AN ANALYSIS OF THE CORTICOLOUS EPIPHYTES ON POPULUS TREMULOIDES IN THE LOWER PENINSULA OF MICHIGAN

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ABSTRACT

AN ANALYSIS OF THE CORTICOLOUS EPIPHYTES ON POPULUS TREMULOIDES IN THE LOWER PENINSULA OF MICHIGAN

By

Steven C. Wang

Twenty five *Populus tremuloides* stands evenly spaced throughout the lower peninsula of Michigan were examined. A prefabricated device was used to standardize data collection and enable the determination of dominance, density and frequency of all epiphytes occurring from 50 to 170 cm above ground level on the north, east, south and west aspects of the tree trunks.

An Importance Value for each species in each community was used as the basic unit of information. Ordination and classification techniques were used to analyse the data.

Sixty three species are described in terms of height and aspect preferences as well as distribution on a regional basis. Ecological parameters believed to be responsible for the patterns of distribution are discussed. Correlations between environmental factors and physiological and morphological adaptations are also introduced.

AN ANALYSIS OF THE CORTICOLOUS EPIPHYTES ON *POPULUS TREMULOIDES* IN THE LOWER PENINSULA OF MICHIGAN

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Steven Chandler Wang

A THESIS

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I. INTRODUCTION

Interest in ecological and phytosociological studies of corticolous vegetation has been increasing rapidly during the past five years (Adams & Risser, 1971; Harris, 1971a; Harris, 1971b; Hinds, 1970; Jesberger & Sheard, 1973; Jonescu, 1970; Sheard & Jonescu, 1974; Yarranton, 1972). Various approaches have been used, with varying degrees of success. Much of the work has concentrated on recording presence or absence of species in one or more cylindrical quadrats on the tree bole (Adams & Risser, 1971; Culberson, 1955a; Culberson, 1958; Garren, 1963; Hale, 1952; Hale, 1955; Hale & Moore, 1968; Hinds, 1970; Jesberger & Sheard, 1973). Beals (1965), Jonescu (1970), and Schwerer (1962) recorded the presence or absence of species but also took aspect into consideration in their data analysis.

The very nature of presence-absence data prevents the detection of subtle changes in abundance that may characterize differences in height (Harris, 1971a) or aspect. An estimate of the abundance of each species in a quadrat is another approach (Hale, 1965; Pearson & Lawrence, 1965), but the subjectivity compounds the problems. A nonsubjective method was introduced in the pioneering work by Billings & Drew (1938) in which the entire epiphytic flora of a portion of trunk was mapped. To obtain a viable sampling procedure, it seems best to strive for a method intermediate to a subjective abundance estimate and the detailed mapping of the entire community.

If sampling a particular aspect is the goal, one could use a <u>line</u> along the bark, facing the appropriate direction. A rectangular quadrat is less appropriate since only due north can be considered north; adjacent bark is an extension of the eastern or western aspect. Jonescu (1970) noted this affect, especially on trees of small diameter. The point sampler technique, first used by Kershaw (1964) and later by Harris (1971a) and Yarranton (1972), employs line sampling. Yarranton (1972) notes, however, problems involved in the "practical impossibility of reproducing a dimensionless point". Ideally, in order to completely, describe an epiphytic flora, one needs information including the number of occurrences and the frequency of occurrence on a number of transects (line quadrats) for each species as well as the size of all thalli, for all heights and aspects. An approach that provides this type of data is introduced in this study.

Using the results of studies by Hale (1955) in southern Wisconsin and Culberson (1955a) in northern Wisconsin, Culberson (1955b) found that cryptogamic epiphytes of Wisconsin have either northern, southern or unlimited distributions. Historical (including glacial), substrate and climatic factors were discussed as causal agents in these distributional patterns. Historically, Michigan's glacial past is similar to that of Wisconsin's (with the absence of an "unglaciated region" in Michigan) and, therefore, the possible influence of the time element due to glaciation on distribution can, as it was by Culberson, be dismissed. The effect of substrate is reduced to a minimum by the examination of only one tree species throughout the study area. Climate (regional and micro-) is the one major factor remaining for consideration in this study).

Phillips (1951) found that the lower peninsula of Michigan may be divided into two regions on the basis of the bryophytes found living on the bark of trees. This division fell at approximately 43° north latitude and was noted that it closely resembled Thornthwaite's (1948) predicted line separating the areas with more and less than an average annual potential evaporation of 24 inches.

A small number of lichen studies have been conducted on Populus in Minnesota and Michigan. Garren (1963) conducted a survey of 10 aspen trees (eight P. tremuloides and two P. grandidentata) at the Itasca Biological Station, Minnesota, and found a number of species to exhibit definite vertical distributional patterns. In Michigan, Schwerer (1962) surveyed the lichen growth on stands of P. grandidentata, in which both aspect and height preferences were noted for many species. Hale & Moore (1968), working on Populus in the northern lower peninsula of Michigan, believed aspect differences to be of negligible significance and combined all aspect data from their cylindrical quadrats.

Populus tremuloides Michx. is an ideal tree species for this type of study. As it is the most widely distributed tree species in North America, it allows for similar studies to be conducted in a variety of climatic regimes, revealing many interesting trends in the analyses of their respective epiphytic floras. Within any one locality, as shown in the present study and in Jonescu (1970), the flora of P. tremuloides is limited to a relatively small number of epiphytic species (63 and 30 species respectively for the two studies), that is relatively easy to analyze.

The purpose of this study was to (1) determine what epiphytes grow on Populus tremuloides in the lower peninsula of Michigan, and show their distribution, (2) define site and species relationships, elucidatin

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elucidating environmental factors responsible for these affinities, (3) continue the work already begun on the epiphytic sociology and geography on P. tremuloides elsewhere in North America and (4) introduce a new technique suited for corticolous phytosociology.

II. THE STUDY AREA

This study was conducted during the summer and fall of 1974, in the lower peninsula of Michigan. Within the 277 mile length from the northern tip of the lower peninsula, to its southern boundary with the states of Ohio and Indiana, many transitions take place, including a major climatic change. Average annual temperature and rainfall (figure 1), both pertinent to this study, are two characteristic features separating the northern and southern portions of the peninsula. These differences are primarily the result of "steep gradients in frequency of tropical maritime (mT) and polar continental (cP) air masses between Grand Rapids and Traverse City" (Niedringhaus 1966), and are exemplified in their climates as humid continental with cool summers in the north and humid continental with warm summers in the southern portion (figure 1b). Not only is this division observable in the meteorological records, but it is well known in terms of soil and vegetation types. The lower peninsula is dominated by two Soil Orders; Spodosols in the northern half and Alfisols in the south. Forest lands of the north are dominated by the hemlock-white pine-mixed deciduous forests, whereas those in the southern half are generally one of two types; the majority are beech-maple forests and a small portion consists of an oak-hickory forest in the southwestern corner of the state. Figure 2 demonstrates the soil and vegetation boundaries.

An additional factor arises from the peninsular nature of the state, as the proximity of the Great Lakes, especially Lakes Michigan and Huron, greatly affect the region. Temperature, precipitation and humidity modified by the lakes, influence sites near the lake shores.

Topographically, the lower peninsula of Michigan varies from 580 feet to 1712 feet above sea level. Local relief is moderate, the principle feature being belts of hills of glacial origin. In a simplified view, two areas of relatively high elevation are noticeable, the highest and more northern is centered in the counties of Crawford, Missaukee, Ogemaw, Osceola, Otsego, Roscommon, and Wexford. The southern highlands are found to be centered in Hillsdale and Oakland counties. Most of the remainder of the peninsula appears as plains or gently rolling hills; see figure 3 for a simplified topographical view of the lower peninsula.

III. METHODS

In order to examine stands of Populus tremuloides from as many sites in the lower peninsula of Michigan as possible, a grid system was developed, beginning with a north-south line from Mackinaw City to the Ohio border. At intervals along this central line, and five lines perpendicular to it, regularly spaced potential sites (areas of approximately 30 square miles where stands would hopefully be found) were chosen. Eleven potential sites were spaced every 25 miles along the central north-south line, with the first near Mackinaw City. The east-west transects crossed the center line at 50 mile intervals, and potential sites were plotted along these lines every 25 miles east and west of the central line. In theory, this grid covered the entire lower peninsula and located 30 evenly spaced potential site locations. Each of these potential sites was visited in order to assess their suitability through presence of a suitable stand of P. tremuloides.

Criteria for suitability of stands were many fold. Of prime importance was the maintenance of a minimum physiognomical variability between stands. To this end I attempted to accept only those stands that (1) were on a well drained site, (2) had a large percentage of P. tremuloides over 7 inches (18 cm) dbh (diameter at breast height), (3) had a similar density (approximately 400 trees per acre or 100 trees per hectare), (4) were made up of similar arboreal components, (5) were within a larger wooded area in order to minimize edge effects, and (6) were without obvious disturbance in recent history.

As a result of the preliminary survey, 25 sites were actually established (see figure 4), three of the bottom tier of potential sites and sites 13 and 16 were eliminated because no suitable stands could be found within the desired area. Under no circumstances was a site rejected or accepted because of the nature of its epiphytic flora.

Once a site was selected, five P. tremuloides trees were randomly selected for examination. Due to the intensive method of analysis preformed on each tree, this number of samples was found to be sufficient; after analysis of the third tree approximately 80% of the species to be found on the five trees had been recorded. In selecting trees, I stood in the approximate center of the stand and walked in a randomly determined compass heading, until the first aspen that fit the requirements was encountered. Requirements for the selection of a tree were simply that the tree had to be between 7 and 11 inches (18 and 28 cm) dbh and have a straight, undamaged nonbranching trunk for the first ten feet in height. Defining a size range is an important consideration in order to minimize the problems of poorly defined aspects in small diameter trees and to reduce the age (important in epiphytic succession) and roughness factors often inherent in trees of greatly differing sizes. The corticolous flora did not influence this choice. Each successive tree was determined in a similar fashion, beginning the search with a new randomly determined compass direction from the tree just sampled.

The commonly used rectangular quadrat was reduced to a vertical line 120 cm in length. Along this vertical line quadrat, the north, east, south, and west aspects of the trees were sampled from a height of 50 cm to 170 cm from ground level. From earlier reconnaissance, this area of

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the trunk seemed well suited to this type of analysis due to the obvious community changes taking place within this 120 cm segment. The flora below 50 cm is primarily an extension of the terricolous communities and has been omitted from this study. On each of the four aspects, along the entire 120 cm transect, all epiphytic thalli (lichens, fungi, mosses and algae) were identified. A prefabricated device (figure 5) was used for determining the transect lines as well as holding the paper on which all information was recorded. This device was positioned on one side of the tree, with an elastic transect line directly on the cardinal direction (aspect), covering the tree from 50 cm to 170 cm. The elastic nature of the line facilitated removal of specimens. For each thallus that the line intersected, its length of intersection with the transect and species name was recorded on the paper attached to the plate. If I was unable to identify the thallus in the field, a code number was recorded in place of its name and the specimen was brought back to the laboratory for examination. In addition to these unknowns, representative voucher specimens of most species were also collected and deposited in the Michigan State University Cryptogamic Herbarium. A total of over 12,000 thalli were thus recorded.

There are a number of ways to summarize the raw data obtained for each species. As regards level of analysis, one may select the entire region as one community for study. Alternatively, one may treat each of 25 sites as a separate community for analysis; or one may group the sites into a number of site groups and treat each site group as a separate community for analysis. In this study, I have grouped the sites into 5

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site groups and divided each site group into 8 communities (4 aspects and 4 heights), i.e., 40 communities have been studied. One may therefore compare, for example, the north aspect community of site group two with the east aspect community of site group three.

The data summarized may have values based on dominance (total length of the thalli of a species), density (total number of thalli of a species) or frequency (total number of trees on which a species occurred). Each of these three measurements has merit, and numerous studies in various fields of specialization have used one, or a combination, of these values in describing the patterns of relative importance of a species. In this study, due to the number of thalli and the variety of growth and distributional patterns present, I incorporated all three measurements into one importance value in order to more fully describe a species' importance in the community.

The _importance value_ (Cain & Castro, 1959 and Curtin & McIntosh, 1951) or IV of species A can be determined as follows:

$$\text{IV(A)} = \text{Relative Dominance (A)} + \text{Relative Density (A)} + \text{Relative Frequency (A)}$$

$$\text{Relative Dominance (A)} = \frac{\text{Dominance of Species A}}{\text{Sum of all Dominances in the sample}} \times 100$$

$$\text{Relative Density (A)} = \frac{\text{Density of Species A}}{\text{Sum of all Densities in the sample}} \times 100$$

$$\text{Relative Frequency (A)} = \frac{\text{Frequency of Species A}}{\text{Sum of all Frequencies in the sample}} \times 100$$

It can be seen that the maximum importance value any species can attain is 300 and that all importance values in any sample must total 300. Importance values are often used in ecologic studies involving vascular plants and their use with the cryptogams can be equally productive.

Techniques of multivariate analysis are also widely used in vascular plant studies and are becoming increasingly utilized in phytosociologic studies of cryptogams. This study employs two basic techniques commonly used in conjunction: ordination and classification. The method of ordination used in the present study was based on principal components analysis (PCA), as discussed in Blackith & Reyment (1971). The computor program was adopted from Wahlstedt & Davis (1968) modified to follow the procedures outlined in Sheard & Jonescu (1974). The data set exists as a matrix of correlation coefficients between species. The classification method used is of the agglomerative-polythetic method, and employed a computor program adopted from McCammon & Wenninger (1970). Input matrices for site classification were correlation coefficients, whereas the matrices for species classification were in terms of a distance function.

All ordinations and classifications were performed with the input of the total importance value of each species for each site. Two sets of data were run, one with the input for all species occurring in more than one site (45 species) and the second utilizing the importance values for the 30 most important species (having the highest regional importance values). The results of these two runs were essentially the same and, except in some cases, the inclusion of the less important species adds little to the understanding of site and species relationships. Unless otherwise noted, all references to classification and ordination are in terms of the 30 species input.

IV. RESULTS AND DISCUSSION

A. Ordination and classification analyses of sites and species

Figure 6 shows three views of site ordination on different combinations of the first three principal components and figure 7 shows the results of the classification of these sites. The three groups (Site Groups 1, 2, and 3) are obvious in the classification and these natural groupings can also be found in the ordinations. The subdivisions of Group 1 into three subgroups was done in order to recognize the natural groups occurring there. The somewhat questionable relationship of site 21 was resolved by placing it with Site Group 1c for several reasons: (1) the 45-species-classification clearly shows this site to have its closest affinities with Site Group 1c, (2) in the 30-species-classification it is only remotely associated with 1a, (3) the ordinations agree with this placement and (4) its geographical affinities are with Site Group 1c.

This is a good example of the need to draw conclusions from both ordination and classification, rather than relying on only one technique. The arrangement of the sites into the five distinct Site Groups 1a, 1b, 1c, 2, and 3 is necessarily the result of subjective observations on the data. However, the detrimental effects of this subjectivity is reduced by the fact that both the ordination and the classification techniques agree closely. Figure 8 shows the geographical distribution of these Site Groups.

The results of ordination (PCA) and agglomerative classification of the thirty species used in the site analysis are given in figures 9 and 10. All except three species (Bacidia naegelii, Bacidia chlorococca and Microthelia micula) are placed into one of five Species Groups defined in both techniques. These three species are not included because of the very low loadings they exhibit on the first three principal components, thus confusing the placement of these taxa into groups using a compilation of information from both PCA and classification. The same subjectivity found in the Site Groups applies here, but the Species Groupings also exhibit a very close adherence in both techniques, lessening the concern over these subjective decisions. Table 1 gives the loadings (transformation coefficients) of these 30 species on the first five principal components. It must be remembered from the onset that these Species Groupings are the result of the analysis of the site importance values. Neither aspect nor height was considered in this input. Further grouping within these five divisions, taking into consideration community structure within a site, will be discussed later. Information concerning dominance (as well as importance value) for all species in each of the 16 communities in each of the 25 sites and for each of the 5 Site Groups is incorporated in the discussion of individual species.

B. Environmental Interpretation

Twenty seven species may be grouped into five distinct groups by utilizing the first two principal components (eigenvector one and two) of the species ordination (figure 9). The third principal component (eigenvector three, figure 9) is helpful in the further separation of these groups. Species Group A is characterized by the species Arthonia caesia, cfr Arthonia caesia, Bacidia populorum, Physcia stellaris, Protococcus spp., and Rinodina pyrina; Group B by Physcia millegrana and Physciopsis elaeina; Group C by Candelaria concolor, Physcia orbicularis-group, and Platygyrium repens; Group D by Bacidia umbrina, Candelariella xanthostigma, Epicoccum sp., Lecidea symmicta, Lepraria B, Ochrolechia arborea, Parmelia subaurifera, Parmelia sulcata, Physcia adscendens, Physcia aipolia, and Xanthoria polycarpa; Group E by Caloplaca cerina, Caloplaca holocarpa, Lecanora sambuci, Leptorhaphis contorta, and Physcia ciliata. The first three axes also separate five Site Groups (figure 6): Group 1a includes sites 1, 2, 3, 9, and 11; Group 1b includes sites 4, 5, 6, 8, and 10; Group 1c includes sites 7, 12, 14, 21, and 22; Group 2 includes sites 17, 18, 24, and 25; and Group 3 includes sites 15, 19, 20, 23, 26, and 27. By examining the species and site ordinations simultaneously, the discovery of possible ecological parameters responsible for these groups is simplified.

Eigenvector one clearly separates the combined sites of Groups 2 and 3 from sites in Groups 1a and 1b, leaving the majority of sites in Group 1c in an intermediate position. This separation of groups closely resembles, although in inverted position, the geographical placement of these groups in the state (see figure 8), suggesting that there is some general (regional) climatic condition responsible for this division. The line separating the sites with positive and negative associations on the first axis is shown by the dotted line in figure 8; its close approximation of the zone demarcating climatic, vegetation and soil changes is readily apparent.

Most of the previous ecological and physiological studies have shown that the major factor affecting epiphytic growth is a moisture element (Adams & Risser, 1971; Harris, 1971a; Sheard & Jonescu, 1974; Blum, 1973; Farrar, 1973). The latter two authors stress the importance of humidity, or some factor influencing the rate at which a thallus dries, in the total water balance of lichens. Of the numerous "moisture factors" that are affecting the growth of epiphytic plants in Michigan, only two were found to be highly correlated with the values for the sites on eigenvector one; potential evapotranspiration (data from Messenger, 1962) and mean annual temperature, with correlation coefficients of 0.85 and 0.87 respectively (see figure 11). Potential evapotranspiration is at least in part a measure of the combined effect of temperature and rainfall. As the latter is not correlated with eigenvector one, it is assumed that temperature is the controlling factor for this axis. Temperature has a direct effect on the epiphytic water balance as the moisture absorbed by a thallus from moist air or recent precipitation will be lost by transpiration in direct proportion to the temperature. The effect of wind on the water regime of cryptogamic epiphytes, as noted by Barkman (1958), can be considerable and will be dealt with below. However, the general wind pattern is similar throughout the lower peninsula and will not effect the north-south distribution of the epiphytes. Within the confines of this study, it appears that the warmer the environment, the less water there is available for metabolic processes in the plants of the epiphytic flora. The high moisture stress associated with a positive association with eigenvector one is characteristic of all sites in

Physciopsis elaeina, and Platygyrium repens) are highly correlated with this third component. These species occur for the large part, if not solely, in the southwest portion of the state, especially in Group 2 sites (17, 18, 24, and 25).

This corner of the state is well documented as being associated with a unique vascular flora, due primarily to the effect of the Great Plains climate. The history and origin of this "prairie peninsula" is discussed by Benninghoff (1964) and the status of present prairies in the state is given by Scharrer (1971), see figure 13. The plains climate is characterized by low winter precipitation, moderate summer precipitation with occasional major droughts and the presence of much continental air (Borchert, 1950) which contrasts strongly with the generalized picture of the Michigan climate as having heavy winter snows, relatively heavy summer precipitation and a relatively low evapotranspiration rate. The climate of the counties in the southwest corner of the state reflects both these regimes. The North American distribution of these species are all either Pan Temperate or Eastern Pan Temperate except for Lecidea symmicta, which is Artic Boreal (Brodo, 1965; Wetmore, 1967). It is concluded that the third axis of the ordination accounts for the great effect that the prairie climate has in the southwest corner of Michigan.

The remaining eigenvectors will not be dealt with in this manner as any associated environmental conditions become increasingly obscure and of less importance in the understanding of the total picture. However, the three species not included in the Species Groups due to their low correlations with the first three axes are highly correlated with the fourth. Of all the species, Bacidia chlorococca and Microthelia micula are the two most negatively correlated species and Bacidia naegelii is

Groups 2 and 3 except sites 24 and 25. Those sites exhibiting large negative associations with this temperature axis are in large part Group 1b sites, and are the backbone of the northern highlands region (sites 3, 4, 5, and 6). Sheard & Jonescu (1974) noted that the correlation between species abundance and the first eigenvector in the species ordination was evidence for the environmental interpretation of that eigenvector to be a moisture gradient. Figure 12 shows the relationship between number of species in each site plotted against eigenvector one (correlation coefficient of -0.84). This eigenvector is clearly a gradient affecting species density. Many of those species negatively correlated with the first principal component (Group D) are found concentrated in the cooler sites and, conversely, those species in Groups A and B tend to be concentrated in the warmer sites. Known North American distribution of these epiphytes also agree with the general temperature gradient. Information gathered from Brodo (1965), Wetmore (1967) and the Michigan State University Cryptogamic Herbarium show that although those species exhibiting a pan temperature distribution are found at all points on the first eigenvector, these species are concentrated in the area of positive association. The 14 species in this study exhibiting artic boreal or pan boreal distributions are negatively associated with eigenvector one.

Species thriving in the more xeric environments (due to high temperatures) are Arthonia caesia, cfr Arthonia caesia, Physcia millegrana, Physciopsis elaeina, and Protococcus spp. Species adopted to the cooler temperatures are Lepraria B, Ochrolechia arborea, Parmelia subaurifera, Parmelia sulcata, Physcia aipolia, and Xanthoria polycarpa. None of these species can necessarily be considered to require warm or cool temperatures as their microclimatic affinities (height or aspect) may show just the opposite.

Eigenvector two separates the combined Species Groups A, B, and D from Groups C and E. These latter two groups are positively correlated with this principal component; the species Caloplaca holocarpa, Lecanora sambuci, Leptorhaphis contorta and Physcia ciliata being the most highly correlated. The former three Groups, especially the species Bacidia chlorococca, Lecidea symmicta, Lepraria B, and Ochrolechia arborea, are negatively associated with this axis. This eigenvector helps very little in the separation of Site Groups, suggesting that the associated environmental conditions (if any present) transcend Site Group lines and affect sites individually. Those sites highly correlated with eigenvector two are sites 2, 9, and 11 (all at the northern tip of the peninsula) and site 21. Those species positively correlated exhibit a characteristic distributional pattern which includes these sites (see Physcia ciliata, figure 62). In order to elucidate the possible environmental parameters lying behind these patterns, the ordination of 45 species is helpful. Although the 15 extra species often make this ordination confusing, these rarer species are beneficial in this case. Catillaria glauconigrans, Hysteriographium mori, and Lecanora allophana are the most highly correlated species, more so than any member of group E. These three species occurred only along the northern lake shores (sites 7, 8, 9, 11, and 12). The distributional patterns of the species negatively correlated are similar to those in the 30 species ordination since all of the same taxa are involved. However, the distribution of the rare species most negatively correlated in the 45 species run, Rinodina willeyi and Xenosporium *sp*., are found to occur only in the northern highlands (sites 3, 4, 5, 6, and 10).

These facts suggest that a positive correlation with eigenvector two reflects the positive effect that the proximity to the northern lake shore (Lakes Michigan and Huron) has on the epiphytic flora. The inclusion of site 21 into this group, as well as the general trend of all Group E species to extend down into this portion of the state may seem anomolous, but explanations can be offered. One feature which makes site 21 (and site 25) different from the rest of the southern half of the study area is their relatively high snowfall and the abnormally cool mean annual temperatures. These attributes liken these sites to the northern lake shore sites. The exclusion of the southern lake shore sites from this group can be explained by the higher temperatures found in these more southerly sites. A major change affected by the proximity of large bodies of water is in the form of a modification of temperatures and a relatively stable source of moist air. The effects of the wind produced by the lake and land breezes that are characteristic of lake shores, also modify the epiphytic environment. Although the air may be relatively moist, its movement is important in its drying capacity on the flora. Although the intricacies are unknown, eigenvector two seems to reflect some effect that the Great Lakes are exerting on the epiphytic flora.

Although two species in Group D (*Bacidia umbrina* and *Lecidea symmicta*) and one in Group A (*Physcia stellaris*) are positively associated with eigenvector three, all species in Groups B and C (*Candelaria concolor*, *Physcia millegrana*, *Physcia orbicularis*-group the most posit

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the most positively correlated species with the fourth eigenvector. The meaning behind this and the remaining axes are unknown.

C. Species distribution and zonation in the lower peninsula of Michigan

One of the first multivariate analyses of lichen phytosociology on Populus tremuloides was performed by Sheard & Jonescu (1974) in west-central Canada (Alberta and Saskatchewan). They found Bacidia populorum to be negatively associated with the moisture gradient and Physcia adscendens, Physcia orbicularis, and Physcia stellaris to be positively associated with moisture. Caloplaca cerina, Physcia aipolia, Rinodina pyrina, and Xanthoria polycarpa were all found to have little or no association with the moisture factor. The present study found that in the lower peninsula of Michigan, on Populus tremuloides, moisture associations for Bacidia populorum, Physcia adscendens, and the Physcia orbicularis-group are similar to those requirements found by Sheard & Jonescu (1974). However, both Physcia stellaris and Xanthoria polycarpa react oppositely in comparison. The remaining species were found to be reacting variously to comparable moisture factors. Both studies found the first principal component to be a factor directly related to water relations.

In comparing the abundances of lichen species found by Hale & Moore (1968) at the University of Michigan Biological Station, with data from the sites of the present study surrounding the Biological

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Station (Site Group 1b), close similarities are found. In both studies Parmelia subaurifera, Parmelia sulcata, and Physcia adscendens were the three most abundant species. Garren (1963), although collecting in Minnesota in a site further north than any site of the present study, described a flora similar to that found in Site Groups 1a and 1c.

Culberson (1955b) in Wisconsin and Phillips (1951) in Michigan, were enabled to divide the two states into two parts by means of an epiphytic flora. This study, too, can divide the lower peninsula of Michigan into two distinct sections by comparing sites with positive and those with negative correlations with eigenvector one. This method gives a division which closely resembles Phillips' division and is directly comparable to Culberson's demarcation in Wisconsin (see figure 14). The lines determined by these epihytic studies are, as one might expect from comparisons with climatic and vascular vegetation studies, expressions of the same environmental gradients.

In the present study, due to the nature of the collection technique and the statistical analyses, both the northern and southern halves of the study area may be divided further, as discussed earlier. It is with consideration to these further subdivisions that species abundances can be compared. Table 2 gives the average importance values for the eight most important (highest importance value) epiphytes for each of the five Groups. Figure 15 shows the five generalized geographical distributional patterns represented by 23 of the 30 species; the seven remaining species have scattered or uninterpretable patterns. The horizontal axis is divided into the five Site Groups and the vertical is the average percent of the state-wide importance value found in each of the Site Groups for each group of species. These graphs demonstrate the various distributional patterns and suggest the complexity beyond simple north or south distributions.

D. Height and aspect preferences

Each of the 25 sites are affected by different combinations of macroclimatic factors working together with other factors to produce 25 unique environments for epiphytic habitation. Within each site, microclimatic forces are also at work shaping the epiphytic flora. The two variables measured that express these forces within each site are height and aspect. For ease of handling, the 120 cm segments were divided into four 30 cm sections and, with this division on the four compass directions, each tree is divided into 16 quadrats. Due to various factors (density of the stand, direction and velocity of winds, etc.) the relative importance that aspect or height has on affecting species distributions is variable between sites. Although these observations are interesting in their own right, this variation between individual sites is an unnecessary variable and is de-emphasized by grouping the sites into the five larger Site Groups.

With an increase in height from 50 to 170 cm, due to the distance from the moisture holding ground layer and an increase in wind velocity, there is a concomitant decrease in humidity. Temperature changes with the increasing height are slight, if present at all, and are considered negligable. In sites with dense growths of Pteridium aquilinum the light intensity may decrease below 100 cm (the average height of the mature fern) during the summer months, but is constant in the 70 cm above this point.

The relative effects of different aspects are most readily noticed between the north and south aspects in which direct sunlight is the major factor. The north aspect receives very little direct sunlight and, therefore, is warmed little by this radiation. The south aspect, with the greatest amount of direct solar radiation, is warmed a great deal, and all epiphytes in this environment must be able to withstand these effects. Although the east and west aspects receive approximately the same amount of sunlight (assuming no differential shading), the west has a more xeric nature since it has all day to dry and warm before the sun reaches it (Geiger, 1966). As a general rule, the south and west aspects are relatively dry and warm and the north and east aspects are relatively cool and moist. There is a continuum of microclimatological factors from the lower portions of the north to the upper reaches of the south or west.

Within any one Site Group, a change in height changes both the number of species present and the percent cover very little, it at all (figures 16a and 17a). Changes in aspect will cause a small change in the number of species but can drastically affect the percent cover of the epiphytic flora (figues 16b and 17b). The frequent depression in percent cover of the south and west aspects without an associated depression due to increasing height, seems to imply an influence due to direct sunlight. However, this certainly does not imply that the species on the south aspect of the trees always grow poorly; those species adapted to growth in this xeric environment often grow luxuriantly. Species composition is one factor that almost always changes from one height or aspect to another.

Whether or not the cover or number of species changes, the relative abundances of the complex of plants present will change with changing microenvironmental conditions.

As many authors have noted (Adams & Risser, 1971; Barkman, 1958; Culberson, 1955b; Hale, 1952; Hale, 1955) the phorophyte on which thalli grow is an important consideration. In the normal development of bark in Populus tremuloides, the phellogen keeps pace with the increasing diameter of the tree, giving rise to the characteristic smooth bark. Bark characteristics such as hardness, pH and relief are important for epiphytic growth in terms of area for colonization, water holding capacity and airborne nutrient and particulate accumulation and availability. Populus tremuloides has a relatively hard bark, measured as approximately 110 (90-140) on the "Presto" scale of hardness (Culberson, 1955a). The water holding capacity of Populus spp. is in the intermediate range and the pH averages 6 (Culberson, 1955a).

Different tree species (as well as some intraspecific examples) exhibit different sets of bark characteristics, and these variations can be critical in determining the composition of the epiphytic flora present on the tree trunk. One should consider these differences before combining phytosociological information from more than one species of tree. Even the two common species of Populus (P. tremuloides and P. grandidentata) support different floras. Geographical, aspect and height preferences change between phorophyte species, and preference generalizations based on several (or even two) species of trees are of questionable value. When a taxon is referred to as requiring high moisture conditions, or that a specific microenvironment is xeric, these statements must be understood relative to the extremes in the study. It is only in the light of these facts that some of the conclusions in this study, and all studies of this type, can be made.

A comparison of two studies done in the British Isles (Harris, 1971a; Kershaw, 1964) and the present study is informative. Harris and Kershaw found Parmelia sulcata to be a tree-top species adopted to a sunlit and relatively xeric environment. Harris (1971b) showed P. sulcata to have a high light compensation point, which correlates well with its dry, sunlit affinities. As a component of the general state wide lichen flora of Michigan this taxon exhibits few xeric adaptations. On P. tremuloides, as revealed in this study, Parmelia sulcata is considered to be a relatively mesic species, prefering northern aspects. Both Schwerer (1962) and Hinds (1972) found P. sulcata to be found primarily low on the tree trunks. These different interpretations of habitat requirements are due in part to varying substrate and primarily to the climatological differences between Michigan and the British Isles. Suggestive of these differences are the results of comparisons of species in common between the studies. Of the species considered xeric in the present study, none were found in the British studies; of the species found by Harris and Kershaw, all were considered moisture or shade-loving species in the Michigan studies. The British study sites apparently afforded the lichens favorable moisture (with the undoubted addition of other factors) at greater heights and drier aspects than the sites in Michigan.

E. Morphological and physiological adaptations

To get a clear understanding of the distribution of epiphytes within a particular site, the roles that morphology and physiology play in interactions with microclimatic conditions, must be examined. In this regard, many species can be grouped in terms of thallus type, cortical features and chemistry. Barkman (1958) included in his Atmophyta the protococcoid algae, strongly sorediose lichens, and fruticose lichens, and states that they utilize mainly atmospheric vapour in their water processes. Most other cryptogamic epiphytes use water mainly in liquid form or from both sources (Barkman, 1958). Although tree trunks are generally considered xeric environments, the lower portions and the north aspects of the tree boles offer a considerable amount of atmospheric water vapour. Of the thirty most important species; Arthonia caesia, cfr Arthonia caesia, Bacidia chlorococca, Bacidia umbrina, Lecidea symmicta, Lepraria B, Ochrolechia arborea, Parmelia subaurifera, and Protococcus spp. are classified by Barkman as belonging to the group requiring water vapour, and of these species all are found to be concentrated on the lower portions of the north aspect. Bacidia chlorococca and Protococcus spp. are also found on the lower portions of the east aspect, also a very moist environment, in great abundance. The distribution of these nine species is attributed to the fact that they are not adapted to absorb and hold moisture to any great degree in any environment subjected to rapid or frequent desiccation. Similarly, fruticose lichens require areas of high relative humidity; because of thier intimate association with the air, they may quickly loose water to a dry environment. The fruticose lichens occurring in this study were Alectoria nidulifera, Evernia mesomorpha, Ramalina fastigiata, Usnea hirta, and Usnea subfloridiana. Although none of these taxa were common, 85.4% of the total dominance that was recorded, was found on the north aspect.

Extremely xeric habitats are also encountered on an individual trunk. The upper section of the southern aspect receives a great deal of direct solar radiation, heats up quickly, receives little moisture from the ground layer, and becomes quite dry. The presence of anthraquinones, pruina, and a thick upper cortex are theorized as being adaptations to prevent water loss and direct damage from high light intensities (Barkman, 1958). Within this study all species lacking an upper cortex occur in moist portions of the transects and only those species with a cortex exhibit the potential for more xeric growth habits. Three species are characterized as occurring high on the southern aspects; Caloplaca cerina, Physcia ciliata, and Xanthoria polycarpa. The genera Caloplaca and Xanthoria contain parietin, an anthraquinone, presumed by Barkman (1958) to be involved in xeromorphic adaptations. Both Caloplaca cerina and Xanthoria polycarpa are found predominantly (chi square, $p < 0.05$) in the upper half of the south and west aspects. Although Caloplaca holocarpa (also containing parietin) exhibits no aspect preferences, it is concentrated on the higher portions of the transects. Xanthoria fallax, although too rare for meaningful generalizations, occurred only on the west aspect above 110 cm. Xerophytism and presence of parietin are highly correlated. It is not obvious why Physcia ciliata grows under xeric conditions; its upper cortex is epruinose, no

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epruinose, not unusually thick, and it contains no anthraquinones. It is, however, closely appressed to the substrate, which will help in water preservation. Only two pruinose species were found in this study, Physcia aipolia, which is concentrated high on the eastern aspects and the relatively rare Physconia detersa, which exhibits few xerophytic tendencies.

Although the highly sorediate nature of the first group of species was in part responsible for its distribution on the tree, there is no cause and effect suggested for the xerophytic taxa. It can only be inferred that because of their adaptations these species are enabled to exist in a hot and dry environment, not obliged to exist there. Unlike those species required to live on the moist portions of the tree, the xerophytes are able to exist in almost any of the various environments found on the tree bole.

V. SUMMARY

Twenty five stands of Populus tremuloides spread uniformly throughout the lower peninsula of Michigan were examined by a vertical transect method which permitted analyses of aspect and height preferences of corticolous epiphytes as well as the determination of importance values (relative dominance + relative density + relative frequency) for each species. Attempts were made to keep the physiognomic variability between stands at a minimum. A total of 63 species (57 lichens, 2 algae, 3 fungi, and 1 moss) were found growing on P. tremuloides in these 25 sites. They are listed in table 3 in order of their dominances.

The epiphytic communities were defined on the basis of aspect and height; 4 aspects (north, east, south, and west) and 4 heights (50-80 cm, 80-110 cm, 110-140 cm, and 140-170 cm). In all, 16 communities were analyzed in each of the 25 sites. Ordination and classification procedures, based on species importance values within each site, were used to divide the species and sites into groups for further analysis. The 25 sites were divided into 5 site groups: Site Group 1a is located in the northern tip of the lower peninsula and is defined by sites 1, 2, 3, 9, and 11; Site Group 1b, in the north central portion of the lower peninsula is made up of sites 4, 5, 6, 8, and 10; Site Group 1c, found across the central portion of the peninsula is made up of sites 7, 12, 14, 21, and 22; Site Group 2, found in the southwest corner of the peninsula is made up of sites 17, 18, 24, and 25; and Site Group 3, which covers most of the southern half of the lower peninsula is made up of sites 15, 19, 20, 23, 26, and 27. These site groups correlate well with previous climatological classifications of Michigan. The 30 species attaining the highest importance values were divided into 5 species groups: Species Group A contains Arthonia caesia, cfr Arthonia caesia, Bacidia populorum, Physcia stellaris, Protococcus spp., and Rinodina pyrina; Species Group B contains Physcia millegrana and Physciopsis elaeina; Species Group C contains Candelaria concolor, Physcia orbicularis-group, and Platygyrium repens; Species Group D contains Bacidia umbrina, Candelariella xanthostigma, Epicoccum sp., Lecidea symmicta, Lepraria B, Ochrolechia arborea, Parmelia subaurifera, Parmelia sulcata, Physcia adscendens, Physcia aipolia, and Xanthoria polycarpa; Species Group E contains Caloplaca cerina, Caloplaca holocarpa, Lecanora sambuci, Leptorhaphis contorta, and Physcia ciliata. Three species, Bacidia chlorococca, Bacidia naegelii, and Microthelia micula, were without definite species group affinities.

The ordinations helped reveal possible environmental factors responsible for the variation of species composition between sites. Earlier analyses have suggested that moisture factors have the greatest effect on epiphytic distributions. The present analysis of the species and site ordinations suggests that the cryptogamic flora on P. tremuloides in the lower peninsula of Michigan is influenced most by temperature, which acts as the major agent in moisture stress. The Great Lakes and the Prairie influences (both of which include some influence of temperature) are secondary to temperature, but their effects are considerable. The first three principal components of the species ordination account for 47% (temperature 24%, lakes 14%, and prairie 9%) of the total variation present in the input data. This relatively low percentage (47%) reflects the large amount of environmental variation inherent in an area as large and diverse as the lower peninsula of Michigan.

Species prefering the higher temperatures are Arthonia caesia, cfr Arthonia caesia, Physcia millegrana, Physciopsis elaeina, and Protococcus spp. The sites exhibiting these temperatures are all sites in Site Group 3 plus sites 17 and 18. Lower temperatures are favored by Lepraria B, Ochrolechia arborea, Parmelia subaurifera, Parmelia sulcata, Physcia aipolia, and Xanthoria polycarpa and are characteristic of the northern highland sites (especially sites 3, 4, 5, 6, and 10).

Those species affected positively by the influence of the Great Lakes (and the conditions met in sites 21 and 25) are Caloplaca holocarpa, Lecanora sambuci, Leptorhaphis contorta, and Physcia ciliata. Four sites (2, 9, 11, and 21) exhibit this positive correlation with the second principal component. Species favoring the environments represented by a negative correlation on this vector are Arthonia caesia, Bacidia chlorococca, Bacidia naegelii, Lecidea symmicta, Lepraria B, Ochrolechia arborea, Parmelia subaurifera, and Parmelia sulcata. Sites exhibiting this correlation are either in Site Group 1b (sites 4, 5, and 6) or in Site Group 3 (sites 20 and 26).

The third principal component represents the influence exerted on the flora by the prairie climate. Bacidia umbrina, Candelaria concolor, Lecidea symmicta, Physcia millegrana, the Physcia orbicularis-group, and Physciopsis elaeina are positively correlated and most of these species are concentrated in the southwest corner of the state (sites 17, 18, 24, and 25).

Distribution patterns of various species on the individual trees reflect height and/or aspect preferences in response to various environmental conditions in different sites. The within-site preferences exhibited by cryptogamic epiphytes in the lower peninsula of Michigan are not necessarily the same as the same species height and aspect preferences in other parts of the world. Even in the lower peninsula of Michigan, the height and aspect preferences of a given species vary from one site to another. Similarly, the height and aspect preferences for species within Michigan differ at times from those reported by other workers in other parts of the world. Two examples may be cited: (1) Physcia ciliata exhibits sun-loving tendencies in Site Groups 1a and 1b, but it obviously prefers shade in Site Group 1c, and (2) Parmelia sulcata is considered mesic in this study but was found to be xeric in the British Isles. These anomalies may be explained, at least in part, by an examination of micro- and macroclimatic conditions. There exists a multidimensional continuum which includes a transition from extremely xeric to extremely hygric environments in the many epiphytic habitats in the world. Each individual collection site lies somewhere in this continuum and, within the limits of conditions defined in that site, its own moisture gradient exists. Comparisons between different sites, without a knowledge of the environmental conditions responsible for the continuum ranges within each site, should be made, and evaluated, with caution. Site and species relationships are summarized in table 4.

Some morphological and physiological adaptations are highly correlated with aspect and height preferences. Of the thirty most important species, all the highly sorediate lichens, granulate lichens, and protococcoid algae primarily occurred low on the north aspects. These epiphytes are Arthonia caesia, cfr Arthonia caesia, Bacidia chlorococca, Bacidia umbrina, Lecidea symmicta, Lepraria B, Ochrolechia arborea, Parmelia subaurifera, and Protococcus spp. Similarly, the great majority of the occurrences of the fruticose lichens (Alectoria nidulifera, Evernia mesomorpha, Ramalina fastigiata, Usnea hirta, and Usnea subfloridiana) are found on the north aspect. These distributions are due primarily to the need of these species for great amounts of atmospheric moisture. The presence of parietin in Caloplaca cerina and Xanthoria polycarpa is suggested as an adaptation for the xerophytic growth habit of these two lichens.

The ability to recognize Species Groups and Site Groups and to assign plausible environmental parameters to the relationships between groups, reflects the value of the collection technique introduced. The recording of all specimens along a relatively long vertical transect (120 cm) on the bark of the tree trunk appears justified. Although the time spent on each tree can be quite long, depending on the number of epiphytes present, a great amount of data may be obtained from a relatively few trees. Although five trees in each site appeared to be an adequate sample, ten trees, if time permitted, would probably prove to be more reliable. This technique permits the recording of large numbers of occurrences of the more common species, as well as the recording of cover, important features in statistical analysis. It also allows the recording of greater number of rare species than might otherwise be detected. In addition, many of the negative features of other methods, e.g., the presence-absence method, the estimation of cover method and the point sampler method, are eliminated.

Table 1 Loadings on the first five principal components and variances for the first three and first five components for the thirty most important species.

Species	Transformation coefficients					Variances	
	Principal components						
Name	1	2	3	4	5	h_3^2	h_5^2
A. caesia	.5144	-.3040	-.0580	.5172	-.0307	.3604	.6288
A. cfr caesia	.6225	-.1694	.2166	-.0938	-.2977	.4631	.5605
B. chlorococca	.0520	-.4034	.0472	-.3208	.1102	.1677	.2827
B. naegelii	.0296	-.2974	-.0157	.6428	-.1651	.0896	.5370
B. populorum	.2149	-.0684	.2769	.4998	.5083	.1275	.6357
B. umbrina	-.6322	-.0493	-.3729	.1868	-.1573	.5412	.6008
C. cerina	-.2985	.2776	.6284	-.2414	-.1263	.5611	.6353
C. holocarpa	-.4792	.6319	.2734	.0102	.2231	.7037	.7536
C. concolor	.0516	.4135	-.4621	-.0430	.1282	.3872	.4055
C. xanthostigma	-.6389	-.0327	-.1965	.2442	-.5347	.4479	.7934
L. sambuci	-.2993	.7607	.0080	.2991	.1158	.6683	.7712
L. symmicta	-.3848	-.4528	-.4290	.1528	.0499	.5371	.5630
Lepraria B	-.7339	-.4082	-.0828	-.0867	-.0606	.7121	.7233
L. contorta	-.4656	.6951	.1711	.0364	-.2326	.7292	.7847
M. micula	.3030	-.1494	.1328	-.6122	-.2007	.1318	.5468
O. arborea	-.7476	-.3957	-.1574	-.0260	-.1799	.7403	.7733
P. subaurifera	-.7799	-.3576	-.0080	-.0224	.1188	.7362	.7508
P. sulcata	-.6950	-.3274	.0328	-.1750	.3745	.5913	.7622
P. adscendens	-.5688	.0927	.1762	.3853	-.0122	.3632	.5118
P. aipolia	-.6948	-.2448	.1510	-.2199	.2989	.5655	.7032
P. ciliata	-.1995	.8427	.1334	-.0335	.0053	.7677	.7689
P. millegrana	.4225	.0119	-.6503	-.2185	.0868	.6015	.6568
P. orbicularis-gp.	-.0721	.3914	-.5651	.1371	-.2425	.4777	.5553
P. stellaris	.1643	.1394	-.3076	.2220	.7021	.1410	.6833

Table 1, continued

P. elaeina	.3669	.0143	-.3050	-.1824	-.0070	.2278	.2612
R. pyrina	.2669	-.2269	.4126	.4220	.0355	.2930	.4723
X. polycarpa	-.7902	-.1854	.1556	-.2179	.2726	.6830	.8048
Epicoccum sp.	-.6275	.0875	[illegible]	[illegible]	[illegible]		

Table 1, continued

P. elaeina	.3669	.0143	-.3050	-.1824	-.0070	.2278	.2612
R. pyrina	.2669	-.2269	.4126	.4220	.0355	.2930	.4723
X. polycarpa	-.7902	-.1854	.1556	-.2179	.2726	.6830	.8048
Epicoccum sp.	-.6275	.0875	-.0188	.1009	-.4624	.4018	.6258
Protococcus spp.	.6249	-.2128	.3327	.0618	-.2675	.5465	.6218
P. repens	.1763	.4913	-.2791	-.2701	.0603	.3504	.4269
Eigenvalue	7.269	4.207	2.639	2.392	2.094	14.115	18.601
% Trace	24.23	14.02	8.80	7.97	6.98	47.05	62.00
% Accumulated Trace	24.23	38.25	47.05	55.02	62.00		

Table 2 Species attaining the eight highest importance values in each site group

Site Group 1a Species	IV
Physcia adscendens	50.20
Caloplaca cerina	39.18
Caloplaca holocarpa	32.06
Lecanora sambuci	25.55
Candelariella xanthostigma	18.64
Arthonia caesia	15.33
Physcia orbicularis-group	13.59
Parmelia sulcata	13.39

Site Group 1b Species	IV
Parmelia sulcata	63.88
Physcia adscendens	35.06
Parmelia subaurifera	25.14
Caloplaca cerina	20.79
Bacidia chlorococca	15.88
Arthonia caesia	15.42
Physcia stellaris	11.90
Lecanora sambuci	11.67

Site Group 1c Species	IV
Arthonia caesia	58.09
Physcia adscendens	45.78
Lecanora sambuci	28.92
Physcia stellaris	20.78
Caloplaca holocarpa	18.53
Caloplaca cerina	14.42
cfr Arthonia caesia	11.09
Protococcus spp.	10.34

Site Group 2 Species	IV
Physcia millegrana	115.20
Arthonia caesia	35.29
Physcia stellaris	30.06
Physcia orbicularis-group	16.41
Microthelia micula	12.03
Protococcus spp.	11.83
Lecanora sambuci	10.46
cfr Arthonia caesia	9.64

Table 2, continued

Site Group 3 Species	IV
Protococcus spp.	94.20
Arthonia caesia	51.57
Microthelia micula	37.26
Bacidia chlorococca	22.81
cfr *Arthonia caesia*	22.05
Caloplaca cerina	17.94
Rinodina pyrina	11.89
Physcia millegrana	11.83

Table 3 Total Dominance (mm) for 63 species

Parmelia sulcata	11,197	Trentepohlia sp.	308
Physcia adscendens	10,133	Xanthoria polycarpa	259
Arthonia caesia	6517	Epicoccum sp.	244
Protococcus spp.	4962	Candelaria concolor	237
Caloplaca cerina	4801	Hypogymnia physodes	233
Parmelia subaurifera	3771	Physciopsis elaeina	146
Physcia stellaris	3747	Lecidia symmicta	136
Caloplaca holocarpa	3521	Catillaria glauconigrans	105
Lecanora sambuci	2951	Evernia mesomorpha	101
Physcia millegrana	2695	Lepraria B	96
Bacidia chlorococca	1921	Candelariella vitellina	94
Physcia orbicularis-group	1593	Parmelia flaventior	94
Candelariella xanthostigma	1564	Rinodina willeyi	72
Physcia ciliata	1488	Physconia detersa	71
Physcia aipolia	1052	Hysteriographium mori	63
Ochrolechia arborea	933	Xenosporium sp.	55
cfr Arthonia caesia (without apothecia)	528	Arthonia patellulata	53
Bacidia populorum	516	Lecania cyrtella	51
Platygyrium repens	514	Lecanora chloropolia	49
Leptorhaphis contorta	448	Lepraria C	36
Rinodina pyrina	376	Xanthoria fallax	24
Microthelia micula	375	Lecanora sp.	20
Bacidia umbrina	350	Lecanora allophana	16
Bacidia naegelii	336	Lecanora chlarona	15
		Usnea subfloridiana	14

Table 3, continued

Rinodina dakotensis	11
Usnea hirta	11
Buellia stillingiana	10
Rinodina populicola	10
Alectoria nidulifera	9
Arthonia willeyi	7
Buellia punctata	7
Ramalina fastigiata	6
Cetraria pinastri	5
Leptorhaphis parameca	4
Catillaria griffithii	3
Melaspilea deformis	3
Buellia polyspora	2
Candelaria fibrosa	2

Table 4 Summary of lichens on Populus tremuloides in the lower peninsula of Michigan. Positive or negative affinities are shown for each of the 30 species for the first five principal components. Aspect preferences are denoted by a + (south or west) or a - (north or east). Similarly, height preferences are shown by a + (above 110 cm) or a - (below 110 cm). Those Site Groups sharing principal component values with species groups are also given.

		Principal components 1	2	3	4	5	Micro-Habitat		Site Group
Species	Group	Temp.	Lake	Prairie	?	?	Aspect	Height	Relationships
Protococcus spp.		+	-	-		-	-	+	
A. caesia w/o		+				-	-	-	
A. caesia	A	+	-		+		-	-	3
R. pyrina			-	-	+				(+1,-2,+3)
P. stellaris				+		+		+	
B. populorum					+	+		+	
P. elaeina	B	+		+				-	2
P. millegrana		+		+			+		(+1,+3)
P. orbicularis			+	+		-	+	-	
C. concolor	C		+	+					
P. repens			+	+					
Lepraria B		-	-				-	-	
O. arborea		-	-				-	-	
P. subaurifera	D	-	-				-	-	
P. sulcata		-	-				-	-	
L. symmicta			-	+			-		1b
P. aipolia		-	-					+	(-1,-2)

Table 4, continued

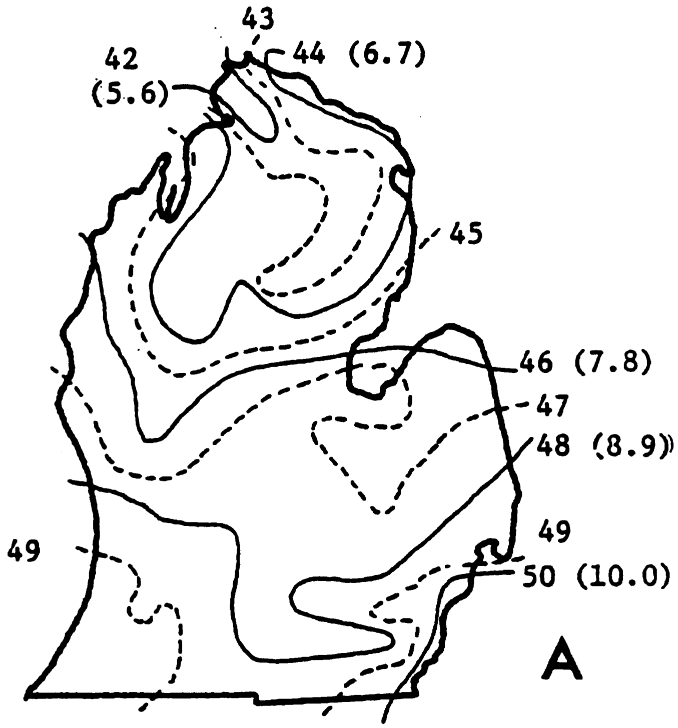
X. polycarpa		-		+	+	+
B. umbrina	*D*	-	+		-	-
Epicoccum [illegible]						

Table 4, continued

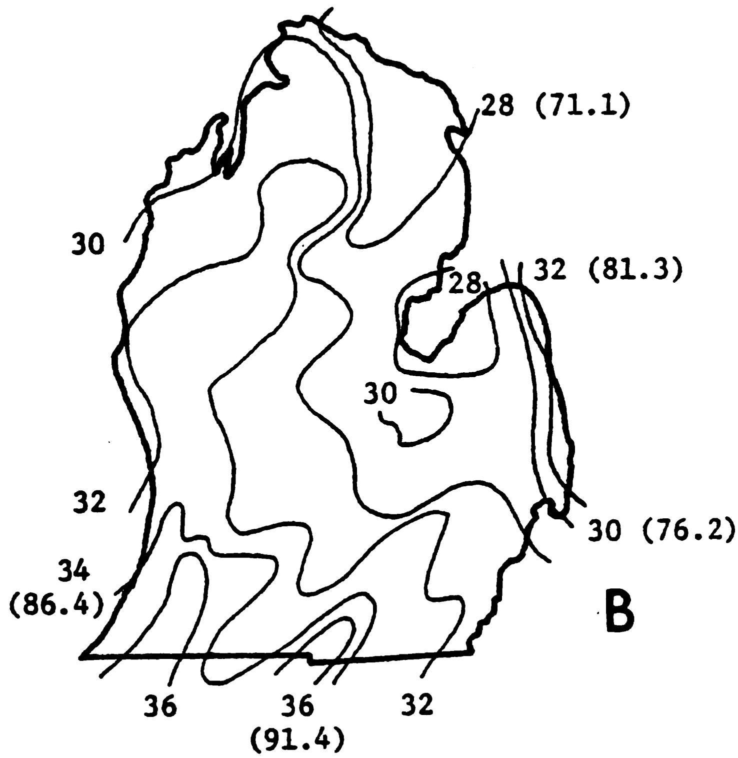
X. polycarpa		-				+	+	+	
B. umbrina	D	-		+			-	-	
Epicoccum sp.		-				-	+	-	
C. xanthostigma		-				-			
P. adscendens		-			+			+	
L. contorta		-	+				+	-	
C. holocarpa		-	+					+	
L. sambuci	E		+		+			+	(+2,3)[1a]
P. ciliata			+					+	
C. cerina				-				+	

Figure 1. A. Annual mean temperature. °F(°C), 1940-1969.

B. Annual mean precipitation. Inches (cm), 1940-1969.


43
42
(5.6)
44 (6.7)
45
46 (7.8)
47
48 (8.9)
49
49
50 (10.0)

A


28 (71.1)
30
28
32 (81.3)
30
32
30 (76.2)
34
(86.4)
36
36
(91.4)
32

B

Figure 2. A. Major forest vegetation of the lower peninsula.

(1) Hemlock-white pine-northern hardwoods

(2) Beech-maple

(3) Oak-hickory

B. Major soil orders of the lower peninsula.

(1) Spodosol region

(2) Transition region

(3) Alfisol region

Figure 3. Generalized view of the lower peninsula highlands.

Figure 4. Geographical location of the collection sites (25). Numbers refer to site number.

Figure 5. Transect and recording device.

A Positioned on tree, covering 50 to 170 cm from ground level.

B Total view of device.

(1) Holes for attaching to tree

(2) Elastic transect line

(3) Aluminum plate, shown without recording paper

C Close-up of section of transect and recording device with thalli.

(1) Elastic transect

(2) Thalli

(3) Codes or names of thalli

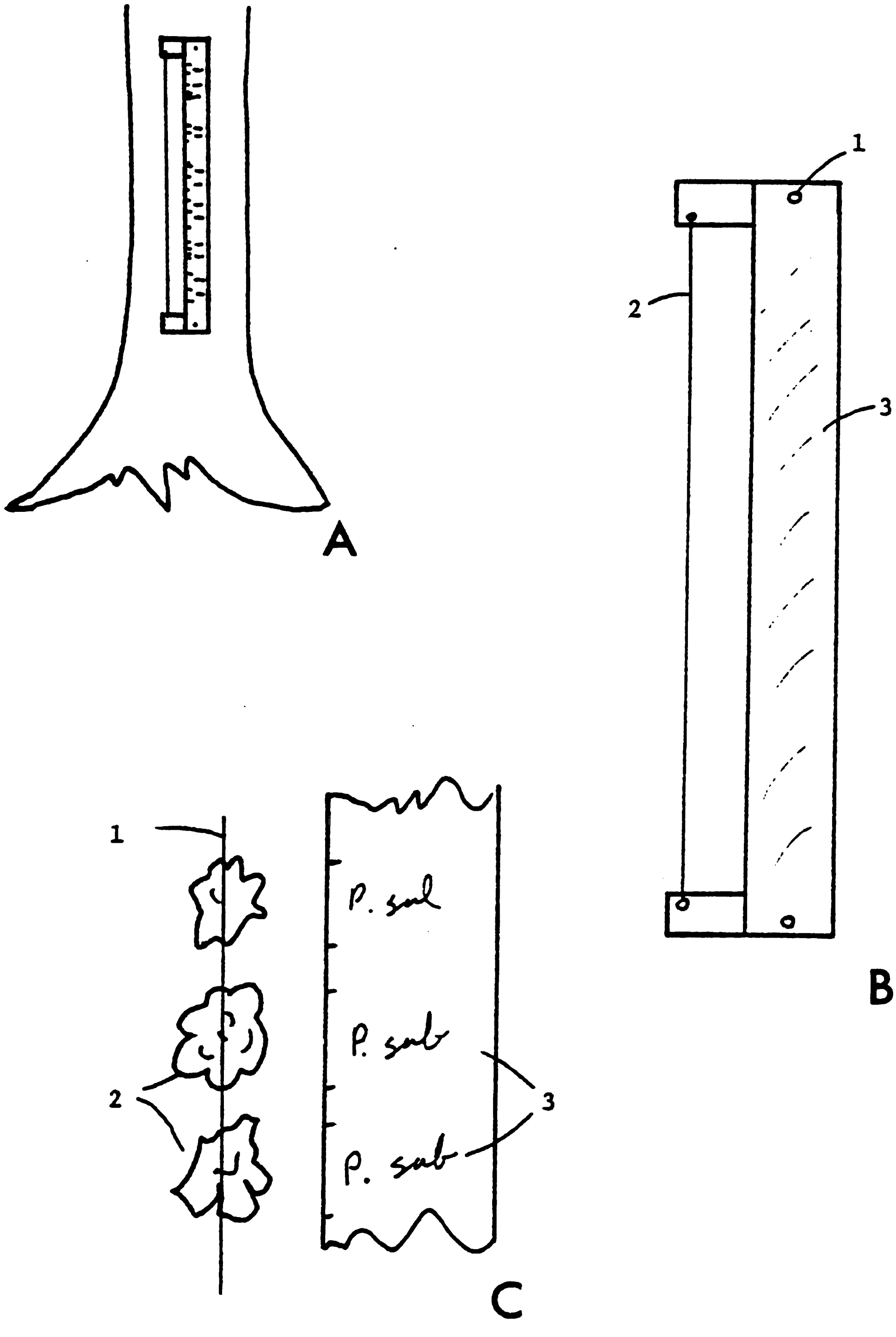

A
1
2
3
B
1
2
P. sal
P. sab
P. sab
3
C

Figure 6. Ordination of sites.

A Plot of eigenvector one and two.

B Plot of eigenvector one and three.

C Plot of eigenvector two and three. ✸ indicates two sites occupying the same coordinates.

Figure 7. Dendrograph resulting from the agglomerative classification of sites. Numbers refer to Site Groups.

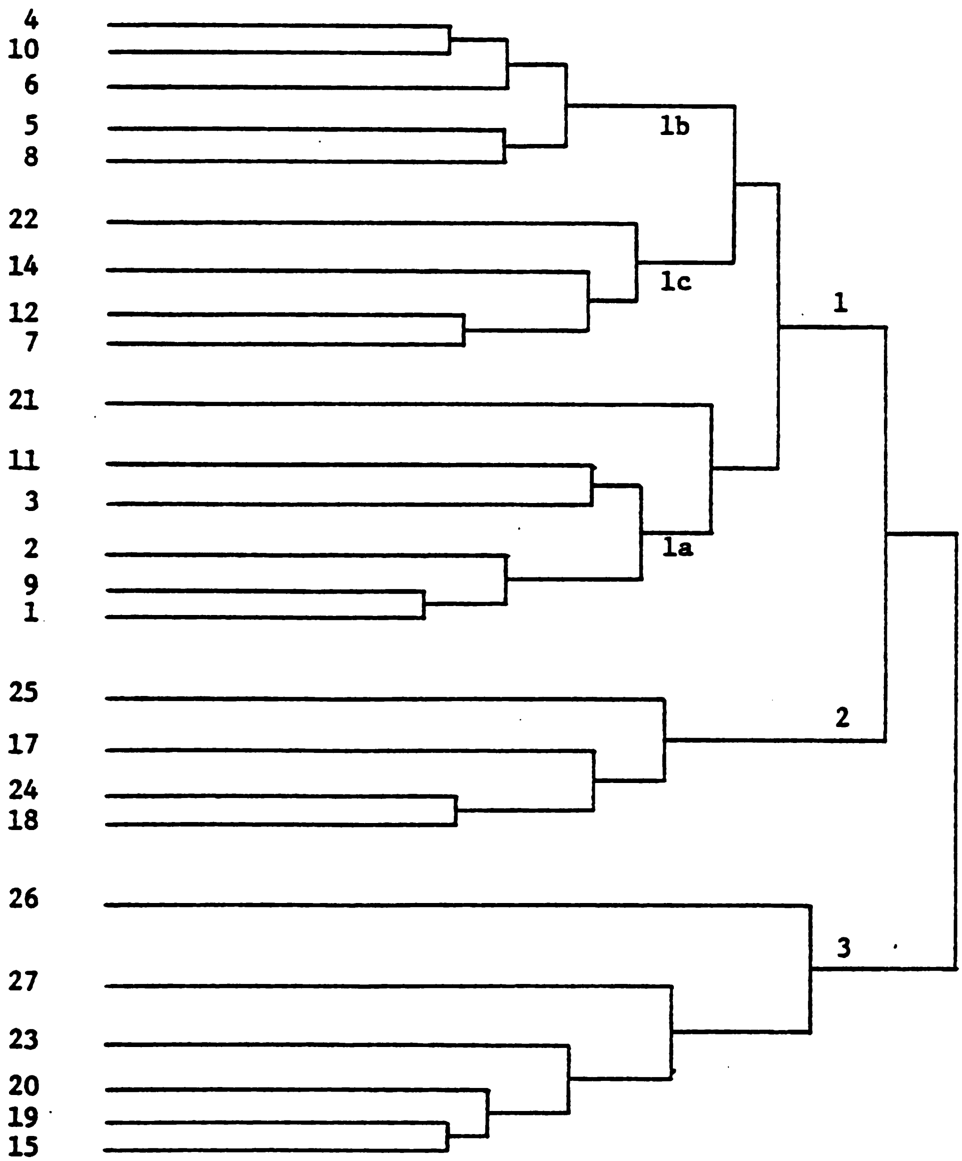

4
10
6
5
8
22
14
12
7
21
11
3
2
9
1
25
17
24
18
26
27
23
20
19
15
1b
1c
1
1a
2
3

Figure 8. Geographical distribution of Site Groups. Dashed line represents division between sites with negative (above the line) and positive (below the line) correlation with eigenvector one.

Figure 9. Ordination of species.

A Plot of eigenvector one and two.

B Plot of eigenvector one and three.

C Plot of eigenvector two and three.

Figure 10. Dendrograph resulting from the agglomerative classification of species. Letters refer to Species Groups.

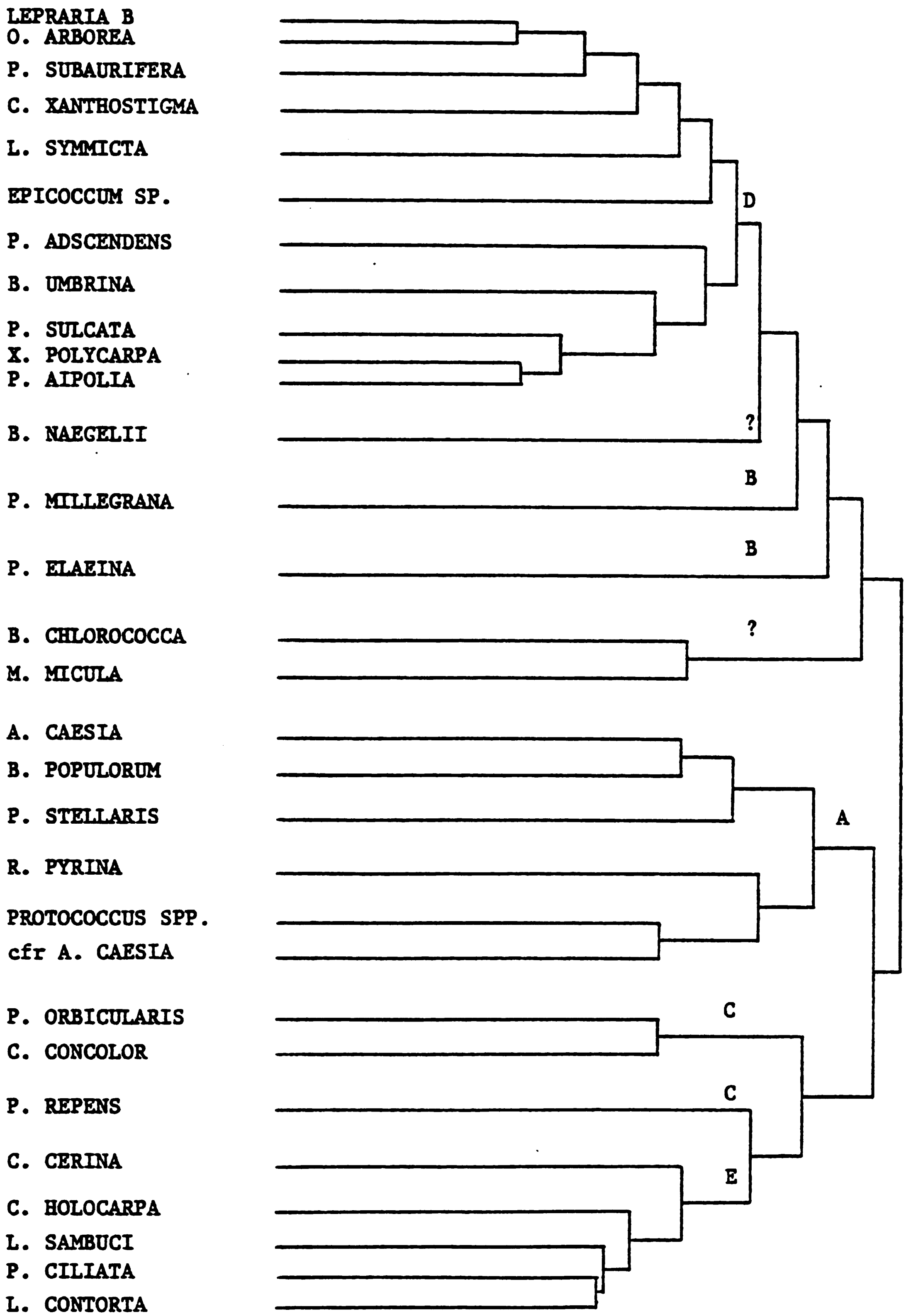
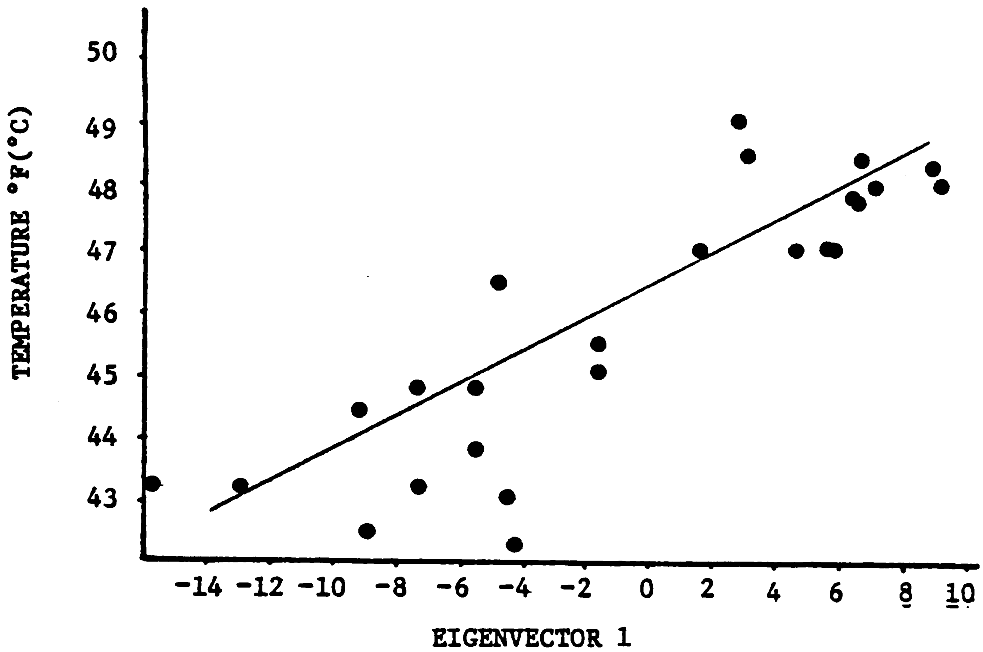
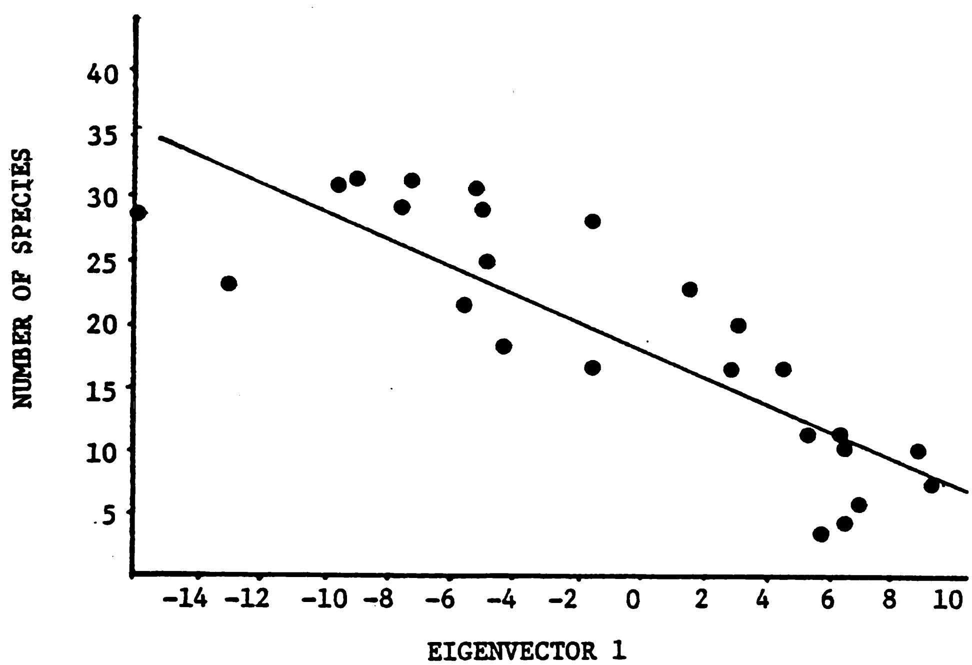

LEPRARIA B
O. ARBOREA
P. SUBAURIFERA
C. XANTHOSTIGMA
L. SYMMICTA
EPICOCCUM SP.
P. ADSCENDENS
B. UMBRINA
P. SULCATA
X. POLYCARPA
P. AIPOLIA
B. NAEGELII
P. MILLEGRANA
P. ELAEINA
B. CHLOROCOCCA
M. MICULA
A. CAESIA
B. POPULORUM
P. STELLARIS
R. PYRINA
PROTOCOCCUS SPP.
cfr A. CAESIA
P. ORBICULARIS
C. CONCOLOR
P. REPENS
C. CERINA
C. HOLOCARPA
L. SAMBUCI
P. CILIATA
L. CONTORTA
D
?
B
B
?
A
C
C
E

Figure 11. Correlation of temperature and eigenvector one.

Figure 12. Correlation of number of species and eigenvector one.



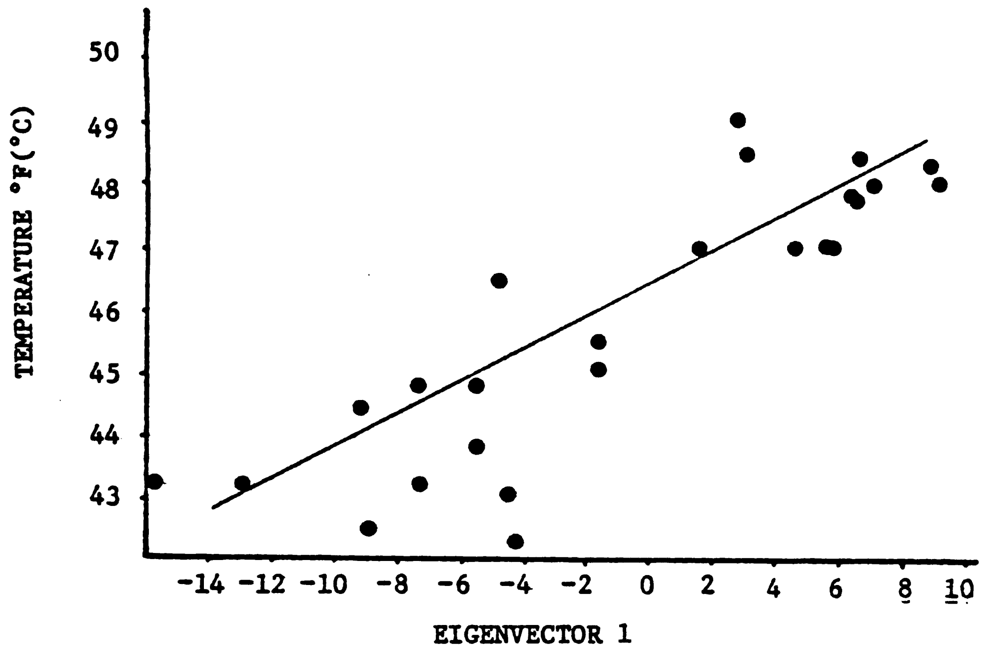
TEMPERATURE °F(°C)
50
49
48
47
46
45
44
43
-14 -12 -10 -8 -6 -4 -2 0 2 4 6 8 10
EIGENVECTOR 1



NUMBER OF SPECIES
40
35
30
25
20
15
10
5
-14 -12 -10 -8 -6 -4 -2 0 2 4 6 8 10
EIGENVECTOR 1

Figure 11. Correlation of temperature and eigenvector one.

Figure 12. Correlation of number of species and eigenvector one.


TEMPERATURE °F(°C)
50
49
48
47
46
45
44
43
-14 -12 -10 -8 -6 -4 -2 0 2 4 6 8 10
EIGENVECTOR 1

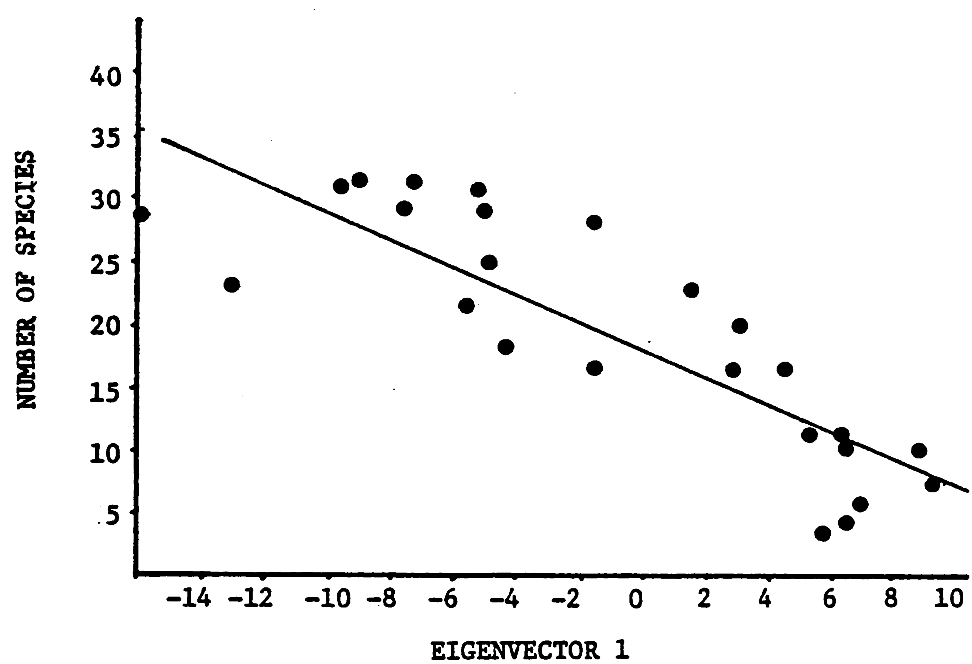
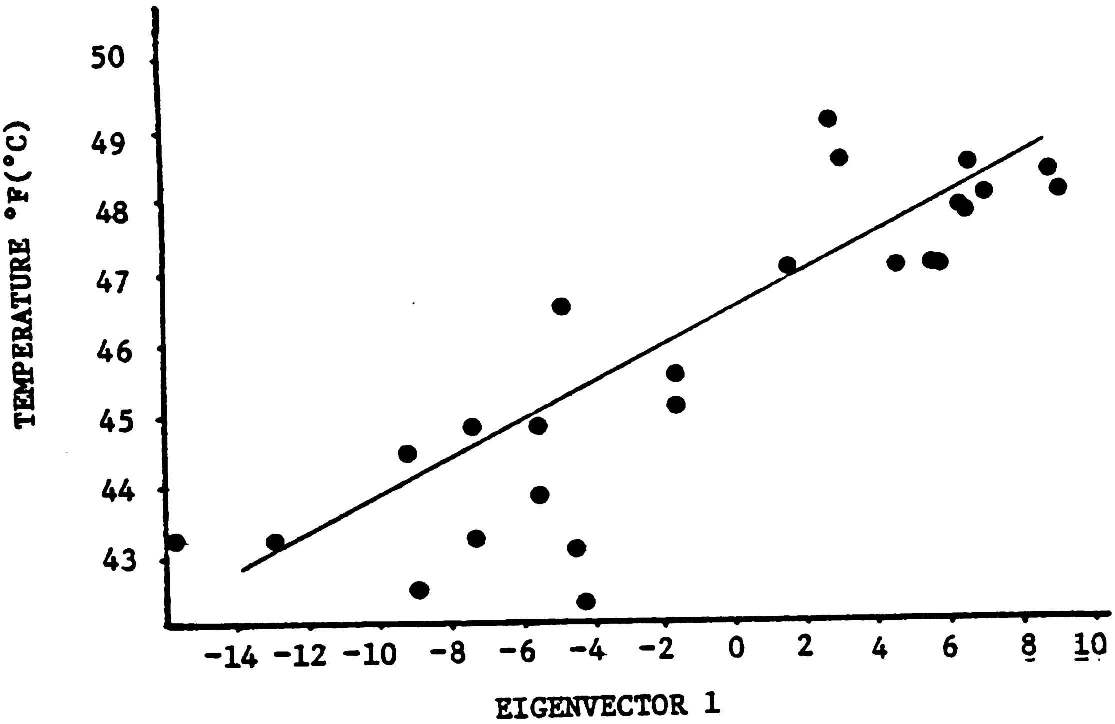

NUMBER OF SPECIES
40
35
30
25
20
15
10
5
-14 -12 -10 -8 -6 -4 -2 0 2 4 6 8 10
EIGENVECTOR 1

Figure 11. Correlation of temperature and eigenvector one.

Figure 12. Correlation of number of species and eigenvector one.


TEMPERATURE °F(°C)
50
49
48
47
46
45
44
43
-14 -12 -10 -8 -6 -4 -2 0 2 4 6 8 10
EIGENVECTOR 1

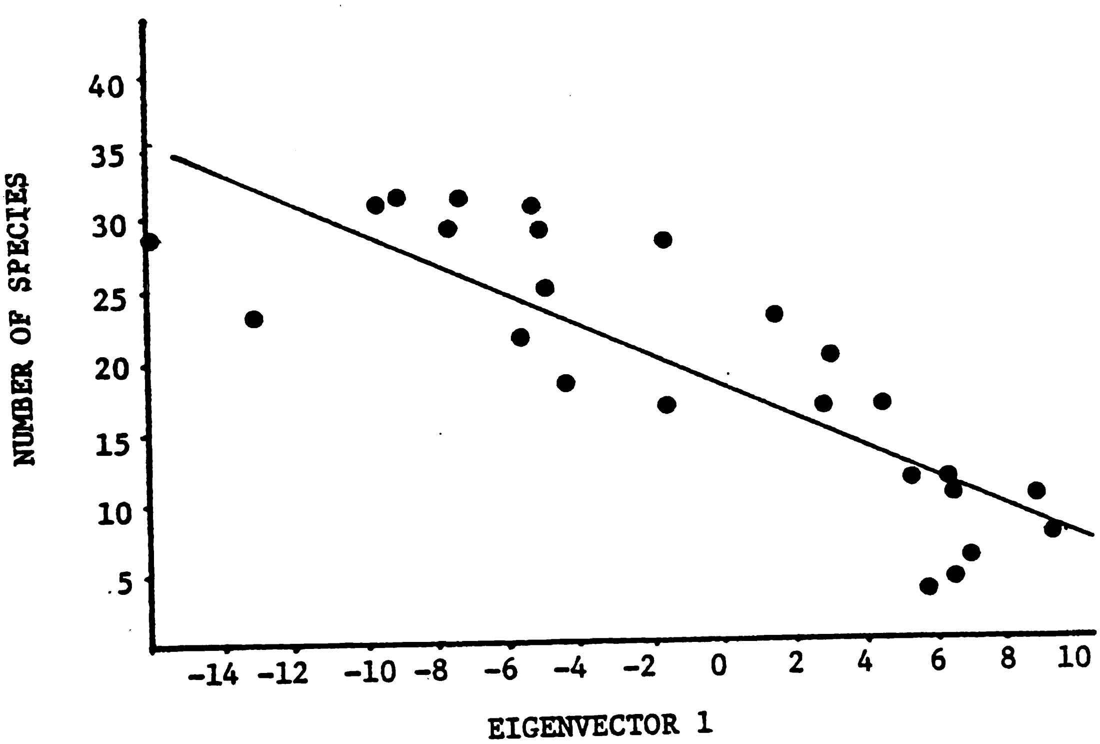

NUMBER OF SPECIES
40
35
30
25
20
15
10
.5
-14 -12 -10 -8 -6 -4 -2 0 2 4 6 8 10
EIGENVECTOR 1

Figure 13. Present prairies in Michigan.

Figure 14. Division of Michigan by epiphytic studies. Dashed (-----) line in Wisconsin represents the approximate location of Culberson's (1955b) north-south division. Dashed line in Michigan is the line between positive and negative correlation with eigenvector one in the present study. Dotted (·········) line in Michigan represents Phillip's (1951) division at approximately 43° north latitude.

Figure 15. Five regional distribution patterns for 23 species. For each distributional pattern only those species (23 out of 30) that fit one of the patterns very closely are included. The vertical axis is the average percent of the state wide Importance Value found in each of the Site Groups for each group of species. The letters A-F refer to the following species

A *Lepraria B*, *Ochrolechia arborea*, *Physcia aipolia*, *Parmelia subaurifera*, *Parmelia sulcata* and *Xanthoria polycarpa*.

B *Caloplaca cerina*, *Caloplaca holocarpa*, *Candelariella xanthostigma*, *Epicoccum sp*. and *Leptorhaphis contorta*.

C *Lecanora sambuci*, *Physcia adscendens* and *Physcia ciliata*.

D *Arthonia caesia* and *Bacidia populorum*.

E *Candelaria concolor*, *Physcia millegrana*, *Physcia stellaris* and *Platygyrium repens*.

F *Microthelia micula*, *Protococcus spp*. and *Rinodina pyrina*.

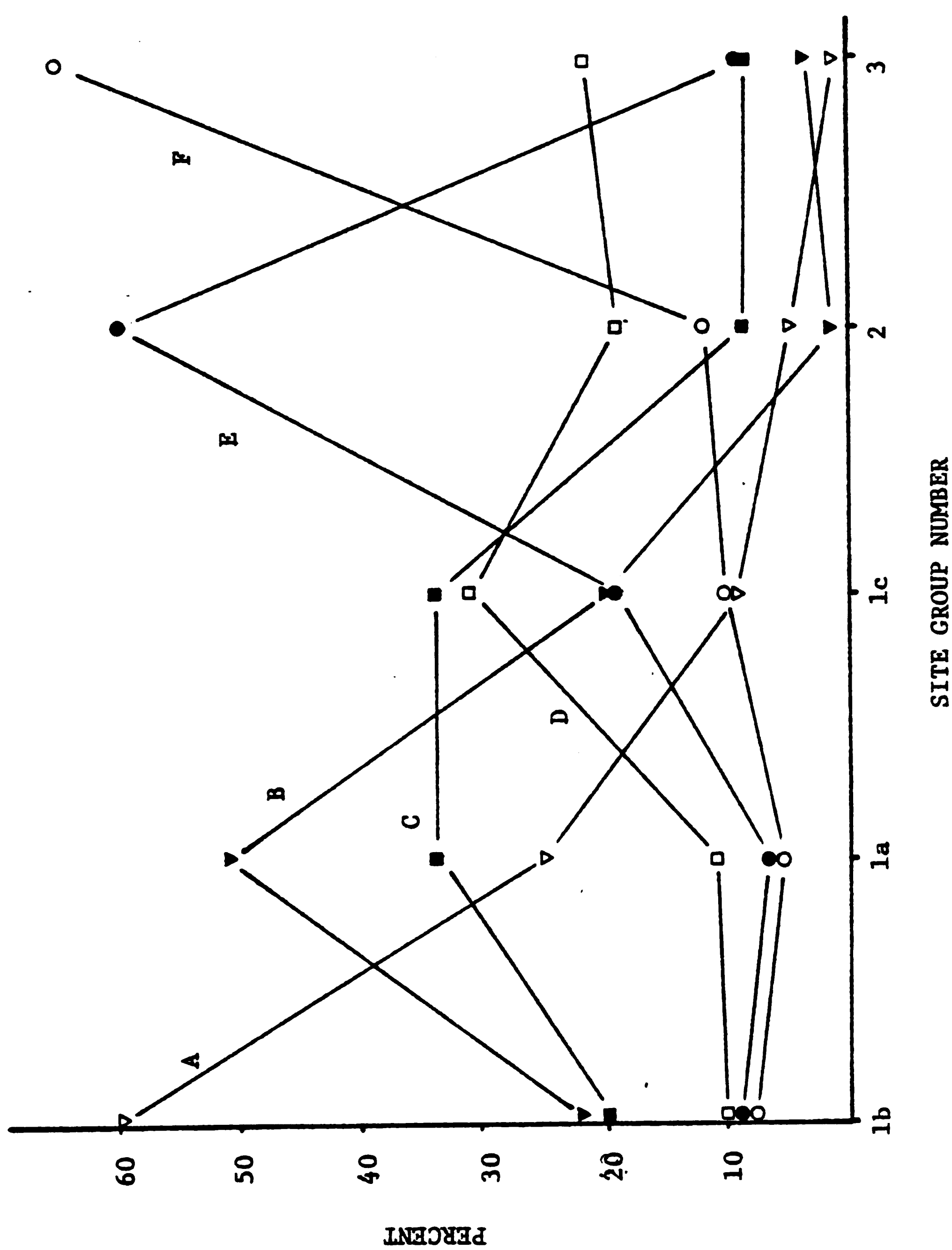
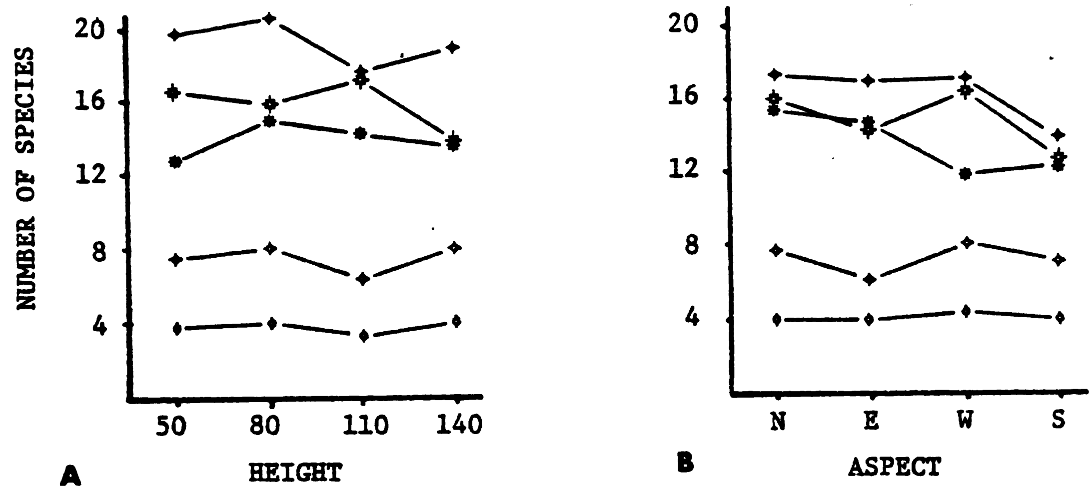

PERCENT
60
50
40
30
20
10
SITE GROUP NUMBER
1b
1a
1c
2
3
A
B
C
D
E
F

Figure 16. A. Number of species at the four heights.

B. Number of species on the four aspects.

Figure 17. A. Percent cover at the four heights.

B. Percent cover on the four aspects.


NUMBER OF SPECIES
20
16
12
8
4
50
80
110
140
A
HEIGHT
20
16
12
8
4
N
E
W
S
B
ASPECT

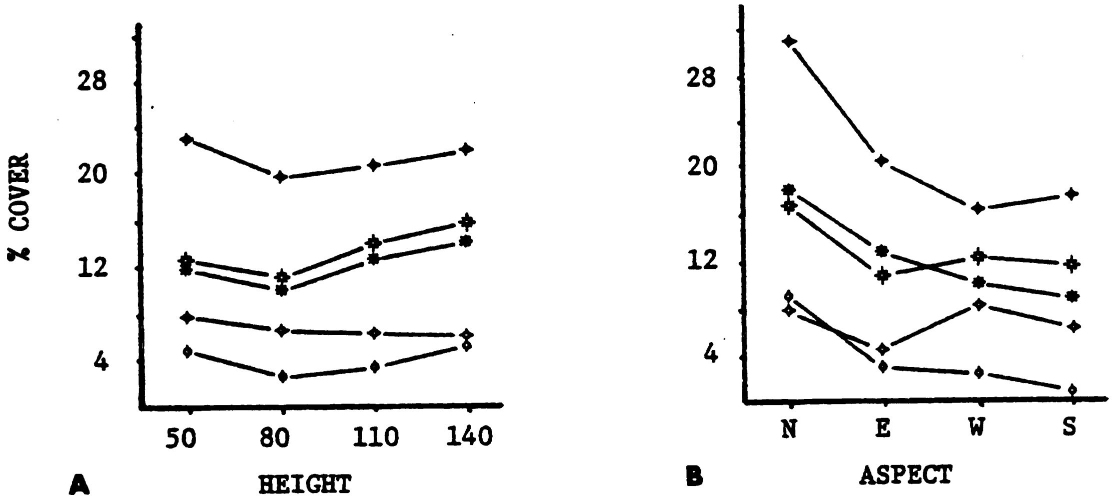
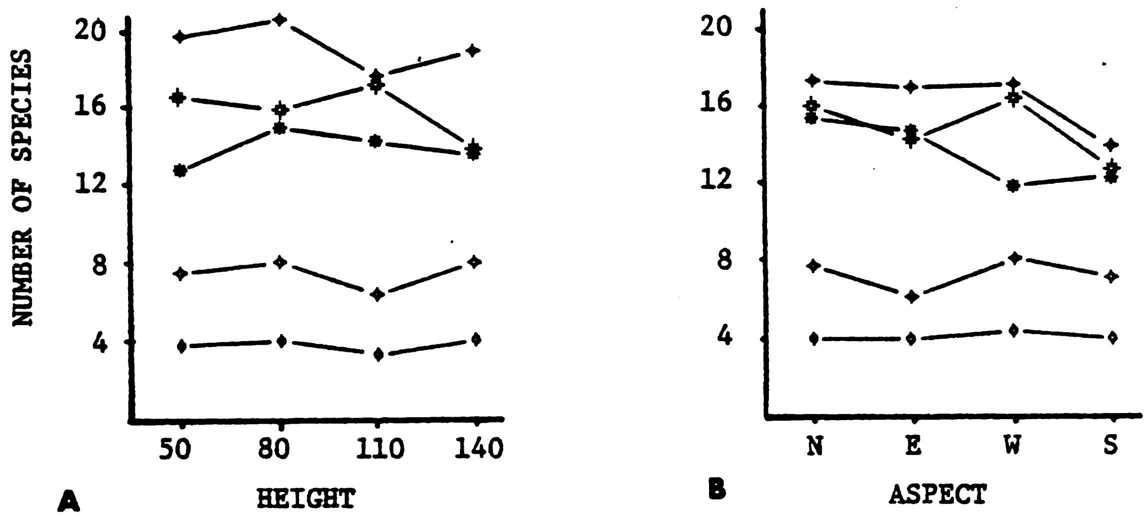

% COVER
28
20
12
4
50
80
110
140
A
HEIGHT
28
20
12
4
N
E
W
S
B
ASPECT

Figure 16. A. Number of species at the four heights.

B. Number of species on the four aspects.

Figure 17. A. Percent cover at the four heights.

B. Percent cover on the four aspects.


NUMBER OF SPECIES
20
16
12
8
4
50
80
110
140
A
HEIGHT
N
E
W
S
B
ASPECT

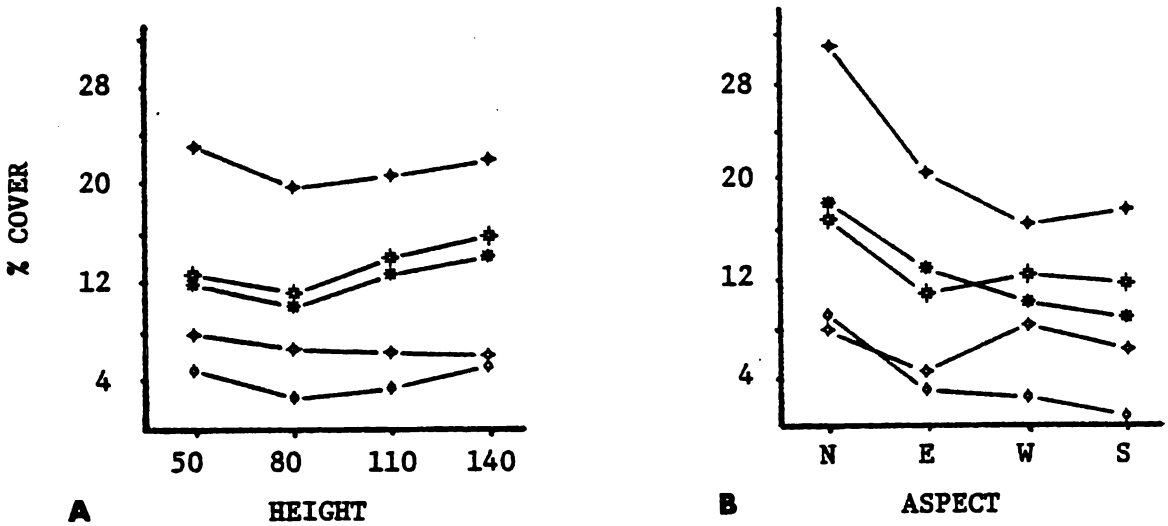
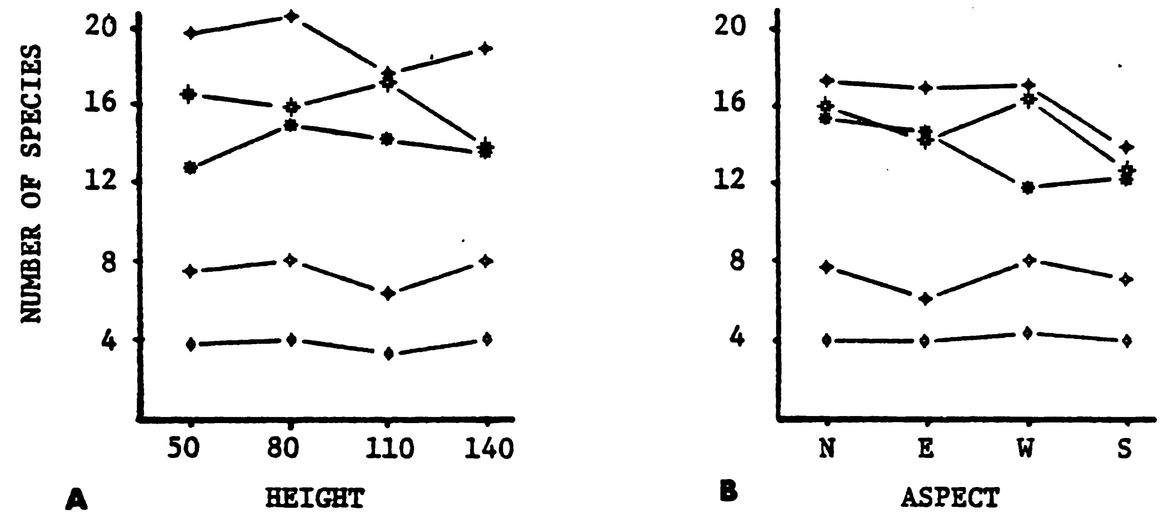

% COVER
28
20
12
4
50
80
110
140
A
HEIGHT
N
E
W
S
B
ASPECT

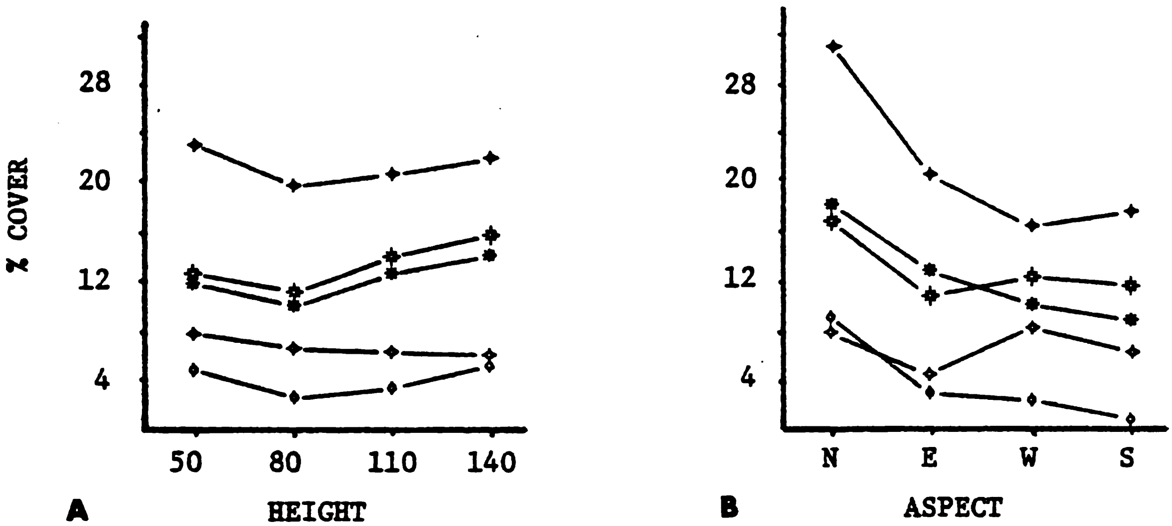
Figure 16. A. Number of species at the four heights.

B. Number of species on the four aspects.

Figure 17. A. Percent cover at the four heights.

B. Percent cover on the four aspects.


NUMBER OF SPECIES
20
16
12
8
4
50
80
110
140
A
HEIGHT
N
E
W
S
B
ASPECT


% COVER
28
20
12
4
50
80
110
140
A
HEIGHT
N
E
W
S
B
ASPECT

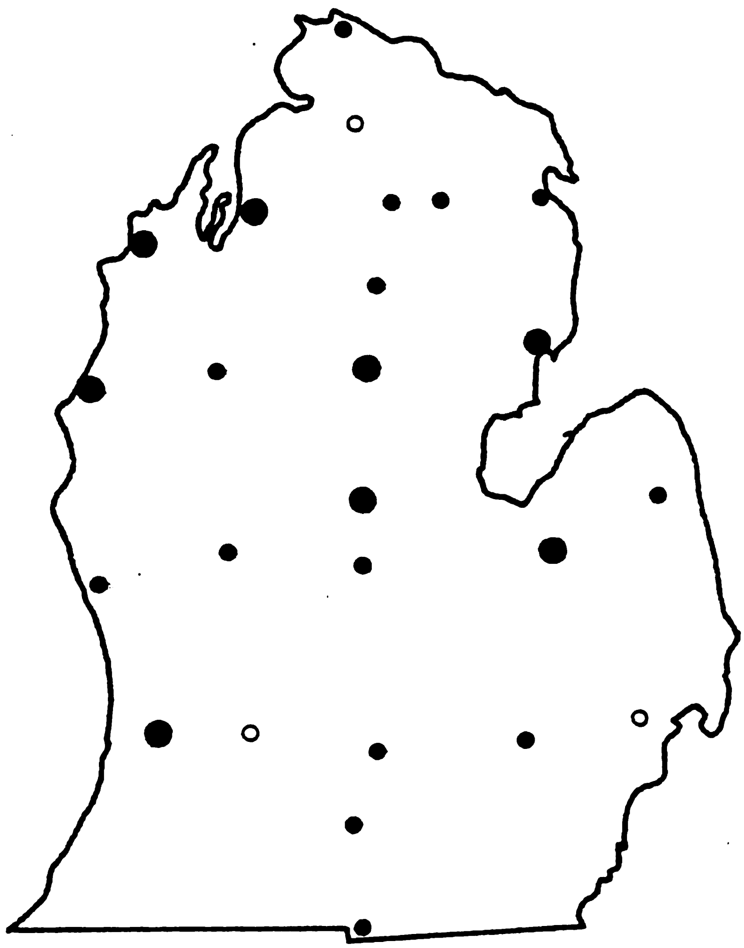


Figure 18. Regional distribution of Arthonia caesia.

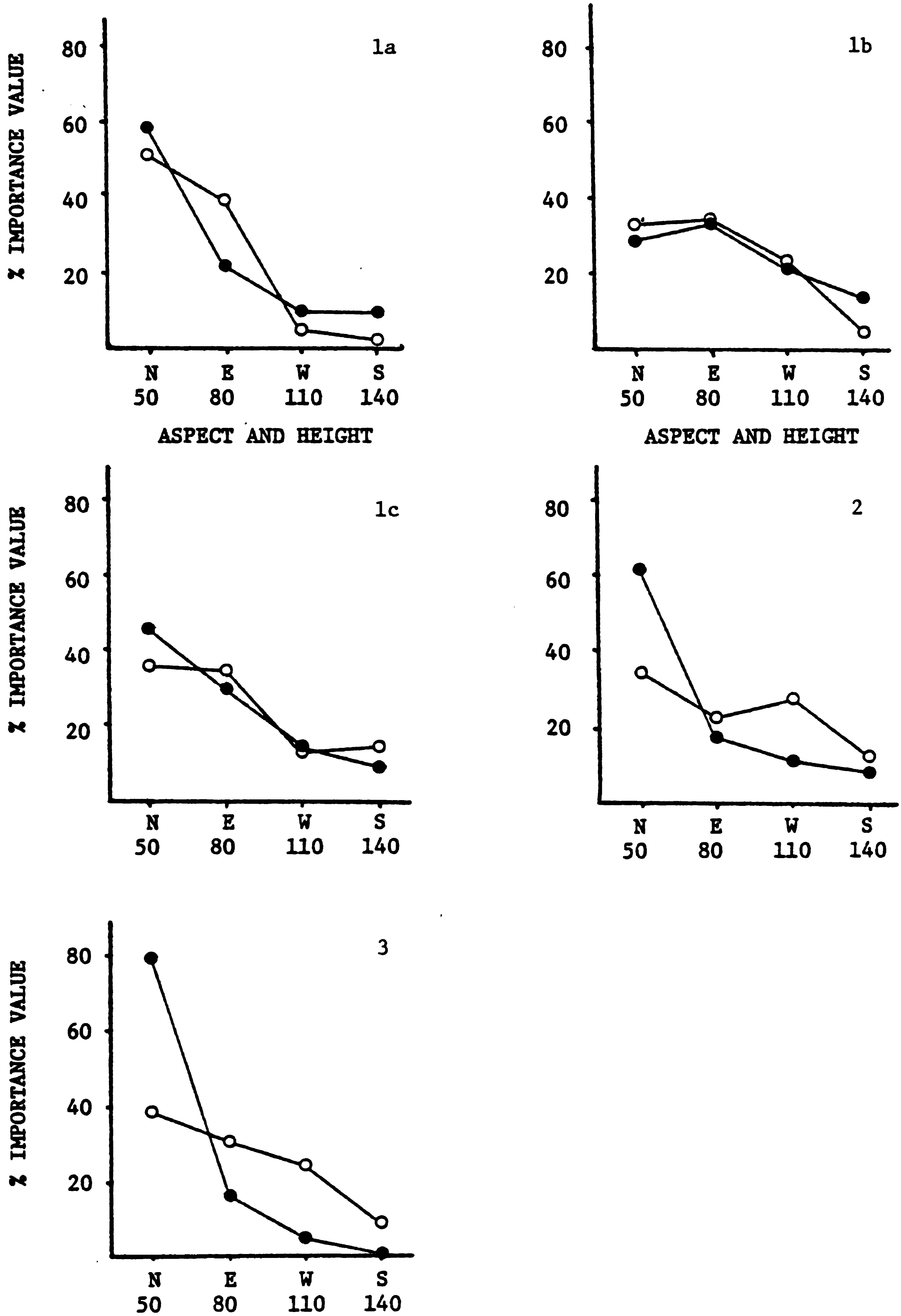


Figure 19. Within site distribution of <u>Arthonia</u> <u>caesia</u>.

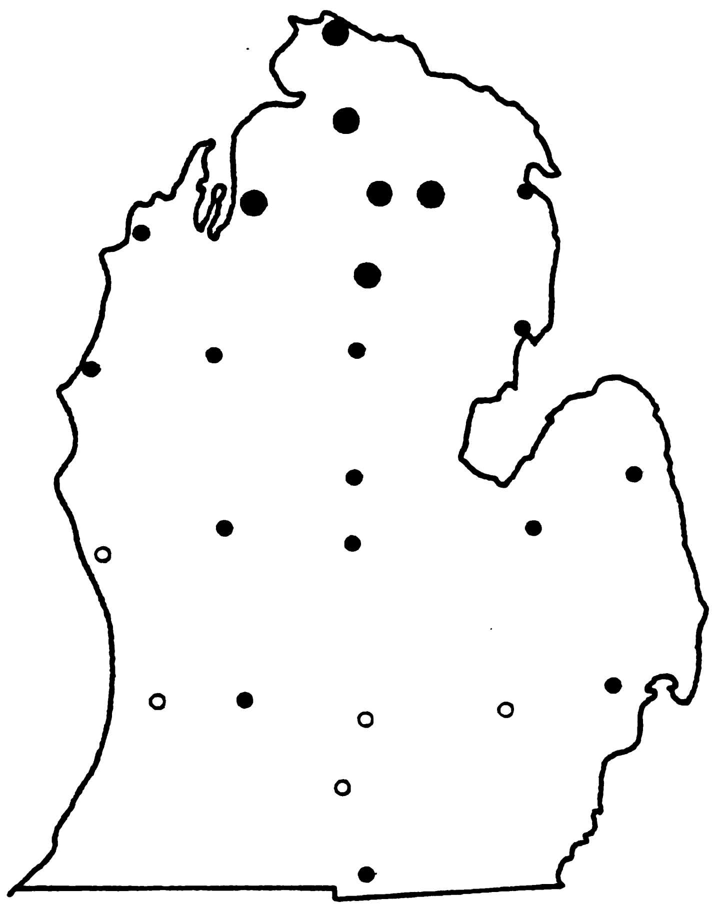


Figure 20. Regional distribution of Caloplaca cerina.

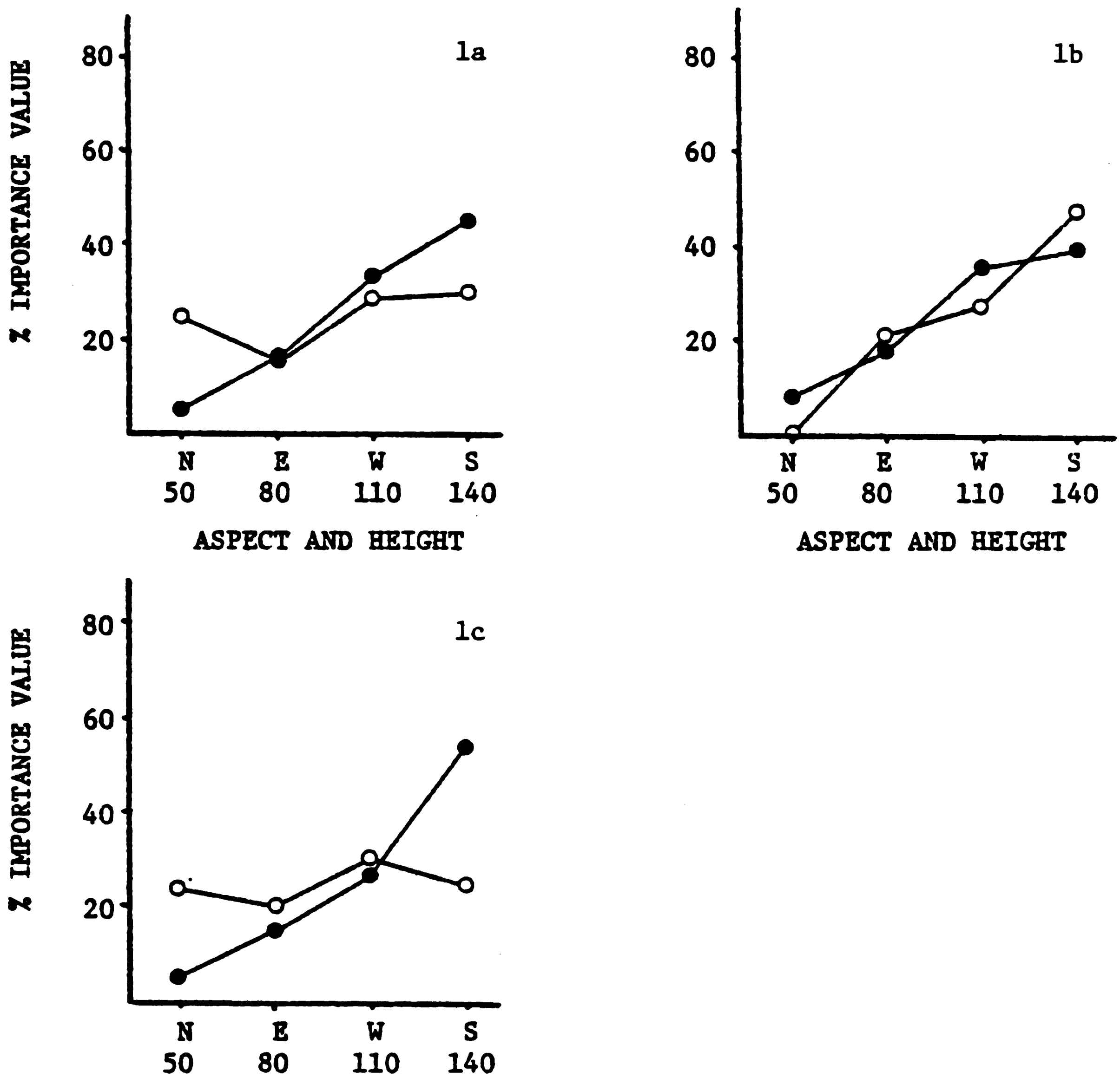


Figure 21. Within site distribution of Caloplaca cerina.

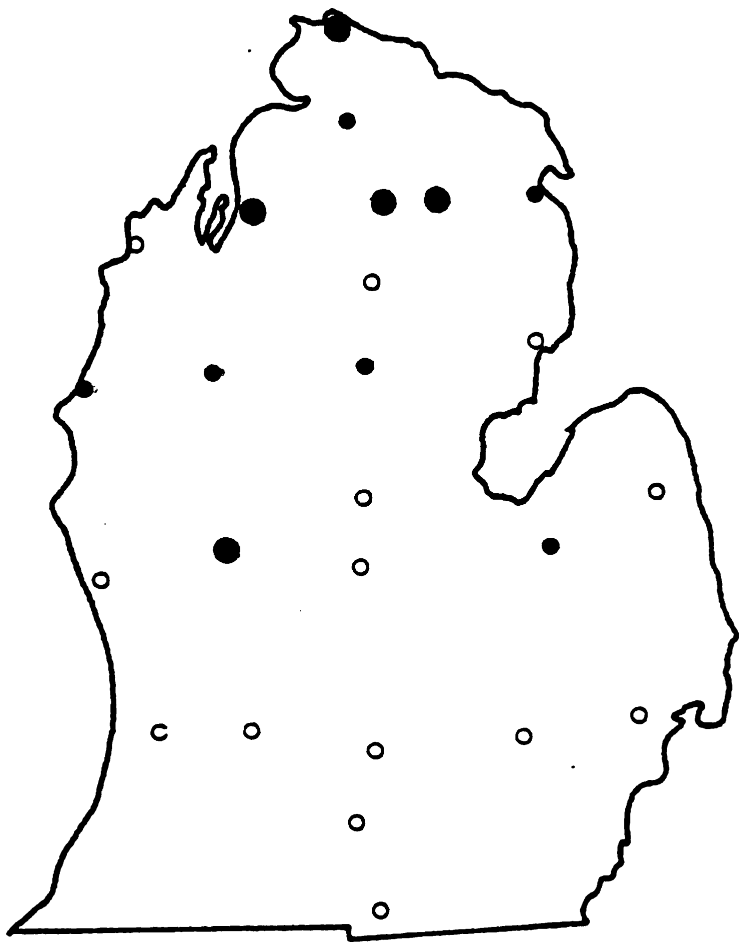


Figure 22. Regional distribution of Leptorhaphis contorta.

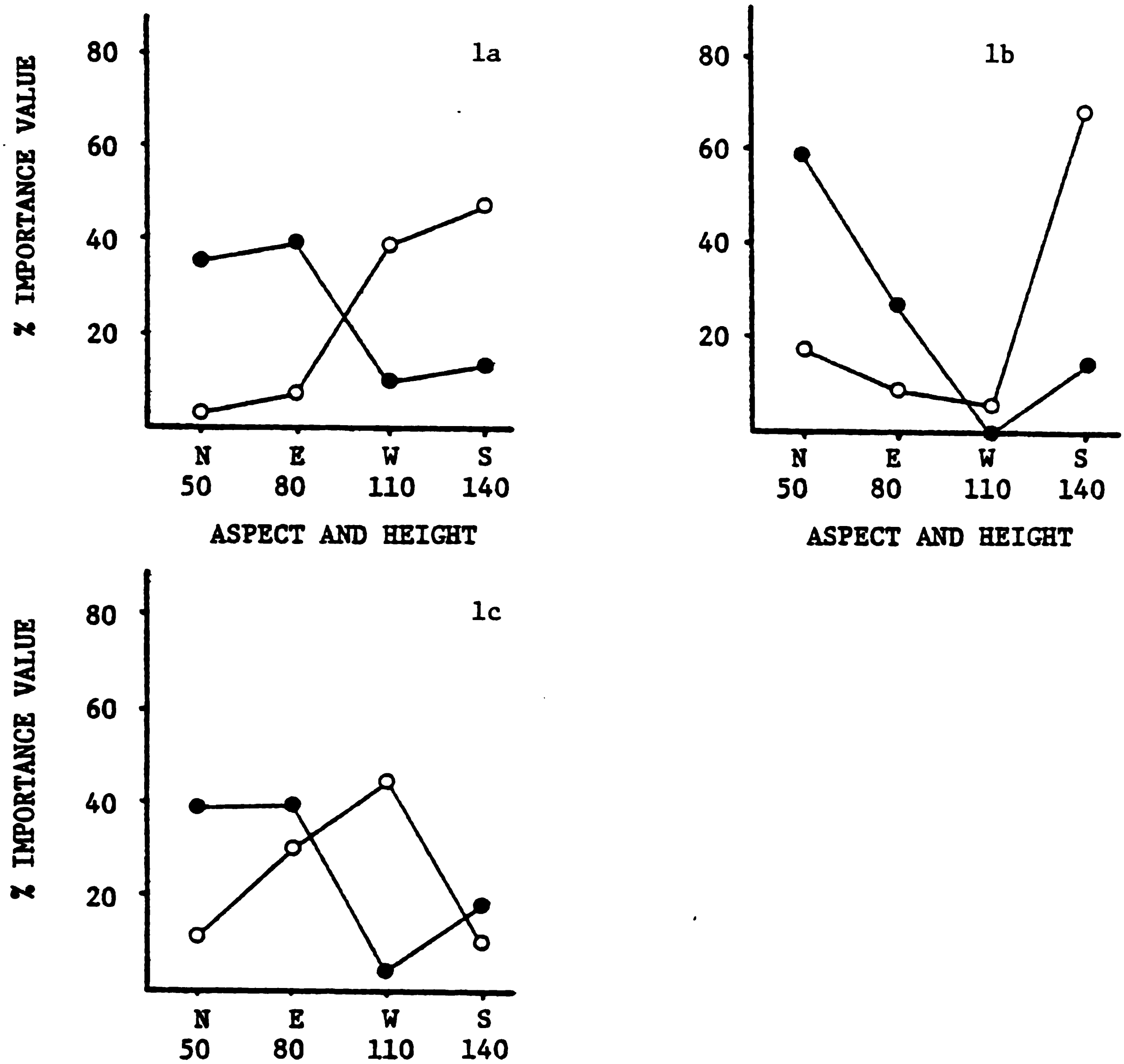


Figure 23. Within site distribution of Leptorhaphis contorta.

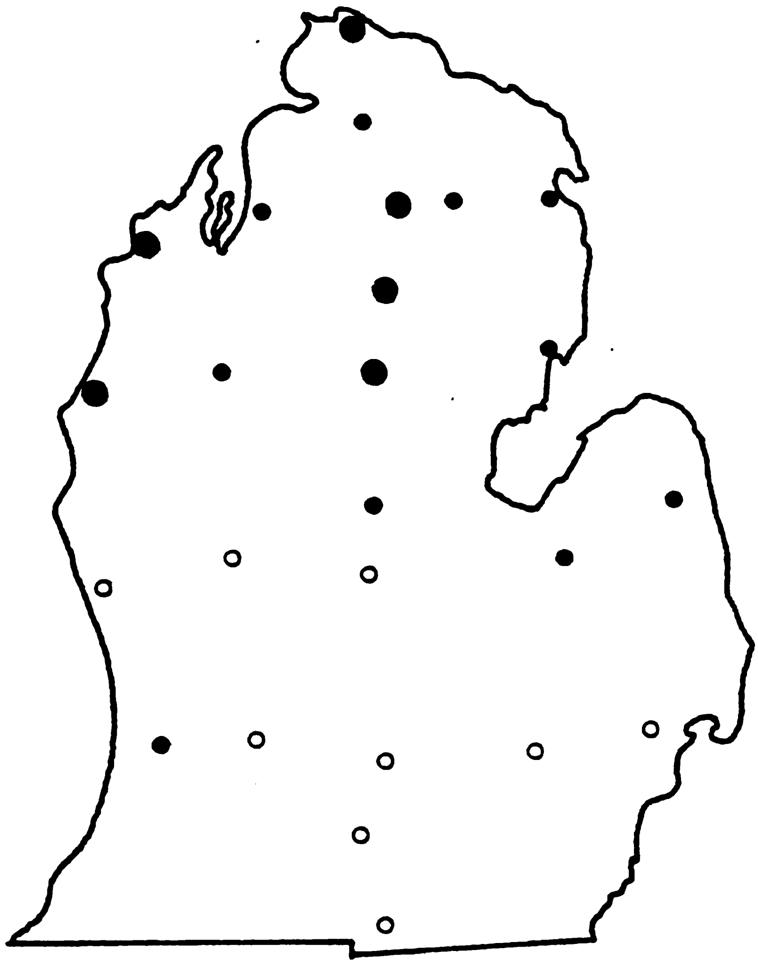


Figure 24. Regional distribution of Parmelia subaurifera.

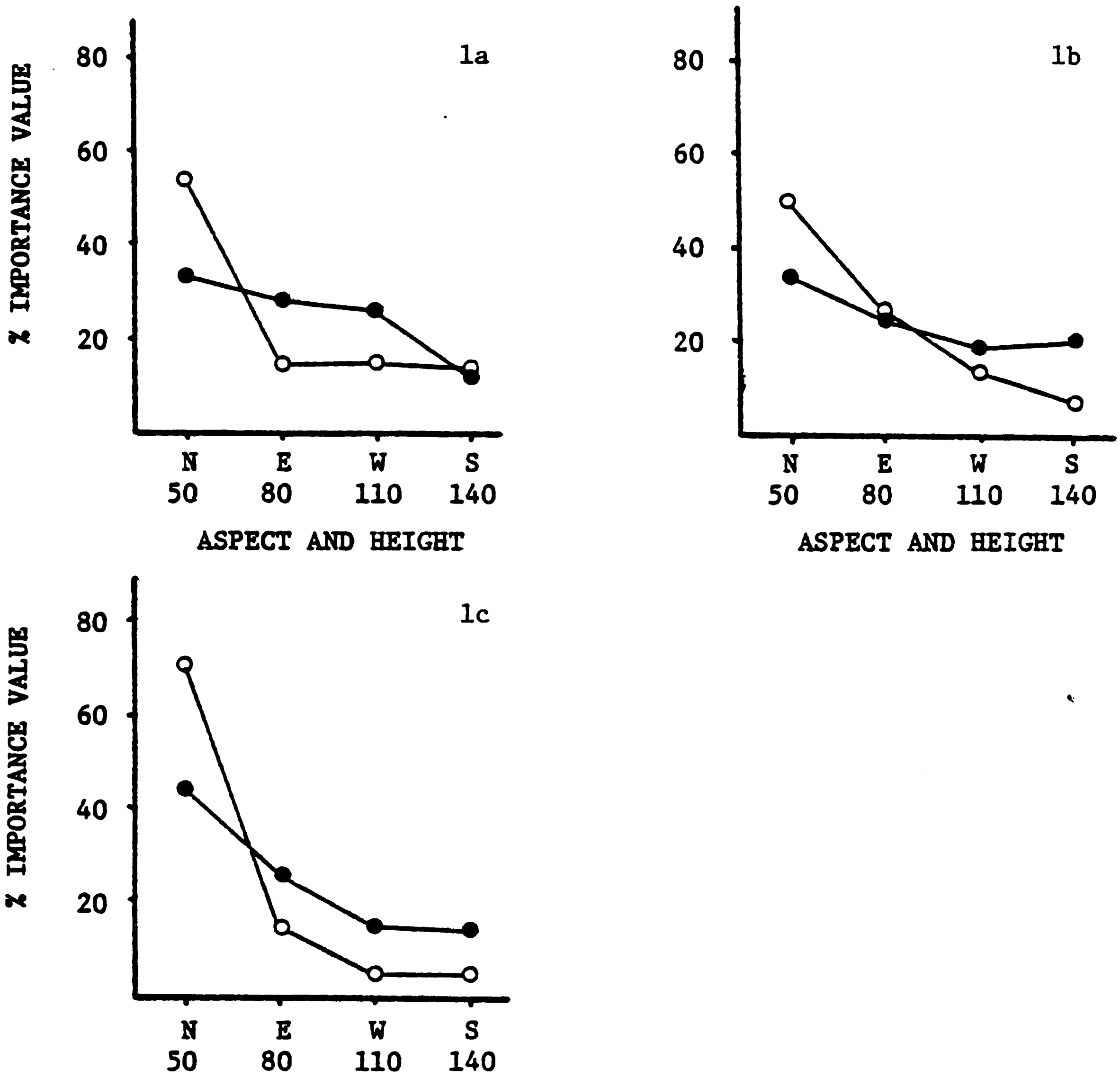


Figure 25. Within site distribution of <u>Parmelia subaurifera</u>.

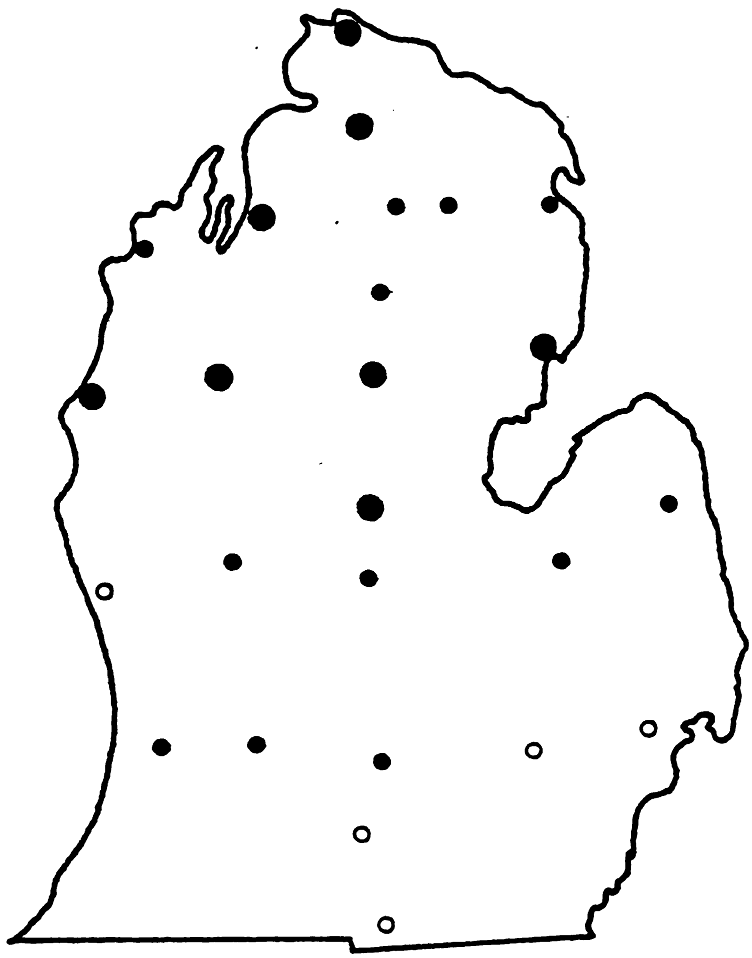


Figure 26. Regional distribution of Physcia adscendens.

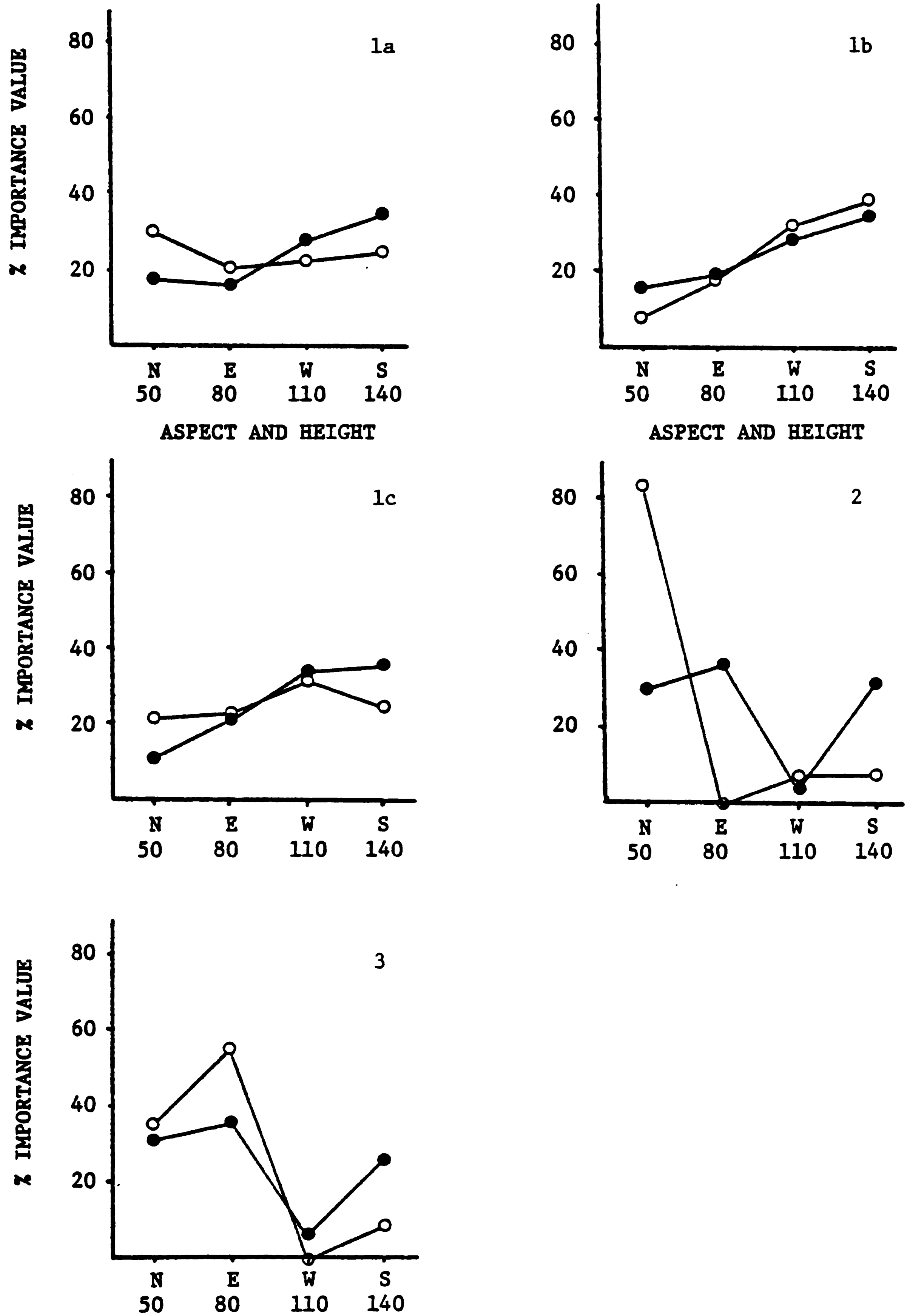


Figure 27. Within site distribution of *Physcia adscendens*.

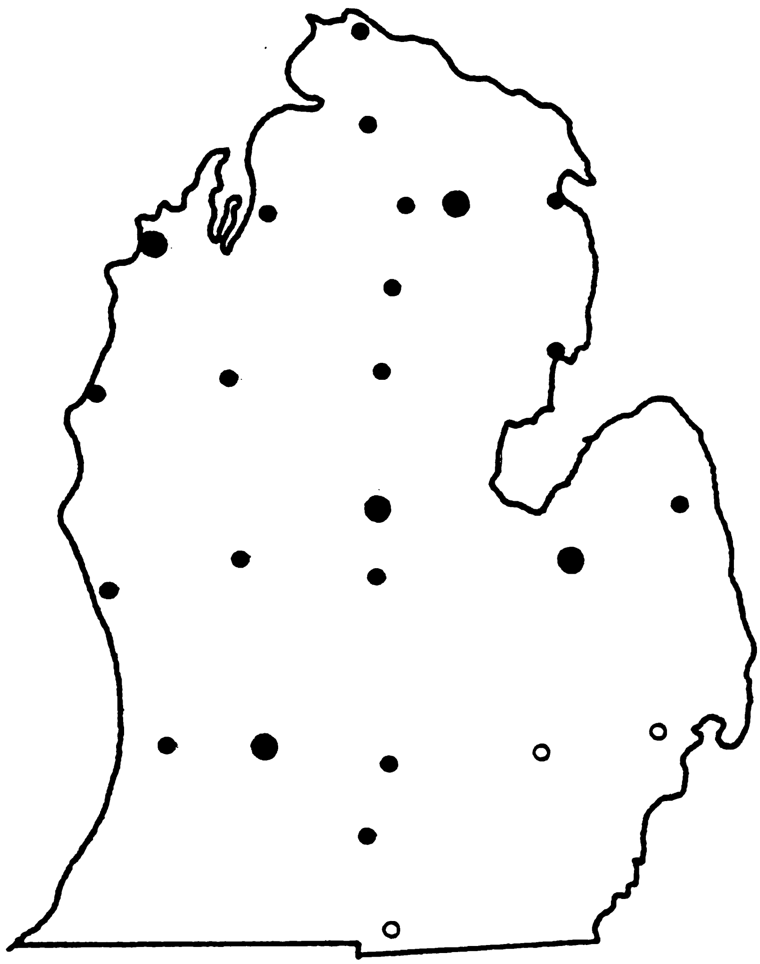


Figure 28. Regional distribution of Physcia stellaris.

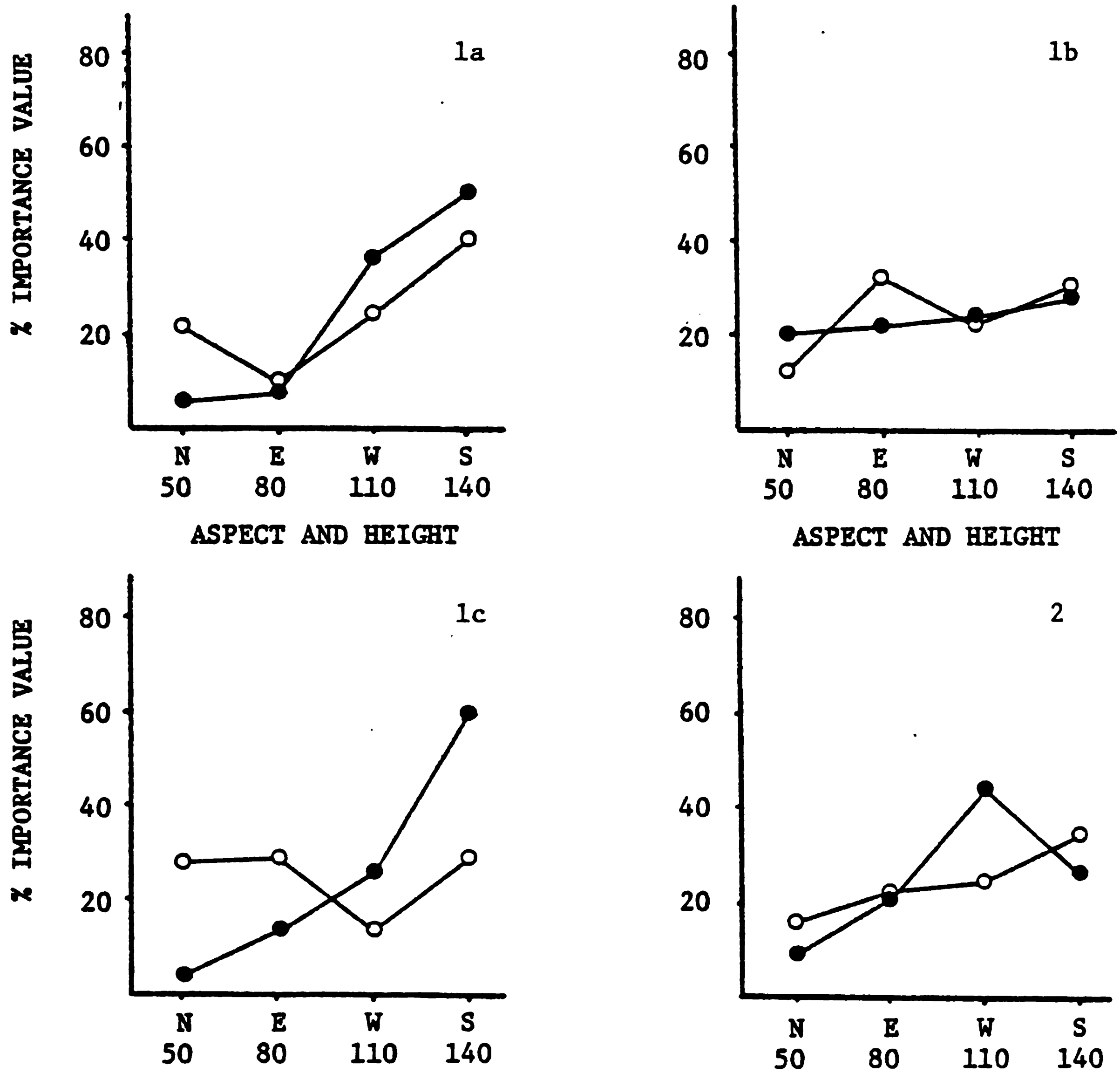


Figure 29. Within site distribution of Physcia stellaris.

Species Group A

Arthonia caesia and Physcia stellaris, although members of this group, are illustrated in figures 18 & 19 and 28 & 29 respectively.

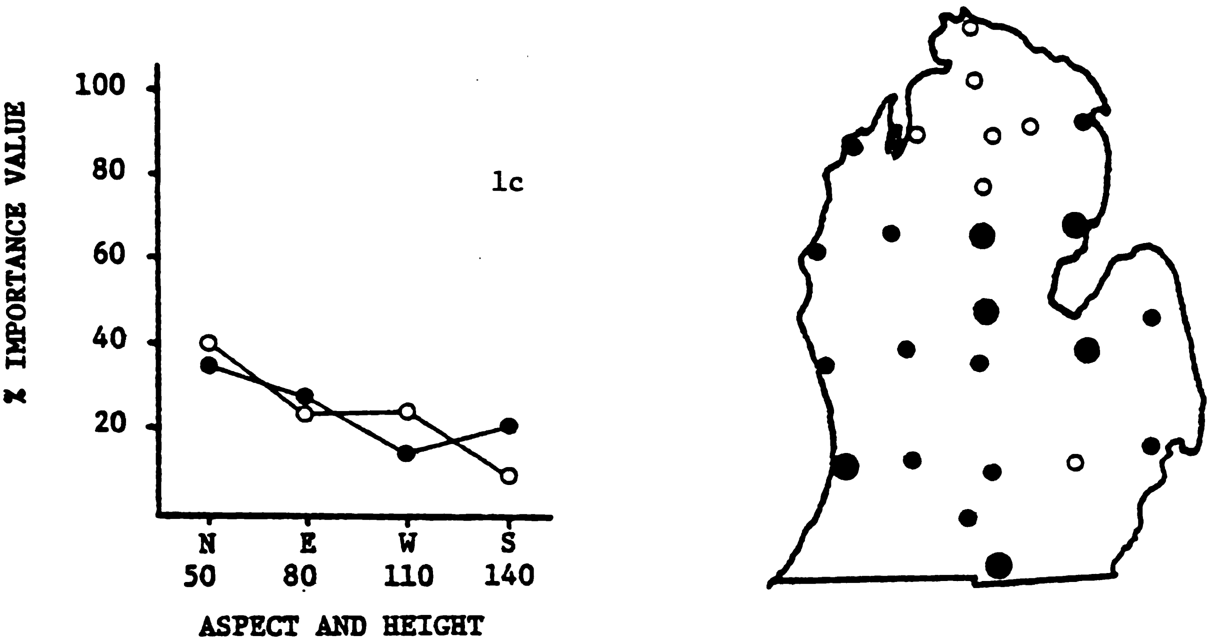


Figure 30. Distribution of cfr Arthonia caesia.

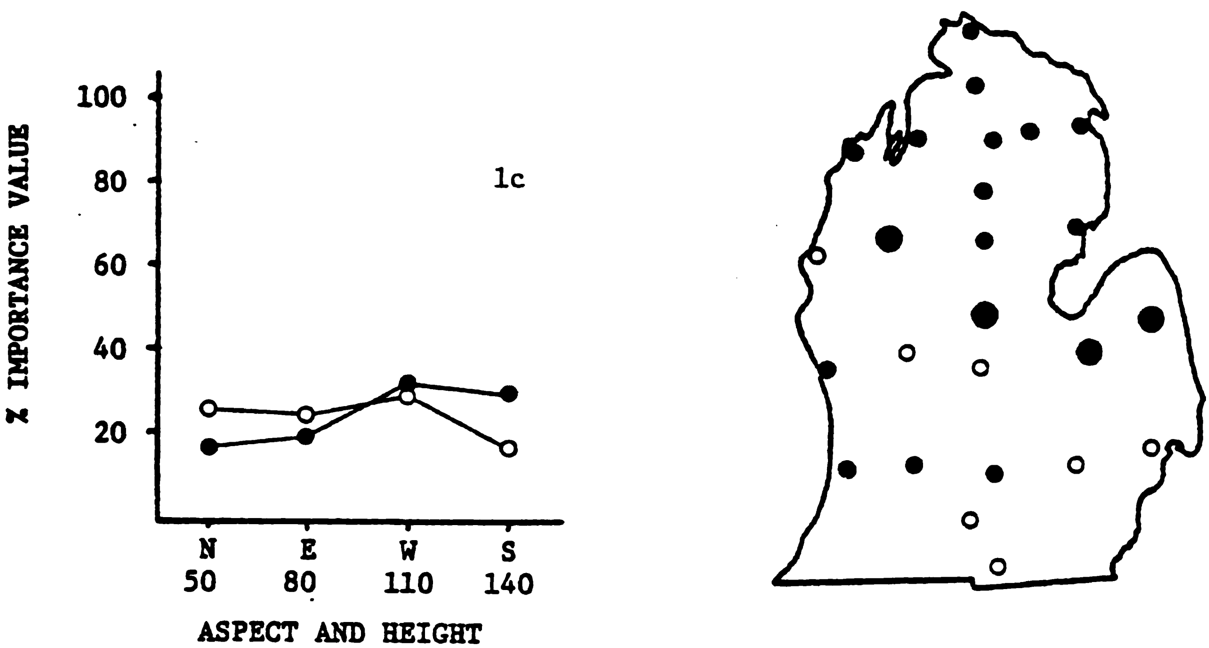


Figure 31. Distribution of Bacidia populorum.

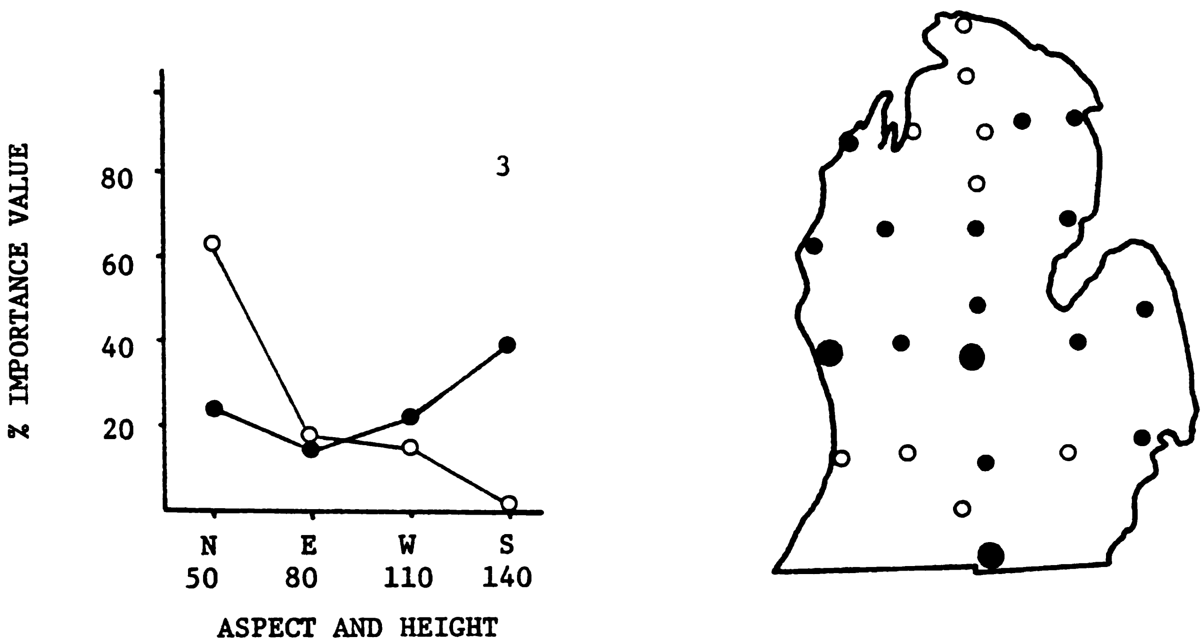


Figure 32. Distribution of Protococcus spp.

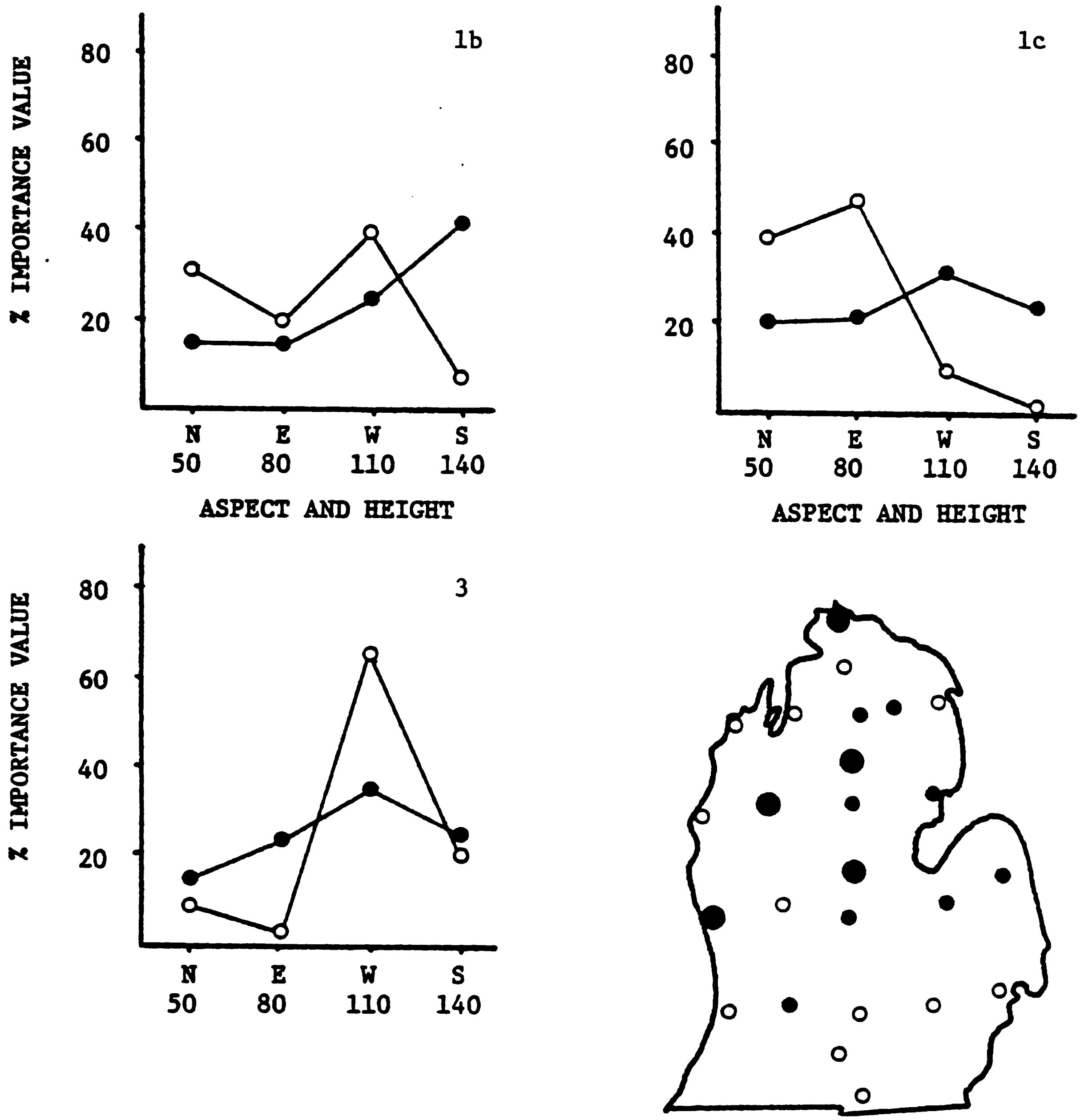
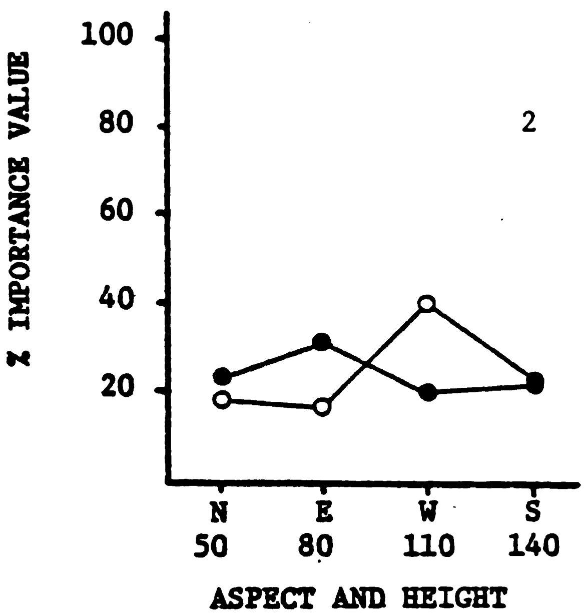


Figure 33. Distribution of <u>Rinodina pyrina</u>.

Species Group B



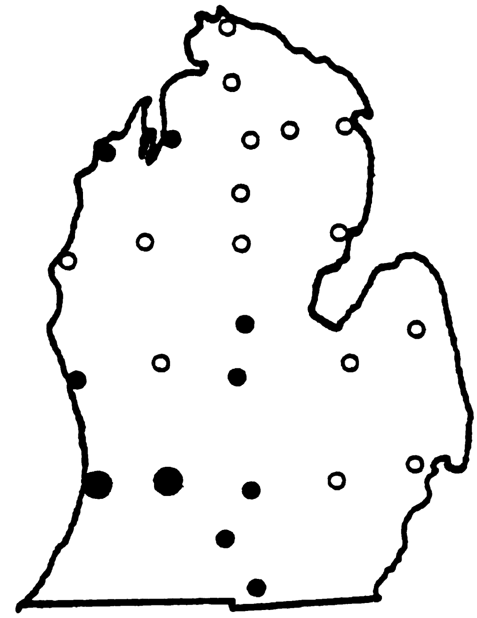
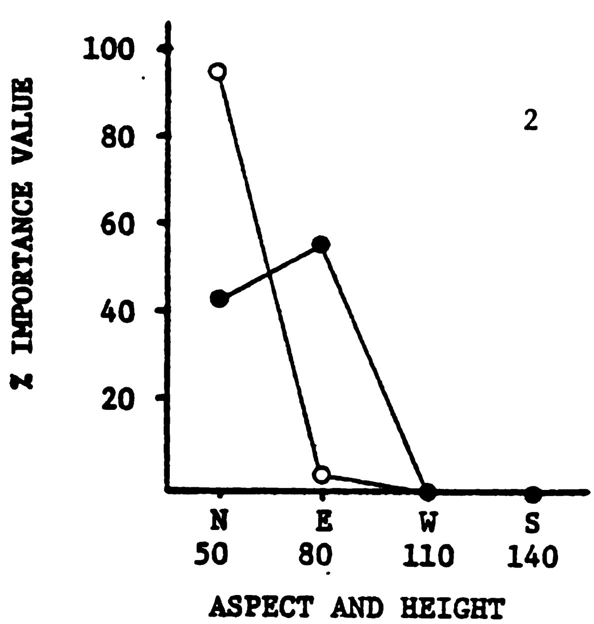


Figure 34. Distribution of Physcia millegrana.



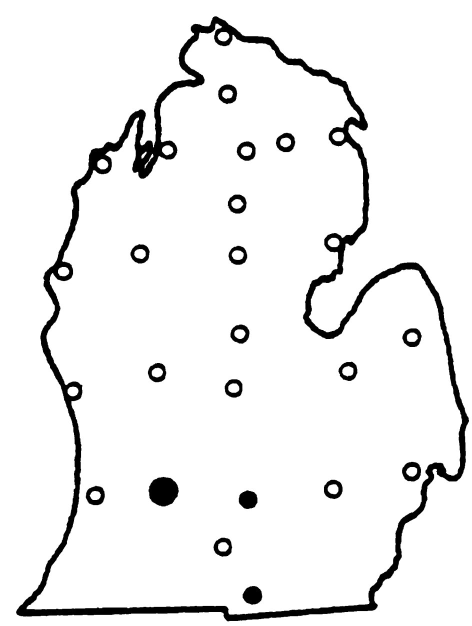


Figure 35. Distribution of Physciopsis elaeina.

Species Group C

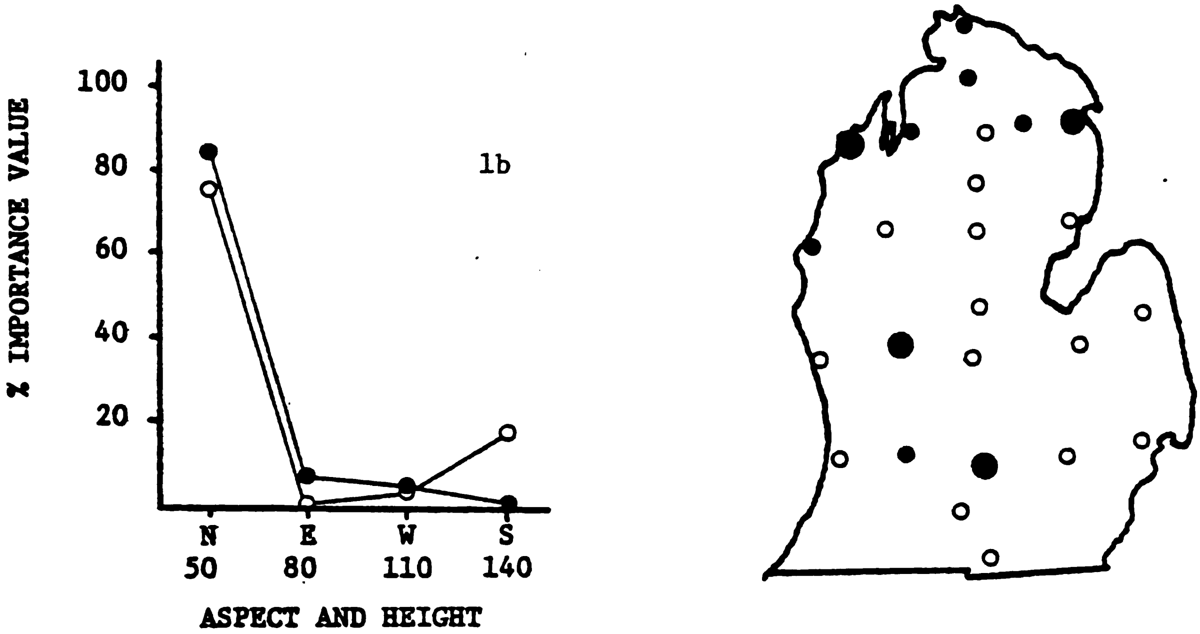


Figure 36. Distribution of Candelaria concolor.

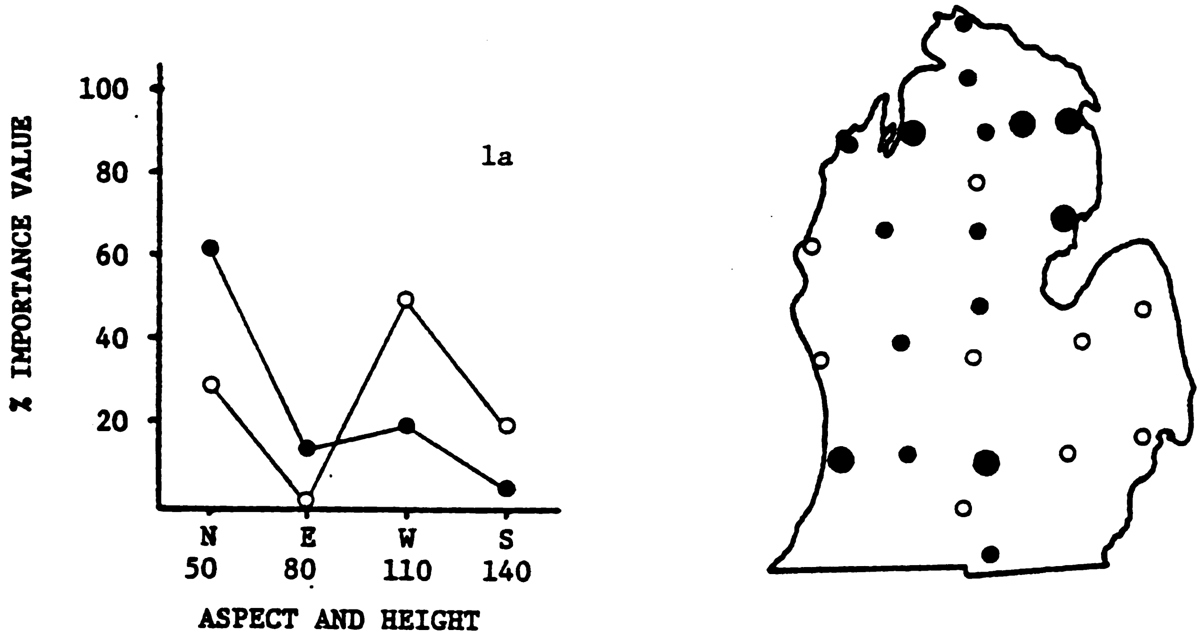


Figure 37. Distribution of Physcia orbicularis-group.

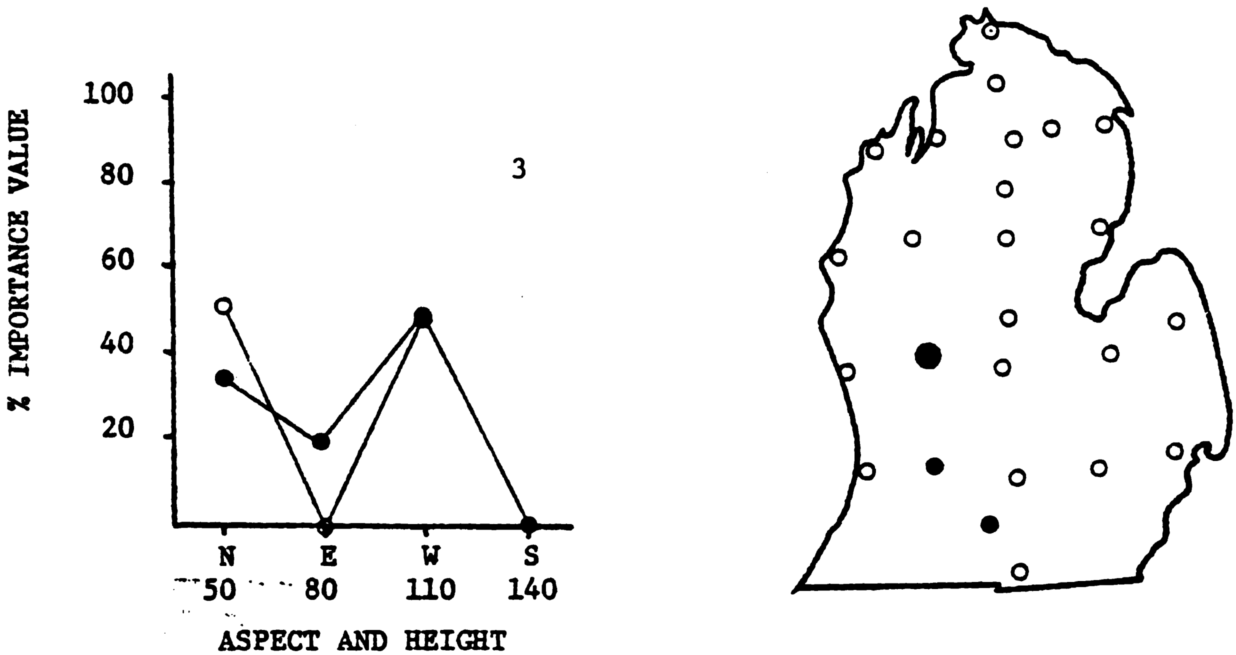
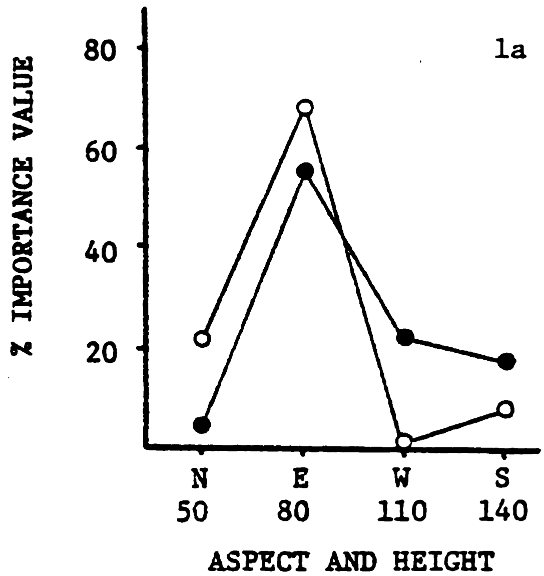
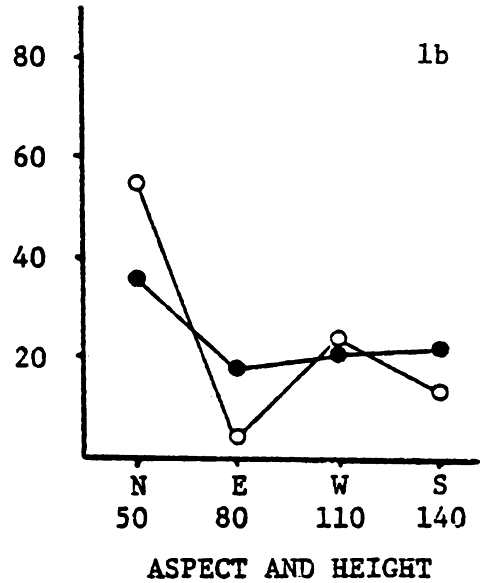


Figure 38. Distribution of Platygyrium repens.

Species Group D

Parmelia subaurifera and Physcia adscendens, although members of this group, are illustrated in figures 24 & 25 and 26 & 27 respectively.





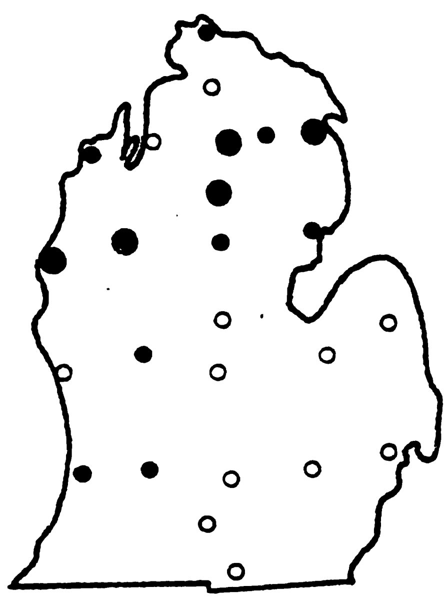


Figure 39. Distribution of Bacidia umbrina.

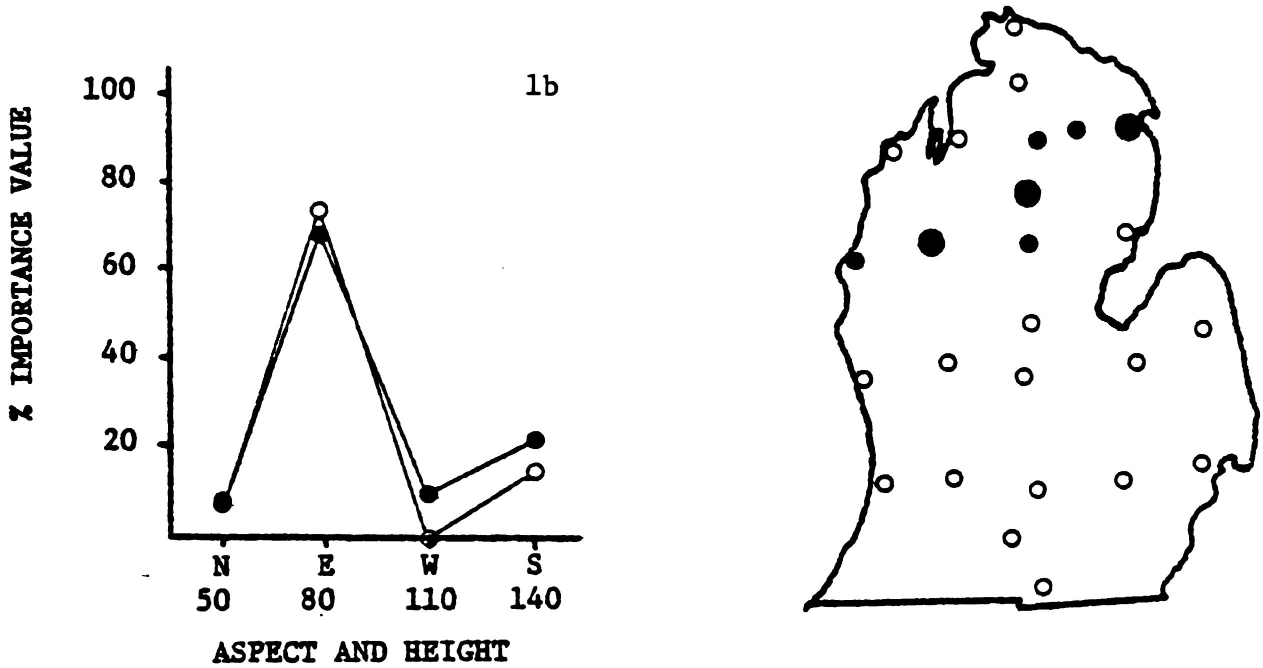


Figure 40. Distribution of Candelariella vitellina.

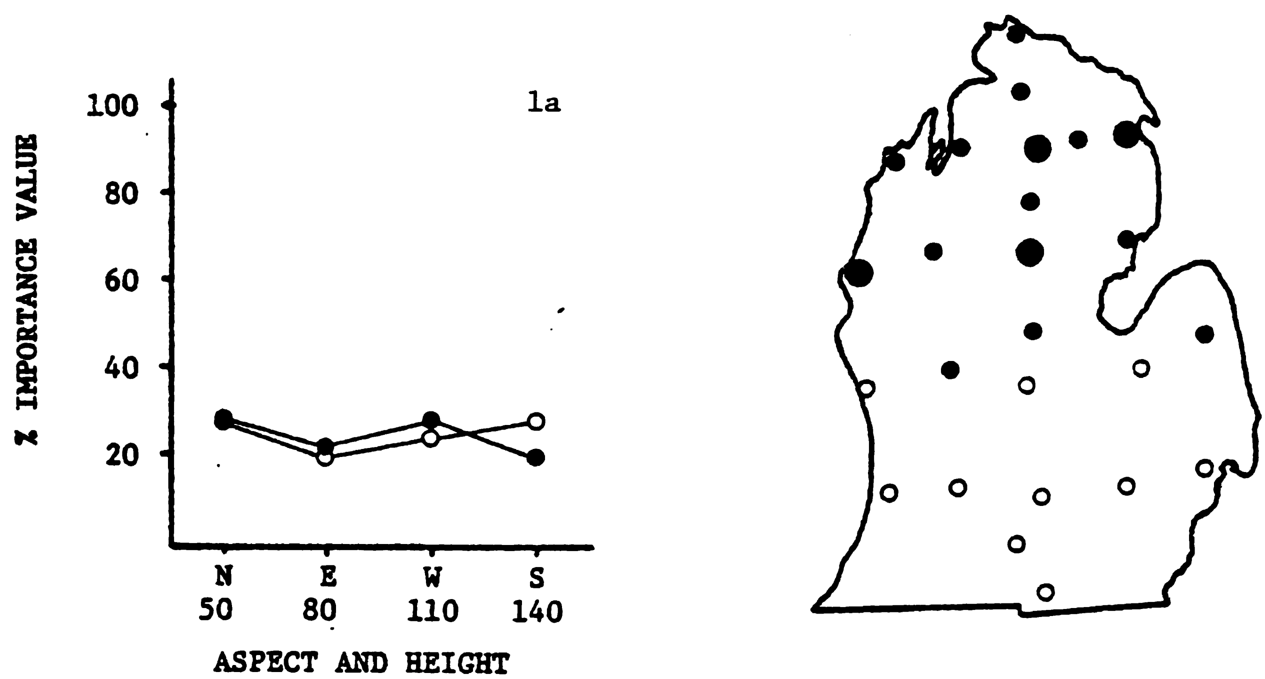


Figure 41. Distribution of Candelariella xanthostigma.

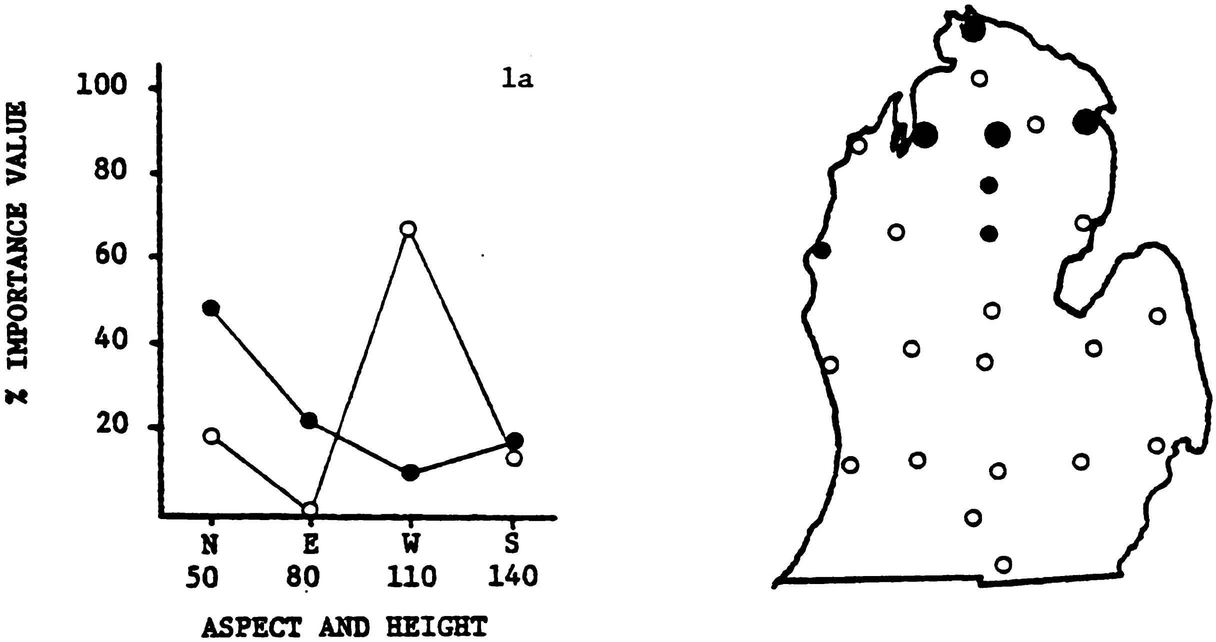


Figure 42. Distribution of Epicoccum sp.

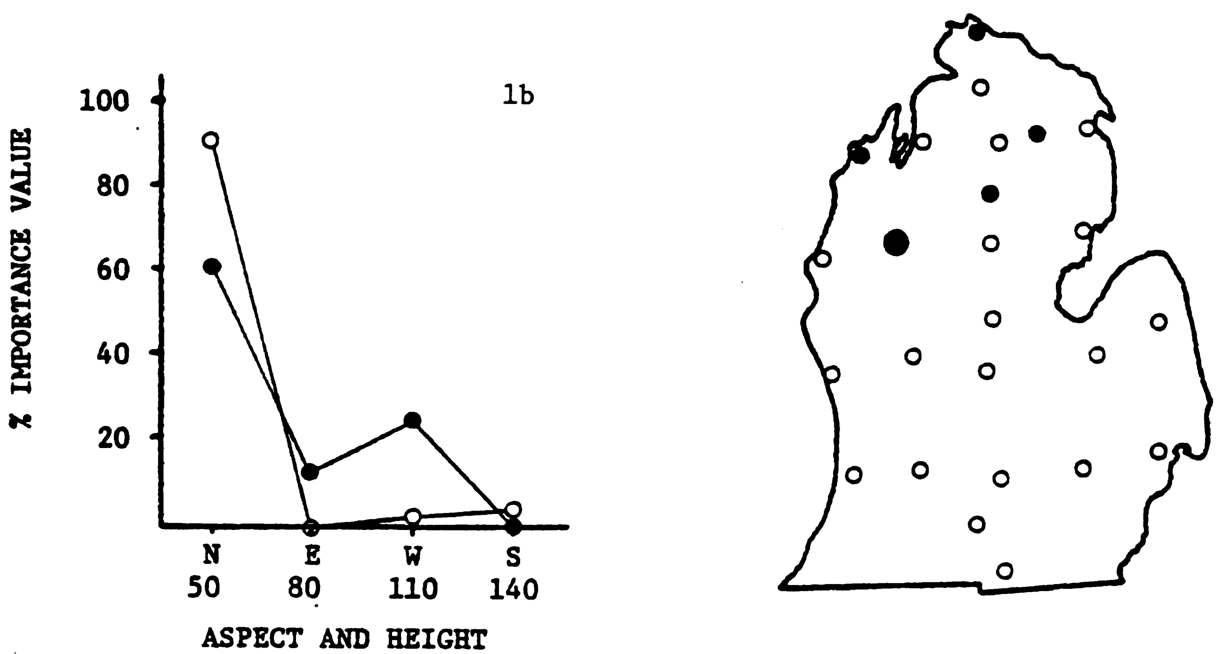


Figure 43. Distribution of Evernia mesomorpha.

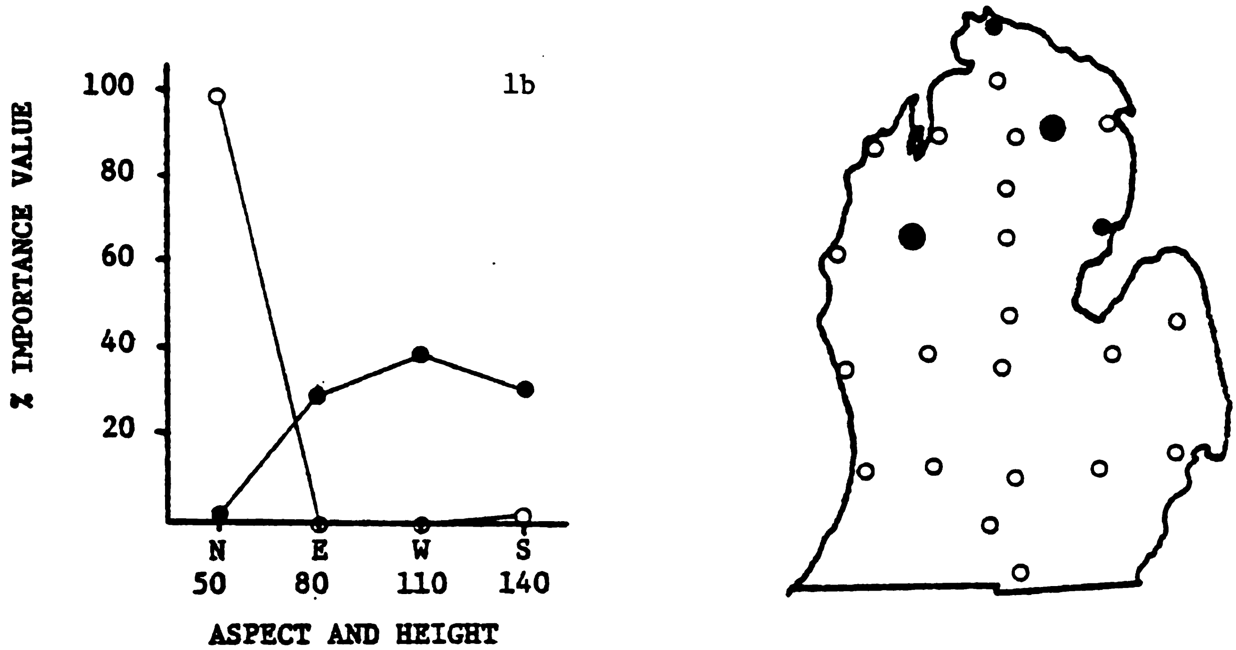


Figure 44. Distribution of Hypogymnia physodes.

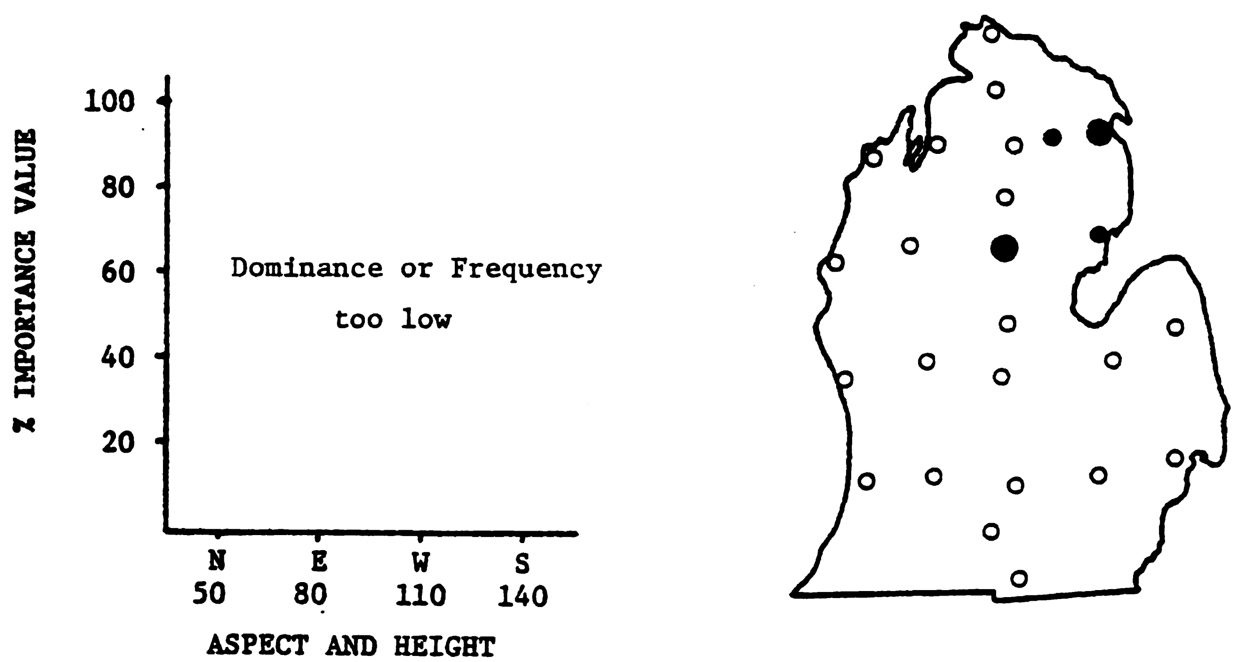
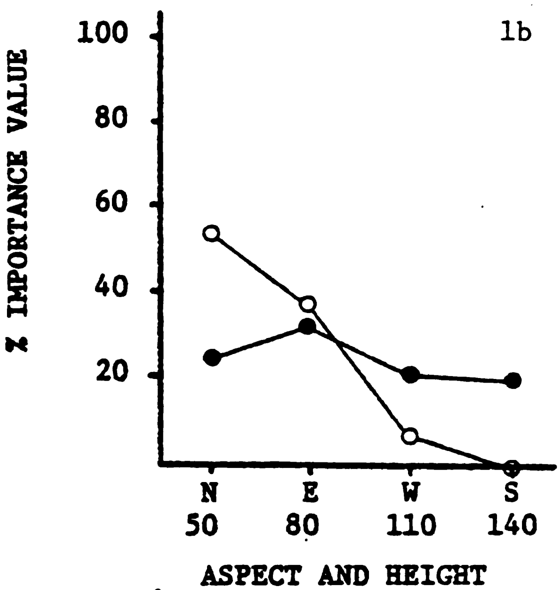


Figure 45. Distribution of Lecanora chloropolia.



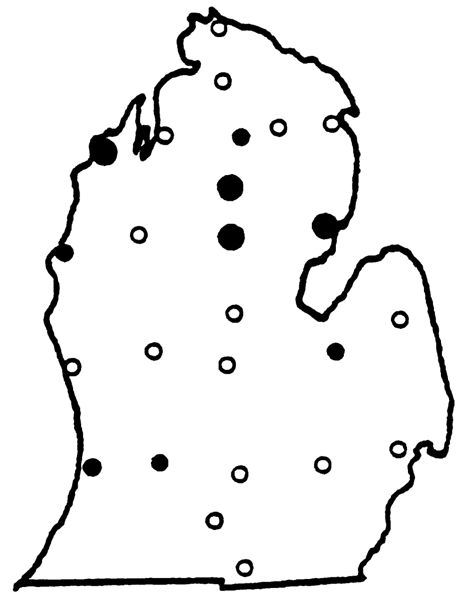
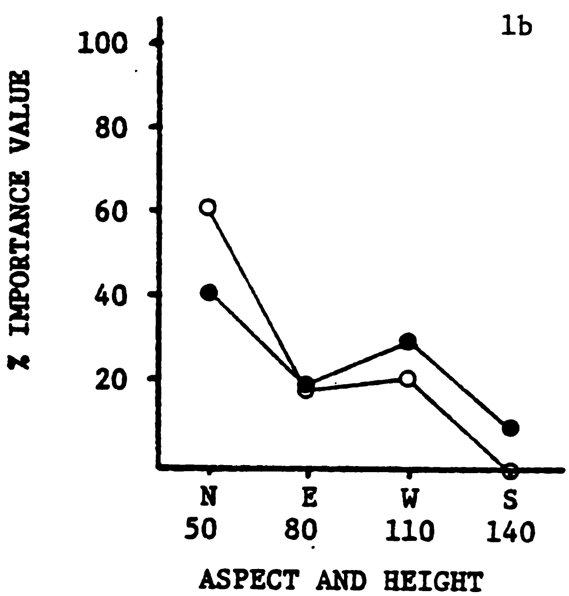


Figure 46. Distribution of Lecidea symmicta.



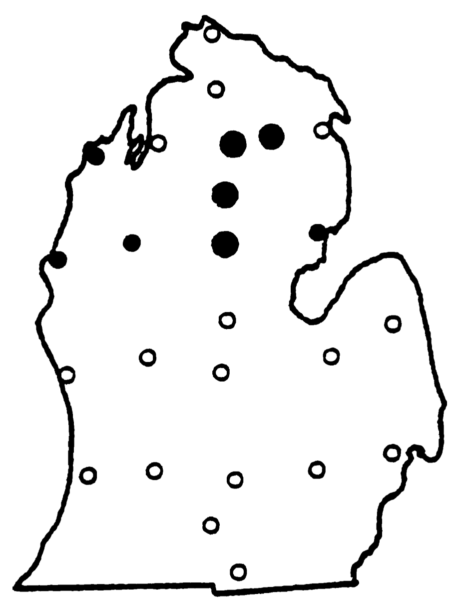


Figure 47. Distribution of Lepraria B.

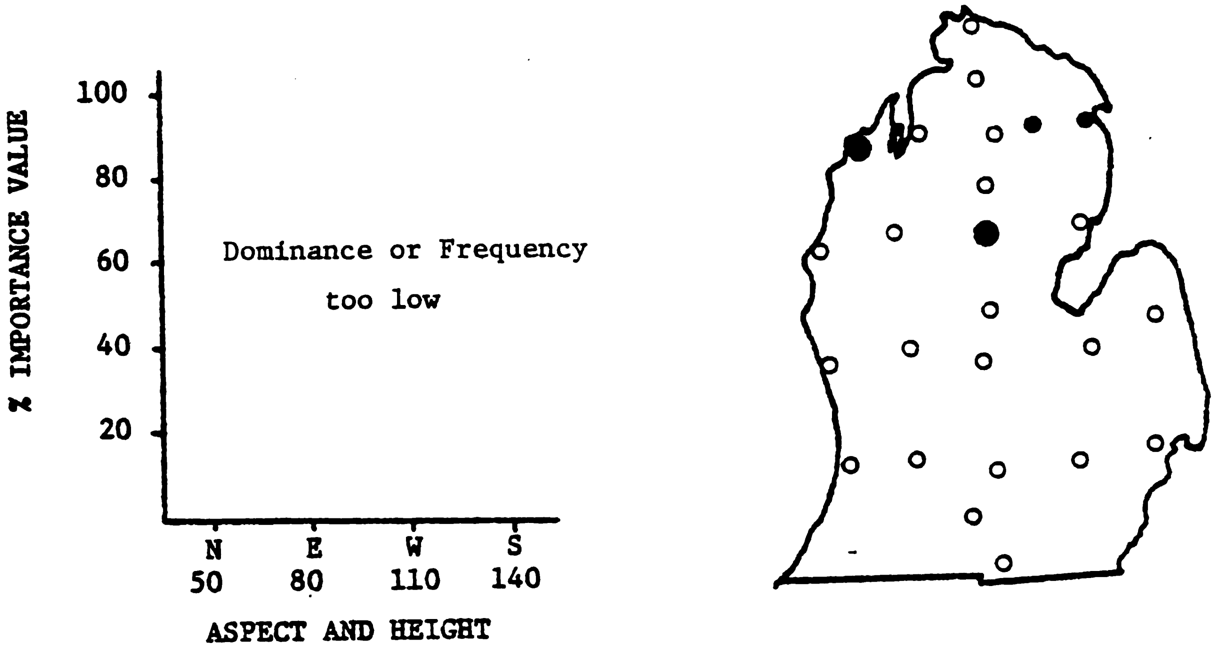


Figure 48. Distribution of <u>Lepraria</u> <u>C</u>.

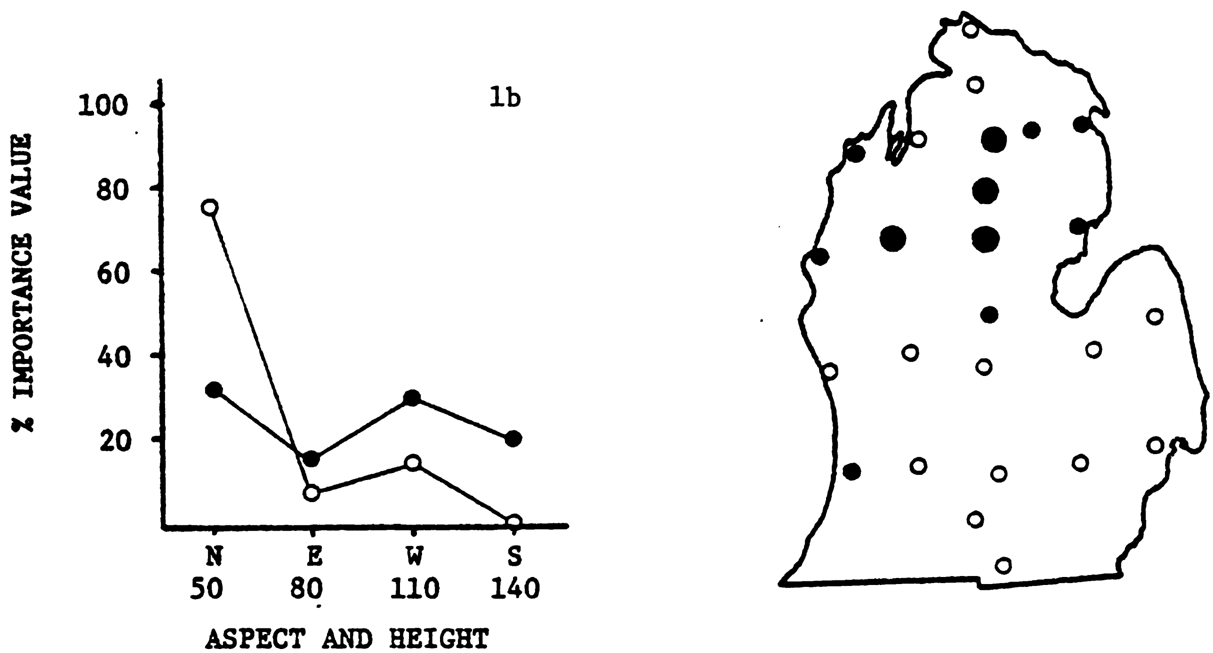


Figure 49. Distribution of <u>Ochrolechia</u> <u>arborea</u>.

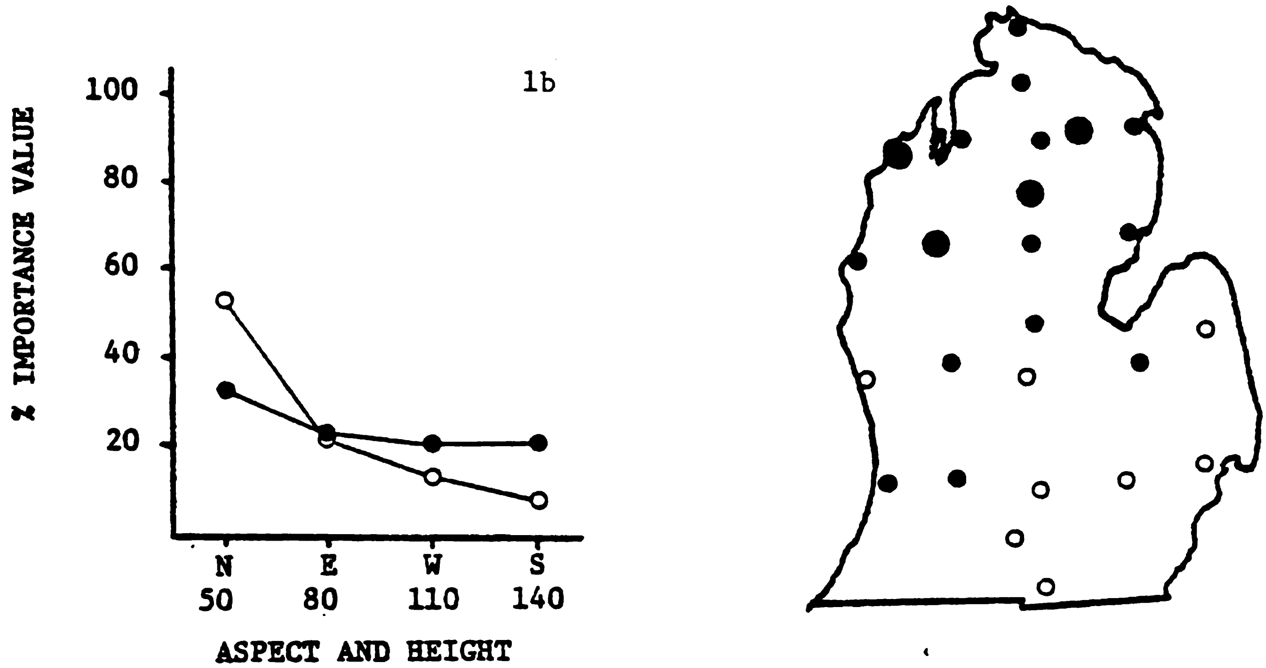


Figure 50. Distribution of Parmelia sulçata.

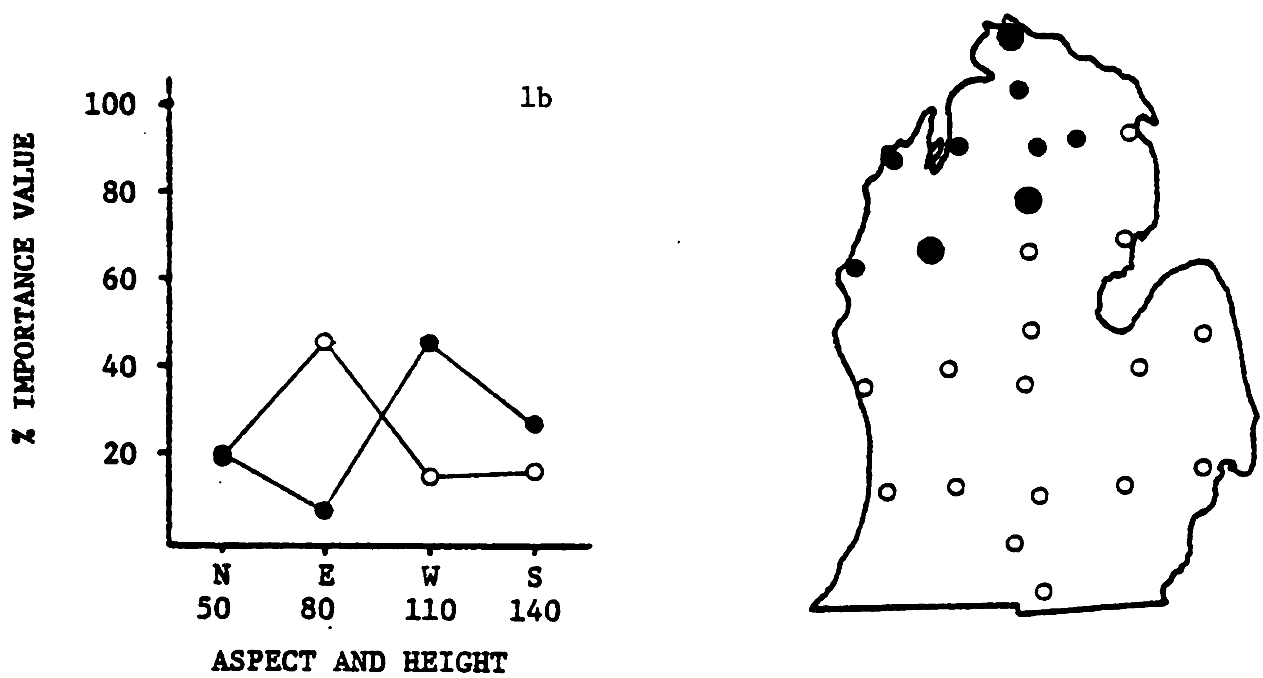


Figure 51. Distribution of Physcia aipolia.

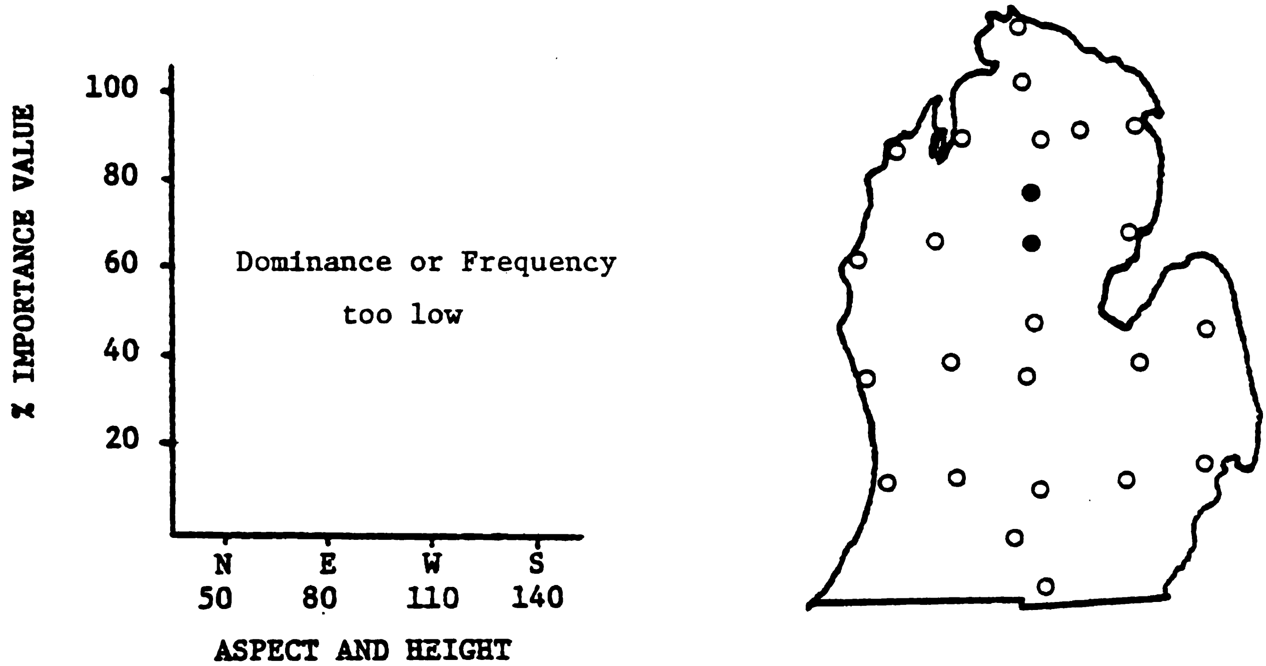


Figure 52. Distribution of Rinodina willeyi.

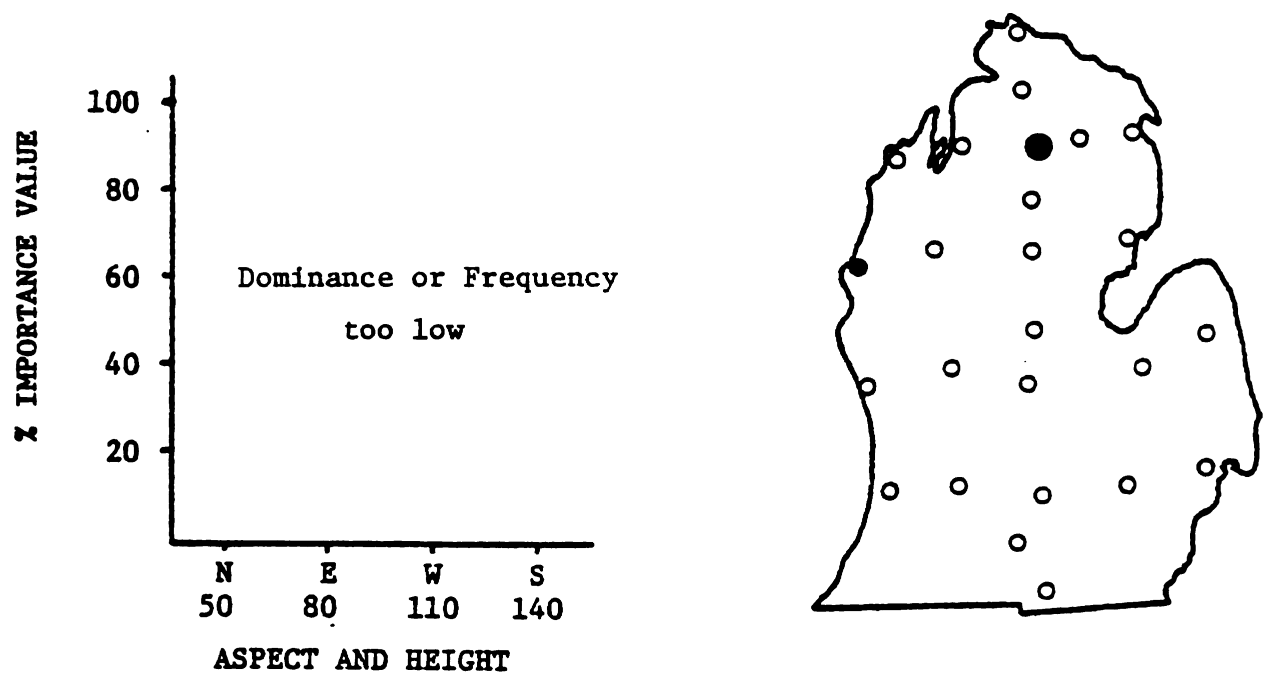


Figure 53. Distribution of Xanthoria fallax.

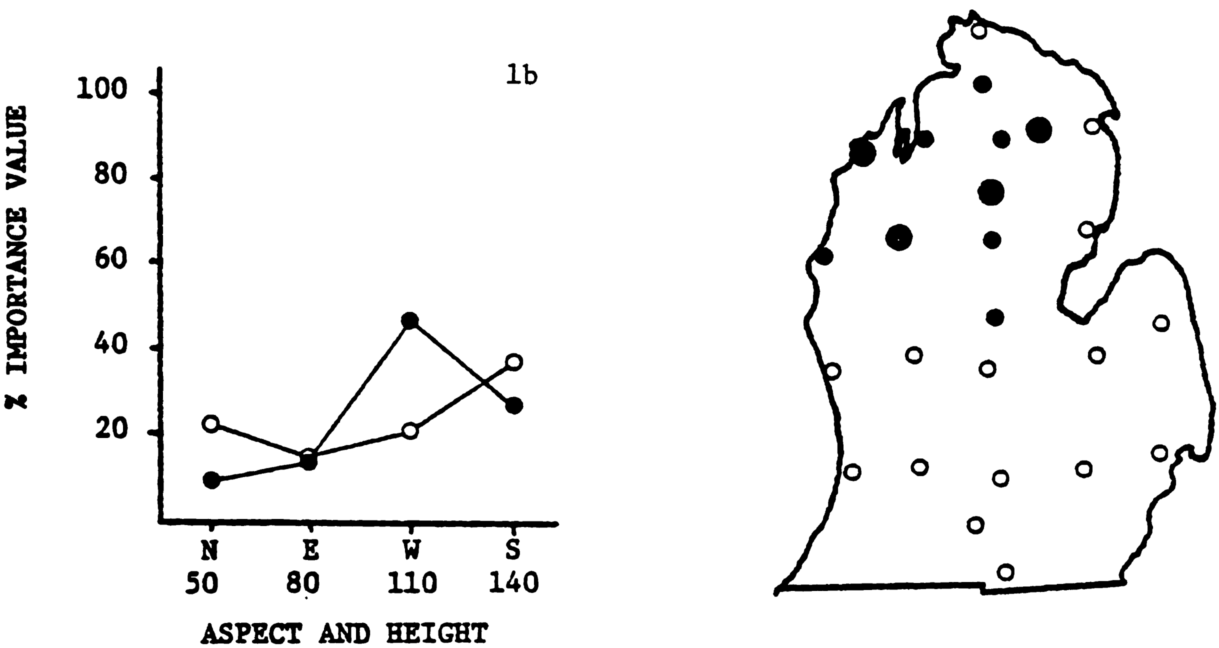


Figure 54. Distribution of Xanthoria polycarpa.

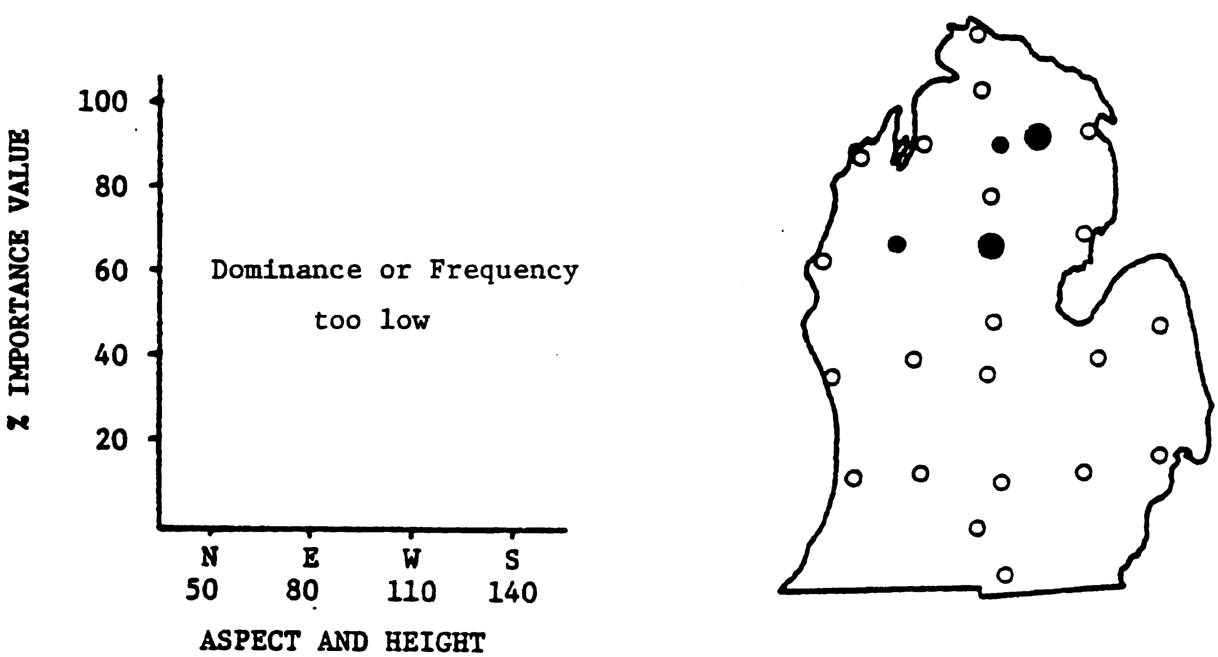


Figure 55. Distribution of Xenosporium sp.

Species Group E

Caloplaca cerina and Leptorhaphis contorta, although members of this group, are illustrated in figures 20 & 21 and 22 & 23.

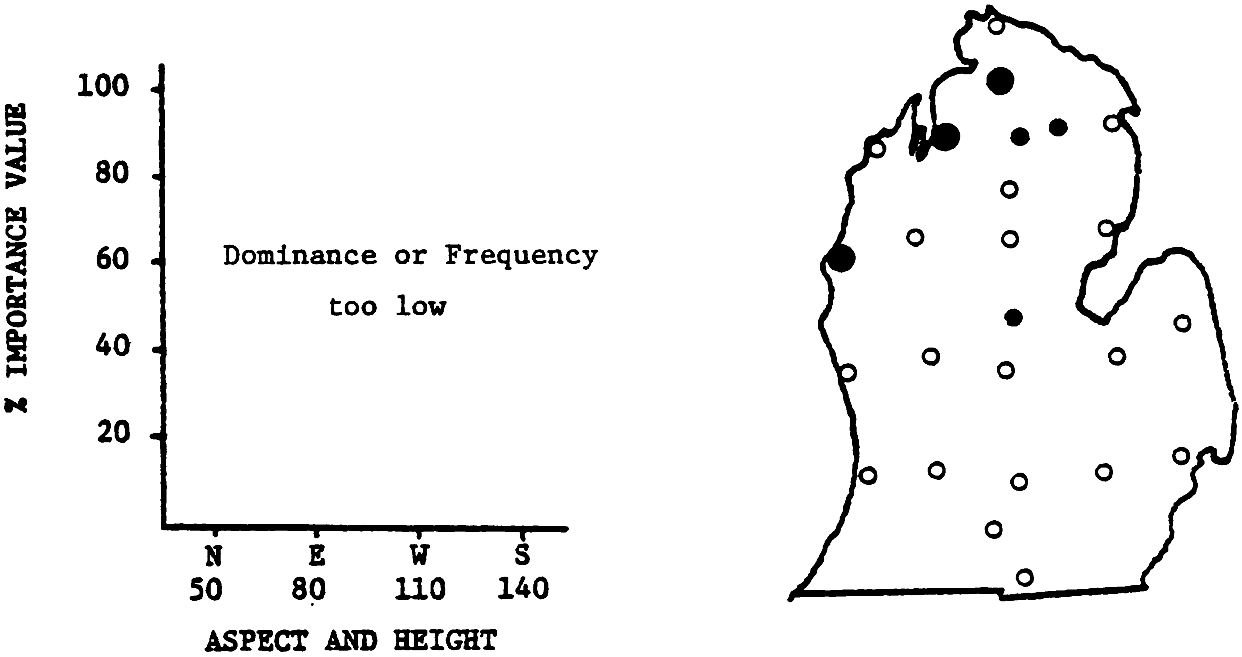


Figure 56. Distribution of Arthonia patellulata.

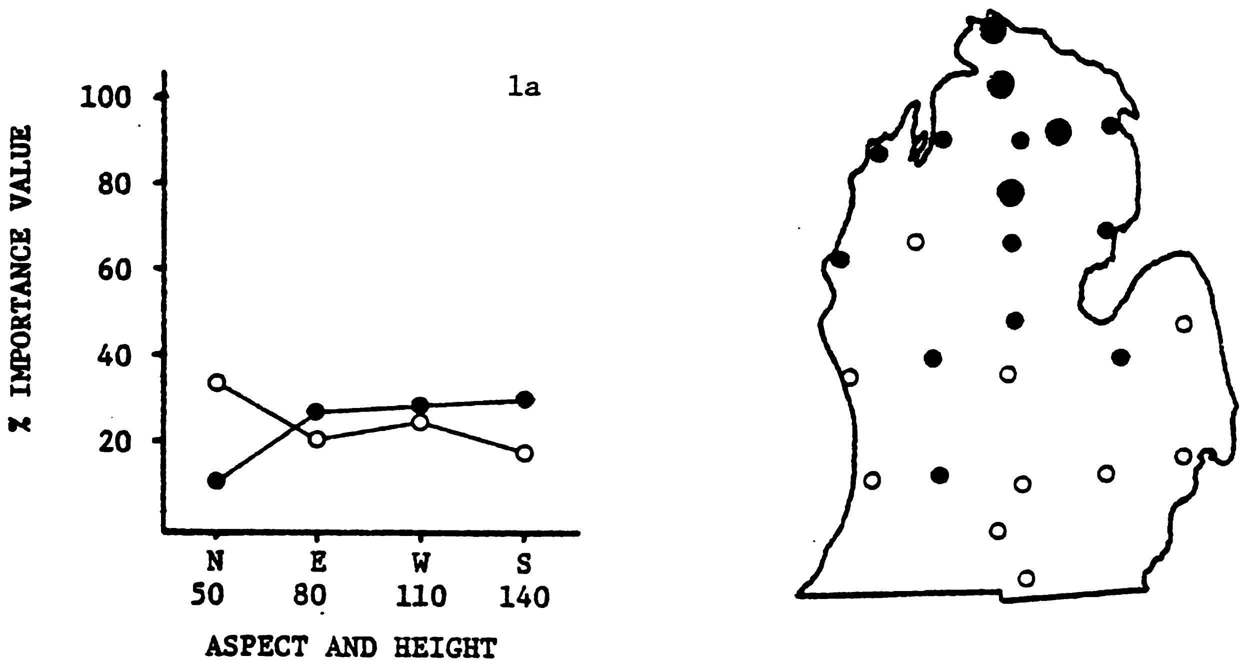


Figure 57. Distribution of Caloplaca holocarpa.

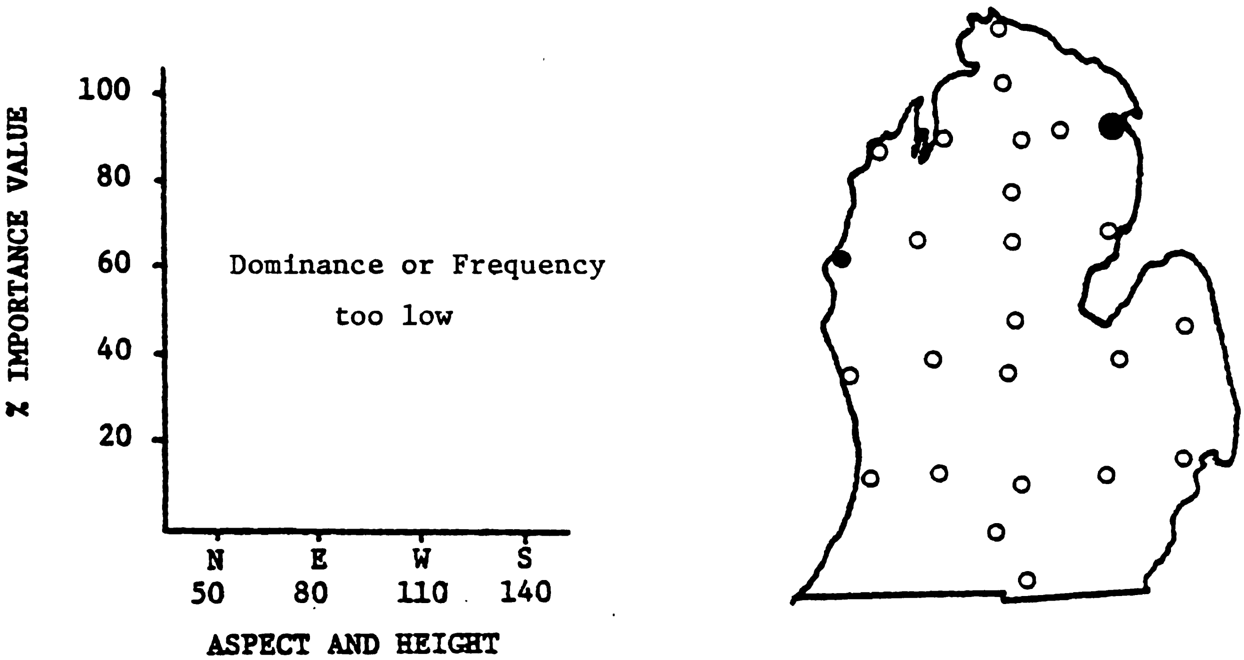


Figure 58. Distribution of Catillaria glauconigrans.

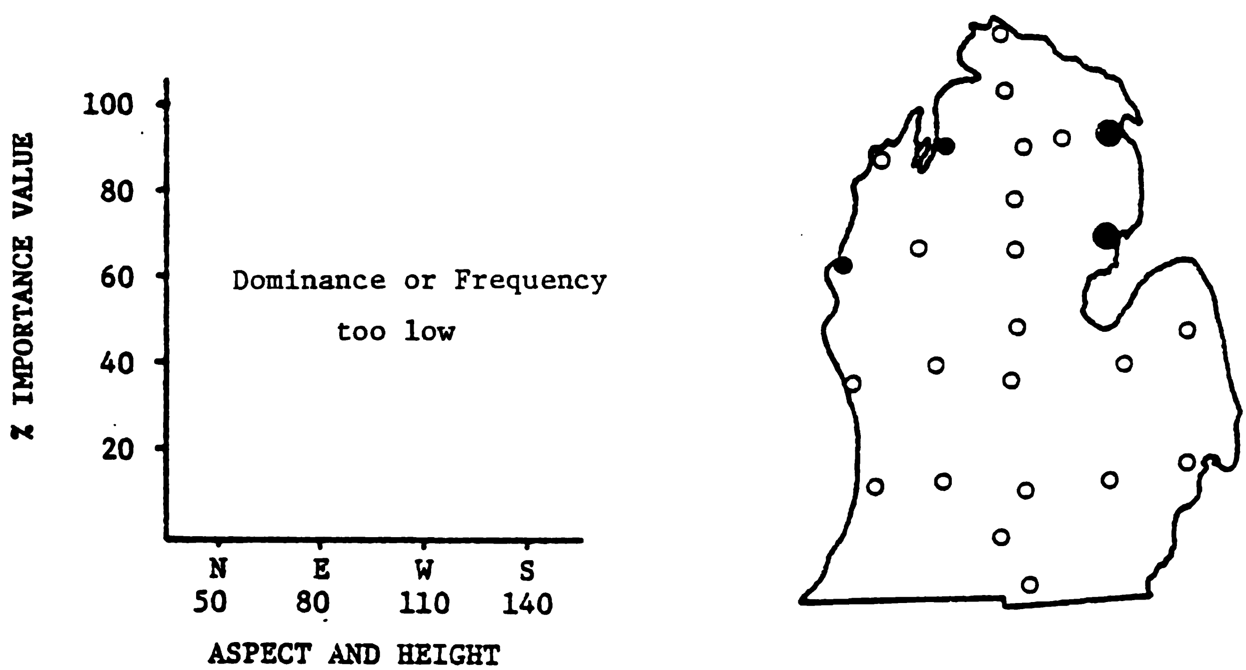


Figure 59. Distribution of Hysteriographium mori.

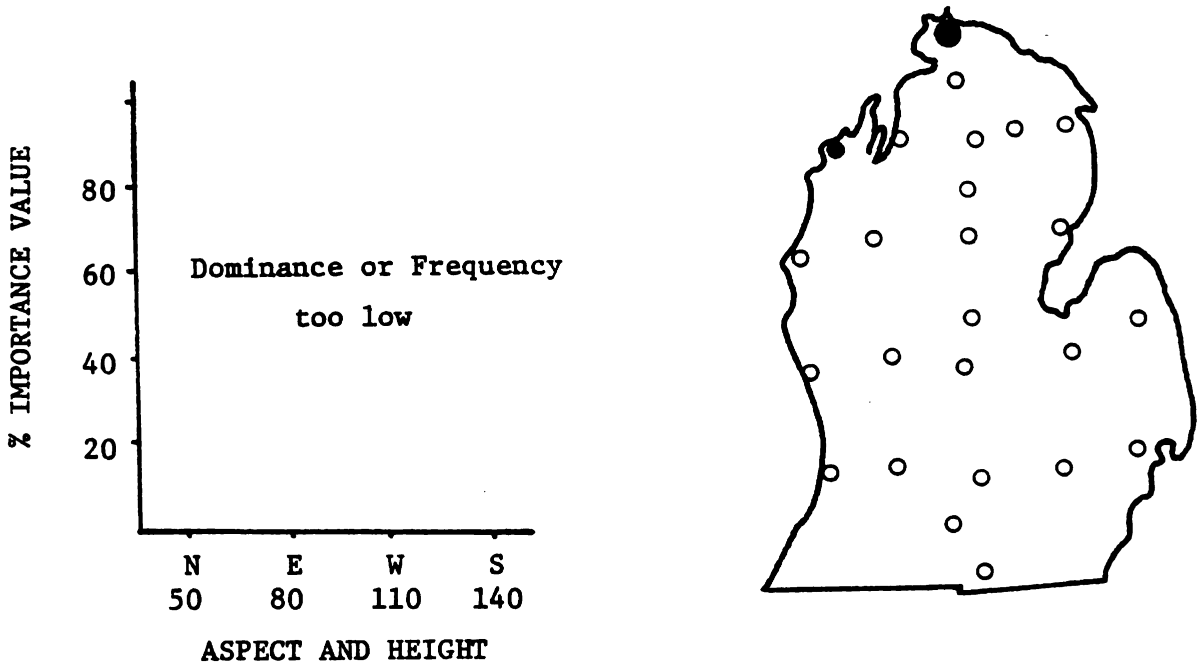
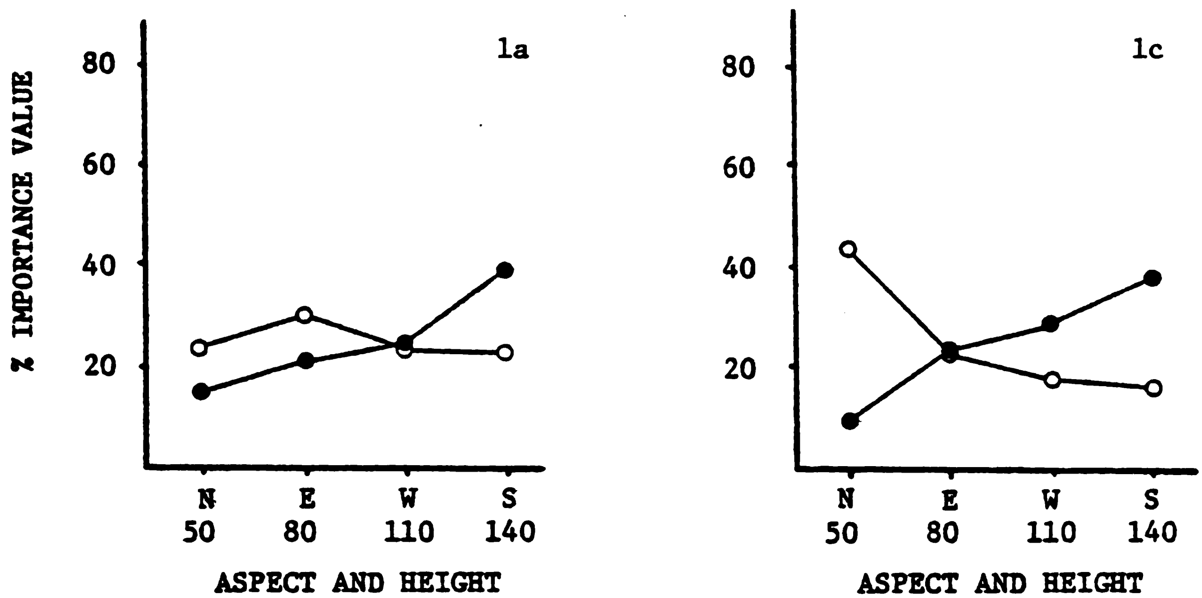


Figure 60. Distribution of Lecania cyrtella.



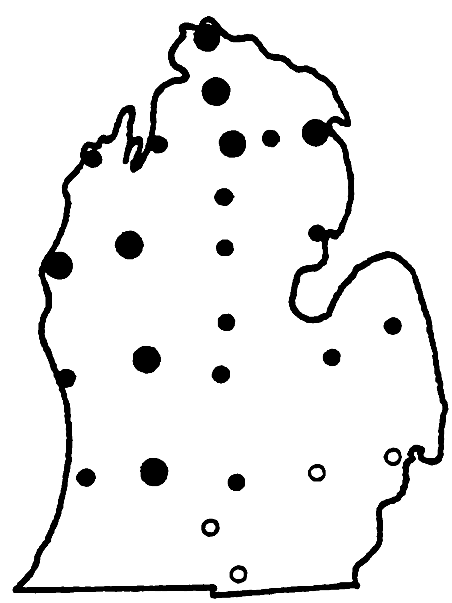


Figure 61. Distribution of Lecanora sambuci.

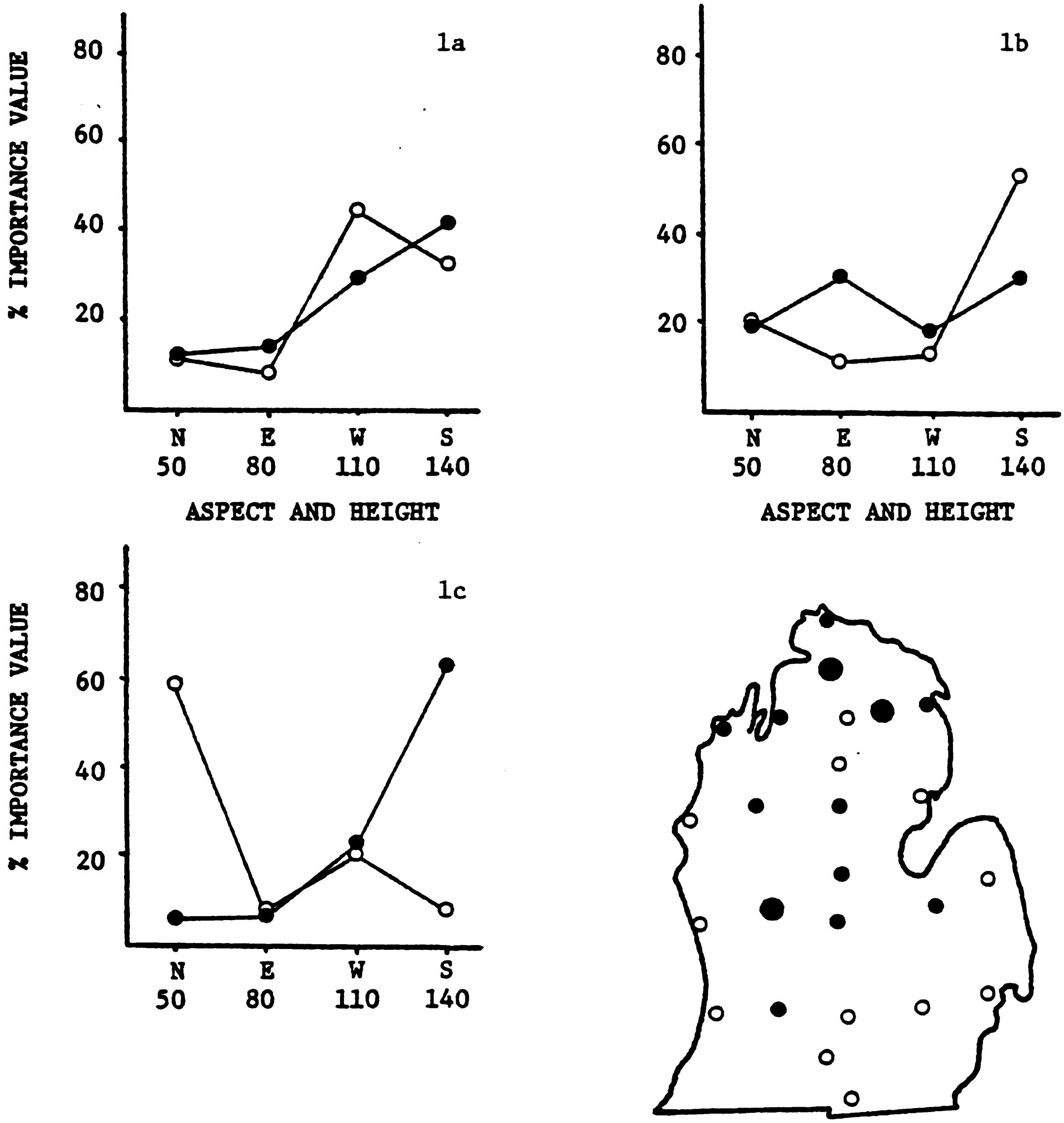


Figure 62. Distribution of <u>Physcia ciliata</u>.

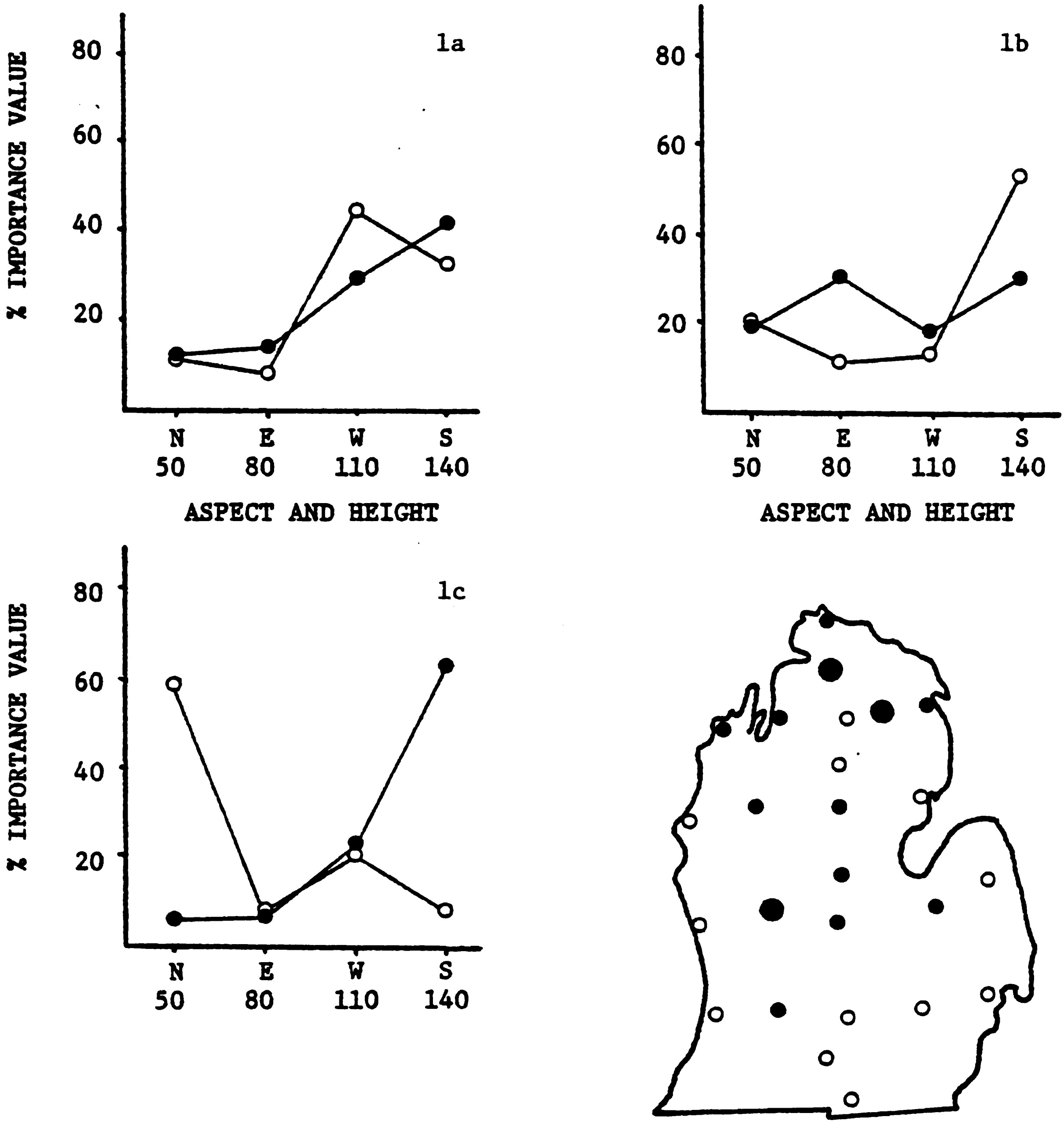


Figure 62. Distribution of Physcia ciliata.

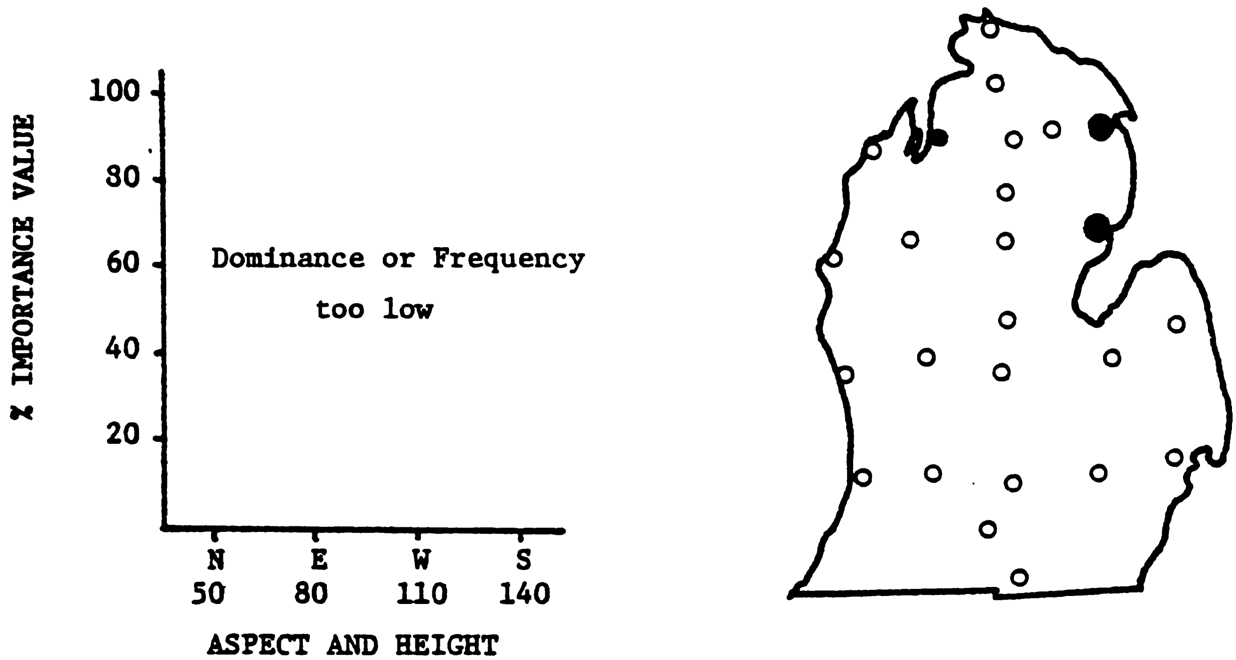


Figure 63. Distribution of Lecanora allophana.

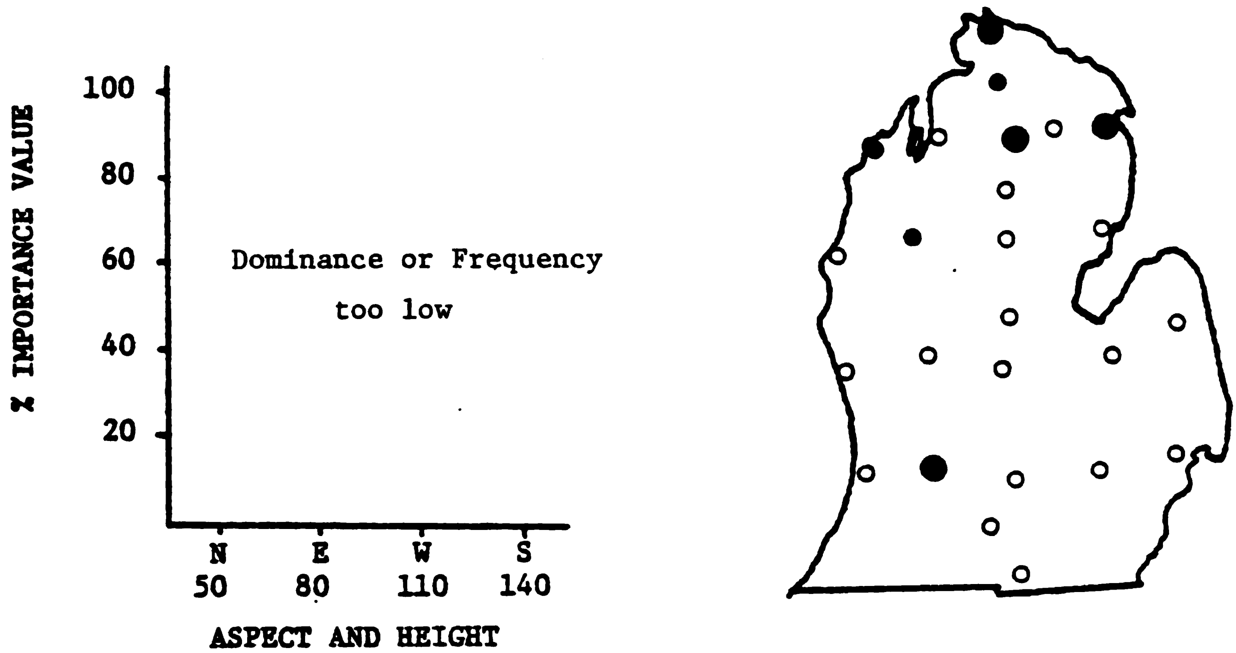


Figure 64. Distribution of Physconia detersa.

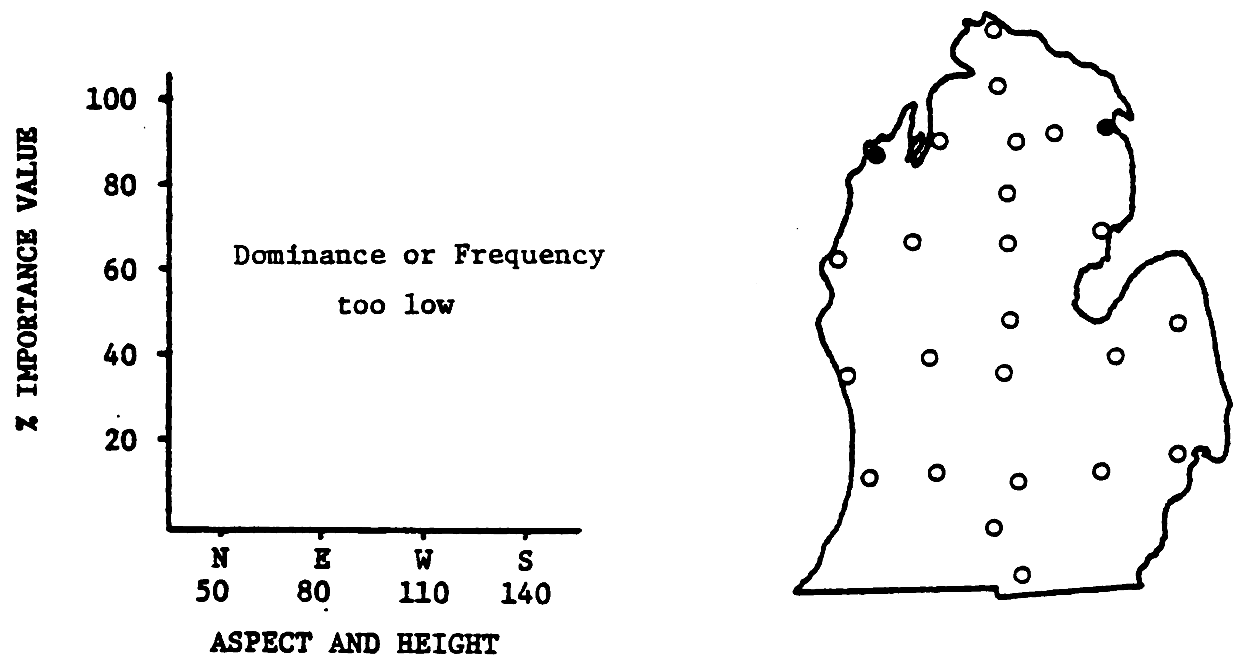


Figure 65. Distribution of Rinodina poplicola.

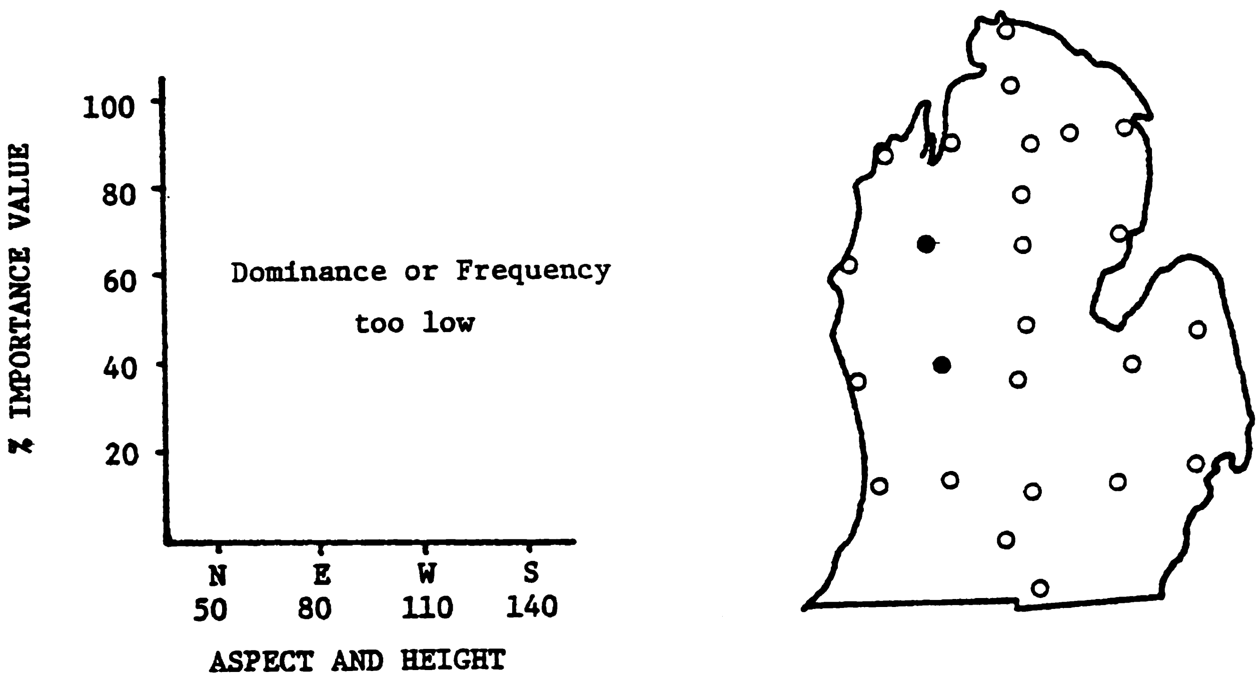


Figure 66. Distribution of Trentepohlia sp.

Species without known Species Group affinities.

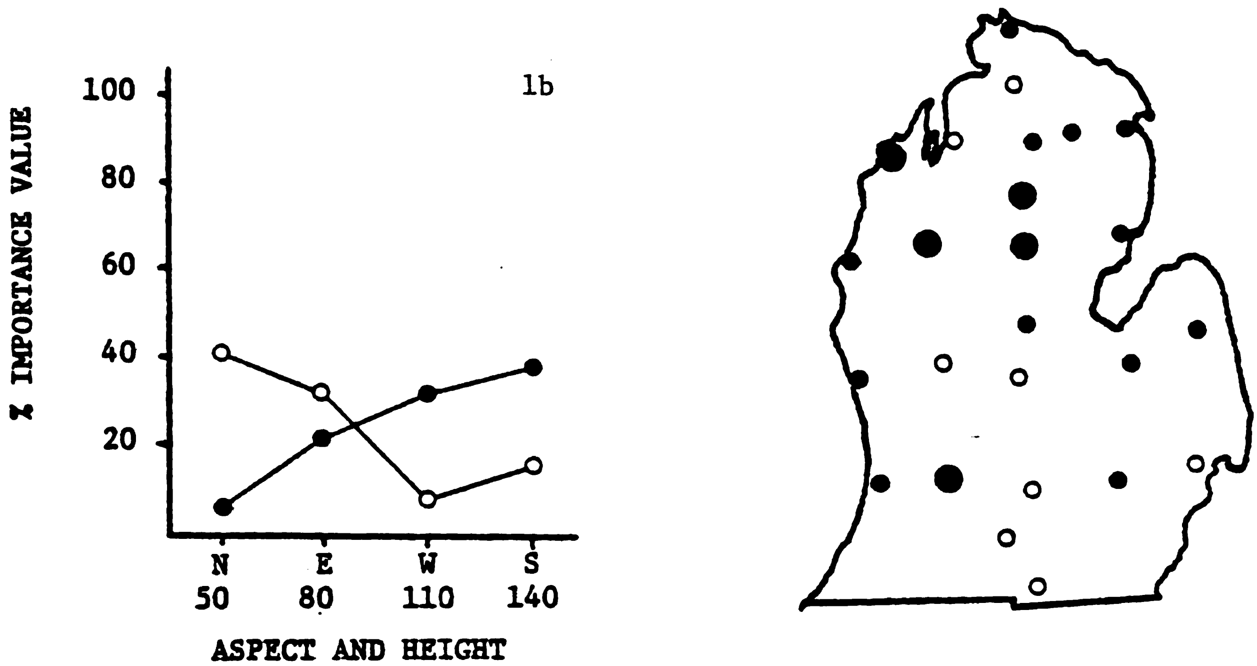


Figure 67. Distribution of Bacidia chlorococca.

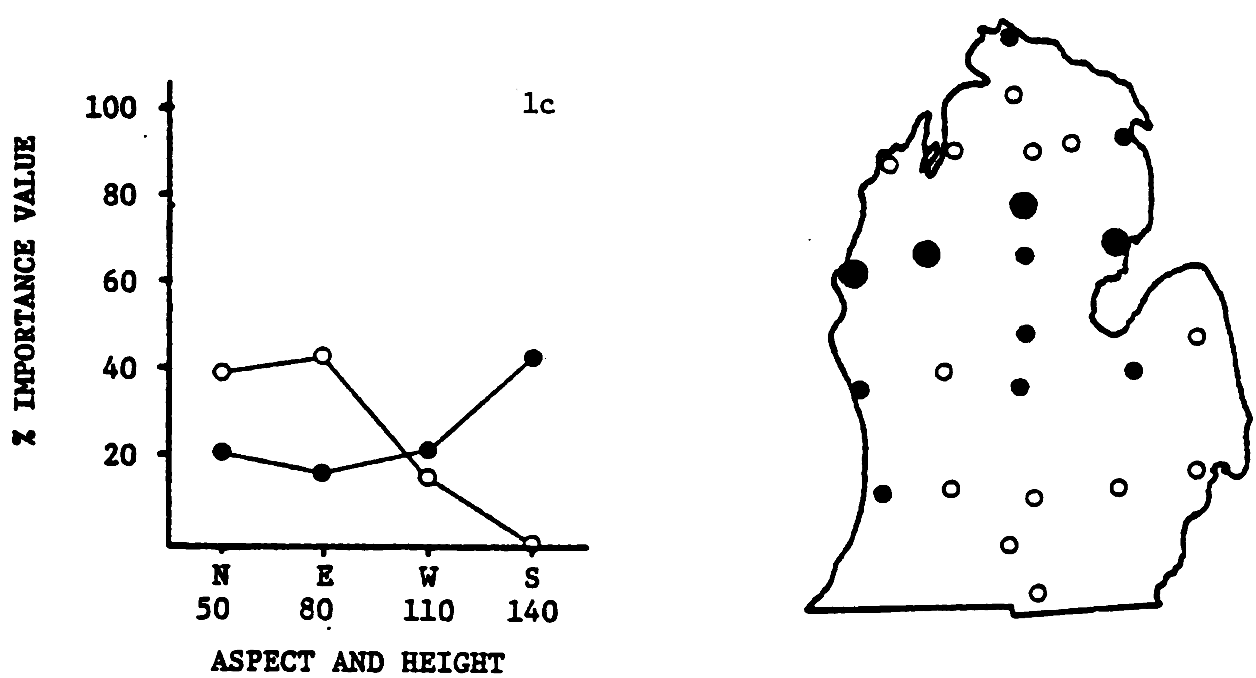
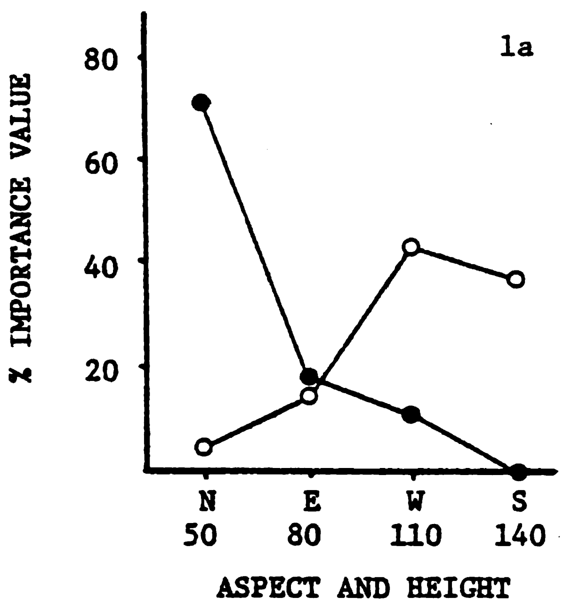
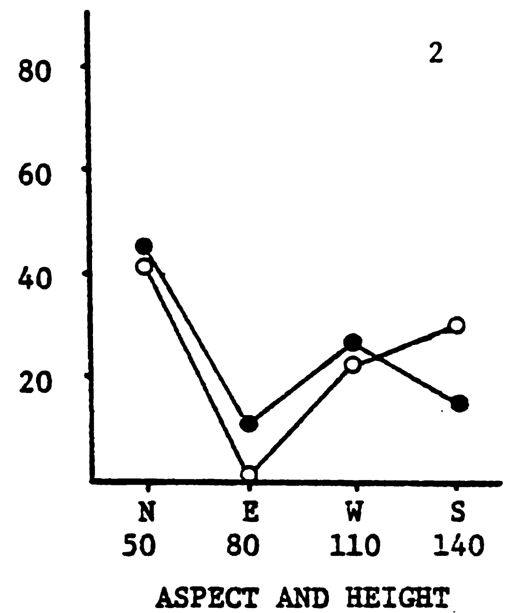


Figure 68. Distribution of Bacidia naegelii.





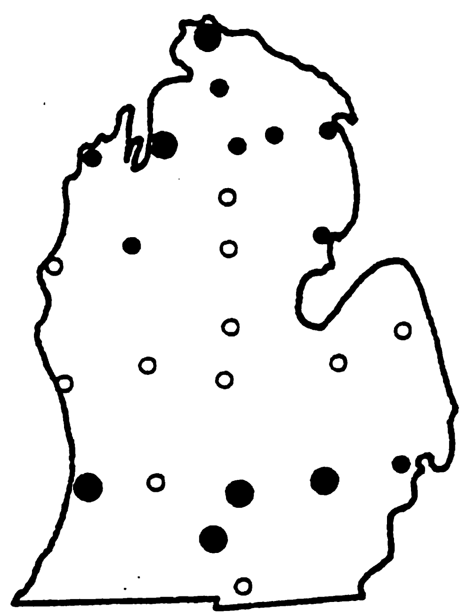


Figure 69. Distribution of Microthelia micula.

Figure 70. Species occuring in only one site. Numbers refer to number of species found only in that site. The following lists these species by site.

Site	Species
1	*Catillaria griffithii*
5	*Candelaria fibrosa* and *Leptorhaphis parameca*
6	*Buellia stillingiana*, *Lecanora chlarona* and *Usnea subfloridiana*
7	*Ramalina fastigiata* and *Rinodina dakotensis*
8	*Cetraria pinastri*
10	*Alectoria nidulifera* and *Usnea hirta*
11	*Melaspilea deformis*
12	*Lecanora sp.*
14	*Arthonia willeyi* and *Buellia punctata*
24	*Buellia polyspora*
25	*Parmelia flaventior*

APPENDIX I

THE SPECIES

The following list and figures describe and/or illustrate all species studied. Within the list each species name is followed by its total (D = number of mm) and relative (percent of the regional total) dominance and a reference to the appropriate figures in which are given a map demonstrating geographical distribution and a graph (for most species) illustrating within site distributional patterns. The list of species includes taxonomic notes wherever necessary. All references loosely termed cover, occurrences or dominance in this section are in terms of dominance. Ecological parameters derived from regional as well as site ordinations, are suggested if possible. References to aspect or height preferences are given only if they are statistically significant (chi square test, $p < 0.05$). Morphological or physiological adaptations, correlated with environmental factors (temperature, light and water) within a site and on a regional basis, are noted.

Maps show each species total distribution as well as the concentration of distribution, when feasible. The concentrations of distribution are determined by arranging the sites in order of the dominances for the species in question and, beginning with the site having the greatest dominance for that species, adding the dominances in each site until 75% of the total state dominance is accounted for. Often this results in a close group of sites representing the center of distribution. The horizontal axis on the graphs is divided into two sets of four quadrats; either north, east, west and south or 50-80 cm, 80-110 cm, 110-140 cm and 140-170 cm for aspect and height respectively and the vertical axis is percent of the dominance accounted for by each quadrat in the Site Group illustrated. Six common species, representing the major within site distributional patterns have graphs of their growth characteristics in all site groups in which they were found. Most other species have a graph representing aspect and height preferences only for the Site Group within which the species attains the greatest dominance. Combined distributions of the rare species occurring in only one site are shown in figure 70.

APPENDIX I

Alectoria nidulifera Norrl. D = 9 mm; 0.01%; figure 70.

The only occurrences were on the north aspect of two trees in site 10.

Arthonia caesia (Flot.) Körb. D = 6517 mm; 9.45%; figures 15D, 18, and 19.

A very widely distributed species, concentrated on the western shores and the Saginaw Valley. The general within-site pattern of distribution is that of a preference for the lower heights and the north aspect. In the northern half of the peninsula, height and aspect are of equal importance in controlling the distribution. In the warmer sites of Groups 2 and 3, aspect attains a secondary importance to height; this high concentration in the lower portions of the tree suggests its great need for moisture. As a leprose species, it requires atmospheric vapour for its water requirements, most easily obtained near ground level. Its high correlation with eigenvector one reflects its ability to grow in warm temperatures.

cfr Arthonia caesia (without apothecia) D = 528 mm; 0.77%; figure 30.

This is very likely Arthonia caesia but the lack of apothecia prevents certain identification. The presence of atranorin (TLC test) and the identical morphological appearance suggest A. caesia. The distribution of the taxon, geographical concentrations, as well as its within-site preferences, are all similar to A. caesia.

Arthonia patellulata Nyl. D = 53 mm; 0.08%; figure 56.

This species occurs in the northwestern sites and is affiliated with the species of Group E. It is a sun and moisture-loving species concentrated on the lower southern exposures.

Arthonia willeyi Tuck. D = 7 mm; 0.01%; figure 70.

A rare species occurring only in site 14.

Bacidia chlorococca (Stizenb.) Lett. D = 1921 mm; 2.79%; figure 67.

A widely distributed species found mainly in the northern highlands and westward. Although its distribution on the individual trees of a site changes with the geographical location, its growth is always concentrated on the north or east aspects, and becomes more abundant as the height is increased. One notable exception is in Site Group 1a, where the abundance decreases with increasing height. This is a granulate species, that requires the high atmospheric humidity available on the north and east aspects.

Bacidia naegelii (Hepp) Zahlbr. D = 336 mm; 0.49%; figure 68.

Distribution, overall ecological parameters and its granular nature are similar to B. chlorococca. In those sites in which it grows well it is most commonly found high on the north and east aspects. In the entire study area, it was recorded only once on the south aspect, covering only 3 mm.

Bacidia populorum (Massal.) Trev. D = 516 mm; 0.75%; figures 15D and 31.

This species was found in 18 of the 25 sites and was concentrated in Group 1c sites where it was found to increase in abundance with height on all sides of the trees. Its preference for aspect varied in other groups; north in 1a and south in 1b and 3, but continued to grow better at the higher heights.

Bacidia umbrina (Ach.) Bausch D = 350 mm; 0.51%; figure 39.

The overall distribution of this species is similar to B. populorum except that its band of concentration is shifted north into the highlands and reflects a considerable difference in environmental preference. Its intrasite growth, found most often on the north and east aspects without clear height preferences, accentuates the differences between these closely related species.

Buellia polyspora (Will.) Vain. D = 2 mm; 0.003%; figure 70.

A rare species found only on the southern aspect in site 24.

Buellia punctata (Hoffm.) Massal. D = 7 mm; 0.01%; figure 70.

Found only in site 14.

Buellia stillingiana J. Stein. D = 10 mm; 0.01%; figure 70.

This species was found only in site 6, a northern highlands site, reflecting its more northern known distribution in this state.

Caloplaca cerina (Ehrh.) Th. Fr. D = 4801 mm; 6.96%; figures 15B, 20, and 21.

This species occurs in all but five sites, concentrated in the northernmost six sites. Tolerating a wide variety of habitats and microclimates, this species prefers the upper heights on the study boles; 77.2% of its total dominance is in the top half of the transects, 44.1% in the top 30 cm segment. Its cardinal preference changes with the macroclimatic and site conditions. In the cool moist sites of Group 1b the majority of the occurrences fall in the upper 60 cm of the south and west aspects. In the much warmer drier habitat of Group 2, this species is rarely found on the south aspect, but has shifted its preference to the east and west aspects in an apparent response to the hot and dry nature of the southern aspect. In Groups 1a and 1c (which fall between the climatic extremes of Groups 1b and 2), height remains an important factor, but the aspect has little effect. This species is adopted to a xeric environment. The presence of parietin is a dominant feature of this genus, and is assumed to help account for its xerophytic adaptations.

Caloplaca holocarpa (Hoffm.) Wade D = 3521 mm; 5.11%; figures 15B and 57.

As C. cerina, this species is concentrated in a few northern sites, and its relatively wide distribution shows the dip into site 25 that is characteristic of the species in Group E. Caloplaca holocarpa and C. cerina are often found growing inseparably on the tree bark. However, as the lack of specimens in any southern sites attest, C. holocarpa may require slightly cooler temperatures. Its within-site distribution suggests this also since it tends to grow more toward the north and east aspects, as well as lower on the tree bole than C. cerina. This species is adapted to xerophytic conditions, the presence of parietin helping in this regard.

Candelaria concolor (Dicks.) Arn. D = 237 mm; 0.34%; figures 15E and 36.

This species is found along the northern and western shores as well as the western interior sites near site 25. Its distribution on trees varies between Site Groups, but in Group 1b (within which 44.7% of the dominance occurred) this species shows strong moist-loving tendencies as a large percentage of the thalli were recorded on the lowest 30 cm segment of the north aspect.

Candelaria fibrosa (Fr.) Müll. Arg. D = 2 mm; 0.003%; figure 70.

A rare species occurring only in the northern highlands (site 5).

Candelariella vitellina (Ehrh.) Müll. Agr. D = 94 mm; 0.14%; figure 40.

Found in the northern highlands and nearby shores, it exhibits a tendency not to grow on the north aspect, nor below 80 cm.

Candelariella xanthostigma (Ach.) Lett. D = 1564 mm; 2.27%; figures 15B and 41.

This species includes a newly proposed segregate, C. efflorescens Harris & Buck ined. These taxa appeared to require the cooler temperatures of the northern half of the study area. In Groups 1b and 1c they grow best on the east and south aspects, but are indifferent in Group 1a sites.

Catillaria glauconigrans (Tuck.) Hasse D = 105 mm; 0.3%; figure 58.

This species occurred in only two sites, 7 and 11, both northern lake shore sites. In both cases, the great majority of occurrences were on the aspect facing away from the lake. In site 7 all occurrences were on the east aspect and in site 11, 85% of the coverage was on the west aspect.

Catillaria griffithii (Sm.) Malme D = 3 mm; 0.004%; figure 70.

Found only in site 1.

Cetraria pinastri (Scop.) S. Gray D = 5 mm; 0.007%; figure 70.

A rare species found only in the lake shore site 8.

Evernia mesomorpha Nyl. D = 101 mm; 0.15%; figure 43.

This species occurs in five sites, but is common only in site 6. Although relatively rare, its distribution relates it to the species in Group D. Most occurrences (88.1% of its total dominance) are on the north aspect, suggestive of its fruticose habit and associated need for relatively great amounts of atmospheric moisture.

Hypogymnia physodes (L.) W. Wats. D = 233 mm; 0.34%; figure 44.

This taxon exhibits a scattered distribution, being abundant only in sites 6 and 10, suggesting the cool temperature and high moisture requirements which are borne out by the distribution within sites (97.9% of the occurrences are on the north aspect). However, only 3.4% of the total is found in the lowest quarter of the north quadrat.

Lecania cyrtella (Ach.) Th. Fr. D = 51 mm; 0.007%; figure 60.

A rare species found only in sites 1 and 8.

Lecanora sp. D = 20 mm; 0.03%; figure 70.

The thallus of this species appears as sterile, large sorediate patches with a conspicuous white margin of fungal hyphae. Atranorin was demonstrated by TLC. It occurred only in site 12, on the lowest portion of the north aspect.

Lecanora allophana (Ach.) Nyl. D = 16 mm; 0.02%; figure 63.

This species was recorded in three northern lake shore sites (9, 11, and 12).

Lecanora chlarona (Ach.) Nyl. D = 15 mm; 0.02%; figure 70.

The fact that this species occurred in one site (6) in the northern highlands and its preference for only the lowest segment of the north aspect, suggests its need for a cool moist environment.

Lecanora chloropolia (Erichs.) Almb. D = 49 mm; 0.07%; figure 45.

This species was found in four sites in the northwestern portion of the study area. It exhibits a preference for the lower sections of the west aspect, suggesting a need for direct light but relatively high moisture.

Lecanora sambuci (Pers.) Nyl. D = 2951 mm; 4.28%; figures 15C and 61.

This species is widely distributed, occurring in all sites except the four southeastern sites. Its inability to survive in this latter area reflects the higher temperatures and industrial-urban nature in this part of the state. Although L. sambuci seems to have few environmental requirements on a regional basis, the within-site distributions reveal definate preferences. In all groups this species becomes more abundant as the height is increased; the aspect preference varies between Site Groups. In Site Group 1b, this species is found primarily on the south and west aspects, reflecting a need for warmth and dryness in this cool and moist environment. In the Group (1a) in which it appears most frequently, L. sambuci has no cardinal preference, but still increases in importance with height. In the warmer environment of Groups 1c and 2 it is found primarily in the northern aspect, an apparent response to this warmer environment.

Lecidea symmicta (Ach.) Ach. D = 136 mm; 0.2%; figure 46.

Although found in nine sites, this species is quite rare in all but a few of the locations. Its within-site distribution places it in the group of species requiring relatively high moisture and low light intensities (occurring primarily on the north and east aspects).

Lepraria B D = 96 mm; 0.14%; figures 15A and 47.

Likely not to be a true Lepraria, this granular soraliate species contains fumarprotocetraric acid (TLC). It is found in eight sites, but is quite rare in most of them. 83.3% of the total coverage was found in the north and east aspects. Of the specimens found on the south and west aspects, all were found below 110 cm. This taxon thrives best in the cool moist environments; its sorediate nature suggests a need for this type of condition.

Lepraria C D = 36 mm; 0.05%; figure 48.

This is a soraliate species without thalline reactions with K, C, KC, or PD. An unknown substance was detected by TLC (brownish-green spot with H_2SO_4 and light yellow with PD, rf = .7-.8, benzene:dioxane: acetic acid, 90:25:4). It favors cool sites as well as the cool and moist sections of the transects. All eight recorded specimens of this taxon were growing on the north and east aspects, 72.2% occurring below 80 cm.

Leptorhaphis contorta Degel. D = 448 mm; 0.65%; figures 15B, 22, and 23.

This is an interesting species due to its requirements for a moist yet sunlit environment. In the Group 1b sites, the apparent requirements of this species are accentuated, as 53.6% of the total is found in the lowest 30 cm segment of the south aspect. Its distribution in the study area is basically northern.

Leptorhaphis parameca (Massal.) Körb. D = 4 mm; 0.006%; figure 70.

Only two specimens of this epiphyte were found, both on the same tree in site 5.

Melaspilea deformis (Schaer.) Nyl. D = 3 mm; 0.004%; figure 70.

Found only in the lake shore site 11.

Microthelia micula Körb. D = 375 mm; 0.54%; figures 15F and 69.

The disjunct distribution of this species is an interesting feature. In the northern sites its requirements are similar to those of L. contorta, favoring the lower segments of the south and west aspects. However, in Group 2 sites, the occurrences were scattered on aspect and height. In the warmest group of sites (Group 3) all of the thalli occurred in the lowest 30 cm segment; none on the north, 73% on the south. Generally, like _L_. _contorta_, this species requires moisture and direct sunlight.

Ochrolechia _arborea_ (Ljubitz.) Almb. D = 933 mm; 1.35%; figures 15A and 49.

This species is abundant only in the cool moist sites of the northern highlands. There were no records in any Group 3 site. In the sites in which it was found, at least 70% of the coverage occurred in the north and east aspects. The height distribution varies; Group 1b has the same distribution at all heights, but in the warmer sites of Group 1a and 1c the great majority of occurrences were on the lower half of the transects. In all respects, this completely sorediate species requires shade, moisture and cool temperatures.

Parmelia _flaventior_ Stirt. D = 94 mm; 0.14%; figure 70.

All seven of the recorded occurrences of this lichen were found in site 25, suggesting a tolerance for relatively high temperatures. All thalli were found on the south aspect, re-emphasizing the high temperature and low moisture tolerances of this lichen.

Parmelia _subaurifera_ Nyl. D = 3771 mm; 5.47%; figures 15A, 24, and 25.

This species is an almost ubiquitous member of the flora in the northern half of the state. Its heavily sorediate surface is not easily wetted; only the northern sites and shaded lower heights can offer it the required humidity. It generally occurs with P. sulcata.

Parmelia sulcata Tayl. D = 11,197 mm; 16.23%; figures 15A and 50.

This is the most common species in the study. Less than 10% of the total cover occurred on the south aspect, and most of these southern occurrences were found in the cooler sites of Group 1b. Over half of the dominance was recorded from the north aspect. Due to its xero-tolerant nature (Barkman, 1958), its height preferences are variable.

Physcia adscendens (Th. fr) Oliv. D = 10,133 mm; 14.70%; figures 15c, 26, and 27.

This species is very common in all but a few sites, notably absent in the four southeastern sites. More than 68% of the occurrences of this species are found in Groups 1a and 1c. In these sites aspect plays little role, whereas height is found to be important as the occurrences increase with increasing height. In the cooler northern highlands (Group 1b) the growth of P. adscendens is greatly influenced by aspect as well as height; occurrences are concentrated on the warmer drier south and west aspects, and the upper sections of all aspects. In the sites of Group 2 and 3, it reacts oppositely to those of Group 1b, as in these more xeric sites this lichen is found primarily on the north or east aspects and its center of height concentration has shifted downward. Barkman (1958) notes that P. adscendens is xerophytic, as this study suggests. However, as in all species, there are optimum conditions for growth, a fact that this taxon demonstrates; the south and west aspects of the warmest sites prove to be too xeric for this lichen.

Physcia aipolia (Ehrh.) Hampe D = 1052 mm; 1.53%; figure 51.

A species that is predominantly found in the Group 1b sites, it is concentrated on the upper portions of the east aspect. In the remaining sites, most occurrences of which are in Group 1a, the majority are found on the higher sections of the south aspect. Although this species desires the cooler sites, it thrives best in the more xeric portions of those sites. The characteristic pruina of this species may be of importance in its xeromorphism.

Physcia ciliata (Hoffm.) Du Rietz D = 1488 mm; 2.16%; figures 15C and 62.

Although this species has a wide distribution, it is only common in four sites. It does equally well in the three northern Site Groups, preferring the highest portions of the transects. In Groups 1a and 1b, P. ciliata thrives on the west and south aspects respectively, but it changes its preference in favor of the northern aspect in the warmer climate of the Group 1c sites. A drastic reduction in its occurrences is found in Groups 2 and 3 as only 2.4% of its total dominance was recorded in these ten sites.

Physcia millegrana Degel. D = 2695 mm; 3.91%; figures 15E and 34.

Most (94.4%) of the total occurrences for this species were recorded in the four sites of Group 2. It had a high preference for the west aspect, with little regard for height. The affect of the prairie wedge on this portion of the state has a profound influence on the distribution of this epiphyte. It was found to be highly correlated with eigenvector one, demonstrating its warm temperature requirements.

Physcia orbicularis-group D = 1593 mm; 2.31%; figure 37.

The group of lichens represented by the species Physcia orbicularis (Neck.) Poetsch. (with red medulla), P. pusilloides Zahlbr., and P. luganensis Mereschk. are included in the P. orbicularis-group for the purposes of this study. During the field work, I was not aware of the taxonomic problem encountered with these species and in the field all were labeled P. orbicularis. Voucher specimens brought back to the laboratory were found to be a mixture of the three species.

This group has a wide distribution, but requires relatively great amounts of moisture evidenced by the fact that in all groups except in the cool 1b sites and the one specimen found in Group 3, at least 62% of the occurrences were found on the lower 30 cm segment. In Groups 1a, 1b, and 2 these species are primarily found on the south and west aspects. As a general rule, this group of species appears to have a high light and moisture requirement.

Physcia stellaris (L.) Nyl. D = 3747 mm; 5.43%; figures 15E, 28, and 29.

This species is one of the most widely distributed epiphytes found in this study. Only the three southeastern sites did not record P. stellaris, reflecting the effective dryness and possible lower air quality characteristic of this section of the state. Aspect and height are of approximately equal importance, often with the warmer, drier, and sunlit regions of the tree having the highest concentrations.

<u>Physciopsis</u> <u>elaeina</u> (Sm.) Poelt D = 146 mm; 0.21%; figure 35.

This species was found only in three southern and western sites, suggesting a need for continental influences available in this portion of the state. Its high correlation with eigenvector one implies a high temperature requirement which agrees with Barkman's (1958) statement that this taxon is found in warm dry habitats in the Netherlands and believes that thermophily is involved in its distribution. Within the sites it avoids the extreme xeric conditions by existing primarily on the north aspect and at low heights.

<u>Physconia</u> <u>detersa</u> (Nyl.) Poelt D = 71 mm; 0.1% figure 64.

This species is distributed like most of the members of Group E, favoring the northern sites but having some occurrences in the west-central sites. This lichen was never common within a site and does not exhibit any detectable height preference. It was never found on the south aspect of any tree and occurred most frequently on the east.

<u>Ramalina</u> <u>fastigiata</u> (Pers.) Ach. D = 6 mm; 0.009%; figure 70.

This species was found only in site 7.

<u>Rinodina</u> <u>dakotensis</u> Magn. D = 11 mm; 0.02%; figure 70.

Found only in site 7.

<u>Rinodina</u> <u>populicola</u> Magn. D = 10 mm; 0.01%; figure 65.

This species occurred on the warmer aspects of the trees in two northern lake shore sites (west in site 8 and south in site 11).

Rinodina pyrina (Ach.) Arn. D = 376 mm; 0.55%; figures 15F and 33.

This species occurs in about one half of the sites, absent from many of the southern and western sites. Like many of the widely distributed species, R. pyrina changes aspects and height preferences corresponding to the climatic regime within which it is found. In the cooler sites of 1b, this lichen is concentrated on the higher portions of the west and north aspects. When this species is found in the warmer sites of Groups 1a and 1c, it grows best on the cooler east and north aspects, generally at lower heights than in Group 1b. Curiously, in Group 3 it is found on the high portions of the south and west aspects.

Rinodina willeyi Sheard ined. D = 72 mm; 0.01%; figure 52.

This species was collected in only two sites, both members of the northern highlands Group 1b. The cool requirements of this lichen suggested by its geographical location is emphasized by the fact that only one specimen (total of ten) was found above 110 cm on the south or west aspects.

Usnea hirta (L.) Wigg. D = 11 mm; 0.02%; figure 70.

A total of three specimens were collected of this lichen, all on the north aspect in site 10. Usnic acid and an unknown substance (low rf and no reaction with Pd) were demonstrated by TLC (Benzene:dioxane: acetic acid (90:25:4)).

Usnea subfloridiana Stirt. D = 14 mm; 0.02%; figure 70.

Only one specimen was found, it occurred on the north aspect of a tree in site 6. It was shown to have usnic and squamatic acids by TLC.

Xanthoria fallax (Hepp) Arn. D = 24 mm; 0.03%; figure 53.

The total of three occurrences in two sites (3 and 7) of this lichen were recorded on the west aspect.

Xanthoria polycarpa (Ehrh.) Oliv. D = 259 mm; 0.38%; figures 15A and 54.

This lichen was found most frequently in Group 1b sites. Within this area it was concentrated on the south aspect and in the higher portions of the transects. In Group 1a, it was primarily found high on the west aspect. Although this species grows best in cool temperatures it requires the direct sunlight received on the southern and western exposures. The anthraquinone (parietin) present is important in its ability to thrive in these xeric habitats.

FUNGI

Epicoccum sp. D = 244 mm; 0.36%; figures 15B and 42.

This epiphyte was characteristically found in the northern sites on the lower portions of the south and west aspects. A cool climate, high humidity, and warmth from the direct sun play a part in the distribution of this species.

Hysteriographium mori (Schwein.) Rehm D = 63 mm; 0.09%; figure 59.

This species was recorded in four of the northern lake shore sites. Most (84.1%) of the occurrences were in the lower 30 cm segments, only 7.9% was found on the southern aspect.

Xenosporium sp. D = 55 mm; 0.08%; figure 55.

Like Epicoccum sp., this species was found principally on the lower south and west aspects in the northern highlands.

ALGAE

Protococcus spp. D = 4962 mm; 7.19%; figures 15F and 32.

These include a number of different protococcoid algae. Although the total distribution of these species is wide, 85.7% of the total occurred in the six sites of Group 3. Even though these algae thrive in higher temperatures, they require the shaded portions of the trees; 64% are found on the north aspects and only 3.7% of the total cover was found on south aspects. As Barkman (1958) noted these species as belonging to the group requiring atmospheric moisture, their occurrence on the north aspects is expected. Their occurrence in all but one of the south-eastern sites may suggest that this whole group of species exhibits the toxitolerance found in Protococcus viridis (Barkman, 1958).

Trentepohlia sp. D = 308 mm; 0.45%; figure 66.

This alga was found in only two sites and appears to require the moisture that is available near ground level. All occurrences were recorded on the lower half of the transects.

MOSS

Platygyrium repens (Brid.) B.S.G. D = 514 mm; 0.75%; figures 15E and 38.

This moss was found low on the north and west aspects in three southwestern sites.

APPENDIX II

THE SITES

The following are descriptions of all sites included in this study. Each site number is followed by county, township, range, section, distinguishing characteristics (if any), and principle associated plant components (arboreal and ground cover) of each site. See figure 4 for geographical position of sites.

APPENDIX II

1. Cheboygan Co. T.38N., R.3W., Sec. 15.

This portion of the state tends to be low and wet. Acer saccharum, Pinus strobus, Populus gradidentata and Pteridium aquilinum.

2. Cheboygan Co. T.34N., R.3W., Sec. 31.

Open to natural field on north side. Acer saccharum and Pteridium aquilinum.

3. Otsego Co. T.29N., R.2W., Sec. 14.

Acer saccharum, Pinus strobus, and Pteridium aquilinum.

4. Crawford Co. T.25N., R.3W., Sec. 22.

Canopy relatively open. Acer saccharum and Pteridium aquilinum.

5. Roscommon Co. T.21N., R.3W., Sec. 13.

Small stand, canopy open in spots. Acer saccharum, Pinus strobus, and Pteridium aquilinum.

6. Wexford Co. T. 20N., R.11W., Sec. 13.

Acer saccharum, Pinus strobus (few), Populus grandidentata, and Pteridium aquilinum.

7. Mason Co. T.20N., R.18W., Sec. 13.

Acer saccharum, Pinus strobus, Quercus velutina, and Pteridium aquilinum.

8. Leelanu Co. T.28N., R.14W., Sec. 15.

Open to natural field on north side. Acer saccharum and Pteridium aquilinum.

9. Antrim Co. T.29N., R.8W., Sec. 13.

Relatively dense stand. Acer saccharum, Pteridium aquilinum, and Rubus sp.

10. Montmorency Co. T.30N., R.3E., Sec. 31.

North side of the trees in this stand were conspicuously roughened. Pinus strobus (few), Quercus velutina, and Pteridium aquilinum.

11. Alpena Co. T.30N., R.8E., Sec. 30.

This portion of the county seemed to have a limited epiphytic flora associated with P. tremuloides. Acer saccharum and Pteridium aquilinum.

12. Iosco Co. T.21N., R.7E., Sec. 18.

Acer saccharum, Populus grandidentata, and Pteridium aquilinum.

14. Midland Co. T.15N., R.2W., Sec. 30.

Stand relatively open. Acer saccharum and Pteridium aquilinum.

15. Gratiot Co. T.11N., R.3W., Sec. 20.

The sides of this site open to agricultural fields. Acer saccharum, Rosa sp., and Rubus sp.

17. Eaton Co. T.2N., R.3W., Sec. 13.

Undergrowth quite dense. Acer saccharum, Fagus pennsylvanica, and Pteridium aquilinum.

18. Calhoun Co. T.3S., R.4W., Sec. 26.

    Acer saccharum, Quercus rubra, and Rubus sp.

19. Hillsdale Co. T.7S., R.2W., Sec. 15.

    Swampy area to the east of this stand. North side of these trees have vertical fissures. Few Populus tremuloides in area. Acer saccharum, Quercus alba, and Cornus sp.

20. Muskegon Co. T.10N., R.17W., Sec. 3.

    North side of trees rough. Pteridium aquilinum, Rubus sp., and Solidago sp.

21. Montcalm Co. T.12N., R.10W., Sec. 17.

    Acer saccharum, Populus gradidentata, Quercus rubra, Pteridium aquilinum, and Rubus sp.

22. Tuscola Co. T.11N., R.8E., Sec. 4.

    Acer saccharum, Hamamalis virginiana, Pteridium aquilinum, and Rubus sp.

23. Sanilac Co. T.14N., R.14E., Sec. 30.

    Acer saccharum, Betula alba, Populus grandidentata, and Pteridium aquilinum.

24. Allegan Co. T.2N., R.15W., Sec. 23.

    Acer saccharum, Pinus strobus, and Pteridium aquilinum.

25. Barry Co. T.3N., R.9W., Sec. 18.

    Juglans nigra, Quercus velutina, Pteridium aquilinum, and Rubus sp.

26. Oakland Co. T.2N., R.7E., Sec. 29.

    Open on west side. Acer saccharum, Quercus spp., and Pteridium aquilinum.

27. Macomb Co. T.14N., R12E., Sec. 30.

Undergrowth relatively heavy, canopy open in spots.

Acer saccharum.

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