AN ANALYSIS OF PATTERN AND INTERSPECIFIC ASSOCIATION ALONG A SOIL MOISTURE GRADIENT ON THE JACK PINE PLAINS OF NORTHERN LOWER MICHIGAN

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AN ANALYSIS OF PATTERN AND INTERSPECIFIC ASSOCIATION ALONG A SOIL MOISTURE GRADIENT ON THE JACK PINE PLAINS OF NORTHERN LOWER MICHIGAN

By

Michael Daniel Byer

AN ABSTRACT

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ABSTRACT

This study deals with correlation and association between the frequent plant species occuring along a soil moisture and vegetation gradient ranging from Jack Pine to Leatherleaf Bog in Crawford Co., Northern Lower Michigan. This was done by first gathering quantitative presence and cover data, as well as environmental data, for 400 1 X 1 meter quadrats located randomly in a study area of 100 X 100 meters. On the basis of examination of the soil profile in the center of each quadrat it was later assigned to one of seven segments corresponding to catenal soil types. For association and correlation analyses, the number of segments was reduced to five by combination of some soil types.

Cole association coefficients, which give an estimate of the tendency of pairs of species to occur together, were calculated on each of five segments of the gradient for all possible pairs of species which occured above a given level of frequency on each segment. Of the 513 association coefficients 29 per cent are significant at the 5 % level, and 16 per cent at the 1 % level. Since far more coefficients were significant than one would expect by chance if none of the species were associated with each other, it seems evident that the species in question exhibit association patterns within the segments of the gradient.

Zero order correlation coefficients were calculated between each of these frequent vascular species and at least one other species. These coefficients show the tendency for high cover values of species to occur or not to occur together. For these determinations, the frequent species were first divided into six groups and correlation coefficients were then calculated for all possible pairs in each group. Of the 70 correlations, 21 per cent

were significant at the 5 % level and 18 per cent at the 1 % level. The different groups were not randomly chosen for the correlation analyses, some were in fact picked because of the apparent ecological similarities of the species. Nevertheless there is a suggestion that high cover values of the species are also non-randomly distributed with respect to one another within the gradient segments.

Zero-order correlation coefficients were also calculated for each frequent vascular species with at least one of the following environmental variables: depth of A_{O_L} soil layer, depth of A_{O_H} soil layer, per cent tree cover, per cent bryophyte cover, and depth of loose moss mat. These computations did not furnish convincing evidence that the variables chosen were particularly influential in determining the distribution patterns of the species.

Partial correlation coefficients, which show the tendency for species to occur together or not to occur together when several other species and/or variables are mathematically held constant, were also calculated for all species-species and species-variable pairs in each group. In some cases discrepencies between the partial and the zero-order correlations for the same pairs, suggested that part of the correlation between species is due to interaction, or to similar reactions of the species to environmental variables.

Differences between the association and correlation coefficients for the same pairs of species, and changes in these coefficients from one segment of the gradient to another, coupled with field observations, data for cover and frequency of species, mean values for environmental variables along the gradient, and

general knowledge of the species were useful in formulating hypotheses concerning certain of the ecological relationships of and among the species studied. Ordinations were constructed of all frequent vascular species on each gradient segment, in which the coordinates of each species were plotted along two axes representing the correlations of the species with two environmental variables. These ordinations show a general tendency for species to keep about the same positions relative to each other on all gradient segments, which strongly suggests that the correlations are generally valid despite their low significance, for if the coefficients represented only random deviations there should be no similarity in species position between the segments.

In general, the association and correlation coefficients agree with field observations of the visually evident association and pattern phenomena. They also agree with our general ecological knowledge of the plants concerned. These agreements, along with the high proportion of significant coefficients and the similarity of ordination figures for different gradient segments, suggest that these coefficients are on the whole valid, though not exhaustive, estimates of the association phenomena which occur. Since some associations and correlations which appeared in the coefficients were not obvious in the field, these techniques would seem to be more than "an elaboration of the obvious" (Cole 1957, Greig-Smith 1957).

Though the techniques used here seem useful in detecting and describing species pattern and association, these are not to be considered ends in themselves. In the present study, the information gleaned therefrom was used in formulating logical hypotheses

concerning the mechanism's responsible for the associations found. It would appear that interspecific interaction and differential tolerance to various past or present environmental conditions, are responsible in some degree for the various positive and negative associations demonstrated. Certain of these association patterns appear to be related to various phases of microcyclic patterns (Watt 1947).

The hypotheses advanced are not intended as proofs for the underlying causes of community structure in the study area, but simply as possibilities which may be tested by experiment. The testing of some of the hypotheses presented here is the objective of work now in progress.

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I

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II

INTRODUCTION
AND
BACKGROUND

A - INTRODUCTION

Interspecific association is the name of a now widely-recognized phenomenon describing the tendency for different species to occur together either more frequently or less frequently than one would expect if the species were randomly (independently) distributed with respect to each other.

A profusion of techniques for describing and exploring interspecific association has come into the literature in recent years, and several are explored in this paper. The main purpose of this study is to advance our knowledge of order-producing phenomena in vegetation with the aid of these techniques. Hypotheses are advanced for explaining the associations which are found. These are based upon comparison of the results of different techniques, and comparisons of the association of the same species in somewhat different habitats. In this way it is possible to obtain clues concerning the ecology and physiology of local species populations and the phenomena producing community structure. These hypotheses must be tested experimentally at some future time, but the analysis presented here should suggest which, of the myriads of experiments possible with each species or species combination, might best help us to approach our ultimate goal of understanding pattern-producing phenomena.

Interspecific association studies are one way of approaching the phenomenon of non-random distribution of species, or pattern, with the unique feature that here we consider non-random distribution of two or more species with respect to each other instead of considering each species by itself. But in reality this is a purely arbitrary distinction, for in studies of patterns

of single species one usually attempts to determine to what features of the environment the patterns are related. Since at the individual species level, other species are as much a part of the environment as are various "abiotic" factors (cf. Odum and Odum 1959), we are merely concentrating on the biotic aspects of the environment in interspecific association studies. Although this study concentrates on interspecific association, and hence on the living portion of the ecosystem, we must consider the system as a whole if we desire information about the operation of the mechanisms which result in pattern. Consequently, correlations of species with some non-living variables were also calculated.

Most of the techniques used here have been used previously, in one form or another, to study interspecific association and other pattern phenomena. So far as the writer is aware, however, this is the first time that several such techniques have been combined in one study, although the problem of changes in interspecific association along a gradient has been touched upon by several authors (e.g. Bray 1956, Hopkins 1957a). I feel that much more can be learned about the biology of particular species and the nature of community phenomena by using several different techniques, each designed to answer somewhat different questions, and comparing the results, than could be gained from the use of any one of the techniques by itself. The study of differences of association between the same species in different habitats along a gradient also yields more information than could analyses in each of the habitats separately.

The study area was a soil moisture gradient in the Jack pine vegetation region in sandy outwash soils in Crawford Co., Northern Lower Michigan. The "dry end" of this gradient was in

open Jack pine forest, the "wet end" was an open Leatherleaf bog with scattered coniferous trees. Ring counts of the largest trees, and examination for charcoal in the soil profile, suggested that the area was burned about 60 years before, near the turn of the century, but that it has remained relatively undisturbed since.

Four-hundred randomly located 1 X 1 meter quadrats were studied in an area of 100 X 100 meters. For each quadrat, per cent cover of each vascular species, and presence of each bryophyte and lichen species, soil profile, and several other environmental variables were recorded, and pH determinations, soil moisture content determinations, and light intensity readings were recorded for sets of 100 quadrats each. For analysis, the gradient was divided into seven segments by soil type, and mean values of frequency and per cent cover of each species and mean values of each environmental variable were calculated for all the quadrats in each segment. The number of segments was then reduced to five, by combination. For each of these five segments, Cole association coefficients were calculated between all possible pairs of those species which occured above a previously determined minimum level of frequency on the segment. The vascular species were then divided into six groups, and zero-order and highest order partial correlation coefficients were calculated for all possible pairs of species within each group. For some of the groups, correlations were run with certain environmental variables also. Multiple correlations of each species or variable in each of the groups with all other species and variables in that group were calculated, and for one group standard partial regression coefficients were calculated. For supplementary

information, species-area curves were constructed for all five gradient segments, and ordinations of the species in relation to two environmental variables were calculated for all but one of the segments.

A high proportion of significant coefficients suggested that association patterns were common among the species in the study area. Correlations of the species with the particular environmental variables chosen for analysis, however, were not nearly so convincing. The validity of the techniques is suggested by the overall agreement of the coefficients with field observations. But in individual cases there were surprises, in that some associations were observed in the field only after the calculations had suggested their presence, and others were not visually evident, suggesting that the techniques are useful in detecting associations and do not merely elaborate the obvious.

The various coefficients were useful in formulating hypotheses concerning the roles of these species in the community and in advancing possible explanations of the mechanisms producing each of the association found. Certain of the possible hypotheses appeared to be mutually exclusive, leaving a residuum of compatable ones some of which complemented one another. This also provides corroborative evidence for the validity and value of the techniques as used here.

The species-area curves seem to indicate that sampling was adequate to characterize the area in all but one segment of the gradient. The ordinations show some possible trends in the correlations of species with environmental parameters, and shifts in these trends along the gradient. They seem to show also that the association between two species cannot be predicted on the

basis of their similarities or differences in tolerance ranges with respect to only one or two environmental variables.

By way of background, a review and discussion of literature pertaining to the whole field of pattern is presented below. In this way, the relative merits and peculiarities of the techniques used here will be more fully understood.

B - PATTERN CONCEPTS

The present state of our ecological knowledge makes it fairly clear that species in nature are not merely randomly dispersed within supposedly "homogeneous" communities and associations. Men have known at least since the dawn of history that plant species have definite habitat preferences, and that they therefore exhibit non-random distribution on a grand scale. Curiosity concerning these distributions and their causes, in fact, was a major factor leading to the beginnings of plant ecology. It was soon discovered that certain characteristic groupings of species tended to occur on sites with certain climatic and physical characteristics, and these observations, coupled with man's "natural tendency to pigeonhole" (Gleason 1926), led to various attempts to classify large natural groupings of species such as the Clementsian "community" (e.g. Weaver and Clements 1938) and the "association" of the Zürich-Montpelier School (e.g. Braun-Blanquet 1951).

Unfortunately, the Clementsian and Braun-Blanquet systems, as well as other similar systems, emphasized the larger units,

giving little attention to the smaller ones. Thus, by implication, the vegetation within these large units was considered to be homogeneous and the plants within them were not examined for small-scale patterns. The "union" of Braun-Blanquet (1951) does recognize such patterns, but little effort is made to explain their causes and significance. However, the physical habitat contains many irregularities (e.g. small hummocks and hollows, boulders near the surface), as does the biotic habitat (e.g. sunlight patterns under a forest canopy, differential accumulation of litter), and these factors interact with each other and with the organisms in the ecosystem in various ways, to which must be added that the organisms themselves also interact directly or indirectly (Odum and Odum 1959). Thus, it is only reasonable that plant species should respond distributionally to the microenvironmental patterns which result, although the situation is further complicated by the non-randomness of dispersal and reproduction.

Within recent years, concepts and mathematical techniques connected with microdistribution patterns have been developed at a rapid rate. As Greig-Smith (1957) points out, however, the study of pattern is not an end in itself. Instead, such studies should provide clues to the biology of the plants studied and should serve as guideposts for future work of an experimental nature.

1. KINDS OF PATTERN. Odum and Odum (1959) show that members of a species population may theoretically be distributed in three basic ways within a community. These are: (1) randomness, where the individuals are distributed with no spatial relationship to one another, somewhat like hailstones which have fallen

from the sky upon a smooth surface without deflection by air currents or irregularities of the surface; (2) clumping ("superdispersion", "overdispersion", or "arrangement" (Hutchinson 1953), "contageous" distribution (Cole 1949 and other authors)), in which the average distance from one individual to its closest neighbor is less than would be expected in a random distribution, and variability in these distances is greater than expected in a random distribution, and (3) uniformity (infradispersion", "regularity", "order", or "underdispersion" (Hutchinson 1953)), where the organisms approach the arrangement of molecules in a crystal lattice, so that the distances between them show less variability than in a random distribution. Of the three, it is now generally agreed that randomness is probably the exception rather than the rule, if indeed it truly occurs in nature at all (e.g. Hutchinson 1953, Cantlon 1958-59). Clumping would occur if the species were reproductive groups, or drawn together by social instincts or favorable interactions, or associated with patches of more favorable habitat. Uniformity might occur if the microhabitat variation was not critical, but the species in question required a minimum distance between individuals for optimum growth, efficient feeding, etc. (e.g. desert shrubs, territorial birds).

According to Greig-Smith (1957) and Odum and Odum (1959), patterns may be either spatial, or temporal (i.e. cycles, succession, etc.). However, the bulk of the existing work has been on two-dimensional (horizontal) spatial patterns, with some work on cyclic patterns (e.g. Watt 1945, 1947, Kershaw 1958), and some on reproductive patterns which act in a time sequence (cf. Kershaw 1958, Kershaw and Tallis 1958, Phillips 1953, 1954). In a way,

succession is also a pattern in a time sequence, but it differs from cyclic patterns described by Watt in that it is unidirectional and not self-perpetuating. Studies of seasonal and long term fluctuations (cf. Elton 1949, Weaver and Albertson 1956) fall into the broad category of temporal pattern studies. Vertical layering as well as horizontal spatial patterns should be considered (Hopkins 1957).

Hutchinson (1953) has classified patterns into five types according to their causes. (1) Vectorial patterns are those reflecting spatial gradients in particular environmental conditions; e.g. a pattern reflecting a "mosaic" of different physical microhabitats in each of which a given species has a different probability of occurence. An example would be frost-fissured arctic tundra, but many vectorial patterns are less striking. (2) Reproductive patterns are determined by the manner in which organisms colonize an area. Thus, a plant which spreads by runners or stolons tends to form clumps or clones, whereas one which spreads by wind-borne seeds might tend towards randomness. (3) Social patterns are limited primarily to animals, and include such things as the territorial patterns of birds (uniformity), and flock and herd patterns as well as colonies (clumping). In animals these patterns are effected frequently by signaling. (4) Coactive patterns are determined by interaction between species. Interspecific association (Cole 1949, 1957, Goodall 1952, De Vries 1953, Greig-Smith 1957), which applies to patterns involving two or more species and with which this paper deals, is often brought about by coaction, (or interaction as it is called in this paper), between species. Thus, if A is a shade-requiring forest species and B is a root parasite on A, then the

two should occur together in patches of shade. Both of them thus show clumping and also positive association with each other. On the other hand, if A secretes an antibiotic substance inhibitory to B, then both might be independently clumped, but the clumps of the two species might be negatively associated with each other. (5) Stochastic patterns depend upon the association of species with certain microenvironmental factors which are in themselves randomly distributed. An example might be the distribution of plankton in relation to random water currents.

Patterns may be thought of either in terms of the way in which individual species are distributed, or in terms of the ecological relationships of species to one another and the "associations" between species. The latter is the tendency of two or more species to occur together more or less frequently than one would predict on the basis of a theoretical random (independant) distribution, and is the way in which the problem of pattern is approached in this paper.

2. COMMUNITY PATTERNS. Krause (1952) suggests that phytosociological associations are arranged in a "mosaic" pattern over the surface of the earth. In this respect he seems to do little except to clarify what should already be evident from the work of the phytosociologists. Whittaker (1956) was able to show somewhat the same thing, with similarly large-sized units, on an altitudinal and slope-directional instead of a latitudinal basis. He perhaps admitted of more intergradation and transition between the units than did Krause. Similar groupings occured in sites with similar moisture and edaphic conditions, within a broad range of altitudes and slope exposures.

But the present trend is towards the study of groupings on a smaller scale, which lends itself somewhat more to unbiased random sampling and statistical analysis. Rommell (1930) and Hopkins (1957a) have suggested that vegetation within a broad "homogeneous" stand consists of a mosaic of repeated elements that Hopkins has termed "basic units". The latter Hopkins defines as groupings of species, all of those within one grouping having mutually significant positive correlation coefficients. His procedure involves separating out all species which are negatively correlated with each other and, using these as centers, building up groups of species which are positively associated with them. Earlier Goodall (1952, 1953) attempted to do somewhat the same thing. Basically, his technique consists of eliminating quadrats containing a particular species or strongly associated species pair from a group, recalculating correlation coefficients, and repeating the process until a group is left which shows no significant correlations among its species. The "residue" of eliminated quadrats is then repeatedly subjected to the same procedure until all quadrats are placed in some group. Goodall's method seems somewhat inferior to Hopkins' for both mathematical and biological reasons, since using the most frequent species as a starting point as Goodall does seems to involve some bias. Also, one of the groups obtained may readily be a group of more or less "independent" species having broad tolerance ranges, which are not strongly associated with each other or with members of other groups.

There is no doubt that patterns are occasionally quite distinct, and that "basic units" may be quite evident to the causal observer. This is certainly true of the patterns on polygonal

ground (Wiggins 1951), where sharp "breaks" in the habitat cause sharp breaks in the vegetation. Certain wetland vegetation types, such as marshes (e.g. Miller and Egler 1950), and some tussock types (Watt 1947), exhibit fairly distinct "mosaics" of basic units", in which the species from one unit seldom overlap very far into another unit and where all the species of a unit exhibit a high degree of positive association. But probably by far the most widespread situation in nature, exhibited for example by the herbs of a forest floor, is one in which each species has a reasonably broad tolerance range with respect to several or many microenvironmental factors (here including the influence of other species). Thus, a species may potentially be able to occur over, say, 90 % of an area, but its probability of occurence will fluctuate rather widely from point to point, so that one could visualize the area in question as composed of "contour lines of probability" for each species. The individuals of each species will be concentrated at the favorable "peaks" for that species, becoming sparser "downslope", but the species may still be represented by scattered individuals in some of the higher "valleys". Thus, a species may be positively associated with another whose "peaks" coincide fairly closely with its own, providing a deleterious interaction does not occur between them. Thus, various species pairs should exhibit all degrees of peak-coincidence and all degrees of positive and negative association, so that one could not simply classify them into separate groups of positively associated species such as "basic units".

I do not mean to completely discredit the "basic unit" and

"mosaic" concepts. They can be useful in the classification and description of vegetation, or as a measure of heterogeneity, and in some cases they may be real entities. But perhaps there is too much effort to pigeonhole, or force every species in every situation into some basic unit or other. This may not only be undesirable but, if one is interested primarily in the actual interactive and environmental causes of pattern, unnecessary. Therefore I would suggest that the continuum concept of Curtis and McIntosh (1951) is as applicable to small-scale as to large-scale patterns.

De Vries (1953) found that in many cases two negatively associated species are tied together by one which is positively associated with both, and I have found this to be true in my own work. This is another argument against indiscriminate use of the "basic unit" concept. It is not difficult to see how such a phenomenon might occur, if we view the niche of a plant as multidimensional (Hutchinson 1953, Kohn 1959). Suppose for example that species A and B, herbs on a pine forest floor, both have a peak probability of occurrence on somewhat more acid patches where pine litter has accumulated in large quantities in the past. B, however, finds the small depressions in the topography more favorable, whereas A is more drought tolerant and peaks on old blowdown hummocks. For this reason the two might be negatively associated. But species C may have a broader tolerance than either A or B with respect to moisture, and so has a high probability of occurrence both on hummocks and in hollows. If A, B, and C are then all more apt to occur below openings in the canopy, C may "bridge the gap" between the two negatively associated species and show positive association with both.

Some work on grasslands (De Vries 1953, De Vries et al. 1954) illustrates one useful method of depicting pattern in vegetation without isolating discreet units. Symbols for the species are arranged in a "constellation" figure, with those species which show high positive association placed close together, insofar as possible, and those which show high negative association far apart. Since this constellation attempts to depict in two dimensions what is really a multidimensional phenomenon, and since two negatively associated species may both have a positive association with one or more other species in common, it is not always possible to represent the association pattern by distances alone. Therefore lines of different colors, or of different widths, are drawn between the symbols to indicate the degree of positive association. The positions of the species may be determined more objectively by using the correlations of each species with two environmental variables, as the x- and y-axes for the constellation. It is interesting that, in De Vries work, species with mutually high positive associations did tend to be grouped closely together when this method was used, so that there were a few groupings which were quite distinct and similar to Hopkinsian "basic units". But other species were "free-floaters" which were not very closely tied with anything else. An attempt has been made in the present study to arrange the species in "constellations".

The ordination technique proposed by Bray and Curtis (1957) was devised to show graphically the relationship of stands to one another in two, three, or more dimensions. Stands are placed along one axis with two of the most dissimilar stands, as determined by an index of similarity, taken as the end points of

this axis. The stands are arranged a distance from these end points which is a function of their degree of similarity to each of the "reference" stands. For the ends of the second axis, two stands which are close together on the first axis, but which themselves have a low index of similarity, are chosen as endpoints. The process can be repeated several times to obtain a multidimensional arrangement. Now when the cover or frequency of particular species was plotted within the ordination figures, the authors found that most of them showed a peak at some point within the figure. There are drawbacks to the technique, however, in that it uses vegetation itself as a criterion for determining the ecological interrelationships of vegetation, and so is somewhat biased in favor of "proving" what it intends to prove.

An "index of amplitudinal correspondence" was devised by Bray (1956) to show how much overlap existed between species frequency or cover curves along an environmental gradient. The same technique, however, could be applied to individual quadrats within an area selected for apparent large-scale homogeneity. The values obtained are similar to other kinds of association coefficients, and Bray obtained good correspondence with Cole's (1949, 1957) association coefficients (discussed later).

So far, only spatial patterns have been discussed. Temporal patterns may be of various sorts, including successional, seasonal, cliseral, and cyclic changes. Since cyclic changes may help to explain some of the association phenomena found in the present study, they deserve some comment.

Watt (1947) gives several examples of cyclic patterns. Perhaps the one involving Calluna, Gaultheria, and lichens on windswept mountains is the most dramatic. Here, successive "waves" of Gaultheria, Calluna, lichens, and bare ground move across the

landscape driven by the wind, each phase being dependent upon the last, and distinct alternating bands of the four stages in that order are evident. In other areas where the same species are abundant, but the wind is not so strong, the same alternation occurs. But here Calluna spreads outward from the centers of clumps and dies in the centers, the latter then being colonized by lichens, left bare, and finally reoccupied by Gaultheria and then Calluna.

Watt gives examples in the same paper of a cyclic pattern governed by the buildup and decline of tufts of the grass Festuca, and also of a cyclic pattern caused by the rhizomaceous spread and eventual death of the bracken, Pteridium, where the litter of this fern is inhibitory to many other plants. Kershaw (1958) and Phillips (1954) describe similar patterns, but these studies concentrate on single species and so will be discussed in the next subsection.

Goodall (1954) used a factor analysis technique to determine association between species. This method has not gained great popularity, judging from the literature, and perhaps with good reason. Clark (1958-59) says that it is mathematically unsound, and points out that the method is biased in favor of showing whatever one sets out to prove. Bray and Curtis (1957) show that the results may be difficult to interpret biologically, and that their meaning may be interpreted in a number of different ways. For these reasons, factor analysis will not be discussed further.

3. PATTERNS OF SINGLE SPECIES. There is not always a sharp distinction between studies of "community" pattern and studies of "species" pattern as they are delimited here. The studies of

Watt (1947), for example, which were discussed above, could be considered species pattern studies if the species involved in the cycles had been considered separately.

As an example of this type of study concentrating on a single species, Kershaw (1958) has done a study of Agrostis patterns in pastures. He found that there were several "size units" of Agrostis patches in most pastures, and he attributed this to its pattern of reproduction, its interaction with other species, and its limitation by environmental variables. Kershaw and Tallis (1958) also showed similar patterns for Juncus tenuis and Festuca, and Phillips (1953, 1954) found a similar pattern in Eriophorum.

For three species of buttercups (Ranunculus spp.), Harper and Sager (1953) have shown a very striking pattern in pastures which is related to microtopography. One of these three species is associated with the tops of small ridges, another with the sides of these ridges, and a third species with the hollows between the ridges. Experimental work showed that, while established individuals of all three species could survive under the moisture conditions present in all three microsites, seed germination seldom occured except under moisture conditions approximating those of their natural habitats.

A word could be said concerning patterns in animal populations, although a detailed discussion of them is beyond the scope of this paper. Elton (1949), who presents a comprehensive review of this problem, states that animal pattern studies must consider the problem of mobility which does not confront the vascular plant ecologist. Consequently, it has proven impractical for zoologists to study associations as intensively as have the plant ecologists. Elton points out, however, that associations are

definitely present among the animals, as well as between animals and plants, and in fact Cole's (1949) association techniques used in this paper was originally developed for animal parasite-host relationships. "Clumped" and "uniform" distributions may indeed be quite marked in animals due to their social and territorial instincts, and the host specificity of some. Transitory variations (temperature changes, light variations, precipitation, wind, etc.) shifting the distribution and the degree of clumping of motile organisms within short periods of time, make the problem of pattern analysis in animals more complex than in plants.

4. TECHNIQUES USEFUL IN PATTERN STUDY. The objective modern methods used in analyzing pattern all depend upon mathematical models and statistical techniques. It is not the purpose of this paper to delve deeply into the mathematical theories involved, although all the steps involved in the calculations used in this paper are presented in Appendix A. Rather, I hope to present a brief resume of the logic behind some of the most common techniques which have been used, and to give the reader a general acquaintance with them.

Aids which may be used to advantage in studies of pattern are: (1) random sampling, (2) the use of a sample-unit size which will yield the most useful information, and (3) the use of some coding system whereby the data may be sorted rapidly and easily.

(1) Random sampling makes the data amenable to statistical analysis and allows one to obtain valid significance tests (Clark 1958-59). Any regular or "grid" sampling pattern is inclined to hit disproportionately small or large portions of certain elements in a vegetational mosaic, since there may be

some regularity in the patterns of species or "basic units", and if the grid is of a particular size it may be laid down so as to avoid or partially avoid a certain species or vegetation unit.

(2) Quadrat size should be larger than the sizes of the smallest patterns present, but not larger than the scale of interaction of the species with one another or with habitat variables (Greig-Smith 1957). If quadrats are of the same order of size as individuals or smaller, negative association will appear simply because there is usually not room for individuals of more than one species in the quadrats. If quadrats larger than the scale of interaction or habitat variability which cause positive or negative association are used association will not be demonstrated. Since the scale of pattern is not often readily discernable, and since there may be association relationships of the same species on several scales, it is desirable where possible to use quadrats of several sizes. The type of community sampled will determine in part the size of the samples used; thus in a desert shrub vegetation the samples would be larger than those necessary to determine the associations of grasses and forbes in a pasture, since in the latter case the scale of pattern for vascular plants is much smaller.

(3) Since the determination of association and other patterns involves a lot of sorting for various parameters, it is often desirable to code the information on punched cards of some kind which may be sorted quickly for various species or species-microenvironmental combinations. One such technique is described by Goodall (1953), another by Byer et al. (1959).

If one is interested primarily in the patterns of a single species, a technique proposed by Greig-Smith (1957), and used by Kershaw (1958), is effective. Cover is recorded in quadrats of various sizes, and the mean square of variability in cover is plotted against quadrat size. The peaks of this curve then indicate the average scales of pattern of the species or size of the clumps. There may be only one scale of clumping or several, with each larger clump itself composed of smaller clumps. The scale of pattern in environmental factors, or of other species, which are thought to be the causal mechanisms of the patterns in the species being studied, can be determined in the same fashion. If the sizes of the patterns of environmental factor and species correspond fairly closely, there is a good chance that the factor in question is indeed one of the causal agents of the pattern, as demonstrated by Kershaw (1958).

The "distance to nearest neighbor" technique of Dice (1952), and further elaborated by Clark and Evans (1954), is useful in the determination of clumping or uniform distribution. Basically, it involves a determination of the average distance one would expect between individuals if a population of this density were distributed randomly. The actual mean distance is then determined, and a comparison is made with the expected distances, along with a comparison of actual and theoretical variances. The technique can be adapted to measurements of interspecific association of one species with several others, also.

In the present paper, we are concerned primarily not with individual species patterns, but with measurements of association between two or more species. There are two ways of approaching this problem, each of which answers a somewhat different question. These are: (1) <u>simple association</u> techniques, which

attempt to discover whether two or more species occur together in a given sized sample more frequently (positive association) or less frequently (negative association) than would be expected if the individuals of the species were randomly distributed with respect to each other, and (2) correlation, techniques in which we attempt to determine whether or not high cover values of two or more species are randomly distributed with respect to each other.

III

METHODS

A - FIELD AND LABORATORY TECHNIQUES

The study area is located on Michigan State Forest land in southern Crawford County, Twp. 25 N, Range 3 W, Sec. 30 S.E. It is in the northern part of the lower peninsula of Michigan, about one mile west of Route M 18-76 between the towns of Roscommon and Grayling, west of the point where this road runs north-south. It is also about one mile east of the northwest corner of Higgins Lake. Its location is shown in Figure 1 (p. 22).

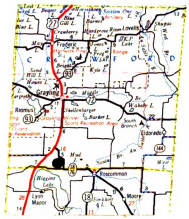
Crawford county is located in what is known as the "Jack pine area" of Michigan. It is characterized by extensive plains of sandy Pleistocene outwash, which have developed into very weakly podzolized Grayling soils on the drier sites and into other, more heavily podzolized soils on moister sites. These outwash plains support, in the present day, a vegetation consisting predominantly of open forest of *Pinus banksiana*[1/] and of open grassy Jack pine savannas.

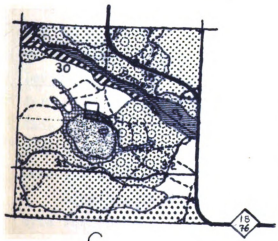
On the hilly sands of the moraines, a soil closely related to the Grayling soils is developed, which is called Roselawn sand. For some at present unknown reason, these moraines support a cover of oaks (particularly *Quercus rubra*, *Q. alba*, *Q. elipsoidalis* complex), with fewer pines, but the understory vegetation on Roselawn and Grayling sands is quite similar. Both of these soils are submarginal for agricultural purposes, and consequently a great deal of Crawford and surrounding counties are in State Forest land. Smaller tongues and patches of more fertile soils, of the same age

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1/ All scientific names of vascular plants cited in this paper follow the eighth edition of *Gray's Manual of Botany* (Fernald 1950).







LEGEND, Fig. 1C

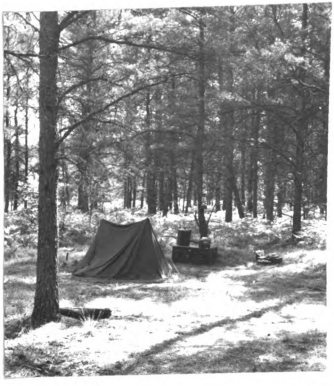
- Dawson-Greenwood Peat
- Grayling Sand
- Grayling Sand, gravelly
- Rifle Peat
- Roscommon Loamy sand
- Roselawn Sand, gravelly
- Roselawn Sandy Loam, gravelly
- Saugatuck Sand
- Highways
- Secondary roads
- Trails
- Section lines
- Study area

FIGURE 1. Location of the study area. A. Map of Michigan, with Crawford Co. and part of Roscommon Co. shaded, dot showing location of the study area. B. Portion of highway map showing the shaded area of A, dot showing the study area. C. Detail from a soil map, showing four sections in Crawford Co., Twp 25N, R 3W. (A from Veatch, Schoenmann, and Moon 1924, C from Michigan Department of Conservation 1927).

as Grayling and Roselawn or older, are present, and are often farmed. Also, several kinds of peats and mucks are present, which have developed in potholes in the Pleistocene drift or along streams. Almost all soils in the area are glacial in origin (Veatch 1953).

The sampling universe was an area of 100 X 100 meters, situated so that it encompassed a fairly broad soil and moisture gradient. The northern side of the area consists of an open Jack pine forest on dry Grayling sand (Figure 2-a, p.24). The southern side is a bog dominated by a thick stand of Leatherleaf shrub (Chamaedaphne calyculata) vegetation on a mat of Sphagnum moss. The soils are Dawson and Greenwood Peats. In the study area, scattered individuals of Black spruce (Picea mariana), Tamarack (Larix laricina) and stunted Pinus banksiana occur on the bog mat (Figure 2-b, p. 24). In other places in this bog Picea and Larix form quite dense stands. The bog margin (Figure 2-b) within the sample area is a dense stand of mature Picea, Larix, and Pinus banksiana. In some places the Larix and Picea predominate, while in other spots Pinus banksiana forms the margin and gives way directly to open bog vegetation. This gradient, though fairly abrupt, included enough area on the soil types transitional between Grayling and Dawson-Greenwood Peat for statistical study.

Ring counts on the largest Jack pines suggested that the tree vegetation had been relatively undisturbed for about 60 years. Charcoal in the soil profile both on the upland and in the bog indicated past fires. Since no fire scars were found on any of the living trees in the area, the last fires probably occured around 1900. The absence of recent stumps suggests that



A



B

FIGURE 2. **A.** Jack Pine forest near the study area. The transition from Carex-Danthonia understory in the foreground to Pteridium in the background corresponds approximately with the Grayling Sand to "Wet Grayling" transition. B. Leatherleaf bog on Dawson-Greenwood Peat in the study area, showing bog margin vegetation at the left and in the background.

there has been no cutting since then either.

A Jack pine-Leatherleaf bog transition was chosen for the study because the "dry" (Jack pine upland) end of such a gradient is on the poorest inorganic soil of the region, and the "wet" (Leatherleaf lowland) end is on the poorest organic soil, which is extremely acid and poorly drained. Consequently, the total flora of such a gradient is small, reducing the number of variables which must be considered both in calculations and in interpretation of the results. Also, this gradient is ecologically broad enough so that only two species (Pinus banksiana and the Low sweet blueberry, Vaccinium angustifolium) bridge the entire gradient from the driest to the wettest soil type. This means that broad-ranging species must of necessity have different associates along the gradient and must exist under different environmental conditions. Furthermore, the study of species associations along an environmental gradient is desirable, since species do not have precisely the same tolerance ranges, and changes in the association of a pair of species, or changes in the associations and correlations of given species with other species and environmental variables along the gradient, can tell us more about their ecology than could such analyses in a relatively homogeneous area.

After a reconaisance of the study area, the sampling universe was so located that a strip about 20 meters wide occured in the peat, giving a relatively equitable distribution of soil types. Accordingly, along what was to be the east side of the area, a base point was located on the bog margin by a stick thrown over the shoulder. A string was then laid out from the base point along a magnetic north-south compass line, extending 80 meters to the north (towards the "upland") and 20 meters to the south (into the bog). The other three sides of the area were then marked off with

the aid of a compass and tapes. The area was divided by strings into 20 X 20 meter squares, in order to facilitate location of the quadrats.

Four hundred 1 X 1 meter quadrats were located randomly within the study area. In order to locate them, the east and west sides of the study area were numbered in one-meter increments from 0 to 100, starting at the south end of the area. The north and south sides were similarly divided and numbered, starting with zero at the east end. Thus the east and south borders of the area corresponded to two axes, and any numbered point could be located by measurement from these axes.

Four hundred four-digit numbers had been chosen from the random number table in Dixon and Massey (1957), before the study area was staked out, and each of these was then considered as two two-digit numbers. Thus "4537" would be "45, 37", the location of the southeast corner of a quadrat along the "east" and "south" baselines respectively.

A metal frame was used to delimit each quadrat, the southeast corner of the frame being placed at the "base point" (i.e. the point "45-37" mentioned above) and the sides being placed parallel to the sides of the study area with the aid of tapes. Where trees were encountered in a quadrat, the bolts holding the frame were disconnected and the frame then reconstituted around the tree, and where trees lay in the path of one or more sides of the quadrat it was sometimes necessary to lay out the quadrat with tapes and strings.

Data for four hundred random quadrats, located in the manner described above, were recorded between early June and late September, 1958. The quadrats were run in four "series"

of 100 each, with the first hundred random numbers chosen corresponding to the first series, the second hundred to the second series, etc. This was done because certain species (for example Bracken, Pteridium aquilinum, and Wood anemone, Anemone quinquefolia) are seasonal, and the size of the vegetative parts may vary during this study period. In this way it was possible to sample completely across the gradient in each part of the area at approximately the same time. Each "series" was run systematically by starting at the NE corner of the study area. The NS 20-meter-wide bands, conveniently marked off with the strings, were run one at a time, by working from north to south within each band, and by starting with the eastern-most band and working westward. In this way it was usually possible to run quadrats on the driest part of the gradient, in the bog, and on all the intermediate soil types on the same day. Admittedly, however, some of the associations, and especially the correlations, such as those involving the two species mentioned above, could still be markedly influenced by the long time span for the sampling as a whole. Thus a negative correlation between two species might mean that they were in their full foliage at different times of year, while a positive correlation could reflect the tendency for the cover of the two species involved to be highest at the same time of year.

One might well ask why it is necessary to take so many samples. Species-area curves, which are explained later in this section, show that according to Vestal's (1949) technique, sufficient samples were taken to characterize the segment in at least four of the five gradient segments. However, in a statistical analysis of association, far more samples are necessary than

for a mere characterization of the area, and the more samples one has, the more critical are the significance tests and the easier it is to demonstrate those associations that exist.

In each quadrat, general character of the vegetation, per cent cover estimates of each vascular plant species, and presence of each bryophyte and lichen species which occured in the quadrat were recorded. Green soil algae and moss protonemata which were visible were lumped as "Protococcus", and included with the bryophytes, since it was not possible to distinguish between them in the field. Total moss cover, lichen cover, and tree cover were recorded for each quadrat; total shrub and herb cover were calculated later by adding the cover values for all the individual species in each quadrat.

For one of the four quadrat series, chosen randomly, light readings were made with a Weston Model 756 sunlight illumination meter, in the center of each quadrat at breast height, on a cloudless day between 11 AM and 2 PM. A series of five light readings was made in full sunlight, in an open area in the bog, at the beginning of the study, another after 50 quadrats had been done, and a third after values for all 100 quadrats had been recorded. A curve of the values of full sunlight was drawn on graph paper, and values for the quadrats plotted against this curve in order to calculate "percentage of full sunlight" for each quadrat. This was done later by allowing 50 spaces between each of the mean "full sunlight" readings on the graph, and plotting the light readings for the quadrats in these spaces in the order in which they were recorded. The estimated full sunlight value at that point could then be divided into the value of that particular quadrat, to obtain an estimate of "percentage of full sunlight". Of course, this technique assumes that an equal amount

of time elapsed between the light readings for each quadrat and the next one, which is not strictly true, but since the quadrats were done systematically without interruption the error is probably not serious. Also, full sunlight showed a variation of only about 7 % during the whole period.

A soil profile was taken for each of the 400 quadrats, after the vegetation data had been recorded on all quadrats. A rectangular block of soil was cut from the center of each quadrat with a spade, except in those few cases where trees or large roots interfered. In the latter, the block was cut as near the center as possible. The soil data were all taken at the same time, because it was felt that variation in judgment of the demarcation between the different layers of the profile would thus be kept to a minimum. The depth of each of the following layers was recorded in millimeters: A_{o_L} (loose leaf and other litter), A_{o_m} (leaf mold, leaves and twigs which are readily identifiable as such but which are tightly packed and mixed with humic materials), A_{o_H} (humus), A_1 (mixed decomposed organic and mineral materials), A_2 (leached zone), B_1 (zone of heavy deposition of iron and organic materials, Orterde), and B_2 (zone of lighter iron deposition, unconsolidated) (modified from Robinson 1936, except for the subdivisions of the A_o which are modified from various sources). Depth to glei was recorded, if glei was present within approximately 75 cm. of the surface, as well as the coloration of the B layer. For the peats, only the first three layers (the A_{o_H} corresponding to the peat proper), and for the Saugatuck and Roscommon soils, only the layers through the A_2 were recorded. Depth of the peats was recorded with a heavy wire used as a sounding device. All data were quantitative except for the coloration of the B_1 and B_2, which

were more or less subjectively called reddish, reddish-brown, or coffee-brown, in lieu of the Munsel color code designations.

On one of the four series of quadrats, the series having been chosen at random, soil samples for moisture, volume-weight, and pH determinations were taken on one day at the end of the study period. All of the loose litter at a point north of the center of each quadrat, just far enough away (10 cm.) from the soil block which had been removed so that the portion disturbed by the soil profile work was not encountered, was brushed aside. A washed soup can 66 mm. in diameter and 100 mm. in height, with both ends cut out with a circular can opener, was driven down vertically until its upper lip was flush with the soil surface. The can was then dug out and the surfaces leveled off. Each sample was then pushed into a separate plastic refrigerator bag, as nearly intact as possible, and labeled with the number of the quadrat on a slip of paper placed inside the bag. Each bag was then secured with a rubber band at the top so that moisture could not escape except by slow diffusion through the plastic. The wet weights were determined in the laboratory over a week later, but several bags which were weighed right after they had been brought back from the field and again just before drying was begun showed no measurable change in weight.

Wet weights were obtained by weighing the samples in the plastic bags. It was previously found that the weight of several unused bags, with labels and rubber bands, had a maximum variation of less than 0.02 grams, so an average value for the weight of the bag, label, and band was considered a constant, and subtracted from each raw weight in order to obtain the wet weight of the soil sample. For dry weight determinations, the samples

were emptied from the bags into 800 ml. beakers, and the beakers of soil were dried in an oven at 105° for four days. The bags, with rubber bands, labels, and all remaining soil and moisture, were also dried for the same period at the same time, but in another oven at 40° C. Both bags and beakers were removed from their respective ovens after drying, and placed in dessicator jars to cool. The soil samples were each placed back in the proper bags and immediately weighed, and constants for bag weight, etc., were subtracted as before. The volume of the soup can used to take the samples was later calculated in order to obtain dry weight of each soil sample per cubic centimeter. The per cent moisture of the samples was calculated simply by dividing wet weight into wet minus dry weight, and multiplying by 100.

In the peat soils, pH and moisture vary so much between one portion of a quadrat and another, because of the hummocky micro-topography, that it was hardly worthwhile to determine values for the individual quadrats for use in the association and correlation analyses. Accordingly, five of the quadrats were chosen at random, so that a rough average could be determined which would be useful in describing the peat area.

PH values were determined for each sample in the laboratory with a Beckman pH meter. For this purpose, a level spatula of soil, from one inch below the top of each sample, was diluted with 10 cc of distilled water. The pH meter was calibrated periodically against Beckman buffer solution.

B - ANALYSIS TECHNIQUES

The data for each quadrat were punched into an "MSU-Bot" modified Royal-MacBee keysort punch card of the type described by Byer *et al.* (1959). These cards may be easily and quickly

sorted with a special sorting needle for values of environmental variables, or over a template if one wishes to determine cover values of species, co-occurence of species, or the cover values in each quadrat of two or more species for use in calculating correlation and regression coefficients.

The quadrats were separated into seven groups by soil type. The descriptions of the various soil types were taken from McKenzie and Whiteside (1956). Unfortunately, there is usually no single criterion for separating a given soil type from other soil types along the gradient, and soil scientists, like vegetation scientists, seldom seem to set exact limits to their types. In order to make the separations as objective as possible, two or more criteria were used for each separation, except where a single criterion was given in the reference. The criteria used for separation are listed in appendix B. These criteria are based upon the descriptions, and insofar as possible an attempt is made to strike an average between the descriptions of two adjacent soil types in the separation. Hence the soils here delimited correspond as closely as possible to my interpretation of McKenzie's and Whiteside's classification.

This technique was sufficient to place all but about 20 of the 400 quadrats into one of the seven soil types. The remainder were referred back to the published description, then placed as objectively as possible by scoring them "1" or "2" for each characteristic according to whether they were closer to the "drier" or "wetter" of two possible soil types, respectively. Those with more "1"s than "2"s were assigned to the "drier" soil type, those with more "2"s to the "wetter". Sometimes it was necessary to use discretion in the assignment of quadrats to a soil type;

i.e. since many of the types are delimited on the basis of the depth of various horizons in the profile, and since the profile depth is dependent upon the age of the profile at a particular spot as much as upon the moisture regimen, recent blowdowns with profiles shallower than normal must be treated individually.

In no case did a soil profile show characteristics of more than two soil types, so it was never necessary to decide between three or more.

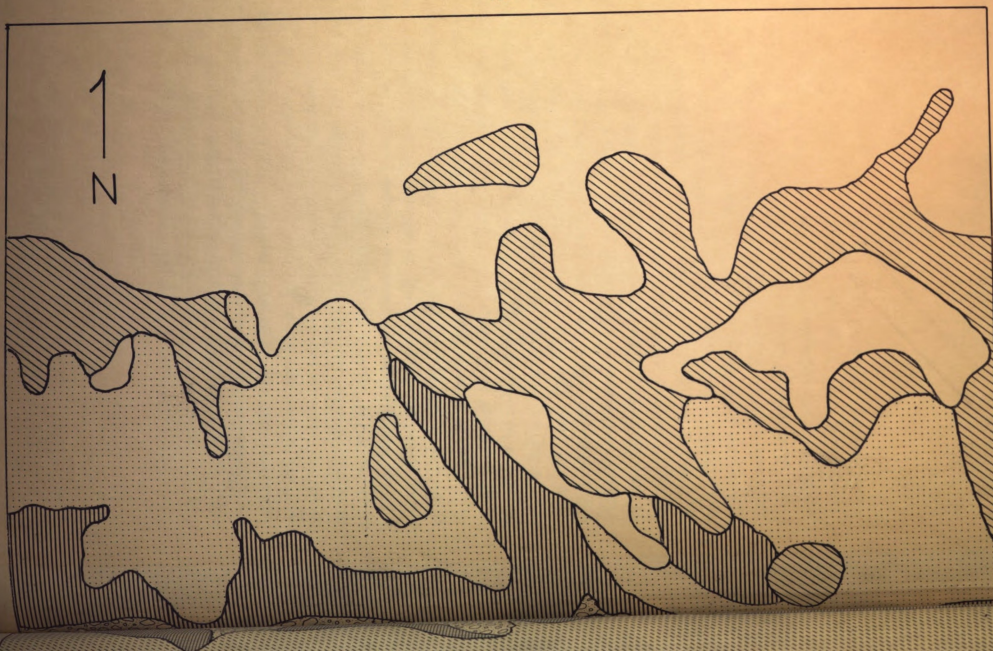
The attempted objectivity in the assignment of quadrats to certain soil types may have certain drawbacks. One is that a few of the quadrats may not correspond, from a Pedologist's viewpoint, to the soil type to which they are assigned, despite all efforts to take age, etc., into consideration. Slight inaccuracies in soil classification, however, may be the cost of statistical objectivity. Furthermore, it is not necessary in this study that all quadrats be assigned to a correct soil type, only that they be placed in relatively homogeneous groups.

Of the 400 quadrats, the original breakdown found 166 in the Grayling sand and only 101 in the Dawson-Greenwood Peat, showing that a slight misjudgment had been made in laying out the sample universe, giving more area on the dry end. There were not enough quadrats for statistically critical association analysis in some of the intermediate soil types. There was enough vegetational variation within the Grayling, however, so that a further separation seemed justifiable; accordingly 46 Grayling quadrats which had a deeper A_2 than the rest and generally better profile development were selected out as an intermediate soil type and called "wet Grayling". This does not

correspond to any soil type in the pedologists' classification. Also, after the initial separation, 15 of the quadrats in the Saugatuck soil type having characteristics close to Roscommon soil were removed and placed with this adjacent soil type. This was done so that the Roscommon quadrats could be included in the association analyses, for the sample of this soil type was not sufficient. These "wet Saugatuck" quadrats were always considered part of the Roscommon soil and were analyzed with it. The criteria used in this paper for the separation of soil types are listed in Appendix B. Because of vegetational similarity and because there were so few quadrats in Greenwood Peat, the Dawson and Greenwood Peats were lumped into a single type. Thus the 400 quadrats were placed in a total of seven different soil types.

A map of the study area, showing a distribution of the soil types, is presented in Figure 3 (p. 35). This map was made by first locating the quadrats on graph paper and marking them in with symbols indicating the soil type to which they belonged. Lines were then drawn separating groups of similar symbols, and these lines were then traced on a plain piece of paper.

In the species-area curves, the horizontal axis of each curve represents the cumulative total number of quadrats, or total area in square meters, the vertical axis represents the cumulative number of species encountered. With the punch cards, it was possible to run the cards for each soil type over a template in a random order and to blacken in spaces on the template for species encountered as the cards were run over it one by one. Thus only new species showed up as unblackened spaces. Any new species encountered in each quadrat were recorded by moving the points for that quadrat a number of units up from the point for



35.

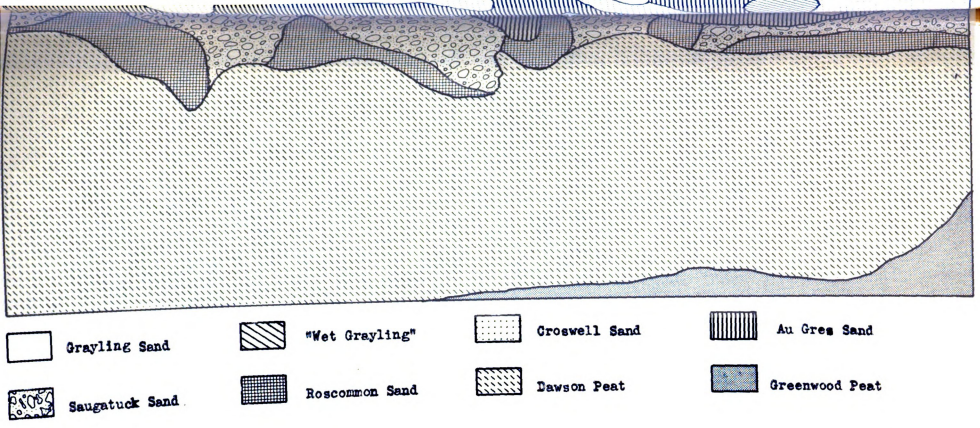


FIGURE 3. Soil map of the study area.

the last quadrat, along the vertical axis of the graph, corresponding to the number of new species in the quadrat.

The per cent frequency and the average per cent cover of each species were calculated for each of the seven soil types. The average values for the following variables were also calculated: thickness of the A_{o_L}, A_{o_m}, A_{o_H}, A_1, A_2, B_1, B_2, total B layers of the soil profile, depth to glei, per cent of quadrats with glei evident, per cent cover of lichen, bryophyte, herb, shrub, and tree layers, per cent of full sunlight, soil pH, percent of moisture in the soil, and dry weight of the soil per cc.

Next, the second and third soil types along the gradient (starting with Grayling, at the "dry" end, as the first and working "down-gradient"), were combined into one group, as were the fourth and fifth, so that there would be enough in each group to warrant statistical treatment. With this rearrangement, there were five groups of quadrats, the smallest of which contained 28 quadrats.

Cole association coefficients were then calculated for each of the five gradient segments, for all possible combinations of those taxa (32 in all) which occurred frequently enough to warrant such analysis. The Cole coefficients for each segment were then arranged in a matrix with that pair of species having the highest positive coefficient taken as a point of reference. The most frequent species of this pair was designated the "reference" species, and all other species were arranged relative to it in the order of their decreasing positive and increasing negative Cole coefficients with it. Thus the species having the highest positive Cole coefficient with the "reference" species was placed adjacent to it in the table, that having the second highest

positive coefficient with it next, etc., until the species exhibiting the highest negative association with it was placed the greatest distance from it.

The original plan was to include in the analysis only those species which occured in 20 or more quadrats in each gradient segment. However, since some of the types included only a small number of quadrats, it was necessary to reduce this figure in some cases. The gradient segments, with the corresponding minimum numbers of quadrats in which a species had to be present in order to be included in the Cole analyses, are listed below, starting at the "dry" end of the gradient:

Grayling	20
Wet Grayling-Croswell	20
Au Gres-Saugatuck	15
Roscommon (with "wet Saugatuck")	12
Dawson-Greenwood	20.

If a species occurs in most or all of the quadrats, the Cole coefficients will be just as invalid as will coefficients involving a too-infrequent species. Accordingly, the median cover value for such species was calculated, and the species were counted as absent if their cover value in a quadrat was below the median value.

Zero-order correlation coefficients with tree cover, and with depth of the A_{o_H} layer, were calculated for each vascular species for which Cole coefficients had been calculated on Grayling, Wet Grayling-Croswell, and Au Gres-Saugatuck. The same was done for the vascular species on Dawson-Greenwood, except that per cent of moss cover and depth of the unconsolidated organic mat were used as the environmental parameters. The number of quadrats in Roscommon was considered too small to warrant this type of analysis.

These correlations of the vascular species on four of the soil types with two environmental parameters were used in constructing combined "ordination" and "constellation" figures, the two environmental parameters being used as X and Y axes. The species were placed in the figures according to their coordinants on these axes, and lines were drawn between those pairs with high positive and high negative Cole coefficients. The magnitude of the Cole coefficients is indicated by the breadth of the lines connecting the species symbols.

The vascular species for which Cole coefficients had been calculated were broken down into six groups for further analysis, and particular environmental variables were included with some groups. The information obtained for each of these groups was: (1) Zero-order correlation coefficients for all possible species-species and species-variable combinations, (2) highest order partial correlation coefficients for all such combinations, and (3) multiple correlation coefficients of each species or variable with all of the others in the matrix. In addition, standard partial regression coefficients were calculated for all possible combinations in Group I, but they were not calculated for the other groups because of the time involved, and because those obtained for Group I were all very similar to the corresponding partial correlation coefficients.

The matrices of the various coefficients were studied for each group, taking into consideration also the association and correlation coefficients of the species and variables in each group with other species and variables not included in the group. Possible postulates for explaining the results were listed.

Certain postulates were mutually exclusive, and others were in direct contradiction with field observations, thus leaving a set of hypotheses for future experimental testing.

C - EXPLANATION OF ASSOCIATION AND CORRELATION TECHNIQUES USED IN THE PRESENT STUDY[2/]

(1) Cole association coefficients are a widely used method for determining association. These coefficients, which are always between minus and plus-one, can be calculated by any of several formulas (i.e. De Vries et al. 1954, Goodall 1952), but perhaps the best known are those proposed by Cole (1949, 1957). The latter is used here. The calculations of this coefficient and of the chi-square test of significance for it, are given in Appendix A-1.

(2) Zero-order correlation coefficients. The calculation technique for these is given in Appendix A-2. They are comparable to the Cole Association Coefficients, except that they are based upon cover (in some other studies density), and they thus show whether or not high cover values of the species tend to occur together, not merely whether or not the species tend to be present together.

2/ Except for the equations for the Cole Coefficient, Dr. Phillip J. Clark of the Department of Zoology, Michigan State University, devised the techniques presented here and in Appendix A. Many of the ideas for analysis are his also.

Quantifiable environmental variables as well as species cover values may be included, and thus species-microhabitat correlations may be obtained. Like the Cole Coefficients, these vary between minus and plus one.

(3) Partial correlation coefficients. The technique for obtaining highest-order partial correlation coefficients is given in Appendix A-3.

They differ from the zero-order correlation coefficients in that they show not the situation in nature, but what the tendency for high cover of two species to occur together or not to occur together would be if a number of other variables were held constant (partialled out). This is in a sense like a consideration of the two species only in those parts of the area where they occur. Thus, it is somewhat analogous to removing from consideration that part of the area where two species are not abundant, or where their probability of occurence is low.

If one wishes to pin down exactly the particular variables which influence the association between two species, it is possible to partial out only one variable or any combination of variables at one time. But only the highest order partial correlations were calculated for this study, due to shortage of time. These are the correlation coefficients between two variables when all other variables in the matrix have been partialed out.

(4) Multiple correlation coefficients. The formulas used in finding and testing these coefficients are given in Appendix A-4.

Multiple correlation coefficients are simply the correlation of one species or variable with several other species and/or variables at once. In this study, they are run for each species

and variable in each correlation matrix against all of the other species and variables in that matrix. Because they are less specific than the other coefficients mentioned here, they are perhaps not as useful. But they do give a clue as to whether a species is a "dependent" or a fairly "independent" one within a community, e.g. whether or not it is greatly influenced by microenvironmental variation and/or association with other species.

Unlike all the other coefficients mentioned here, multiple correlation coefficients vary between zero and plus one, making no distinction between positive and negative association.

(5) Partial regression coefficients may be found by the formulas given in Appendix A-5.

The regression coefficients are more critical than partial correlation coefficients in that they show the association of each member of a variable pair with the other.

Because the standard partial regression coefficients require several times as much calculation as the highest order partial correlation coefficients when both are found by the matrix method, it is probably best to use the latter if time is in short supply, and if an electronic computer is not available.

IV

RESULTS

A - DESCRIPTION OF THE AREA

1. VEGETATION.-The general character of the area has been treated in the introduction and methods sections.

The total flora of the study area is small. The 400 1 X 1 meter quadrats were found to contain a total of only 84 vascular species, 24+ bryophytes, and 6+ lichen species,[3/] not including mosses and lichens on the upright branches of trees and shrubs which were not recorded. Thus 114+ embryophyte and lichen species in all were found in the quadrats. A thorough reconnaisance of the area showed only three other vascular species to be present, as listed at the end of Table 1. It is possible that an additional small number of species, present in very low abundance, was not encountered.

3/ Species of Sphagnum and cup-shaped species of Cladonia (pyxidata-group) were lumped in the analysis, since they were not identified in time, hence the "plus" signs after the figures for bryophytes and lichens. Proper identifications would raise these figures by 5 or 6 species, at most.
Voucher specimens of most of these species are on file in the Michigan State University Herbarium. This includes all taxa studied in the association and correlation analyses.

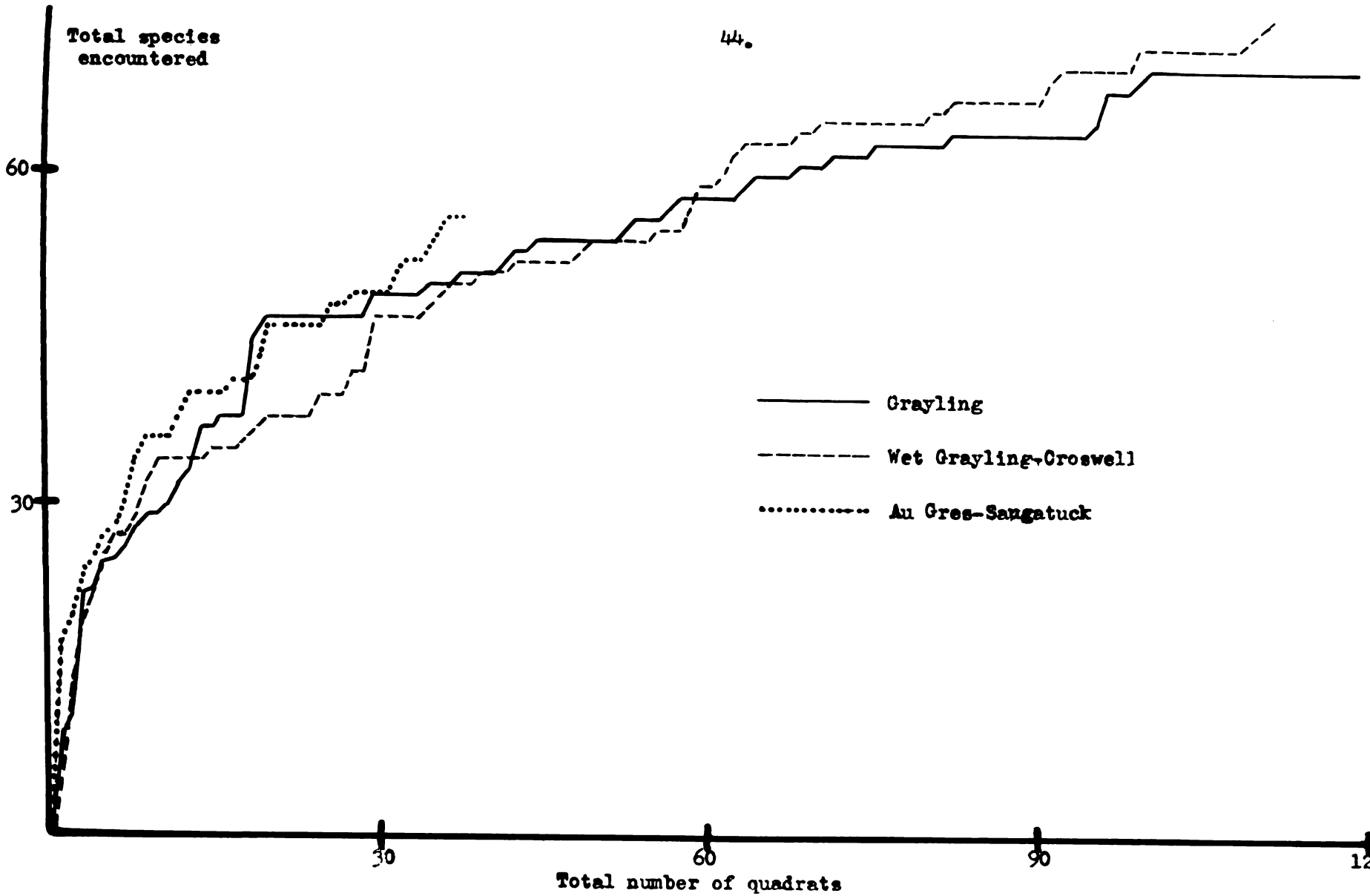
The species-area curves (Figures 4, 5, p. 44-45) rise to a height which is a function of the richness of the flora. The rapidity with which the curve rises is also dependent upon the richness of the flora (Hopkins 1957). It is thus evident that the flora of Roscommon is the richest, that of Dawson-Greenwood the poorest. Grayling is intermediate between the two, and the total flora seems to increase slightly from Grayling through Au Gres-Saugatuck, going from the "dry" end of the gradient towards the bog margin.

A quantitative description of the vegetation of each segment of the area is presented in Tables I (p. 46-53) and II (p. 54-59).

Grayling sand (G)[4/] is characterized by Pinus banksiana as the only dominant in the tree layer, the pine forming a semi-closed canopy. Prunus serotina (Black cherry) is of sporadic occurence as a large shrub. Vaccinium angustifolium (Low sweet blueberry) dominates the shrub layer and is nearly ubiquitous, and Comptonia peregrina (Sweet-fern) occurs sporadically but is fairly frequent in the quadrats. Among the herbs and ground shrubs, Carex pensylvanica (Pennsylvania sedge) is definitely dominant with high average cover, and occurence in nearly every quadrat. More or less in order of importance, other common members of this layer are Pteridium aquilinum (Bracken), Melampyrum lineare (Cow-wheat), Gaultheria procumbens (Teaberry),

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4/ Appendix C-3 lists these symbols, and the soil types to which they correspond.



44.

FIGURE 4. Species-Area curves for Grayling, Wet Grayling-Croswell, and Au Gres-Saugatuck soil types.

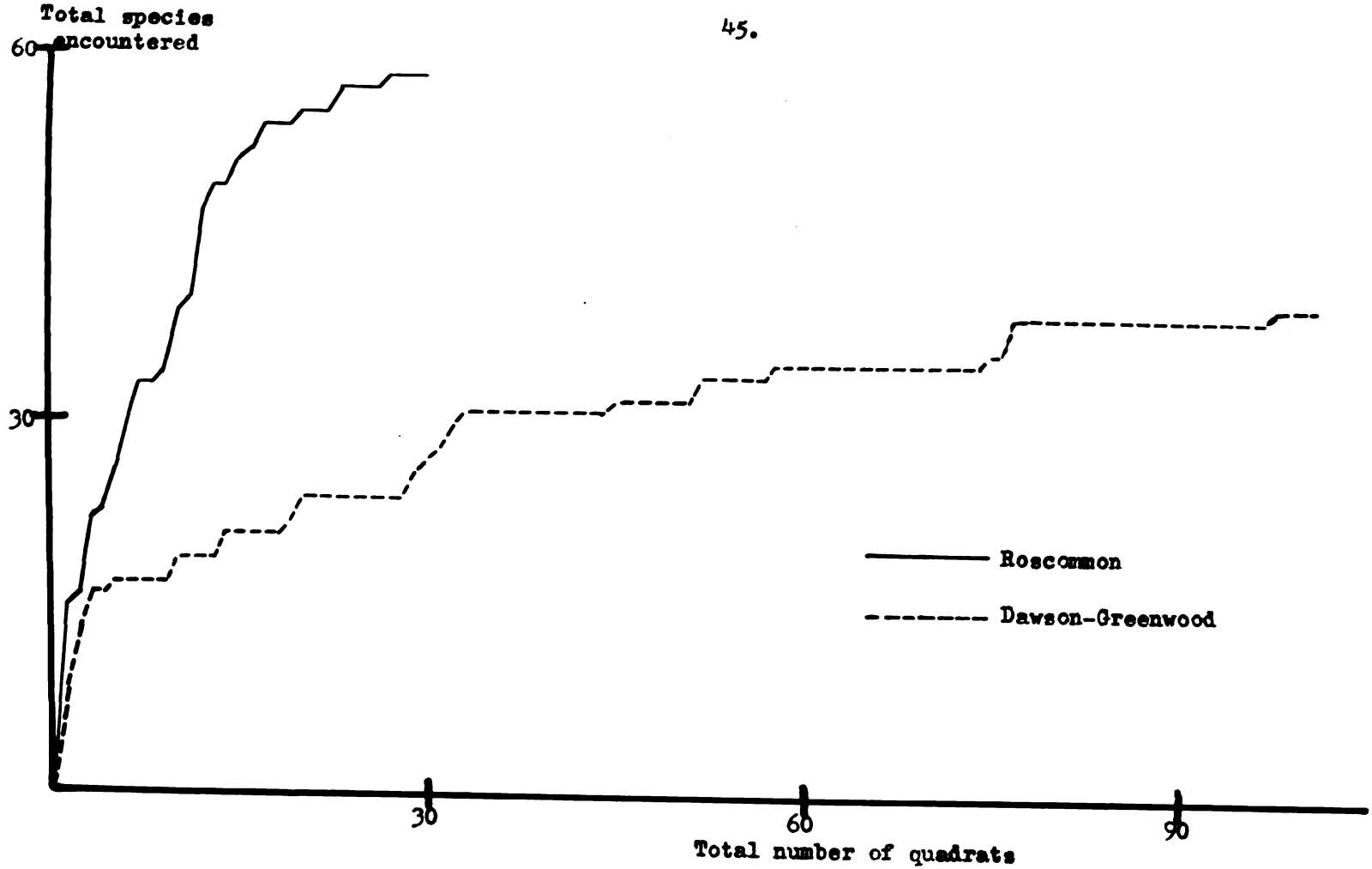


FIGURE 5. Species-area curves for Roscommon and Dawson-Greenwood soil types.

45.

TABLE I

SUMMARY OF PER CENT FREQUENCY ACROSS THE GRADIENT*

Species VASCULAR		Soil Type # G	WG	C	AG	S	R	DG
Acer rubrum	(h)	-	-	1.52	-	-	-	-
Amelanchier humilis	(s)	-	2.17	9.09	-	-	3.45	-
	(h)	0.83	-	1.52	7.14	-	-	-
Amelanchier "large toothed"	(t)	-	-	-	-	-	-	-
	(s)	-	-	-	3.57	-	-	-
	(h)	-	-	-	-	-	-	-
Amelanchier oblongifolia	(t)	-	2.17	1.52	-	-	-	-
	(s)	4.17	2.17	4.55	7.14	-	3.45	-
	(h)	10.00	8.70	15.15	14.29	10.00	-	-
Amelanchier sanguinea	(t)	-	-	-	3.57	-	-	-
	(s)	-	-	3.03	3.57	20.00	6.90	-
	(h)	-	-	1.52	7.14	30.00	3.45	-
Anemone quinquefolia		20.00	15.22	9.09	-	-	-	-
Antennaria neodioica		3.33	-	-	-	-	-	-
Apocynum androsaemifolium		3.33	2.17	-	-	-	-	-
Arctostaphylos uva-ursi		6.67	10.87	-	-	-	-	-
Aster "hairy ovate"		8.33	6.52	7.58	3.57	-	-	-
Aster laevis		13.33	10.87	6.06	-	-	-	-
Aster "lanceolate"		0.83	-	1.52	-	-	-	-
Aster macrophylla		-	2.17	1.52	-	-	-	-
Bromus ciliatus		0.83	-	-	-	-	-	-
Campanula rotundifolia		2.50	-	1.52	-	-	-	-

* See page 53

TABLE I continued

Species	Soil Type#						
	G	WG	C	AG	S	R	DG
Carex "fine"	3.33	2.17	-	-	-	3.45	-
Carex pedunculata	10.83	6.52	9.09	10.71	-	3.45	-
Carex pensylvanica	98.33	97.83	93.94	82.14	40.00	3.45	-
Chamaedaphne calyculata	-	-	-	3.57	20.00	58.62	100.00
Commandra umbellata	-	-	1.52	3.57	-	-	-
"Composite small narrow"	0.83	-	-	-	-	-	-
Comptonia peregrina	16.67	21.74	48.48	50.00	30.00	3.45	-
Coptis groenlandica	-	-	10.61	35.71	50.00	10.34	-
Cornus canadensis	-	2.17	7.58	39.29	60.00	17.24	-
Cypripedium acaule	-	-	6.06	7.14	-	-	-
Danthonia spicata	19.17	10.87	4.55	-	-	-	-
"dead bush"	-	-	1.52	3.57	-	-	-
Epigaea repens	4.17	8.70	31.82	57.14	10.00	13.79	-
Eriophorum spissum	-	-	-	3.57	-	37.93	48.51
Fragaria vesca	1.67	-	-	-	-	-	-
Gaultheria procumbens	32.50	60.87	87.88	96.43	100.00	58.62	0.99
"grass big hairy"	1.67	2.17	-	-	-	-	-
"grass smooth"	0.83	-	-	-	-	-	-
"grass smooth broad"	0.83	-	-	-	-	-	-

* See page 53

TABLE I continued *

Species		Soil Type # G	WG	C	AG	S	R	DG
Hieracium venosum		2.50	-	9.09	-	-	-	-
Ilex verticillata	(s)	-	-	7.58	17.46	20.00	24.14	2.97
	(h)	-	-	6.06	21.43	10.00	3.45	-
Kalmia angustifolia		-	-	1.52	-	10.00	6.90	6.93
Kalmia polifolia		-	-	-	-	-	20.69	55.45
Krigia biflora		-	-	4.55	-	-	-	-
Krigia virginica		0.83	-	-	-	-	-	-
Larix laricina	(t)	-	-	-	-	30.00	17.24	11.88
	(s)	-	-	-	-	-	-	0.99
	(h)	-	-	1.52	-	-	3.45	1.98
Ledum groenlandicum	-	-	-	-	10.71	30.00	79.31	31.68
Liatris sp.		2.50	-	-	-	-	-	-
Lycopodium obscurum		-	-	12.12	14.29	10.00	-	-
Maianthemum canadense		25.83	34.78	74.24	82.14	60.00	10.34	-
Melampyrum lineare		36.67	30.43	53.03	67.86	40.00	3.45	-
Nemopanthus mucronata	(s)	-	-	-	3.57	10.00	13.79	1.98
	(h)	-	-	-	-	10.00	6.90	-
Oryzopsis asperifolia		19.17	15.22	21.12	14.29			
Oryzopsis pungens		16.67	10.87	4.55	-	-	-	-
Panicum "basal inflor."		0.83	-	-	-	-	-	-
Panicum "broad leaved"		0.83	2.17	-	-	-	-	-
Panicum "narrow leaved"		0.83	-	-	-	-	-	-
Panicum sp.		0.83	2.17	-	-	-	-	-

* See page 53

TABLE I continued *

Species		Soil Type # G	WG	C	AG	S	R	DG
Picea mariana	(t)	0.83	-	1.52	7.14	50.00	41.38	14.85
	(s)	-	-	-	-	10.00	10.34	3.96
Pinus banksiana	(t)	97.50	95.65	87.88	92.86	40.00	24.14	6.93
	(s)	1.67	-	1.52	-	-	3.45	1.98
	(h)	0.83	2.17	-	-	-	-	1.98
Pinus resinosa	(t)	0.83	-	-	-	-	6.90	0.99
	(s)	0.83	-	-	-	-	-	-
	(h)	-	-	1.52	-	-	-	-
Pinus strobus	(t)	-	-	-	-	-	6.90	0.99
	(s)	-	-	-	-	-	-	2.97
Polygonum sp.		-	2.17	-	-	-	-	-
Populus grandidentata	(t)	-	-	1.52	-	-	-	-
Populus tremuloides	(t)	-	2.17	-	3.57	10.00	3.45	-
	(s)	-	-	3.03	-	-	-	-
Prunus serotina	(t)	1.67	-	6.06	17.86	10.00	-	-
	(s)	7.50	15.22	12.12	21.43	-	-	-
	(h)	10.80	8.70	18.18	35.71	40.00	-	-
Prunus virginiana	(t)	-	-	-	3.57	-	-	-
	(s)	0.83	-	-	-	10.00	3.45	-
	(h)	0.83	-	-	-	-	-	-
Pteridium aquilinum		61.67	76.09	65.15	53.57	10.00	-	-
Quercus rubra	(s)	5.00	4.35	-	-	-	-	-
	(h)	2.50	-	-	-	-	-	-
Ribes "dull"	(s)	0.83	-	-	-	-	-	-
	(h)	0.83	-	-	-	-	-	-
Ribes "seedling"	(h)	0.83	-	-	-	-	-	-
Ribes "shiny"	(h)	-	-	1.52	3.57	-	-	-

* See page 53

TABLE I continued*

Species		Soil Type # G	WG	C	AG	S	R	DG
Rubus canadensis		9.16	6.52	6.07	14.29	-	3.45	-
Rubus hispidus var. obovalis		0.83	4.35	43.94	64.29	50.00	13.79	-
Rubus idaeus		-	-	3.03	-	-	-	-
"snag unidentified"		-	-	-	-	-	3.45	-
Solidage "lanceolate long petiole"		10.00	13.04	-	-	-	-	-
Solidago "narrow"		0.83	-	-	-	-	-	-
Solidago rugosa		0.83	-	-	-	-	-	-
Solidago "sessile"		0.83	-	-	-	-	-	-
Solidago "sharp teeth"		0.83	-	-	-	-	-	-
Solidago "white bloom"		-	-	-	-	-	-	0.99
Trientalis borealis		1.67	6.52	40.91	71.43	60.00	10.34	-
Vaccinium angustifolium var. nigrum		69.17	82.61	93.94	100.00	100.00	75.86	13.86
Vaccinium angustifolium (typical)		60.00	71.74	96.97	96.43	100.00	79.31	20.79
Vaccinium myrtilloides		0.83	4.35	37.88	50.00	70.00	37.83	1.98
Vaccinium oxycoccus		-	-	-	-	-	13.79	91.09
Viburnum cassinoides	(s)	-	-	4.55	14.29	50.00	31.03	0.99
	(h)	-	-	-	10.71	10.00	-	-
Viola adunca		14.17	4.35	3.03	-	-	-	-

* See page 53

TABLE I continued*

Species	Soil Type# G	WG	C	AG	S	R	DG
Viola "larger"	-	2.17	-	-	-	-	-
MOSSES							
Amblystegium varium	-	2.17	-	-	-	-	-
Aulocomium palustre	-	-	-	-	-	3.45	0.99
Brachythecium salebrosum	9.17	21.74	18.18	32.14	30.00	13.79	2.97
Calliergonella schreberi	42.50	28.26	28.79	39.29	80.00	48.28	6.93
Campylium hispidulum	-	-	-	-	-	3.45	-
Ceratodon purpurascens	12.50	2.17	4.55	-	-	-	-
"delicate tiny bristle leaved"	-	-	-	-	-	-	0.99
Dicranum undullatum	43.33	26.09	21.21	14.29	20.00	24.14	3.96
"ferny moss"	-	-	3.03	-	-	3.45	-
"ferny big moss"	1.67	-	3.03	3.57	10.00	3.45	-
Geocalyx graveolens	0.83	-	-	-	-	-	-
? Lophocolea	-	-	-	-	20.00	6.90	1.98
Plagiothecium sp.	-	-	-	-	-	-	0.99
Pohlia nutans	0.83	-	-	-	-	-	-
Polytrichum commune	13.33	4.35	6.06	10.71	-	6.90	0.99
Polytrichum "little"	-	-	-	-	10.00	6.90	-

* See page 53

TABLE I continued *

Species	Soil Type# G	WG	C	AG	S	R	DG
Polytrichum strictum	-	-	1.52	25.00	70.00	44.83	81.19
"Protococcus"	9.17	10.70	4.55	-	-	-	-
? Ptilidium	2.50	-	1.52	-	-	6.90	-
Rhyncostegium serrulatum	-	-	1.52	-	-	10.34	5.94
Sphagnum "big" #	-	-	-	12.50	33.33	100.00	95.83
Sphagnum "compact" #	-	-	-	-	-	33.33	70.83
Sphagnum plumosum	-	-	1.52	7.14	40.00	89.66	98.02
Sphagnum spp.	-	-	-	7.14	30.00	79.31	98.02
Tetraphis pellucida	-	2.17	-	-	20.00	6.90	1.98
? Tortella	0.83	2.17	1.52	3.57	20.00	20.69	5.94
"twisted orange stalk"	-	-	-	-	10.00	-	-
LICHENS							
"chalky thallus"	-	-	-	-	-	3.45	-
Cladonia coccifera	-	-	-	-	-	-	0.99
Cladonia cristatella	28.33	23.91	12.12	-	20.00	24.14	6.93
Cladonia pyxidata-group	40.83	30.43	22.73	7.14	30.00	37.93	16.83
Cladonia mitis	11.67	4.35	1.52	-	-	-	0.99
Cladonia rangiferina	29.17	8.70	9.09	-	-	6.90	1.98

* See page 53

TABLE I continued*

SPECIES SEEN, BUT NOT FOUND IN QUADRATS

Cirsium hillii

Poa pratensis

S piranthes lacera

* Frequency is based upon presence in randomly located 1 X 1 meter quadrats.

These two Sphagnum "species" are the components of "Sphagnum spp.," two lines down.

Explanation of soil type symbols is given in Appendix C-3.

The symbols in parentheses indicate: (h), herb size class (under 1 foot tall); (s), shrub size class (1 ft-6 ft tall); (t) tree size class (over 6 ft tall).

TABLE II

SUMMARY OF PER CENT COVER ACROSS THE GRADIENT (VASCULAR SPECIES)*

Species		Soil Type#						
		G	WG	C	AG	S	R	DG
Acer rubrum		-	-	T	-	-	-	-
Amelanchier humilis	(s)	-	0.01	0.03	-	-	0.02	-
	(h)	T	-	T	0.01	-	-	-
Amelanchier "large toothed"	(s)	-	-	-	0.01	-	-	-
Amelanchier oblongifolia	(t)	-	0.11	0.05	-	-	-	-
	(s)	0.06	0.15	0.02	0.04	-	0.04	-
	(h)	0.01	0.03	0.03	0.04	0.01	-	-
Amelanchier sanguinea	(t)	-	-	-	0.07	-	-	-
	(s)	-	-	0.01	0.01	0.12	0.01	-
	(h)	-	-	0.01	0.03	0.10	0.01	-
Anemone quinquefolia		0.09	0,05	0.02	-	-	-	-
Antennaria neodioica		0.04	-	-	-	-	-	-
Apocynum androsaemifolium		0.02	0.01	-	-	-	-	-
Arctostaphyles uva-ursi		0.21	0.10	-	-	-	-	-
Aster "hairy ovate"		0.03	0.02	0.02	0.01	-	-	-
Aster laevis		0.03	0.03	0.03	-	-	-	-
Aster "lanceolate"		T	-	T	-	-	-	-
Aster macrophylla		-	T	0.01	-	-	-	-
Bromus ciliatus		0.06	-	-	-	-	-	-
Campanula rotundifolia		T	-	T	-	-	-	-
Carex "fine"		0.02	0.02	-	-	-	0.07	-
Carex pedunculata		0.45	0.05	0.07	0.25	-	0.02	-

* See page 59

TABLE II continued*

Species	Soil Type#						
	G	WG	C	AG	S	R	DG
Carex pensylvanica	9.75	8.85	4.55	3.48	1.02	0.02	-
Chamaedaphne calyculata	-	-	-	0.01	4.03	5.99	23.58
Commandra umbellata	-	-	T	0.05	-	-	-
"composite small narrow"	T	-	-	-	-	-	-
Comptonia peregrina	0.71	0.63	1.25	0.99	0.27	0.05	-
Coptis groenlandica	-	-	0.07	0.39	0.28	0.03	-
Cornus canadensis	-	0.03	0.31	1.63	0.57	0.18	-
Cypripedium acaule	-	-	0.02	0.09	-	-	-
Danthonia spicata	0.28	0.03	0.01	-	-	-	-
"dead bush"	-	-	T	0.01	-	-	-
Epigaea repens	0.04	0.09	0.99	0.95	0.04	0.16	-
Eriophorum spissum	-	-	-	T	-	0.20	0.66
Fragaria vesca	0.01	-	-	-	-	-	-
Gaultheria procumbens	0.52	1.78	3.23	3.99	2.42	1.93	0.01
"grass big hairy"	0.01	T	-	-	-	-	-
"grass smooth"	T	-	-	-	-	-	-
"grass smooth broad"	T	-	-	-	-	-	-
Hieracium venosum	0.04	-	0.03	-	-	-	-
Ilex verticillata (s)	-	-	0.08	0.06	0.05	0.20	0.05
(h)	-	-	0.01	0.05	0.02	0.02	-
Kalmia angustifolia	-	-	0.09	-	0.80	0.37	0.31
Kalmia polifolia	-	-	-	-	-	0.10	0.54
Krigia biflora	-	-	0.02	-	-	-	-

* see page 59

TABLE II continued*

Species		Soil Type#						
		G	WG	C	AG	S	R	DG
Krigia virginica		T	-	-	-	-	-	-
Larix laricina	(t)	-	-	-	-	8.00	5.03	1.58
	(s)	-	-	-	-	-	-	0.01
	(h)	-	-	T	-	-	T	T
Ledum groenlandicum		-	-	-	1.06	0.80	5.34	1.98
Liatris sp.		0.01	-	-	-	-	-	-
Lycopodium obscurum		-	-	0.04	0.06	0.02	-	-
Maianthemum canadense		0.12	0.17	1.24	1.04	0.88	0.03	-
Melampyrum lineare		0.09	0.08	0.25	0.35	0.16	T	-
Nemopanthus mucronata	(s)	-	-	-	0.03	0.20	0.37	0.03
	(h)	-	-	-	-	0.30	0.16	-
Oryzopsis asperifolia		0.30	0.05	0.08	0.31	-	-	-
Oryzopsis pungens		0.06	0.03	0.01	-	-	-	-
Panicum "basal inflor".		T	-	-	-	-	-	-
Panicum "broad leaved"		T	T	-	-	-	-	-
Panicum "narrow leaved"		T	-	-	-	-	-	-
Panicum spp.		T	T	-	-	-	-	-
Picea mariana	(t)	0.33	-	0.68	0.39	7.70	10.80	3.21
	(s)	-	-	-	-	1.20	0.11	0.21
Pinus banksiana	(t)	25.97	27.52	21.15	25.82	14.80	4.66	0.32
	(s)	0.03	-	T	-	-	0.17	0.06
	(h)	T	T	-	-	-	-	T

* See page 59

TABLE II continued*

Species		Soil Type #						
		G	WG	C	AG	S	R	DG
Pinus resinosa	(t)	0.01	-	-	-	-	0.21	0.02
	(s)	0.04	-	-	-	-	-	-
	(h)	-	-	T	-	-	-	-
Pinus strobus	(t)	-	-	-	-	-	1.38	0.10
	(s)	-	-	-	-	-	-	0.14
Polygonum sp.		-	T	-	-	-	-	-
Populus grandidentata	(t)	-	-	0.30	-	-	-	-
Populus tremuloides	(t)	-	0.57	-	0.71	3.50	0.34	-
	(s)	-	-	0.01	-	-	-	-
Prunus serotina	(t)	0.37	-	0.88	5.04	6.50	-	-
	(s)	0.19	0.23	0.42	0.33	-	-	-
	(h)	0.03	0.01	0.06	0.75	0.07	-	-
Prunus virginiana	(t)	-	-	-	0.21	-	-	-
	(s)	0.15	-	-	-	0.10	0.01	-
	(h)	T	-	-	-	-	-	-
Pteridium aquilinum		6.34	5.97	6.88	6.04	0.90	-	-
Quercus rubra	(s)	0.22	0.01	-	-	-	-	-
	(h)	0.01	-	-	-	-	-	-
Ribes "dull"	(s)	T	-	-	-	-	-	-
	(h)	T	-	-	-	-	-	-
Ribes "seedling"	(h)	T	-	-	-	-	-	-
Ribes "shiny"	(h)	-	-	T	T	-	-	-
Rubus canadensis		0.03	0.04	0.04	0.12	-	T	-
Rubus hispidus var. obovalis		T	0.09	0.92	1.59	0.19	0.14	-
Rubus idaeus	-	-	-	T	-	-	-	-

* See page 59

TABLE II continued*

Species	Soil Type#						
	G	WG	C	AG	S	R	DG
"snag unidentified"	-	-	-	-	-	0.03	-
Solidago "lanceolate long petiole"	0.03	0.03	-	-	-	-	-
Solidago "narrow"	T	-	-	-	-	-	-
Solidago rugosa	T	-	-	-	-	-	-
Solidago "sessile"	T	-	-	-	-	-	-
Solidago "sharp teeth"	T	-	-	-	-	-	-
Solidago "white bloom"	-	-	-	-	-	-	0.01
Trientalis borealis	0.01	0.04	0.20	0.44	0.29	0.27	-
Vaccinium angustifolium (typical)	1.67	2.08	3.78	4.36	2.61	4.09	1.20
Vaccinium angustifolium var. nigrum	2.86	5.02	4.25	5.39	2.99	4.48	0.89
Vaccinium myrtilloides	0.01	0.17	0.55	1.61	3.27	2.07	0.01
Vaccinium oxycoccus	-	-	-	-	-	0.08	1.65

* See page 59

TABLE II continued*

Species		Soil Type#						
		G	WG	C	AG	S	R	DG
Viburnum cassinoides	(s)	-	-	0.12	0.49	2.22	1.24	T
	(h)	-	-	-	0.03	0.03	-	-
Viola adunca		0.03	T	T	-	-	-	-
Viola "larger"		-	T	-	-	-	-	-

* Explanation of soil type symbols is given in Appendix C-3.

The symbols in parentheses indicate: (h) herb size class (under 1 foot tall); (s) shrub size class (1 ft. - 6 ft. tall); (t) tree size class (over 6 ft. tall).

Maianthemum canadense (False lily-of-the-valley), Oryzopsis asperifolia (Harsh-leaved mountain-rice), O. pungens (Sharp-pointed mountain-rice), Danthonia spicata (Poverty-grass, which is very lush in a few patches but which has a relatively low frequency), Anemone quinquefolia (Wood anemone), Aster laevis (Smooth aster), and Viola adunca (Hooked violet). Important mosses on the dry end are Dicranum undulatum[5/], Calliergonella schreberi, and Polytrichum commune; important lichens are Cladonia pyxidata-group[6/], ("cup" Cladonias), C. rangiferina, C. cristatella, and C. mitis.

On Wet Grayling Sand (WG) and Croswell Sand (C), the cover of Pinus banksiana remains about the same as on Grayling. Some of the other characteristic dry end species, however, begin to drop out here, notably Anemone quinquefolia, Aster laevis, Danthonia spicata, Oryzopsis pungens, Viola adunca, (nearly disappearing), Dicranum undulatum, Polytrichum commune, Cladonia cristatella, C. pyxidata-group, C. mitis, and C. rangiferina (the last two nearly disappearing). Comptonia peregrina, Gaultheria procumbens, Maianthemum canadense, Vaccinium angustifolium increase in importance on this soil type. Species important farther down the gradient, appearing for the first time in the samples here, are Coptis groenlandica (Goldthread Canker-root), Cornus canadensis (Bunchberry), Ilex verticillata (Black alder),

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5/ Bryophyte nomenclature follows Grout and Evans (1940).

6/ Lichen nomenclature follows Hale and Culberson (1956).

Rubus hispidus var. obovalis (Obovate bristly blackberry, which increases rapidly on Croswell), Viburnum cassinoides (Witherod) and Sphagnum spp. In addition certain species which are very rare on Grayling, such as Epigaea repens (Trailing arbutus, May-flower), Trientalis borealis (Star-flower) and Vaccinium myrtilloides (Sour-top-blueberry), become fairly common here, though not ubiquitous.

On Au Gres-Saugatuck Sand, most of the "dry end" species, which began to decrease in importance on Wet-Grayling-Croswell, drop out completely in the samples. Such are Anemone quinquefolia, Aster laevis, Danthonia spicata, Oryzopsis asperifolia, O. pungens, Polytrichum commune, and Cladonia rangiferina. While they do not drop out completely, Carex pensylvanica, Pteridium aquilinum, and Dicranum undulatum, decrease rapidly and become relatively unimportant. The cover of the characteristic "dry end" tree, Pinus banksiana, is fairly uniform over the first two segments of the gradient already described and on Au Gres, but it drops rapidly on Saugatuck and is largely replaced here by Larix laricina (Tamarack) and Picea mariana (Black spruce), giving Saugatuck a "bog margin" aspect. Some species, notably Melampyrum lineare and Prunus serotina, have about the same importance throughout the first three segments of the gradient on the "upland" side of the bog margin. Some characteristic species, which extend farther up the gradient and even into Grayling, reach a sharp maximum here, particularly Epigaea repens, Coptis groenlandica, Cornus canadensis, Gaultheria procumbens, Ilex verticillata, Maianthemum canadense, Rubus hispidus var. obovalis, Trientalis borealis, and Vaccinium myrtilloides. Vaccinium angustifolium, which is quite extensive on the drier soils of the gradient and a dominant in the shrub layer on Grayling, none-

theless reaches a maximum on Au Gres-Saugatuck. "Bog" species which appear for the first time on Au Gres-Saugatuck, mainly on the latter, are Chamaedaphne calyculata (Leatherleaf), Eriophorum spissum (Hare's-tail), Ledum groenlandicum (Labrador tea), Nemopanthus mucronata (Mountain-holly), and Polytrichum strictum (large haircap moss), besides the two trees already mentioned, Larix laricina and Picea mariana.

Roscommon soil (R), together with Saugatuck, is coincident with the hingeline of the bog. The transitions between the three non-organic or "dry" segments of the gradient, elaborated above, are gradual and almost imperceptable. Here, however, there is an abrupt change in the character of the vegetation, and in fact the quadrats classified as Roscommon contain two quite different associations. Some of them have characteristic "bog margin" vegetation, with a dense overstory of Larix laricina and Picea mariana and some Pinus banksiana. Others appear to be in the bog proper, except that the organic soil layer is not deep enough to be classified as a peat (see Appendix B), and they have a somewhat richer flora than does the peat itself. Upland species which "stick it out" on Roscommon, though their per cents cover drop to a fraction of what they are on Au Gres-Saugatuck, are Amelanchier spp. (Shadbush), Melampyrum lineare, and even Carex pensylvanica and Comptonia peregrina. Pinus banksiana and Vaccinium angustifolium are present here, and sporadically even on the peat itself. Characteristic Au Gres-Saugatuck species which begin to drop out here are Cornus canadensis, Epigaea repens, Gaultheria procumbens, Maianthemum canadense, Trientalis borealis, Vaccinium myrtilloides, the mosses Brachythecium salebrosum and Calliergonella schreberi. Other species seem to reach their maxima here: Coptis groenlandica,

Ilex verticillata, Ledum groenlandicum, Nemopanthus mucronata, and the mosses Tetraphis pellucida and ? Tortella sp. All of the common bog species are present on Roscommon also, though some in lesser quantities than in the bog proper. In general, this segment of the gradient seems to be dominated either by an overstory of Picea and Larix, with a discontinuous Sphagnum mat underneath, or else by an almost treeless, dense shrubbly vegetation dominated by Chamaedaphne and to a lesser extent Ledum, below which is a nearly continuous Sphagnum mat. The latter type has a distinct "boggy" aspect.

Dawson and Greenwood Peat (DG) are similar to the "shrubby" phase of Roscommon in their vegetation, except that there is less admixture of upland and bog-margin species and the Sphagnum mat is essentially unbroken. Chamaedaphne calyculata is the undisputed dominant here, forming a nearly continuous cover above the Sphagnum mat, making the bog look superficially, from a distance, like a broad green pasture with scattered stunted Picea, Larix, and Pinus (Figure 2b, p. 24). The more open places on the mat are occupied by Eriophorum spissum, Kalmia polifolia (Bog-laurel), Ledum groenlandicum, and Vaccinium angustifolium, the last two particularly on the shallower peats adjacent to the bog margin. Vaccinium oxycoccus, the Small cranberry, thrives on the abrupt and high hummocks of the Sphagnum mat where Chamaedaphne is present, but not too dense. Unimportant constituents are several species which reach their peaks on the upland and bog margin, notably Gaultheria procumbens, Ilex verticillata (occuring here only near larger trees), Nemopanthus mucronata (near trees only), stunted Pinus banksiana, and the mosses Brachythecium salebrosum, Calliergonella schreberi, and Dicranum undullatum. Polytrichum strictum reaches a maximum here, and is

a codominant with Sphagnum on the highest hummocks. Perhaps because of the great profusion of dead Chamaedaphne branches here, the upland lichens become somewhat more important on Roscommon and Dawson-Greenwood than they were on Au Gres-Saugatuck. The Chamaedaphne branches seem to serve as a suitable substrate particularly for Cladonia cristatella and Cladonia pyxidata-group.

Looking at the cover of the various layers or synusia in the vegetation (Table III, p. 65-66), lichen cover appears to have a peak on Grayling and another on Roscommon, with the lowest cover on the Croswell and Au Gres soil types. The mosses have a slight peak on Grayling, drop on Wet Grayling and Croswell, and understandably begin to rise again on the wetter soil types, reaching a maximum on Dawson-Greenwood. Herb cover falls steadily from the dry to the wet end of the gradient as shrub cover steadily rises, the former perhaps being at least partially due to the latter. The curve for tree cover rises gradually from Grayling to Roscommon, then drops precipitously on Dawson-Greenwood.

A general graphic picture of the vegetation and soil profile across the gradient is shown in Figure 6 (p. 67).

2. NON-LIVING VARIABLES.-From Table III and Figure 5, it is evident that on the whole, the soil profile becomes deeper from the "dry" to the "wet" end of the gradient. The study area just falls within the limits of the podzol region in Michigan (Veatch 1953), and the deepening of the profile is due to (1) the increase in podzolization from the dry to the wet end of the gradient (note the increased depth of the A_2 horizon in Figure 6 as one approaches the middle of the gradient), and (2) the

TABLE III

MEAN VALUES OF VARIOUS VARIABLES ON EACH SOIL TYPE*

Variables	Soil Type G	WG	C	AG	S	R	DG
SOIL PROFILE							
Thickness Ao_L, mm	13.6	14.1	13.3	14.1	13.2	12.3	12.2
Thickness Ao_m, mm	14.3	13.1	11.6	14.9	29.1	42.8	62.0
Thickness Ao_H, mm	28.7	35.2	37.2	57.1	60.0	139.3	579.2
Thickness A_1, mm	26.1	34.9	30.5	37.3	36.0	27.0	-
Thickness A_2, mm	9.7	27.0	62.4	86.9	183.8	216.7	-
Thickness B_1, mm	35.4	38.5	32.9	72.5	14.5	103.8	-
Thickness B_2, mm	103.2	109.2	110.1	112.5	168.8	89.0	-
Thickness B, mm	138.6	147.7	143.0	185.0	183.3	192.8	-
Depth to Glei, mm	86.1	107.0	123.7	134.8	152.5	92.9	-
Percent of quadrats with Glei evident	15.0	50.0	83.3	96.4	100.0	100;0	-
COVER OF VEGETATION LAYERS							
Percent Lichen	0.69	0.38	0.10	0.01	0.15	0.69	0.17
Percent Moss	2.95	1.96	0.99	8.42	24.36	55.91	74.47
Percent Herb	18.17	17.20	19.58	21.35	7.71	3.38	2.29
Percent Shrub	5.82	8.66	11.18	15.34	18.25	24.76	29.39
Percent Tree	26.03	26.58	20.80	29.45	37.70	21.72	5.12
PERCENT OF FULL SUNLIGHT	12.6	16.7	22.5	33.4	9.33	76.25	84.5

* See page 66

TABLE III continued*

Variables	Soil Type						
	G	WG	C	AG	S	R	DG
SOIL pH	4.57	4.25	4.04	4.13	3.45	3.51	3.34
SOIL MOISTURE-WEIGHT							
Percent moisture in soil by weight	12.6	16.3	19.4	25.4	45.5	35.9	65.8
Gms. dry wgt./cc	1.16	.99	.95	.83	.42	.60	.14

* Explanation of soil type symbols is given in Appendix C-3.

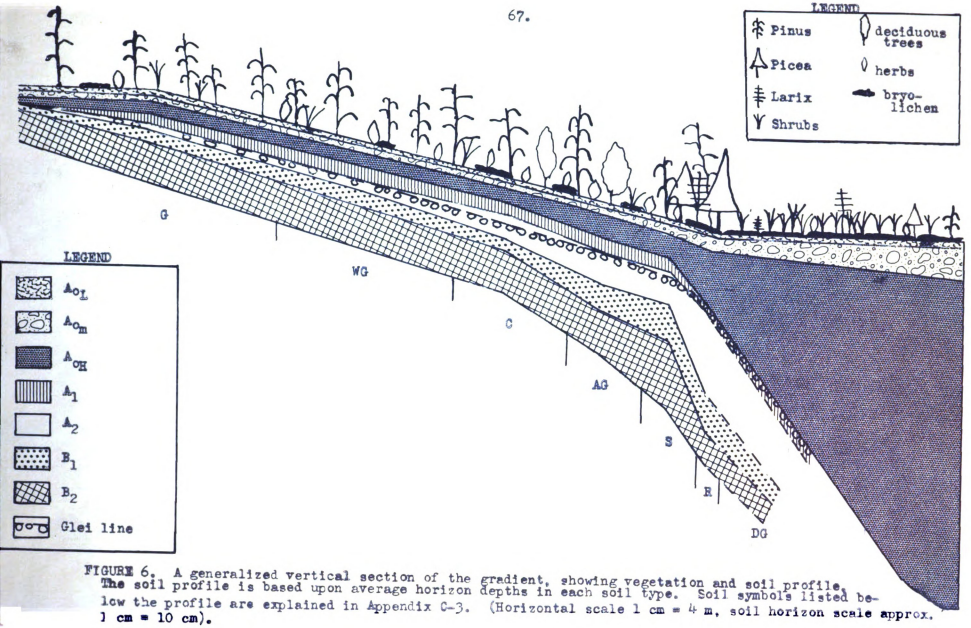


FIGURE 6. A generalized vertical section of the gradient, showing vegetation and soil profile. The soil profile is based upon average horizon depths in each soil type. Soil symbols listed below the profile are explained in Appendix C-3. (Horizontal scale 1 cm = 4 m, soil horizon scale approx. 1 cm = 10 cm).

increased accumulation of organic material (note the increase in the depths of the A_o horizons from the "dry" to the "wet" end of the gradient, Figure 6). The B_1 horizon, where the humus and sesqueoxides leached out of the A_2 horizons have been deposited, also tends to increase in thickness from the dry to the wet end, but then to decrease in thickness again, and if the A_2 layer were followed far enough into the organic soils it would be found to decrease in thickness and disappear. It is also darker in color, and there is generally a sharper distinction between the B_1 and B_2 horizons near the wet end. The B_1 shows an increasing tendency towards cemetation from Grayling to Saugatuck (the latter is in fact distinguished from Au Gres by this character), and then cementation tends again to diminish as the bog margin gives way to the bog. The A_2 also varies in color, being a light grayish brown on the Grayling, and becomming almost pure white in some of the Saugatuck and Roscommon quadrats, indicating that podzolization may be more thorough on the latter soil types.

Per cent of total sunlight at breast height is greatest in the bog proper, with a secondary peak on Au Gres. The lowest light intensity seems to be on the Saugatuck, where tree cover is greatest, and in general light intensity is inversely proportional to tree cover. Though even the dry end of the gradient is fairly acid (mean pH of Grayling, 4.57), acidity increases steadily from the dry to the wet end, until in the bog mean pH is only slightly above 3.0. Soil moisture increases about fourfold from Grayling through Saugatuck, as might be expected, and is highest on Dawson-Greenwood. However, there is a slight drop in soil moisture on Roscommon. Soil dry weight is essentially a

reciprocal function of organic matter, which also is reflected in the soil moisture. Volume weights drop from relatively high values on Grayling to low values on Saugatuck. They increase again on Roscommon before finally reaching their lowest value on Dawson-Greenwood. Possible reasons for the "discontinuity" on Roscommon will be brought forth in the discussion.

The peat contains at least two discontinuous lenses of sand, with charcoal below the sand. These are probably the result of fires, which burned over the peat surface, followed by deposition of sand eroded from the denuded upland. The top lens of sand may be connected with the fire of about 60 years ago, following which the present individuals of Pinus became established. If so, the rate of peat accumulation has been about 0.1-0.2 inches per year since the turn of the century, which agrees with the generally accepted rate of accumulation (Dachnowski 1921).

B - COLE COEFFICIENTS AND ORDINATIONS

The Cole coefficients are presented in matrix form for each soil type in Table IV (p.70-73). Ordination constellation diagrams are shown in Figures 7-14 (p.74-81).

Certain generalizations can be made concerning the Cole association coefficients, and the ordination figures which are based upon them. These are listed in the ensuing paragraphs.

1. Positive associations are far more prevalent than negative associations.

TABLE IV-A - COLE COEFFICIENTS, GRAYLING#

	Vyp	Vang	Vig	Cal	Gau	Mel	Mai	Anem	Oras	Dic	Pter	Prun	Opun	Car	Cran	Com	Dan	Cris	Cup
Vyp	1.000**	.595**	.595**	.501*	.484**	.477*	.459	.295	.266	.211	.073	.027	.054	.157	.205	.309*	.336**	.436**
Vang		1.000**	.643**	.670**	.610**	.724**	.821*	.814*	.353	.363*	.388	.022	.196	.133	.152	.206*	.380**	.441**
Vig			.479**	.423*	.602**	.516**	.479*	.565*	.245	.275**	.405	.167	.010	.259*	.083	.275	.459**	.389**
Cal				.231*	.242*	.301*	.306*	.130	.403**	.239	.127	.250	.010	.167	.250	.348	.189	.265*
Gau					.231*	.283**	.254	.103	.036	.532**	.153	.692**	.103	.012	.077	.599*	.252	.276
Mel						.185	.166	.245	.104	.005	.398**	.045	.167	.242	.211	.170	.337	.412**
Mai							.382**	.297**	.249	.327	.230*	.032	.032	.355	.191	.327	.686**	.469**
Anem								.348**	.179	.239	.226*	.125	.167	.028	.250	.348	.865**	.216
Oras									.143	.083	.234*	.134	.130	.130	.134	.093	.718**	.386
Dic										.027	.137	.015	.104	.403**	.547**	.114	.080	.017
Pter											.073	.432**	.158	.144	.189	.436**	.036	.055
Prun												.152	.206	.683*	.143	.503	.537	.552*
Opun													.083	.143	.100	.134	.189	.130
Car														.074	.000	.203	.009	.069
Cran															.167	.130	.438**	.517**
Com																.072	.060	.043
Dan																	.057	.471**
Cris																		.671**
Cup																		

#/ - Symbols are explained in Appendix C-1
Underlined coefficients are negative.
Species counted as absent below their median cover value are circled.
* - Significant at 5 % level
** - Significant at 1 % level

70.

TABLE 4-B - COLE COEFFICIENT, WET GRAYLING-CROSWELL#

	Mai	Rho	Tri	Epig	Vam	Gau	Com	Mel	(Vang)	(Vyp)	(Vig)	Pter	Cal	Prun	Bra	(Car)	Cup	Dic
Mai		1.000**	.919**	.903**	.729**	.457**	.420**	.304*	.246*	.188	.107	.040	.011	.021	.074	.110	.122	.217
Rho			.631**	.613**	.693**	1.000**	.535**	.427**	.438*	.323*	.166	.171	.097	.043	.343	.217	.626*	.444
Tri				.508**	.444**	1.000**	.360**	.348*	.419*	.183	.282	.091	.067	.212*	.661*	.129	.485	.138
Epig					.473**	.831*	.296*	.502**	.004	.160	.225	.311**	.020	.262	.389	.104	.691*	.311
Vam						.834**	.407**	.342*	.263	.286*	.170	.255*	.222	.088	.434	.239	.714*	.202
Gau							.467*	.543**	.465**	.440*	.328*	.183	.048	.665*	.005	.255	.190	.158
Com								.299**	.585**	.375**	.282*	.153	.083	.138	.055	.067	.488*	.590**
Mel									.289*	.185	.077	.163	.111	.316*	.434**	.086	.448*	.209
(Vang)										.793**	.627**	.341	.222	.100	.321	.282*	.193	.036
(Vyp)											.103	.074	.125	.282	.125	.222*	.195	.372
(Vig)												.240	.260	.172	.119	.047	.034	.089
Pter													.074	.116	.102	.102	.318	.006
Cal														.031	.491**	.183	.035	.569**
Prun															.171	.337	.014	.048
Bra																.119	.019	.171
(Car)																	.099	.006
Cup																		.170
Dic																		

#/- Symbols are explained in Appendix C-1. Underlined coefficients are negative. Species counted as absent below their median cover value are circled.

* - Significant at 5 % level

** - Significant at 1 % level

71.

TABLE IV-C - COLE COEFFICIENTS, AU GRES-SAUGATUCK#

	Cop	Corn	Vam	Rho	Cal	Tri	Epig	(Vig)	(Vang)	Prun	Mai	Gau	Car	Mel	(Vyp)	Com	Pter
Cop		1.000**	.553*	.493*	.333	.309	.276	.276	.276	.156	.050	.035	.050	.119	.240	.255	.525*
Corn			.606**	.404	.294	.321	.255	.042	.224	.131	.162	.080	.022	.156	.329	.211	.441*
Vam				.397*	.059	.162	.211	.361	.042	.218	.208	.042	.095	.106	.131	.042	.435*
Rho					.467*	.208	.404	.056	.056	.367	.309	.156	.367	.119	.156	.035	.079
Cal						.250	.176	.143	.143	.333	.000	.176	.375	.067	.111	.059	.125
Tri							.208	.321	.013	.208	.406	.162	.224	.367	.169	.548**	.109
Epig								.095	.042	.131	.162	.343	.095	.035	.007	.080	.162
(Vig)									1.000**	.321	.013	.095	.321	.095	.050	.521*	.013
(Vang)										.186	.260	.224	.321	.276	1.000**	.361	.260
Prun											.169	.007	.604**	.113	.050	.503**	.076
Mai												.095	.109	.309	.169	.441*	.136
Gau													.162	.035	.007	.211	.162
Car														.367	.340	.208	.460*
Mel															.113	.255	.683**
(Vyp)																.106	.340
Com																	.095
Pter																	

#/- Symbols are explained in Appendix C-1. Underlined coefficients are negative. Species counted as absent below their median cover value are circled.

* - Significant at 5 % level.

** - Significant at 1 % level.

72.

TABLE IV-D - COLE COEFFICIENTS, ROSCOMMON#

	Vig	Vang	Gau	Cal	Spha	Vyp	(Cham)	Led
Vig		.828**	.628*	.265	.163	.094	.094	.142
Vang			.396**	.044	.142	.628*	.245	.024
Gau				.033	.094	.195	.195	.245
Cal					.108	.310	.365	.108
Spha						.265	.070	.024
Vyp							.799**	.245
(Cham)								.442
Led								

TABLE IV-E - COLE COEFFICIENTS, DAWSON-GREENWOOD#

	Vyp	Vang	Led	Erio	Kal	(Spha)	Voxy	(Cham)
Vyp		1.000**	.257	.223	.025	.190	.335	.612**
Vang			.429**	.328*	.046	.192	.256	.701**
Led				.176	.165	.183	.219	.647**
Erio					.110	.176	.123	.287**
Kal						.291	.072	.157
(Spha)							.248	.072
Voxy								.211
(Cham)								

#/- Symbols are explained in Appendix C-1. Underlined coefficients are negative. Species counted as absent below their median cover value are circled.

* - Significant at 5 % level ** - Significant at 1 % level.

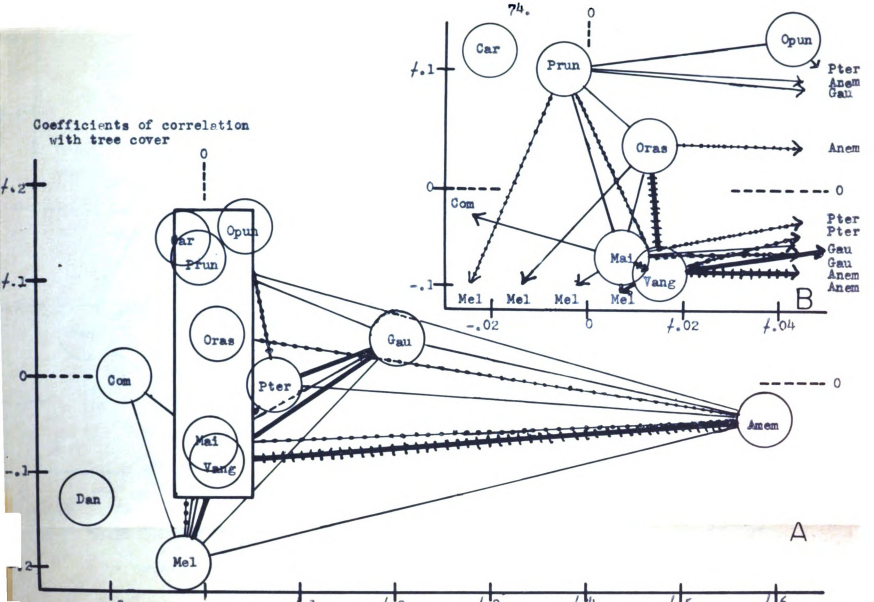


FIGURE 7. A. Ordination-constellation figure of frequent species on Grayling Sand, with lines representing positive Cole coefficients. Line width legend with Figure 10, p. 77. B. Inset showing blocked section of A, with x-axis enlarged 5 times. (Species abbreviations explained in Appendix C-1).

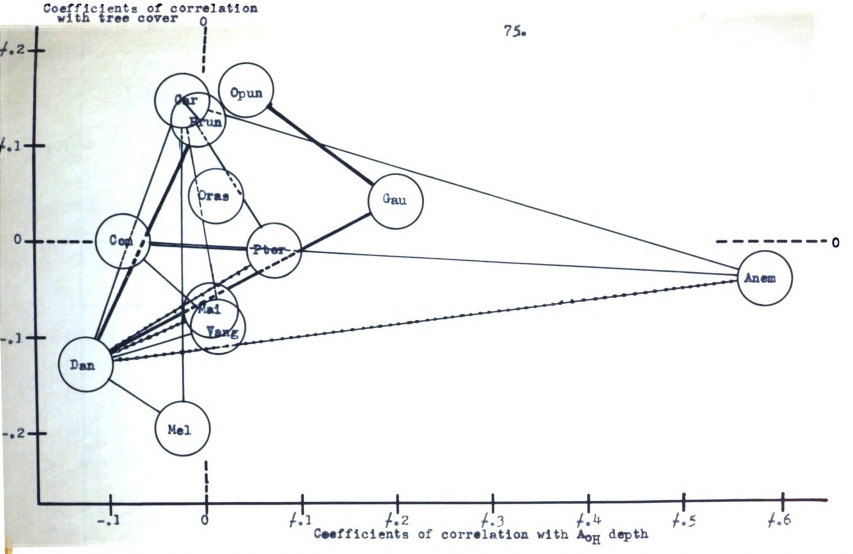


FIGURE 8. Ordination-constellation figure of frequent species on Grayling Sand, with lines representing negative Cole coefficients. Line width legend with Figure 10, p. 77. (Species abbreviations explained in Appendix C-1).

75.

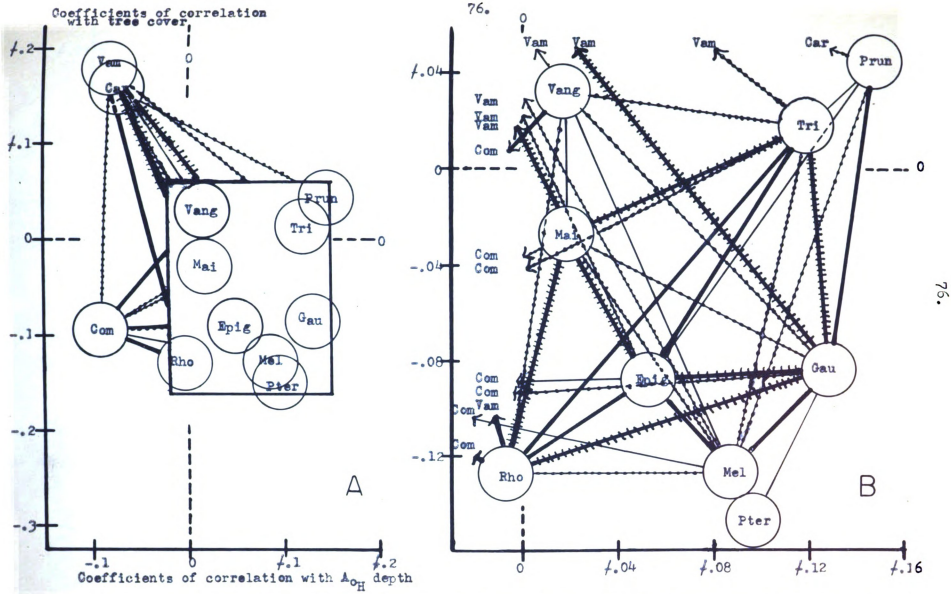
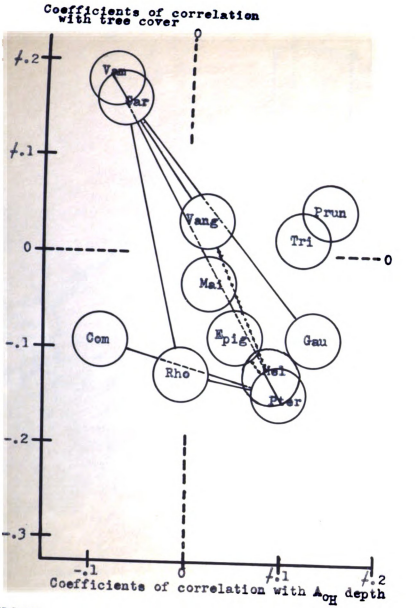


FIGURE 9. A. Ordination-constellation figure of frequent species on Wet Grayling-Croswell Sand, with lines representing positive Cole coefficients. Line width legend with Figure 10, p. 77. B. Insert showing blocked section of A, with x- and y-axes enlarged 2½ times. (Species abbreviations explained in Appendix C-1).



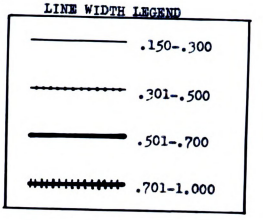


FIGURE 10. Ordination-constellation figure of frequent species on Wet Grayling-Croswell Sand, with lines representing negative Cole coefficients. (Species abbreviations explained in Appendix C-1).

77.

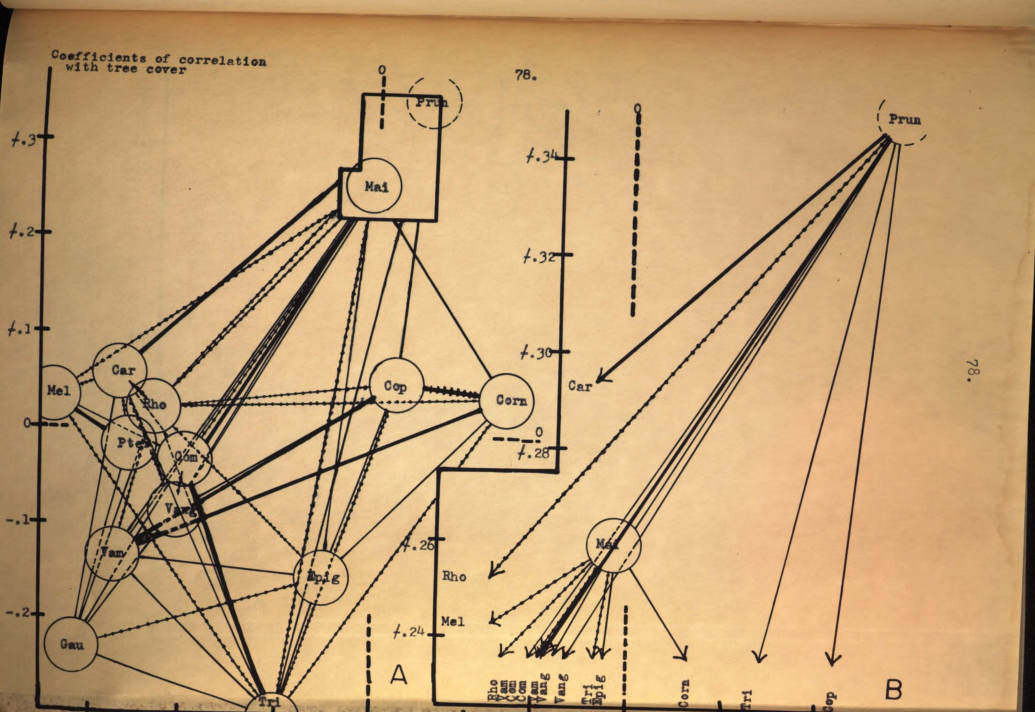


FIGURE 11. A, Ordination-constellation figure of frequent species on Au Gres-Saugatuck sand, with lines representing positive Cole coefficients. Line width legend with figure 10, p. 77. B. Insert showing blocked section of A, with x- and y-axes enlarged 5 times. (Species abbreviations are explained in Appendix C-1).

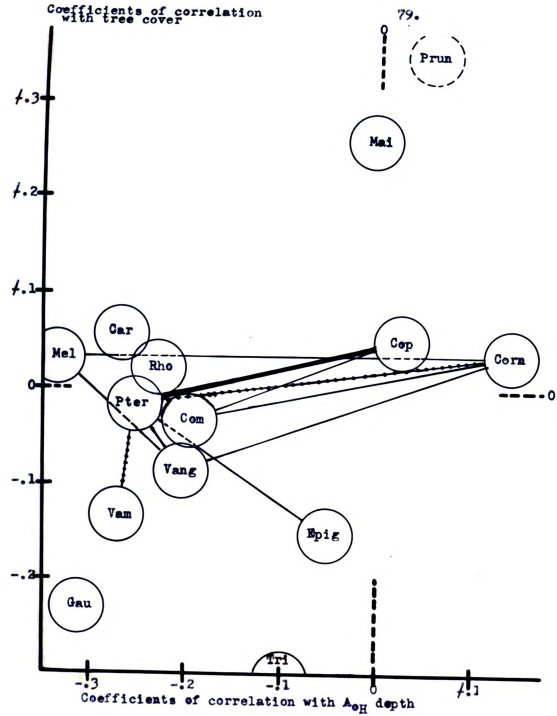


FIGURE 12. Ordination-constellation figure of frequent species on Au Gres Saugatuck Sand, with lines representing negative Cole coefficients. Line width legend with Figure 10, p. 77. (Species abbreviations are explained in Appendix C-1).

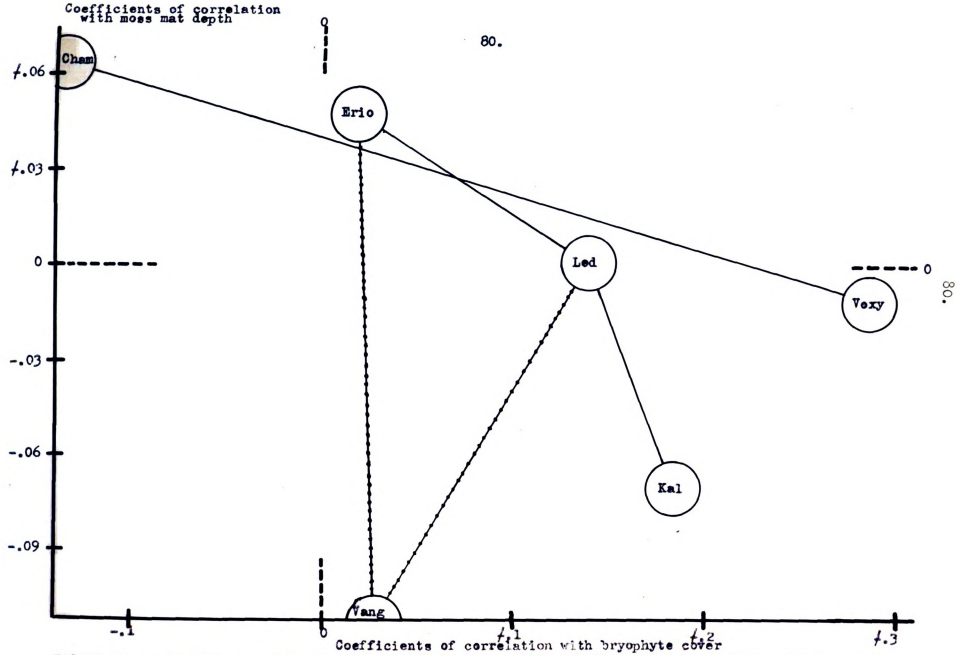


FIGURE 13. Ordination-constellation figure of frequent species on Dawson-Greenwood Peat, with lines representing positive Cole coefficients. Line width legend with Figure 10, p. 77. (Species abbreviations are explained in Appendix C-1).

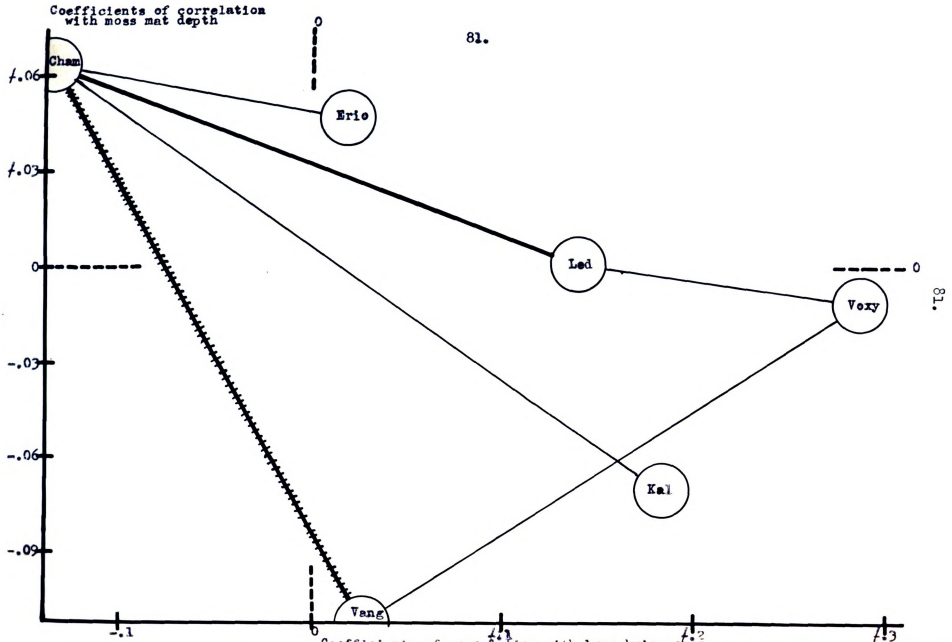


FIGURE 14. Ordination-constellation figure of frequent species on Dawson-Greenwood Peat, with lines representing negative Cole coefficients. Line width legend with Figure 10, p. 77. (Species abbreviations are explained in Appendix C-1).

2. There are certain species on each soil type with which most of the other species are negatively associated. In general, these are species having very high cover values in this soil segment.

3. If two species are highly positively associated on segments where both are relatively rare, they are usually less positively or even negatively associated where both are more abundant.

4. The large majority of vascular species exhibit a positive association with mosses and a negative association with terrestrial lichens, especially on the dry end of the gradient.

5. The degree of positive or negative association of pairs of species does not seem to be a function of their distance apart on the axes of the ordination figures.

6. On Grayling soil, there is a fair variation with respect to correlation of species with tree cover. On Wet Grayling-Croswell, however, there is a slight tendency towards negative correlation with tree cover, and on Au Gres-Saugatuck, there is a stronger tendency in this direction though the majority of these negative correlations are slight. Nevertheless, this general tendency of the bulk of the species is noteworthy (see also Table V, p. 83-84).

7. On Grayling, with four notable exceptions, all of the species exhibit near-neutral correlation with A_{oH} depth. This also seems to be true on wet grayling-Croswell, but on Au Gres-Saugatuck the tendency of most species to be negatively correlated with A_{oH} is striking, particularly for wide-ranging species which are not restricted or nearly restricted to the bog margin.

TABLE V

ZERO-ORDER CORRELATIONS OF SPECIES WITH ENVIRONMENTAL PARAMETERS #

I - Correlations with per cent tree cover (tre) and depth of the A_{O_H} soil layer (hum) on G, WGC, and AGS

Species	G		WGC		AGS	
	tre	hum	tre	hum	tre	hum
Anem	.037	.586**				
Car	.147	.021	.159	.072	.057	.266
Com	.001	.083	.093	.091	.032	.195
Cop					.052	.024
Corn					.037	.140
Dan	.127	.123				
Epig			.088	.051	.152	.052
Gau	.043	.201*	.084	.128	.231	.312
Mai	.070	.007	.027	.019	.260	.003
Mel	.194*	.022	.127	.087	.033	.335*
Opun	.159	.043				
Oras	.047	.013				
Prun	.126	.005	.045	.146	.510**	.055
Pter	.008	.074	.147	.096	.015	.253
Rho			.128	.006	.022	.228
Tri			.018	.118	.306	.099
Vam			.179	.083	.133	.270
Vang	.087	.015	.032	.017	.085	.204

* See page 84.

TABLE V continued #

Species	mat	moss
Chem	.064	.138
Erio	.047	.019
Kal	.070	.182
Led	.001	.139
Vang	.113	.027
Voxy	.011	.286**

The high positive correlation of Prun with tree cover on AGS (circled) may be due to the cover contributed by Prun trees themselves.

Blank spaces indicate that the category is not applicable.

Explanations of species, parameter, and soil type symbols are found in Appendices C-1, C-2, and C-3 respectively.

Underlined coefficients are negative.

* Significant at 5 % level.

** Significant at 1 % level.

8. Species tend to retain about the same relative positions with respect to each other on the ordination axes. This tendency is strongest between Grayling and Wet Grayling-Croswell, but is not very evident between Wet Grayling-Croswell and Au Gres-Saugatuck. Since different variables were used on the peat and since there are few species in common, there is no basis for comparison of peat and non-organic soils.

9. On peat, there is a general tendency for the vascular species to exhibit positive or neutral correlation with depth of the loose Sphagnum-Polytrichum mat.

10. Again on peat, most species exhibit fairly highly positive though usually non-significant[7/] correlations with bryophyte cover.

11. A total of 150 of the 513 Cole coefficients calculated, or 29 per cent of them, are significant at the 5 % level, and 84 of these (16 per cent of the total) are significant at the 1 % level. This indicates that interspecific association is extensive in the study area.

Possible reasons for these trends are suggested in the discussion.

7/ The term "non-significant", as used in this paper, means not significant at the 5 % level.

C - CORRELATION ANALYSES

In the assignment of species and variables to groups for these analyses, in which an attempt was made to place species together in such a way as to yield most useful information, the following groups resulted.[8/]

Group I. Gaultheria procumbens (Gau), Maianthemum canadense (Mai), Melampyrum lineare (Mel), Vaccinium angustifolium (Vang), along with depth of the litter or A_{o_L} layer (lit). This group was chosen for its mutually high Cole coefficients on the Grayling segment of the gradient, and because all of its members continued from the Grayling through the Saugatuck soil types in sufficient abundance to warrant analysis. It was analysed separately on the three "dry end" segments of the gradient; Grayling, Wet Grayling-Croswell, and Au Gres-Saugatuck.

Group II. Carex pensylvanica (Car), Comptonia peregrina (Com), Prunus serotina (Prun), and Pteridium aquilinum (Pter) were selected as the only species remaining after Group I had been designated, for which Cole coefficients had been calculated on all three of the "dry end" gradient segments. As with Group I, these species were analysed on each of the three segments separately. Depth of the A_{o_H} layer (hum) was included as an environmental parameter.

Group III. This is a group of primarily "dry end" species; Anemone quinquefolia (Anem), Danthonia spicata (Dan), Oryzopsis asperifolia (Oras), and O. pungens (Opun), which were run with tree cover (tre). They were abundant enough for analysis only on the "driest" segment of the gradient, Grayling.

8/ The symbols listed after each species or variable in parentheses are used in some of the tables and figures to indicate the species or variables named. They are explained in Appendices C-1 and C-2.

Group IV. On both Wet Grayling-Croswell and on Au Gres-Saugatuck (the second and third segments of the gradient-respectively starting from the "dry" end) four species which peak on the "upland" side of the bog margin, but which tend to be most abundant on the wetter non-organic soil types, were analysed with tree cover (tre). The species are Epigaea repens (Epig), Rubus hispidus var. obovalis (Rho), Trientalis borealis (Tri), and Vaccinium myrtilloides (Vam).

Group V. The two remaining vascular species occuring abundantly enough in the samples on the "dry" side of the bog margin to warrant calculation of Cole coefficients were analysed on the Au Gres-Saugatuck, the only segment on which these species were sufficiently frequent. They are Coptis groenlandica (Cop) and Cornus canadensis (Corn), which were analysed with the two variables tree cover (tre) and depth of the A_{O_H} soil layer (hum).

Group VI. The six vascular species which characterize the bog proper were analysed on the "bog" segment of the gradient (Dawson-Greenwood). Chamaedaphne calyculata (Cham), Eriophorum spissum (Erio), Kalmia polifolia (Kal), Ledum groenlandicum (Led), Vaccinium angustifolium (Vang), and V. oxycoccus (Voxy) were run through the correlation analysis. No environmental variables were included in the matrix, although zero-order correlation coefficients were calculated for each species with depth of mat (mat) and per cent moss cover (moss) in the ordination studies.

Thus, all of the common vascular species except trees on each of four segments of the gradient were run through one correlation matrix, and correlation coefficients were calculated for each species with several others. The Roscommon segment, it was felt, did not contain enough samples to warrant correlation analysis. Where possible, each species was analysed with the same group on more than one gradient segment.

The results of these studies are found in Tables VI-XI (p. 88-95) and Figures 15-28. The figures are included

TABLE VI #

GROUP I DATA

Soil Type: GRAYLING

WET GRAYLING-CROSWELL

AU GRES-SAUGATUCK

I - Cole Association Coefficients

	Gau	Mai	Mel	Vang
Gau	--	.283**	.231*	.670**
Mai		--	.185	.724**
Mel			--	.610**
Vang				--

	Gau	Mai	Mel	Vang
Gau	--	.457**	.543**	.465**
Mai		--	.304*	.246*
Mel			--	.289**
Vang				--

	Gau	Mai	Mel	Vang
Gau	--	.095	.035	.224
Mai		--	.309	.260
Mel			--	.<u>276</u>
Vang				--

II - Zero-Order Correlation Coefficients

	Gau	Mai	Mel	Vang	lit
Gau	--	.399*	.033	.200*	.199
Mai		--	.091	.103	.029
Mel			--	.201*	.<u>074</u>
Vang				--	.178
lit					--

	Gau	Mai	Mel	Vang	lit
Gau	--	.344**	.113	.201*	.<u>102</u>
Mai		--	.160	.128	.<u>069</u>
Mel			--	.<u>008</u>	.<u>204</u>*
Vang				--	.<u>030</u>
lit					--

	Gau	Mai	Mel	Vang	lit
Gau	--	.203	.025	.344*	.061
Mai		--	.<u>006</u>	.<u>026</u>	.033
Mel			--	.<u>152</u>	.<u>012</u>
Vang				--	.038
lit					--

- Underlined coefficients are negative.

Species symbols (capitalized, e.g. Gau, Mel) explained in Appendix C-1, Parameter symbols (not capitalized, e.g. lit) in Appendix C-2.

* - Significant at 5 % level

** - Significant at 1 % level.

TABLE VI SUBSTANCES

TABLE VI continued #

Soil Type: GRAYLING — WET GRAYLING-CROSWELL — AU GRES-SAUGATUCK

III - Highest Order Partial Correlation Coefficients

	Gau	Mai	Mel	Vang	lit	Gau	Mai	Mel	Vang	lit	Gau	Mai	Mel	Vang	lit
Gau	--	.393**	.019	.145	.176	--	.313**	.054	.169	.069	--	.229	.087	.364*	.058
Mai		--	.076	.017	.052		--	.127	.069	.010		--	.029	.107	.045
Mel			--	.211*	.109			--	.042	.193*			--	.174	.012
Vang				--	.164				--	.016				--	.016

IV - Standard regression Coefficients@

	Gau	Mai	Mel	Vang	lit	Gau	Mai	Mel	Vang	lit	Gau	Mai	Mel	Vang	lit
Gau	--	.405**	.020	.154	.191	--	.316**	.057	.180	.073	--	.245	.094	.368*	.064
Mai	.382**	--	.081	.018	.055	.311**	--	.132	.072	.011	.214	--	.030	.101	.046
Mel	.017	.071	--	.207*	.109	.052	.122	--	.043	.195*	.080	.029	--	.162	.013
Vang	.135	.019	.217*	--	.167	.160	.065	.041	--	.016	.360*	.113	.187	--	.019
lit	.163	.045	.112	.162	--	.065	.010	.191*	.016	--	.053	.043	.013	.015	--

V - Multiple Correlation Coefficients

Gau	Mai	Mel	Vang	lit	Gau	Mai	Mel	Vang	lit	Gau	Mai	Mel	Vang	lit
.460**	.410**	.242	.308*	.272	.389**	.371**	.259	.215	.220	.415	.231	.176	.398	.079

See page 88.

@ For the regression of each species on the others, read the columns down.

TABLE VII #

GROUP II DATA

Soil Type: GRAYLING | WET GRAYLING-CROSWELL | AU GRES-SAUGATUCK

I - Cole Association Coefficients

	Car	Com	Prun	Pter	Car	Com	Prun	Pter	Car	Com	Prun	Pter
Car	--	.000	.206	.158	--	.067	.337	.102	--	.208	.601	.460
Com		--	.143	.189		--	.138	.153		--	.503	.095
Prun			--	.073			--	.116			--	.076
Pter				--				--				--

II - Zero-Order Correlation Coefficients

	Car	Com	Prun	Pter	hum	Car	Com	Prun	Pter	hum	Car	Com	Prun	Pter	hum
Car	--	.122	.088	.093	.021	--	.101	.006	.155	.072	--	.133	.034	.256	.266
Com		--	.037	.164	.083		--	.176	.336**	.091		--	.049	.134	.195
Prun			--	.012	.005			--	.092	.146			--	.233	.055
Pter				--	.074				--	.096				--	.253
hum					--					--					--

see page 88.

TABLE VII continued #

Soil Type: GRAYLING | WET GRAYLING-CROSWELL | AU GRES-SAUGATUCK

III - Highest Order Partial Correlation Coefficients

	Car	Com	Prun	Pter	hum	Car	Com	Prun	Pter	hum	Car	Com	Prun	Pter	hum
Car	--	.112	.092	.072	.006	--	.046	.005	.125	.055	--	.130	.025	.224	.186
Com		--	.049	.150	.070		--	.231*	.344**	.094		--	.014	.207	.209
Prun			--	.012	.003			--	.153	.157			--	.219	.004
Pter				--	.061				--	.036				--	.228
hum					--					--					--

IV - Multiple Correlation Coefficients

Car	Com	Prun	Pter	hum	Car	Com	Prun	Pter	hum	Car	Com	Prun	Pter	hum
.169	.214	.101	.190	.103	.172	.407**	.282	.389**	.201	.353	.300	.235	.430	.383

See page 88.

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TABLE VIII #

GROUP III DATA

Soil Type: GRAYLING

I - Cole Association Coefficients

	Anem	Dan	Opun	Oras
Anem	--	.348	.125	.348**
Dan		--	.134	.093
Opun			--	.134
Oras				--

II - Zero-Order Correlation Coefficients

	Anem	Dan	Opun	Oras	tre
Anem	--	.099	.008	.368**	.037
Dan		--	.012	.014	.127
Opun			--	.064	.159
Oras				--	.047
tre					--

III - Highest Order Partial Correlation Coefficients

	Anem	Dan	Opun	Oras	tre
Anem	--	.022	.007	.371**	.059
Dan		--	.032	.026	.132
Opun			--	.056	.158
Oras				--	.058
tre					--

IV - Multiple Correlation Coefficients

Anem	Dan	Opun	Oras	tre
.373**	.134	.172	.377**	.216

See page 88.

TABLE IX #

GROUP IV DATA

Soil Type: WET GRAYLING-CROSWELL AU GRES-SAUGATUCK

I - Cole Association Coefficients

	Epig	Rho	Tri	Vam	Epig	Rho	Tri	Vam
Epig	--	.613**	.508**	.473**	--	.404	.208	.211
Rho		--	.631**	.693**		--	.208	.397*
Tri			--	.444**			--	.162
Vam				--				--

II - Zero-Order Correlation Coefficients

	Epig	Rho	Tri	Vam	tre	Epig	Rho	Tri	Vam	tre
Epig	--	.270**	.537**	.065	.088	--	.232	.196	.132	.151
Rho		--	.450**	.275**	.128		--	.108	.031	.022
Tri			--	.193*	.018			--	.095	.306
Vam				--	.179				--	.133
tre					--					--

III - Highest Order Partial Correlation Coefficients

	Epig	Rho	Tri	Vam	tre	Epig	Rho	Tri	Vam	tre
Epig	--	.028	.468**	.033	.102	--	.221	.147	.163	.132
Rho		--	.356**	.249**	.195*		--	.086	.002	.081
Tri			--	.072	.110			--	.084	.276
Vam				--	.189*				--	.127
tre					--					--

IV - Multiple Correlation Coefficients

Epig	Rho	Tri	Vam	tre	Epig	Rho	Tri	Vam	tre
.547**	.519**	.634**	.356**	.283	.345	.253	.359	.220	.350

See page 88.

TABLE X #

GROUP V DATA

Soil Type: AU GRES-SAUGATUCK

I - Cole Association Coefficients

	Cop	Corn
Cop	--	1.000
Corn	--	--

II - Zero-Order Correlations

	Cop	Corn	tre	hum
Cop	--	.813**	.052	.024
Corn		--	.037	.140
tre			--	.115
hum				--

III - Highest-Order Partial Correlations

	Cop	Corn	tre	hum
Cop	--	.818**	.019	.152
Corn		--	.016	.205
tre			--	.117
hum				--

IV - Multiple Correlation Coefficients

Cop	Corn	tre	hum
.818**	.822**	.128	.237

See page 88.

TABLE XI #

GROUP VI DATA

Soil Type: DAWSON - GREENWOOD

I - Cole Association Coefficients

	Cham	Erio	Kal	Led	Vang	Voxy
Cham	--	.287**	.157	.647**	.701**	.211
Erio		--	.110	.176	.328*	.123
Kal			--	.165	.046	.072
Led				--	.429**	.219
Vang					--	.256
Voxy						--

II - Zero-Order Correlations

	Cham	Erio	Kal	Led	Vang	Voxy
Cham	--	.098	.010	.255**	.191	.043
Erio		--	.021	.000	.145	.029
Kal			--	.010	.010	.032
Led				--	.361**	.168
Vang					--	.183
Voxy						--

III - Highest Order Partial Correlations

	Cham	Erio	Kal	Led	Vang	Voxy
Cham	--	.086	.011	.208*	.097	.015
Erio		--	.022	.073	.143	.011
Kal			--	.005	.007	.030
Led				--	.315**	.112
Vang					--	.131
Voxy						--

IV - Multiple Correlations

Cham	Erio	Kal	Led	Vang	Voxy
.289*	.178	.041	.428**	.416**	.216

See page 88

with the discussions of the groups to which they pertain, in order to facilitate reference. The general tendencies which were observed throughout the various groups are outlined below. Possible interpretations of them are presented in the discussion.

(1) There was a generally good agreement between Cole association coefficients, correlation coefficients, and regression coefficients for the same variable pairs on any particular gradient segment.

(2) The correlation coefficients tended generally to be lower in magnitude, either positively or negatively, than the corresponding Cole coefficients.

(3) Overall, the highest order partial correlation coefficients correspond closely to the zero-order correlation coefficients, but are slightly lower in magnitude.

(4) For the most part, if the correlation between two species is highly positive on a gradient segment where both are relatively infrequent, the correlation between them where both are abundant tends to be less highly positive or even negative.

(5) The partial regression coefficients, where calculated, show little difference from the corresponding highest order partial correlation coefficients.

(6) In some cases, there are notable discrepancies between Cole coefficients and correlation coefficients. The Cole coefficient may be highly positive and the correlation circumneutral or negative, or the Cole coefficient may be circumneutral and the correlation highly negative. The converses of these situations are sometimes true also (interchange "Cole coefficient" and "correlation" in the previous sentence).

(7) In several cases, the highest order partial correlation coefficient shows a notable difference, in either a positive or a

negative direction, from the zero-order correlation coefficient, though in no case is there a discrepancy of more than approximately 0.1.

(8) A high proportion of significant correlation coefficients (21 per cent or 15 of 70 significant at the 5 % level or better, 16 per cent or 11 of 70 significant at the 1 % level) indicates that association can be demonstrated in the study area on the basis of amounts of cover, as well as on the basis of presence or absence.

The proportion of significant correlation coefficients is somewhat lower than the proportion of significant Cole coefficients, however.

(9) The correlations of the species with the environmental parameters chosen (per cent tree cover, depth of humus, depth of litter, depth of moss mat, and per cent moss cover) do not show a proportion of significance notably higher than one would expect if the species were distributed at random with respect to these parameters. But in some cases general tendencies towards positive or negative correlation with these parameters are apparent (see the previous subsection on Cole coefficients and ordinations, and the subsequent discussion of these).

V

DISCUSSION

A - VEGETATION, SOILS, AND OTHER FEATURES OF THE AREA

The relative smallness of the total flora found in the study area, despite the variety of habitats found across the gradient, may be due to the characteristics of the soils. Grayling Sand, and the other non-organic soils of wetter sites which have developed from the same pleistocene outwash substrate, are singularly poor in nutrients. Also, the coarseness of the soil particles gives the soils an extremely high porosity, and consequently low moisture-holding capacity (Veatch 1953). The organic soils, including the Dawson-Greenwood Peat and Roscommon, contain an abundance of nutrients, but these are essentially unavailable to most plants because the acidity of peats makes base exchange unfavorable. Also, the nearly anaerobic conditions caused by saturation of such peats with water, especially in the spring, creates a problem of nutrient absorption (Oosting 1956). According to Veatch (1953), the Dawson-Greenwood Peat complex is composed of the most poorly-drained, and consequently the most acid and poorly oxygenated soils in the northern part of Michigan's lower peninsula.

The species-area curves (Figures 4, 5, p.44-45) strongly suggest that the peat is the most unsuitable habitat for plants in general along this gradient, more so even than Grayling sand. Its curve flattens out quite quickly and does not reach nearly as high a level as the curves for the other soil types. Going "down-gradient" from Grayling sand to the bog margin soils (Au Gres-Saugatuck) the species-area curves have a slightly higher slope on each of the three successive segments of the gradient, and also rise to higher levels or at least appear to be "headed"

for higher levels where there is a small number of quadrats (on Au Gres-Saugatuck). This suggests that, starting with the same parent material, the habitat becomes slightly more favorable where the water table is nearer the surface, and where consequently there is a deeper organic layer, more favorable habitat for necessary mycorrhizal associates, etc. Looking at it in another way, one could postulate that the number of different possible microhabitats is greater on the wetter than on the drier non-organic soils.

The species-area curve for Roscommon soil has the highest slope of any of the curves, possibly because of the mixture of vegetations from the "dry" and "wet" ends of the gradient, or the presence of microhabitats similar to those found on both the organic and inorganic soils.

Hutchinson (1957) among others, has criticized the use of the breaking point of the curves as a criterion for adequate sampling, but since in this paper we are dealing primarily with the most common species this is perhaps not critical.

The mean cover values of the different synusia (Table III, p.65-66) show that the cover of herbs is greatest on Au Gres, the cover of trees greatest on the Saugatuck soil type. Shrub cover is highest on the peat, but here tree cover is low, so the largest biomass per unit area probably occurs on the Saugatuck, and to a lesser extent on Au Gres soils. This fits well with the suggestion, based on the species-area curves, that Au Gres-Saugatuck is the most favorable plant habitat along the gradient. Though the curve for Roscommon has a steeper slope than any of the other curves, this soil type is probably not the most favorable habitat for plants in general. Here the species-area curve merely reflects the "tension zone" nature of this

segment of the gradient, where elements of the floras from the "dry" and "wet" sides of the bog margin come together. These floras are elsewhere quite distinct, and the three "inorganic" segments of the gradient have very few species in common with the peat.

Odum and Odum (1959) suggest that tension zones are areas of rapid change in both habitat and vegetation, the latter being a consequence of the former. Here, on the Roscommon soil, the habitat certainly changes rapidly, for the Saugatuck and Roscommon soils lie across the "hinge-line" separating the "solid" from the "floating" substrate. (The point where the floating mat begins was easily determined by simply jumping up and down on the substrate to test for "give").

The drop in lichen and moss cover from the "dry" to the "middle" segments of the gradient, and the rise of both again between the "middle" and "wet" portions of the gradient, deserves comment. The Grayling soil type contains many small patches which are essentially bare of either litter or vascular plants, thus providing the preferred microhabitats of both the terrestrial lichens and certain xerophytic mosses. These "bare" spots (not to be confused with "sparse" patches, a term which, as used in this paper, denotes areas where vegetation is essentially absent but which are usually amply covered with litter) rapidly disappear down-gradient making the WG-C and AG-S less capable of supporting lichens and xerophytic mosses. On the peat, however, the dead and decaying branches of Chamaedaphne, which are quite numerous, seem to be an excellent substrate for some of the lichens which occur on the dry end. These lichen are thus an exception to the general

rule that few species occur on both the "dry" and "wet" sides of the hingeline. The mosses on the peat, which begin to appear on AG-S, are not the same as the upland mosses, however. Rather, they are Sphagnum spp. and Polytrichum strictum, which form the nearly continuous moss mat. Nonetheless, mosses "as a whole" are probably not so much restricted by moisture conditions as they are by accumulations of deep leaf litter, as one might expect from their very low-statured growth form. Naturally, litter excludes most of the light. Thus the greater frequency of "litterless" patches on both the dry and wet than on the middle segments of the gradient, probably explains in part the bimodal distribution of the mosses.

Before leaving the mosses and lichens, it should be pointed out that the bimodal distribution of lichens found here is somewhat misleading. Only those lichens which appeared to be growing directly on the ground surface were recorded, while epiphytic lichens, including those on recently fallen loose branches, etc, were ignored. Since the lichens present on fallen twigs are hardly a permanent part of a quadrat's vegetation, it was felt that it would be meaningless to include them. The lichens recorded on Grayling were true "bare ground" lichens to a large extent, but those recorded on the peat were actually growing, for the most part, on branches covered by Sphagnum so that they only appeared to be growing on the surface of the mat. If it had been possible to record lichens on the tree trunks and on all loose litter,a different picture might have been obtained.

Just why "bare patches" should be present on Grayling, but not on the other non-organic soil types, is difficult to explain. This situation generally holds on most similar gradients in

Northern Lower Michigan, also perhaps because of the generally more favorable growth conditions on the "moister" soil types. More litter is produced on the latter than in more xeric sites, and the more continuous ground cover tends to check "drifting" of the litter and keep it evenly distributed.

The fluctuations in herb, shrub, and tree cover across the gradient are also noteworthy. Tree cover has a unimodal peak on AG-S, particularly on Saugatuck, but is much higher on the "dry" side of this peak than in the bog. Probably bog conditions restrict most trees, and the growth even of typically bog species such as Picea mariana and Larix laracina is very slow here. In fact Pinus banksiana seems to grow faster here, according to comparisons of ring counts with trunk diameter, than do either Picea or Larix, despite the fact that the former species is most characteristic of the driest upland soils. It probably requires a hard burn removing the loose Sphagnum, and possibly also a thin cover of sand washed in from the upland, before it can germinate on peat, however, for no Pinus seedlings were found on the present bog surface.

Shrub cover increases steadily from Grayling Sand to Peat. The high shrub cover on peat is at least partially a consequence of the low tree cover here, and partially also a result of the peculiar adaptation of Chamaedaphne to occupation of, and reproduction by rhizomes on, the Sphagnum mat. Buell and Cantlon (1950) showed that shrub cover was sometimes negatively associated with tree cover within a "homogeneous" vegetation, apparently because of the tendency for heavy tree cover to shade out the shrubs (though occasionally the reverse was true). Shrub cover probably does not drop on the bog margin where tree

cover is highest, because this margin lies north of the open bog so that light penetrates the edge here. The suitability of the bog margin soils for Chamaedaphne, whose cover is already quite high here, may contribute to this continued rise of shrub cover also.

If we extend Buell and Cantlon's findings to apply more generally, we can postulate that each layer (synusium) of the vegetation tends to inhibit the one below it (for which there is some evidence from the correlation coefficients obtained in the present study). Then it is not surprising that herb cover dips sharply on Saugatuck, and that it continues to drop on Roscommon and DG. Without the heavy tree cover which cuts down light on Saugatuck, it is not probable that herb cover would continue to rise here as well, which was in fact demonstrated in a cutover area by Cantlon and Gillis (1956). On Roscommon and on the peat, shrub cover is so dense that it probably has a similar inhibitory effect on the herbs below it. The near-absence of herbs on these organic soils cannot be attributed entirely to the shading effects of dense Chamaedaphne, however, for there are apparently few herbs which are well-adapted to the acid Dawson-Greenwood peat even in the open areas on the mat. Furthermore, the "characteristic" peat herbs and ground shrubs themselves (Eriophorum spissum, Vaccinium oxycoccus) are thrifty plants even where Chamaedaphne cover is extremely light.

The general tendency for soil moisture to increase, while soil dry weight decreases, from the "dry" to the "wet" end of the gradient, is readily understandable. The water table is nearer the surface and more organic materials are present proceeding from the "dry" to the "wet" end of the gradient.

The general trends of both volume weight and soil moisture show anomalies in the Roscommon segment (see Table III, p.65-66). Assuming that the discontinuities are not merely the result of sampling error, which is a distinct possibility because of the small number of quadrats in the Roscommon soil type, this is probably related to the slightly more compact organic layer in Roscommon than in either Saugatuck or Dawson. This in turn is probably due on the one hand to the low light intensity on Saugatuck which tends to prevent drying, and on the other hand to the nearness of the water table to the surface on Dawson, which keeps the organic material spongy. On Roscommon, conditions of periodic wetting and "baking" by the sun tend to compact the humus. The more compact material of course weighs more and holds less moisture.

Moisture per se is in all probability not the direct governing factor determining the distribution of all species across a moisture gradient (Whittaker 1956, Curtis and McIntosh 1951). The role of litter cover and a suitable substrate in moss and lichen distributions, for example, have been discussed. Moisture, or more specifically depth of the water table, is by and large the primary, or ultimate, cause of the macro-distribution patterns of most plants on this gradient. But the plants themselves are certainly as much influenced by the secondary, tertiary, or "n-ary" consequences of a deep or a shallow water table as they are by moisture itself, if not more so. Thus moisture influences pH, pH influences the nature of the soil biota, these in turn determine the rates of organic decomposition and mineral turnover, and in themselves influence pH. Furthermore, the soil biota operate directly upon vascular plants as herbivores and pathogens.

Depth of the water table, however, in a sense triggers major segments of the complex network which ultimately leads to direct reactions between each plant and its surroundings. Therefore following Whittaker (1956), it seems appropriate to call the gradient with which we are dealing a moisture gradient.

B - COLE COEFFICIENTS AND ORDINATIONS

Goodall (1952) points out that if any species is absent in very few quadrats, the results of the test are as invalid as if it were present in only a very few, because the value could fluctuate more than 100 % by chance. He suggests finding the mean cover value for such a species, and counting the species as present in only those quadrats where its cover exceeds the mean value. I have found it useful, however, to use the approximate median rather than the mean as a breaking point in the present study, so that about half of the quadrats fall into the "present" and half into the "absent" category.

The generalities concerning Cole coefficients and ordinations, which were listed in the results, are discussed below in the order of listing.

1. The prevalence of positive associations over negative associations throughout the gradient may be a result of a general tendency towards a mosaic of lushly-vegetated(hereafter called "lush") and sparsely-vegetated (hereafter referred to as "sparse") patches. This in turn may reflect the generally low cover associated with the litter cones and droughty conditions at the bases of

tree trunks. It may also reflect one or more cyclic patterns.

In the discussion of Group I, it is postulated that there may be a "Vaccinium-Carex-Pteridium-unvegetated" cycle, or something similar, on the non-organic soils, with various species associated with each stage in the cycle. Similarly, on the peat, there may be a "hummock leveling-colonization-Chamaedaphne" cycle as explained in the discussion of Group VI.

Superimposed upon these may be a general "disturbance-colonization-senescence" cycle, which would help to explain the prevalence of positive association and the mosaic of "lush" and "sparse"patches. E.g. if a disturbance such as a blowdown occurs, it provides a bare area suitable for colonization, and also overturns some of the minerals which have been leached downward. The plants which colonize such an area, however, and help to re-establish the leaching process store some of the minerals so that in time the nutrients may again become scarce in the upper horizons. In the blowdown hollows, there are conditions which appear to inhibit certain plants, particularly annuals such as Melampyrum, and deciduous herbs and ground shrubs such as Coptis. Part of this may be due to the accumulation of loose litter, which inhibits spring photosynthesis, and the accumulation of duff, which causes poor spring aeration, making it increasingly difficult for plants to send shoots through the deepening litter each spring.

Other possible factors include: release of specific inhibitory substances from the litter of certain species, buildup of general decomposition products from the accumulating humic material with resultant increasing acidity and oxygen tension, shifts in soil organism populations, etc. In any case the general pattern seems to suggest a decline in abundance and vigor of most species during

late stages of the cyclic sequence. Whether this "senescence" is only transitory, and whether some sort of equilibrium would in time be restored if blowdowns ceased to occur, it is difficult to say.

Though this hypothesis has not been tested, I have noted a clear tendency for younger blowdowns to have more vigorous vegetation and for older blowdowns, especially the hollows, to be nearly devoid of vegetation, in several forest types in the podzol region of Northern Lower Michigan. Blowdown and other cyclic disturbance patterns are not nearly so evident in Jack pine as they are in deciduous forest types, but they could be operating here nevertheless. Less drastic disturbances such as might be caused by deer pawing, deposition of feces by animals, burrowing by animals which turns over the minerals leached out of the soil, etc., might have similar though less dramatic effects. If such a pattern is operating and is obscure to the observer of the study area, it may become evident through statistical techniques.

On peat, the observed patterns, possibly of cyclic nature, may be dependent upon the deterioration of Sphagnum hummocks. The hummocks are disrupted by deer, hunters, frost action, and possibly other factors.

A way of testing the "cyclic pattern" hypothesis in future studies is being worked out.

2. The few species in each gradient segment which tend to be negatively associated with most other species generally have high cover values. It is possible, therefore, that these particular species are so well adapted to the segment in which they are most abundant that, where they are present, they tend to outcompete everything else. It is also possible that these

species occupy microsites to which most other species are poorly adapted.

3. If two species are highly positively associated on segments of the gradient where both are relatively uncommon, it may be because both are near their tolerance limits for the same factor or set of factors, so that they tend to occur together in microsites where these conditions are relatively favorable for both. Where both species are more abundant, and a larger proportion of the area is relatively favorable for their occurence, then differences in tolerance with respect to certain other factors, or unfavorable interaction between the two, may cause the positive association between them to be numerically lower.

4. The tendency of vascular species to be positively associated with mosses on the dry end may be due to the tendency of these vascular plants to grow best under moist conditions. Most of the mosses tend to occupy the moister spots on the dry end of the gradient, despite the fact that the species tend to be relatively xerophytic. Part of this association could also be due to the "disturbance-colonization-senescence" cycle suggested above, with mosses perhaps tending to colonize disturbed microsites first, followed by vascular plants.

The tendency of vascular plants to be negatively associated with lichens may be most easily explained by the moisture preferences of the former, and the drought tolerance of the latter. Most of the "dry" end mosses, though xerophytic <u>for mosses</u>, tend nonetheless to occupy what, on Grayling, are relatively moist microsites; hence the overall difference in the response of vascular plants to mosses and lichens.

5. The apparent absence of a tendency for species close together on the ordination axes to be more positively associated

than those which are far apart on these axes contradicts the findings of De Vries (1953) and De Vries et al. (1954) to some extent. However, there are at least three possible reasons for this.

Firstly, since species respond to many variables, species which happen to be close together on the two axes chosen for the ordinations might be widely separated on several axes of a multidimensional ordination figure, containing other possible variables. In the ordinations here presented, we are looking at only one possible facet of such multidimensional figures. Two species which appear close together on the axes used here might be likened to two widely-separated stars, which appear close together from our viewpoint. Conversely, two species which appear widely separated on one or both of the axes chosen for these ordinations might have similar requirements and tolerances for many other variables.

Secondly, species which are close together on these axes may have tolerances and requirements so similar that where one is present, it tends to outcompete or exclude the other. This might be particularly true for large and clonal species. Or two such species with similar tolerances might tend to occupy the same microsites during different portions of a temporal cycle. In any case, as explained by Volterra (1931), Gause (1934) and Hutchinson (1957) they could not both occupy exactly the same niche without one tending to become extinct in that region. They might nevertheless alternate on similar sites due to some factor(s) which exhibit(s) a temporal fluctuation (Hutchinson 1953).

Thirdly, De Vries may have found a tendency for species close together on his ordination figures to be positively associated because of the way in which he chose his data. He did not

work within a single relatively homogeneous area, but with a wide variety of different stands. Species were positively associated if they showed a tendency to occur in the same stands, and the stands were chosen purposely for their wide variation in the very factors which were used as axes. Thus purposeful selection of data, and increasing heterogeneity with respect to the variables used as axes in the ordination, will tend to bring positively associated species close together in the figures (Cole 1949, Greig-Smith 1957). Even on the present gradient, if soil moisture and depth of organic layer were used as axes and all segments of the gradient were lumped for the calculation of ordinations and Cole coefficients, we could predict a tendency for positively associated species to be close together. But such an effort, I feel, would be of less value than the drawing of ordination figures for each segment of the gradient separately, for the majority of the information which it would yield could be gleaned with far less effort from reconnaissance observations in the field.

6. The increasing (though slight) tendency for forest floor species to be negatively correlated with tree cover from the "dry" to the "wet" end of the gradient (exclusive of peat), might be explained in either or both of two ways.

Firstly, the tree canopy is more open on the "dry" end, and forest floor species may tend to occur where desiccation is relatively slow, since moisture may be fairly critical for many species here. But on the wet end, where available moisture is fairly adequate and tree cover more continuous, the majority of species perhaps "express their preferences" for microsites with higher light intensity.

Secondly, on Au Gres-Saugatuck, the deepest humus often occurs in those Saugatuck quadrats under the dense tree canopy. Since most species are negatively correlated with humus depth on this soil type, they may be "vicariously" negatively correlated with tree cover for this reason.

7. The tendency which most species show towards negative correlation with deep humus, such as that found on Au Gres-Saugatuck, may have to do with the relative age of the soils. Those microsites with the greatest humus accumulation are probably, in general, the oldest, and hence senescent according to our senescence-cycle hypothesis. Or humus may be directly or indirectly inhibitory to most "upland" ("non-bog") species for reasons which are not fully understood. It is also possible that the last proposal made in "5" above should be reversed. Thus species may be "vicariously" negatively correlated with humus depth because they are inhibited by the dense tree cover in quadrats which have deep humus.

Past fires, by removing accumulated organic material and opening the canopy, may have displaced many species down-gradient. The present vegetation of the study area is rather young successionally, and the humus of the Au Gres-Saugatuck soils is not yet "mature"; that is, it is extremely loosely-packed and poorly decomposed. This humus may not be suitable for colonization by "down gradient" species (the Roscommon is more decomposed and more firmly packed), and because of its small extent in time and space plants may not yet have evolved which "fit" into the hybrid niches (Anderson 1949) present here. Therefore, it would not be surprising if a lag occured between accumulation of organic matter and the establishment of

"down gradient" species. With further successional development and the establishment of a better equilibrium in the accumulation-decomposition balance, however, species of the lower segments should tend to extend upslope.

8. The trend shown by most species to keep the same relative positions in the ordination figures on Grayling and on Wet Grayling-Croswell is not surprising. It suggests that the requirements and tolerances of most species are similar on the two segments. It also gives one confidence in the general validity of the correlation coefficients, for if they were chance deviations there should be no demonstrable similarity of species positions between segments.

The relative positions of species may shift greatly between Wet Grayling-Croswell and Au Gres-Saugatuck because there is a sharper break in the character of the habitat between these types than between Grayling and Wet Grayling-Croswell. Predominantly "dry-end" species perhaps respond primarily to different factors on Wet Grayling-Croswell than they do on Au Gres-Saugatuck, because on the latter they are near their tolerance limits, and in time may have these limits exceeded through habitat change (see "7" above). The appearance of several "new" species on Au Gres-Saugatuck or at least the first abundant occurence of them as one proceeds from the dry to the wet end of the gradient, is another possible contributing factor in that these species may interact with "dry end" species. Also, due to the unique set of conditions on Au Gres-Saugatuck, there may be a survival of genotypes on this soil type different from those surviving on the "dry" segments of the gradient.

9. The vascular species on peat, which exhibit a generally somewhat positive correlation with loose mat depth, perhaps exhibit this tendency because of a tendency to occur on the better drained hummocks, where the mat is generally deepest.

10. On peat, most shrub and herb species seem to be inhibited by the cover of Picea and Larix, and by extremely dense Chamaedaphne. Both the trees and Chamaedaphne seem to inhibit or kill Sphagnum. This, then, may explain the tendency for all vascular shrubs and herbs except Chamaedaphne to be positively, or at least neutrally, correlated with bryophyte cover.

11. The proportion of significant Cole coefficients is far higher than could reasonably be expected if the species were distributed at random with respect to each other. Hence, it seems quite evident that interspecific association is common among the species in the study area.

C - CORRELATION ANALYSES - GENERAL

The general findings of the correlation analyses are discussed below, in the same order in which they were listed in the results.

1. The generally good agreement between the Cole, correlation, and regression coefficients for the same pair of species is according to expectation.

2. The tendency for the zero-order correlation coefficients to be somewhat closer to neutral than the Cole association coefficients is probably due in part to different deviations from

linearity of the two coefficients, and hence to a tendency for a Cole coefficient to have a higher numerical value than the corresponding correlation coefficient, though they may both represent the same degree of association. But perhaps also, there is a general tendency for the cover of one species to be low where the other has high cover, due to competition or unfavorable interaction between them. This would give a numerically lower correlation value to two species with a positive association coefficient, even though the microhabitat requirements of the two might be similar.

3. The general tendency for highest order partial correlation coefficients to be slightly lower in magnitude than the corresponding zero-order correlations is according to expectation (Clark 1958-59). Any positive or negative correlation between two species is certainly due in part to the degree of coincidence of environmental tolerance ranges of these species, and to their interaction with other species. As we partial out more and more of these other species, and the environmental variables which may influence the association, we begin to see more and more clearly the effects of the interaction between the two species themselves in a mathematically-created "uniform" environment (of course, this "uniform" environment could never be completely realized, when we are dealing with natural situations, because it is impossible to partial out all variables). Thus we usually get a lower correlation between two species when we "remove" some of the causal factors of this correlation. For a discussion of the converse of this situation see "7" below.

4. The reasons for the positive correlation between two

species often being lower in magnitude where both species are relatively abundant than where both are relatively scarce are probably similar to the reasons for a similar tendency found among the Cole coefficients. The reader is therefore referred back to "3" (p. 108) in Section V-B.

5. The similarities between the highest order partial correlation coefficients and the corresponding standard partial regression coefficients found in this study probably would not hold in all situations. One can visualize situations, e.g. certain host-obligate parasite relationships, where one species of a pair is relatively "dependent" upon the second, but where the second is "indifferent" to the first, or slightly inhibited by it. In these cases, the "dependent" species might have a very high positive regression upon the "independent" one, but the regression of the "independent" upon the "dependent" species might be substantially lower. It is interesting to note that no such discrepency occured among the regression coefficients calculated in the present study, despite the fact that a suspected host-parasite relationship (Melampyrum lineare, Vaccinium angustifolium) was among them (See Group I discussion). In any case, the highest order partial correlation coefficient should approximate the mean of the two reciprocal standard partial regression coefficients.

6. Possible general explanations for the discrepencies between the Cole and correlation coefficients for the same pairs of species are listed categorically below.

(a) Positive Cole coefficient, neutral correlation coefficient. If the scale of pattern of microhabitat to which two species respond were of about the same size as the quadrat used, two

species which had peaks of occurrence probability on small hummocks, or other microtopographic features, would probably be positively associated on the basis of presence alone. But suppose that there is a deleterious interaction between the species, for example species B might be an herb intolerant of the shade of shrub species A. Then, both species might be present on most hummocks and both absent in the hollows, resulting in the positive association coefficient. But on the hummocks with a high cover of the shrub, A, the herb, B, would have a low cover value, and on those hummocks where, by chance, A had very little cover to inhibit B, the cover of the latter might be high. So the correlation coefficient would have a near-neutral or even a negative value. This is illustrated in Figures 15-a and 15-b (p. 117).

Slightly different microhabitat requirements by two species could also contribute towards shifting the correlation coefficient towards neutrality, even though the two species involved have a positive association coefficient. Both species must be fairly restricted spatially, and the microhabitats where each reaches its optimum cover must be close together or adjacent with fairly large spaces in the sampling universe where both species have a low probability of occurrence. If, for example, species A tended to occupy the tops of high, fairly small hummocks, and B had a peak probability of occurrence on the slopes of these hummocks, then one might get a situation where "islands" of A were surrounded by "borders" of B. If one used quadrats of the proper size, most quadrats would then tend to fall so that both species were included, or neither. But those which fell with the top of a hummock in their centers would have a high cover of A and little of B; conversely, those which landed on the side of a

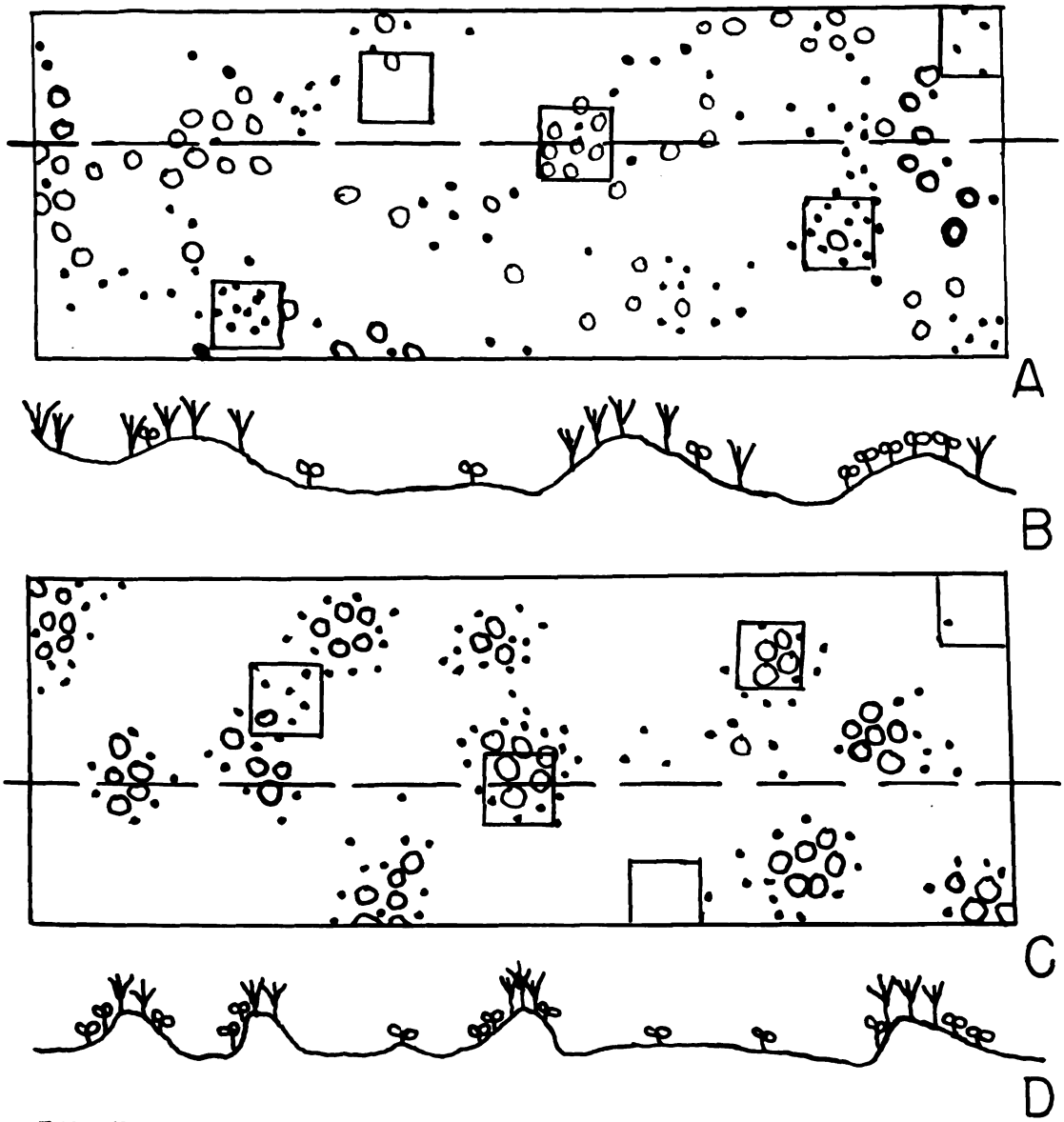


FIGURE 15. A. Diagram showing how it is theoretically possible to get a positive association coefficient and a neutral correlation coefficient, if the two species are restricted in microhabitats and are competing (see text). B. Vertical section of A. C. Diagram showing how it is theoretically possible to get a positive association coefficient and a neutral or negative correlation coefficient, if microhabitat requirements are slightly different but suitable microhabitats are contiguous (see text). D. Vertical section of C. Legend with Figure 16, p. 120.

hummock would have much B and little A. So the correlation, based upon cover and not presence alone, could be circumneutral or even negative. This is illustrated in Figures 15-c and 15-d (p. 117).

The possible explanations for correlation coefficients being smaller numerically than Cole coefficients (see "2" above, p. 113) may apply here also.

(b) Neutral Cole Coefficient, negative correlation coefficient. Two relatively wide-ranging species with broadly overlapping tolerance ranges, at least one of which tended to inhibit the other or which had a peak probability of occurrence and lush growth in somewhat different microhabitats, might exhibit this tendency.

The situations illustrated in Figures 15-a and 15-b (p. 117) might also produce this combination of coefficients if the scale of pattern were a great deal larger, or the quadrats a great deal smaller, so that more of the quadrats contained one species without the other, and so that the cover of one species would be extremely high and that of the other extremely low in most quadrats.

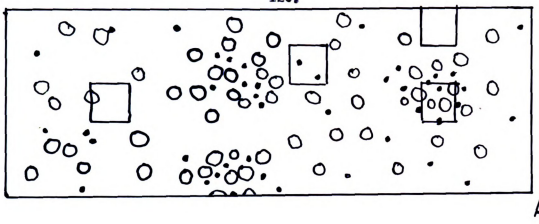
(c) Neutral Cole coefficient, positive correlation coefficient. This situation might occur if two species had fairly broad tolerance ranges, that is, if they had some probability of occurrence over all or most of an area. If a particular environmental variable were one of the major controlling factors in both of their distributions, and if both species also had a sharp peak of occurrence probability at about the same values of this variable, then associations might be near-neutral or only slightly positive. Over most of the area, the two species would each have about the same chance of occurrence, and they might occur separately in quadrats about as frequently as they did together. But many of the quadrats where both occurred together would have extremely high cover of both species because

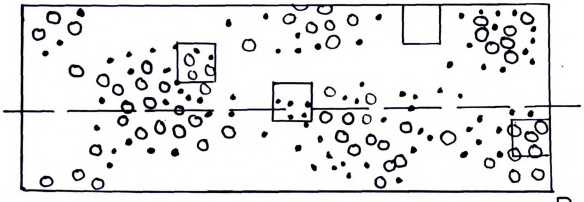
of the particularly favorable conditions for both at these points. Consequently, the correlations might be moderately to highly positive. This situation is illustrated diagramatically in Figure 16-a (p. 120) and in Figure 17 (p. 121).

This combination of coefficients might also be possible if the situations shown in Figure 15 (p. 117) were true, but if the scale of pattern were only slightly larger than the quadrat. Then, many quadrats might contain species A or species B alone, or neither species, but those which happened to include both A and B would, because of the high cover of both species at the junctures between patches or clones, usually include high cover of both.

(d) Negative Cole coefficient, neutral correlation coefficient. This combination might be possible if certain restricted portions of the sampled area had conditions particularly favorable to lush growth of most species (e.g. recent blowdowns with exposed concentrated mineral nutrients) so that even two negatively associated species might both have high cover in these spots. The particularly high cover of both species in these "cases" might offset, in the correlation coefficient, the differing habitat preference of the species or the unfavorable interaction between them in more stabilized microsites, which make them appear negatively associated on the basis of presence alone.

Another situation which might give these results is illustrated in Figures 16-b and 16-c (p. 120). This is similar to the situation shown in Figures 15-c and 15-d (p. 117), except that the scale of pattern is much larger relative to quadrat size. The species are almost completely separated environmentally but occur in usually adjacent microsites. Most quadrats might thus include individuals of only species A or species B, giving a negative association, but the lush cover of both, where quadrats happened







LEGEND, Figures 15 and 16

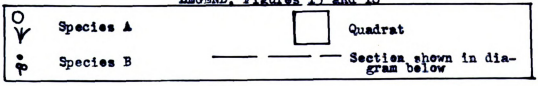


FIGURE 16. A. Diagram showing how it is theoretically possible to get a neutral association coefficient and a positive correlation coefficient, if both species have a broad tolerance range but peak in particularly favorable microsites (see text). B. Diagram showing how it is theoretically possible to get a negative association coefficient and a neutral correlation coefficient, if both species exhibit large-scale pattern but occupy similar or contiguous microsites (see text). C. Vertical section of B.

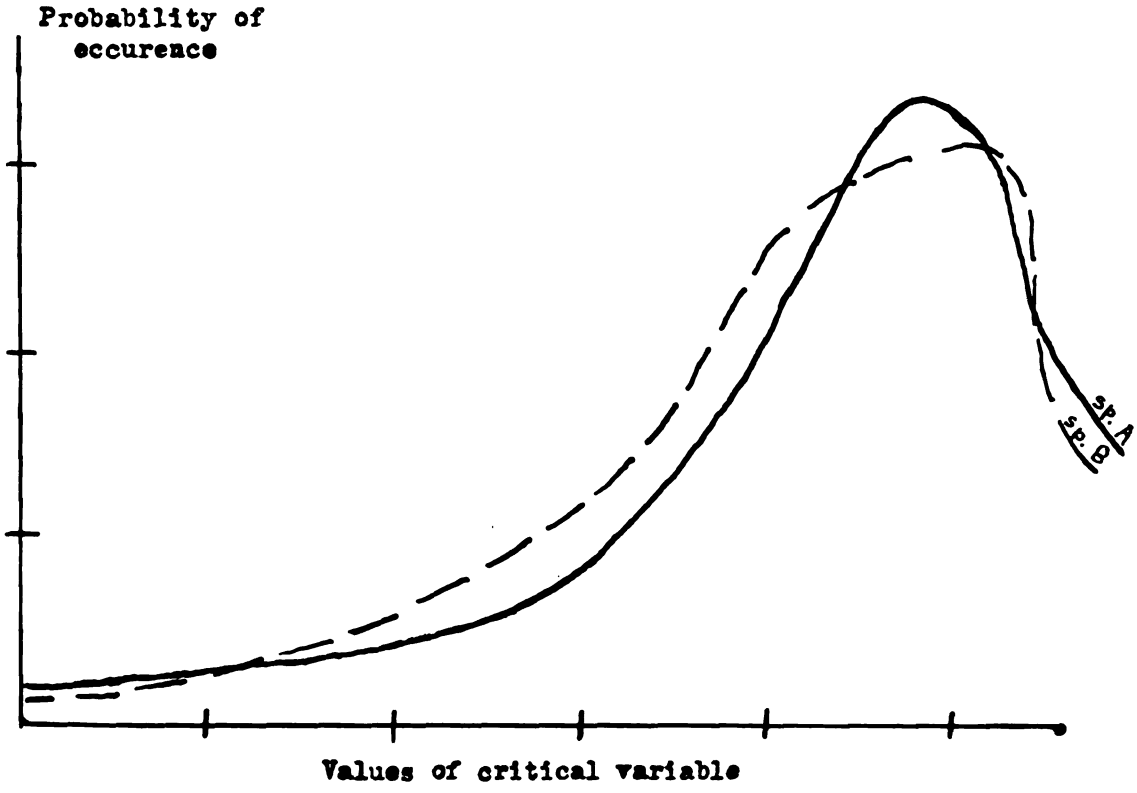


FIGURE 17. Graphs showing theoretical probability of presence or high cover of the two species in Figure 16A, in relation to some critical variable.

to fall so as to include both, might shift the correlation towards neutral.

The overall trend towards correlation coefficients which are lower numerically than the association coefficients (see "2" above, p. 113) may play a role in creating this combination of coefficients also.

These attempts to explain discrepencies between association and correlation coefficients are probably oversimplified, and they are perhaps seldom as clear-cut in nature as they are in the illustrations. I feel, however, that the hypotheses which have just been presented serve as a useful "rough framework" within which we can interpret the various combinations which occur, if only somewhat naively. Re-examination of the study area with them in mind has proved rewarding in considering particular species pairs.

7. The discrepencies between zero-order and highest order partial correlation coefficients, if the partial correlations are lower numerically than the zero order correlations, may be due to the factors mentioned in "3" above (p. 114). But it may be that occasionally these factors work "in reverse". For example there might be a favorable interaction between two species, but they might be "held apart" by differences in microenvironmental requirements with respect to a particular variable, or by an unfavorable interaction of one of them with a third species with which the other interacts favorably. When this variable or third species is partialled out, then the partial correlation should be positive and higher numerically than the zero-order correlation coefficient. In other cases a particular set of environmental conditions, or a favorable interaction of both species of a pair

with a third species, or unfavorable interaction of both with a third species which occupies an extensive portion of the area, all might tend to either "hold" or "push" two species together spatially. If these species themselves interact unfavorably, or are quite different in their tolerance ranges, then partialling out of the variables which function in keeping them together should give the partial correlation a higher negative value than the zero-order correlation.

8. The proportions of significant correlation coefficients are not quite as high as the proportions of significant Cole coefficients, even though the groups were in some cases chosen because the species had mutually high positive Cole coefficients, or because they peaked in the same part of the gradient. In the latter case, the Cole coefficients of the majority of pairs often tended to be highly positive also, perhaps because of their somewhat similar microhabitat requirements.

It seems probable, then, that although interspecific associations are clearly demonstrable on the basis of cover values, they are not quite as strong as those based upon presence or absence. The reasons for this are not clear at present, but perhaps a general tendency for high cover values of two species to be mutually exclusive (see "2" above, p. 113) is a factor.

9. The generally low and non-significant correlations of the species with environmental parameters suggests that the variables chosen, within the limits of their variability in the study area, are not especially critical for most of the common plants. A second possibility is that interaction between species is really more important in determining plant distributions

in the study area than are microenvironmental factors, and a third is that the quadrats were not small enough to detect responses of the species to environmental variables.

D - GROUP I

GAULTHERIA PROCUMBENS (GAU), MAIANTHEMUM CANADENSE (MAI), MELAMPYRUM LINEARE (MEL), VACCINIUM ANGUSTIFOLIUM (VANG), AND LITTER DEPTH (LIT) ON GRAYLING, WET GRAYLING-CROSWELL, AND AU GRES-SAUGATUCK SOILS (TABLE VI, p. 88)

In general, the associations and correlations of these species are highly positive on the dry end of the gradient on Grayling Sand soil type (G), and become lower as one approaches the moister central portion of the gradient on Au Gres-Saugatuck soil types (AGS) (Figures 18c-h, p. 125). This is not surprising when one examines the frequency and cover curves for these species (Figures 18a, 18b, p. 125), for all four tend to peak in the AG-S segment of the gradient. Therefore, one might suspect at the outset that these are all "moisture-requiring" species, which are positively associated on the "dry" portions of the gradient where they occur together in isolated "islands", where moisture or moisture-dependent conditions are relatively favorable for all of them. This would also help to explain the "breakdown" of association between these species on AG-S, where a greater portion of the area is available to the species and where, since most of the area is suitable so far as moisture is concerned, differences in the

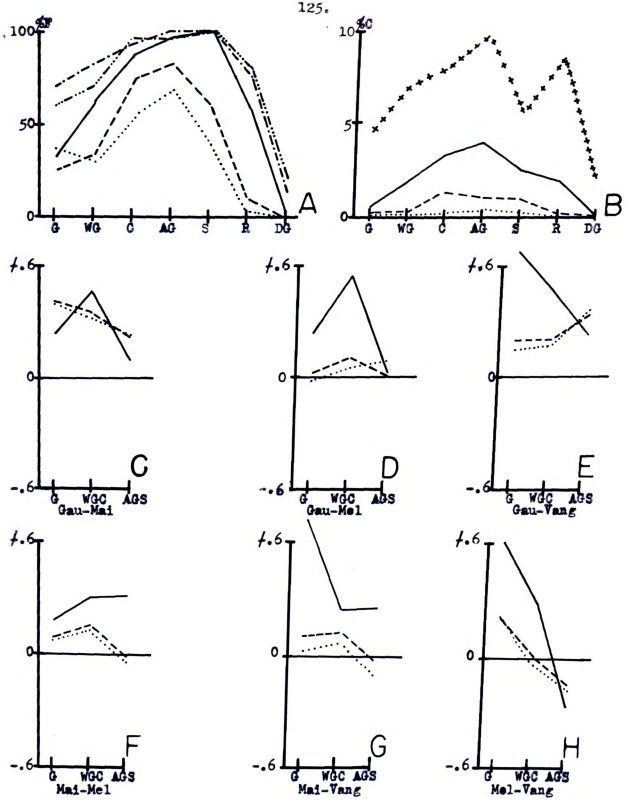


FIGURE 18. Graphs of Group I data. A. Frequency, B. Cover. C through H. Cole association, zero-order correlation, and highest order partial correlation coefficients of the species pairs indicated. Legends with Figure 19, p. 131.

requirements of the species for factors other than moisture are liable to become more influential in the association and correlation coefficients. An examination of field notes for the four species, and the association and correlation coefficients themselves, make it clear that factors besides moisture must be partially responsible for the patterns found here.

All of these species tend to be somewhat positively associated with mosses on the "dry" end of the gradient, and somewhat less so on the wetter AG-S segment. All are somewhat negatively associated with lichens throughout. Though the majority of common vascular species studied exhibit a similar relationship to mosses and lichens, especially on the "dry" end of the moisture gradient, this does perhaps corroborate the hypothesis that Group I species may "prefer" relatively mesic sites.

In actuality, the four species included in this group are probably quite different in their physiology and environmental relations. Their general tendency to be positively associated may be a result largely of somewhat different forces acting on each one, or each interacting with the others in a different way, in a manner which somehow causes them to generally have fairly closely corresponding "contour lines" of probability of occurrence throughout the area. In short, they all occupy about the same microsites in the study area, but possibly each for a different reason.

In general, there is a tendency for species pairs in this group to exhibit stronger positive associations on Wet Grayling-Croswell (WG-C) than on either G or AG-S. There is a tendency for "sparse" patches of several square meters to be more

prevalent on WG-C than on G and AG-S. The extensive "sparse" areas would mean that a large number of quadrats would contain neither one of a pair of species, and hence that associations would be shifted in a positive direction.

Speculations upon the general position of each species in the community will be enumerated, and postulates concerning the reasons for the patterns exhibited by this species will be summarized.

1. GAU. This distinctly clonal species peaks on AG-S, but has a fairly broad amplitude, occurring on all the segments of the gradient. It seems to require some organic material on the dry end, occurring frequently on buried logs, etc. Whether this is actually a reflection of a requirement for organic material, for symbiotic fungi and bacteria which occur with the organic matter, or for the increased moisture content of buried logs, it is difficult to say. At any rate, Gau is quite negatively correlated with deep humus on the "wet" end of the gradient, and occurs frequently on tree-base hummocks on the dry end where it may obtain the benefit of moisture in the form of stem flow, suggesting that the requirement may be at least partially for moisture. Possibly also, since this evergreen plant is favored by early spring sunlight, it is concentrated around tree bases where the snow melts off relatively early. Correlations with tree cover (Table V, p. 83-84) suggest that Gau is actually something of a sunlight-requiring species, but perhaps the advantages of stem flow or early spring photosynthesis around tree bases are enough to offset this on the dry end. Also, tree cover is less continuous on the "dry" than on the "wet" end, and sunlight may be sufficient for Gau around tree bases on G but not on AG-S. The postulate concerning spring

photosynthesis may be sounder than the one concerning moisture. There is little soil around some of the tree bases where Gau is found and consequently they must dry out rather quickly, despite the infrequent "shots" which they get from stem flow.

Gau tends to be positively associated and correlated with the other species in the Group I matrix; with Mai perhaps because both are moisture and humus requiring species, with Mel perhaps because Gau serves as one of the hosts of this apparent parasite, and with Vang perhaps because it is favored by the shade of this shrub, provided that this shade is not too deep, and because both species occur during approximately the same stages of cyclic patterns. There is a suggestion of some indirect interaction between Mel and Gau, through Vang. The latter two may be hosts of Mel, and Gau tends to occur with Vang, but Vang when very lush is perhaps inhibitory to Mel (though to Gau also to a lesser extent), and hence the positive correlation of Gau with Mel is slightly larger numerically when Vang is partialled out (Table VI, p. 88 - Figure 18-d, p. 125).

2. MAI. This liliaceous perennial herb has a sharper "peak" in cover and frequency on AG-S than does Gau (Figures 18-a, 18-b, p. 125), though it is fairly abundant on all segments of the gradient but the peat. Mai on the "dry" end tends to occur more in hollows in the microtopography than does Gau. However, there is some tendency, observed in the field and supported by a high positive correlation for it to be lushest near the latter (i.e. in the hollows around tree base hummocks). It is very likely a less drought-tolerant plant than is Gau, as suggested by field observations and by its very strong tendency toward

negative association with lichens and positive association with mosses. Often Mai seems to occur on areas where other vegetation is sparse, on both the "dry" and the "wet" ends, and in general its correlation with other species in this group, except Gau, are near-neutral or only slightly positive. But the corresponding association coefficients are highly positive, suggesting that it frequently occurs with high cover of these species, though its vigor may be low when it occurs with them.

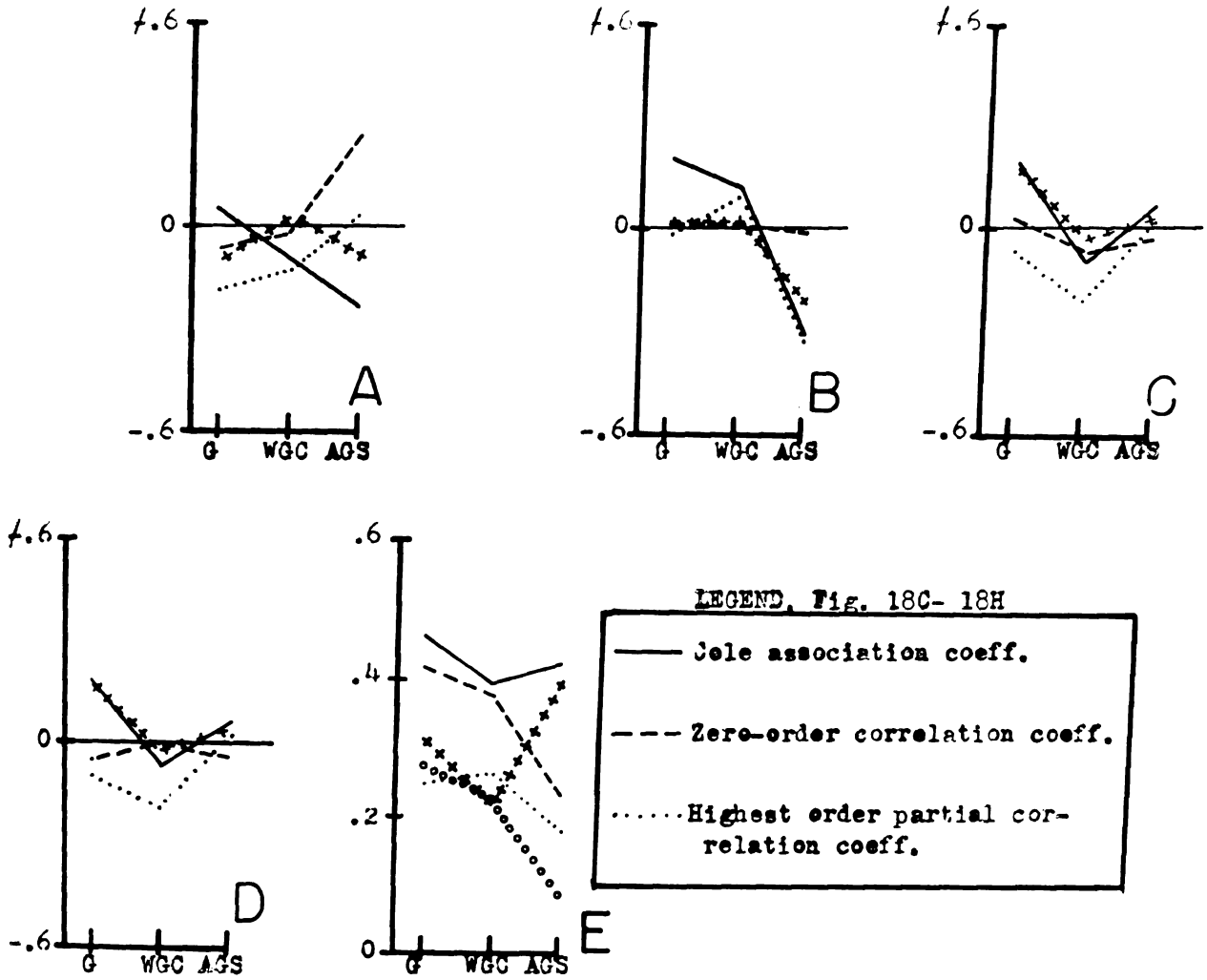
Mai exhibits a near-neutral correlation with A_{o_H} depth (hum) throughout the gradient, but strangely does not occur in the samples on the peat. The deep mat of loose Sphagnum, the acidity, the generally nearly direct sunlight, lack of oxygen in the spring when the mat is inundated, and the dense Cham cover are possible factors restricting it on peat. Since Mai does occur on somewhat similar, but better drained and aerated, less acid peats in white cedar (Thuja occidentalis) swamps, acidity and direct sunlight are among the most probable factors restricting it on the peats of the study area. If Mai's slightly positive correlation with tree cover on AG-S, and its circumneutral correlation with it elsewhere, is not due to sampling error, perhaps it means that Mai really "prefers" shade, but that the generally higher areas around tree trunks are too dry for it, particularly on the "dry" end.

Mai exhibits generally positive associations with the other vascular species throughout the gradient, though it is negatively associated with the apparently quite drought tolerant Car and Com.

Mai perhaps occurs on microsites close to Gau, especially on the "dry" end, though the differences in the reactions of these species to hum and per cent tree cover (tre) on AG-S (Figure 19, p. 131) may make for their circumneutral correlation on this segment. The generally low positive correlation of Mai with Mel (Figure 18-f) may be explained by the former's being the least, and the latter's being the most drought tolerant of the four species in this group, and by Mai's being an unlikely host of Mel, an alleged parasite. Both species have a tendency to occur in areas of sparse vegetation cover, however. Mai may be somewhat inhibited by Vang where the cover of the latter is great(see the circumneutral correlation of these two on AG-S Figure 18-g) though Mai may tend to be associated with Vang in a cyclic pattern, and may also be favored by the light shade of this shrub, which retards desiccation.

3. MEL. This is the only annual among the common species analysed in this study, and there is some indication (Cantlon 1958-59, Piehl 1959, personal observation in the area) that it is also a root parasite on other plants. In any case, its root system is usually surprisingly small, for the size of the plant, and like the European species (Heinricher 1909, 1917) it makes root connections with other vascular plants. Root swellings have also been found / attached to the subterranean fruiting bodies of the Tuberalian fungus Elaphomyces, but at present it is questionable whether these are true connection or superficial.

Mel plants are often distinctly clumped and give a "clonal" appearance. Since this species is a non-rhizomaceous annual, however, this appearance is due to the normally small dispersal distance (one or two feet) of seeds from a parent plant



LEGEND, Fig. 18A, 18B, 19

GAU (Gaultheria procumbens)	VIG (Vaccinium angustifolium var. nigrum)
MAI (Maianthemum canadense)	VVP (Vaccinium angustifolium "typical")
MEL (Melampyrum lineare)	LIT (litter depth)
VANG (Vaccinium angustifolium)	

FIGURE 19. Graphs of Group I data, continued. A. Zero-order correlations with tree cover, B. Zero-order correlations with humus depth, C. Zero-order and D. Highest order partial correlations with litter depth. E. Multiple correlations.

(Cantlon 1958-59) or to the sprouting of rodent seed caches, and perhaps in part to differential survival in different microhabitats, or differential host availability.

Mel seems to do best where other vegetation is present. There is, however, some indication, from field observations and from the association measurements, that particularly lush vegetation cover tends to inhibit it, particularly lush Vang on the moister non-organic soils. The general tendency of Mel to be positively associated, but neutrally correlated with the other Group I species (Figures 18-d, 18-f, 18-g, 18-h) tends to support this hypothesis.

Field observations show no observable preference for any particular abiotic habitat features on the part of Mel. But on the wet end, according to the correlations, it appears to be fairly intolerant of deep humus and on the dry end somewhat intolerant of heavy shade. A possible explanation of Mel's positive correlation with tree cover on AG-S and not on G is that, if Mel's parasitism is facultative, then with the lusher vegetation on AG-S Mel has a better chance of "finding" a host than it does on the "drier" soil types. Hence, if a host can partially replace a requirement for sunlight, Mel might, on the average, require less sunlight for manufacturing its own food material on AGS than it does on the "dry" end of the gradient, where it is perhaps less frequently associated with a host. Though Mel's cover is everywhere low, because of its small size, it has a sharp peak on the Au Gres soil type, and the individual plants tend to be lusher here. Like Mai it was not observed to occur at all on the peat, and understandably it might be

difficult for the seeds of this annual to germinate and reach maturity each year in the deep mat of loose Sphagnum. It is interesting to note in this regard that most of the species of plants which occur on the peat are rhizomaceous perennials, which are able to gain a firm "foothold" in this loose mat.

In accord with the postulate that all members of Group I are associated with Vang in a cyclic pattern, Mel exhibits a similar tendency to be positively associated with most other species except for negative associations with some of the presumably very drought-tolerant species (Dan and Car on Grayling soil). On WG-C, it shows negative association with Pter (the latter being particularly lush on this segment and perhaps shading Mel out), and on AG-S with Vang itself (the latter perhaps being lush enough to inhibit it here), despite the fact that Mel forms root connections with Vang and very probably parasitizes it.

The generally near-neutral correlation between Gau and Mel may be due, as already suggested, to an inhibitory effect of very lush Vang on Mel, since Gau tends to have high cover in or near these lush Vang patches. Mel seems to require less organic matter (humus) than do Gau and the other species in the matrix, especially where humus is generally shallow on the dry end. Mel perhaps occurs with Mai and Vang in a cyclic pattern, since it is difficult to completely explain the mutually positive correlation and association coefficients of these species in any other way, but the data suggest that Mai is the least and Mel the most drought-tolerant of the Group I species, and Mai is an unlikely host of Mel. Mai and Mel may both be inhibited by very lush vegetation, but both may occur near lush vegetation

patches for different reasons, as explained above. Vang may be a host of Mel, but lush Vang cover seems at the same time to inhibit Mel (see preceeding paragraph).

The regression coefficients of the Mel-Vang pair deserve a word. It has been postulated ("5" in Section V-C) that if one member of a species pair is relatively "dependent" for its existence upon the second, but the growth of the second is not markedly influenced by the presence or absence of the first, then the regression of the first upon the second should be positive and substantially higher numerically than that of the second upon the first. Table VI (p. 89) makes it clear that this is not the case here. Therefore, we may conclude: (a) that Mel is not host-specific, despite the fact that it has been found on Vang and not on many of the other species in the vegetation of the study area, or (b) that the quadrats used were of the wrong size to show this feature, or (c) that Mel may connect with Vang rhizomes an average distance from the aereal parts of this shrub greater than the width of the quadrat. Other factors being equal, Mel should have an increasing probability of occurence at diminishing distances from the host, since the concentration of host roots and rhizomes is greatest near the aereal shoots, but a depressing effect of Vang shade upon Mel may tend to offset this, especially since clones of Vang are often quite extensive and lush. Since Gau is also a suspected host of Mel, this pair might also be expected to show a discrepency between the reciprocal regression coefficients, and here too the extent of underground rhizomes of the host may mean that Mel often occurs at a distance greater than quadrat width from above-ground parts of the host.

4. VANG. Vang is definitely the dominant in the shrub layer over most of the area on non-organic soils. It has a relatively broad amplitude, though it peaks on AG-S, and is very sparse on the Saugatuck soil where tree cover is very dense. It is possibly a somewhat shade-intolerant species, as suggested also by its slight negative correlation with tree cover throughout the gradient. Though Vang does occur on the fairly high hummocks throughout the peat, and is therefore not beyond the limits of its tolerance on deep organic matter, it is highly negatively correlated with humus depth on AG-S, suggesting that it "prefers" microsites where physical conditions permit no more than a moderate amount of organic accumulation (Figure 19-b) Vang's tendency to be lushest on the highest hummocks on AG-S, and also where it occurs on the peat, suggest that it may be basically a drought-tolerant species (Its ecological counterpart in New Jersey has a root system penetrating deeply into mineral soil, whereas many shrubs do not (Laycock 1959)). But its negative association with drought-tolerant Car on the dry end may be due to the alternation of these two plants in a cycle (see above, this section). On AG-S, Vam, the other blueberry species found on this gradient, shows a tendency to occupy the depressions in the microtopography, while Vang occupies the hummocks. Interestingly, however, Vang is positively associated with Car on AG-S, perhaps a reflection of the restriction of both species to the same high and dry microsites despite their mutual "repulsion".

Vang is distinctly clonal, and where the clones are particularly large and lush the correlation coefficients indicate that they tend to inhibit the cover of other species, including

all of those in this group (Mel, Mai, and Gau in apparent order of greater to lesser inhibition by Vang), even though these species may show positive association coefficients with Vang.

Other possible ecological relationships of Vang with the other species in this group have been discussed.

5. THE TWO FORMS OF VANG. Vang deserves mention from another point of view. There are two readily distinguishable forms called, by Fernald (1950), Vaccinium angustifolium (typical) (Vyp) and Vaccinium angustifolium var. nigrum (Vig). The former is distinguished by having a whitish bloom on the fruits but no bloom on the leaves, while the latter possesses a whitish bloom on the leaves and has shiny dark blue berries. Cover curves plotted separately for the two varieties (Figure 18-a) do not show any differences so great between the cover of the two varieties along the gradient that they could not easily be due to sampling error, but Cantlon and Gillis (1956) found that Vig tended to be more important on the dry end of similar moisture gradients within a 100 mile radius of the present study area, and Vyp more important on the wet end. There may be a slight tendency in this direction here.

Differences between the two varieties are more striking when the associations between each variety and other species are compared, however. To begin with, the two are only slightly positively associated with each other, except on Grayling. It is possible that this could be due to the fact that the association coefficients for both varieties are based upon counting the variety as "absent" if it is below its median cover value for the soil type in which a quadrat occurs (see Section III-B). When a clone of one variety happens to get

started in a particular spot, it may spread and tend to exclude the other, so the cover of one variety may be high in quadrats where that of the other is low. But of the associations of the two varieties with the other common species, several of them differ widely between the two varieties. In some cases, Vig seems to show less negative association with drought tolerant species (e.g. Car, Com, Cladonia pyxidata-group (Cup)) and less positive association with moisture-requiring species (i.e. Mai, Dicranum undullatum (Dic))than does Vyp, which fits well with the hypothysis that Vig is better adapted to the dry end and hence more drought-tolerant than is Vyp. But in other cases just the opposite seems to be true (i.e. the associations of each variety with Calliergonella schreberi (Cal), Cladonia rangiferina (Cran)). Also, in some cases, the Cole coefficients of the two varieties shift in opposite directions from one gradient segment to the next (e.g. Pteridium aquilinum (Pter), Epigaea repens (Epig), Rubus hispidus var. obovalis (Rho)), so that it is difficult to make any generalization. Nevertheless, there is overall a high degree of correspondence between the association coefficients of each of the two varieties with most species. As a matter of fact, these two varieties show a much higher degree of such correspondence than any other pair of the taxa studied.

A question remains concerning the taxonomic position of the two varieties. According to many authors (i.e. Stebbins 1950, Clausen and Hiesey 1958, Anderson 1949), two distinct varieties cannot remain distinct if they are sympatric and occupy the same habitats, simply because they would interbreed and intermediates would be produced. It is thus necessary to postulate that the

two "varieties" dealt with here are either distinct species with a genetic barrier between them, or that they are simply "forms" of the same species. It seems to me that the latter hypothesis must almost surely be the correct one, judging from the association coefficients obtained, for no two species in the matrix show nearly so good a correspondence in their cover curves and in their associations with other species. This includes Oras and Opun, which belong to the same genus, and also Vam with either of the forms of Vang, all of which are members of the same section of Vaccinium. Since in no case do the associations of the two V. angustifolium varieties with another taxon differ numerically by more than about 0.2, a good bit of the apparent difference between the two varieties may be due to sampling error.

The writer feels justified in using Vang in the correlation analysis, instead of running the two "varieties" through the analysis separately, because there may conceivably be genetic forms among the other species which are just as different physiologically as are the two forms of Vang. If such forms do exist among the other species, however, they are not easily distinguishable morphologically, and hence there may be just as much error involved in the correlations of some of the other species because of diversity within them as one invites by lumping the two "varieties" of Vang (see Whittaker 1956).

Since there were no obvious intermediates found between the two blueberry "varieties", either in the study area or in observations upon V. angustifolium in a wide variety of habitats in the northern part of Michigan's lower peninsula, it seems most likely that the characters which separate Vig and Vyp are contained

in a single pair of alleles, one of which is completely dominant, or else that a system of epistatic genes is involved, certain combinations giving the form called "var. nigrum" and others producing the "typical variety".

While the present work is certainly not intended to be a revision of the genus Vaccinium, and in any case experimental work is necessary before a definite statement can be made, this is one instance where ecological work has quite by accident called attention to a taxonomic riddle, which a fairly recent and thorough work (Camp 1945) did not clarify. Camp seems not to recognize the "varieties", though according to Fernald (1950) they have been called separate species.

The sharp drop in the cover of Vang on Saugatuck, and its rise again on Roscommon, suggests that there may be a sorting of ecotypes adapted to organic and non-organic soils superimposed upon the segregation of the two "varieties".

6. CORRELATIONS WITH LITTER. Average litter depth changes little over the entire portion of the gradient analysed in Group I, from Grayling to AG-S, (Table III, p. 65-66). The character of the litter does change somewhat, for cover of deciduous ground vegetation near the bog margin is greater than on the "dry" end, and contributes a larger portion of the total litter. On the bog margin proper, in which some of the quadrats classified as Saugatuck soil type lie, spruce-larch litter predominates over pine litter. But litter character is generally quite similar, and in most spots it is composed almost entirely

of Jack pine needles and some dead branches, with very small proportions of litter from herbs and ground shrubs. It seems likely, therefore, that relative rates of decomposition of the litter, and the consequent buildup of acids, rates of turnover of minerals, etc., along the gradient, are relatively more important than are differences in litter composition in influencing plant distributions, association patterns, etc. Of course, litter depth, discussed here, is probably an important factor, also, though local litter depth itself is largely dependent upon the size of the annual increment falling on a microsite, microtopography, depth to water table, soil flora and fauna, and other factors. Therefore, the correlation of a species with litter depth does not necessarily represent a direct effect of litter depth upon the species.

All four species in the present group exhibit their greatest tendency towards negative correlation with litter depth on WG-C. This is perhaps due to the extensive "sparse" patches on this segment of the gradient, where litter is usually comparatively deep. Only one of the four negative coefficients on this segment is significant, but nevertheless the general trend is evident from the graphs (Figures 19-c, 19-d).

In general, the correlations of each of the Group I species with litter are not very striking, the only significant one being the negative correlation of Mel and litter on WG-C. On the "dry" end, Gau's moderate positive correlation with litter may be due to Gau's tendency to occupy tree base hummocks here, where litter tends to accumulate. Vang, along with Gau, shows the least inhibition by litter on WG-C, according to the correlations obtained, and seems moderately favored by deeper litter on

Grayling. Perhaps litter is inhibitory to Car on Grayling, thus allowing Vang to colonize those microsites covered by deep litter. Also, Vang is a perennial shrub whose above-ground branches do not have to push through the litter each spring, and Gau is an evergreen ground shrub whose photo-synthetic surface is ready to function as soon as the snow melts. Mai and Mel, on the other hand, and particularly the latter, do not have a positive correlation with litter any-where on the gradient above about $\neq .025$, and especially Mel exhibits negative correlation with litter on Grayling and WG-C. In contrast to Gau and Vang, Mai and Mel must send up new shoots through the litter each spring. So plants of these latter two species which were buried under deep litter and had to push up through it might have less chance of survival. Mel, being an annual which must start from seed each spring, should be more adversely influenced than Mai in this respect, and in-deed Mel does have a more highly negative correlation with litter depth overall than does Mai. If Mel seeds germinate on top of the litter, a possible inability of the germinating roots to reach a host root through deep litter may be critical also.

In no case was there a marked discrepency between the zero-order and partial correlations of any species with litter depth, so the partial litter-species correlations need not be discussed further.

7. MULTIPLE CORRELATIONS. The multiple correlations exhibited by this group (Figure 19-e), in general, give a picture of the increasing "independence" of these species as one follows them from an area near the limits of their tolerance range for

drought (on Grayling) to an area nearer the optimum habitat for all of them (on AG-S). The multiple correlation of Mai decreases markedly from Grayling to AG-S, and those of Gau and Mel show a slight tendency in this direction. Also, the four species on the whole become increasingly "independent" of litter cover as they near their optimum habitat. This is the result one would predict, since on Grayling all four species are probably narrowly restricted in certain particularly favorable microsites. On AG-S, on the other hand, they seem to be essentially ubiquitous, and hence relatively "indifferent" to small differences in microhabitat or to interactions among themselves.

Only the multiple correlation of Vang rises from Grayling to AG-S; probably Vang itself is relatively "independent", but since its cover is high it exerts an inhibitory influence on the other three species. Gau is seemingly the most "dependent" species throughout the gradient, perhaps because of its organic material requirement on the dry end and its interaction with Vang on the wet end. Mai is somewhat less "dependent", especially on the wet end, and Mel is the most "independent" of all, which suggests that this alleged parasite may have a wide host range. Litter depth apparently has relatively little influence on the species in this group as a whole, anywhere on the gradient, though it seems to have more on AG-C than elsewhere.

E - GROUP II

CAREX PENSYLVANICA (CAR), COMPTONIA PEREGRINA (COM), PRUNUS SEROTINA (PRUN), AND PTERIDIUM AQUILINUM (PTER) ON GRAYLING, WET GRAYLING-CROSWELL, AND AU GRES-SAUGATUCK SOILS. (TABLE VII, p.90).

In contrast to Group I, Group II was chosen not because its members exhibited in common any particular association tendencies, but rather because these four species were a "residuum" left over after the four species in Group I were removed. They are the only other four species which bridge the three "driest", or inorganic-soil segments of the gradients, in sufficient abundance so that Cole association coefficients were calculated for them on all of these segments.

The four species do, nevertheless, have certain things in common. Their frequency and cover curves (Figures 20a, 20b, p. 144), for example, show that three of them peak somewhere on the "dry" side of AG-S, and begin to decrease on AG-S itself. The fourth, Prun, does peak on AG-S, but this is probably due to the occurrence of four Prun trees here and not on the other gradient segments. The occurrence of the Prun trees on AG-S and not elsewhere on the area studied is probably a result of different fire histories or other phenomena of the past which varied, and which happened to be favorable for Prun maturation, in the area studied, only on the AG-S segment. Outside of the study area, Prun often attains a large size on the driest of Grayling soils, so the fact that it "peaks" on AG-S, on this particular area, does not necessarily reflect a partiality to moist conditions on the part of Prun. It seems fair to conclude, then, that the four Group II species are somewhat more xerophytic

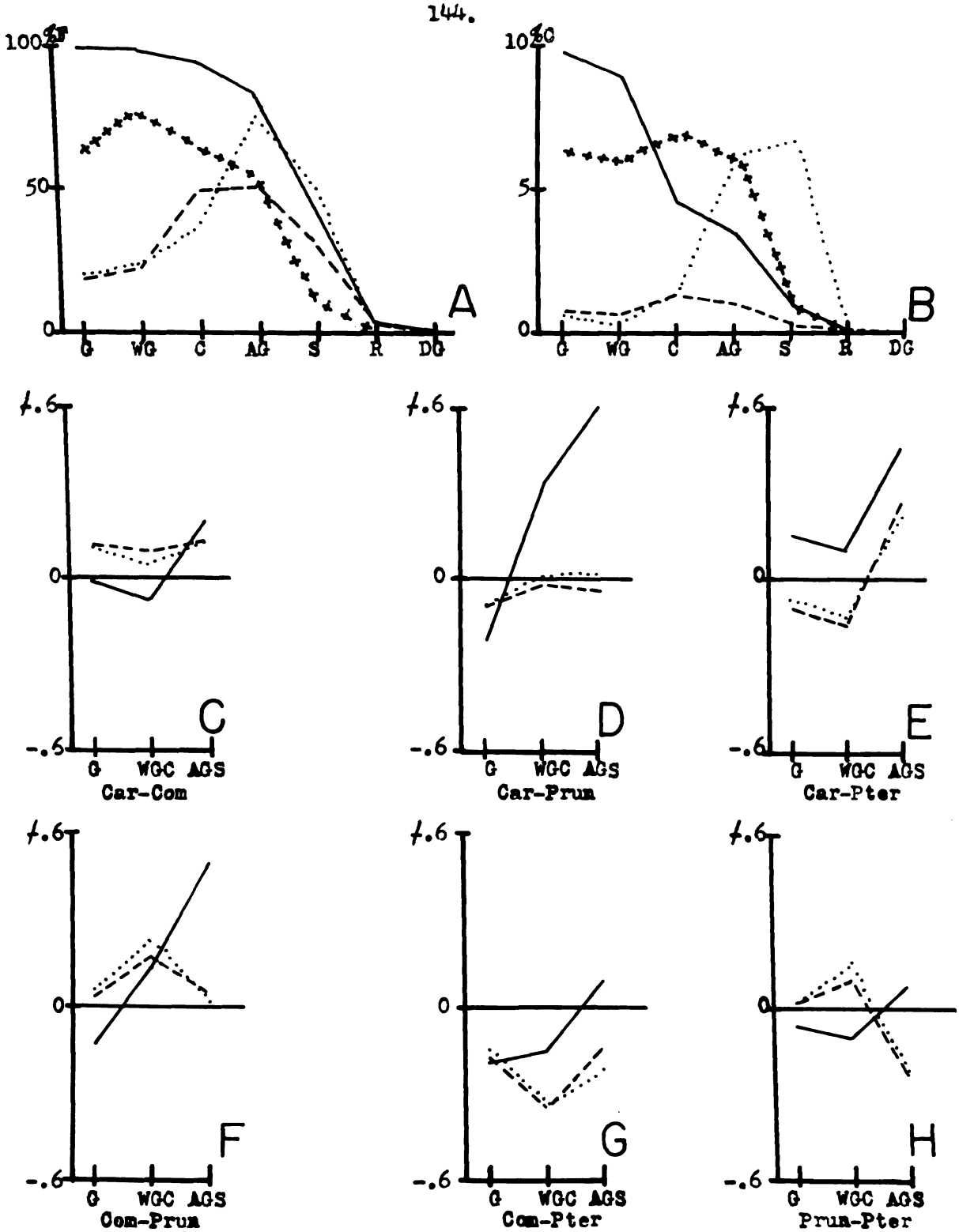


FIGURE 20. Graphs of Group II data. A. Frequency, B. Cover. C through H. Cole association, zero-order correlation, and highest order partial correlation coefficients of the species pairs indicated. Legends with Figure 21, p. 154. Prun frequency obtained by summing frequency of tree, shrub, and herb size classes.

than their counterparts in Group I.

Another thing which the Group II species exhibit in common, and in contrast to the Group I species, is their general tendency to be negatively, or only slightly positively, associated with mosses. This may also be a reflection of their generally more xerophytic nature, and their tendency not to occur in the wetter spots where mosses are most abundant. In this connection, it is rather surprising that Com shows a stronger negative association with mosses than do the other three species, for Com's cover curves suggest that it is not as xerophytic as Car. Mosses are often colonizers of disturbed microsites, particularly blowdowns in forested areas, and Com seems to be a colonizer of disturbed sites also. Mosses may occupy disturbed spots which are generally moister than those occupied by Com, however, and mosses may "prefer" exposed humus whereas Com tends to do well on bare mineral soils, as in roadcuts etc. Since Com is quite resinous, it is also possible that its litter is inhibitory to the mosses in the segments involved.

The four Group II species, with the exception of Prun, show a generally less negative association with lichens than do the species in Group I. Since lichens generally occur on the drier sites, and on those which are nearly bare both of other vegetation and litter, this tendency also suggests that the Group II species may be more drought-tolerant and more capable of invading bare spots than the Group I species. The general tendency among the species pairs of this group is a shift from generally near-neutral correlation and association on the dry end of the gradient, to at least positive association on the AG-S segment. On Grayling, there is only one significant (5 %) association

coefficient and that is negative. On WG-C, there is one significant (5 %) positive association, but on AG-S, there are three significant positive associations. Furthermore, the other three associations, while not significant, are slightly to moderately positive, so the overall tendency is fairly strong. Group II might thus be considered as a rough "reciprocal" of Group I. It is fairly "close-knit" on the moister non-organic soils and "breaks apart" on the drier soils, though nowhere is it as close-knit as is Group I on Grayling. Members of both groups thus tend to show strong positive associations with other species having similar habitat requirements, in segments of the gradient where both species of such pairs are near the limits of their tolerance, since both species of such a pair will occur together on particularly favorable "islands".

The fact that the correlations between members of this group do not show the same trend towards positiveness on AG-S which the association coefficients do may be due largely to some competition or shading effects. Both Prun and Pter, where they are fairly lush, apparently inhibit other species in some fashion; whether by shading, nutrient or moisture competition, antibiosis, or in some other way is not clear. Evidence for the existence of this inhibition is presented in Table VII (p. 90), Figure 20, and under the subsections dealing with these species below.

1. CAR. Car is nearly ubiquitous on the non-organic part of the gradient, and is definitely the dominant in the herb layer on the dry end. Of the four fairly xerophytic species in Group II, Car appears at first glance to be the most drought-tolerant since it peaks on Grayling, the soil type with the least available moisture. Also, Car is nearly restricted to hummocks on the

wet end, and seems to "prefer" them even on the "dry" end. Car does not show a strong tendency towards either positive or negative association with mosses on the dry end, however, suggesting that other species such as Com may be more drought-tolerant, and in fact Car (possibly different genotypes) is fairly abundant on finer-textured soils in more mesic sites in Northern Lower Michigan, whereas Com is practically restricted to dry Jack pine and Oak barrens. Perhaps, then, Car is limited on the "wet" end not entirely by excess moisture, but also by competition from other species better adapted to this habitat. The latter factor, as well as drought-tolerance, may explain Car's peak on Grayling.

Car exhibits only a slight tendency towards negative association with lichens, suggesting that it is more efficient at colonizing "sparse" and "bare" sites than, for example, Prun or Pter. It may also mean that Car is somewhat inhibited by excess litter cover, since lichens generally occur in spots where litter is shallow.

Car shows a slight tendency towards positive correlation with tree cover. It seems to be markedly inhibited by the deep humus on the AG-S segment, but has a near-neutral correlation with humus on G and WG-C. It is possible, then, that the deep humus on the "wet" end directly or indirectly restricts Car on AG-S rather than moisture or competition from other species, though the moisture regimen in deep depressions where the humus is usually also deepest could also be a factor.

On Grayling soil, Car shows no positive associations of even a moderate magnitude, and is negatively (but not significantly) associated with some other fairly drought tolerant species (Anemone quinquefolia (Anem) Pter, Danthonia spicata (Dan)).

On Grayling, then, Car may be a relatively "independent" species, and other species may have difficulty in invading solid Car patches. Perhaps where it is lush, Car does exclude Anem and Dan to some extent, and evidence suggests that Pter may inhibit Car. Since Car perhaps "prefers" microsites where these three relatively drought-tolerant species also occur, Car may therefore be particularly lush on some of these microsites and tend to exclude the other drought-tolerant species. But perhaps Car is not lush enough where it is present on more mesic sites to inhibit the more mesophytic species, and its tolerances may at the same time not be specific enough to produce significant positive or negative association with any other species. The negative association of Car and Vang on Grayling may be due to the alternation of these species in a cyclic pattern, as discussed in the section dealing with Group I.

On WG-C, Car is somewhat negatively associated with Rubus hispidus var. obovalis (Rho), and again with Vang. The former may be a result of the mesophytic Rho occurring in depressions while Car remains on the "high" dry microsites, while the latter is perhaps due again to the alternation of Car and Vang in a cyclic pattern. On AG-S, Car exhibits fairly positive associations with seven species, and no markedly negative associations. Since of the seven positive associates, five are characteristic "dry end" species, including even Vang and Pter, it is probable that here all such relative xerophytes tend to "congregate" on high ground and are essentially absent from the areas in between (See "3" and "6" in Section V-B), The "dry-end" species may have the same competitive and inhibitory effects upon other "dry end" species here that they exhibit farther up the gradient, but perhaps the large "gaps" in the habitat where all

"dry-end" species are essentially absent, shifts their association in a positive direction, so that "misery makes strange bedfellows" despite the operation of the phenomena which tend to "hold them apart".

It is rather surprising, especially since the median cover value technique was used in calculating Cole coefficients for Car and hence the association coefficients are to some extent a measure of the tendency of high cover values of Car to occur with other species, that Car does not exhibit negative association with some of the characteristic "wet end" species on AG-S. Perhaps a tendency for even the "wet end" species to tend to do better on hummocks on the AG-S, as well as a tendency for most species to "avoid" deep humus here ("7" in Section V-B) have so much influence that even very mesophytic species are not negatively associated with the dry-end sedge. This is in fact suggested to some extent by field observations, which show that AG-S depressions are quite sparsely vegetated in comparison to the hummocks.

As one might expect, the association of Car with the other three Group II species in the matrix is generally near-neutral on Grayling, and increases to a moderately or highly positive value on AG-S. This, as suggested above, perhaps reflects a tendency for all to be mutually restricted to the highest and driest microsites on the wet end. The correlation coefficients between Car and the other species, however, are much closer to neutral than the Cole coefficients or negative. This suggests that very high cover values of Car and other Group II species are mutually exclusive.

Turning now to the individual pairs, Car and Com may occur during different phases of a cyclic pattern, but Com, which in the field appears to be something of a "pioneer", may be lushest towards the end of the phase during which it is abundant, whereas Car, which seems to move into more mature microsites, may be lushest during the beginning of its period of colonization so that both tend to be vigorous on microsites of about the same age, and their correlation is perhaps more highly positive than their association coefficient for this reason (Figure 20-c). An examination of their relative abundances on abandoned sandy farm land may shed some light on this question. On WG-C, the highest order partial correlation, positive and numerically higher than the zero-order correlation coefficient between Car and Com (Figure 20-c) suggests that they may appear slightly more positively correlated than they might be on this soil if the lush patches of Pter were absent. Pter may inhibit both of them, and thus high cover of Com and Car may occur outside of Pter patches only.

The statistical data coupled with field observations suggest that Prun and Car both tend to occupy hummocks, especially on the "wet end", but that Prun does not germinate and/or survive well in the seedling stage in lush Car patches, and that Car may be somewhat inhibited under the dense cover of Prun trees (Note the high positive association on two segments and the circumneutral correlation, Table VII and Figure 20-d). A moderate difference between the zero-order and highest-order partial correlations for these two species on AG-S is difficult to explain.

Car and Pter apparently tend to occur together, especially where both are restricted to hummocks on the wet end (high positive association). But Pter seems to be definitely inhibitory to Car where the former is lush (positive association, negative or less positive correlation, Figure 20-e).

2. COM. This is a loosely clonal shrub, nearly ubiquitous on the study area's inorganic soils, and characteristic of Jack pine barrens generally. But its cover is nowhere high. In actuality, it may be more drought-tolerant than Car, though it peaks lower down on the moisture gradient (Figure 20-a, 20-b). It is perhaps not as markedly influenced by competition from other species on the "wet end" as is Car, which may explain the fact that it peaks lower on the gradient than the latter species.

Com shows no marked "preference" for tree cover or openings (Figure 21-a, p. 154). On the AG-S, it is the most negatively correlated with humus of the four Group II species, however, and it even exhibits a tendency in this direction on Grayling and WG-C (Figures 21-b, 21-c). This fits with Com's observed tendency, in other areas, to colonize bare and newly-eroded roadcuts and to be quite abundant on such sites, and further suggests that Com is a colonizer of newly-exposed mineral soils and tends to die back as organic material builds up.

Com is the most negatively correlated with mosses of the four species in this group. As explained early in this subsection, this does not necessarily negate the hypothesis that Com is a colonizer of recently disturbed areas, as are many mosses. Com may "prefer" exposed mineral soil, while the mosses are partial to overturned humus, or its litter may be inhibitory to the

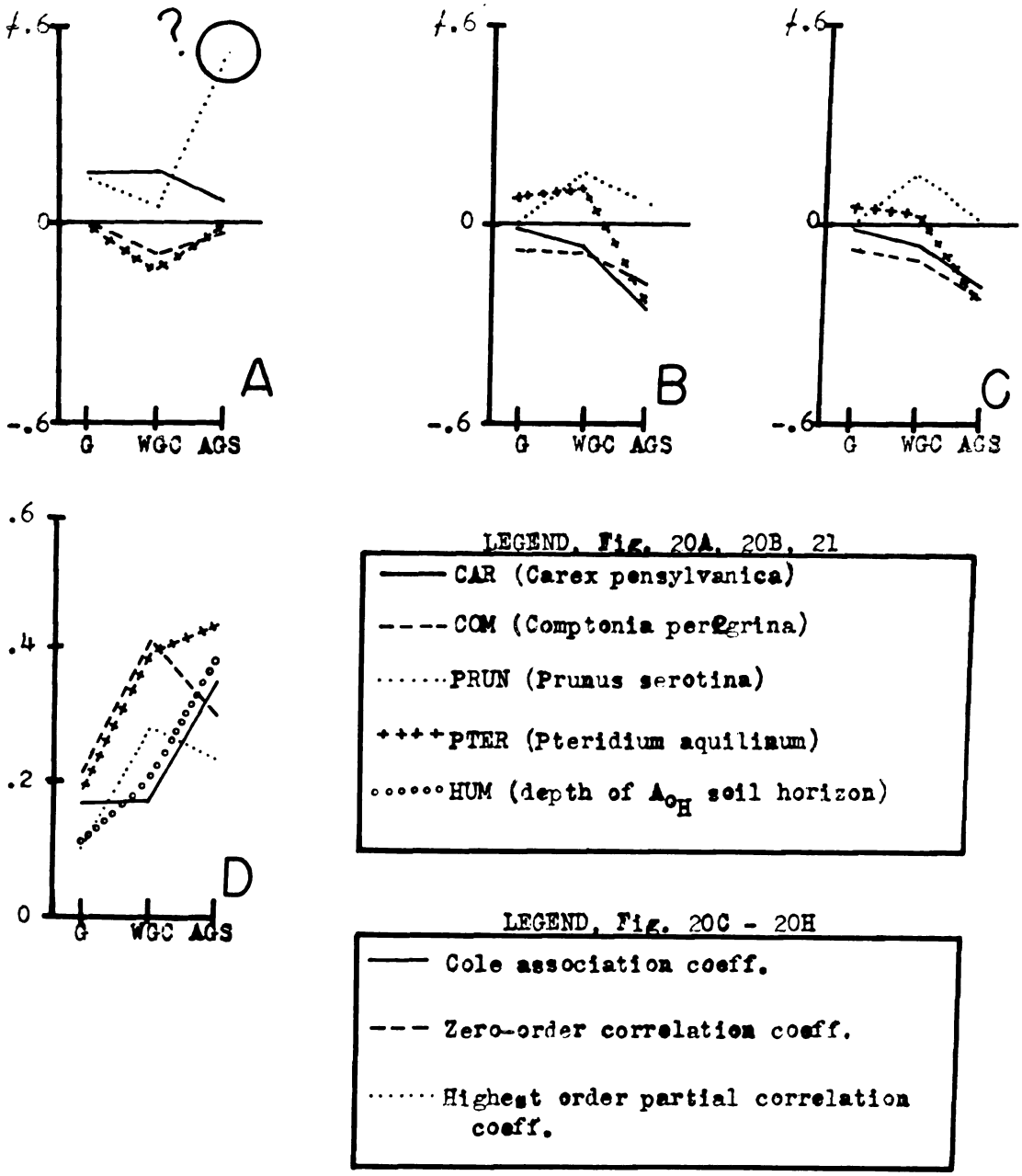


FIGURE 21. Graphs of Group II data, continued. A. Zero-order correlations with tree cover, B. Zero-order, and C. Highest order partial correlations with depth of A_{OH}. D. Multiple correlations. The correlation of Prun with tree cover is somewhat inaccurate because some of Prun's own cover is included.

common mosses.

Com exhibits a general tendency towards positive association with other species. On Grayling soil it is negatively associated with Anem and Pter as well as Vang, on WG-C, only with Pter. Lush Pter perhaps inhibits Com, despite the former's being an herb and the latter's being a shrub. Vang may also inhibit Com, or Vang may be the more mesophytic of the two, on Grayling. On WG-C, however, Com and Vang are highly positively associated. This may reflect a tendency for Vang, which is probably less drought-tolerant than Com, to occupy the "wetter" microsites on Grayling, while even here Com may be most at home on the driest microsites. But on the moister WG-C, Vang may "retreat" to the hummocks with Com. Also, the exclusion of both species from extensive "sparse" patches and also from the particularly lush Pter patches on WG-C is probably a factor tending to raise the Cole coefficient, by increasing the number of quadrats in which both species are absent. On AG-S, Com is negatively associated with Cop and Corn. This is in harmony with the apparent inhibition of Com by excess humic material, while Cop and Corn seem to be very much at home with it.

Com and Car may belong to different phases of a cyclic pattern but may both be vigorous during the same phase (See Car discussion).

Com and Prun, judging from field observations, both tend to occupy high, dry hummocks on AG-S. But the highly positive association coefficient and circumneutral correlation (Figure 20-f), suggest that the cover of Prun trees may inhibit Com

growth here. On the "dry" end, Com and Prun, like Com and Car have a negative Cole coefficient and circumneutral correlation.

Both may occur during different phases of a cycle but both may be most vigorous at about the same time during such a cycle, as we have postulated for Car-Com (See Car discussion above). On the other hand, one of them may occur mostly where values of a particular environmental variable are low, the other where such values are high, with both however having a "peak" of lush-cover probability in microsites where values of this variable are intermediate. In either case, a modification of Figure 17 (p. 121) might serve to illustrate the situation, with the horizontal axis representing time in the former case, and the "tail" of one of the curves to the right in either case.

Predominantly negative correlations and associations between Com and Pter (Figure 20-g) suggest that Pter is inhibitory to Com, especially where Pter is particularly lush on WG-C, but that both are probably essentially xerophytic species (i.e. Cole coefficient circumneutral, correlation negative on AG-S). Both species are probably excluded from large parts of the area on AG-S and are restricted to the same high, dry microsites, despite their "mutual aversion".

3. PRUN. Prun is a difficult species to evaluate, since it is present in very few quadrats in all three segments of the inorganic-soil part of the moisture gradient.

In the study area, all individuals of this species on G and WG were in the seedling or sapling (to 6 feet high) size classes, and the oldest individuals on the dry end were perhaps 3 feet tall, and 7 or 8 years old. On AG-S, and on some of the

Croswell soil bordering this segment, several "trees" (individuals over 6 feet tall in this study) were present, the largest of which were perhaps 25 feet in height and up to 30 years old, with trunks to 2 inches in diameter. Since it was necessary to "lump" all of the size classes in the data in order to have a minimum number of "present" quadrats for this species for the Cole and correlation analysis, a coefficient of a particular magnitude on the different segments may mean quite different things. E.g., a negative association coefficient between Prun and another species on Grayling might reflect a tendency for Prun not to germinate well where the second species is abundant, but on AG-S the same value might be due to the inhibition of the second species by the shade or litter of the Prun trees. The last is especially likely since the several young trunks of this root-sprouting tree usually form quite a dense canopy.

Prun shows no marked microhabitat preferences which are evident in field observations. It appears to "prefer" higher ground near the bog margin, on AG-S, however.

Prun appears essentially indifferent to humus depth throughout the gradient, and is one of the few species apparently not inhibited where deep humus is present on AG-S (Figures 21-b, 21-c). Caution is required in interpreting this however, since a quadrat may have high Prun cover due to the crown of one of the "trees" which overlaps the quadrat, and yet be several meters removed from the actual base of the tree. Actually, humus seems to be relatively shallow about the bases of these trees, and the association and correlation coefficients of other species with Prun are interpreted on this assumption.

Prun may do slightly better where shade is relatively deep, but here again the correlation coefficients with tre may be misleading. The very highly positive correlation between Prun and tree cover on AG-S (Figure 21-a) is almost undoubtedly due to the large amount of cover contributed by Prun itself.

Prun exhibits no even moderately negative associations with any other species anywhere on the gradient. It exhibits a number of positive associations on each segment, however. This suggests that, on the "dry end" of the inorganic soil gradient, Prun becomes established most readily where other species are abundant, perhaps in the moister microsites. On AG-S, perhaps the shade, litter, or other conditions associated with Prun trees, or the hummocks on which they occur, provide a favorable environment for the occurrence of other species. Correlation coefficients of Prun with other members of Group II, however, as well as casual observation, suggest that the cover of other species may be inhibited under dense Prun cover, other species being unable to grow very vigorously under these trees. Whether the shade of Prun is inhibitory, or some toxic substance in the litter of this species, or some factor associated with Prun, is not clear at present.

Prun has a slight tendency towards positive association with mosses, and a fairly marked tendency towards negative association with lichens, especially on the "dry end". This suggests that Prun litter or cover may inhibit lichens and not mosses, or that Prun is not as much of an "obligate xerophyte" as, for example, Com or Car. The positive association with mosses may reflect a slight "preference" on the part of Prun for the

moister microsites where these mosses usually occur. The negative association with lichens suggests that Prun does not do well in lichen-covered microsites, probably because of the dry conditions here and/or because of Prun's apparent tendency to germinate and survive best where the vegetation is lusher than it is on lichen-covered areas.

The correlation and association coefficients between Prun and Car (Figure 20-d) suggest that Prun may be inhibited in its germination by lush Car. But Car occurs with mature Prun trees on the "wet" end, perhaps because the high, dry sites where Prun occurs are favorable sites for it. At the same time Prun tree cover seems to inhibit good growth of Car, by shading it out or in some other way (See Car discussion).

A similar ecological relationship is possible between Prun and Com, on AG-S. The possibility that Prun and Com occur during different phases of a cyclic pattern is discussed in the subsection dealing with Com. It is possible that Com occupies microsites on the dry end which are too dry for Prun. But on the moister part of the gradient Prun also may come to occupy what are, for these gradient segments, the drier spots, along with Com. The inhibition of Com, but not of Prun, in lush Pter patches, may shift the partial correlation of the Prun-Com pair in a positive direction as explained under the discussion of Com.

Pter too seems to be favored by the high hummocks on which Prun trees grow, on the "wet end", but like other species is probably inhibited in its growth under Prun cover, giving a fairly negative correlation between this pair though the Cole coefficient is slightly positive. There is evidence

that higher up on the gradient, where most of Prun cover consists of seedlings and saplings, rather than trees, the two species reverse roles and Pter inhibits Prun. However, it is also possible that, for some reason which is presently obscure, young Prun individuals are abundant and vigorous about the peripheries of Pter patches. This would explain the neutral to positive correlation between these two slightly negatively associated plants on G and WG-C, for quadrats on the periphery of a Pter patch might contain a high cover of both species (Figure 20-h). A difference between zero-order and partial correlations for this pair on WG-C is somewhat difficult to explain.

4. PTER. Pter may be somewhere intermediate between Com and Prun in its moisture requirements and tolerances. This is suggested in part by its near-neutral correlation with both lichens and mosses. Like Car, Pter peaks higher up on the gradient than Com, but it drops out down-gradient perhaps because of a tendency to be outcompeted by more characteristic "wet-end" species, to be directly or indirectly inhibited by humus, etc., and not because it has any particular "aversion" to higher moisture. In this respect it may be similar to Car.

Pter is a distinctly clonal species, spreading only by rhizomes in Michigan and sometimes forming quite dense clumps. It seems to do best on hummocks even on the "dry end", and is definitely restricted to them on the "wet end".

The largest and lushest patches of Pter occur on WG-C. This is not reflected to any great extent in the cover curve (Figure 20-b), perhaps because there are large "sparse" patches where Pter does not occur at all on this soil type,

(though Cantlon and Gillis (1956) found a distinct peak on WG-C in other areas). Thus Pter cover is concentrated in dense patches of the WG-C gradient segment. This does not necessarily mean that WG-C is a more favorable soil type for the formation of large, high-density clones of Pter than is Grayling, since equally dense clones of this species often occur on the driest Grayling in areas near the study area. However, the height and surface area of fronds is greater on WG-C in the study area, producing essentially continuous cover. Possibly, this is a combined response to more available moisture and lower light intensity, but it may also be related to fire history and soil nutrient conditions. Whatever the cause of this phenomenon, it is useful in interpreting the ecological relationships of Pter with other species, as we shall see presently.

Pter seems to be definitely inhibitory to most other species, where its cover is high. Two of the other three species in Group II have negative correlations with it, yet a number of species including the two negatively correlated ones show circumneutral to positive associations with it. Although this is too small a number of correlations to provide convincing evidence, the hypothesis that though many other species "prefer" microsites which are also favorable for Pter, their vigorous growth is by and large inhibited in lush Pter patches, seems tenable.

There is an alternative to this hypothesis. The fronds of this fern tend to unroll rather late in the spring, and are usually not in "full leaf" until sometime in July. Consequently, one would expect the cover of Pter to be low in the first quadrats studied, since the field work was begun in early June,

and an inspection of the raw data indicates that this is indeed the case. This factor would tend to shift the correlations of Pter with other species, which are already "in full leaf" when the cover of Pter is very low or when Pter might even be recorded as absent in a quadrat where it will later be lush, in a negative direction. It is doubtful if all of the apparent "inhibition" of other species by Pter could be attributed to this factor, since field observations do suggest that many other species do poorly under the fern's lush cover, and Watt (1947) has found that Pteridium in England inhibits other species, perhaps through secretion of an antibiotic substance. However, the inhibition may not be as great as the association and correlation coefficients would suggest.

Pter frequently is absent from tree-base hummocks, even though lush all around them. It is likely that the soil is too shallow on these tree-base hummocks for Pter and/or that they are too dry even for this relative xerophyte.

Pter, like most species, is quite negatively correlated with hum on AG-S. This probably reflects its distinct "preference" for the higher hummocks here, which generally possess a relatively shallow humus layer. Elsewhere on the gradient, Pter may even be slightly favored in patches with relatively deep humus.

There is possibly a slight tendency for Pter to be inhibited by tree cover. This may be due in part to Pter's "aversion" of tree-base hummocks.

Pter exhibits almost an equal number of positive and negative associations along the gradient. Since the associations exhibited by most other species are primarily positive, the larger proportion of negative associations exhibited by Pter may reflect the observed tendency for lush clones of this species to inhibit other species. The lushest patches of Pter occur on WG-C, and here it is quite negatively associated with five species (two significant) and highly positively (non-significantly) associated with only one other vascular species, again suggesting that it may be most inhibitory where it is particularly lush.

Pter is positively associated with Gau in all three segments of the gradient, despite Gau's tendency to occur on tree base hummocks and Pter's apparent tendency not to do so. This may mean that both species are somewhat favored by not-too-deep humus, and that Pter is not as inhibitory to Gau as it is to some other species. (Observations indicate, however, that Gau does have less cover under very lush bracken than elsewhere).

On Grayling soil, Pter is negatively associated with Dan and Com, suggesting that it inhibits them or requires more moisture than they do. On AG-S, Pter's negative associations with Cop, Corn, and Vam suggest that the latter three usually occur in microsites where humus is too deep for Pter and/or where moisture is too high for it. The alleged parasite, Mel or its hosts, are perhaps inhibited by Pter on WG-C. On AG-S there is a positive association between these two species,

which suggests that they may be "thrown together" on the dry hummocks here.

On WG-C, Pter has a tendency to be somewhat positively associated with both mosses and lichens, though on G it is more or less negatively associated with lichens. This may be an indirect result of the inhibition of most vascular plants under Pter, for the sparsely-vegetated ground under lush patches of Pter may be a favorable habitat for both mosses and lichens. It may be pertinent here that Pter develops very slowly in early summer, contributing little shade to inhibit the moist season activities of mosses and lichens, yet intercepts the hot summer sun which might otherwise cause excessive desiccation.

The possible interpretations of association and correlation coefficients between Pter and the three other species in Group II have already been discussed in the preceeding subsections. Reviewing these briefly, it appears that Pter is somewhat inhibitory to both Car and Com, although both of these species may do well in microsites similar to those "preferred" by Pter. But on AG-S all three species are perhaps restricted to "islands" where the soil surface is higher and, consequently, drier than in surrounding microsites, giving positive associations between Pter and these species here. Prun seedlings and saplings may be inhibited by Pter, the older trees in turn perhaps inhibiting Pter to some extent. The peculiar combination of the correlation and association coefficients between Prun and Pter, however, permit one to hazard a guess that Prun is better able to germinate and survive as a seedling in the vicinity of lush Pter

clones than elsewhere. This could also be due to the slow vernal development of Pter fronds.

5. CORRELATIONS WITH HUMUS. The zero-order correlations of the Group II species with humus depth have been discussed in connection with the ordinations and at the beginning of this section, as well as in the subsections dealing with each of the species.

The partial correlations of the species with humus depth (Figure 21-c) do show at least three noteworthy aberrations from the zero-order correlations (Car, Prun, and Pter). They are all difficult to explain, and could be due to chance. Nonetheless, it would be as inadvisable to positively write these discrepencies off to sampling error as it would be to assume implicitly that the possible explanations for the correlation and association coefficients presented in this study could all be experimentally substantiated. It is perhaps noteworthy that in all three cases the partial correlations are closer to neutral than are the zero-order correlations. The three cases by themselves are too small a sample to show a trend statistically, but they do suggest that in some fashion, other species markedly influence the distribution of certain species with respect to humus depth.

6. MULTIPLE CORRELATIONS (Figure 21-d). Car exhibits a fairly low multiple correlation coefficient on Grayling. This rises slightly on WG-C, and is about twice as large on AG-S as it is on Grayling. One might expect this on the basis of the hypothesis that Car is relatively "independent" on Grayling, but becomes "dependent" on AG-S where it can occupy only restricted

portions of the area which are "dry enough" for it. Pter exhibits a similar tendency, again as one might expect on the basis of Pter's cover curves (see next paragraph). Com and Prun both exhibit their lowest multiple correlations on Grayling, but the coefficients are highest on WG-C and then fall slightly on AG-S. This may be due to the way in which Pter influences the distribution of both these species, with Pter being especially lush on WG-C.

The general tendency is for the multiple correlations of this group to be lowest on Grayling, higher on WG-C, and highest on AG-S. This one might predict on the basis of the cover curves for the four species in Group II. Since cover and frequency generally are high on Grayling or Wet Grayling and then drop off "down-gradient", these species probably occupy more restricted and less abundant microsites on AG-S. Hence their multiple correlations may reflect their more "dependent" and "specialized" nature on the "wetter" soil types.

The multiple correlation of humus depth, which increases about fourfold between Grayling and AG-S, probably reflects the tendency, which becomes more evident as average humus depth becomes greater and greater "down-gradient", for deep humus to directly or indirectly inhibit growth of most species, or for organic accumulation to be favored by conditions which are also inhibitory to plants.

DISCUSSION
F- GROUP III
ANEMONE QUINQUEFOLIA (ANEM), DANTHONIA SPICATA (DAN), ORYZOPSIS PUNGENS (OPUN), ORYZOPSIS ASPERIFOLIA (ORAS), ON GRAYLING SOIL (TABLE VIII, P. 91)

Group III consists of all the remaining species which were common enough to warrant statistical analysis on Grayling, but which were not included in Groups I or II.

All four of these species appear to be characteristic "dry end" species (See frequency and cover curves, Figures 22-a,22-b, p.168). Three of them peak on Grayling and begin to drop rapidly through Wet Grayling and Croswell, disappearing on Au Gres. The fourth (Oras) peaks on Croswell and drops out on Saugatuck, but it is abundant on Grayling also, and because there were a few more quadrats on Grayling than on WG-C, it was abundant enough for the calculation of Cole Coefficients only on the former soil type. In fact none of the four species were abundant enough for Cole association analysis on any of the segments except Grayling.

The habitat relationships and ecological interrelationships of members of this group cannot be studied in as much detail as in Groups I and II, because Group III was analysed on one segment only, and hence there are no changes in associations and correlations in different segments of the gradient which might yield valuable clues. Also, the associations and correlations in this group are not as strong as in the first two groups, and this makes it more difficult to suggest hypotheses explaining their ecological interrelationships. A third factor which makes statistical analysis difficult is the fact that all four species occurred in barely enough quadrats to warrant statistical analysis, so that relative large deviations from zero may easily be due to

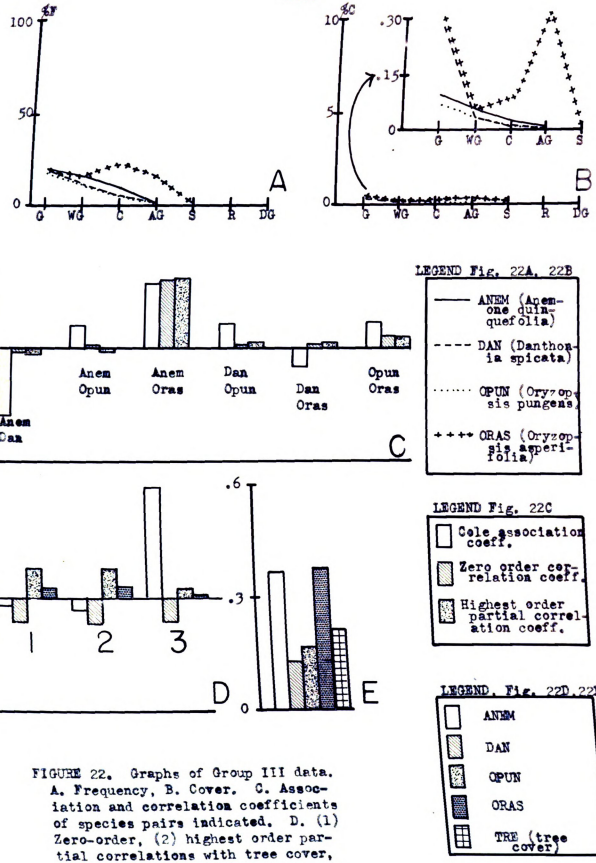


FIGURE 22. Graphs of Group III data. A. Frequency, B. Cover. C. Association and correlation coefficients of species pairs indicated. D. (1) Zero-order, (2) highest order partial correlations with tree cover, (3) zero-order correlations with A_{OH} depth. E. Multiple correlations. C, D, and E apply to Grayling soil only.

chance and it is difficult to achieve significance. Therefore, in attempting to explain the mostly non-significant association and correlation coefficients obtained here we are on shakier ground than we have been in dealing with the foregoing groups.

Only one pair of species (Anem-Oras) exhibits a significant association and correlation coefficient; beyond this all of the correlation coefficients, at least, are close to neutral. It should not be assumed, however, that this means that the species in this group are "independent" with respect to each other and to environmental factors. Rather, it is probable that these species exhibit a complex of patterns, and that they interact with other species and react the environment in a number of ways. It probably happens that, in quadrats 1 m^2 in size, many of the various pattern-inducing phenomena for these species "average out" to give a circumneutral coefficient, so that the species appear "independent".

Judging from field observations, and from correlations with lichens and mosses, one of the species in this group, Dan, is extremely xerophytic; another, Opun, somewhat less xerophytic. But Oras and Anem, especially the latter, seem to be species which require a reasonable amount of moisture. The reasons why Oras and Anem drop out rapidly from the dry to the wet end of the gradient are probably not intolerance of greater moisture, but rather an intolerance to interactions with wet-end species and with the generally lusher vegetation on the "wet end", and/or an intolerance to deep humus or certain soil organisms in this humus, or a need for mineral soil for germination.

1. ANEM. Anem is a small perennial herb, which does not present a particularly clonal appearance and which has little cover anywhere. It is probably a species which requires a fair amount of moisture, despite its tendency to peak on Grayling and to drop out rapidly "down-gradient". Accordingly, it is most abundant on mossy hummocks, on the lower parts of tree-base hummocks with Mai, and in low hollows in the microtopography. Incidentally, these microsites are among the most sparsely-vegetated on the Grayling soil, which is in harmony with the hypothesis mentioned above that Anem drops out down-gradient because it interacts unfavorably with other species.

Unlike the other Group III species, Anem is hardly ever present on really open areas on the Grayling soil outside of the study area. The correlation of Anem with tre (Figure 22-d) is however, near-neutral, or even slightly negative, contrary to expectation. This is difficult to explain except by sampling error, or by assuming that excess shade is as inhibitory to Anem as is full sunlight.

The correlation of Anem with hum (Figure 22-d) is very highly positive and significant. This may be due in part to Anem's tendency to occupy the moister microsites on Grayling where humus is, on the average, deeper than the overall average for this soil type, or it may be that Anem requires the moisture held in the matted organic material rather than requiring the organic matter itself. The hypothesis mentioned above, that Anem drops out on the wet end because of the deep humus there, is not necessarily in discord with this very high positive correlation between Anem and humus on Grayling.

Inhibitory soil organisms and decomposition products could be present in the humus on AG-S which are absent on G. Or the deep humus on AG-S, deeper than any on G, may restrict the germination or establishment of Anem on the wet end even though the mature plant may need some humus.

Anem is fairly positively associated with most other vascular species, particularly with Vang, Mai, and Oras. All of these are also relatively "mesophytic" species, and in addition Mai tends to occur, with Anem, where other vegetation is sparse. Anem is negatively associated only with Car, Com, and Dan, all of which are presumably relatively heliophytic-xerophytic species.

If correlation coefficients were run between Anem and all of the other species, there might not be the same tendency towards positiveness shown in the association coefficients, since Anem seems to grow best where other vegetation is sparse.

Anem and Dan (Figure 22-c) are quite negatively (though not significantly) associated, seemingly because of the former's mesophytism and the latter's xerophytism. Despite this, the correlation of this pair is circumneutral, perhaps because both tend to occupy recently disturbed and/or litter-bare patches. Though Anem perhaps occupies small depressions in these patches and Dan the hummocks, these microsites may be close enough together so that relatively high cover of both species often occurs in the same quadrat. Also, it may be that the tolerance ranges of the species overlap only slightly, but that the cover of both is lushest at the point of overlap.

Since their association coefficient is somewhat positive, Anem and Opun (same figure) may both have a tendency to occur

during the same phase of a cyclic pattern, both perhaps colonizing litter-bare or recently disturbed microsites or "avoiding" lush patches of Car. But the circumneutral correlation coefficients may reflect a tendency for Anem to require more moisture than Opun, so that the cover of one is low where that of the other is high.

Anem and Oras (Same figure) perhaps reflect, in their significant highly positive association and correlation coefficients, the tendency of both to require a relatively high and constant supply of moisture, the inhibition of both by lush Car and Dan patches and the poor competitive ability of both. It is noteworthy that both of these species react similarly with the other two Group III species.

2. DAN. Dan must be an extremely xerophytic species, which tends to invade dry, sunny, recently-disturbed microsites and "hard-burn" patches where lichens abound, and where litter and vascular plants are sparse. This tendency is reflected in Dan's positive correlations with lichens and negative correlations with mesophytic mosses, and in its distribution pattern across the gradient. Even on Grayling it tends to be lushest on the higher hummocks.

A rough grass which grows in tufts, Dan forms extensive clones often with very small interstices between the clumps. In this latter respect it is similar to Car. Like Car, it very likely inhibits the growth of other species mechanically, for where the Dan clumps are crowded together in this fashion there is little room for individuals of other species.

The correlations of Dan with tre and hum (both somewhat negative, Figure 22-d) suggest that Dan is a plant of open,

sunny situations where humus is shallow. Indeed, Dan is a dominant in an open field adjacent to the study area, and seems to do better in openings than it does under Jack pine cover. Dan's somewhat negative correlation with humus depth is also in accord with the observation that Dan tends to occur in spots where litter is sparse, since the humus is usually shallower than average in these spots also. Removal of litter by wind from such places probably contributes to the poorly developed A_o horizons.

Whereas Anem is positively associated with most other species, Dan is negatively associated with a majority of them, due perhaps to its xerophytism and its ability to spatially exclude other plants. It is particularly negative with Gau, Mai, and Anem, which appear to be among the most "mesophytic" species on Grayling, and also with Pter, which perhaps inhibits Dan as it seems to certain other species, and/or is inhibited by it. Dan has some tendency towards positive association with the presumably "xerophytic" species Com and Opun, though it is negatively associated with Car. Possibly Dan tends to exclude Car or vice-versa, so that competition between clones of the two species may be responsible for their negative association with each other.

The data suggest that Dan and Anem tend to occupy somewhat different microsites because of their differing moisture requirements, but occur close together in relatively bare areas (See Anem above).

Dan and Opun show a slightly positive (not significant) association (Figure 22-c) which, if not due to sampling error, is in accord with the apparent xerophytic nature of these species. But lush Dan patches tending to spatially exclude Opun, and the somewhat negative responses of the latter and positive responses of the former to tree cover and humus (Figure 22-d), may be responsible for the neutral correlation coefficients.

Dan and Oras are slightly negatively associated, perhaps because of Dan's xerophytism and Oras' mesophytism. As with many such small Cole coefficients in this group, this one could be due to sampling error. But as with Anem-Dan, both species may have optima during the same phase of a cyclic pattern; for example, they may both tend to colonize recently disturbed and litter-bare microsites, tending to shift the correlation of this pair towards neutral.

3. OPUN. This is a seemingly xerophytic species, but probably not so xerophytic as Dan. The less positive correlations with lichens and more positive correlations with mosses suggest this, as does the somewhat positive correlation with tree cover (Dan-tre is somewhat negative). It is a relatively small grass occurring in small, scattered tufts.

On G, Opun does not seem to exhibit any observable marked habitat preferences. On the wet end of its range (AG-S), however, (where statistical analyses were not carried out for this species), Opun is quite infrequent and definitely restricted to relatively dry hummocks, as we might expect. On AG-S moisture per se may not be the factor limiting Opun to the convexities. Thickness of organic layer, distribution of soil organisms, or other vascular plants could be important.

Opun may be indifferent to humus depth on G, however, and it is slightly positively correlated with tree cover even though it is apparently a "xerophytic" species (Figure 20-d).

For the most part, both the positive and negative association coefficients exhibited by Opun are weak. Perhaps the tufts and patches of Opun are not large enough to mechanically exclude other species, as Dan and Car seem to do. Opun actually seems to have more of a tendency toward positive than toward negative association. This tendency may be due to the mutual exclusion of Opun and many other species from large patches of Dan and Car, so that these species occur mostly in "Carex-less" and "Danthonia-less" microsites. If they are thus essentially absent from a large portion of G, they may occur together more than one would expect if they were randomly distributed. Also, Opun may not be as "partial" to sparsely-vegetated microsites as is Dan. Opun exhibits significant negative association only with Gau. Though both are positively associated with humus depth, Opun may do poorly where the humus is unusually deep, while Gau seems to thrive on such deep humus on the "drier" soil types. Also, Opun does not seem to do well on tree-base hummocks as Gau does.

Opun tends toward positive association with several other more-or-less "mesophytic" species (Anem, Oras, Pter, Prun). It may be one of the few species fairly tolerant of dense Pter cover. Opun is slightly positively associated with the presumably xerophytic species Dan and Com, and is slightly negatively associated with Car, which may inhibit or exclude it.

The Opun-Anem and Opun-Dan pairs are discussed above, under the latter species of each pair. Opun and Oras exhibit a slightly positive association and correlation (Figure 22-c). This may reflect their mutual "preference" for bare areas, and the partial exclusion of both from Dan and Car patches, despite their somewhat different moisture requirements.

4. ORAS. Oras is a coarse, strongly caespitose grass resembling Opun, but much larger and broader-leaved. Like the latter, it seems to be definitely restricted to hummocks on the "wet" end of the gradient, although its associations with lichens and mosses (negative and positive respectively) suggest that it is a more mesophytic species, more like Anem in its moisture requirements than like Dan or Opun. It is sometimes associated with large mossy hummocks, perhaps because it is favored in moist, recently disturbed spots where mosses tend to occur. It is perhaps also favored in spots relatively bare of vegetation and litter, like the other Group III species, and like Anem it may be inhibited by deep litter, factors connected with deep humus, or interactions with other species on the "wet end".

Oras does not seem to be influenced by humus depth on Grayling, but it does appear to be somewhat favored by the shade of trees (Figure 22-d). This may explain why Oras is not found in abundance in open savanna-type vegetation or open fields on Grayling, whereas Dan and Opun frequently are.

Oras, like Anem, exhibits a majority of positive associations with other vascular species. But unlike the latter, it

exhibits no negative associations which are anywhere near significance. Therefore Oras is, perhaps, more able to compete with certain other species and/or is more drought-tolerant than Anem, but at the same time more "dependent" and specialized in its requirements than is Opun.

Oras' highest positive associations are mostly with relatively "mesophytic" species (Vang, Mel, Mai, Anem), as one might expect. The three slight negative associations are with Pter, Car, and Dan, all presumably "xerophytic" species. Pter may be antibiotically inhibitory to Oras, while Car and Dan may tend to exclude Oras spatially, or to occur on sites which are too dry for the latter.

Summarizing the postulates relating to the "behavior" of Oras with other Group III species, we find that the high positive association and correlation between Oras and Anem are in accord with the apparent relative mesophytism of both species, and the apparent tendency of both to "prefer" disturbed or litter-bare microsites. The slight (non-significant) negative association between Oras and Dan is perhaps not as great as one would expect on the basis of the former's mesophytism, the latter's xerophytism, and the latter's possible tendency to spatially exclude the former. Both are perhaps lush in litter-bare spots. Despite their apparently different moisture requirements, Oras and Opun may both tend to occupy litter-bare or disturbed microsites, and both may be excluded from Car and Dan patches while neither one tends to exclude the other.

5. CORRELATIONS WITH TREE COVER (Figure 22-d). Tree cover was used as an environmental variable for Group III before it was decided to use this as one of the variables for the ordinations. Therefore, the ecological relationships of these species with tree cover have already been covered in the discussions of each species. Since the partial correlation coefficients in no case differ by more than a few thousandths from the zero-order correlations, no more need be said about them here.

6. MULTIPLE CORRELATIONS (Figure 22-e). Anem and Oras have high multiple correlation coefficients significant at the one-per cent level, largely because of the high positive correlation between them. This does not necessarily mean that these are the most "dependent" species on the whole, however. Anem and Dan are probably the most "dependent" species, judging from a survey of all association and correlation coefficients; the former because it must generally occur in rather specialized microsites with a favorable moisture situation, and the latter because it tends to exclude mechanically other species. Although other considerations suggest that it is a "dependent" species, Dan has a weak multiple correlation with the other three species in the group and with tree cover. Oras is perhaps more "dependent" than Opun, but less so than Anem and Dan, despite its high multiple correlation with other Group III variables.

Tree cover shows a non-significant multiple correlation, and appears to be of only minor importance per se in determining the microdistribution of the species in Group III.

G - GROUP IV
EPIGAEA REPENS (EPIG), RUBUS HISPIDUS VAR. OBOVALIS (RHO), TRIENTALIS BOREALIS (TRI), AND VACCINIUM MYRTILLOIDES (VAM) WITH TREE COVER (TRE) ON WET GRAYLING-CROSWELL AND AU GRES-SAUGATUCK SOILS. (TABLE IX, p.93)

The four species included in this group are relatively mesophytic species. Three of them have a frequency and cover peak on Au Gres, and the fourth, Vam, has a peak on Saugatuck (Figures 24-a, 24-b, p.181). Furthermore, all of them have relatively sharp peaks. All are absent or only very sparsely represented on Grayling, all are sparse on Wet Grayling. All begin to increase rapidly on Croswell. On Saugatuck, Epig falls rapidly while Vam rises slightly to its maximum cover value; Rho and Tri fall only slightly on this soil type. Three species fall rapidly on Roscommon, while Epig, which has already fallen off on Saugatuck, remains about the same on Roscommon. All are absent from the peat proper.

Fairly sharp peaks in the middle portion of the gradient, indicating that these species may have a fairly narrow tolerance range with respect to soil moisture or certain variables related to soil moisture, are not the only things which the four have in common. All of them are similar in their associations with other vascular species and with lichens and mosses. All tend to be quite negatively correlated both with the three mosses and the one lichen for which association coefficients were calculated on these soil types. The only aberrant one seems to be Tri with Calliergonella schreberi (Cal), which is moderately positive (non-significant) on AG-S and incidentally rather difficult to explain.

With the vascular plants, abundant enough for study, all four Group IV species exhibit generally high positive association coefficients on WG-C, and less highly positive associations on AG-S. This suggests that all of them are relatively "dependent" species, and occur generally in spots where other species are present in abundance also. Since the Group IV species reach their modes on AG-S, it is possible that inhibitory effects of their increased cover are responsible for the overall drop in association coefficient values from WG-C to AG-S. Partly, it may also be due to the fact that more of the area is generally suitable for plant growth on AG-S, leaving fewer "sparse" patches where both species of any pair are usually absent. On WG-C, where such "sparse" patches are present, they apparently tend to make Cole coefficients more highly positive. Also on AG-S, where the more "mesophytic" species are presumably more "at home" than on WG-C, the Group IV species may be less dependent upon the cover of other species to prevent desiccation of the soil surface than they are on the "drier" soil type. Finally, most of the more "xerophytic" species with which Group IV species had Cole coefficients calculated on AG-S may "retreat to the hummocks" here, while the Group IV species themselves tend even here to remain in the hollows, or remain on the general surface levels.

All four Group IV species exhibit a tendency towards negative association with Car and Pter, at least on WG-C. This is probably due in part to the inhibition of these species, as of most others, by Pter and by lush Car patches. In part, it

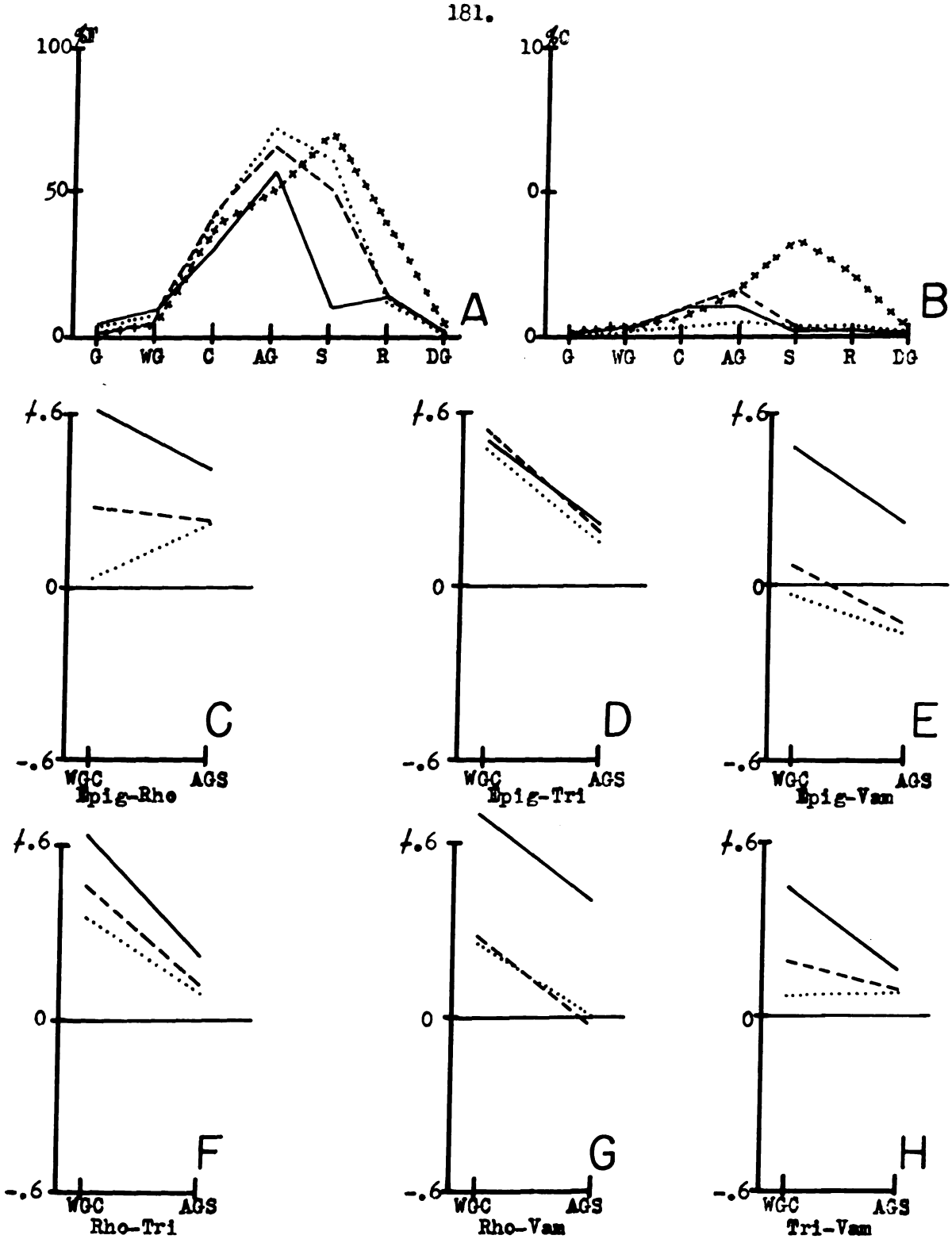


FIGURE 23. Graphs of Group IV data. A. Frequency, B. Cover. C through H. Cole association, zero-order correlation, and highest order partial correlation coefficients of the pairs indicated. Legends with Figure 24, p. 185.

may also be due to the general restriction of these two xerophytes to drier microsites than are occupied by Group IV species. From WG-C to AG-S, the associations of all Group IV species with Car become less negative or even positive, and Epig and Rho become less negatively associated with Pter. Perhaps Group IV species, despite their apparently greater tolerance of moister conditions than most other non-bog species, tend on the very moist AG-S to "climb out" onto the hummocks, with Car and Pter, and thus to become less negatively associated even with these quite xerophytic species.

The associations and correlations of Group IV species work out quite nicely and are almost a "textbook example" of the tendency for associations and correlations to decrease when suitable habitats for the species are more abundant and widespread. All Group IV species are relatively sparse on WG-C, especially on Wet Grayling, so that on this segment of the gradient they probably occur together mostly on relatively small "islands" on Croswell, and are all but absent from a large portion of the segment. On AG-S, on the other hand, all four of the species are more abundant, suggesting that this "wetter" soil type is closer to an optimum habitat for them and that, consequently, more abundant and extensive microsites are open to them. As we might expect, then, all but one of the associations and correlations between these species are positive on WG-C, and most of them are still positive on AG-S. But all of the associations and most of the correlations drop appreciably on AG-S, where the four species are less insular in their microdistribution. A number of quite high positive associations and correlations is evident, especially on WG-C,

a probable reflection of the similar microhabitats which these species require. A number of differences between zero-order and partial correlation coefficients suggests a fair amount of interaction among the species of this group.

The four species might thus be considered to comprise a fairly good "basic unit" in the sense of Hopkins (1957), and their requirements seem to be so similar that one might suspect a great deal of niche overlap. In reality, however, each species probably occupies many microsites in common with the other three but operates within them in unique ways.

Since some of the distribution and association patterns of these species have been discussed in the preceeding paragraphs, and because all the species exhibit them in common, they need not be mentioned again under the headings dealing with the individual species. In order to avoid repetition, the behavior of an individual species is mentioned only insofar as it appears unique.

1. EPIG. Epig is a creeping woody perennial which is markedly clonal. On Grayling soil (where it was not analysed because of its scarcity), Epig often occurs in "bare" spots. On WG-C and AG-S, clones occur in both high and low spots, but they seem generally to be much lusher on the hummocks. Often Epig is lush where blueberry cover is sparse, and in fact where other vegetation is generally sparse. On the "drier" soils, Epig nodes are much closer together, and the leaves are much smaller, than they are on the "moister" soils, suggesting that growth rates are slower on "drier" soils, and by extrapolation perhaps on the drier microsites within a segment also.

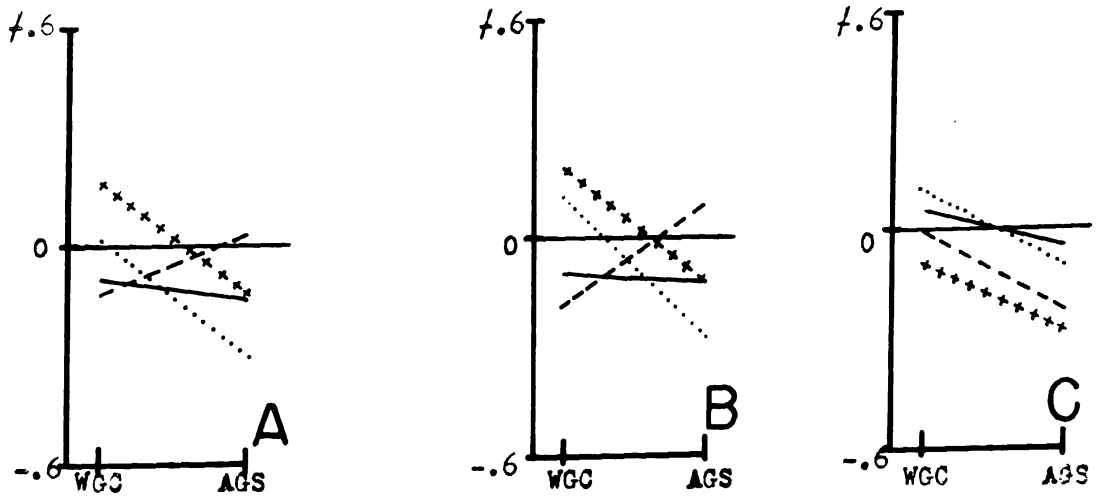
Vang and Vam seem distinctly inhibitory to Epig, for often Epig clones at the edges of blueberry clones are very lush adjacent to the Vaccinium clone, but depauperate underneath the Vaccinium cover. The transitions between lush and sparse Epig are often quite abrupt in such cases. Similarly, lush clones of Epig stop abruptly at the edges of Sphagnum (Sphag) patches. Thus, Sphag could be inhibitory to Epig, which may explain why Epig is not found at all on the peat.

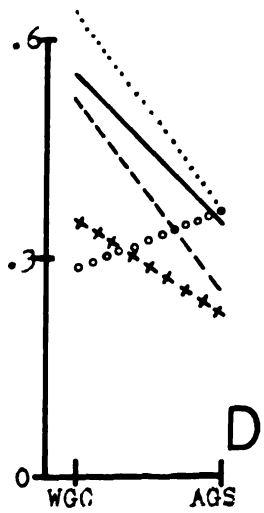
Epig may be slightly adversely influenced by heavy tree cover (Figures 24-a, 24-b, p. 185), but it is one of the few species which seem nearly indifferent to humus depth (Figure 24-c). It is only slightly negatively correlated with humus depth on AG-S, and it may be only the loose Sphagnum-Polytrichum mat and not the peat itself which prevents it from occurring on the peat proper.

In its behavior with the other three Group IV species, Epig seems more or less typical for the group. In each case, however, the partial correlation coefficient differs appreciably from the zero-order correlation on one or both segments of the gradient.

On WG-C the partial correlation of Epig-Rho which is far lower numerically than the positive zero-order correlation and is circumneutral (Figure 23-c), may reflect a three-way interaction between Epig, Rho, and Tri. Both Epig and Rho show high positive correlations with Tri, and so if they themselves interact positively they may somehow be "held together" by the interaction of one or both with Tri, with mycorrhizal fungi associated with Tri, etc.

The partial correlation slightly lower numerically than the positive zero-order correlation between Epig and Tri on





LEGEND, Fig. 23A, 23B, 24

——— EPIG (Epigaea repens)

- - - - RHO (Rubus hispidus var. obovalis)

..... TRI (Trientalis borealis)

+++++ VAM (Vaccinium myrtilloides)

••••• TRE (percent tree cover)

LEGEND, Fig. 24C - 24H

——— Cole association coeff.

- - - - Zero-order correlation coeff.

..... Highest order partial correlation coeff.

FIGURE 24. Group IV data, continued. A. Zero-order, and B. Highest order partial correlations with tree cover, C. Zero-order correlations with A_{o_H} depth. D. Multiple correlations.

WG-C (Figure 23-d) may be due to the partialling out of Rho, with which both species are quite highly positively correlated here. On AG-S, a similar discrepancy may be the result of the partialling out of tree cover, since both species are seemingly somewhat inhibited by shade.

The inhibition of Epig by Vam, observed in the field, probably shows up in the circumneutral correlation coefficient between these two (Figure 23-c). An interaction of Vam and/or Epig with Tri and/or Rho is suggested by the correlation on WG-C, which is slightly negative when the latter species are partialled out though slightly positive otherwise. This may be a reflection of the three-way interaction mentioned two paragraphs back.

2. RHO. This somewhat clonal creeping woody species exhibits no marked microhabitat preferences which are evident from field observations, but the strong association coefficients suggest that Rho, along with the other Group IV species, is in fact quite "dependent" and fairly restricted by moisture conditions. Rho does appear to "avoid" the "sparse" patches, and it may be associated with recently disturbed microsites. It does poorly under dense Vaccinium cover, but often is lush near lush clones of Vaccinium and in openings within these clones. Sometimes it also seems to be lush in deer trails, and in the bottoms of deep hollows with Sphagnum moss where other vegetation is sparse. As might be expected, Rho is generally absent or poorly represented in patches of vegetation with a particularly "dry-end" aspect (lush Car clones, Pter patches, etc.).

Rho is slightly negatively correlated with tree cover on WG-C (Figures 24-a, 24-b), perhaps because it has a propensity

to occur on recent blowdowns above which the canopy is relatively open. But on AG-S, this correlation is near-neutral despite the denser tree cover here, perhaps because under more optimum moisture conditions here Rho is not so "particular" about shade, or because Rho must occur on the higher ground on this "wetter" soil type. Since the "higher and drier" microsites are very often the tree-base hummocks, Rho may be "forced" to grow in the shade.

Rho appears "indifferent" to humus depth on WG-C but on AG-S, like most species, it seems to be inhibited where the humus is deepest (Figure 24-c).

In its associations with other species, Rho is typical for the group except in the case of Com. Why the Rho-Com association goes from highly positive on WG-C to circumneutral on AG-S is difficult to explain. Perhaps it is due to the inhibitions of both by lush patches of Pter, Car, and Vang, as well as "sparse" patches, on WG-C. Rho also follows the general pattern in its associations and correlations with other members of Group IV.

The difference between the zero-order and partial correlations of Rho-Epig suggest a three-way interaction involving Epig, Rho and Tri, as explained under Epig. This is suggested also by the discrepency between the zero-order and partial correlation of Rho-Tri on WG-C (Figure 23-f). Since both are highly positively correlated with Epig here, the lowering of the correlation when Epig is partialled out suggests that the latter, in some fashion, "holds them together".

Vam cover seems to inhibit Rho, as it does Epig. This is suggested by the correlation coefficients of Rho-Vam being numerically much smaller than the positive Cole coefficient between these two, or even circumneutral (Figure 23-g).

3. TRI. Tri is a perennial herb which spreads vegetatively by rhizomes. It is not so evidently clonal as Epig or Rho, and shows no marked microhabitat preferences on either the "wet" or the "dry" end of its range across the gradient though it is probably inhibited directly or indirectly by Sphagnum. This inhibition where Sphagnum is present may explain Tri's absence from the peat.

Examination of the rhizome system of Tri shows that shoots usually arise only where two rhizomes of the plant cross. At present the reason for this peculiarity is not known, though Kershaw and Tallis (1958) mention a similar phenomenon in the grass Agrostis. This behavior, at any rate, probably intensifies the clonal appearance of Tri and keeps it from spreading rapidly from year to year.

Clones of Tri do occur sometimes in spots with a "dry end" aspect on the wet end, such as lush Car or Pter clones. But the shoots of Tri tend to be fairly small in such spots.

Negative correlation with tree cover on AG-S (Figures 24-a, 24-b) suggest that Tri is favored by relatively high light intensity, but the circumneutral correlation on WG-C suggests that, on the drier soil types, it may require some shade to prevent desiccation. It may be slightly inhibited by deeper humus on AG-S, but not as much so as the majority of vascular species, and it seems to be slightly favored by deeper humus on WG-C (Figure 24-c).

As far as its associations and correlations with other Group IV species are concerned, Tri is essentially typical. The differences between partial and zero-order correlations of Tri with Epig and Rho, which suggest a three-way positive

interaction complex have already been discussed under Epig and Rho. On AG-S, Tri and Epig may be "held together" by their mutual "avoidance" of shade (see Epig discussion above).

A glance at the positive association and correlation coefficients of Tri and Vam (Figure 23-h) suggests that lush Vam may not be so inhibitory to Tri as it is to the other two Group IV species. The partial correlation coefficient is slightly lower than the zero-order correlation on WG-C. This is perhaps because here, both Tri and Vam are quite positively correlated with Rho, with which one or both may interact favorably, and somewhat positively correlated with tree cover. The mathematical "elimination" of these factors may remove two of the "bonds" between these species.

4. VAM. This is a clonal low-bush blueberry related to Vang, and occuring intermixed with it on the "wetter" non-organic soils. Vang, however, tends to occupy the tops of hummocks on the "wet end", whereas Vam seems to occupy the sides of depressions, particularly deep depressions with precipitous sides. Neither Vang nor Vam seems to occur, however, where Sphagnum is present in the bottoms of the hollows, though Vang does so occasionally and Vam almost never. Vam may be inhibited by or in Sphagnum, which would explain why it was never found on peat. Vang thus seems to have a much broader tolerance range in both directions than does its "cousin", perhaps a result of greater genetic variability (Section V-D-5).

Vam seems to be similar to Tri in its correlations with tree cover (Figures 24-a, 24-b). It may require shade to prevent desiccation on the drier WG-C, but may in reality be benefited by relatively direct sunlight and so tends to occur under the lighter part of the canopy on AG-S, where desiccation

is not such a serious problem.

Vam may be slightly more moisture tolerant and moisture requiring than the other three Group IV species, since it peaks on Saugatuck soil whereas the other three peak on Au Gres (Figures 23-a, 23-b). Yet it seems to be more strongly inhibited where humus is deep than any other Group IV species (Figure 24-c).

The associations of Vam with the other Group IV species are typical for the group. But on the basis of the correlations, which are generally much lower numerically than the positive Cole coefficients or even negative, it is likely that Vam is directly or indirectly inhibitory to them. Of the three other species, Epig seems to be the most inhibited, Rho somewhat less so, and Tri very little or not at all (Figures 23-e, 23-g, 23-h).

Possible interpretations of differences between zero-order and partial correlations of the Vam-Epig and Vam-Tri pairs are discussed above under Epig and Tri respectively.

5. CORRELATIONS WITH TREE COVER (Figures 24-a, 24-b). Since tree cover is one of the variables used in the ordinations, and since the zero-order correlations of each Group IV species with it have already been discussed, they are not treated separately. However, in the correlations between the Group IV species and tree cover, as in the correlations between the species themselves, there are some noteworthy differences between the zero-order and partial correlations. Of the four species, only Epig and Vam show no such differences. The Rho-tre partial correlation on AG-S is circumneutral in contrast to the slightly positive zero-order correlation. This is

difficult to explain, and does not seem to be in accord with the rest of the data. The difference between the two correlations of this species with tre on WG-C, however, may reflect an interaction involving Rho, Tri and Vam. Both Tri and Vam have positive partial correlations with tre, and if they somehow interact favorably with Rho they may cause it to occur in deeper shade than it otherwise might. When Vam and Tri are "removed", the Rho-Tre correlation becomes more negative.

Tri has a circumneutral partial correlation with tre on WG-C, whereas the zero-order correlation of this pair is slightly positive. This may again reflect an interaction of Tri with Vam, the latter being positively correlated with tree cover and perhaps providing a favorable habitat for Tri, so that in a sense it "pulls Tri into the shade".

6. MULTIPLE CORRELATIONS (Figure 24-d). As one might expect, the multiple correlation of each of the four species in Group IV is much higher on WG-C than is the corresponding coefficient on AG-S. This is probably because almost all the individual correlation coefficients are higher on WG-C than are the corresponding coefficients on AG-S. All four of the species multiple correlations on WG-C are significant at the one-percent level, while none of them are significant even at the 5 % level on AG-S.

It would be difficult to single out any particularly "dependent" or "independent" species within the group, though on both segments of the gradient Epig and Tri are somewhat higher in their multiple correlations than Rho or Vam. Vam probably has a relatively low multiple correlation because of the tendency for its shade to inhibit other species, thereby "driving" the correlations between Vam and these species

towards neutral, and not because it is truly "independent".

Tree cover has not been demonstrated to be of particular importance.

H - GROUP V
COPTIS GROENLANDICA (COP), AND CORNUS CANADENSIS (CORN) WITH TREE COVER (TRE) AND DEPTH OF HUMUS (HUM) ON AU GRES-SAUGATUCK SOIL (TABLE X, p. 94)

After the analysis of Groups I, II, III, and IV only two frequent vascular species were "left over" on the part of the gradient on the "dry side" of the bog margin. Accordingly, these were included in a group of their own, along with two environmental parameters.

It turns out that the two species have a good deal in common, for they are similar in their frequency and cover curves across the gradient (Figures 25-a, 25-b, p. 193), and in their associations with other species. As one might expect, they are also highly and very significantly positively correlated and associated with each other (Figure 25-c).

Both Cop and Corn are perennial herbs which spread by rhizomes. Cop is a small, delicate evergreen herb, never contributing appreciably to the total vegetation cover. The larger Corn, on the other hand, is one of the dominants in the herb layer on AG-S, and in some spots it forms a nearly continuous cover.

Both Cop and Corn appear to have very narrow tolerance ranges, for both are absent from Grayling and from the peat.

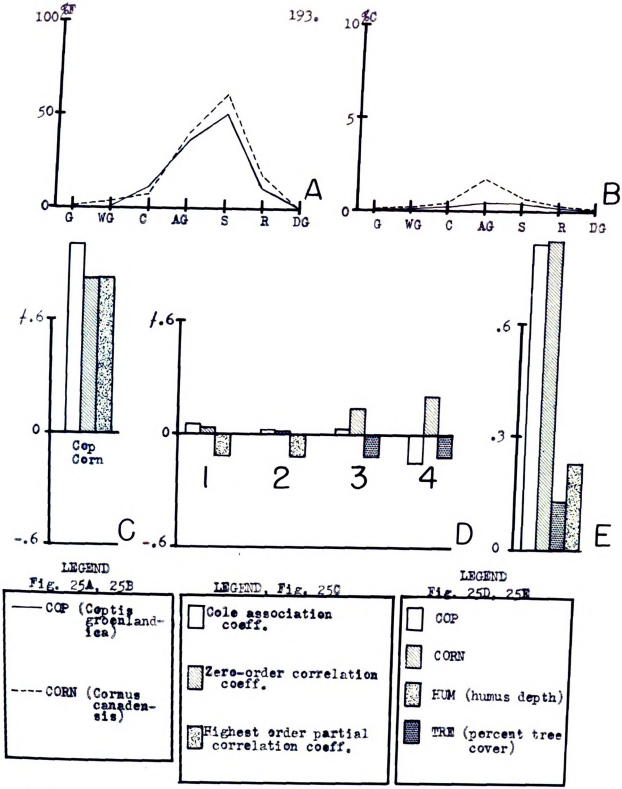


FIGURE 25. Graphs of Group V data. A, Frequency, B, Cover. C, Cole association and correlation coefficients between Cop and Corn. D, (1) Zero-order, (2) highest order partial correlations with tree cover, (3) zero-order, (4) highest order partial correlations with A_{oH} depth. E, Multiple correlations. C, D, and E apply to Au Gres-Sauigatuck soil only.

Both have frequency peaks on Saugatuck and cover peaks on Au Gres, and the frequency peaks are quite sharp (Figures 25-a, 25-b). Cop and Corn therefore appear to have quite narrow tolerances with respect to moisture or some moisture-dependent factor.

Both Cop and Corn exhibit generally high positive association with the more "mesophytic" vascular species and with the moss Cal. They are somewhat negatively associated with Com and very negatively associated with Pter, perhaps because Com and Pter occur in spots too dry for Cop and Corn. It is rather surprising, then, that both Cop and Corn are only slightly negatively associated with Car. Perhaps Car, despite its xerophytism, in some obscure fashion provides a favorable habitat for Cop and Corn. Even the order of magnitude of the association of each of the two Group V species with each other species is quite similar in most cases.

Cop and Corn do differ rather markedly in their associations with Vang. The former is moderately positively, the latter moderately negatively associated with this shrub. Although this difference may be due to chance, it does, if it is real, give valuable clues to the reasons for the association between Cop and Corn. These will be taken up presently.

Both species seem to be fairly definitely restricted to deep hollows on the "dry end" of their range on the gradient (WG-C), though they do occasionally occur on the mossy hummocks. In either case the moisture in such spots is relatively high compared with WG-C as a whole. Corn appears in the field to be more indifferent to microtopography than is Cop. One shoot of Corn in fact, was found growing atop an old stump, certainly not a "low" microsite. Perhaps a rotting stump does tend to

absorb and hold moisture, but Corn's requirement may not be for moisture but for organic material, perhaps to sustain its mycorrhizal fungus. So it may usually occur in the low spots because of the deeper humus there.

The associations of these two species with Vang suggest that the relationships between them may be interactive. Corn is somewhat negatively associated with Vang, and may be inhibited by the summer shade of the latter species. The positive association of Cop with Vang, on the other hand, suggest that it is tolerant of Vang's dense summer shade. This is not surprising, for Cop is an evergreen and can probably carry out the major portion of its photosynthesis in the spring before Vang leafs out whereas Corn cannot. If Cop can "stand" Vang shade, it can perhaps grow well in the summer shade of dense Corn cover also. An interaction between Cop and Corn is probably more complex than a simple "preference" for Corn summer shade on the part of the smaller evergreen Cop, but in any case it appears that Corn is relatively "independent" and that Cop is somehow dependent upon Corn, as discussed under subsection 2 below.

1. CORRELATIONS WITH TREE COVER (Figure 25-d). Both species, according to their zero-order correlations with tree cover, are unaffected by it or perhaps even slightly favored by shade. Perhaps Cop, at least, should be more positively correlated with tre if it is a shade-tolerant species as we have postulated, but perhaps the high, dry conditions around tree bases, where tree cover is concentrated, tends to offset an "indifference" or "affinity" towards shade.

2. CORRELATIONS WITH HUMUS DEPTH (Figure 25-d). Unlike most species, Cop and Corn do not have negative zero-order correlations with humus depth. In fact, Corn is actually moderately positively correlated with it, which is in accord with the hypothesis that Corn actually requires fairly deep humus.

The partial correlations of each species with hum give a further insight into the ecological relationships between them. The partial correlation of Corn-hum is a good deal more highly positive than the zero-order correlation, and the partial correlation of Cop-hum is moderately negative in contrast to a circumneutral zero-order correlation. Thus we see the species as somehow interdependent, directly or indirectly, with the "humophile" Corn tending to "pull up" the correlation of the Cop with humus, and the "humophobe" Cop similarly tending to lower the positive correlation of Corn with humus. The associations with Vang, discussed above, suggest that the small evergreen Cop may be the more dependent of the two.

3. MULTIPLE CORRELATIONS. The multiple correlations do not give any additional information, in this case, which has not already been discussed. The multiple correlations of Cop and Corn are naturally much higher than those of the two environmental parameters, because of the very high positive correlation between these two species.

I - GROUP VI
CHAMAEDAPHNE CALYCULATA (CHAM), ERIOPHORUM SPISSUM (ERIO), KALMIA ANGUSTIFOLIA (KAL), LEDUM GROENLANDICUM (LED), VACCINIUM ANGUSTIFOLIUM (VANG), AND VACCINIUM OXYCOCCUS (VOXY) ON DAWSON-GREENWOOD PEAT
(TABLE XI, p. 95)

This group includes all of the vascular species which occurred in any abundance on the peat proper.

One interesting feature of the group is that a cyclic pattern can definitely be detected by coupling field observations with information derived from the association and correlation coefficients. While a cyclic pattern is probably important in the vegetation structure on the inorganic soil types also, it is not well understood at the present time because of the comparatively large number of species found on these soil types, and because no environmental factor varies so conspicuously on the "upland" as does microtopography on the peat.

Following the individual analysis of each of the six Group VI species, which appears below, a synthesis is presented in which a possible cyclic pattern, and the roles which these species may play in it, is described.

1. CHAM. This rank evergreen shrub is definitely the only dominant on the peat of the study area, unless one considers the scattered spruces and larches to be dominants in the tree layer. From a distance, Cham appears to form a solid green "field" (Figure 2, p. 24), but closer observation reveals a wide variation in its cover in different spots. The "gaps" in the Cham "canopy" are often occupied by other species of vascular plants, primarily the five other species analysed in this group.

Cham is apparently clonal. Its frequency and cover curves (Figures 26-a, 26-c, p. 199), show that it is present, though sparse and depauperate, as far up the gradient as Au Gres soil type. It increases rapidly in abundance and frequency on Saugatuck and Roscommon (R) to a maximum on peat (DG). Strangely enough, it seems mostly to occupy the highest hummocks on the "dry end" of its range on the gradient as it does in the bog, suggesting that an extreme moisture "preference" may not be the primary factor involved in its distribution. It is possible that these "hummocks" represent reminants of the former bog surface, lowered by recurrent fires of the late 1900's. Possibly Cham (with many other bog species) is largely excluded from the non-organic soils because it is "out-competed" here by upland species. Also, it appears to be somewhat shade-intolerant. On the other hand, it is obviously capable of withstanding conditions of extremely low pH, low levels of available nitrogen and phosphorous, and high oxygen tension better than most species, so that it can flourish in the bog where it "leaves its competitors behind".

Cham's correlations with mat depth (mat) and per cent moss cover (moss) are respectively the most highly positive and the most highly negative among the six Group VI species (Figure 27-c, p. 200). Though these correlations are not near the 5 % significance level, they suggest, as does the general lushness of Cham on the higher hummocks, that Cham is the "end point" in a microcycle. If the oldest hummocks are the largest and highest, and evidence will be presented presently suggesting that they are, then it appears that Cham spreads vegetatively and eventually "crowds out" other species. It seems eventually to kill back even Sphagnum and Polytrichum mosses, as well as vascular plants which may have thrived on the hummocks in the

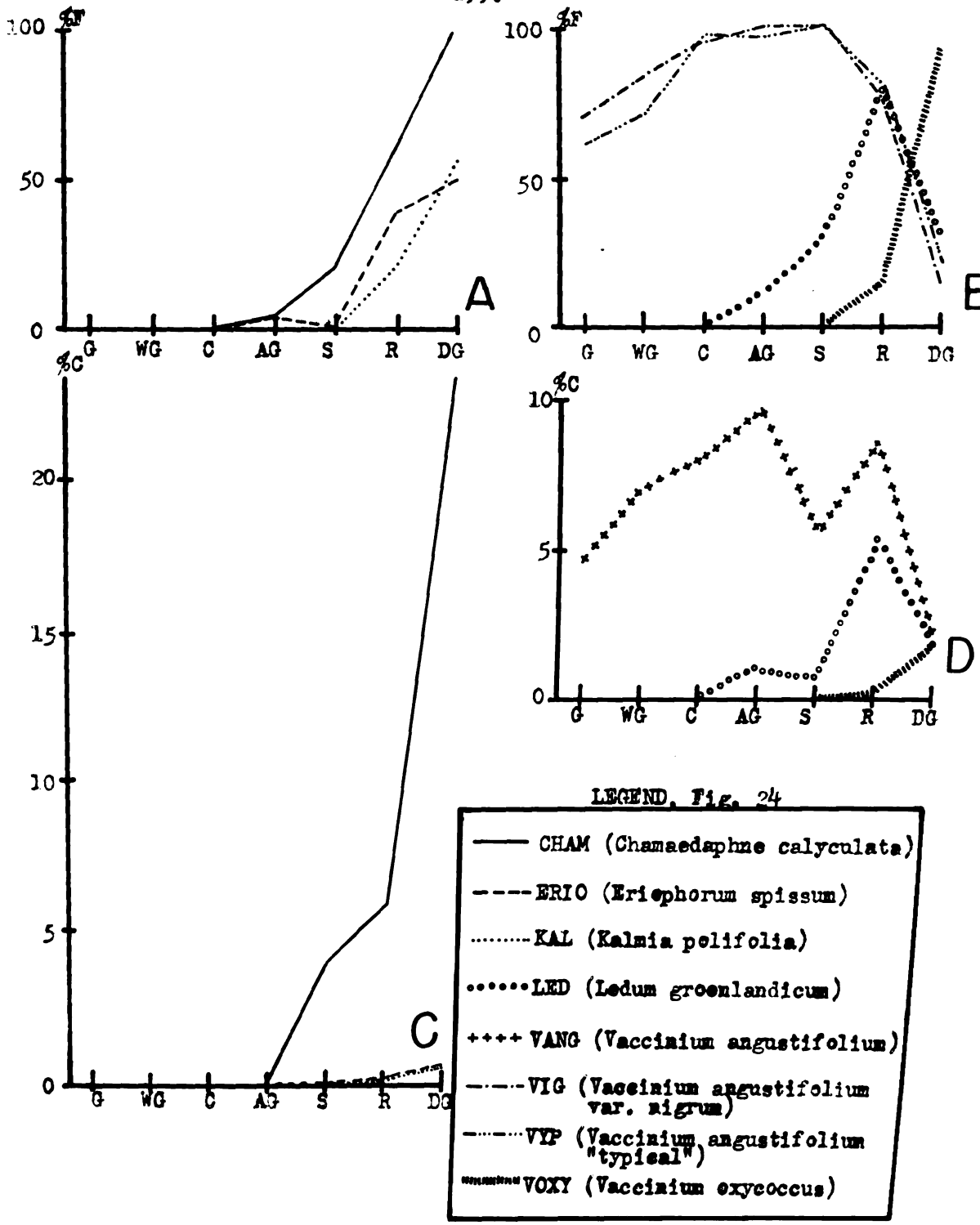


FIGURE 26. Graphs of Group VI data. A and B. Frequency, C and D. cover.

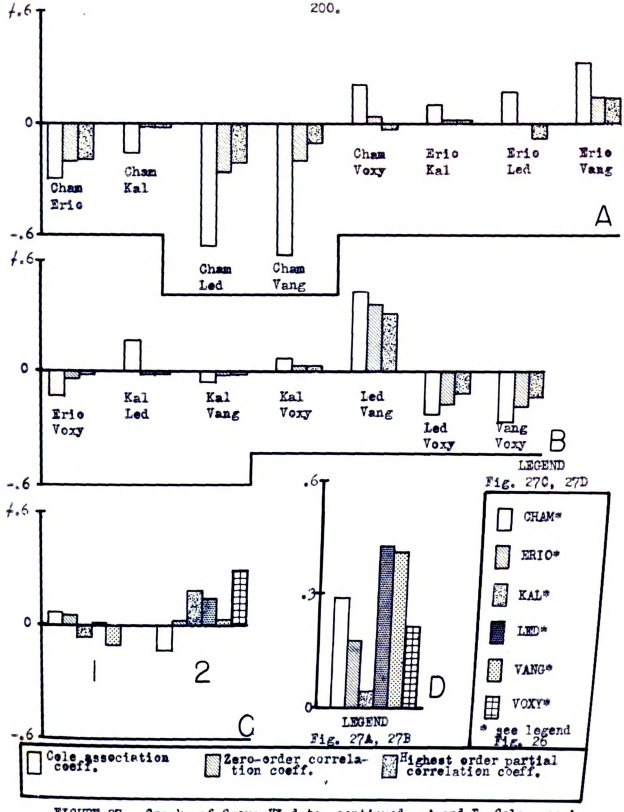


FIGURE 27. Graphs of Group VI data, continued. A and B. Cole association and correlation coefficients of the pairs indicated. C. Zero-order correlations with (1)moss mat depth and (2) bryophyte cover (where the bars are too short to show the code design, they are ordered from left to right in the same order in which they are listed in the legend). D. Multiple correlations. All graphs apply to Dawson-Greenwood Peat only.

earlier stages of the hummocks' development. The depth of the loose moss mat appears greatest where Cham is lushest, if we can trust the slightly positive correlation of Cham with mat. This suggests again that those hummocks where Cham has its highest cover are among the oldest, and that the mat has had the most time to develop on such hummocks.

The correlations and associations of Cham with the other abundant vascular species of the peat augment the evidence for Cham's "climax" position in a cycle of hummock buildup. Most of them are negative, probably reflecting Cham's tendency to inhibit other species as it spreads and becomes lusher. This is especially so since the "median" technique (Section III-b) was used in calculating Cole coefficients for Cham, and thus the negative association coefficients as well as the correlations show that other species are sparse under high Cham cover.

Specifically, Cham is quite negatively associated and correlated with Vang and Led (Figure 27-a, p. 200). This may be due to a tendency not only for Cham to exclude these two shrubs, but for these species, once clones of them become established, to effectively exclude Cham. A tendency for the partial correlations of these two species with Cham to be less strongly negative than the zero-order correlations may be due to the high positive correlation between Vang and Led, and their mutual "aversion" to Cham. Thus if Led and Vang interact positively, then since they are both negatively correlated with Cham, each may "hold" the other "away" from Cham to some extent. Further evidence suggests, however, that Led and Vang do not interact positively, but merely tend to occur together on the shallower peats (see Led discussion), so the

discrepencies between zero-order and partial correlations of these species with Cham become hard to explain. It may be that a clone of Vang can invade a clone of Led, or vice versa, much more easily than either of them can invade a dense clone of Cham, so that Vang and Led do provide relatively more favorable habitats for each other than Cham clones provide for either one. This would account for the aforementioned discrepencies.

That the negative association and negative correlation of Erio with Cham have low (and non-significant) numerical values is a bit surprising, in view of the tendency apparent in the field for the former to occur in open, relatively level spots on the peat, where Cham is sparse and where hummock leveling may have recently occurred. But the scale of pattern here may be smaller than the size of the quadrats used, so that a lush old Cham patch on a high hummock, and tufts of Erio in an adjacent hollow, often occur in the same quadrat. Led and Vang clones, on the other hand, are often larger than the quadrat used, and probably for this reason the negative association of these species with Cham is stronger than the negative Cham-Erio association.

The slightly negative association and circumneutral correlation of Cham and Kal probably reflects a tendency for Kal to be lushest with moderately lush Cham, but for extremely dense Cham to inhibit Kal as it does everything else. Voxy is the only species positively associated with Cham, probably because the former "prefers" above-average Cham cover (recall that the "median" technique was used in calculating Cole coefficients of Cham with other species). It seems most likely, however, that Voxy is in no way "aided" by Cham, but that both

species tend to do best on relatively old and high hummocks. The circumneutral correlation of these two species, in fact, seems to reflect the tendency for extremely lush Cham to inhibit even Voxy. This tendency is strongly suggested by field observations also, to which should be added that Voxy tends to grow slightly down the sides of hummocks whereas Cham occupies the crests. The slight discrepency between zero-order and partial correlation coefficients between Cham and Voxy is most easily attributable to sampling error.

The "common sense" reason for the seeming inhibition of all other species by Cham would be that Cham simply shades the other species out or outcompetes them, or that the litter of extremely lush Cham does not allow light to penetrate to the plants whose photosynthetic parts are near the ground surface (Voxy, Erio, Sphagnum). However, the ecological relationships involved here are probably more complex; for example mycorrhizal phenomena might be involved or an "antibiotic" substance might be secreted by Cham leaves or rhizomes. Perhaps future studies will clarify this issue.

2. ERIO. This is a sedge which forms small tussocks. If Cham is a "climax" in a cyclic pattern, then Erio would appear to be a "pioneer". These terms are borrowed from the terminology of succession ecology, and in a discussion of cycles are dealing with autogenic, repeating processes. But at least Erio appears to be important on recently disturbed microsites.

Whereas Cham is lushest on the "roughest" microtopography, Erio is prevalent on the most gently rolling microtopography (actually on the very low, broad hummocks), on microsites generally substantially lower than the overall level of the bog mat. These microsites may be spots where hummocks have

recently become "senescent" and have broken down. Possible reasons for such hummock breakdown will be discussed towards the end of this section.

In the light of the field observations, the correlations and associations exhibited by Erio are somewhat surprising. Erio is circumneutrally or slightly positively (not by any means significantly) correlated with both mat depth and bryophyte cover (Figure 27-c). One might expect that the correlation with mat depth would be negative, since presumably Erio gets its start on microsites where the tall moss hummocks have just recently broken down and where the mat, consequently, is just beginning to build up again. Similarly, one might expect Erio to show a high positive correlation with bryophyte cover, since Erio occurs mainly on open microsites where there is no Cham or other vascular cover to inhibit moss growth. It is not necessary to discard the hypothesis which is based upon field observations, however. As mentioned in the discussion of Cham above, there is reason to believe that the scale of pattern of alternating patches of Cham and Erio may be somewhat smaller than, or only slightly larger than, the quadrat used. So Erio may, for whatever reason, tend to occupy "flat" spots in the bog, adjacent to the highest hummocks where Cham is lush, the mat is deep, and much of the moss cover has been killed back under the lush Cham.

In addition to its negative association and correlation with Cham (see Cham discussion), Erio shows a slight tendency towards negative association with Voxy (Figure 27-b). This is because of the latter's affinity for the upper slopes of the high abrupt hummocks where Cham, apparently inhibitory to Erio, is moderately lush. Cham seems to eventually exclude both Erio and Voxy, however, which may explain the weakness of the

Erio-Voxy negative association.

In view of Erio's apparent "aversion" to lush cover of other species, its general tendency towards positive association with the shrubs Kal, Led, and Vang(Figure 27-a) is also somewhat surprising. Perhaps this tendency reflects the relatively sparse cover of these shrubs (compared to that of the lushest Cham) where they occur (Figures 26-a, 26-b, 26-c, 26-d), so that habitats for Erio are relatively favorable where clones of Kal, Led, and Vang occur. Erio and Kal exhibit circumneutral correlation and association with only a slight tendency towards positiveness. This may be due to the tendency of both species to be inhibited by the lushest Cham, but for Kal to "prefer" moderate Cham cover and for Erio to do best where Cham is very sparse or absent. Erio and Led are more positively associated than Erio and Kal, but perhaps the lusher Led patches inhibit Erio just as Cham cover does, giving the circumneutral correlation between these species. More likely, however, suitable recently disturbed microsites for vigorous colonization by Erio are rare in the spots occupied by Led clones, which will become clear in the discussion of the latter species. The positive association and correlation of Vang with Erio is stronger than the Erio-Led association and correlations, the association being significant at the 5 % level. Perhaps this is because Vang, like Led, is inhibited by Cham, or because Vang is seldom lush enough in the bog to exclude Erio, or because Vang microsites are somehow more favorable for Erio colonization than are Led patches. Vang, Led, and Erio may all do well on the shallower peats, another factor which would tend to make them all mutually somewhat positively associated.

The discrepency between the zero-order (exactly zero) and the partial (slightly negative) correlation coefficients of the Led-Erio pair (Figure 27-a) is possibly due only to chance, but could be due to the exclusion of both species by lush Cham, so that they are "pushed together" on microsites where Cham is scarce despite their somewhat differing tolerances and requirements. Thus, the true ecological differences between Erio and Led may show up only when Cham, the "force" pushing them together, is partialled out. It would seem, though, that the same phenomenon should cause a similar discrepency between the two correlation coefficients for Erio-Kal and Erio-Vang.

3. KAL. Kal is an evergreen shrub,(present only on R and DG,) whose cover is nowhere very high. It seems to be somewhat clonal, and occurs with light Cham cover on microsites which, judging from the "roughness" of the microtopography, are somewhat older than the optimum microsites for Erio. But it seems to drop out where Cham cover is lusher than average and where the hummocks are particularly abrupt and high.

Kal is slightly negatively correlated with mat depth and slightly positively correlated with bryophyte cover (Figure 27-c), which is in accord with the hypothesis that it "prefers" relatively "young" microsites where the mat has not yet become too deep, and where Cham has not become lush enough to kill much of the moss. The Kal-Cham and Kal-Erio coefficients (Figure 27-a) have been discussed under the subheading pertaining to the latter species of each pair. Led and Kal (Figure 27-b) may have a positive association due to a mutual inhibition by Cham, but Led itself may be slightly inhibitory to Kal, or Led and Kal may "prefer" different microsites, giving a circumneutral correlation between the latter two.

A similar situation may pertain between Kal and Vang (same figure), though here even the association coefficient is circumneutral. This suggests that perhaps microsites favorable for Led are, for some reason, more favorable for the occurrence of Kal than are the interiors of Vang clones. A slight tendency towards positiveness between Kal and Voxy, though weak, could result from a tendency on the part of both species to occur with Cham, though Voxy seems much more tolerant of moderate to heavy Cham cover than is Kal.

4. LED. This is a distinctly clonal evergreen shrub which often forms "islands" in the sea of Cham, especially on the shallower peat close to the bog margin. Indeed, though Cham occurs mixed in these clones of Led, it is sparse here, suggesting that Led clones may nearly exclude Cham once they become established just as Cham seems to exclude Led. An alternative hypothesis, however, is that Led clones became established during the period immediately following a fire, and that the seedlings became established in mounds of sand washed down from the upland at this time. The microtopography where Led clones occur, which is generally less rough than the hummocks occupied by Cham, could be explained by the shallowness of peat over a lens of sand, as well as by the relative youth of a microsite, but unfortunately no data on thickness or depth below the surface of sand lenses in the peat are available for individual quadrats, so that this hypothesis cannot be tested for the present.

Led has a circumneutral correlation with mat depth and a moderately positive (non-significant) one with bryophyte cover (Figure 27-c). This is what one might expect of a relatively thrifty species occurring on relatively recently disturbed microsites, or on microsites with a shallow layer of

peat over a lens of sand. In either case the mat would not be very deep, and the cover of Led is not usually great enough to kill back the mosses,so that microsites where Led clones are present may have a relatively continuous and shallow moss mat.

The Led-Cham coefficients may reflect a tendency for clones of these species to inhibit one another, and to have somewhat different microhabitat preferences, while the Led-Erio coefficients suggest a mutual exclusion from Cham clones, and a tendency for Erio to be favored by the relatively light cover of Led but to have low cover on the broad low hummocks occupied by Led. Results for the Led-Kal pair suggest that Kal can occur with Led and that, like Led, it is inhibited by very lush Cham cover but that it may do best in the vicinity of Cham.

The high positive association between Led and Vang (Figure 27-b) may be the product of both species' tending to occupy the shallower peats, and hence for parts of clones of each species to frequently occur in the same quadrat.

Voxy and Led may (Figure 27-b) exhibit a tendency towards negative association and correlation because of the "repulsion" between Led and Cham, and the tendency for Voxy to be somewhat positively associated with the latter species. This statement is not meant to imply that there is a negative interaction between Led and Voxy or a positive one between Cham and Voxy, but simply that Voxy "prefers" the upper slopes of the more abrupt, high Sphagnum and Polytrichum hummocks where clones of Cham and not of Led are typically found.

Led shows a number of discrepencies between its zero-order and partial correlation coefficients with other species, some of which are rather difficult to explain. The slight shift in a negative direction of the partial correlation coefficients of the Led-Erio and Led-Vang pairs may be due to the

partialling out of Cham. Cham may "drive these species together" in nature because of their mutual exclusion from lush Cham clones, so that their true "affinity" for one another is evident only when Cham is partialled out. The partial correlation of Led-Voxy, on the other hand, is shifted slightly in a positive direction, perhaps showing that Led and Voxy are negatively correlated partly because of the former's incompatability with the fairly lush Cham, on the upper slopes of high hummocks, with which the latter apparently must occur.

VANG. This distinctly clonal, deciduous, low shrub is the only non-arborescent / true "upland" species which occurs in the bog proper in any abundance (Figures 26-b, 26-d), and like Led it forms "islands" in the nearly solid Cham, especially on the shallower peats. It seems to occur on somewhat higher hummocks than does Led, but like the latter may have a history of establishment on sand pockets following the erosion of the upland after fire.

Vang exhibits a negative correlation with mat depth, suggesting that it may tend to occur on even shallower and/or younger peats than does Led. But unlike the latter it has only a circumneutral correlation with bryophyte cover, suggesting that it may be inhibitory to Sphagnum and Polytrichum just as Cham seems to be, either shading the moss out or covering it with leaf litter.

We may approach the associations and correlations of Vang with other species by comparing them with the associations and correlations of Led with these same species, for both Vang and Led seem to occupy similar positions in the bog community. Both the association and correlation coefficients between Vang and Led (Figure 27-b) are quite highly positive and quite significant, probably because clones of both species tend to

occupy the shallower peats with interspersed sand lenses and hence occur in adjacent sites, and not because clones of the two are truly intermingled.

Vang and Voxy (same figure) are somewhat negatively associated and correlated as are Led and Voxy, probably for similar reasons. Voxy occurs usually with fairly lush Cham and Cham and Vang seem to "avoid" one another.

The partial correlation of Vang with Voxy, of somewhat less magnitude negatively than the zero-order correlation, may be due to the partialling out of Cham, with which there is some evidence that Vang interacts negatively and that Voxy is compatable (the latter provided that the cover of Cham is not extremely lush, as just beyond the edges of Cham clones or on the upper slopes of Cham-occupied hummocks).

Reviewing the "behavior" of Vang with species which have already been discussed, we find that Vang and Cham clones seem to be mutually exclusive (perhaps not quite so much so as in the case of Led and Cham). This negative relationship may be due to unfavorable interaction between them or microsite environmental differences (e.g. Vang on shallower peats over sand). Erio and Kal perhaps tend to occur with Vang more frequently than they would if randomly distributed because of the mutual exclusion of all three species from lush Cham, though Vang microsites are perhaps not particularly favorable for vigorous growth of either Erio or Kal. The latter, in fact, seems to do better with medium or light Cham cover than with Vang.

VOXY. This creeping, distinctly clonal, evergreen dwarf shrub, with its rhizomes running a short distance below the surface of the moss mat, represents a life form nearly unique to the bog and "upland" both. Gau, Epig and Arctostaphylos uva-ursi

(common bearberry) are similar but many times larger. Voxy and Kal are the only two bog species totally restricted to peat and to Roscommon in the samples (Figures 26-a, 26-b, 26-c, 26-d). Voxy seems definitely to be favored on the upper slopes of large and abrupt hummocks, and, though it occurs with Kal, Led and Vang occasionally, it seems to be definitely at its best with moderately lush Cham. Whether this reflects an interaction between Cham and Voxy, or merely means that both species "prefer" high and abrupt hummocks, it is difficult to say.

Voxy's circumneutral correlation with mat depth (Figure 27-c) fits well, since this species presumably occurs on the younger hummocks where the mat may not yet have become built up to a great extent. But its fairly positive correlation with bryophyte cover (same figure), the highest exhibited by any of the six species in this group, is rather puzzling, since Voxy seems to occur on the upper slopes of high hummocks with moderately lush Cham. Hence one would expect that the Cham close to Voxy might be lush enough to inhibit moss growth so that the correlation of Voxy with bryophyte cover would tend towards negativeness. Nonetheless the positive correlation of Voxy with bryophyte cover, if not due to sampling error, may be due to Voxy's dependence upon living moss for its existence, for this small plant which is superficially "rooted" in the moss may obtain moisture and nutrients via mycorrhizae from the Sphagnum.

The association and correlation coefficients of other species with Voxy seem to be explicable on the basis of the latter's somewhat positive association with Cham, its apparent "preference" for the upper slopes of abrupt hummocks adjacent

to the lushest Cham clones on the tops, and its possible ability to grow contiguously with lush cover of Cham better than the other Group VI species. Next to Voxy, Kal is perhaps the most tolerant of these species to moderate Cham cover. It has only circumneutral association and correlation coefficients with Voxy, while Erio, which apparently cannot grow with lush Cham but often grows adjacent to it, has a slightly negative Cole coefficient with Voxy but a circumneutral correlation. Led and Vang, which seem to definitely exclude Cham as well as being excluded by it, and which usually occur nowhere near lush Cham, are negative both in their association coefficients and in their correlation coefficients with Voxy. For a more detailed discussion of these coefficients refer to the appropriate subheadings.

THE MULTIPLE CORRELATIONS (Figure 27-d). Led and Vang have the highest multiple correlation values among the Group VI species. This is probably due to their strong positive correlation with each other, and the moderate negative correlation of both with Cham. Cham also has a fairly high multiple correlation, probably because of its tendency to "exclude" other species and its tendency towards negative correlation with them. The other three multiple correlations are non-significant, but they suggest that of the three remaining species Voxy may be relatively "dependent", and Erio somewhat less so, perhaps because of their dependence upon the degree of Cham cover. Kal may be relatively "independent", though field observations suggest that it is inhibited by the densest cover of Cham.

THE BOG CYCLE (Figure 28, p. 213). Though it was difficult to detect with any degree of exactness the manner in which a

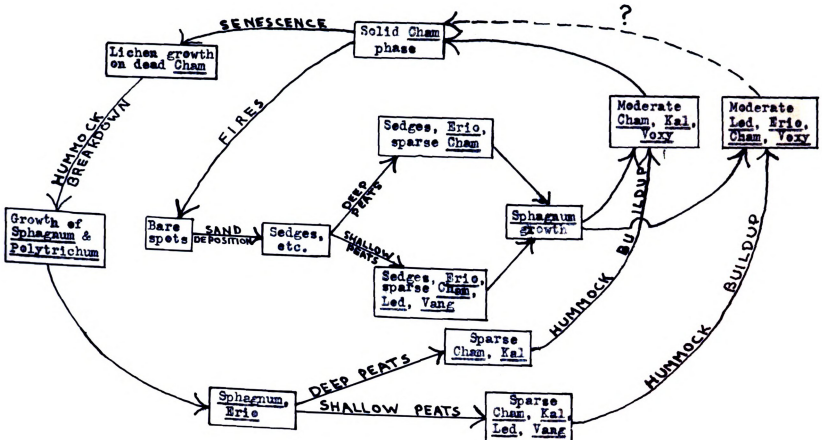


FIGURE 28. A hypothetical diagram of the bog cycle.

213.

cyclic pattern might operate in the upland vegetation, it seems possible to work out a reasonable hypothesis, if only a rough one, for such a pattern in the bog. This is partly because of the small number of species with which we have to contend here, and partly because of the very abrupt nature of the microtopography, with which the cycle seems to be associated.

The last deserves a word as to its possible causes. The hummocky nature of the peat may be due partly to frost action (Sigafoos and Hopkins 1951), and partly to the more rapid growth of clones of Sphagnum and Polytrichum in certain spots than in others. Cham, which seems to occupy the most abrupt hummocks, may or may not have something to do with their formation and breakdown. It is possible that clones of this species at least do something to bind the Sphagnum hummocks together, as Watt (1947) has suggested that certain grasses do in pasture hummocks. When a clone of Cham dies and its roots and rhizomes decay, therefore, possibly the now loose Sphagnum of a hummock is easily eroded down by rain or frost action not to mention passing animals, hunters, and botanists. Indeed, animals probably have a great deal to do with the pattern in the bog, for numerous animal trails run through the Sphagnum and along these trails the mat is compressed and water remains standing in the spring. Frost action may be greater along these trails because of the water accumulating in them, and may affect microtopography in a manner similar to the way in which it causes formation of tussocks in the arctic (Sigafoos 1952). As trails are abandoned, Erio and bog shrubs may move into them and the cycle may be renewed. In two cases during the period of study, fairly large hummocks were found freshly

knocked over near these trails, most likely by deer.

The depth of the peat may affect the abruptness of microtopography. As suggested in the discussion earlier, hummocks may be broader and flatter in spots overlying shallowly-buried sand lenses. This may be related to the shallowness of the peat in such places, and the consequent lessened effects of frost action. Also, more effective decomposition along the bog margin, due to better aeration, may lessen these effects. The shrubs Led and Vang perhaps are influential in hummock buildup in these "shallow-peat" microsites, as Cham may be on the deeper peats.

At any rate, according to the sequence here suggested, the broad, flat microsites seem to be most often colonized by Erio. Then, on the deeper peats, Cham may invade, accompanied by Kal, and the Cham clones may gradually build up, accompanied by a buildup of hummocks. As Cham becomes lusher, first Kal begins to drop out as Voxy invades on the upper slopes of the hummocks, then even Voxy drops out as Cham forms a solid "canopy" and kills back the moss. Eventually, Cham may die and leave the hummocks to be eroded, or the hummocks may become "topheavy" and deteriorate, beginning the cycle over again. On shallower peats, or where clones of the other shrub species may be present in the vicinity, Led or Vang may replace Cham in the early stages of hummock development. These may eventually be replaced by Cham, as the bog becomes filled in (Buell and Buell, 1941), but perhaps they remain as fairly stable "islands" in the Cham "sea" for some time. The role of blowdown of the scattered trees in the cycle is unclear also, though Sigafoos and Hopkins (1951) suggest that blowdowns are unimportant in creating hummocks.

Judging from other bogs in similar sites, fires may induce a temporary vegetation of sedges in bogs of this sort, and may also aid in the establishment of Led and Vang on sand washed from the upland. But Cham, or a mixture which may include Cham, Led, Vang, Andromeda glaucophylla (bog rosemary), Myrica gale (sweet gale), and various sedges and orchids may take over eventually. The exact nature of the vegetation may depend largely upon local nutrient conditions and pH (Conway 1949, Parmelee 1947).

A diagram of the hypothetical cycle is shown in Figure 28.

J - GENERAL DISCUSSION

It has already been emphasized in this paper that the demonstration of the existence of pattern and of interspecific association is not the ultimate goal of such studies as this. Since the ecologist is, or should be, concerned with the functional organization of that complex known as the ecosystem, we must try to delimit as nearly as possible the natural processes which produce these association patterns. So far, I have only advanced a series of hypotheses concerning the causes of the detected association patterns on this soil moisture gradient. The testing of some of these hypotheses by field experiments is planned for the future, however, and it seems worthwhile to give a very brief and rough idea of the types of

tests contemplated.

We wish to test hypotheses concerning both vectorial and interactive patterns (Hutchinson 1953). The former are those patterns which indirectly cause positive and negative interspecific association through biotope overlap, while interaction between species may cause it directly. Consequently, some of our experiments must be designed to test the behavior of species under various controlled field conditions. This may be done by transplanting individuals or planting seeds of the species to be tested in randomized plots in different parts of the gradient, and then varying moisture, leaf litter cover, light intensity, etc. Blocks of soil may be transposed between plots in different parts of the gradient also. If it is suspected that ecotypic differences within some species are responsible for the broad range of a species across the gradient, or for its different association behavior in different parts of the gradient, then individuals from different parts of the gradient may be subjected to the same treatments. Interaction experiments may be designed which will measure the growth, flowering behavior, etc., of individuals of a species when surrounded by individuals of a second species. Such a technique is described in detail by Sakai (1955). In order to pinpoint more accurately the actual conditions bringing about a particular association pattern of a species, greenhouse experiments may be performed to supplement the necessarily less well controlled field experiments.

VI

CONCLUSIONS
AND
SUMMARY

A - CONCLUSIONS

The major conclusions which may be drawn from this study are listed below.

1. The high percentage of significant coefficients suggests strongly that association patterns are numerous in all segments of the gradient.

2. Sampling seems to be adequate to characterize the area in all but the Roscommon segment of the gradient.

3. Vegetation as a whole in the study area seems to be "clumped", lushly vegetated patches alternating with sparsely vegetated spots.

4. The degree of positive or negative association between two species cannot necessarily be predicted on the basis of the similarity or non-similarity of their correlations with one or two environmental factors.

5. Each of the several kinds of coefficients used yields somewhat unique information, and the use of several different measures of association yields more information about the position of each species in the community than would any of the coefficients by themselves.

6. The study of the changes in the cover contributions, associations, and correlations of species across a soil moisture gradient is useful in that it provides clues to the ecological nature of the species concerned which could not be obtained from study of the associations of the same species in any one segment of the gradient.

7. It is possible to construct hypotheses concerning the causes of the interspecific associations which are found, by considering information derived from the mathematical estimates

of association and correlation together with field observations and general biological knowledge. These hypotheses may serve as guideposts for experimental testing of some of the mechanisms bringing about organization in the community.

8. The validity of the various coefficients is suggested by their general agreement with observations in the area and knowledge of the plants macro- and microdistribution, and by the generally positive association and correlation between apparently ecologically similar species and the generally negative association and correlation between species which seem in the field to be ecologically dissimilar.

9. Cyclic patterns seem to occur in the study area, and the various techniques are useful in detecting the nature of these patterns.

10. The validity of the various hypotheses can only be determined experimentally, but the association studies and the hypotheses formed on the basis of them suggest which, of the many experiments possible, might be most worthwhile if we are trying to determine the mechanisms of species patterns and community structure.

B - SUMMARY

1. It is clear that species in nature exhibit patterns of microdistribution, as a result of both small-scale non-uniformity of the habitat, and interactions between the species themselves.

2. Such non-random distribution naturally leads to interspecific association, since the tolerance ranges of certain species to factors which fluctuate within short distances may overlap broadly, leading to positive association, or overlap relatively little, leading to negative association. Similarly, positive and negative interactions lead to positive and negative associations respectively. This paper approaches the problem of community structure primarily from the angle of interspecific association.

3. As a background for the present study, pattern concepts in general are examined. We may find that a species is either "uniformly" distributed or "clumped", and it may exhibit patterns in time (cyclic and successional patterns) as well as in three-dimensional space. For convenience, patterns may be classified according to their causes, which may be either physical or biological, though this is not a fundamental distinction.

4. Communities have been defined as "mosaics of basic units", but probably completely discreet "basic units" do not often exist in nature. Since the environment varies in a continuous fashion, we might expect also that there should be a "continuum" of association, with negatively associated species "interconnected" by species, or series of species, with which they are at least vicariously mutually positively associated.

5. It is well to study patterns of single species and their relationship to environmental patterns, as aids to explaining the association patterns found and for supplementary information.

6. Modern methods of pattern and association study rely heavily upon statistical techniques. Therefore random sampling,

rather than the more classical "grid" arrangement, is desirable. Sampling units of a size corresponding to the scale of pattern in the community studied are necessary, and a coding system whereby the data may be easily and rapidly sorted is helpful. The relative merits of several statistical techniques previously used in studying pattern, as well as the ones used here, are discussed.

7. The purpose of the present study may be defined as: (a) an attempt to formulate hypotheses concerning the way in which individual species "operate" within the framework of the plant community, the mechanics of community function and interspecific association in the study area, (b) an attempt to show the existence and extent of interspecific association in the study area and (c) an attempt to explore several mathematical techniques which may prove useful in association studies. Some of the hypotheses may be tested experimentally, and the association studies show us the lay of the land in this respect, suggesting which experiments might be worthwhile.

8. The study area was a 100 X 100 meter plot traversing a soil moisture gradient from Jack pine (Pinus banksiana) open forest to Leatherleaf (Chamaedaphne calyculata) bog on sandy outwash soils in Crawford Co., Northern Lower Michigan. Such a gradient was chosen for the study, rather than a relatively homogeneous vegetation, because the changes in species distribution and association across such a gradient can provide valuable clues as to the ecological positions of the species in the community. Also, the small total flora of both ends of this gradient reduces the number of variables with which we have to deal, and few species can occur all the way across the gradient.

9. Four hundred random 1 X 1 meter quadrats were located on the area, in each of which presence estimates and per cent cover were recorded for each macroscopic plant species (exclusive of fungal fruiting bodies), along with soil profile data. Total lichen, moss, herb and seedling, shrub and sapling, and tree cover were determined for each quadrat by summing the cover values of the species in each category. Foot-candle readings were made for a random set of 100 of the quadrats, and soil volume-dry weight, moisture content, and pH determinations were made for another such set.

10. For analysis, the quadrats were placed into seven groups by soil type, the number of groups being later reduced to five by combination of contiguous types for the association studies. Per cent frequency and mean per cent cover of each species, and mean values of the recorded environmental variables, were determined for each of the seven original gradient segments. For the five segments left after combination, species-area curves were constructed, and Cole association coefficients were calculated for all possible pairs of non-arborescent species occurring above a given level of frequency in each gradient segment. The Cole coefficients were used to construct ordination-constellation figures for all soil segments but Roscommon, with correlations of the species with two environmental variables used as axes for the figures in each case. In these figures the species were placed along the axes according to their correlations with the two variables. Lines were drawn between the species symbols to show the magnitude of positive or negative association.

11. The vascular species for which Cole coefficients had been calculated were then divided into six groups, and for all

possible species pairs in each group, zero-order and highest order partial correlation coefficients were calculated. Where possible this was done for two or more segments of the gradient. With some groups, correlations with environmental variables were included also. Multiple correlations were calculated for each species or variable in each group. In addition, partial regression coefficients were calculated for all species combinations in one of the groups.

12. The Cole association coefficients show the tendency which pairs of species have to occur together or not to occur together. The zero-order correlation coefficients show the tendency for high or low cover values of species to occur together or to "repel" one another. The highest order partial correlation coefficients show the tendency of high cover values of two species to occur together when all other variables in a matrix are mathematically held constant. The regression coefficients show separately the tendency for high cover values of each species or high values of a variable to occur with high values of each other variable with which we are dealing.

13. The species-area curves suggest that sampling was adequate to characterize the area in all segments of the gradient save Roscommon soil. The flora is apparently richest in the "middle" segments of the gradient, and poor on both the "wet" and the "dry" ends. We might predict this, for general growing conditions seem to be more favorable in the "middle" than on either of the "ends", and there is a mixing of the bog and upland floras in the "middle".

14. Several observations suggest that the study area was burned for the last time about 60 years ago, but that it has otherwise been essentially undisturbed since. In this respect it probably does not differ markedly from similar areas in the Northern part of Michigan.

15. The Cole coefficients and ordinations suggest that the degree of association between species cannot be predicted solely on the basis of the similarity or dissimilarity of their correlations with one or two environmental variables. They also suggest that the vegetation as a whole tends to be non-randomly distributed, that it is distributed in lush clumps with interstices sparsely vegetated. Mossy patches seem to be generally favorable for lush cover of vascular species, whereas lichens seem to "prefer" the sparsely vegetated patches. On the upland, there seems to be a fairly marked tendency on the part of most species to be inhibited where humus is particularly deep, for whatever reasons, and also a slight tendency towards avoidance of the heaviest tree cover.

16. In general, on the basis of the work with the Cole coefficients and the six "groups", species do seem to exhibit both positive and negative association and correlation. Approximately 29 per cent of the association coefficients are significant at the 5 % level, about 16 per cent at the 1 % level, very much greater percentages than one would expect if the species were randomly distributed with respect to each other. The 21 per cent of the correlation coefficients which are significant at the 5 % level, and the 18 per cent significant at the 1 % level, strongly suggest that cover of the species is non-randomly distributed also.

17. It was possible to construct postulates concerning the causes of the association behavior of species in each intensively analysed group, and these hypotheses will serve as a basis for future experimental work.

18. We can say that the positive and negative associations and correlations between species seem to be due to similarities and differences in the tolerances of the species to environmental variables (e.g. humus depth and soil moisture), as well as to interaction.

19. Pairs of species that peak at about the same point on the gradient tend towards positive association and correlation where they are both near the limits of their range across the gradient. This is probably due to the generally similar requirements of the species, and to the fact that on these "fringes" of their ranges, sites where both can occur are limited. Probably because microsites where both species of such pairs can occur are more extensive on gradient segments where the species are near their optima, the association and correlation of such species on such segments is generally lower positively than it is at the margins of the range, or even negative. On such optimal sites small differences in niche requirements are more evident because the species are not "pushed together" on relatively small "islands".

20. Some species, notably the important shrubs and Pteridium, show a marked tendency towards negative association, and more particularly towards negative correlation with other species. This is perhaps because they inhibit the smaller species by cutting down the light reaching them, or because "antibiotic" substances are present in their litter, or because their litter covers the photosynthetic parts of smaller plants.

21. Discrepancies between zero-order and partial correlation coefficients for the same pair of species sometimes suggest interaction. Some positive interactions are suggested in addition to the negative interactions mentioned above, but the reasons for some of them are not at all clear. Some of the discrepancies are almost surely due to sampling error. In some cases, such discrepencies may be due to the partialling out of a third species which is associated with some microenvironmental factor with which both of the species for which the coefficients were calculated are associated also. Thus, the "interaction" may be vicarious.

22. Time factors seem to influence association patterns as do environmental and interactive factors. Several cyclic patterns are tentatively postulated: one is connected with the spread and senescence of clones of Pteridium aquilinum, Carex pensylvanica, and Vaccinium angustifolium on the upland, another with blowdown and subsequent profile development on the upland, and still another with hummock buildup and Chamaedaphne calyculata growth in the bog.

23. The standard regression coefficients calculated here do not seem to yield information different from that available from the highest order partial correlation coefficients.

24. The validity of the various techniques is suggested by the general good agreement of the coefficients with field observations, and the fact that species apparently similar in their ecological requirements are usually positively associated and correlated, and those which seem ecologically dissimilar negatively associated and correlated.

25. Surely some of the hypotheses proposed here will prove invalid upon testing, and some of the highly positive and negative coefficients may be due to chance. Through

experimental testing we can further delimit the possibilities, and gain a deeper insight into the phenomena causing the association patterns which are a part of the organization of biotic communities.

VII

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APPENDICES

APPENDIX A-1

COLE ASSOCIATION COEFFICIENTS

I - CALCULATION OF ASSOCIATION COEFFICIENTS. In calculating association coefficients (Cole 1949, 1957) between two species, the sample quadrats are assigned to four categories by sorting data code cards or data sheets. These are: "a", species A and species B both present, "b", species A present, species B absent, "c", species A absent, species B present, "d", species A and B both absent. The number in each category is then placed in the appropriate block in a 2 X 2 contingency table, and the marginal totals are obtained, as follows:

		SPECIES B present	SPECIES B absent	
SPECIES A	pres.	a	b	$a \neq b$
	abs.	c	d	$c \neq d$
		$a \neq c$	$b \neq d$	$a - b - c - d = N$.

As an example, we have the table for Maianthemum canadense (Mai) and Vaccinium angustifolium (Vang) on Grayling sand:

		MAI pres.	MAI abs.	
VANG	pres.	29	63	92
	abs.	2	26	28
		31	89	120 .

In this example, it is readily seen that there is a marked tendency for the quadrats to contain either both species or neither, rather than one or the other alone.

The following formulas are identical with those proposed by Cole (1957), except that a less complex notation is used. They give a coefficient of association between + 1 and -1.

$$1.\ C = \frac{\frac{ad - bc}{N}}{\left(\begin{array}{c}\text{b or c, which-}\\ \text{ever is smaller}\end{array}\right) + \left(\frac{ad - bc}{N}\right)}$$ (used when $ad > bc$, positive association).

$$2.\ C = \frac{\frac{ad - bc}{N}}{\left(\begin{array}{c}\text{a or d, which-}\\ \text{ever is smaller}\end{array}\right) - \left(\frac{ad - bc}{N}\right)}$$ (used when $ad < bc$, negative association).

For our example, we use the first formula, obtaining C = + .724.

II - CHI SQUARE TEST OF SIGNIFICANCE. For a 2 X 2 table, chi-square may be approximated by a short-cut formula (Greig-Smith 1957):

$$3.\ \chi^2 = \frac{(ad - bc)^2 N}{(a + c)(b + d)(c + d)(a + b)},$$

which is an approximation to the exact chi-square for a 2 X 2 table:

$$\chi^2 = \frac{\left(ad - bc - \frac{N}{2}\right)^2 N}{(a + c)(b + d)(c + d)(a + b)}.$$

For our example, using the approximate formula, $\chi^2 = 6.659$, which for one degree of freedom (in 2 X 2 tables df is always 1) is significant at the 1 % level.

APPENDIX A-2

ZERO-ORDER CORRELATION COEFFICIENTS

The zero-order correlation coefficients are found in the conventional fashion, as suggested for example by Snedecor (1956). However, they are arranged in a matrix so that they can be used later in finding highest order partial and multiple correlation coefficients, as well as standard partial regression coefficients, by the shortcut method devised by Clark (1953-59), which is presented in parts 3, 4, and 5 of Appendix A.

First, find $\sum X_i$, $\sum X_j$, and $\sum X_i X_j$ for each pair of species or other variables where:

$\sum X_i$ is the sum of values for the first variable,

$\sum X_j$ is the sum of values for the second variable,

$\sum X_i X_j$ is the sum of the products of the values of the two variables in each quadrat.

The values of $\sum X_i X_j$ are then arranged in a matrix:

	X_1	X_2	X_3	X_4
X_1	$\sum X_1^2$	$\sum X_1X_2$	$\sum X_1X_3$	$\sum X_1X_4$
X_2		$\sum X_2^2$	$\sum X_2X_3$	$\sum X_2X_4$
X_3			$\sum X_3^2$	$\sum X_3X_4$
X_4				$\sum X_4^2$

For example, we have the values for Group I, consisting of Gaultheria procumbens (Gau), Maianthemum canadense (Mai), Melampyrum lineare (Mel), Vaccinium angustifolium (Vang), and depth of leaf litter (lit):

	Gau	Mai	Mel	Vang	lit
Gau	200.56	27.06	6.31	466.16	982.80
Mai		16.07	1.95	92.93	201.20
Mel			4.79	76.26	135.50
Vang				7633.76	8053.40
lit					25194.00

.

Next, find $x_i x_j$ for each pair, by the formula:

1. $$\sum x_i x_j = \sum X_i X_j - \frac{(\sum X_i)(\sum X_j)}{N}$$,

where N is the number of quadrats in the sample. The values of $\sum x_i x_j$ are then arranged in a matrix as were the values of $\sum X_i X_j$, as follows. (Note that the symbol "x" (small "x") differs from "X" (large "X")).

	x_1	x_2	x_3	x_4
x_1	$\sum x_1^2$	$\sum x_1 x_2$	$\sum x_1 x_3$	$\sum x_1 x_4$
x_2		$\sum x_2^2$	$\sum x_2 x_3$	$\sum x_2 x_4$
x_3			$\sum x_3^2$	$\sum x_3 x_4$
x_4				$\sum x_4^2$

.

From our example, using the values of $\sum X$ for the five variables (Gau = 61.8, Mai = 14.4, Mel = 10.6, Vang = 541.0, lit = 1626.0), we have:

	Gau	Mai	Mel	Vang	lit
Gau	168.73	19.64	0.85	187.55	145.41
Mai		14.34	0.68	28.01	6.08
Mel			3.85	28.47	-8.13
Vang				5194.75	722.85
lit					3161.70

Now the zero-order correlation coefficients are calculated by the formula:

$$2.\quad r_{ij} = \frac{\sum x_i x_j}{\sqrt{\sum x_i^2 \sum x_j^2}} .$$

It is desirable to save the denominators, $\sqrt{\sum x_i^2 \sum x_j^2}$, in a separate matrix, since they will be used later in calculating the standard partial regression coefficients. The zero-order correlation coefficients are now arranged in a matrix:

$$\begin{matrix} r_{11} & r_{12} & r_{13} & r_{14} \\ & r_{22} & r_{23} & r_{24} \\ & & r_{33} & r_{34} \\ & & & r_{44} \end{matrix}$$

For the example, the zero-order correlation coefficients are:

	Gau	Mai	Mel	Vang	lit
Gau	1	.3993**	.0333	.2003*	.1991*
Mai		1	.0914	.1026	.0286
Mel			1	.2013	-.0737
Vang				1	.1784
lit					1 .

The above matrix is symmetrical (i. e. $r_{ij} = r_{ji}$), so that the lower left portion may be copied from the upper right portion. It is convenient to do this when the matrix is to be used to calculate highest order partial correlation coefficients.

It is usually sufficient to round these coefficients off to two or three decimal places, but if they are to be used in order to find the highest order partial correlation coefficients, then at least four places are necessary.

The significance of these coefficients is read directly from the usual correlation tables, such as that on p. 174 of Snedecor (1956), with N - 2 degrees of freedom (N = number of quadrats). The significance of the figures above is indicated by a single asterisk (*) after the figure for significance at the 5 % level, and a double asterisk (**) for significance at the 1 % level.

APPENDIX A-3

HIGHEST ORDER PARTIAL CORRELATION COEFFICIENTS

The matrix of zero-order correlation coefficients (r_{ij}), which we have obtained (Appendix A-2), is now placed in the upper left-hand corner of a larger matrix, with the identity matrix in the upper right (see below). The combined correlation and identity matrix is now "reduced" by the square root method (Dwyer 1951) as follows:

r_{11}	r_{12}	r_{13}	r_{14}	1	0	0	0
r_{21}	r_{22}	r_{23}	r_{24}	0	1	0	0
r_{31}	r_{32}	r_{33}	r_{34}	0	0	1	0
r_{41}	r_{42}	r_{43}	r_{44}	0	0	0	1
s_{11}	s_{12}	s_{13}	s_{14}	s_{15}	s_{16}	s_{17}	s_{18}
	$s_{22.1}$	$s_{23.1}$	$s_{24.1}$	$s_{25.1}$	$s_{26.1}$	$s_{27.1}$	$s_{28.1}$
		$s_{33.2}$	$s_{34.2}$	$s_{35.2}$	$s_{36.2}$	$s_{37.2}$	$s_{38.2}$
			$s_{44.3}$	$s_{45.3}$	$s_{46.3}$	$s_{47.3}$	$s_{48.3}$.

The various values of s_{ij} and $s_{ij.h}$ are found as follows.

(1) The values of s_{ij} are identical with the corresponding values of r_{ij}. Thus the top row of the s-matrices may be copied directly from the top row of the r- and identity matrices;

$$1. \quad s_{ij} = r_{ij},$$

for example:

$$s_{12} = r_{12}, \qquad s_{16} = 0.$$

(2) The diagonals in the lower left s-matrix ($s_{ii.h}$) are found by subtracting the squares of all the terms which are <u>above</u> this diag-

onal term in the s-matrix, namely $s_{ij.h}$, from the corresponding r_{ii}, and taking the square root of this quantity;

$$2.\ s_{ii.h} = \sqrt{r_{ii} - s^2_{(i-1)i.h-1} - s^2_{(i-2)i.h-2} - \cdots - s^2_{2i.1} - s^2_{1i}}\ ,$$

for example:

$$s_{44.3} = \sqrt{r_{44} - s^2_{34.2} - s^2_{24.1} - s^2_{14}}\ ,$$

$$s_{22.1} = \sqrt{r_{22} - s^2_{12}}\ .$$

(3) Each of the other s-values ($s_{ij.h}$) is obtained by first multiplying each value in the column above it in the s-matrix ($s_{(i-1)j.h-1}$, $s_{(i-2)j.h-2}$, etc.) by the term in the same row as the latter value, but in the column containing the diagonal ($s_{ii.h}$) of the row in which the value we are trying to find lies ($s_{(i-1)i.h-1}$, $s_{(i-2)i.h-2}$, etc.). "Diagonal" in this case refers to the lower left matrix only. These products are summed, and the sum is subtracted from the r-value (r_{ij}) corresponding to the value we wish to find. The difference is then divided by the diagonal of the row in which the unknown lies, namely $s_{ii.h}$. Thus:

$$3.\ s_{ij.h} = \frac{r_{ij} - (s_{(i-1)j.h-1})(s_{(i-1)i.h-1}) - (s_{(i-2)j.h-2})(s_{(i-2)i.h-2}) - \cdots - (s_{2j.1})(s_{2i.1}) - (s_{1j})(s_{1i})}{s_{ii.h}}\ ,$$

for example:

$$\frac{0 - s_{35.2}s_{34.2} - s_{25.1}s_{24.1} - s_{15}s_{14}}{s_{44.3}}\ ,$$

$$s_{27.1} = \frac{0 - s_{17}s_{12}}{s_{22.1}}$$

Now, we obtain the inverse of the correlation matrix (c_{ij} matrix) from the reduced identity matrix (the matrix in the lower right in the table at the beginning of Appendix A-3). For a particular value of c_{ij}, each value in column "$i \neq 1$" is multiplied by the corresponding value in column "$j \neq 1$" (n being equal to the number of columns in the left-hand matrices), and the products are summed;

$$4.\ c_{ij} = (s_{1(i\neq n)})(s_{1(j\neq n)}) + (s_{2(i\neq n).1})(s_{2(j\neq n).1}) + \cdots + (s_{n(i\neq n).n-1})(s_{n(j\neq n).n-1}) \ .$$

for example:

$$c_{23} = s_{16}s_{17} + s_{26.1}s_{27.1} + s_{36.2}s_{37.2} + s_{46.3}s_{47.3} \ .$$

Arranging these values in matrix form, we have: .

$$\begin{matrix} c_{11} & c_{12} & c_{13} & c_{14} \\ c_{21} & c_{22} & c_{23} & c_{24} \\ c_{31} & c_{32} & c_{33} & c_{34} \\ c_{41} & c_{42} & c_{43} & c_{44} \end{matrix} \ ,$$

the matrix being symmetrical ($c_{ij} = c_{ji}$).

As a check, we can multiply the c_{ij} matrix by the r_{ij} (zero-order correlation coefficient) matrix, which should yield the identity matrix. To get the value in the ith row, jth column of the identity matrix, multiply each of the values in the ith column of the c_{ij} matrix by the corresponding value in the jth column of the r_{ij} matrix, and sum these products. For example:

$$r_{12}c_{13} + r_{22}c_{23} + r_{32}c_{33} + r_{42}c_{43} = 0 \ ,$$

$$r_{14}c_{14} + r_{24}c_{24} + r_{34}c_{34} + r_{44}c_{44} = 1 \ .$$

For our example of Appendix A-2, we obtain the following matrices.

Negative values are underlined in order to save space.

r_{ij}	Gau	Mai	Mel	Vang	lit					
Gau	1	.3993	.0333	.2003	.1991	1	0	0	0	0
Mai	.3993	1	.0914	.1026	.0286	0	1	0	0	0
Mel	.0333	.0914	1	.2013	.0737	0	0	1	0	0
Vang	.2003	.1026	.2013	1	.1784	0	0	0	1	0
lit	.1991	.0286	.0737	.1784	1	0	0	0	0	1
s_{ij}	1	.3993	.0333	.2003	.1991	1	0	0	0	0
		.9168	.0852	.0247	.0555	.4355	1.0908	0	0	0
			.9958	.1933	.0759	.0038	.0933	1.0042	0	0
				.9602	.1610	.1982	.0093	.2022	1.0414	0
					.9621	.1986	.0571	.1129	.1733	1.0394

c_{ij}

1.2684	.4849	.0215	.1720	.2064
.4849	1.2019	.0854	.0196	.0593
.0215	.0854	1.0620	.2301	.1173
.1720	.0196	.2301	1.1145	.1801
.2064	.0593	.1173	.1801	1.0804

Identity matrix (c_{ij} matrix times r_{ij} matrix)

.9999	.0001	.0000	.0001	.0002
	1.0001	.0000	.0000	.0001
		.9999	.0000	.0001
			1.0000	.0001
				1.0002

This "check" identity matrix suggests that there have been no errors in the calculations save those caused by rounding off to four places, or that if there are other errors they are very slight.

All the highest order partial correlation coefficients, $r_{ij.h}$, are now obtained by the formula;

$$5.\ r_{ij.h} = \frac{-c_{ij}}{\sqrt{c_{ii}c_{jj}}} ,$$

for example:

$$r_{12.34} = \frac{-c_{12}}{\sqrt{c_{11}c_{22}}} ,$$

$$r_{24.13} = \frac{-c_{24}}{\sqrt{c_{22}c_{44}}} .$$

As with the zero-order correlation coefficients, significance of the highest order partial correlation coefficients is ascertained directly from tables such as those on p. 174 of Snedecor (1956), with N - (h/2) degrees of freedom, with N sets of observations (quadrats) and h variables partialled out. For our example we obtain:

	Gau	Mai	Mel	Vang	lit
Gau	-	.393**	-.019	.145	.176
Mai		-	.076	.017	-.052
Mel			-	.211*	-.109
Vang				-	.164
lit					-

where significance at the 5 % level is indicated by a single asterisk (*) after the figure, and significance at the 1 % level by a double asterisk (**).

APPENDIX A-4

MULTIPLE CORRELATION COEFFICIENTS

These coefficients show the correlation between a particular variable, which we shall call "y", and several others. In the present study, multiple correlations are calculated between each variable in a matrix and all of the others.

The matrix of zero-order correlation coefficients (Appendix A-2) must be arranged so that the zero-order correlation coefficients of "y" with each other variable are in the right-hand column. This correlation matrix must then be reduced by the technique given in Appendix A-3, except that $s_{yy.h}$ need not be found. The multiple correlation coefficient between variable y and all the others ($R_{y.h}$) is then found by taking the square root of the sum of squares of all $s_{iy.h}$ values in the right-hand column of the reduced correlation matrix (the lower left matrix on p. 239) except $s_{yy.h}$. Using the matrix on p. 239, we have:

$$R_{4.123} = \sqrt{s^2_{14} + s^2_{24.1} + s^2_{34.2}} \quad .$$

This formula may also be applied in a stepwise fashion, thus:

$$R_{4.1} = \sqrt{s^2_{14}} \quad , \qquad R_{4.12} = \sqrt{s^2_{14} + s^2_{24.1}} \quad , \qquad \text{etc.}$$

If a correlation matrix and a reduced correlation matrix have already been obtained, one can save time by keeping rows and columns of this correlation matrix in the original order, as each multiple correlation coefficient is calculated, except for the row and column representing variable "y" which are placed to the bottom and right. If n rows lie above the interchanged row "y" in the original correlation matrix, then the first n rows in the reduced correlation matrix may be copied directly from the original $s_{ij.h}$-matrix, taking care to

rearrange columns to correspond to the rearrangement in the r_{ij} matrix. Thus with k variables, the reduced correlation matrix must be completely recalculated for $x_1 = y$, but for $x_{k-2} = y$ we need only recalculate five s-values, for $x_{k-1} = y$ only two, and for $x_k = y$ none.

The significance of $R_{i.h}$ may be conveniently tested by the F-test:

1. $$F = \frac{R^2/P}{1-R^2/N-P-1},$$

where degrees of freedom are P and N - P - 1 for the numerator and denominator, respectively. N is equal to the number of sets of observations (quadrats), and P is the number of independent variables or "predictors" (the number of variables in the matrix minus one).

For our example from Appendices A-2 and A-3, we have:

SPECIES or VARIABLE

Gau	$R_{1.2345} = .460^{**}$,	F = 7.719
Mai	$R_{2.1345} = .410^{**}$,	F = 5.800
Mel	$R_{3.1245} = .242$,	F = 1.786
Vang	$R_{4.1235} = .308^{*}$,	F = 3.006
lit	$R_{5.1234} = .272$,	F = 2.298 ,

where one asterisk after the figure (*) indicates significance at the 5 % level, and two asterisks (**) indicate significance at the 1 % level.

APPENDIX A-5

STANDARD PARTIAL REGRESSION COEFFICIENTS

The first steps in the calculation of these regression coefficients is the same as the first steps in the calculation of correlation coefficients, and the reader is refered to Appendices A-2 and A-3 for formulas and procedures. Recapitulating these steps briefly, with the necessary modifications: (1) obtain all the sums of squares and products of deviations from the mean ($\sum x_i^2$, $\sum x_i x_j$), and arrange in a matrix; (2) compute all the zero-order correlation coefficients, retaining the denominators ($\sqrt{\sum x_i^2 \sum x_j^2}$) in a matrix for later use; (3) construct the correlation matrix, as shown on p. 239, but leave out the value of x_i which is to be the dependent variable, y; (4) obtain the matrix of the inverses of the zero-order correlation coefficients r_{ij}, namely c_{ij}, as explained in Appendix A-3; (5) check the latter, as before, by multiplying by the r_{ij} matrix in appropriate fashion.

Still using our example from Appendices A-2 and A-3, if we wish to let x_2, Mai, be equal to y, we obtain:

$\sum x_i x_j$	Gau-x_1	Mel-x_3	Vang-x_4	lit-x_5	Mai-y
x_1	168.73	0.85	187.55	145.41	19.64
x_3	0.85	3.85	28.47	-8.13	0.68
x_4	187.55	28.47	5194.75	722.85	28.01
x_5	145.41	-8.13	722.85	3161.70	6.08
y	19.64	0.68	28.01	6.08	14.34

(By comparing the above with the matrix on the bottom of p. 236, one can see that the two are identical except that the row and column representing x_2 in the latter are labeled "y", and are placed to the bottom and right, respectively).

$\sqrt{\Sigma x_1^2 \Sigma x_2^2}$

	x_1	x_3	x_4	x_5	y
x_1	168.73	25.49	936.22	730.39	49.19
x_3		3.85	141.42	110.33	7.43
x_4			5194.75	4052.68	272.93
x_5				3161.70	212.93
y					14.34

(Negative values are underlined in the following matrices).

r_{ij}	x_1	x_3	x_4	x_5				
x_1	1	.0333	.2003	.1991	1	0	0	0
x_3	.0333	1	.2013	.0737	0	1	0	0
x_4	.2003	.2013	1	.1784	0	0	1	0
x_5	.1991	.0737	.1784	1	0	0	0	1
s_{ij}	1	.0333	.2003	.1991	1	0	0	0
		.9994	.1947	.0804	.0333	1.0006	0	0
			.9602	.1606	.2016	.2029	1.0414	0
				.9634	.1752	.1173	.1736	1.0380

c_{ij}

1.0727	.0130	.1794	.1825
.0130	1.0561	.2317	.1218
.1794	.2317	1.1147	.1802
.1825	.1218	.1802	1.0774

Identity matrix (c_{ij} matrix times r_{ij} matrix)

1.0000	.0000	.0003	.0000
	1.0000	.0000	.0000
		1.0000	.0000
			.9999 .

It is well to note here that the $\sum x_i x_j$, r_{ij}, and identity matrices are identical to the corresponding matrices for the correlation coefficients, but with the row and column for values of y omitted or (in the $\sum x_i x_j$ matrix) changed in position. So if the correlation coefficients have already been calculated these need not be redone. The "lower" matrices ($s_{ij.h}$ matrices), on the other hand, may be copied, keeping all values in the same order as in the correlation matrices with the y column omitted, only as far down as the omitted row, and from this point on must be recalculated. The inverse of the correlation matrix (c_{ij}) must be completely redone, as must the check.

We now obtain the inverse of the matrix of sums of squares and products, d_{ij}, by the formula;

$$1.\ d_{ij} = \frac{c_{ij}}{\sqrt{\sum x_i^2 \sum x_j^2}} ,$$

using the values from the inverse of the correlation matrix and from the matrix of denominators used in calculating the zero-order correlation coefficients. For example:

$$d_{23} = \frac{c_{23}}{\sqrt{\sum x_2^2 \sum x_3^2}} .$$

The various partial regression coefficients ($b_{iy.h}$) are now obtained from the formula;

$$2.\ b_{iy.h} = d_{i1}\sum x_1y + d_{i2}\sum x_2y + \dots + d_{in}\sum x_ny = \sum(d_{ij}\sum x_jy) \quad ,$$

where i is constant and j is variable. For example:

$$b_{32.145} = d_{31}\sum x_1y + d_{33}\sum x_3y + d_{34}\sum x_4y + d_{35}\sum x_5y.$$

The error, ss, is obtained from:

$$3.\ ss = y^2 - b_{1y.h}\sum x_1y - b_{2y.h}\sum x_2y - \dots - b_{ny.h}\sum x_ny \quad ,$$

with N - p - 1 degrees of freedom, N observations (quadrats), and p independent variables. Consequently, we obtain the variance from the formula;

$$4.\ s^2_{y.h} = \frac{ss}{N - p - 1} \quad ,$$

and the standard deviation is found in the usual fashion by taking the square root of the above. We also have the formula for the variance of the individual regression coefficients;

$$5.\ s_{b_{iy.h}} = \sqrt{c_{ii}}\,(s_{y.h})$$

The t-test is used to test the significance of each of these coefficients, as follows;

$$6.\ t_{b_{iy.h}} = \frac{b_{iy.h}}{s_{b_{iy.h}}} \quad .$$

It is convenient to arrange the various values in a particular form in a table, as demonstrated by using the figures from our example. Negative values are underlined in this table.

$x_i y$	(Gau) 19.64	(Mel) 0.68	(Vang) 28.01	(lit) 6.08	$\sqrt{d_{ii}}$
d_{ij}	.0063575	.0005101	.0001916	.0002499	.079734
	.0005101	.2743117	.0016384	.0011040	.523748
	.0001916	.0016384	.0002146	.0000445	.014649
	.0002499	.0011040	.0000445	.0003408	.018461
$b_{iy.h}$	.118	.137	.001	.003	

$y^2 = \text{Mai} = 14.34$ $\quad s_{y.h} = \sqrt{.10364826} = 0.3219445$

$s_{b_{iy.h}}$	.026	.169	.005	.006
$t_{b_{iy.h}}$	4.538**	.811	.200	.500

If now the standardized regression coefficients, $\beta_{iy.h}$ (which are pure numbers comparable to the highest order partial correlation coefficients) are wanted, they may be computed from:

$$7. \quad \beta_{iy.h} = b_{iy.h} \sqrt{\Sigma x_i^2 / \Sigma y^2} \quad .$$

For our example, we have:

$$\beta_{12.345} = .405^{**}$$

$$\beta_{32.145} = .071$$

$$\beta_{42.135} = .019$$

$$\beta_{52.134} = .045 \quad ,$$

where two asterisks (**) after the figure indicate significance at the 1 % level.

APPENDIX B

CRITERIA USED TO SEPARATE SOIL TYPES

SOIL TYPE*	SYMBOL	LIMITS OF TYPE AS HERE DEFINED*
GRAYLING	G	A_2 depth 0-14 mm., or A_2 depth 15-19 mm., B color 1 to 2 on an arbitrary scale, or A_2 depth 20-24 mm., B color 1.
"WET GRAYLING"	WG	A_2 depth 15-19 mm., B color 2.5 to 3, or A_2 depth 20-24 mm., B color 2 to 3, or A_2 depth 25-49 mm., B color 1 to 3.
CROSWELL	C	A_2 depth 25-49 mm., B color 3.5 to 5, or A_2 depth 50 mm. or over. } $A_{o_L} \neq A_{o_m} \neq A_{o_H}$ depth under 50 mm., and/or B texture "unconsolidated".
AU GRES	AG	B texture "chunky", or B texture "crumbly", $A_{o_L} \neq A_{o_m} \neq A_{o_H}$ depth over 80 mm.
SAUGATUCK	S	B texture "cemented", A_{o_H} depth under 90 mm.
ROSCOMMON (and "WET SAUGATUCK")	R	B texture "crumbly", or B texture "unconsolidated" or "chunky", A_1 depth over 50 mm., or B texture "cemented", A_{o_H} depth over 90 mm. } B color 5, A_{o_H} depth under 12 inches.

* See p. 253.

SOIL TYPE*	SYMBOL	LIMITS OF TYPES AS HERE DEFINED*
DAWSON PEAT	DG	A_{O_H} depth 12-42 inches.
GREENWOOD PEAT		A_{O_H} depth over 42 inches.

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* Some of the soil "types" used here, for the sake of convenience, are not types recognized by the Michigan Department of Agriculture (McKenzie and Whiteside, 1956), and the descriptions of the types are not to be regarded as "official" designations. B color, on a scale from 1 to 5, refers to the degree of brown ferrous-organic color in the horizon, with 1 designating the least and 5 the most coloration.

APPENDIX C-1

SPECIES SYMBOLS USED IN TABLES, FIGURES, AND TEXT

SYMBOL	SPECIES NAME*
Anem	Anemone quinquefolia
Bra	(M) Brachythecium salebrosum
Cal	(M) Calliergonella schreberi
Car	Carex pensylvanica
Cham	Chamaedaphne calyculata
Com	Comptonia peregrina
Cop	Coptis groenlandica
Corn	Cornus canadensis
Cran	(L) Cladonia rangiferina
Cris	(L) Cladonia cristatella
Cup	(L) Cladonia pixydata-group ("cup" Cladonias)
Dan	Danthonia spicata
Dic	(M) Dicranum undullatum
Epig	Epigaea repens
Erio	Eriophorum spissum
Gau	Gaultheria procumbens
Kal	Kalmia polifolia
Led	Ledum groenlandicum
Mai	Maianthemum canadense

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* See p. 255.

SYMBOL	SPECIES NAME*
Mel	Melampyrum lineare
Opun	Oryzopsis pungens
Oras	Oryzopsis asperifolia
Prun	Prunus serotina
Pter	Pteridium aquilinum
Rho	Rubus hispidus var. obovalis
Spha	(M) Sphagnum spp.
Tri	Trientalis borealis
Vam	Vaccinium myrtilloides
Vang	Vaccinium angustifolium (both varieties)
Vig	Vaccinium angustifolium var. nigrum
Voxy	Vaccinium oxycoccus
Vvp	Vaccinium angustifolium "typical"

* Mosses are designated by an (M) preceding the species name, lichens by an (L). Names without prefixes designate vascular species.

APPENDIX C-2

PARAMETER SYMBOLS USED IN TABLES, FIGURES, AND TEXT

SYMBOL	ENVIRONMENTAL PARAMETER DESIGNATED
hum	depth of the A_{O_H} horizon of the soil profile.
lit	depth of loose leaf litter (A_{O_L} horizon of the soil profile).
mat	depth of the loose mat of dead Sphagnum and Polytrichum moss in the bog
moss	percent cover of mosses (mostly Sphagnum and Polytrichum) in the bog quadrats
tre	percent cover of the tree canopy above the quadrats

APPENDIX C-3

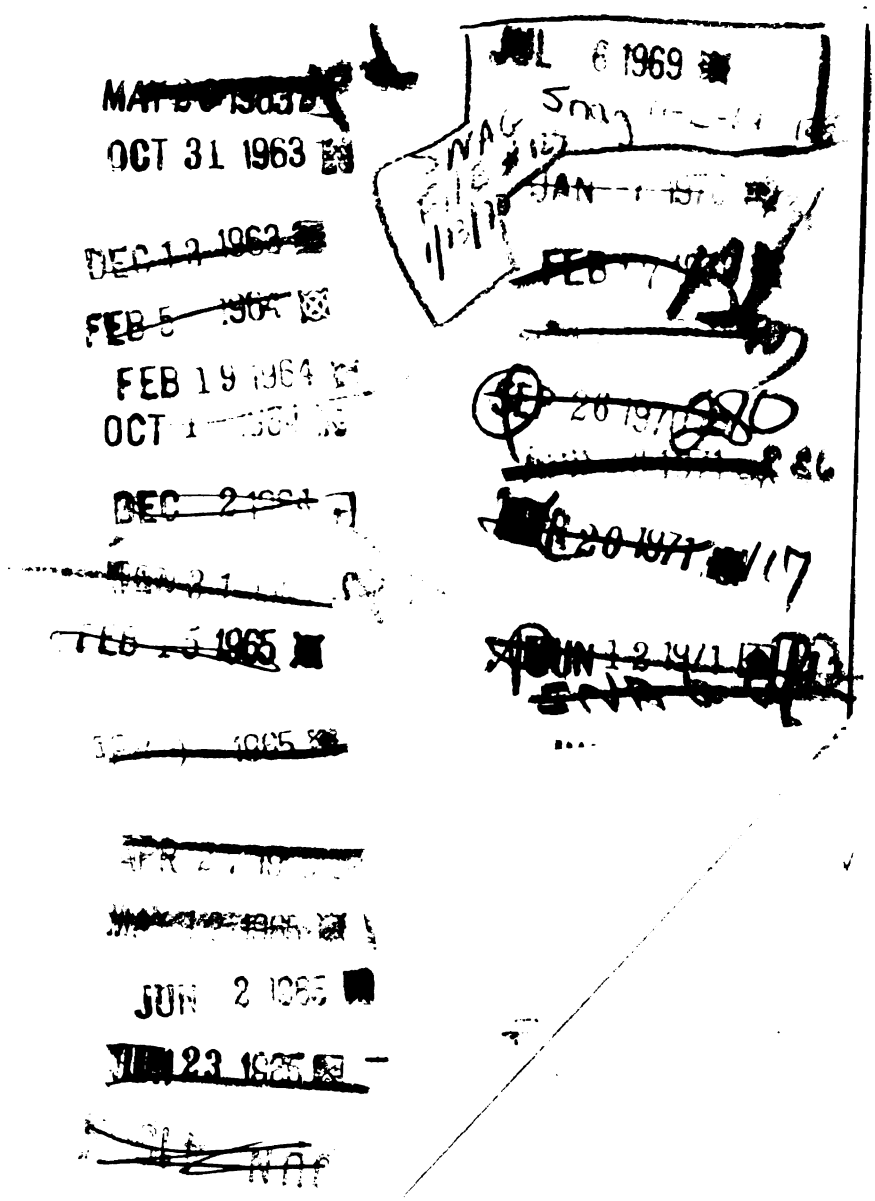
SOIL TYPE SYMBOLS USED IN TABLES, FIGURES, AND TEXT

SYMBOL	SOIL TYPE*
a - individual soil types	
G	GRAYLING SAND
WG	"WET GRAYLING" SAND
C	CROSWELL SAND
AG	AU GRES SAND
S	SAUGATUCK SAND
R	ROSCOMMON SAND (including "WET SAUGATUCK")
DG	DAWSON PEAT GREENWOOD PEAT
b - combined soil types (gradient segments)	
G	GRAYLING SAND
WG-C or WGC	WET GRAYLING-CROSWELL SAND
AG-S or AGS	AU GRES-SAUGATUCK SAND
R	ROSCOMMON SAND
DG	DAWSON-GREENWOOD PEAT

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* The soil types named here are based upon types designated by the Michigan Department of Agriculture (McKenzie and Whiteside, 1956), but their primary use here is as reference points for the division of the gradient into convenient "homogeneous" segments. The names and delimiting characters of these types do not correspond exactly to standard definitions.

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