PATTERN ANALYSIS
ALONG A
PINUS-CHAMAEDAPHNE TRANSITION
AS A KEY TO
VEGETATIONAL STRUCTURE AND ORGANIZATION

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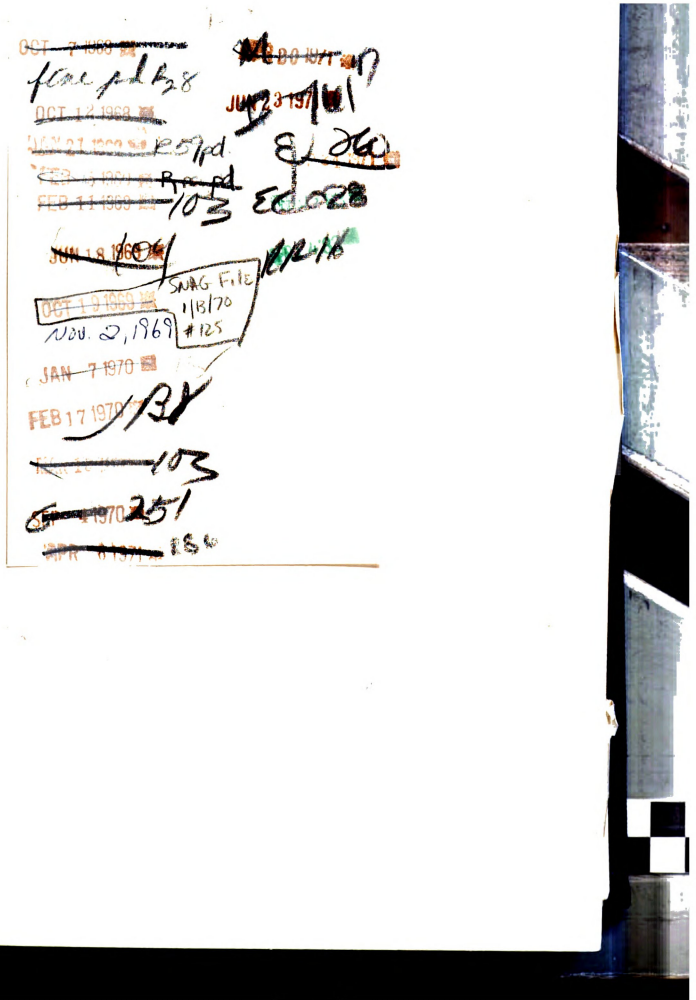
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PATTERN ANALYSIS ALONG A *PINUS-CHAMAEDAPHNE* TRANSITION AS A KEY TO VEGETATIONAL STRUCTURE AND ORGANIZATION

By

Michael Daniel Byer

AN ABSTRACT OF A THESIS

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ABSTRACT

PATTERN ANALYSIS ALONG A
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by Michael Daniel Byer

This study investigates the use of microdistribution and interspecific association patterns as possible tools for unravelling the cause-effect heirarchy of biological community organization. Changes in these patterns along a gradient of soil drainage and development, with its associated vegetational transition from *Pinus banksiana* forest on the well-drained soils to open *Chamaedaphne calyculata* bog on the most poorly-drained sites, were also examined for clues to this heirarchy. The spatial scale of patterns, investigated via quadrats of different sizes, also proved helpful.

Measures of association are designed to show whether high values of two species or other variables are found together more frequently (positive association) or less frequently (negative association) than one would expect of entities independently distributed with respect to each other. Here, a number of correlation and regression measures proved their worth, as have these and other techniques

in previous studies. Used here were the phi coefficient (ϕ), which shows the degree to which two species tend to occur in the same or in different quadrats, the zero-order product-moment correlation coefficient (r), which measures the tendency for high values (i.e. per cent cover or thickness in this study) of species and other variables to occur together, the first-order partial correlation coefficient ($r_{ij.h}$), which determines the influence of correlations with other single variables on the correlation between particular variable pairs, and the fitting of linear, quadratic and cubic regression curves.

The uniqueness of the present study lies largely in its examination of environmentally-related changes in association and in its use of several association measures in conjunction. The great bulk of pattern studies use only one method, thereby examining but one property of patterns which have a multiplicity of properties. The use of several techniques and the study of changes lessen the chance that we, like the blind men examining the elephant, may emerge from our data with an impression completely out of proportion with respect to reality.

Attempts to place the species into natural mutually positively associated groupings by means of simple mathematical formulas based upon these association measurements

seem not to yield meaningful answers, at least in the vegetation studied. Perhaps the grouping tendencies within it are too complex to produce such distinct units. Moreover, there are various theoretical objections to such grouping techniques, for in attempting to oversimplify extremely complex situations they may tend to obscure rather than reveal relationships. It is therefore postulated that the several grouping techniques tested are best used merely as guides, or reserved for those cases where one has reason to suspect a distinct vegetational mosaic to begin with. An effort is made here, instead, to "subjectively" reconstruct organizational hierarchies on the basis of all the available information about the species involved.

An abundance of non-random microdistribution of species with respect both to one another and to variables of the physical environment, within relatively homogeneous gradient segments, is clearly demonstrated in the study area. This comes as no suprise, in the light of the findings of similar studies and of the theoretical improbability of randomness in nature. Part of the demonstrated pattern may be attributable to large-scale heterogeneity within gradient segments, and as might be expected positive and negative associations seem stronger on the physically more heterogeneous segments, but a major portion can only

be explained by small-scale, or microdistributional responses of the species.

A tendency of xerophytic species to exhibit stronger positive and negative correlations on the margins of their ranges across the gradient than on those segments where they reach their greatest abundance and vigor is perhaps a consequence of greater sensitivity to small changes where conditions approach the tolerance limits of the species, and of those portions of the marginal segments least similar to a species' optimal habitat being unsuited to it. An opposite trend, i.e. a general reduction in positive intercorrelation among them near their range margins, may be related to a reduction in competitive vigor as conditions close to the tolerance limits of these species are approached.

The larger, more abundant, and more clonal species seem, in general, to exhibit stronger correlations, probably because they themselves constitute a strong patterning force with their large sphere of interactive influence and ability to exclude spatially the entry of other species into a microsite. But on all but the most poorly-drained gradient segment, there is an overwhelming preponderance of positive over negative interspecific correlation, apparently reflecting a relatively large-scale patterning of

areas more and less favorable to plant growth generally. Thus the preponderance of relatively weakly positive, circumneutral or slight negative correlations of the rarer and smaller species suggests inability of these plants to survive or grow well with the larger and more abundant species. Probably in this community the former play the role of opportunists temporarily utilizing unoccupied space (and hence do not reach clonal size or large dimensions), and it is postulated that such opportunists may be an important component of natural communities in general.

In contrast to the aforementioned large-scale environmental variations which produce predominantly positive correlations, there seems, on the basis of changes in correlation with quadrat size and distributions of positive and negative correlation values, to be a small-scale interspecific competition and spatial exclusion effect which tends to produce negative association. This combination of large-scale environmental, small-scale interactive patterning is in agreement with the findings of other studies, and is corroborated by the much higher proportion of high positive ϕ coefficients (based upon presence or absence) than of r_s (based upon per cent cover). The larger scale patterning, according to this hypothesis, must tend to

bring most species together in the favorable patches, where interaction tends to preclude luxuriant growth of any one of them near heavy cover of another.

The "environmental" factors considered in this study, namely cover of vegetation synusia, thickness and cover of litter, and thickness of soil horizons, are relatively weakly correlated with species, especially the second. Perhaps these factors are not the ones most directly influencing species performance here, or perhaps interspecific interaction is really a more important pattern-inducing force here than the physical part of the plants' environment.

Field experiments were designed to test separately the responses of selected species to the environmental gradient and to certain other species. The species were selected on the basis of changes in correlation or unusual patterns of correlation and association discovered in a preliminary study. Seed, seedling, and mature plant performance were tested.

These experiments demonstrated that representative species of the poorly-drained and imperfectly-drained segments of the gradient are not excluded from the better-drained portions by any inability to survive there, as

adults, in the absence of natural interspecific interaction. There is an indication, from plots soon excessively flooded for further plant survival, that certain species naturally restricted to well-drained and intermediately-drained soils might be able to survive on poorly-drained organic soils under artificial culture conditions. In these excessively flooded plots, there seemed to be no semblance of proportionality between ability to survive inundation and a species' natural position on the drainage gradient. With one and possibly two bog species, inability of seeds to germinate on inorganic soil clearly seems to be one factor which could limit their spread to such soils, but with the tested species native to inorganic soils there is no demonstrable difference in ability to germinate across the whole range of soil-drainage conditions. Most probably, then, species distributions across the gradient are limited primarily by ability of adults to spread vegetatively under natural conditions of interspecific interaction, but in some cases by germination and seedling survival requirements.

Growth rates and vigor, as estimated from various morphological measurements, as well as performance in a manipulated environment (in this case one having exces-

sively droughty conditions) show up much more difference between species, and within the same species on different gradient segments, than do straight survival measurements. The former two thus show more promise as keys to the physio-ecological nature of species than does the latter. The more sophisticated measurements sometimes yield results unexpected from species' natural distributions, although in the case of the manipulated environment some of the differences seem attributable to differences in transplant hardiness.

Controlled experiments designed to test interaction between species deal more directly with the major questions of a study such as this one than do simple transplant experiments. Unfortunately, meaningful results were obtained from only two such experiments.

As to specific patterns found in this study area, moss and lichen cover as a whole, as well as individual species within these categories, show a bimodal distribution across the gradient. Although the primary moss species are relatively mesophytic and the lichen species relatively xerophytic, members of both categories seem to require sites sparsely covered by litter or vascular plants, and the low points of moss and lichen cover seem to be re-

lated respectively to a scarcity of bare patches and a maximum of vascular plant ground cover. This ground cover is itself perhaps reduced by thick litter cover, possibly because this litter retards soil warming necessary to vigorous bud expansion in the spring.

Also noteworthy are two mutually positively correlated groupings of species among those which seem to reproduce primarily from seed in the study area; they are likely brought about by similarities in germination or seedling survival requirements among the grouping members. There is a distinct tendency on the better-drained inorganic soils for the more xerophytic species to have an affinity for Carex pensylvanica, the more mesophytic ones to have an affinity for Vaccinium species. Thus, these two dominant entities may be visualized as the nuclei of two "phases" in the vegetation, but these "phases" are by no means clear-cut spatially, and the two dominants themselves are found together in all sorts of combinations. The "phases" are therefore best thought of merely as trends.

A probable inhibition of understory species by Prunus serotina litter and an apparent strong interaction between Coptis groenlandica and Cornus canadensis are other highlights suggested by the correlation analyses of the

mineral soil segments.

In the bog, mature Chamaedaphne calyculata and other shrubs seem to inhibit herbs and Sphagnum moss, and possibly a shrub and an herb-Sphagnum stage are associated in a cycle of hummock buildup and breakdown. Rarity of interspecific interdigitation between shrub clones suggests a strong amensal reaction between bog shrub species or their associated mycorrhizae.

Incidentally, the study provides some evidence which might be helpful in solving a taxonomic problem. Two phyletically close Vaccinium taxa, which have essentially identical overall distributions and cover modes across the gradient, show differences in their association patterns of about the order of magnitude exhibited by distinct species. They must represent two partially or completely isolated gene pools, each with its own unique potential for environmental response and niche occupancy. Such isolation could result from one entity being diploid V. boreale, the other tetraploid V. angustifolium var. nigurm, which morphological evidence suggests to be the case.

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CHAPTER I

INTRODUCTION

Statistics is regarded today by virtually all scientists as one of the basic weapons in their arsenal. So universal is the acceptance of biometric techniques for the objective testing of hypotheses that we are, perhaps, too seldom moved to question their worth. Yet these methods are most frequently used to help answer specific questions which one has in mind. Nonetheless, it is in the nature of science, as indeed of any inquiry into the nature of the universe, that we sometimes come upon areas fertile for investigation, but so unexplored that we simply do not know <u>what</u> questions to ask. In such cases, a statistical procedure which would suggest the best places to start investigation would be most helpful.

The organizational basis of a biological community is, I submit, a little known area which could benefit from just such treatment. On the one hand, we have excellent autecological "life history" studies of many species, in which the performance of organisms is too frequently viewed as a result of physiological reactions to rather than in-

teractions with an integrated biotic-abiotic system. On the other, we have a fairly recent body of descriptions of the detailed structure of the communities containing such species. Yet this structure must surely result in large measure from the nature and activities of the individual species making up the vegetation. Only by using the two approaches in conjunction can we avoid the "apparently barren nature of some statistical work in ecology" which Greig-Smith (1964) attributes to failure to recognize empirical description of structure as "a starting point for further investigation of the factors responsible and not an end in itself". The autecological study of a whole natural assemblage of organisms is vastly more complex than the investigation of a single species' interrelationships with its environment. Statistical procedures revealing the distribution patterns resulting from the interactions among the biotic and abiotic components of the assemblage help to suggest which, among literally thousands of possible experiments involving these species, should prove most rewarding. Thus one may avoid the fruitless testing of countless postulates which the existing structural patterns indicate to be false.

The present thesis, representing some earlier ef-

forts in a projected continuing study, is necessarily largely descriptive and concerned with methods. But it is done in the spirit of thus using statistics primarily to suggest questions rather than to test the validity of hypotheses already formulated. By pointing the way to some of the best avenues of investigation and contraindicating many which are doomed to failure, it will hopefully make possible, in the long run, a far greater return per unit of expended energy than would otherwise be obtainable. Thus the seeming prodigality of the vast initial calculation operation may be compensated many times over. Besides, the organizational analysis of whole communities, which is thus greatly facilitated, should in the end also prove more productive than isolated life history studies done with only rudimentary knowledge of, or regard for, the communities which the organisms occupy. It is doubtful that such investigations of community organization will replace intensive investigations of single species or make them obsolete. They can, however, pave the way for more realistic treatment of these species as working components of the biogeochemical wholes with which they evolved, not as isolated active entities pulling and tugging at a sort of inert physio-chemical conglomeration which envelops them.

The research herein discussed has the following objectives: (1) characterization of the large-scale (macrodistributional) and various small-scale (microdistributional) patterning present in a particular plant community, and changes in these patterns along a drainage-related gradient of vegetation and soil development, (2) an exploration of several types of correlation-regression analyses as techniques for elucidating these patterns, (3) the construction of plausible postulates concerning the phenomena responsible for the patterns, which will thereby suggest the nature of some aspects of community organization, and (4) the testing of a few of these postulates by means of field experiments.

"Macrodistribution", as the term is used in this thesis, refers not to geographic distribution, but rather to changes in frequency and per cent cover related to the area sampled on the soil-vegetation gradient, and hence to change in the distribution of populations. "Microdistribution", on the other hand, refers to variation in the location and luxuriance of individuals and small aggregations (or other convenient units such as individual shoots of a clone) within areas of a few square meters or less.

By "patterning" is meant non-random distribution.

Randomness, i.e. the kind of distribution which would result if every point in the study area had an equal chance of containing an individual of a species, has been shown to be rare and possibly nonexistent in nature. Species usually tend to be clumped or overdispersed (points nearer an individual having a greater chance of containing another), occasionally regularly distributed or underdispersed (points nearer an individual having a smaller chance of containing another) in response to their own reproductive patterns and the patterns existing in other elements of the community with which they interact (Odum and Odum 1959, Hutchinson 1953, Cole 1949, Greig-Smith 1964).

Correlation-regression analysis (2 above) is here used to show the degree of non-random distribution of species with respect to these other elements, the latter being either other species or environmental variables. The regression coefficient or the plotted regression curve shows the changes in a dependent variable, y, as an independent variable, x, changes. The product moment correlation coefficient, on the other hand, indicates the relative goodness of fit of a series of points (values in each sample) to the best-fitting regression curve, no matter the slope of this curve. Thus, in a sense, the regression

answers the question of "how much?" or "how strong?" the mathematical effect of one variable upon the distribution of another may be (not necessarily implying a biological cause-effect relationship). The correlation coefficient shows the consistency or reliability of the relationship. Since the present study is more concerned with the existence of relationships than with their magnitudes, greater attention is given here to correlation, although regressions may sometimes answer important questions which correlations cannot (Chapter VI).

If non-randomness consists of a tendency for higher values (e.g. cover, density, frequency) of a species to occur with the higher values of a second species or other variable it is called positive association, whereas if each variable tends to be relatively high in value where the other is relatively low it is called negative association (cf. Greig-Smith 1964). The same definitions and techniques can be extended to combinations of three or more variables, but this is not done in the present study.

The correlation and regression techniques are not designed to reveal the spatial details of pattern (e.g. size of clumps, spacing between them, etc.), as some other procedures are, but since they deal with combinations of

variables the correlation and regression coefficients are more efficient in unravelling the complexities of an organizational heirarchy. Moreover, they put the investigator in a relatively favorable position for seeking the causes of this organization. The knowledge that two species are positively or negatively associated is obviously more valuable in attempting to ascertain whether they interact favorably or unfavorably with each other, or respond similarly or differently to various factors, than are figures on mean number of individuals per quadrat or breadth of their clumps. (The latter may also be of some help if the scale of variation of certain possible causative factors is already known). The choice of correlation and regression analysis over some other possible techniques was also based partly upon the relative ease of the calculations and the availability of computer programs.

The "causes" sought for existing patterns in the present study are mostly on a level which might concern a practicing agriculturist, e.g., Species A inhibits or stimulates the growth of Species B. We should not lose sight, however, of a more ambitious level of understanding which hopefully will be possible in the future, a level at which we can describe biological communities as functional

networks of chemical reactions, energy flux, and information transfer. The theories of the trophic-dynamic ecologists (e.g. Lindemann 1942) do visualize biotic-abiotic assemblages in this way but are inadequate to describe the detailed organization within a single trophic level, with which I am dealing here. H. T. Odum (1960) has been exploring the question via his analog circuit studies.

Concerning objective number 1 again, the planners of the study felt that an investigation of changes in small scale community organization as a function of community change along a gradient of some kind would add another meaningful dimension. Shifts in abundance and pattern relationships among species in response to varying conditions along this gradient may provide clues to the roles of these species in community structure unobtainable from an examination of association on any portion of the gradient separately. There has been considerable attention to vegetational changes along large-scale gradients (e.g. Curtis and McIntosh 1951, Curtis 1959), and emphasis upon changes in association patterns on a similar scale by a few workers (e.g. Whittaker 1956). But relatively few ecologists (notably Bray 1956, Kershaw 1963) seem to have explored gradient-related microdistribution and association changes

in some detail.

The present study is unique, to my knowledge, in this investigation of association changes along a gradient combined with the use of several different measures of association. Each of these measures answers somewhat different questions about the patterns present, and thus permits the viewing of several facets of these departures from randomness.

CHAPTER II

GENERAL PROCEDURE

A. LOCATION AND CHARACTER OF THE AREA. The area used for all phases of this study was located in extreme south central Crawford County, in the northern part of Michigan's lower peninsula (Figure 1 A, page 12). It is on State Forest land in the southeast 1/4 of Section 30, Township 25 North, Range 3 West. As shown in Figures 1 B and 1 C, it is approximately one mile west of Route 18-76 between the towns of Grayling and Roscommon, one mile north of the Roscommon County line, about two miles east of Higgins Lake and County Road 270 (Old U.S. 27) and two and one-half miles east of the Lansing-Mackinaw Bridge Throughway (Present U.S. 27).

The soil parent materials in this part of Michigan include extensive areas of sandy and gravelly tills and outwashes of late Wisconsin glacial origin (Veatch et al. 1924). The tills (formerly mapped as Roselawn sand and related soils by Veatch et al. 1924), which comprise the low rolling topography of the ground moraines, support a tree cover of the oaks Quercus rubra, Q. alba, and members

of the Q. ellipsoidalis complex.[1] The extensive outwash plains, on the other hand, characteristically support forests or savannas of Pinus banksiana, the mid-western Jack pine (Figure 2 A, page 19), often with interspersed Quercus ellipsoidalis and Pinus resinosa. More rarely, P. resinosa may form the dominant tree cover and occasionally the Quercus spp. characteristic of tills may dominate. Stands of Bigtoothed aspen, Populus grandidentata, may occur on both tills and outwashes as may Red maple, Acer rubrum, as a subordinate component. Understory vegetation in both pine and oak stands is strikingly similar, dominated by two Vaccinium species (blueberries, huckelberries), Pteridium aquilinum (bracken), Carex pensylvanica (a sedge), Comptonia perigrina (Sweet fern), and (more prevalent in treeless sites and savannas) Danthonia spicata (Poverty oat grass). The outwash soils, formerly the only ones designated Grayling sand and its relatives, on the whole are said to be poorer in fine materials and soluble materials than the hilly sand areas mapped earlier as Roselawn complex. But an individual sample of outwash may assay higher

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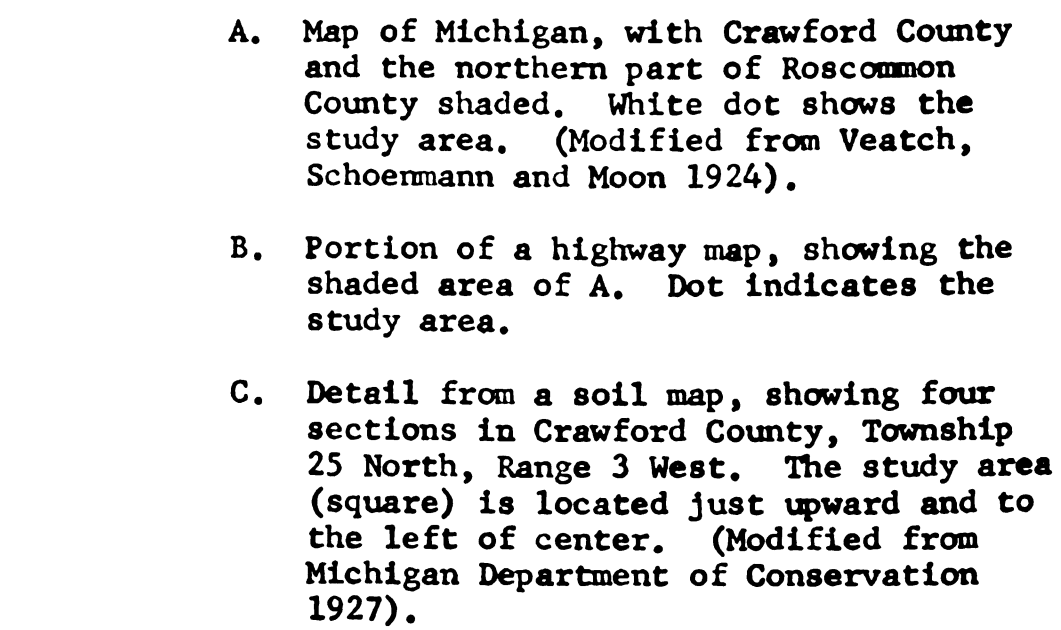
[1]Scientific names of vascular plants cited in this thesis follow Fernald (1950), except when an author is given the first time the species is mentioned.

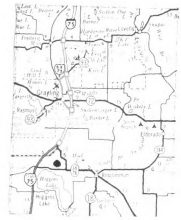
FIGURE 1. Location of the Study Area

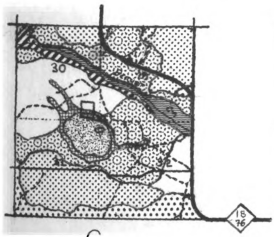


A. Map of Michigan, with Crawford County and the northern part of Roscommon County shaded. White dot shows the study area. (Modified from Veatch, Schoenmann and Moon 1924).

B. Portion of a highway map, showing the shaded area of A. Dot indicates the study area.

C. Detail from a soil map, showing four sections in Crawford County, Township 25 North, Range 3 West. The study area (square) is located just upward and to the left of center. (Modified from Michigan Department of Conservation 1927).





LEGEND, FIGURE 1 C

- Dawson-Greenwood peat
- Grayling sand
- Grayling sand, gravelly
- Rifle peat
- Kinross loamy sand
- Roselawn sand, gravelly[X]
- Roselawn sandy loam, gravelly[X]
- Saugatuck sand
- Highways
- Secondary roads
- Trails
- Section lines
- Study area

[X]Now mapped as Grayling

in both than one of till of similar geological origin (cf. data of Veatch 1953). It is quite probable, then, that the vegetational differences arise from topography related drainage and evapo-transpiration differences and/or the greater intensity and rapidity with which fires can burn over a flat surface, rather than from parent material differences. The existing oak, aspen, and Jack pine stands are all apparently successional, dating from the early 1900's when the fire frequency began to decline following the regional clearcutting and subsequent slash fires of the late 1800's (Veatch et al. 1924, Kilburn 1960).

The current soil classification combines soils in sandy outwash and till deposits into one soil series, if there are no other observed profile differences; hence Roselawn is now included in Grayling (Whiteside et al. 1955).

The Jack pine-supporting outwashes are pitted with glacial potholes. Various types of bog and marsh vegetation have developed in them, and it is along the border of one such pothole that the study area is located. It is a poorly-drained, acid (non-calcareous) bog of the type known as leatherleaf for the dominant shrub, Chamaedaphne calyculata (the type is also known locally as "huckelberry

swamp" although the plants referred to, Vaccinium boreale Hall and Aalders and V. angustifolium var. nigrum, rarely comprise more than 10-20% of the biomass). The area was chosen so that it would encompass roughly equal proportions of Grayling sand, the bog soil type Dawson-Greenwood peat, and soils intermediate between them. Because of scale limitations only Saugatuck sand, among these intermediate types, is shown in the soil map from which Figure 1 C was taken. The Dawson-Greenwood peat is a poorly descomposed, fibrous type.

Grayling sand is characterized by the near absence of a leached, or A_2 horizon and a very yellowish zone of accumulation, or B horizon; that is, the B has minimal sesquaoxide and organic deposition and so is not very different in color from the parent material. "Wet Grayling" (an arbitrary unit separated from Grayling sand when the latter proved to occupy a disproportionately large area) reflects slightly poorer drainage in an increased leaching and increased deposition, which become more pronounced on the still less effectively drained Croswell sand. On the latter, also, the red-black coloration of the B horizon becomes quite intense. Continuing in the direction of poorer drainage, Au Gres sand is distinguished from Croswell sand

primarily on the basis of the former's pronounced B horizon aggregation; firm pressure of the fingers is required to break the chunks. This tendency reaches its maximum on Saugatuck sand, where the B forms a hardpan which can be broken only by chipping. This cementing begins to decrease on Kinross sand, and concomitantly organic matter (A_0 horizons) increases to a depth and consistency resembling that of the peat. The Dawson-Greenwood peat is distinguished from Kinross by having a thickness of incompletely decomposed organic matter of 12 inches or greater. The areal divisions between soil types, as listed in Appendix A (page 373) are measurements intermediate between those chosen by McKenzie and Whiteside (1956) as "typical" for each type (except in the case of "Wet Grayling").

From Grayling through Au Gres the overstory vegetation remains Pinus banksiana, its cover varying little throughout this portion. The associated understory vegetation, however, changes radically. On Grayling, it is characterized by extensive sparse patches and a dominance of Carex pensylvanica, Vaccinium angustifolium var. nigrum and V. boreale (Figure 2 A, page 19). The primary change on "Wet Grayling" is a tendency for the tall bracken fern Pteridium aquilinum, growing in fairly scattered patches

on Grayling, to become extremely lush and sometimes to form almost solid cover. On Croswell, as one follows the gradient in the direction of progressively less efficient drainage, certain species relatively minor on Grayling and "Wet Grayling" such as Gaultheria procumbens, Epigaea repens and Maianthemum canadense increase to near their maximum cover. Concomitantly, several important species of the middle gradient ("bog margin") first appear in any but sporadic quantities: Coptis groenlandica, Cornus canadensis, Rubus hispidus var. obovalis and Vaccinium myrtilloides. In addition, total ground cover increases (Figure 2 B). But the vegetation of Croswell is still predominantly "dry end", in contrast to that on Au Gres where Gaultheria etc., Coptis etc., and the two gradient-spanning Vaccinium taxa (which reach their maxima here) form an unusually continuous ground cover. This lushness could be due to several factors, such as drainage favorable to plant growth generally, a B horizon texture which is neither impenetrable to water nor conducive to excessively rapid percolation, and an "edge effect" which provides considerably more light (from the nearly treeless bog) to this band than to the better-drained soils. The portion of Saugatuck adjacent to Au Gres is vegetationally similar to

the latter, but with considerably sparser ground cover. Closer to the bog, however, the tree cover becomes much more continuous, and along either side of the Saugatuck-Kinross line runs a band of tall, closely spaced trees not only of Pinus banksiana, but of Picea mariana and Larix laricina as well (Figure 2 C, left). Approaching this band from the "dry end" side, the Au Gres ground vegetation begins to thin out, and a few shrubs such as Ledum groenlandicum, Kalmia polifolia, Nemopanthus mucronata and Viburnum cassinoides assume some importance (they do not penetrate to soils which are much better drained than this). Under the heavy marginal tree canopy itself, ground cover becomes sparse; there are usually depauperate individuals of the shrubs just mentioned, as well as of species characteristic of both bog and "bog margin" and even the "dry end", but apparently light intensity is simply too low here for good plant growth. The part of Kinross sand lying on the "wet end" side of this tree border supports a vegetation typical of the bog; dominant Chamaedaphne as well as scattered clones of Ledum, Vaccinium angustifolium var. nigrum and V. boreale rooted in a mat of living Sphagnum moss, with occasional scattered small trees of Larix, Picea, Pinus banksiana, P. strobus and P. resinosa.

On Dawson-Greenwood peat Ledum cover drops but otherwise the vegetation remains similar (Figure 2 C, right).

In summary, then, there is a gradual shift in the pine forest floor vegetation between the "dry end" and mid-gradient, then a sudden transition across a narrow zone of bog margin trees to the open bog vegetation. There are but two shrub-herb species which extend to both sides of the marginal band of trees to any great extent, so that this transition satisfies the definition of an ecotone (Whittaker 1956, Curtis 1959, Becking 1957).

This particular drainage-related soil and vegetation gradient was chosen for this study because the vegetation is floristically poorer than that on any other gradient of comparable range in drainage in the region. This is thought to result from the relative coarseness and low nutrient content of the inorganic parent material, and the low pH, low oxigination, and possibly low availability of nutrients on the organic soil. Floristic paucity is desirable in a pioneering study of pattern, particularly one which emphasizes association between species as this one does, because the number of variables and consequently of possible combinations is thus minimized.

Indications are that the area remained essentially

FIGURE 2. Photographs of the Vegetation of the Study Area.

A. Pinus banksiana stand on Grayling sand, showing characteristic sparse understory vegetation.

B. Pinus banksiana stand on Au Gres or Saugatuck sand looking towards the better drained portion of the gradient. Note the very lush understory vegetation.

C. Left, zone of dense trees (Pinus, Picea and Larix) on Saugatuck and Kinross sands along the bog margin or hingeline. Right, characteristic open bog vegetation on Dawson peat, dominated by the shrub Chamaedaphne calyculata.

A

B

C

undisturbed during the 55 years or so preceding the beginning of the study. Rings were counted on several Pinus banksiana on the inorganic soil, and on several stumps of each conifer species present in the bog in the western portion of the study area, which was clearcut for experiments. These were supplemented by core borings on three Pinus banksiana, two Picea and two Larix distributed throughout the remainder of the area studied. They revealed that most trees began growth 55 $\pm$ 3 years before the 1958 sampling, probably following a fire. Virtually all the Pinus on inorganic soil probably originated at this time, since closing of the vegetation cover would have tended to prevent sufficicient light from reaching younger seedlings of this shade-intolerant tree. Seedlings have continued to establish themselves in the more open bog up to the present time, however, although some of the oldest trees here are but 3 inches in DBH. The bog vegetation did not give evidence of recent rising or lowering of the water table. The vegetation thus seems to have reached the relative equalibrium characteristic of older Jack pine. If the findings of Kittridge (1934) hold for the region in question here, this vegetation might remain somewhat as is for another 40-50 years.

B. FIELD METHODS. 1958 Sampling. A square area of 100 X 100 meters was staked out in such a way that it embraced the entire soil-vegetation transition discussed above. Prior inspection suggested that an area of this size would be sufficient to encompass the normal range of macrodistributional variation found on each of the soil types in this and similar stands in northern lower Michigan. Thus, the results should be fairly indicative of what one might expect generally in the vegetation types studied. The square shape was chosen because it best fit the particular gradient, a rather abrupt one. An oblong sample universe whose long axis paralleled that of the gradient would have included too little of the soils developed under intermediate drainage conditions. Orientation was with the sides running approximately East-West and North-South, the latter closely following the orientation of the gradient.

Four hundred 1 X 1 meter quadrats were randomly located within the area, as many as time permitted, so that standard errors of the coefficients to be calculated later would be as small as possible. The 1 X 1 meter quadrat was several times larger than the individual shoots or tussocks of any species dealt with, so this seemed about

the right size to show up the largest scale association patterns present. Sampling was carried out between mid-June and mid-September of 1958. With one or two exceptions (pointed out where appropriate) the aerial portions of the species seemed neither to grow nor to die back to any extent during this period, so it is unlikely that seasonal changes affected the measurements appreciably despite the relatively long sampling period. Nonetheless, reading of the quadrats was done in such a fashion as to insure that all parts of the study area would be proportionately represented in the sampling done during each of several relatively short time intervals. In this way, apparent differences between segments of the gradient due to temporal factors was minimized.

The reason for a complete random sample, rather than a stratified one which would have insured a reasonably large number of quadrats and consequently lower standard errors on the arealy smaller gradient segments, was a practical one. Any detailed soil mapping done before the vegetation sampling would have disturbed the plants unduly. Moreover, since exploratory soil profiles close to the sample universe had revealed that soils varied greatly within a space of two or three meters, it was obvious that

profiles dug in the center of each quadrat after vegetation sampling would insure more accurate determination for each quadrat than would a soil map based upon profiles dug every ten meters or so. In the latter case, some quadrats would have been five meters from the closest soil reference point.

Each 1 X 1 meter quadrat contained a centrally located 1/2 X 1/2 meter quadrat, and the latter a central 1/10 X 1/10 meter quadrat. The smaller quadrats are not randomly located, since their positions are predetermined by those of the largest sized quadrats. However, they may be thought of as being centered at some of the intersections of a 1 X 1 meter grid, these intersections having been chosen at random. Their location is thus similar to that of randomly located point quadrats, used by many workers including Greig-Smith (1964) and Kershaw (1964), but they have non-zero area. Location at grid intersections makes the assumption that there is no spatially regular variation in the vegetation of about the same scale as that of the grid, such as that which Harper and Sager (1953 in fact demonstrated in a field containing old plow furrows. But that does not seem a likely eventuality, and so it is probably safe to assume that the smaller quadrats give an unbiassed sample, though of course

randomness cannot be assumed in comparing results from units of one size with those from units of another size.

For each of the three quadrat sizes, presence of all vascular species was recorded and their cover estimated. Presence of all bryophyte and lichen species was recorded also, but their cover was estimated only in the smallest quadrats. Voucher specimens for all species encountered in the quadrats are on file in the Beal-Darlington herbarium at Michigan State University. Total moss, lichen and tree cover were also estimated for each quadrat, while total shrub and herb cover were calculated later by summing cover of the component species. Litter thickness in each of the largest quadrats was estimated by measuring it at five equidistant points within the quadrat and taking an average. Per cent of bare ground and per cent of litter covered ground were estimated for all three quadrat sizes. After the vegetational sampling had been completed, a soil profile was dug in the center of each group of nested quadrats and thickness of each soil horizon (to as great a depth as feasible), depth to gley, and degree of cementing and color of the B horizon were recorded (the B horizon characteristics were later used only in the separation of soil types).

Experimental Plots. Two pieces of the 1958 study area were used in 1960 and 1961, to begin transplant and germination experiments. Because the details of these experiments, unlike those of the sampling, are pertinent only to chapter 7, they are included with that chapter in order to make of it a better integrated whole.

C. ANALYSIS TECHNIQUES. Each quadrat was assigned to a soil type according to the criteria listed in Appendix A (Page 373). The seven soil types originally designated were subsequently combined into five segments, for some of the less extensive types did not contain enough quadrats for a worth-while correlation analysis. Per cent frequency and mean per cent cover of each species considered were calculated for each of the seven soil types and each of the five segments. Standard deviations of the cover of each species were calculated also, as were the means and sample standard deviations of the other variables recorded. Such data for those 47 species common enough for further analysis (present in at least five 1 X 1 meter quadrats) and for the other 16 measured variables are summarized in Table I (page 27). A complete listing of the species encountered, together with their frequency and cover, is found in Tables I and II of Byer (1960).

Several types of correlation and regression coefficients were calculated for these species and other variables. For the sake of greater unity of the individual sections of the work, discussions of these coefficients and details of the analyses are presented with the appropriate chapters. Similarly, statistical handling of the data from experimental plots is described in Chapter VII, to which it pertains.

The R technique is used throughout the association studies, i.e., the quadrats are treated as the individual objects observed, and their various characteristics (presence or cover of species, values of "environmental" parameters) correlated with one another. The interrelationships between these characters themselves are thus revealed, rather than similarities and differences between quadrats in terms of their species composition, soil profile development, etc.

TABLE I

Frequency, cover, means and standard deviations of species and other variables across the gradient.

Symbols for soil type names (listed across the top of the table's pages) and for species and other variables (listed in the left-hand columns) are listed together with their meanings in Appendix B (page 375).

The variables are listed in the following sequence: species in alphabetical order (nos. 1-47), synusia in order of decreasing height (nos. 48-52) and then total cover of all synusia combined (no. 53), litter parameters (nos. 54-58), soil horizons in the order in which they occur starting at the surface (nos. 57-62, if A_{0L} and A_{0M} horizons are counted here as well as with litter), and depth to gley (no. 63).

LEGEND

quadrat size	
symbol	meaning
1	1 m^2
4	1/4 m^2
H	1/100 m^2

parameter measured	
symbol	meaning
F	per cent frequency
FC	per cent frequency for combined gradient segments (see text, page 25).
C	mean per cent cover
CC	mean per cent cover for combined gradient segments
$\bar{X}$	mean value
XC	mean value for combined gradient segments
s	standard deviation of CC or $\bar{X}$C

TABLE I, cont.

VARIAB	QDT SIZE*	PAR MEAS*	SOIL TYPE G	WG	C	AG	S	R	DG
1 AMD	1	F	14.17	10.87	18.18	21.43	10.00	3.45	-
		FC	14.17	15.18		18.42		-	-
		C	0.07	0.18	0.05	0.08	0.01	0.04	-
		CC	0.08	0.10		0.06		-	-
		s	0.44	0.67		0.18		-	-
	4	CC	0.08	0.19		0.13		-	-
		s	0.44	1.20		0.52		-	-
2 AMS	1	F	-	-	4.55	10.71	40.00	10.35	-
		FC	-	-		18.42		-	-
		C	-	-	0.02	0.04	0.22	0.02	-
		CC	-	-		0.09		-	-
		s	-	-		0.24		-	-
	4	CC	-	-		0.10		-	-
		s	-	-		0.47		-	-
3 ARM	1	F	20.00	15.22	9.09	-	-	-	-
		FC	20.00	11.61		-		-	-
		C	0.09	0.05	0.02	-	-	-	-
		CC	0.09	0.04		-		-	-
		s	0.27	0.14		-		-	-
	4	CC	0.14	0.04		-		-	-
		s	0.58	0.21		-		-	-
4 ARC	1	F	6.67	10.87	-	-	-	-	-
		FC	6.67	-		-		-	-
		C	0.21	0.10	-	-	-	-	-
		CC	0.21	-		-		-	-
		s	1.12	-		-		-	-
	4	CC	0.21	-		-		-	-
		s	1.17	-		-		-	-
5 ASH	1	F	8.33	6.52	7.58	3.57	-	-	-
		FC	8.33	7.14		-		-	-
		C	0.03	0.02	0.02	0.01	-	-	-
		CC	0.03	0.02		-		-	-
		s	0.15	0.08		-		-	-
	4	CC	0.03	-		-		-	-
		s	0.22	-		-		-	-

* Legend on page facing the first page of the table

TABLE I, cont.

VARIAB	QDT SIZE*	PAR MEAS*	SOIL TYPE G	WG	C	AG	S	R	DG
6 ASL	1	F	13.33	10.87	6.06	-	-	-	-
		FC	13.33		8.93		-	-	-
		C	0.03	0.03	0.03	-	-	-	-
		CC	0.03		0.02		-	-	-
		s	0.10		0.07		-	-	-
	4	CC	0.04		0.02		-	-	-
		s	0.15		0.10		-	-	-
7 BRA	1	F	9.17	21.74	18.18	32.14	30.00	13.79	2.97
		FC	-		19.64		-	-	-
	H	CC	-		0.21		-	-	-
		s	-		1.00		-	-	-
8 CAL	1	F	42.50	28.26	28.79	39.29	80.00	48.28	6.93
		FC	42.50		28.57		50.00	48.23	-
	H	CC	1.34		0.25		6.39	5.00	-
		s	7.77		1.92		18.83	17.26	-
9 CPD	1	F	10.83	6.52	9.09	10.71	-	3.45	-
		FC	10.83		8.04		7.89	-	-
		C	0.45	0.05	0.07	0.25	-	0.02	-
		CC	0.45		0.06		0.19	-	-
		s	2.85		0.27		0.83	-	-
	4	CC	0.39		0.05		-	-	-
		s	2.82		0.28		-	-	-
	H	CC	0.10		-		-	-	-
		s	0.65		-		-	-	-
10 CAR	1	F	98.33	97.83	93.94	82.14	40.00	3.45	-
		FC	98.33		95.54		71.05	-	-
		C	9.75	8.85	4.55	3.48	1.02	0.02	-
		CC	9.93		6.41		2.85	-	-
		s	13.24		10.86		4.25	-	-
	4	CC	10.34		6.92		3.56	-	-
		s	13.78		11.09		5.62	-	-
	H	CC	8.96		6.67		2.80	-	-
		s	14.29		14.03		7.14	-	-

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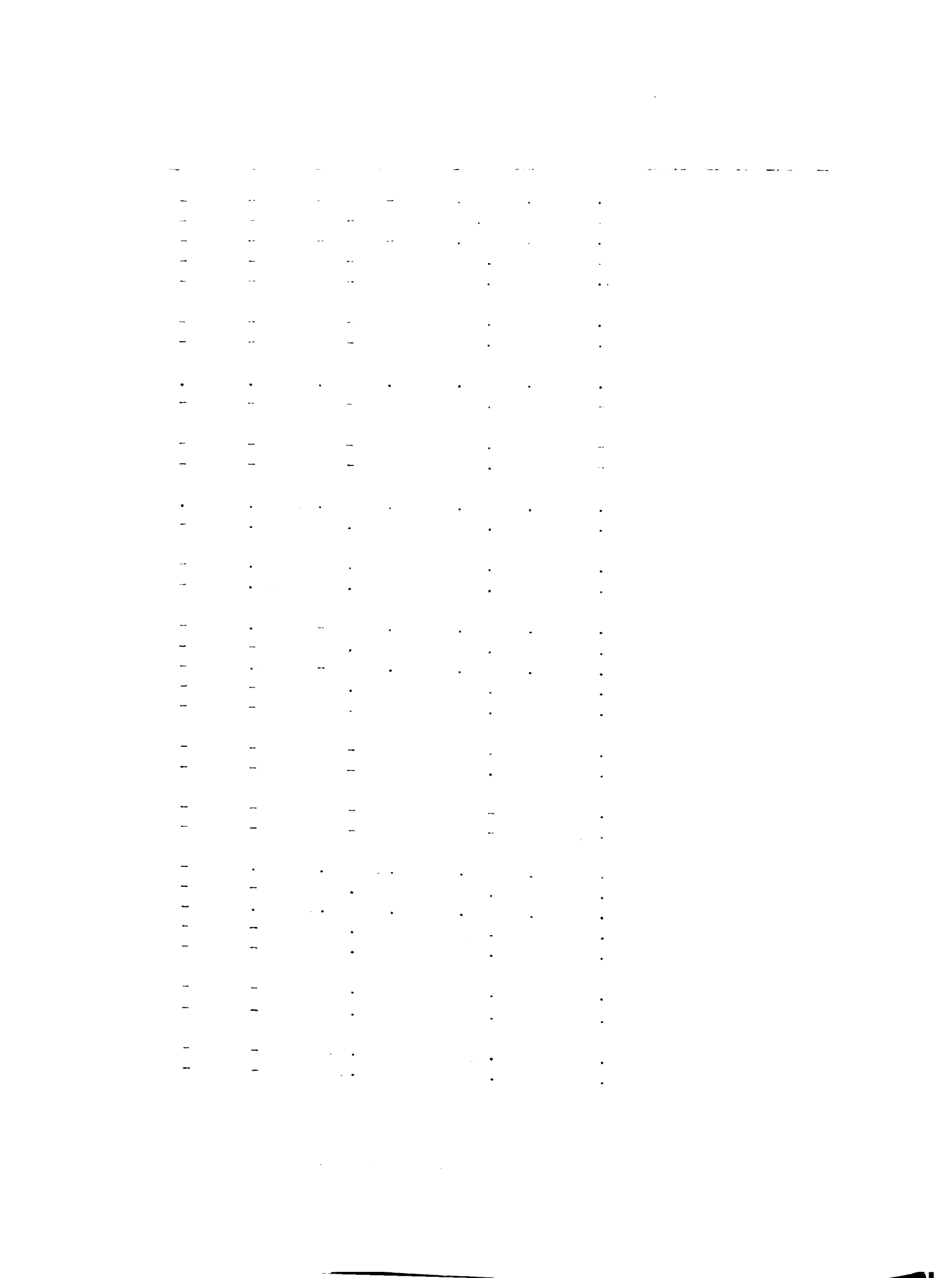

TABLE I, cont.

VARIAB	QDT SIZE*	PAR MEAS*	SOIL TYPE G	WG	C	AG	S	R	DG
11 CRM	1	F	-	-	-	3.57	20.00	58.62	100.00
		FC	-	-		-		58.62	100.00
		C	-	-	-	0.01	4.03	5.99	23.58
		CC	-	-		-		5.85	23.51
		S	-	-		-		8.41	15.97
	4	CC	-	-		-		5.36	26.12
		S	-	-		-		8.29	17.70
	H	CC	-	-		-		3.55	26.02
		S	-	-		-		8.48	20.67
12 COM	1	F	16.67	21.74	48.48	50.00	30.00	3.45	-
		FC	16.67	37.50		44.74		-	-
		C	0.71	0.63	1.25	0.99	0.27	0.05	-
		CC	0.71	1.00		0.80		-	-
		S	2.80	2.00		1.55		-	-
	4	CC	0.66	1.02		0.67		-	-
		S	2.74	2.55		1.97		-	-
	H	CC	1.06	0.53		1.11		-	-
		S	7.10	2.38		4.08		-	-
13 COP	1	F	-	-	10.61	35.71	50.00	10.34	-
		FC	-	6.25		39.47		-	-
		C	-	-	0.07	0.39	0.28	0.03	-
		CC	-	0.04		0.36		-	-
		S	-	0.23		0.62		-	-
	4	CC	-	0.05		0.37		-	-
		S	-	0.28		0.65		-	-
	H	CC	-	0.12		1.05		-	-
		S	-	0.75		2.88		-	-
14 COR	1	F	-	2.17	7.58	39.29	60.00	17.24	-
		FC	-	5.36		44.74		17.24	-
		C	-	0.03	0.31	1.63	0.57	0.18	-
		CC	-	0.19		1.35		0.18	-
		S	-	0.95		2.35		0.75	-
	4	CC	-	0.18		1.35		0.18	-
		S	-	0.90		2.46		0.63	-
15 CRM	1	F	29.17	8.70	9.09	-	-	6.90	1.98
		FC	29.17	-		-		-	-

* Legend on page facing the first page of the table

TABLE I, cont.

VARIAB	QDT SIZE*	PAR MEAS*	SOIL TYPE G	WG	C	AG	S	R	DG
16 CRS	1	F	28.33	23.91	12.12	-	20.00	24.14	6.93
		FC	28.33	16.96		-	-	-	-
17 CUP	1	F	40.83	30.43	22.73	7.14	30.00	37.93	16.83
		FC	40.83	25.89		-	-	-	-
	H	CC	0.34	0.19		-	-	-	-
		s	1.13	1.10		-	-	-	-
18 DAN	1	F	19.17	10.87	4.55	-	-	-	-
		FC	19.17	8.04		-	-	-	-
		C	0.28	0.03	0.01	-	-	-	-
		CC	0.28	0.02		-	-	-	-
		s	1.40	0.12		-	-	-	-
	4	CC	0.20	0.02		-	-	-	-
		s	1.11	0.10		-	-	-	-
	H	CC	0.18	-		-	-	-	-
		s	1.29	-		-	-	-	-
19 DIC	1	F	43.33	26.09	21.21	14.29	20.00	24.14	3.96
		FC	43.33	23.31		-	-	-	-
20 EPI	1	F	4.17	8.70	31.82	57.14	10.00	13.79	-
		FC	4.17	22.32		44.74		13.79	-
		C	0.04	0.09	0.99	0.95	0.04	0.16	-
		CC	0.04	0.62		0.71		0.16	-
		s	0.28	1.69		1.35		0.49	-
	4	CC	-	0.65		0.82		0.11	-
		s	-	1.85		1.91		0.32	-
	H	CC	-	1.22		-		-	-
		s	-	4.83		-		-	-
21 ERI	1	F	-	-	-	3.57	-	37.93	48.51
		FC	-	-		-		37.93	48.51
		C	-	-	-	T	-	0.20	0.66
		CC	-	-		-		0.20	0.50
		s	-	-		-		0.44	1.15
	4	CC	-	-		-		0.25	0.60
		s	-	-		-		0.78	1.63
	H	CC	-	-		-		0.13	0.34
		s	-	-		-		0.41	1.05

* Legend on page facing the first page of the table

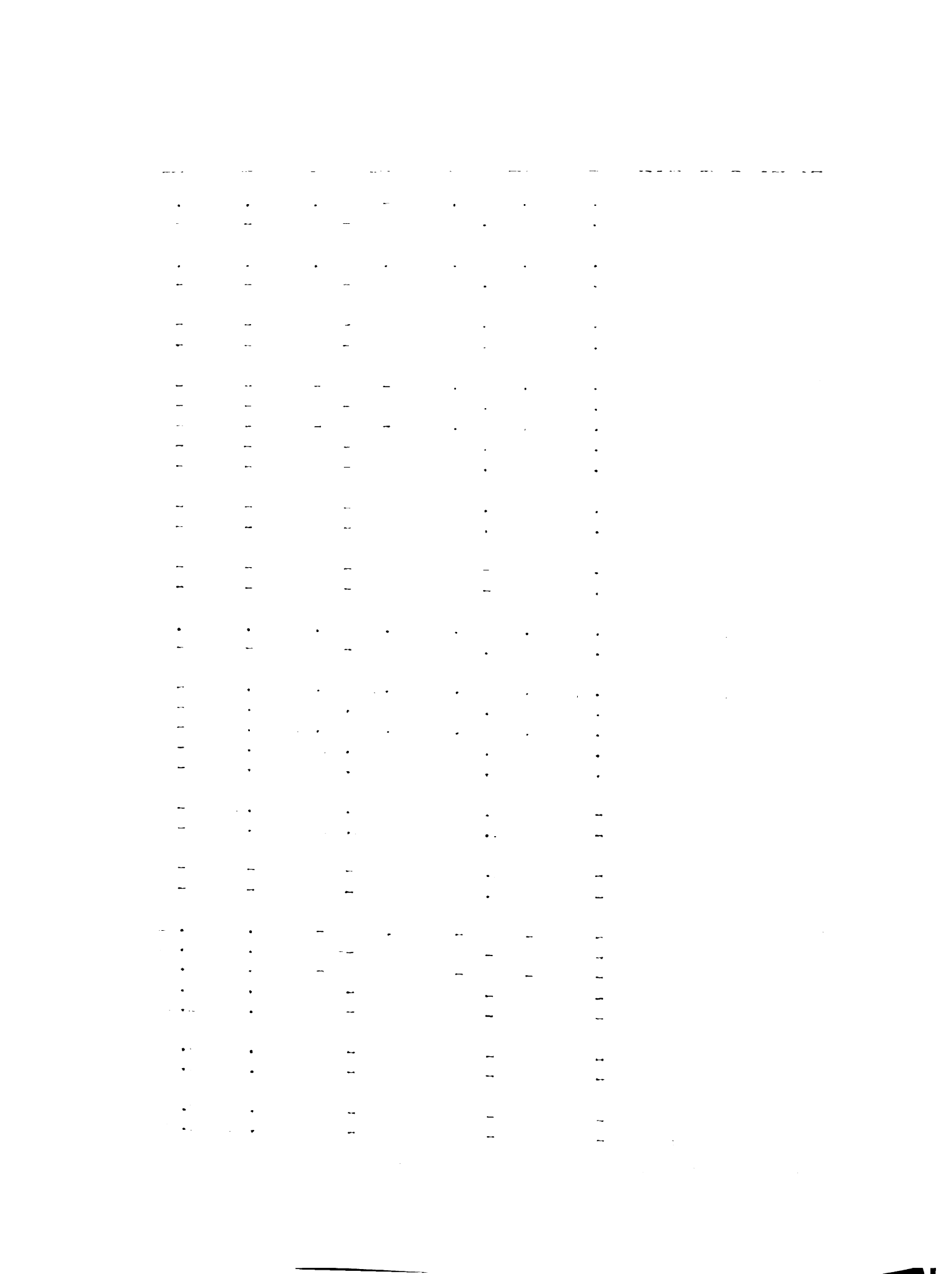

TABLE I, cont.

VARIAB	QDT SIZE*	PAR MEAS*	SOIL TYPE G	WG	C	AG	S	R	DG
22 GAU	1	F	32.50	60.87	87.88	96.43	100.00	58.62	0.99
		FC	32.50	76.79		97.37		58.62	-
		C	0.52	1.78	3.23	3.99	2.42	1.93	0.01
		CC	0.52	2.38		3.60		1.93	-
		S	1.10	3.12		3.15		3.44	-
	4	CC	0.55	2.60		3.51		1.76	-
		S	1.28	3.70		3.75		3.48	-
	H	CC	0.40	3.39		3.68		2.03	-
		S	1.64	6.99		7.96		4.72	-
23 ILX	1	F	-	-	10.61	39.29	30.00	27.59	2.97
		FC	-	6.26		36.84		27.59	-
		C	-	-	0.09	0.11	0.07	0.22	0.05
		CC	-	0.03		0.10		0.22	-
		S	-	0.15		0.16		0.60	-
	4	CC	-	0.02		0.18		0.13	-
		S	-	0.13		0.55		0.43	-
24 KAL	1	F	-	-	-	-	-	20.69	55.45
		FC	-	-		-		20.69	55.45
		C	-	-	-	-	-	0.10	0.54
		CC	-	-		-		0.10	0.47
		S	-	-		-		0.27	0.58
	4	CC	-	-		-		0.14	0.76
		S	-	-		-		0.39	2.57
	H	CC	-	-		-		-	1.29
		S	-	-		-		-	3.79
25 KAN	1	F	-	-	1.52	-	10.00	6.90	6.93
		FC	-	-		-		-	6.93
		C	-	-	0.09	-	0.80	0.37	0.31
		CC	-	-		-		-	0.30
		S	-	-		-		-	1.87
	4	CC	-	-		-		-	0.36
		S	-	-		-		-	2.10
	H	CC	-	-		-		-	0.54
		S	-	-		-		-	3.60

* Legend on page facing the first page of the table

TABLE I, cont.

VARIAB	QDT SIZE*	PAR MEAS*	G	WG	C	SOIL TYPE AG	S	R	DG
26 LED	1	F	-	-	-	10.71	30.00	79.31	31.68
		FC	-		-	15.79		79.31	31.68
		C	-	-		1.06	0.80	5.34	1.98
		CC	-		-	0.99		5.34	1.98
		S	-	-		4.64		7.59	4.02
	4	CC	-	-		0.73		4.90	1.95
		S	-	-		3.32		7.97	4.62
	H	CC	-	-		*		6.62	2.73
		S	-	-		-		15.84	8.49
27 LYC	1	F	-	-	12.12	14.29	10.00	-	-
		FC	-	-		13.16		-	-
		C	-	-	0.04	0.06	0.02	-	-
		CC	-	-		0.05		-	-
		S	-	-		0.17		-	-
28 MAI	1	F	25.83	34.78	74.24	82.14	60.00	10.34	-
		FC	25.83	58.93		76.32		-	-
		C	0.12	0.17	1.24	1.04	0.88	0.03	-
		CC	0.12	0.52		0.99		-	-
		S	0.35	0.88		1.01		-	-
	4	CC	0.16	0.55		0.96		-	-
		S	0.55	1.13		1.10		-	-
	H	CC	-	1.00		1.21		-	-
		S	-	2.83		3.43		-	-
29 MEL	1	F	36.67	30.43	53.03	67.86	40.00	3.45	-
		FC	36.67	43.75		60.53		-	-
		C	0.09	0.08	0.25	0.35	0.16	T	-
		CC	0.09	0.18		0.30		-	-
		S	0.17	0.39		0.38		-	-
	4	CC	0.11	0.18		0.45		-	-
		S	0.34	0.46		0.87		-	-
	H	CC	-	0.41		0.24		-	-
		S	-	1.85		1.17		-	-
30 MEM	1	F	-	-	-	3.57	20.00	20.69	1.98
		FC	-	-		-		20.69	-
		C	-	-	-	0.03	0.50	0.53	0.03
		CC	-	-		-		0.53	-
		S	-	-		-		1.73	-

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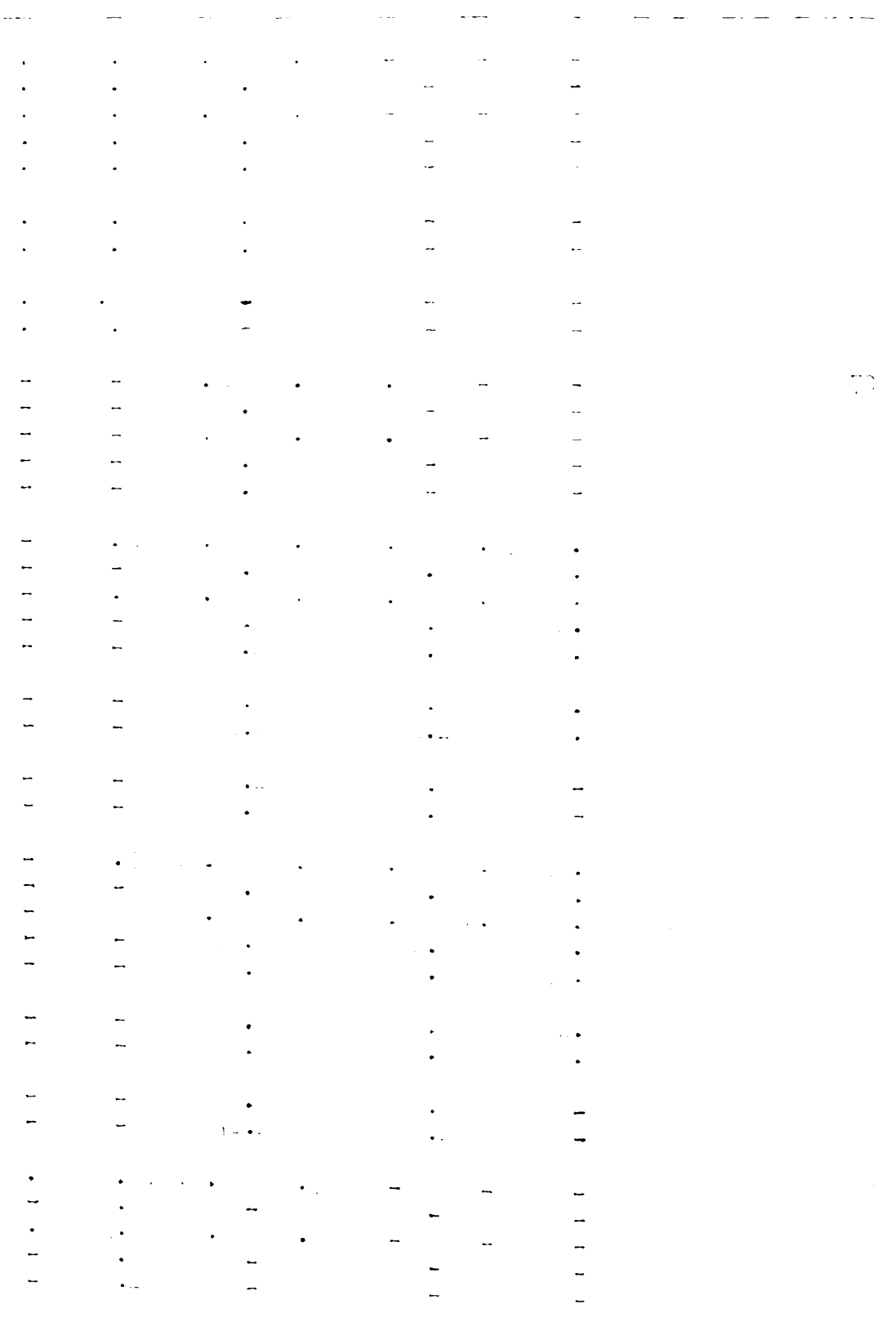

TABLE I, cont.

VARIAB	QDT SIZE*	PAR MEAS*	SOIL TYPE G	WG	C	AG	S	R	DG
30 MEM (cont.)	4	CC	-	-		-		-	-
		S	-	-		-		0.38	-
						-		1.18	-
31 OPU	1	F	16.67	10.87	4.55	-	-	-	-
		FC	16.67	-					
		C	0.06	0.03	0.01	-	-	-	-
		CC	0.06	-			-	-	-
		S	0.23	-		-		-	-
						-		-	-
	4	CC	0.05	-		-		-	-
		S	0.24	-		-		-	-
32 ORS	1	F	19.17	15.22	21.12	14.29	-	-	-
		FC	19.17	18.75		15.79		-	-
		C	0.30	0.05	0.08	0.31	-	-	-
		CC	0.30	0.07		0.23		-	-
		S	1.12	0.27		1.15		-	-
	4	CC	0.24	0.02		0.30		-	-
		S	1.53	0.12		1.37		-	-
	H	CC	0.19	-		-		-	-
		S	1.44	-		-		-	-
33 POS	1	F	-	-	1.52	25.00	70.00	44.83	81.19
		FC	-	-		-		-	81.19
	H	CC	-	-		-		-	5.72
		S	-	-		-		-	14.23
34 PRU	1	F	17.50	23.91	25.76	50.00	40.00	-	-
		FC	17.50	23.21		47.37		-	-
		C	0.22	0.24	0.48	1.08	0.07	-	-
		CC	0.22	0.38		0.39		-	-
		S	0.81	1.53		0.71		-	-
	4	CC	0.16	0.32		0.44		-	-
		S	0.84	1.88		1.21		-	-
	H	CC	-	-		0.53		-	-
		S	-	-		2.50		-	-
35 PER	1	F	61.67	76.09	65.15	53.57	10.00	-	-
		FC	61.67	68.75		42.11		-	-
		C	6.34	5.97	6.88	6.04	0.90	-	-
		CC	5.74	6.51		4.68		-	-
		S	6.93	7.09		7.11		-	-

* Legend on page facing the first page of the table

TABLE I, cont.

VARIAB	QDT SIZE*	PAR MEAS*	SOIL TYPE G	WG	C	AG	S	R	DG
35 PER (cont.)	4	CC	5.85	6.41		5.99		-	-
		S	9.10	9.22		8.99		-	-
	H	CC	4.08	6.83		9.32		-	-
		S	12.88	15.92		17.68		-	-
36 RHO	1	F	0.83	4.35	43.94	64.29	50.00	13.79	-
		FC	-	27.68		60.53		13.79	-
		C	T	0.09	0.92	1.59	0.19	0.14	-
		CC	-	0.57		1.22		0.14	-
		S	-	1.39		2.32		0.46	-
	4	CC	-	0.63		1.40		-	-
		S	-	1.70		3.12		-	-
	H	CC	-	0.97		2.18		-	-
		S	-	2.89		5.64		-	-
37 RUB	1	F	9.16	6.52	6.07	14.29	-	3.45	-
		FC	9.16	6.25		10.53		-	-
		C	0.03	0.04	0.04	0.12	-	T	-
		CC	0.03	0.03		0.04		-	-
		S	0.12	0.14		0.14		-	-
	4	CC	0.05	-		-		-	-
		S	0.32	-		-		-	-
38 SPL	1	F	-	-	1.52	7.14	40.00	89.66	98.02
		FC	-	-		15.79		89.66	98.02
	H	CC	-	-		2.97		45.47	47.85
		S	-	-		15.46		40.45	37.48
39 SPP	1	F	-	-	-	7.14	30.00	79.31	98.02
		FC	-	-		-		79.31	98.02
	H	CC	-	-		-		2.60	15.35
		S	-	-		-		6.87	24.68
40 SOL	1	F	10.00	13.04	-	-	-	-	-
		FC	10.00	5.36		-		-	-
		C	0.03	0.03	-	-	-	-	-
		CC	0.03	0.01		-		-	-
		S	0.11	0.06		-		-	-
	4	CC	0.04	-		-		-	-
		S	0.22	-		-		-	-

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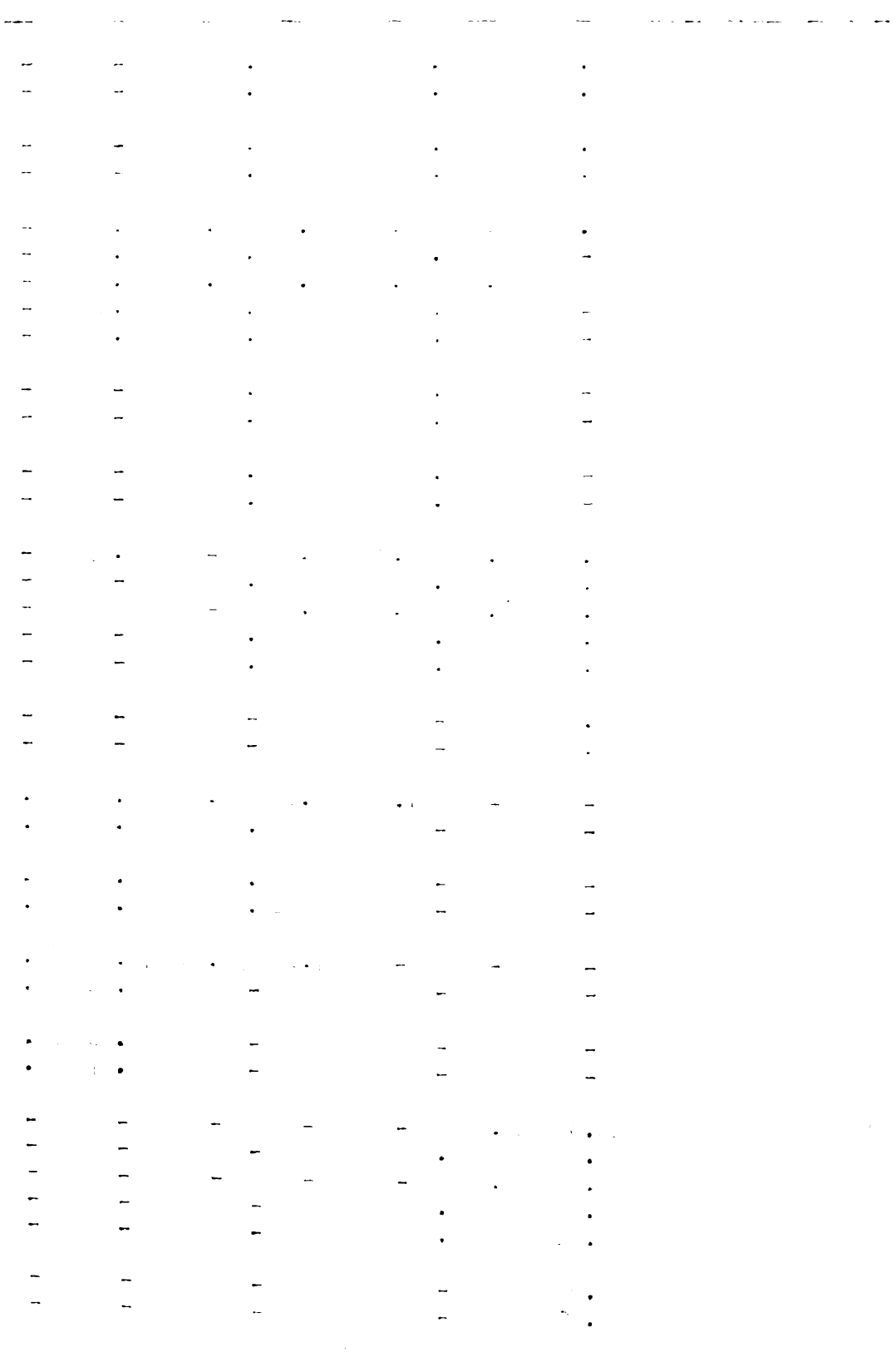

TABLE I, cont.

VARIAB	QDT SIZE*	PAR MEAS*	SOIL TYPE G	WG	C	AG	S	R	DG
41 TRI	1	F	1.67	6.52	40.91	71.43	60.00	10.34	-
		FC	-	26.79		68.42		-	-
		C	0.01	0.04	0.20	0.44	0.29	0.27	-
		CC	-	0.14		0.41		-	-
		S	-	0.28		0.43		-	-
	4	CC	-	0.17		0.41		-	-
		S	-	0.49		0.74		-	-
	H	CC	-	-		0.75		-	-
		S	-	-		3.11		-	-
42 VAM	1	F	0.83	4.35	37.88	50.00	70.00	37.83	1.98
		FC	-	24.11		55.26		37.83	-
		C	0.01	0.17	0.55	1.61	3.27	2.07	0.01
		CC	-	0.52		2.05		2.07	-
		S	-	1.69		2.96		5.35	-
	4	CC	-	0.43		1.84		1.88	-
		S	-	1.29		3.40		3.79	-
	H	CC	-	0.37		2.29		1.45	-
		S	--	2.53		7.93		4.23	-
43 VIB	1	F	-	-	4.55	17.86	50.00	31.03	0.99
		FC	-	-		26.32		31.03	-
		C	-	-	0.12	0.52	2.25	1.24	T
		CC	-	-		0.98		1.48	-
		S	-	-		2.58		2.83	-
	4	CC	-	-		1.05		1.24	-
		S	-	-		4.64		3.40	-
	H	CC	-	-		1.13		-	-
		S	-	-		5.09		-	-
44 VIC	1	F	69.17	82.61	93.94	100.00	100.00	75.86	13.86
		FC	69.17	89.29		100.00		75.86	13.86
		C	1.67	2.08	3.78	4.36	2.61	4.09	1.20
		CC	1.64	2.90		3.90		4.31	1.19
		S	2.15	2.96		3.81		5.68	3.88
	4	CC	1.88	3.24		4.79		4.74	1.44
		S	2.90	3.73		4.90		5.45	5.17
	H	CC	1.99	3.73		6.59		6.07	1.30
		S	4.96	7.12		11.55		9.21	6.23

* Legend on page facing the first page of the table

TABLE I, cont.

VARIAB	QDT SIZE*	PAR MEAS*	SOIL TYPE G	WG	C	AG	S	R	DG
45 VIO	1	F	14.17	4.35	3.03	-	-	-	-
		FC	14.17	-			-	-	-
		C	0.03	T	T	-	-	-	-
		CC	0.03	-			-	-	-
		s	0.09	-		-		-	-
	4	CC	0.02	-		-		-	-
		s	0.09	-		-		-	-
46 VOX	1	F	-	-	-	-	-	13.79	91.09
		FC	-	-		-		13.79	91.09
		C	-	-	-	-	-	0.08	1.65
		CC	-	-		-		0.08	1.65
		s	-	-		-		0.29	1.95
	4	CC	-	-		-		0.05	2.18
		s	-	-		-		0.16	3.20
	H	CC	-	-		-		-	2.84
		s	-	-		-		-	6.30
47 VIP	1	F	60.00	71.74 96.97		96.43 100.00		79.31	20.79
		FC	60.00	86.61		97.37		79.31	20.79
		C	2.86	5.02 4.25		5.39 2.99		4.48	0.89
		CC	2.45	4.48		4.76		4.31	0.89
		s	3.15	5.09		3.76		5.55	2.94
	4	CC	2.58	4.69		5.12		5.76	1.08
		s	3.87	6.24		4.73		6.79	4.09
	H	CC	2.39	5.02		6.00		9.14	1.09
		s	6.61	10.54		9.14		17.93	4.38
48 TRE	1	F	98.33	97.83 92.42		100.00 100.00		82.76	30.69
		FC	98.33	94.64		100.00		82.76	30.69
		C	26.03	26.58 20.80		29.45 37.70		21.72	5.12
	4	CC	33.31	29.06		41.61		28.75	6.06
		s	25.37	25.72		30.14		29.00	16.20
49 SHR	1	C	5.82	8.66 11.18		15.34 18.25		24.76	29.39
	4	CC	5.88	10.18		16.33		25.36	31.70
		s	6.80	8.91		10.36		15.89	16.20
50 HER	1	C	18.17	17.20 19.58		21.35 7.71		3.38	2.29

* Legend on page facing the first page of the table

TABLE I, cont.

VARIAB	QDT SIZE*	PAR MEAS*	SOIL TYPE G	WG	C	AG	S	R	DG
50 ERB (cont.)	4	CC	18.54	18.75		20.14		2.96	2.78
		s	15.84	14.34		14.19		3.89	3.54
51 MOS	1	F	61.67	50.00	46.97	64.29	100.00	100.00	100.00
		FC	61.67	48.21		73.68		100.00	100.00
		C	2.95	1.96	0.99	8.42	24.36	55.91	74.47
	4	CC	2.42	1.65		12.54		59.08	74.39
		s	7.35	5.43		25.60		35.93	27.41
52 LCH	1	F	56.67	41.30	30.30	7.14	30.00	44.83	20.79
		FC	56.67	34.82		13.16		44.83	20.79
		C	0.69	0.38	0.10	0.01	0.15	0.69	0.17
	4	CC	0.74	0.24		0.08		0.32	0.16
		s	1.72	0.89		0.49		1.48	0.85
53 TOT	4	CC	-	-		-		431.86	-
		s	-	-		-		97.56	-
54 LIT	4	$\bar{X}c$	11.43	13.46		11.42		6.00	3.18
		s	9.18	13.61		9.44		9.40	5.78
55 BAR	4	CC	0.42	0.09		0.26		0.25	0.38
		s	2.12	0.51		0.92		0.78	1.46
56 LIP	4	CC	91.93	93.36		80.58		33.31	20.26
		s	10.82	8.45		28.88		36.02	25.65
57 AOL	1	$\bar{X}$	13.6	14.1	13.3	14.1	13.2	12.3	12.2
	4	$\bar{X}c$	13.60	13.70		14.03		12.17	11.47
		s	5.04	5.83		7.22		8.45	4.91
58 AOM	1	$\bar{X}$	14.3	13.1	11.6	14.9	29.1	42.8	62.0
	4	$\bar{X}c$	13.88	12.13		18.79		41.59	60.55
		s	7.75	5.49		12.45		33.96	41.08
59 AOH	1	$\bar{X}$	28.7	35.2	37.2	57.1	60.0	139.3	579.2
	4	$\bar{X}c$	25.17	34.26		57.53		136.24	23 in.
		s	9.83	17.27		33.83		55.69	9.04

* Legend on page facing the first page of the table

TABLE I, cont.

VARIAB	QDT SIZE*	PAR MEAS*	SOIL TYPE G	WG	C	AG	S	R	DG
60 A-1	1	$\bar{X}$	26.1	34.9	30.5	37.3	36.0	27.0	-
	4	$\bar{X}C$	25.13	31.93		32.26		28.59	-
		s	14.48	17.46		15.64		24.41	-
61 A-2	1	$\bar{X}$	9.7	27.0	62.4	86.9	183.8	216.7	-
	4	$\bar{X}C$	9.58	46.17		110.11		213.28	-
		s	8.36	28.27		95.94		99.54	-
62 EEE	1	$\bar{X}$	138.6	147.7	143.0	185.0	183.3	192.8	-
	4	$\bar{X}C$	46.20	108.23		190.58		-	-
		s	29.20	75.53		76.11		-	-
63 GLI	1	F	15.0	50.0	83.3	96.4	100.0	100.0	-
	4	$\bar{X}C$	-	-		149.32		-	-
		s	-	-		47.45		-	-

* Legend on page facing the first page of the table

CHAPTER III

ZERO-ORDER CORRELATION COEFFICIENTS

A. METHODS. For each quadrat size on each gradient segment, the following statistics were calculated.

1. Zero-order product moment correlation coefficients, based upon per cent cover, were found between all possible pairs of those species occurring in five or more quadrats, between all possible combinations of one of these species with another measured ("environmental") variable and between all pairs of such "environmental" variables. Assuming a normal distribution, it is found that, for all segments, presence in five or more quadrats will leave more than 95% of the observations within the 2σ confidence interval, which Sokal and Sneath (1963) deem sufficient. With a skewed distribution, probably more common in nature, the per cent falling within this interval is even higher. Rarer species were ignored both because of possible decrease in this percentage, and because distributions depart increasingly from the normal as the number of occurrences becomes lower. Normal distribution is assumed in the correlation coefficient. The small letter

$\underline{r}$ is conventionally used to designate this statistic.[2] A complete list of the $\underline{r}$ values calculated is presented in Table VII (page 91).

The assumption of normality is probably violated in most cases by biological data, which tends to be skewed either to the right or to the left (Clark 1961), but not so far in most cases as to preclude the usefulness of $\underline{r}$ as an approximate measure of association (cf. Snedecor 1956). In addition to normality, the correlation coefficient assumes linearity, which is shown in Chapter VI to be invalid in a minority of cases. But even in the latter instances the correlations reflect the general or average slope of the regression. For reasonably rapid elucidation of the associations between a large number of variables, therefore, $\underline{r}$ seemed the most satisfactory among the available measures.

2. So-called phi coefficients (ϕ) were calculated for all possible pairs of those species which were present in at least the number of quadrats indicated below for each segment, and also absent in at least the same number.

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[2]This statistic is defined by the standard formulas found for example on page 214 of Yule and Kendall (1940), page 184 of Fisher (1958), page 234 of Walker and Lev (1953), and page 200 of Dixon and Massey (1957).

Segment Symbol[3]	Name	Drainage Characterization	Minimum No. of Quadrats for Presence and Absence
G	(Grayling Sand)	Dry	20
WC	(Wet Grayling-Croswell Sand)	Dry-Mesic	20
AS	(Au Gres-Saugatuck Sand)	Mesic	15
R	(Kinross Sand)	Wet-Mesic	12
DG	(Dawson-Greenwood Peat)	Wet	20

We shall allow the letters a, b, c, and d to represent respectively the numbers of samples having both species A and B present, species A only, species B only, both absent. Then ϕ is calculated by the formula:

$$\phi = \frac{ad - bc}{\sqrt{(a + b)(c + d)(a + c)(b + d)}},$$

found on page 272 of Walker and Lev (1953). It is a product moment correlation, actually a special case of r in which only two categories, zero and non-zero, are recognized.

This reduction to two categories makes necessary

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[3]Definitions of these segments are given in Appendix A (page 373). The legend for the symbols is given in Appendix B (page 375).

the larger number of quadrats containing the species than for the calculation of $\underline{r}$, where continuous variation is taken into account. A minimum of five samples in each of the categories a, b, c and d is generally accepted as adequate; a smaller number in any category may lead to too large a standard error (cf. Cole 1949). If one species of a pair were present in fewer than 12 quadrats, there would be virtual certainty of having one or more of the four categories fewer than five; it is for this reason that such species are not considered in the ϕ calculations. If a species is present or absent in fewer than 20 quadrats, in fact, the chances of making such an error are quite great, but the smaller numbers were permitted on AS and R because there was unused space on the IBM cards used to record data for these two segments. Several of the pairs whose ϕs were calculated did have one category of 4 or 3, but in no case were the corresponding chi squares significant. There seemed to be no harm, therefore, in including such ϕs in the Table VII in order to help round out the general picture.

The ϕ coefficients are presented together with the $\underline{r}$ values in Table VII (page 91), in the pink-shaded rows. A few "environmental" variables, with values of zero in the

requisite number of quadrats, e.g., cover of moss and lichen synusia, were included in the ϕ calculations also.

The ϕ coefficient was specifically designed for answering questions in which at least one of the variables is of a qualitative nature and measurable only on a nominal scale, e.g., eyes brown or not brown, male or female. Thus it might seem a superfluous calculation here, merely a simplification of $\underline{r}$ and hence cruder and less sensitive. In reality, each coefficient answers somewhat different questions, as explained in Section G of this chapter, and comparisons between them can be valuable.

3. Significance tests were carried out for the above coefficients, $\underline{t}$ in the case of $\underline{r}$ and chi-square in the case of ϕ, to determine the probability that these coefficients were different from zero. Significance levels of $P < .05$ or higher for all coefficients are indicated after the numbers in Table II with symbols, as explained in the legend preceding that table.

4. A number of special calculations involving the ϕ and $\underline{r}$ coefficients were used in analyzing tendencies. These are explained at the appropriate points later in this chapter.

B. DEMONSTRATION OF THE EXISTENCE OF PATTERN.

Perhaps the most striking and convincing result of this study is the demonstration of the existence of pattern within each of the five gradient segments, i.e., the vegetation within each such segment, though relatively homogeneous, on a large scale, is evidently heterogeneous on a small scale. Probably the spatial repetition of two or more elements, each tending to be restricted to areally small microsites, creates the appearance of large-scale homogeneity.

Considering all soil types and quadrat sizes combined, we find 12% of the rs and 38.1% of the ϕs significant at the $P < .05$ level or higher. Since by definition we would expect 5% of the possible pairs of randomly distributed variables to give significant correlations at this level purely by chance, we have 2.4 and 7.6 times the expected numbers of significant correlations, respectively. Even the former figure could scarcely be due to chance when one considers that some 3700 coefficients were calculated! At higher levels of significance, moreover, the ratio of actual to expected proportion of significant coefficients becomes progressively greater so that 4.4% of the r's are significant at $P < .001$, as are 18.1% of the ϕs at

$P < .005$. These are respectively 44 and 36 times the expected percentages. Practically every individual species or variable also exhibits many times the expected proportion of significance in its correlation with other variables, and the general picture is similar if proportions are calculated for individual soil types and quadrat sizes separately (Table II, page 55). These high proportions of significance cannot be attributed merely to a high number of "obvious" or "meaningless" correlations. After we have discounted all of these the remaining percentages of significant coefficients remain about as high, on the whole. This can be seen by comparing the subcolumns headed SS, CX, etc. on the left-hand side of column 3 of Table II (Proportions of Species-"environmental" correlations which are significant, including those of synusia with their major components) with the series SS', CX' etc. to the right of them (the same, excluding the synusia-component coefficients).

Some of these correlations may result from responses of species to gross environmental patterns within the gradient segments, particularly in the three middle segments which are obviously heterogeneous. Some, however, seem attributable to the microdistributional phenomena which,

because they are generally not conspicuous in the field, are of more interest to us.

The mere discovery of patterns on a small scale within vegetation is by no means an original one, as Kershaw (1963) clearly indicates. Among dozens of papers published during the past few years in which the authors attempted to demonstrate pattern on a scale of several square meters or less in the most diverse vegetation types imaginable (e.g. Goodall 1952, 1953, 1954, Cole 1949, Dice 1952, Kershaw 1958, Kershaw and Tallis 1958, Phillips 1953, 1954), I have encountered none in which they failed to do so. It is in its examination of changes in these patterns as a function both of environmental differences along a gradient and differences in quadrat size that this study attempts to reveal previously unreported characteristics of pattern and to provide useful suggestions for future investigations.

The phenomenon of the much higher actual-expected ratio at higher than at lower significance levels suggests that a relatively high proportion of the microdistribution patterns present are quite marked and distinct. The higher levels of significance probably represent strong ecological interactions between variables or narrow tolerance ranges,

with strong coincidence (in the case of positive correlation) or non-coincidence (in the case of negative correlation) in spatial optima. The lower levels may reflect broader tolerances, weaker ecological interactions and more overlapping optima.

C. INFLUENCE OF SOIL, DRAINAGE. Table II (page 55) was constructed in order to compare the proportions of coefficients significant on the various gradient segments and quadrat sizes, for groupings of species with similar distributions across the gradient and for groups of "environmental" variables which had certain characteristics in common. A listing of the species and variables found in the different categories is found in Appendix C (page 377), and the criteria used for separating the species into these convenient categories is explained in detail in Chapter IX.

We must caution ourselves, before interpreting the propositions of significant correlations found on each soil type, that they are not strictly comparable with one another. The number of samples is not constant, and it is increasingly difficult to establish significance as sample size decreases. Thus, all other things being equal, we would expect a far higher proportion of the coefficients

on G, on which 120 quadrats were sampled, to be significant than on R, which includes only 29, but if we find the reverse to be true or even the same proportion on both segments it is noteworthy. G, WC, and DG are roughly comparable with 120, 112, and 101 quadrats respectively, as are AS and R with 38 and 29. We must also be aware that a few of the proportions listed in the table are based on such a small number of coefficients that they cannot be taken seriously. These are indicated in Table II by parentheses.

The lowest proportion of significance is found among those relatively rare and/or small species occurring on the inorganic soils, most of which possess optima on the drier G or WC segments rather than on the moister AS (called "small solitaries" and symbolized as (SS) in the table).[4] The more clonal and areally extensive of the species which possess cover optima on one of the two best-drained segments (here designated "clonal xerophytes" (CX)) seem generally to be more strongly correlated with other species on the relatively more mesic WC segment, perhaps

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[4]In order to avoid confusion with the symbols for the soil types, symbols for these species groupings will be shown in parentheses.

because their clonal organization itself imposes a non-randomness upon their own microdistribution which is reflected in these coefficients. The positive relationship between frequency and proportion of significant correlation (next section) suggests this also, for the more frequent species are also the more clonal. But these more clonal species are scarcely more often significantly correlated than the (SS). Those species whose higher cover is found on the mesic AS ("Margin Drys" (MD) which are also abundant enough on G for correlation analysis there and "Margin Wets" (MW) which are not), on the other hand, exhibit almost twice as high a proportion of significant coefficients as the two relatively xerophytic group just mentioned (see grand totals, lower right in (Table II).

In looking at the proportion of significant coefficients for these groupings of species on different soil types, one finds some tendency for species to display higher correlations at the margins of their ranges along the gradient than in habitats seemingly optimal for them. Thus the bog margin species, (MD) and (MW), exhibit a much higher proportion of significance on G, WC and R relative to sample size ((MD) only on the latter) than on the AS segment where they reach their maximum cover. On R, the

(MD) and the distinctly bog species (B) exhibit proportions of significance about twice as high as do the (MW), which are apparently closer to their optimum habitats there than are the former two. These results suggest that species on their optimum segments of the gradient tend to have tolerance ranges embracing most of the conditions found within those segments, that they consequently tend towards more nearly ubiquitous distribution within these segments, and thus to circumneutral correlations with other species. But on segments which are more "marginal" for them, the same species may be restricted to relatively small portions of the segment, or may only grow well in these portions. Accordingly, they perhaps exhibit high positive correlations with other species which are similarly spatially restricted, high negative correlations with those restricted to different microhabitats.

A dramatic instance of such increase in correlation at range margins is the prevalence of high <u>positive</u> correlations on WC between the clonal xerophytes, (CX), and the (MD) and (MW) groups that reach peak cover on the bog margin. The (CX) are approaching the most poorly-drained limits of their range, the (MD) and (MW) the best-drained limits of theirs. Hence all may be relatively poor com-

petitors on this common "meeting ground" and so tend to be mutually more successful in those microsites most favorable to plant growth generally, or where the species dominating the ground cover on WC are sparse (indicating, perhaps, relative unfavorableness to plant growth generally). Now on AS, the mesic segment where the (MD) and (MW) have their cover maxima, the majority of these correlations disappear. The (CX)-(MD) and (CX)-(MW) correlations shifting in a negative direction by 0.2 or more between the dry mesic WC and the mesic AS (including positive to less positive and circumneutral to negative shifts) are about twice as numerous as those shifting positively by the same amount (15 against 7, only 2 shifting by less than 0.2). Moreover, the seemingly less drought-tolerant (MW) exhibit only negative shifts above this magnitude (9 of them) in their coefficients with (CX), whereas about half of the corresponding shifts in the (MD)-(CX) correlations are positive (6 of 13). Hence xerophytes and mesophytes tend to produce high cover in the same spots relatively less frequently on the more mesic segment, most especially in the case of more extreme mesophytes. Possibly the mesophytes have a competitive edge on the more poorly drained segment and effectively exclude the (CX) from the moister

and/or abiotically more favorable microsites by thriving there themselves. The experiments (Chapter VII) demonstrate that the xerophytes grow on these bog margin soils about as well as on the better-drained segments when such competition is excluded.

Maximal or minimal conditions may increase the sensitivity of species to interactions or small environmental differences, just as reduced vigor in many populations may decrease disease resistance.

Among themselves, the relatively mesophytic (MD) and (MW) exhibit a trend opposite to that of most other species, being more positively correlated with each other in their optimum habitat, the mesic AS, than on the dry mesic WC where all are less abundant. This suggests either that very different factors limit the distribution of different mesophyte species on the drier segment, or that they cannot compete very successfully with one another in the restricted areas relatively favorable to them at their range margin.

Time and again, we find that species tend to appear indifferent to a parameter on those segments where the parameter's values are low, but are strongly correlated with it (positively or negatively) where its values are

high. This is especially true in the soil horizon correlations. For example, there are overall much stronger correlations with soil horizon thicknesses on deep-profiles of the mesic AS than on G or WC, and correlations with bracken, Pteridium aquilinum (Ptr, no. 35 in the tables) are much the strongest on WC where cover of this large fern is so high as to make it decidedly the dominant among the high herbs. One might expect that if a species were positively correlated, for instance, with humus thickness (aoh)[5] on AS, it should be even more strongly positively correlated with it on G where humus is in such short supply. In fact, however, the latter correlation turns out to be circumneutral much more frequently than not. This leads us to postulate that there may be thresholds, i.e., values below which a parameter can have but little influence, favorable or adverse, upon the growth of a plant. Thus 10 mm. or 20 mm. of humus may make little difference to a plant because in any case there is an insufficient volume of this organic material in which roots

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[5]Abbreviations used for species and other variables used in the tables are listed in Appendix B (page 375). They may be distinguished from symbols for gradient segments and species groups by their being underlined and consisting of three rather than one or two letters or other symbols.

of a species favored by it can grow and proliferate. But 30 mm., for example, might be the minimal thickness in which roots of such a species could grow without becoming dessicated by the sun striking the ground surface. Then 60 mm. would provide twice as much root-expansion volume as 30 mm. and accordingly favor more vigorous shoot proliferation.

As a demonstration of the value of examination of correlation and other information from different parts of the gradient in specific cases, let us examine the pair Carex pensylvanica (Car) and Epigaea repens (Epi). From Table VII (page 97) we see that on AS, the correlation (r) between this part is 0.48 and 0.55 on 1 m^2 and 1/4 m^2 scales respectively, both positive and highly significant ($P < .01$ and .001). But the corresponding correlations on the better drained segments are circumneutral, even slightly negative (non-significant) on WC.

We see from the summaries of per cent cover across the gradient (Table I, page 27) that Carex' cover is greatest on well-drained G while Epigaea produces its greatest growth on the moister AS. This suggests that the first is a relative xerophyte, the latter a mesophyte, so the circumneutral correlation between them on the "dry end"

(which might be negative were not both scarce in sparsely vegetated patches) is not surprising. Possibly, then, their positive correlation on the bog margin results from both growing relatively poorly on the more poorly drained Saugatuck portion of this soil despite Epigaea's apparent mesophytism; their maximum tolerances for moisture or flooding may coincide though their optima are decidedly different. Another possibility is that certain other species, at their optima on this part of the gradient and so vigorous competively, preempt large parts of the area, mutual absence of Carex and Epigaea from these parts making their correlation positive. But the latter species do not both exhibit any high negative correlation with the same third species, so the first alternative appears more plausible. By comparing correlations and cover on several soils we have avoided some possible pitfalls, that Carex' and Epigaea's optima for moisture, humus, or something else coincide, for instance, or that they interact positively. In these last cases there would probably be at least a suggestion of positive correlation on the "dry end".

If we compare the gradient segments themselves with each other in regard to the proportions of significant

correlations found upon them, we see from Table II that R contains a higher proportion of significant correlations at all four levels than does AS. Since there are about one third more quadrats on AS than on R, so that coefficients of somewhat lower value are significant on the former, the higher proportions on R take on added import. This implies that R, is indeed more heterogeneous than AS, as suspected from field observations that the former contains both inorganic soil and bog elements, and also that its tipup-mound microrelief is much more extreme than AS's. Such heterogeneity would tend to make all but the most broadly-ranging species strongly predominate in distinct patches of one or the other environmental types represented, and hence give rise to many high correlations. Similarly, among the segments whose sample sizes are large WC, with about 7% fewer quadrats than G, appears to support the stronger correlations, possibly because it contains both dry end and bog margin elements. But DG, with fewer quadrats than G or WC, is the locus of considerably higher percentages of significance at all levels than either of the latter. In the case of DG, however, it is probably a sharply defined small-scale heterogeneity caused by the marked hummock-and-hollow microtopography found on that

segment (and discussed in more detail elsewhere) which is the cause. The DG segment, on a scale several times that of the largest quadrats appears more homogeneous than any other, and it embraces neither broad vegetational extremes nor conspicuous elements of other segments. The absence of drainage-influencing slope may be an important factor in this.

D. RELATION BETWEEN FREQUENCY OR COVER AND STRENGTH OF CORRELATION. It appeared frequently during the analyses that the more abundant species or those with the highest cover might exhibit the strongest correlations overall. As a partial test of this question, a series of linear regressions of the standard form,

$$y = a + bx,$$

whose computational formulas are given for example on pp. 230 ff. of Walker and Lev (1953), were calculated for the data from gradient segment G (Grayling Sand). In these regressions, frequency or cover of species (dependent variable y) were plotted upon per cent of all correlations of the species significant (independent variable x). Letter a represents the y - intercept and b, the regression coefficient or slope, the increase in y per unit increase in x. This was repeated for each of four different significance

levels of the correlations, both for the coefficients from all three quadrat sizes treated as a single population and for those from the 1 m X 1 m size only. Relevant results are presented in Table III, page 60).

At the three lower significance levels ($P < .01$, .02 or .05) frequency of a species and its correlation strength, as measured by the proportion of its coefficients significant, do indeed seem to be positively related as predicted. This is especially true when coefficients from all three quadrat sizes are considered together, and the regression of frequency upon per cent significance at $P < .05$ for all quadrat sizes, is itself significant at $P < .01$. There are no other significant regressions but their overwhelming positive trend is fairly convincing. Per cent cover and per cent significance in all three quadrat sizes are similarly positively related (the low magnitude of the b's being due to the relatively low values of cover as compared to frequency). But on the 1 m^2 scale alone, the regressions of cover on significance proportion range from flat to quite negative.

The import of these results would seem to be that the more commonly encountered species and those with the highest cover, which are usually one and the same, tend to

TABLE III

The regression coefficient (column 4) of frequency and cover of species on per cent of correlation coefficients of these species significant on gradient segment G (Grayling Sand). The significance levels at which these per cents were calculated are listed in column 2, the quadrat sizes which were considered in column 3. Symbols used are 1 = $1m^2$, 4 = $1/4\,m^2$, H = $1/100\,m^2$.

1 y (abundance criterion)	2 Significance level, of correlations, P≤	3 Quadrat Sizes	4 b	5 Significance of b (dash = P >.05)
Frequency	0.05	1, 4, H	+ 2.68	P <.01
(ϕ coefficients)	0.025		+ 2.29	–
	0.01		+ 2.41	–
	0.005		– 0.57	–
	0.05	1 only	+ 1.09	–
	0.025		+ 0.63	–
	0.01		+ 0.13	–
	0.005		+ 0.00	–
Per cent cover	0.05	1, 4, H	+ 0.13	–
(r coefficients)	0.02		+ 0.05	–
	0.01		+ 0.07	–
	0.001		– 0.19	–
	0.05	1 only	– 0.00	–
	0.02		– 0.07	–
	0.01		– 0.12	–
	0.001		– 0.12	–

exhibit the strongest correlations as postulated. Since these species are generally the more clonal ones, their wide sphere of influence upon other species may bring this about. But the decrease in positive slope of the regression upon significance proportion at progressively higher significance levels, and the negative regression of both frequency and cover on these proportions at the highest significance level of the correlations, ($P < .001$) appear to reflect a counteracting force. This force probably consists in the specialized requirements of the relatively rare species which exhibit a somewhat higher proportion of very high correlations than the large, clonal, extensive species. Perhaps the highly significant correlations of the rare species reflect their specialized requirements, environmental specificity and dependence upon the more robust and ubiquitous elements in the community. The higher proportion of low-value correlations exhibited by the more ubiquitous species may reflect their relatively broad tolerances and non-specificity of influence.

The overall negative regressions of cover on significance proportion data for 1 m^2 quadrats alone seem unaccountable to anything other than small sample size.

E. INFLUENCE OF QUADRAT SIZE. The measurement of correlation on the basis of data from different quadrat sizes should reveal something of the spatial scales of patterns present (Goodall 1952, Kershaw 1963, 1964, Greig-Smith 1964 among others).

Greig-Smith (1964) and Kershaw (1964) point out that we should expect more and more species to be positively correlated as we increase the size of the sample units, and conversely fewer positive and more negative correlations as we decrease unit size. On the basis of quadrats 30 or 40 miles square randomly located over the whole surface of the earth, such unlikely things as wheat and spruce trees might be positively correlated while intertidal organisms would be found to be associated with benthic forms of the same latitude. Diminishing the scale toward the other extreme, we would reach a point where the organisms were larger than the sample quadrats, so that the probability even of parts of two individuals' in the same quadrat would be small. In this case we would obtain predominantly negative associations. As Greig-Smith (1964) theorizes, and as Kershaw (1961) found in practice, positive correlations should then generally shift in a negative direction as we reduce the size of the sample

units, because of both this factor and the increased intensity of competition on a small scale.

Figure 3 (page 64) illustrates, for the data of this study, the influence of quadrat size upon strength of positive or negative correlation. The bar graphs show the frequency (y-axis) with which correlations of variable pairs, based upon data for quadrats of a given size, exhibit positive or negative shifts of various magnitudes (x-axis) from correlations of the same pairs based upon larger quadrats. These graphs are based upon data for all gradient segments combined. For example, eleven variable pairs have correlations based upon data for the 1/4 m^2 quadrats which are between .23 and .27 (inclusive) algebraically lower than their correlations based upon 1 m^2 quadrat data. Accordingly the bar between - 0.23 and - 0.28 shaded in Figure 3A has a height of 11. The values of the correlation coefficients themselves have no effect upon this graph. Three variable pairs with correlations in 1 m^2 and $\frac{1}{4}$ m^2 quadrats respectively of + 0.90 and + 0.65, + 0.15 and - 0.10, and - 0.15 and - 0.40 will all have a shift of - 0.25, and accordingly all will be represented in the - 0.23 to - 0.28 bar.

Table IV (page 65) lists the numbers of positive

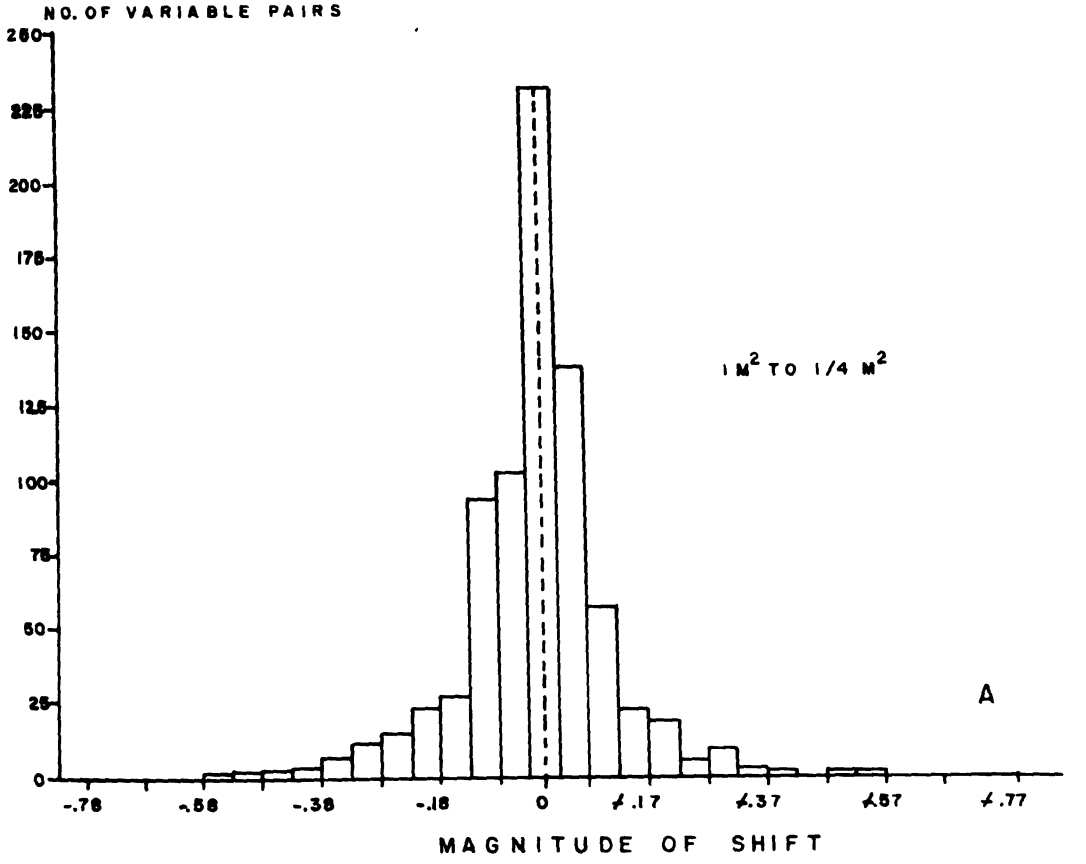
FIGURE 3. Shifts in correlation with quadrat size

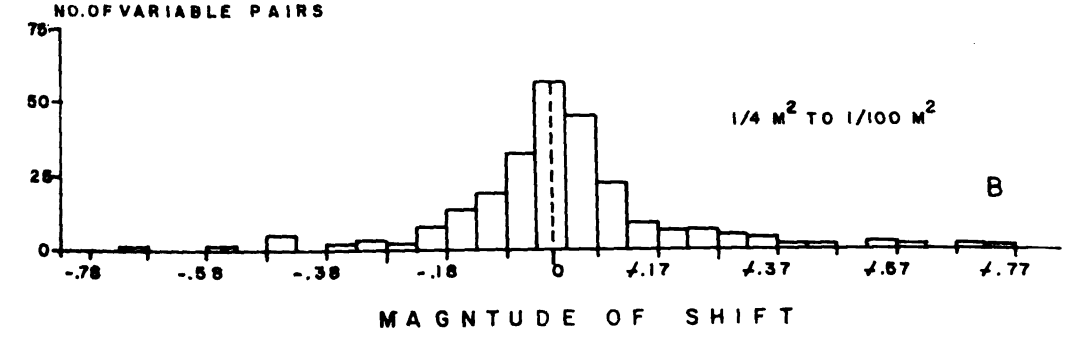
The horizontal axes represent the magnitudes of changes in the correlation coefficient between particular variable pairs, the vertical axes the number of variable pairs exhibiting changes of these magnitudes.

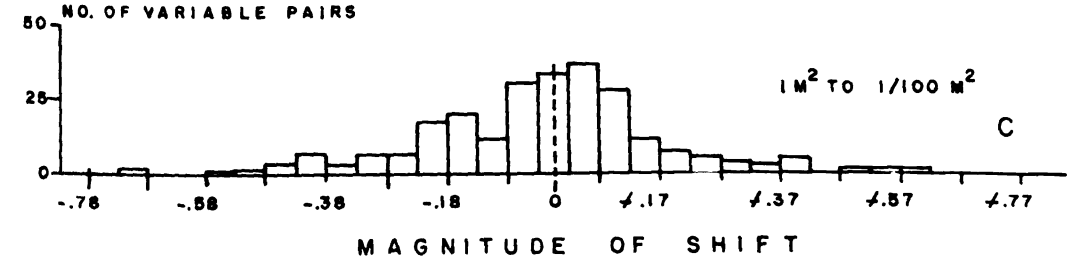
A. Changes between 1 m^2 and 1/4 m^2 quadrats.

B. Changes between 1/4 m^2 and 1/100 m^2 quadrats.

C. Changes between 1 m^2 and 1/100 m^2 quadrats.


NO. OF VARIABLE PAIRS
250
225
200
175
150
125
100
75
50
25
0
1 M² TO 1/4 M²
A
-.78
-.58
-.38
-.18
0
+.17
+.37
+.57
+.77
MAGNITUDE OF SHIFT


NO.OF VARIABLE PAIRS
75
50
25
0
1/4 M² TO 1/100 M²
B
-.78
-.58
-.38
-.18
0
+.17
+.37
+.57
+.77
MAGNTUDE OF SHIFT


NO. OF VARIABLE PAIRS
50
25
0
1 M² TO 1/100 M²
C
-.78
-.58
-.38
-.18
0
+.17
+.37
+.57
+.77
MAGNITUDE OF SHIFT

and negative changes above certain arbitrary values, in order to call attention to a fact not immediately evident from looking at the graphs; that the really large shifts with decreasing quadrat size are indeed predominantly negative. The tendency is, however, not nearly so pronounced as Greig-Smith's reasonable hypothesizing might lead one to expect, and seems to occur primarily between the 1 m^2 and $\frac{1}{4}$ m^2 quadrat sizes with little if any change between the latter and $\frac{1}{100}$ m^2.

TABLE IV

Correlation shifts between large and smaller quadrat sizes. Explanation in text.

Magnitude of shift	Numbers of correlations exhibiting shifts of the magnitudes and signs listed at the left between the quadrat sizes indicated					
	$1m^2$ to $\frac{1}{4}m^2$		$\frac{1}{4}m^2$ to $\frac{1}{100}m^2$		$1m^2$ to $\frac{1}{100}m^2$	
	-	+	-	+	-	+
0.30 or over	19	11	10	12	18	14
0.20 or over	58	28	17	25	36	23
0.15 or over	79	47	30	30	58	33
0.10 or over	137	92	46	43	70	49
	mean shift=	-0.013	mean shift=	+0.007	mean shift=	-0.017

The modes, or values exhibited by the largest number of correlation pairs, are very slightly on the positive side of zero, and small shifts are seen to be predominantly positive in Figure 3. But this is counterbalanced by both greater numbers and higher values of negative shifts. This combination makes for nearly equal area under the curve on either side of the mean, and hence for mean shifts (bottom of Table IV) as well as coefficients of skewness, g_3 (Clark 1961) not significantly different from zero and, in fact, very close to it numerically.

A possible cause of the slight predominance of small positive shifts in correlations with decreasing quadrat size, despite the tendency of larger shifts to be negative, might be a pronounced tendency of species to be grouped together on a small scale. The decrease in negative shifting between the 1/4 m^2 and the 1/100 m^2 quadrats tends to corroborate this hypotesis. Such small scale grouping might be largely independent of larger-scale patterns or groupings, which would tend to break down on a smaller scale due to spatial limitations and competition as discussed above. Thus, it is possible to postulate patterning forces of at least two distinct scales in the ecosystems of the study gradient. The larger may be large-

scale heterogeneity within gradient segments such as parent material or soil moisture differences, whereas the latter may be related to changes in exchangable soil ion concentrations brought about by the species which recently occupied a microsite, or to the approximate area occupied by interacting species themselves. At any rate, the smaller scale patterns would appear to be stronger and more specific than the larger ones, for the Greig-Smithian factors predisposing toward negative shifts should otherwise tend to move the modes as well as the longer and areally larger tails of the Figure 3 curves to the negative (left) side.

As an example of the uses to which correlations from quadrats of different sizes may be put, let us examine the pair Rubus hispidus var. obovalis (Rho, no. 36 in the tables) and Vaccinium boreale (Vyp, no. 47). On WC the correlations are + 0.01 on the basis of data from 1 m^2 quadrats, - 0.00 from 1/4 m^2 quadrats and + 0.35 from 1/100 m^2 quadrats; on AS the respective correlation are - 0.13, - 0.09, and + 0.47 (Table VI, page 114). The high positive correlations on a 1/100 m^2 scale, significant at the $P < .001$ and $P < .01$ levels respectively on the two segments, are in vivid contrast to the circumneutral ones from larger quadrats. This combination rules out the pos-

sibility that the correlation is due to mutual optima with respect to any environmental variable acting on a fairly broad scale, such as tree cover or parent material textural variations. An examination of the correlations of Rubus and Vaccinium with other variables and species reveals none with which both have a significant positive or negative correlation on both soil types, so similar responses to such a species or to one of the environmental variables measured is also ruled out as a possible cause. Moreover, Vaccinium is a shrub and Rubus a repent vine, and both form large clones and spread by rhizomes. Thus the microsite where the cover of both is measured in a 1/100 m^2 quadrat is usually some distance from the bulk of the underground parts of each, and a correlation between them on this scale could scarcely be the result either of interactions between them underneath the ground, or of mutual responses to a soil factor varying on a small scale. By a process of elimination we are almost forced to the conclusion that a positive interaction is occurring between the aereal parts of the two species, and that where a Rubus vine passes beneath a lush Vaccinium clump it puts forth more and/or larger leaves. At present we do not know whether this might be related, for example, to a simple stimulation

of Rubus leaf expansion in dense blueberry shade (a response similar to "shade-leaf" formation in many trees), to a metabolic exudate released by one of these species and stimulatory to leaf and shoot growth of the other upon contact, or to some other factors perhaps beyond our wildest imagination. What is important is that by examination of correlation behavior in quadrats of different sizes, we have considerably narrowed down and crystalized the field of possible causes. Some now absurd ones might easily have seemed acceptable postulates had we possessed only the information from the smallest quadrats, and the relationship would not have come to our attention at all had we used only one of the larger sizes.

The information from two gradient segments has been useful in this case also, but here the two coefficients reenforce one another, instead of indicating a change as do the examples cited in Section C.

F. PREVALENCE OF POSITIVE CORRELATION. Almost as striking as the unusually high proportion of significant coefficients is the undeniable predominance of high positive over high negative correlation values. If we count those coefficients from all three quadrat sizes whose absolute values are 0.2 or over, (which approximates the

lowest value significant for any segment), we obtain the figures presented in Table V below. The complete distributions of coefficient values are illustrated in Figures 4 and 5 (pages 76, 77).

TABLE V

The numbers of coefficients for all quadrat sizes of 0.2 or over in absolute value which are positive and negative, the mode and the mean of all coefficients on each soil type. See also Figures 4, and 5, pages 76 and 77.

Soil Type	G	WC	AS	R	DG	Total	Total
Coefficients +0.2 or more positive	77	125	164	101	26	493	126
Coefficients -0.2 or more negative	21	20	91	65	21	218	51
Mode of all coefficients	-.03	-.03	-.08	-.12	-.05	---	---
Mean of all coefficients	+.020	+.029	+.005	+.007	-.015	---	+.067

Overall, over twice as many of the r's above 0.2 are on the positive side as are on the negative. Similarly, the number of positive ϕs larger than 0.2 is about two and one-half times the number of negative ones. By contrast, the modes, i.e. the intervals which contain the most coefficients, are slightly negative on all five gradient seg-

ments. This means that, among coefficients of low value, there are many more negative than positive ones. In combination with the prevailing positiveness of high values, this accounts for the nearly neutral mean correlation values on each soil type, and for our inability to statistically demonstrate skewness in the distribution of coefficient values just as was the case with the distributions of correlation shifts with quadrat size. (Here, however, the curves are mirror images of those of the shifts, with the right-hand tail longer, the left-hand tail higher near the zero point).

The striking tendency towards positive correlation could possibly be due to a clustering or overdistribution of the vegetation as a whole, such as is visually evident in the field. Lush and sparse multispecific patches would correspond to a mosaic of microsites relatively more and less favorable for growth of vascular plants generally. Such a mosaic could theoretically owe its presence to the distribution of some dominant and inhibitory species, but such a species should exhibit predominantly strong negative correlations with others. Only on one segment, DG, is there in fact a dominant species which does (Chamaedaphne calyculata). On G and WC dominant bracken (Pteridium

aquilinum), which is known to inhibit other species in an antibiotic fashion and which may leave behind a concentration of inhibitory substances in patches where it has recently died (Watt 1947), shows only a weak negative trend in its coefficients. Nonetheless, the antibiotic-impregnated patches need not necessarily be strongly correlated with patches of living Pteridium, and hence might be the sparse patches in a vegetational mosaic despite living bracken's lack of a striking negative correlation trend with other species.

But there are no plausible causative species on the remaining two segments where Pteridium and Chamaedaphne are sparse or absent, nor in fact do any of the measured physical factors exhibit the unusually strong trends toward high positive or negative correlation which one would expect of a dominant patterning force (Prunus serotina demonstrates possible antibiotic activity on AS, but is scarcely widespread enough to account for the positive correlation trend). It thus appears, then, that the patterning force consists of some unmeasured abiotic parameter, or in the distribution of unmeasured organisms such as soil microbiota or insect larvae.

The negative modes may reflect the same general

tendency towards negative correlation on a small scale due to interspecific competition and spatial exclusion mentioned by Greig-Smith, and postulated above (Section E) as a reason for the predominance of high negative over high positive correlation shifts with decreasing quadrat size. They may, on the other hand, be a result of large-scale patterning which, as mentioned in Section E, perhaps produces relatively weak correlations. If so, then it also tends to produce negative ones, while the correlations attributable to the more sharply-defined, hence high correlation-producing forces on a small scale are mostly positive.

On those gradient segments which contain much sparsely vegetated space and where such spaces are relatively large, namely G and WC, the number of large positive coefficients according to Table V is respectively about four and six times as large as the number of negatives. But on segments where vegetation is more uniformly dense and competition would appear to be at a maximum we obtain less than twice as many positives (as on AS) or only a few more (as on DG). The modes on the latter two segments, moreover, are more negative (-.08 and -.05 respectively) than those on the two better drained, more sparsely vege-

tated segments (-.03 on both), and considering the several hundred coefficients contributing to each of these figures it is improbable that the differences are trivial. This is just what we would expect; the most marked positive trend should occur where a force like spatial or moisture competition, predisposing to negative correlation, is relatively important (although under extreme drought conditions moisture competition might be more vigorous on the "dry end" than elsewhere). A relatively high proportion of slight to moderate negative correlation on R and the lowest mode of all here (-.12) may be due, not to competition, but rather to the great heterogeneity of the physical environment here.

We can now utilize the predominance of positive correlation in conjunction with information previously discussed in order to demostrate additional aspects of pattern in the study area.

Overall, proportions of significant coefficients decrease on the smaller quadrat sizes (Table II, page 55). Since most significant coefficients are positive, including nearly all on AS and R, the negative shift with decreasing quadrat size discussed in the preceeding section would tend to make most coefficients less positive and hence less

significant as this size becomes smaller.

If we now examine the behavior of different physio-ecological groupings of species separately, we find the bog species (B) on DG exhibiting by far the greatest decrease in correlation significance proportions between 1 m^2 and 1/100 m^2. The mesophytic, mostly clonal (MD) and (MW) as well as the larger clonal xerophytes (CX), each exhibit a somewhat weaker tendency of the same sort on at least one soil type, but for the small, mostly non-clonal (SS) species of the inorganic soils there seems to be no such trend whatever.

The lack of any apparent general trend as to the part of a species' range where the greatest quadrat size-related significance decrease is found makes interpretation of these results difficult. The (CX), (MW), and (B) exhibit their greatest decreases on their optimal segments, WC, AS and DG respectively. The (MD), on the other band, decrease most on G, the xeric end of their range. The better the drainage where a grouping has its optimum, the less the tendency of its positive correlations to decrease in value as quadrat size does, but this may be a coincidence.

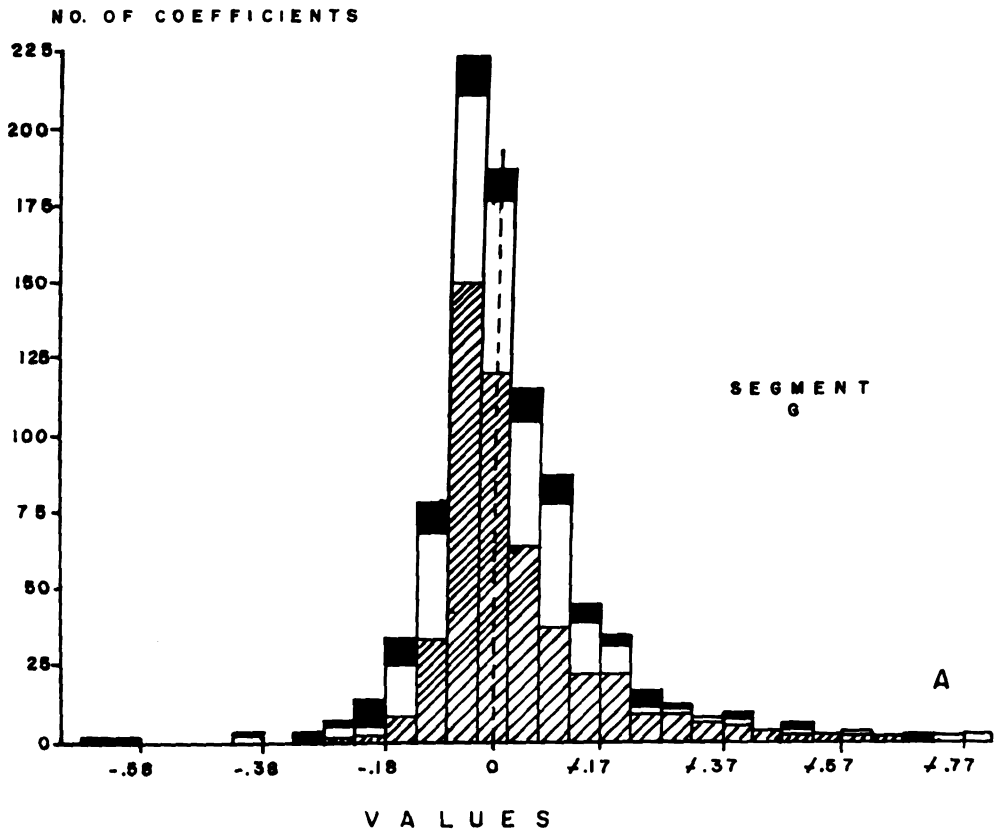
The (B), the only species exhibiting a really

FIGURE 4. Correlation Values for each Segment

The number of correlations within each value range are indicated by the height of the bars. Diagonal hatching = species-species correlations, clear = species-environment correlations, black = environment-environment correlations.

A. Correlations on Segment G, r

B. Correlations on Segment WC, r


NO. OF COEFFICIENTS
225
200
175
150
125
100
75
50
25
0
SEGMENT
G
A
-.58
-.38
-.18
0
+.17
+.37
+.57
+.77
VALUES

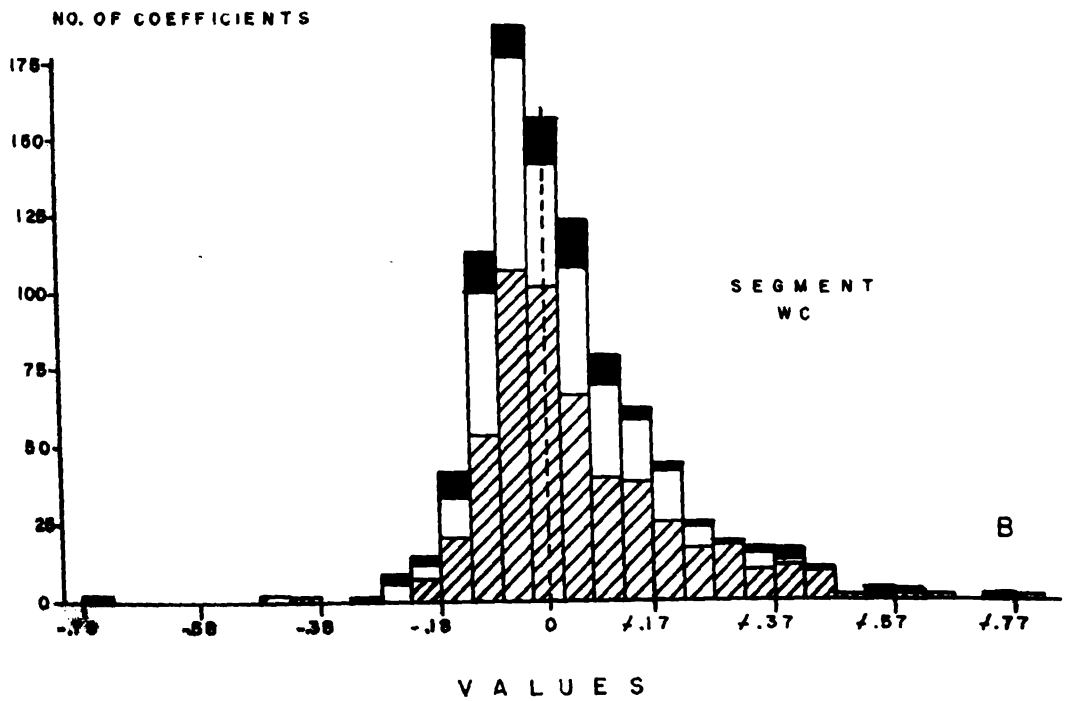

NO. OF COEFFICIENTS
175
150
125
100
75
50
25
0
SEGMENT
WC
B
-.58
-.38
-.18
0
+.17
+.37
+.57
+.77
VALUES

FIGURE 5. Correlation Values for each Segment, cont.

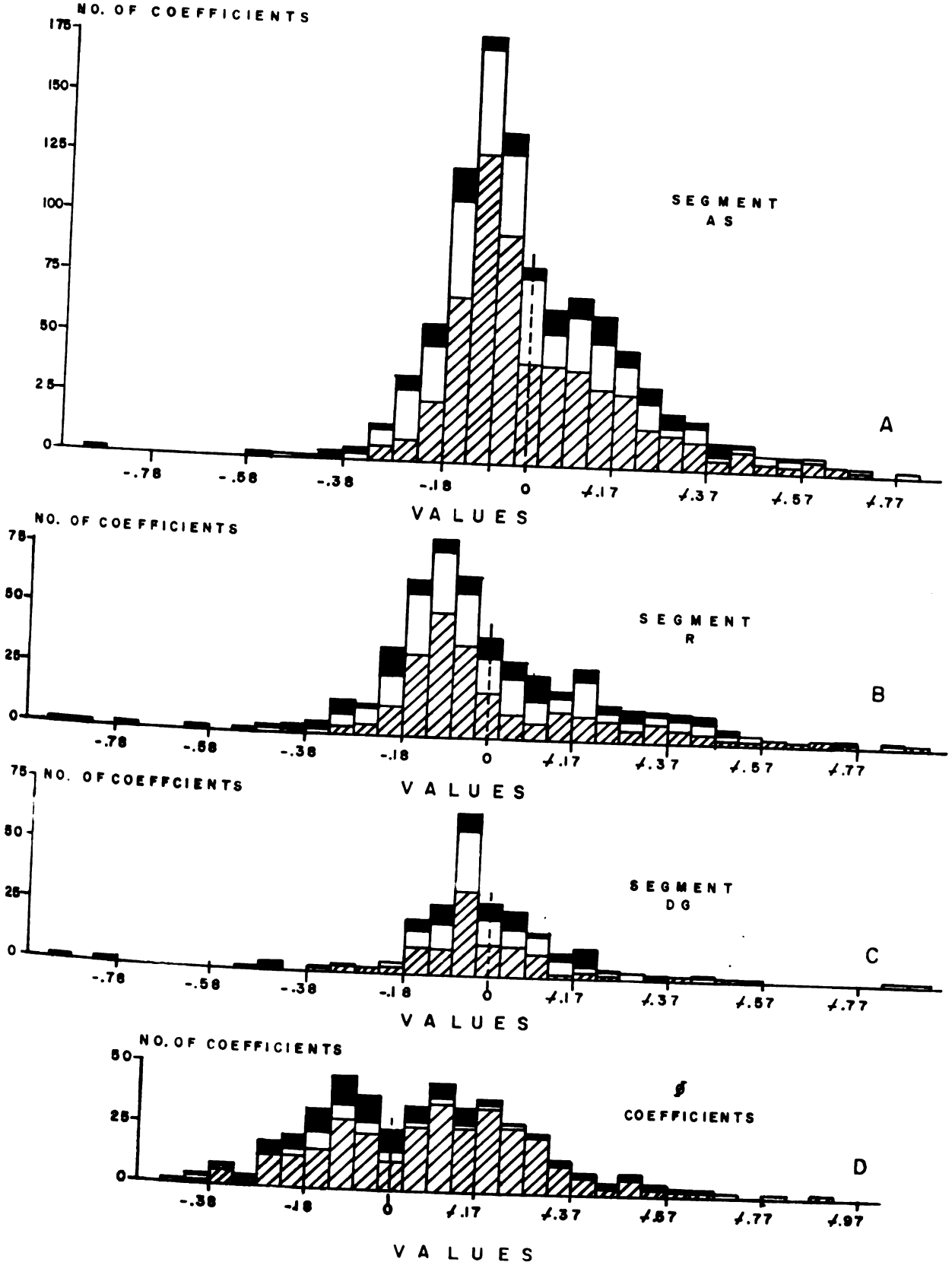
Explanation and legend as for Figure 4, page 76.

A. Correlations on Segment AS, r

B. Correlations on Segment R, r

C. Correlations on Segment DG, r

D. Correlations on all segments combined, ϕ


NO. OF COEFFICIENTS
175
150
125
100
75
50
25
0
SEGMENT
A S
A
-.78
-.58
-.38
-.18
0
+.17
+.37
+.57
+.77
VALUES
NO. OF COEFFICIENTS
75
50
25
0
SEGMENT
R
B
-.78
-.58
-.38
-.18
0
+.17
+.37
+.57
+.77
VALUES
NO. OF COEFFCIENTS
75
50
25
0
SEGMENT
DG
C
-.78
-.58
-.38
-.18
0
+.17
+.37
+.57
+.77
VALUES
NO. OF COEFFICIENTS
50
25
0
ϕ
COEFFICIENTS
D
-.38
-.18
0
+.17
+.37
+.57
+.77
+.97
VALUES

strong decrease in significance in smaller quadrats, are also the only species which exhibit a high proportion of significant negative correlations. As we can see from Table VI (page 79), the proportion of negative coefficients does not change appreciably or even decrease slightly with decreasing quadrat size, although on the basis of prior results we might reasonably expect it to increase. But the proportion of positive coefficients for the smaller quadrats decreases tremendously, a probable consequence of interspecific inhibition on a relatively small scale by clonal shrubs such as Chamaedaphne. The large number of high negative correlations may owe itself to this inhibition also. The relatively large scale of the hummock-and-hollow microtopography, probably the primary "environmental" pattern-inducing factor here, perhaps accounts for the higher proportions of positive correlations on a larger scale.

G. COMPARISON OF ϕ AND r COEFFICIENTS. The much higher proportion of significance among the ϕ coefficients than among the rs is striking. On G, WC and AS there are considerably more significant ϕs at each significance level and only on DG are the proportions about the same (Table II, page 55)(the proportions on R cannot be taken

TABLE VI

A comparison of the percentages of positive and negative coefficients which are significant on the DG gradient segment.

Significance level, P<	Quadrat size								
	1 m^2			1/4 m^2			1/100 m^2		
	+	-	total	+	-	total	+	-	total
0.05	12.7	5.5	18.2	5.2	8.8	14.0	2.6	5.3	7.9
0.025	5.4	5.5	10.9	5.2	5.3	10.5	1.4	3.9	5.3
0.01	5.4	5.5	10.9	3.5	3.5	7.0	1.3	1.3	2.6
0.001	0.0	3.6	3.6	3.5	3.5	7.0	1.3	0.0	1.3

seriously because of the small number of coefficients calculated there). Part of this may be due to the predominance of the more abundant species in the ϕ coefficient calculations, and to these species' tendency to have higher $\underline{r}s$ than the rarer species also (see Section D of this chapter). Yet even among just those species for which ϕs were calculated on each soil type and quadrat size, there are nearly twice as many significant ϕs as $\underline{r}s$ at corresponding significance levels (bottom of Column 9, Table II, page 55).

Probably this again reflects a mosaic of patches of

lush and patches of sparse vegetation generally. If we postulate such a mosaic then, in the sparsely vegetated microsites, only the most common species may have much probability of occurring; accordingly most of the species may be clustered together in the lushly vegetated spots, mutually absent from sparse locations, and so are positively correlated on the basis of presence. But within each lushly vegetated microsite, interspecific competition and spatial exclusion may tend to make the cover of species inversely proportional to one another, as already explained in other connections. Now, most of the significant correlations on the inorganic soils are positive (the import of which was discussed in Section F above) so that the proportion of significant correlations is a good measure of the proportion of high positive correlations. Thus, correlations based upon cover, although overwhelmingly positive on the whole, are numerically lower than the ϕs and hence less liable to be significant. The similarity in the proportions of significant rs and ϕs on DG may be due in part to the absence of extensive sparse patches, and to the absence of slope or level differences with respect to the water table making for nearly ubiquitous presence of the common species on this segment. Both conditions

would tend to lower the proportion of positive and significant ϕs. At the same time, the rather distinct and sharply-defined nature of the microtopography and its related clear-cut vegetation mosaic, plus the apparent inhibition effects of lush bog shrubs, may tend to increase the numbers of both high positive and high negative rs.

It is evident, then, that the ϕ and r calculations do not yield the same information and do not duplicate one another, although if we allow the two types of coefficients for each variable pair themselves to be variables the correlation between them comes out very highly positive ($r_{\phi r} = +0.70$, $P < .001$). The ϕ coefficients, by merely considering presence or absence, without regard to the amount of cover, are more inclined to reflect preferences of species with regard to broadly-varying factors, such as soil moisture or texture or minerals perhaps. The rs , on the other hand, may reflect competition or interaction between species, as well as response to factors varying sharply on an extremely small scale, to a much greater degree. This is interrelated also with quadrat size (Section E of this chapter).

As another illustration, if two species possessed quite different microhabitat optima but a great deal of

niche overlap, then the two would occur together much of the time, perhaps giving a positive ϕ, but the per cent cover of each would be high in different microsites giving a circumneutral r. Or a combination of circumneutral ϕ, negative r would be possible under similar circumstances. Thus we see that similar ϕ - r combinations could be due to quite different sets of circumstances.

There is in addition a substantial minority of instances in which either r is greater than ϕ positively, or where r is circumneutral or even positive while ϕ is substantially negative. A good case in point is the pair Gaultheria procumbens (Gau, no. 22 in the tables) - Maianthemum canadense (Mai, no. 28), which on both 1 m^2 and 1/4 m^2 scales, on both G and WC, yields quite positive and highly significant r values with $P < .01$ or .001 (see Table VII, page 106). The corresponding ϕ coefficients, while also positive, are consistently much lower in value and significance (one of them not even significant at $P < .05$). The situation here may indeed be somewhat the opposite of the one just mentioned; the two species may have a relatively small area of overlap within the range of habitat conditions under which they have a high probability of growing, so that Maianthemum is frequently found

without Gaultheria and Gaultheria without Maianthemum. The area of overlap, however, could include the cover optima of both (observations suggest the remains of old logs, stumps, and other large bodies of decomposing organic matter in this case), giving rise to a correlation based upon amount of cover which would be more highly positive than one based upon simple presence.

H. "ENVIRONMENTAL" PARAMETERS. It is incorrect to arbitrarily designate particular variables "environmental" when, in fact, every species is in some degree part of the environment of every other growing within its sphere of influence. In fact one group of variables which are here called "environmental", the layers of vegetation or synusia,[6] are themselves made up of species. They are included in the analysis because frequently they may have an influence on members of other synusia which are not evident from individual species correlations. Also included are characteristics of the litter, non-living but

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[6]As designated here, tree and shrub synusia are separated on the basis of height (below 6 feet for shrubs). Those woody species with a repent habit are included with all the species having non-woody stems in the herb category, whereas all other woody plants less than 6 feet in height are designated shrubs.

organic, and the soil, most of whose mass (but not necessarily influence) is inorganic. The epithet "environmental" is patently one of convenience, and should not be thought of as implying any fundamental differences in the ways in which "environmental" factors as opposed to other species impinge upon organisms.

The "environmental" parameters which at first glance seem to exert the strongest influence upon species distributions are the synusia ((SY) Column 2 in Table II, page 55). However, a considerable proportion of the high synusium-species correlation is due to the fact that the correlated species themselves constitute these synusia. For example, the positive correlation between shrub cover and Chamaedaphne in the bog is nearly unity (+0.83), which looks most exiting until we realiza that this species, making up over 80% of the shrub cover here, is practically synonymous with the shrub synusium. If we now consider only those species-synusium correlations for which the species is not a member of the synusium with which it is correlated or does not comprise over 20% of that synusium in more than two quadrats, we obtain the proportions listed just to the right of the synusia (SY) in Column 2 of Table II, namely (S-). (S-), it should be stressed, is no perfect

gauge of the relationship between variation in the synusia and in the cover of species, either. For one thing, there are almost certainly relationships between cover of synusia and that of the species which comprise them aside from the participation of the latter in the former. For another, the species for which correlations have been eliminated are naturally the more common ones, leaving a disproportionately high number of correlations with relatively rare species. Now, as discussed in Section D above, the rarer species tend to exhibit the lower proportions of correlations. The combined effect may be to make the adjusted figures lower than they should be.

In so far as these figures can be trusted, it is evident that the synusia have considerably less influence upon the microdistribution of species than might have been assumed. On G, WC, and DG the corrected proportions of significance in these synusium-species correlations ((S-), Column 2 of Table II) are now somewhat lower on each segment than similar means for all correlations ("tot" in Column 4), and on AS they are only about one-third as high. Only on R do synusia seem to be strongly correlated, probably because of the heterogeneity in that segment, and the great variation in tree and shrub cover associated with

the coming together of upland and bog elements. But based upon these adjusted proportions of significance, the synusia do seem to exert (or merely predict?) as much patterning influence as the horizons overall ((HO) in Column 2) and somewhat more than the litter parameters (LI). Synusial correlations appear particularly strong on G and WC.

Soil horizon thicknesses ((HO), Column 2) seem to be more closely related to species distributions on WC than elsewhere. This most probably stems from the relatively higher cover of vegetation as a whole on relatively deep-horizoned Croswell, that part of WC which borders on AS. Also, there is a surprisingly large proportion of highly significant coefficients with the horizons on DG, the bog soil, which means here entirely with the thickness of the peat itself. One would think that here, where the organic matter is several times thicker than most roots can penetrate, its thickness would be less related to species distributions than elsewhere. Also, the zone of possible root penetration or shading by upland species is relatively small. But concentrations of mineral nutrients may be differentially stimulatory to different species, and may be inversely proportional to distance to mineral

substrate below from which they can seep upward, or to upland soils from which they can wash and seep laterally. Or possibly the patterns reflected here are relict ones; the peats farther from the margin, though thicker, are younger and in the more recently filled-in part of the lake basin. Conversely, the marginal peats are more likely to have been dry at the time of fires, and so to have been more recently replaced. Local differences in the magnitude of surface level fluctuations, such as those described by Buell and Buell (1941), may also have their effect.

But overall, the proportions of species-environment coefficients significant are generally smaller than those of species-species correlations, particularly at the high significance levels ($P < .01$ and .001). This is true for each gradient segment as well as the five segments combined, and suggests that these parameters have rather less pattern-inducing influence than species upon other species. If we now examine the significance of correlations of "environmental" parameters with other such parameters (Column 3 of Table II), however, just the opposite seems to be true, both generally and for specific categories of parameters and segments.

As a corollary of the last-mentioned trend, the

cover of synusia should be more strongly influenced by the distribution of other synusia and other "environmental" parameters than are the individual species which constitute them. Thus shrub cover may be reduced under tree cover, herb cover reduced under shrub cover, or either increased in patches of relatively thick humus, etc. Competition and spatial exclusion of species within these synusia may tend to lower individual species -"environment" correlations.

The importance of "environment" in the microdistributions of particular groupings of species can be inferred from the proportions listed in Columns 3 and 4 of Table II, uncorrected and corrected for "ridiculous" correlations respectively. The "small solitaries" (SS) seem to be relatively little influenced throughout. The more abundant "clonal xerophytes" of well drained soils (CX), on the other hand, exhibit a proportion of significant correlations with "environmental" variables two to four times as high as do the (SS). This parallels the statistical behavior of the two groups with other species, but here the difference is more marked. Similarly, as in their correlations with other species, those species with cover optima on the more poorly-drained soils, (MD), (MW) and

(B), seem from the uncorrected proportions (SS, CX etc.) of Column 3 more strongly correlated with "environmental" parameters than are the aforementioned xerophytes, especially far from their optimal habitat as on G or WC. But this difference disappears when the corrected proportions are considered (SS', CX' etc., Column 3), suggesting that it reflects nothing but correlations of synusia with their components. The relatively high corrected proportions for (MW) on R are based on very few coefficients, so probably reflect chance fluctuations.

A more detailed discussion of the roles played by individual environmental parameters follows in Chapter VIII.

I. USEFULNESS OF NON-SIGNIFICANT CORRELATIONS. Isolated non-significant correlation coefficients naturally cannot be given much credence, since we have no assurance that their magnitude is not due to random sampling error, or to random fluctuation in nature which represents a sort of "background noise" in the system. However, a whole series of non-significant positive or negative correlations with a common reference point may indicate a trend. To my knowledge, no significance test for the difference of series of correlation values taken as a whole from random expectation has yet been devised. It is, accordingly, im-

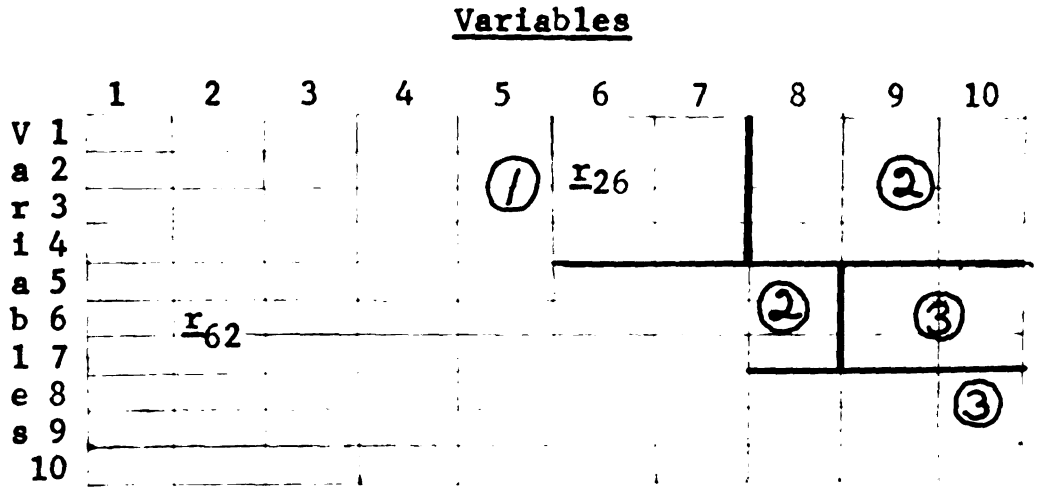
possible to state that this or that trend is "significant", and the use of such tendencies in interpreting the data may receive criticism for that reason. By the same kind of inductive reasoning which first led men to seek objective significance tests, however, it seems permissable to now consider seriously those trends which, according to our experience and judgement, stand a very small chance of being due to random fluctuation. An objective measure of this "very small" chance would, of course, increase one's conviction. But in the meantime it seems pointless, indeed irresponsible, to ignore perfectly useful information.

As an example, bracken fern (Pteridium aquilinum, abbreviated Ptr, no. 35 in the tables) on the Wet Grayling-Croswell (WC) soil type, in the 1 m^2 quadrats, exhibits with other species two positive correlations and one negative which are significant at the $P < .05$ level, and none more highly significant. But if we count the non-significant positive and negative correlations whose absolute values are above 0.05, we obtain only 2 positive and 11 negative coefficients, apparently corroborating the rather obvious field observation that other species tend to be absent or to grow poorly under or near lush bracken cover.

TABLE VII

Complete listings of correlation coefficients, r and ϕ.

This is a right-hand matrix, i.e. the lower left half of the matrix (shaded portion in the example below) has been eliminated because each coefficient in the ith row, jth column, r_{ij}, is identical with the reciprocal one in the jth row, ith column, r_{ji}. This is illustrated by r_{26} and r_{62} in the example. The diagonals r_{ii} are also eliminated, since the correlations of variables with themselves are unity.



The table is divided into pages as indicated in the example by circled numbers and heavy lines. As many of the lowest numbered rows as will fit are placed on the first page, and the columns are placed on the first and as many subsequent pages as necessary with this series of rows. Then the next lowest numbered sequence of rows is begun, and the columns within it treated in the same fashion, etc., until the end is reached.

Within each block, gradient segments are listed vertically from the top down in order of increasingly poor drainage, and quadrat sizes are arranged horizontally with the largest size at the left.

Number of quadrats upon which these coefficients are based are for G, 120; for WC; 112, for AS, 38; for R, 29; and for DG, 101.

Rows of ϕ coefficients are shaded in red.

The variables are ordered as explained on the page preceding Table I, page 27.

Decimal points are omitted and negative coefficients are underlined. Significance is indicated by symbols after the numbers as follows:

	P<	
symbol	r	ϕ
'	0.05	0.05
"	0.02	0.025
!	0.01	0.01
#	0.001	0.005

The legend for all abbreviations for species and variable names, soil types and quadrat sizes is found in Appendix B, pages 375-376.

For example, on page 91, last figure in the top row of coefficients, we see that r for the pair Amo-Car on Segment G, 1/4 m^2 quadrats is +0.24, significant at P<.01.

TABLE BEGINS ON THE NEXT PAGE

1	2	3	4	5	6	7	8	9	10	11
	ANS 1 4	ANM 1 4	ARC 1 4	ASH 1 4	ASL 1 4	BRA 1 H	CAL 1 4 H	CFD 1 4 H	CAR 1 4 H	CHM 1 4 H
A G 1 M WC 0 AS	04 05	03 12 03 03	03 03	03 02 03	01 03 05 02			03 03 02 03 07	17 24" 05 07 22 33'	
A 2 M AS S								09	23 14	
A G 3 N M WC		11 25"	01 01 07	05 04 04 03		19'		04 03 02 03	00 05 04 02	
A 4 R G C			03 02	06 04				03 02	07 07	
			A G 5 S WC H	03 03 27"				03 02 06	02 04 04	
				A G 6 S WC L				04 03	10 09	
						B WC 7 R A	18' 01		08	

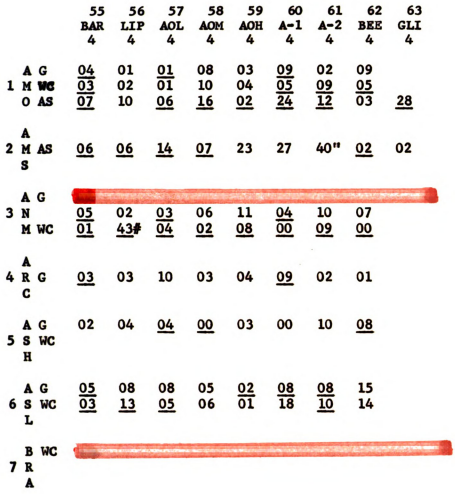
		12 COM 1 4 H	13 COF 1 4 H	14 COR 1 4	15 CRN 1	16 CRS 1 4	17 CUP 1 4 H	18 DAN 1 4 H	19 DIC 1 4	20 EPI 1 4 H	21 ERI 1 4 H
1	A G M WC O AS	14 07 02 02 10 09	00 01 42'07	00 00 38"19				03 03 01 03		01 03 04 11 33'	
2	A M AS S	19 08	16 12	12 07						14 10	
3	A G N M WC	06 07 03 03 05	05 04	06 04	01	29#	09	08 01 04 01 03	10	03 02 03	
4	A R G C	01 04						00 03		03	
5	A G S WC H	02 03 02	05	05				00 04 05		03 07	
6	A G S WC L	03 03 12 06	06 03	06 03				06 02 03 03		04 11 05	
7	B WC R A	03 06	04				04	02	15	10 05	

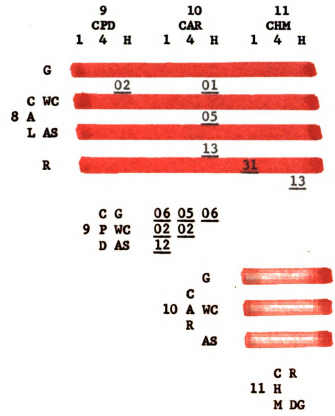
		22 GAU 1 4 H	23 ILX 1 4	24 KAL 1 4 H	25 KAN 1 4 H	26 LED 1 4 H	27 LYC 1	28 MAI 1 4 H	29 MEL 1 4 H	30 NEM 1 4	31 OPU 1 4
1	A G M WG O AS	03 10 18 13 04 12	02 03 02 08			07 06	10	06 03 03 06 01 04	05 05 06 05 10 01		08 03
2	A M AS S	23 14	17 07			05 02	11	16 04	26 12		
3	A G N M WC	19* 01 04 03 03	06 04					32# 05 02 13 08	18' 03 03 09 07		01 05
4	A R G C	06 06						03 05	01 06		06 04
5	A G S WC H	02 01 02	05					02 01 01	37#51# 03		07 06
6	A G S WC L	01 02 03 01	06 03					06 10 13 06	13 07 15 04		07 04
7	B WC R A	04 06						04 01	23" 05		

		32 ORS 1 4 H	33 POS 1 4 H	34 PRU 1 4 H	35 PTR 1 4 H	36 RHO 1 4 H	37 RUB 1 4	38 SPL H	39 SPP H	40 SOL 1 4	41 TRI 1 4 H
1	A G	02 00		01 04	07 02		00 03			01 12	
	M WC	01 01		03 03	13 03	01 01	03			02	00 07
	O AS	04 05		01 02	01 05	19 32	07				14 08
2	A M AS S	07 05		20 07	03 15	17 10	10				25 07
3	A G N	34# 37#02		21" 39#22"	09 03 00		02 04			08 22"	
	M WC	38#02		03 03	01 02	12 07	03			33#	05 05
4	A R G C	18'02		05 03	06 05		05 03			31#07	
5	A G S WC H	01 01 06		25"30# 03	03 06 07	03	05 13 05			12 31# 00	05
6	A G S WC L	09 02 00 03		08 03 06 11	01 16 01 04	11 06	06 04 12			01 01 07	14 05
7	B WC R A			15	03 01	10 03					16

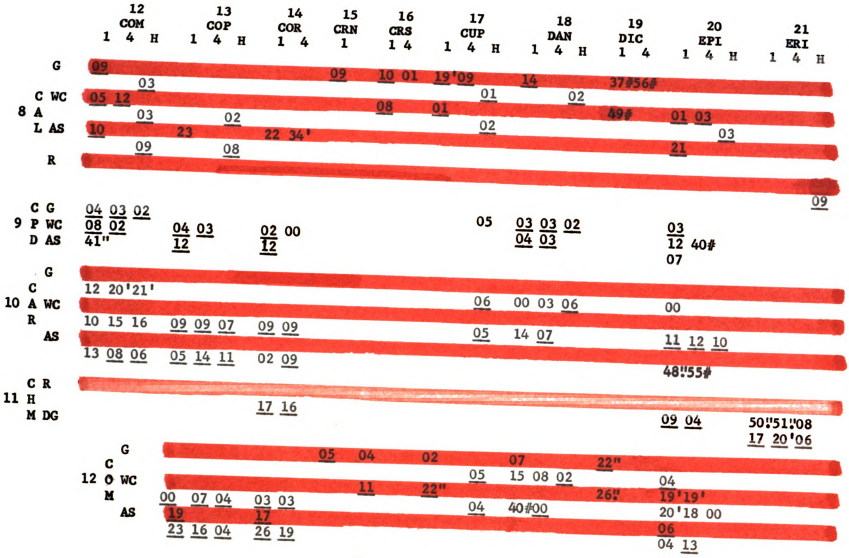
TABLE VII, cont.

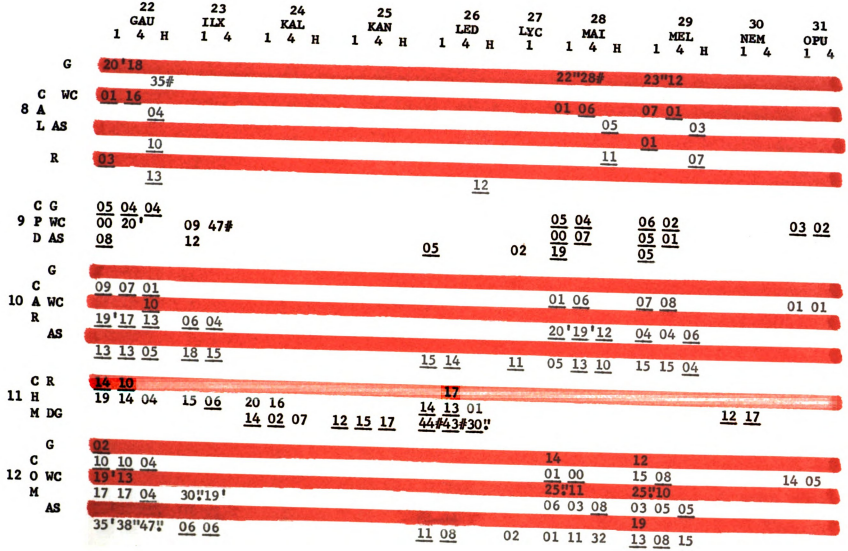
		42 VAM 1 4 H	43 VIB 1 4 H	44 VIG 1 4 H	45 VIO 1 4	46 VOX 1 4 H	47 VYP 1 4 H	48 TRE 4	49 SHR 4	50 HRB 4	51 MOS 4	52 LCN 4	53 TOT 4	54 LIT 4
1	AG			01 06	03 04		08 00	08	10	22"	11	06		08
	MWC	03 03		07 02			07 10	01	17	04	03	03		15
	OAS	10 08	09 06	25 29			15 10	17	00	21	09	04		11
2	AMS	08 04	12 08	05 13			21 17	06	06	17	09	03		14
3	AG			20'			15							
	NMWC	09 07		15 09 01 04	03 03		20' 31# 27" 16	08 03	26" 09	01 02	02 40#	06 05		11 08
4	ARC			01 04	07 03		03 01	13	13	09	04	05		00
5	AGSWCH	01		06 11 05	12 41#		05 03 01	06	04	00	03	05		07
6	AGSWCL	09 05		30#17 01 03	33#05		17 11 09 06	07 11	10 03	02 06	03 21'	09 04		03 04
7	BWCRA	12 04		01			08							

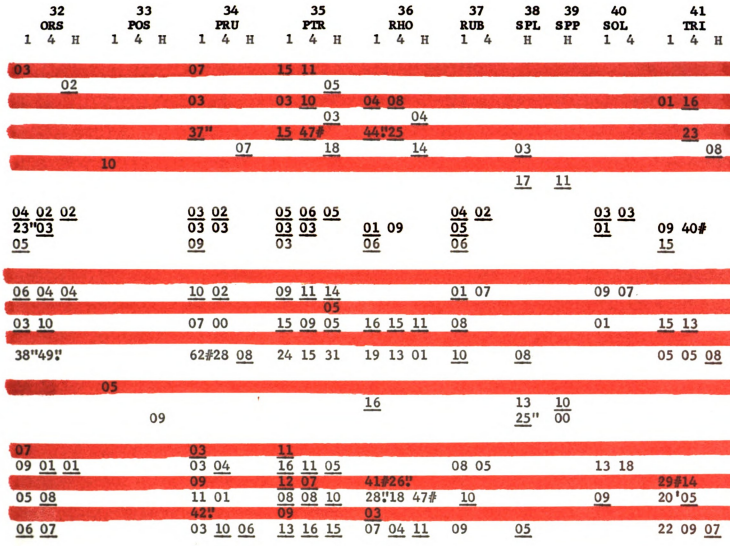

55 BAR 4
56 LIP 4
57 AOL 4
58 AOM 4
59 AOH 4
60 A-1 4
61 A-2 4
62 BEE 4
63 GLI 4
A G 04 01 01 08 03 09 02 09
1 M WC 03 02 01 10 04 05 09 05
O AS 07 10 06 16 02 24 12 03 28
A
2 M AS 06 06 14 07 23 27 40" 02 02
S
A G
3 N 05 02 03 06 11 04 10 07
M WC 01 43# 04 02 08 00 09 00
A
4 R G 03 03 10 03 04 09 02 01
C
A G 02 04 04 00 03 00 10 08
5 S WC
H
A G 05 08 08 05 02 08 08 15
6 S WC 03 13 05 06 01 18 10 14
L
B WC
7 R
A


9 CPD 1 4 H
10 CAR 1 4 H
11 CHM 1 4 H
G
02
01
C WC
8 A
L AS
05
13
R
31
13
C G 06 05 06
9 P WC 02 02
D AS 12
G
C
10 A WC
R
AS
C R
11 H
M DG

12
COM
4
13
COF
4
14
COK
1
4
15
CRN
1
16
CRS
1
4
17
CUP
4
18
DAN
4
19
DIC
1
4
20
EFL
4
21
ERI
4

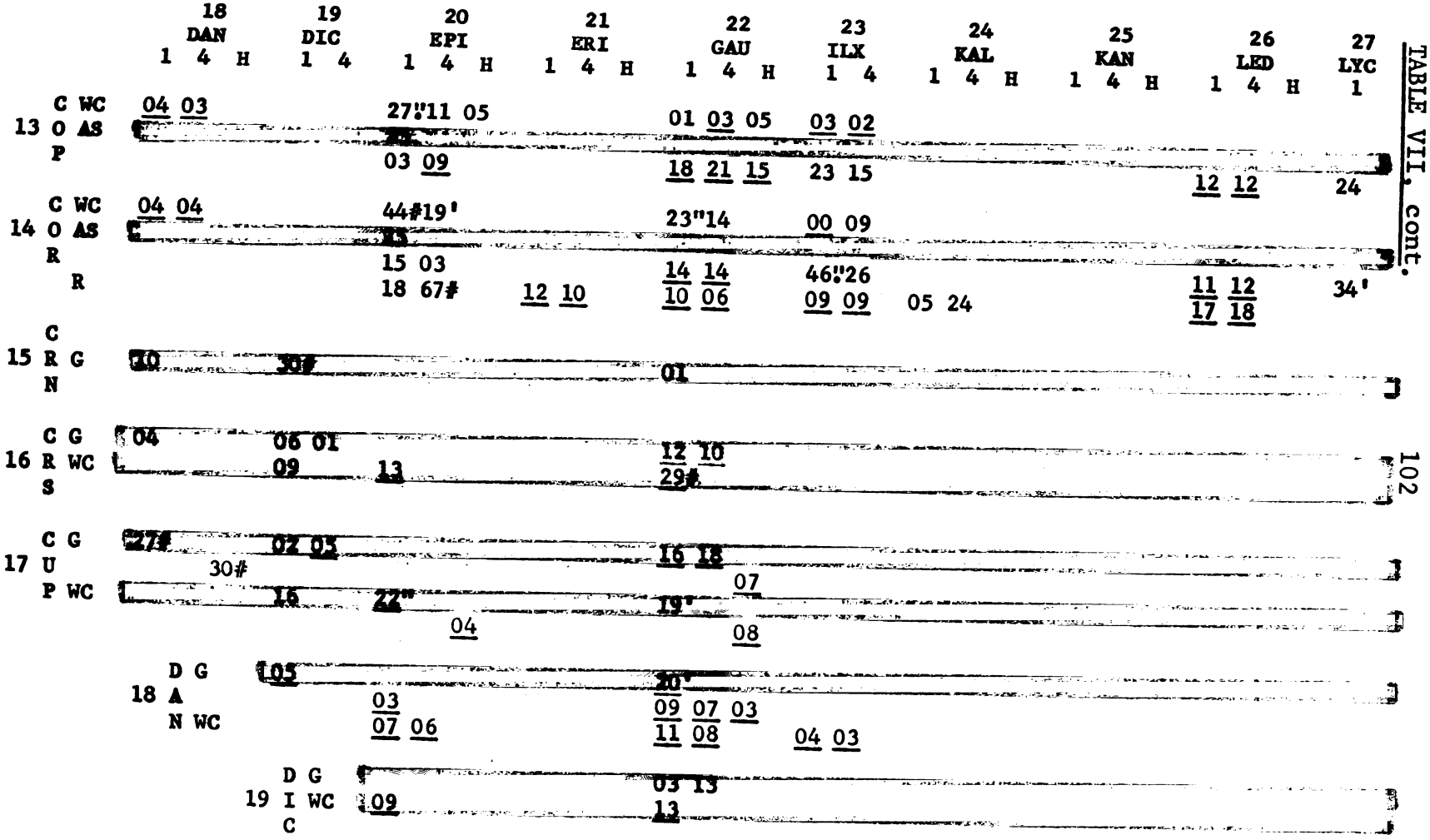

12 COM 1 4 H
13 COP 1 4 H
14 COR 1 4
15 CRN 1
16 CRS 1 4
17 CUP 1 4 H
18 DAN 1 4 H
19 DIC 1 4
20 EPI 1 4 H
21 ERI 1 4 H
8 G C WC A L AS R
9 G C P WC D AS
10 G C A WC R AS
11 C R H M DG
12 G C O WC M AS


22 GAU 1 4 H
23 ILX 1 4
24 KAL 1 4 H
25 KAN 1 4 H
26 LED 1 4 H
27 LYC 1
28 MAI 1 4 H
29 MEL 1 4 H
30 NEM 1 4
31 OPU 1 4
8 G C WC A L AS R
9 C G P WC D AS
10 G C A WC R AS
11 C R H M DG
12 G C O WC M AS


32 ORS 1 4 H
33 POS 1 4 H
34 PRU 1 4 H
35 PTR 1 4 H
36 RHO 1 4 H
37 RUB 1 4
38 SPL H
39 SPP H
40 SOL 1 4
41 TRI 1 4 H
8 A
9 P
10 A
11 H
12 O
G
C WC
L AS
R
C G
D AS
C
M DG
M
03 07 15 11
02 05
03 10 04 08 01 16
37" 03 04 23
15 47# 44#25
07 18 14 03 08
10 17 11
04 02 02 03 02 05 06 05 04 02 03 03
23"03 03 03 03 03 01 09 05 05 09 40#
05 09 03 06 06 01 15
06 04 04 10 02 09 11 14 01 07 09 07
05
03 10 07 00 15 09 05 16 15 11 08 01 15 13
38"49" 62#28 08 24 15 31 19 13 01 10 08 05 05 08
05 16 13 10
09 25" 00
07 03 11 08 05
09 01 01 03 04 16 11 05 08 05 13 18
09 12 07 41#26" 29#14
05 08 11 01 08 08 10 28"18 47# 10 09 20'05
42" 09 03
06 07 03 10 06 13 16 15 07 04 11 09 05 22 09 07

		42 VAM 1 4 H	43 VIB 1 4 H	44 VIG 1 4 H	45 VIO 1 4	46 VOX 1 4 H	47 VYP 1 4 H	48 TRE 4	49 SHR 4	50 HRB 4	51 MOS 4	52 LCN 4	53 TOT 4	54 LIT 4
	G			32#20'			32#32#				71#	02		
				11			01							
	C WC	08 11		06			00				66#	00		
8	A	02		07			01							
	L AS	11 03												
		08	09	11			18							
	R													
		03		22			05							
	C G			11 08 05	45#01		01 03 04	08	04	08	04	04		08
9	P WC	01 10		05 01			04 11	08	09	10	01	05		07
	D AS	01	08	15			09							
	G			04			26#							
	C			02 00 05	05 06		20'27:16	19'	07	78#	08	05		25"
10	A WC			01			14							
	R	11 13 05		22'17 11			16 16 09	12	18	61#	11	04		23"
	AS			32										
		13 08 11	16 10 08	21 20 07			11 08 07	05	07	56#	30	11		00
	C R													
11	H	06 36 10	27 21	07 01 06		42'70#	03 11 16	35	47"	14	11	15	41'	18
	M DG			18 15 14		08 11 03	29:25"21'	12	83#	01	35#	05		16
	G			05			14							
	C			09 03 01	20'03		14 12 05	06	33#	10	07	09		13
12	O WC	28#26"		10			20'				08	10		
	M	11 29:12		09 05 03			11 07 36#	07	38#	16	10	09		20'
	AS	04												
		11 06 12	13 08 06	28 05 06			18 09 03	15	10	10	16	06		07

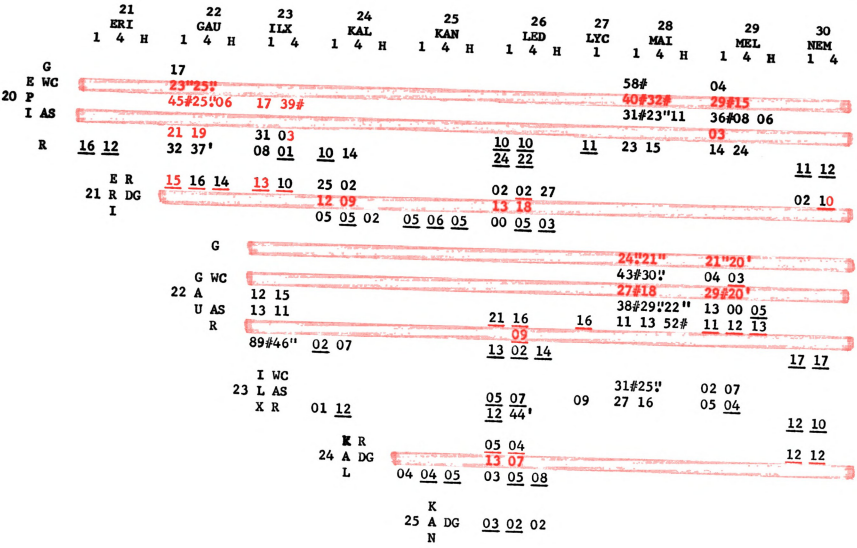
55 BAR 4
56 LIP 4
57 AOL 4
58 AOM 4
59 AOH 4
60 A-1 4
61 A-2 4
62 BEE 4
63 GLI 4
14 COR 1 4
15 GRN 1
16 CRS 1 4
17 CUP 1 4 H
G
C WC
8 A L AS
R
C G 9 P WC D AS
C 10 A WC R AS
C R 11 H M DG
G 12 WC M AS
02/03
02 03
01 02
08 10
01 04
11 14
05 10
10 31
16 14 04 06 01 14 02 00
05 07 03 07 11 10 11 08
17 31 15 08 34' 38" 21 29 16
21/04 22 26#, 11 21', 04 13 21 32# 27 22
02 06 08 08 04 03 11 03
03 07 04 02 07 03 18 08
10 18 24 02 22 32 18 26 03
C WC 13 O AS P
80#74#
90#
81#69#
C WC 14 O AS R
R
C 15 R G N
43#
39#
C G 16 R WC S
52#
38#
C G 17 U P WC


18 DAN 1 4 H
19 DIC 1 4
20 EPI 1 4 H
21 ERI 1 4 H
22 GAU 1 4 H
23 ILX 1 4
24 KAL 1 4 H
25 KAN 1 4 H
26 LED 1 4 H
27 LYC 1
13 COPP
14 COR R
15 CRN
16 CRS
17 CUP
18 DAN
19 DIC
C WC
C AS
C WC
C G
R WC
C G
U G
P WC
D G
A WC
D G
I WC
C

		28 MAI 1 4 H	29 MEL 1 4 H	30 NHM 1 4	31 OPU 1 4	32 ORS 1 4 H	33 POS 1 4 H	34 PRU 1 4 H	35 PTR 1 4 H	36 RHO 1 4 H
13	C WC	14 16 13	16 30"65#			05 04		02 03	22'24"04	42#32#29"
	O AS		12					10	36'	32'
	P	04 15 02	17 18 20			12 13		16 16 22	17 05 25	34'22 15
14	C WC	22'30"	10 22"			05 04		03 03	17 14	34#28"
	O AS		14					10	34'25	29 29
	R	09 27	35'22			12 12		21 31	10 12	59#43"
	R			12 29						13
15	C R G N	14	12			04		21"	12	
16	C G R WC S	27#18' 20'	17 06 02			23"		17 08	03 06 19'	23"
17	C G U P WC	24"26# 09	27#10 24"			16 04		22" 01	05 15 12	10 23"
		06	03							08 03
18	D G A N WC	09 07 05 02 01	06 01 03 07 07		01 27"	02 01 02 02 02 28"		11 02 01 05 03	27# 14 11 05 14 09	26"45#
19	D G I WC C	17 25" 14	09 00 11			04		06 05	02 02 00	15

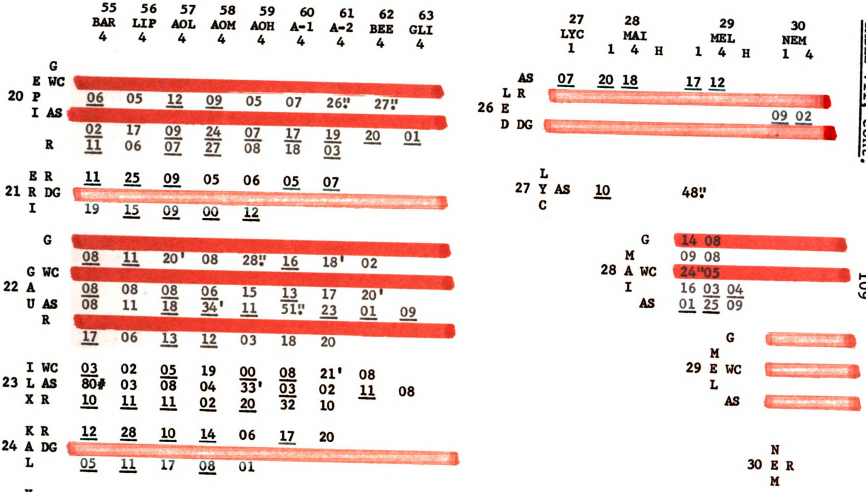
		37 RUB 1	4	38 SPL H	39 SPP H	40 SOL 1	4	41 TRI 1	4	H	42 VAM 1	4	H	43 VIB 1	4	H	44 VIG 1	4	H	45 VIO 1	4	46 VOX 1	4	H	47 VYP 1	4	H
	C WC	04				04		30"43#			06	01	04				07	04	04						05	01	01
13	O AS										40"																
	P	16		07				29	01	25	47"37'08			23	08	08	14	17	12						02	00	00
	C WC	03				04		22'29"			14	05					08	10							04	08	
14	O AS							12			[illegible]																
	R	16						12	19		15	15		04	04		09	02							00	08	
	R										05	12		08	00		57"02					06	09		35	15	
	C																										
15	R G																21"								13		
	N																										
	C G																38#23"								34#13		
16	R WC							23"			25"																
	S																										
	C G																38#55"								34#20'		
17	U																		12								09
	P WC							18			24"																
													03						07						05		
	D G																16								23"		
18	A	09	02			01	01										01	01	06	11	01				12	11	05
	N WC	04				04		00	06		06	06					09	14							07	18	
	D G																18	15							16	29#	
19	I WC							01			06																
	C																										

			48 TRE 4	49 SHR 4	50 HRB 4	51 MOS 4	52 LCN 4	53 TOT 4	54 LIT 4	55 BAR 4	56 LIP 4	57 AOL 4	58 AOM 4	59 AOH 4	60 A-1 4	61 A-2 4	62 BEE 4	63 GLI 4
	C	WC	00	03	23"	04	05		07	03	03	08	19'	24"	11	14	01	
13	O	AS																
	P		04	09	08	05	10		17	02	01	07	06	09	26	53#	19	06
	C	WC	07	01	24"	05	05		10	04	02	14	11	21'	02	09	01	
14	O	AS																
	R		01	08	35'	03	09		26	15	06	10	11	13	24	18	23	24
		R	07	14	23	05	43'	08	14	02	01	08	24	10	06	05		
	C																	
15	R	G																
	N																	
	C	G				18*	61#											
16	R	WC																
	S																	
	C	G				08	80#											
17	U																	
	P	WC																
	D	G																
18	A		15	08	02	04	38#		15	73#	38#	21"	13	12	06	10	08	
	N	WC	09	16	09	03	03		03	11	04	16	17	08	13	10	03	
	D	G				56#	06											
19	I	WC																
	C																	


21 ERI 1 4 H
22 GAU 1 4 H
23 ILX 1 4
24 KAL 1 4 H
25 KAN 1 4 H
26 LED 1 4 H
27 LYC 1
28 MAI 1 4 H
29 MEL 1 4 H
30 NEM 1 4
G
E WC
20 P
I AS
R
E R
21 R DG
I
G WC
22 A
U AS
R
I WC
23 L AS
X R
K R
24 A DG
L
K
25 A DG
N
17
23"25"
45#25"06
17 39#
21 19
32 37'
31 03
08 01
10 14
16 12
15 16 14
13 10
25 02
12 09
05 05 02
05 06 05
10 10
24 22
02 02 27
13 18
00 05 03
11
23 15
58#
40#32#
31#23"11
04
29#15
36#08 06
03
14 24
11 12
02 10
24"21"
43#30"
27#18
38#29"22"
11 13 52#
21"20'
04 03
29#20'
13 00 05
11 12 13
16
12 15
13 11
89#46"
02 07
21 16
09
13 02 14
17 17
31#25"
27 16
09
02 07
05 04
05 07
12 44'
12 10
05 04
13 07
03 05 08
12 12
04 04 05
03 02 02

		31 OPU 1 4	32 ORS 1 4 H	33 POS 1 4 H	34 PRU 1 4 H	35 PTR 1 4 H	36 RHO 1 4 H	37 RUB 1 4	38 SPL H	39 SPP H	40 SOL 1 4	41 TRI 1 4 H
	G	02	01		04	13		04			06	
	E WC				16	25"14	53#53#					48#51#
20	P		03 04		03 03	20'20'11	27"30"18	07			08	52#35#
	I AS				10	12	29					
			04 07		18 11	25 17	23 19	14				19 03
	R						03					
	E R						15		36	05		
21	R DG			11 12 22'						01		
	I			13					23"	04		
	G		07		10	29#32#						
		12 08	02 02 03		06 05	22"18'24"		07 05			11 07	
	G WC				18	13 05 06	32#35#					32#30#
22	A		05 06		22"37#	22'16 01	20'23"31#	07			10	38#10
	U AS		11 01		20 08 05	04 06 11	06 08 12	08	09			15 04 10
	R			09								
							05		02	03		
	I WC		13 04		03 04	18 12	14 04	04			04	26"38#
23	L AS		12 07		05 10	14 04	21 10	14				15 15
	X R						29					
	K R						05					
24	A DG			20'14								
	L			05					09	07		
	K											
25	A DG			06					04	09		
	N											

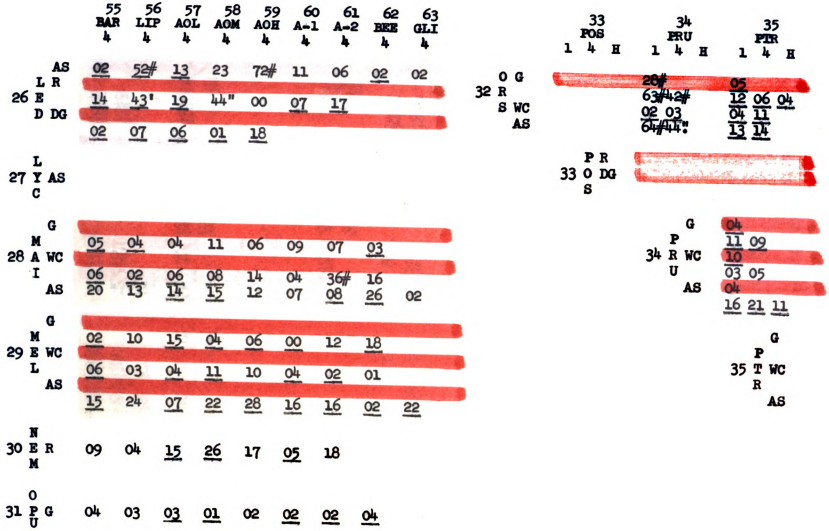
		42 VAM 1 4 H	43 VIB 1 4 H	44 VIG 1 4 H	45 VIO 1 4	46 VOX 1 4 H	47 VYP 1 4 H	48 TRE 4	49 SHR 4	50 HRB 4	51 MOS 4	52 LGN 4	53 TOT 4	54 LIT 4
	G			07	01		00							
	E WC	45#36#		11			11				08	17		
20	P	12 06 03		05 05 03			21'13 17	01	12	06	08	09		13
	I AS	17												
		22 17	05 09	06 09			37'36'	09	01	57#	16	07		15
	R	69#19	09 13	05 07		05 11	38'28	10	03	51"	02	08	04	03
	E R	13 42'03	06 11	05 15 25		35 18	21 18 16	22	40'	01	27	07	05	18
21	R DG			11		03		04						
	I			21'11 04		02 03 06	04 05 08	04	22'	43#	13	04		14
	G			24"30#			23"16				17	17		
				11 07 15	02 02		20'21'16	09	10	12	13	14		13
	G WC	24"32#		52#10			27#05				13	37#		
22	A	13 42#29"		21'22"06			16 08 10	02	33#	33#	10	16		05
	U AS	00 06 14	17 14 06	30 10 11			53#65#09	24	16	14	06	12		27
	R													
		34 60#08	06 16	03 10 17		14 16	38'36 62#	10	31	85#	16	10	22	10
	I WC	24"16		04 02			07 18	16	22'	04	01	05		10
23	L AS	06 05	00 08	28 04			22 12	01	01	04	04	06		13
	X R	21 16	05 12	06 03		10 10	19 07	12	22	43"	10	07	05	16
	K R	07 08	20 14	02 05		73#23	18 15	08	04	10	34	08	14	22
24	A DG			03				02						
	L			04 05 07		12 01 09	12 03 07	09	10	03	12	06		09
	K													
25	A			05 05 03		20'15 03	02 04 04	29"	08	11	03	03		06
	N													


55 BAR 4
56 LIP 4
57 AOL 4
58 AOM 4
59 AOH 4
60 A-1 4
61 A-2 4
62 BEE 4
63 GLI 4
20 G E WC P I AS R
06 05 12 09 05 07 26" 27"
02 17 09 24 07 17 19 20 01
11 06 07 27 08 18 03
21 E R DG R I
11 25 09 05 06 05 07
19 15 09 00 12
22 G G WC A U AS R
08 11 20' 08 28" 16 18' 02
08 08 08 06 15 13 17 20'
08 11 18 34' 11 51" 23 01 09
17 06 13 12 03 18 20
23 I WC L AS X R
03 02 05 19 00 08 21' 08
80# 03 08 04 33' 03 02 11 08
10 11 11 02 20 32 10
24 K R A DG L
12 28 10 14 06 17 20
05 11 17 08 01
25 K A DG N
04 02 01 02 06
27 LYC 1
28 MAI 1 4 H
29 MEL 1 4 H
30 NEM 1 4
26 AS L R E D DG
07 20 18 17 12
09 02
27 L Y C AS
10 48"
28 G M A WC I AS
14 08
09 08
24"05
16 03 04
01 25 09
29 G M E WC L AS
30 N E R M

		31 OPU 1 4	32 ORS 1 4 H	33 POS 1 4 H	34 PRU 1 4 H	35 PTR 1 4 H	36 RHO 1 4 H	37 RUB 1 4	38 SPL H	39 SPP H	40 SOL 1 4	41 TRI 1 4 H
	AS		04 05		12 08	15 15	12 10	06				19 12
	L R											
26	E						04		33	22		
	D DG			16 21'								
				13					07	17		
	L											
27	Y AS		06		14	05	36'	08				06
	C											
	G		24"		18'	15 20"						
	M	04 06	05 03		04 05	23"35#		08 07			02 07	
28	A WC				01	08 13	52#55#					48#32#
	I		06 07		11 07	13 13 15	57#42#32#	08			11	46#23"
	AS		24 02		21 09 59#	23 31 18	09 00 24	08		07		20 04 60#
	G		16		24"	00 20'						
	M	00 02	06 01		07 09	01 05		42#45#			08 08	
29	E WC				19'	11 08	33#12					29#10
	L		03 06		14 11	12 06 00	08 10 06	00			06	14 14
	AS				12	47#	12					
			12 11		14 47"02	32'32'11	58#60#63#	17	04			29 04 05
	N											
30	E R						10					
	M											
	O											
31	P G	06 02			03 02	15 14		03 00			14 01	
	U											

TABLE VII, cont.

		42 VAM 1 4 H	43 VIB 1 4 H	44 VIG 1 4 H	45 VIO 1 4	46 VOX 1 4 H	47 VYP 1 4 H	48 TRE 4	49 SHR 4	50 HRB 4	51 MOS 4	52 LCN 4	53 TOT 4	54 LIT 4
	AS	12 08	08 05	10 01			20 17	21	18	28	60#	21		25
	LR													
26	ED	22 14 11	31 23	23 45"08		12 10	20 04 20	15	47"	04	41'	13	06	29
	DG			18				06						
				07 03 07		17 17 09	50#42#10	05	07	17	10	08		09
	LYC													
27	AS	05	08	07			09							
	G			25"29#			19'13				19'	21"		
	M			20'06	01 10		13 10	17	06	21'	12	12		05
28	AWC	34#36#		14			09				08	05		
	I	62#33#33#		19'06 04			07 13 13	10	16	05	09	09		01
	AS	03 05 00	03 15 08	14 20 07			10 21 03	34'	25	09	14	15		08
	G			37#34#			25"28#				10	05		
	M			31#20'	19'26"		22"10	17	09	03	07	02		07
29	EWC	25"22"		19'			09				10	14		
	L	01 04 03		02 02 08			01 07 07	07	02	15	04	09		12
	AS	08												
		02 02 04	19 10 05	23 10 02			00 19 56#	12	32	52#	23	09		09
	NER													
30	M	07 17	05 27	04 32		06 01	24 28	00	07	04	01	74#	16	15
	OPG													
31	U			01 06	03 00		01 08	01	02	05	06	05		04


55 BAR 4
56 LIP 4
57 AOL 4
58 AOM 4
59 AOH 4
60 A-1 4
61 A-2 4
62 BEE 4
63 GLI 4
26 LED AS
02 52# 13 23 72# 11 06 02 02
DG
14 43' 19 44" 00 07 17
02 07 06 01 18
27 LYC AS
28 MAI G
WC
AS
05 04 04 11 06 09 07 03
06 02 06 08 14 04 36# 16
20 13 14 15 12 07 08 26 02
29 MEL G
WC
AS
02 10 15 04 06 00 12 18
06 03 04 11 10 04 02 01
15 24 07 22 28 16 16 02 22
30 NEM R 09 04 15 26 17 05 18
31 OPU G 04 03 03 01 02 02 02 04
32 ORS G
WC
AS
33 POS 1 4 H
20# 63#42# 02 03 64#44"
34 PRU 1 4 H
05 12 06 04 04 11 13 14
35 PIR 1 4 H
PR
33 OS DG
34 PRU G
WC
AS
04 11 09 10 03 05 04 16 21 11
35 PTR G
WC
AS

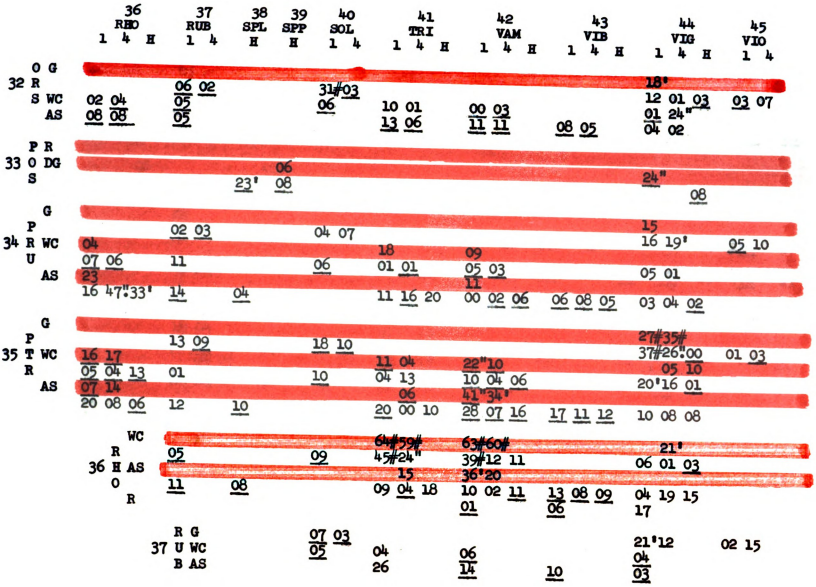
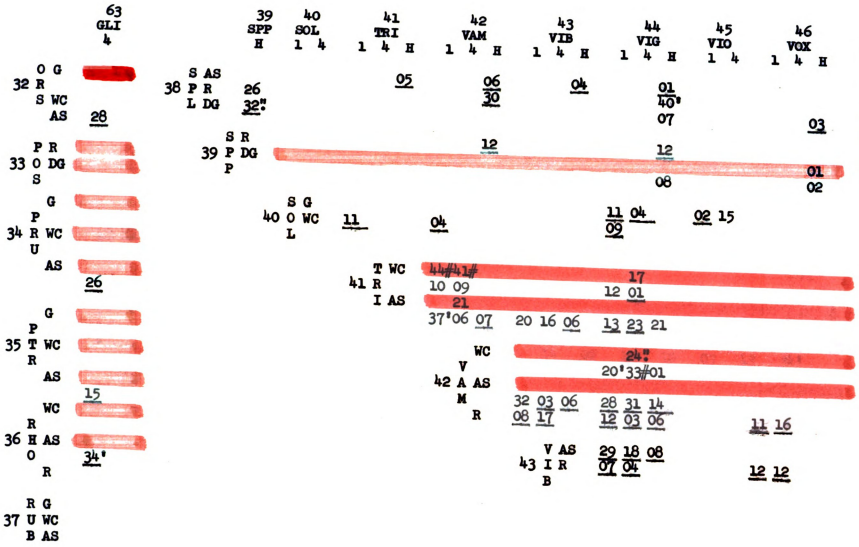

36 RHO 1 4 H
37 RUB 1 4
38 SPL H
39 SPP H
40 SOL 1 4
41 TRI 1 4 H
42 VAM 1 4 H
43 VIB 1 4 H
44 VIG 1 4 H
45 VIO 1 4
O G
32 R
S WC
AS
P R
33 O DG
S
G
P
34 R WC
U
AS
G
P
35 T WC
R
AS
WC
R
36 H AS
O
R
R G
37 U WC
B AS

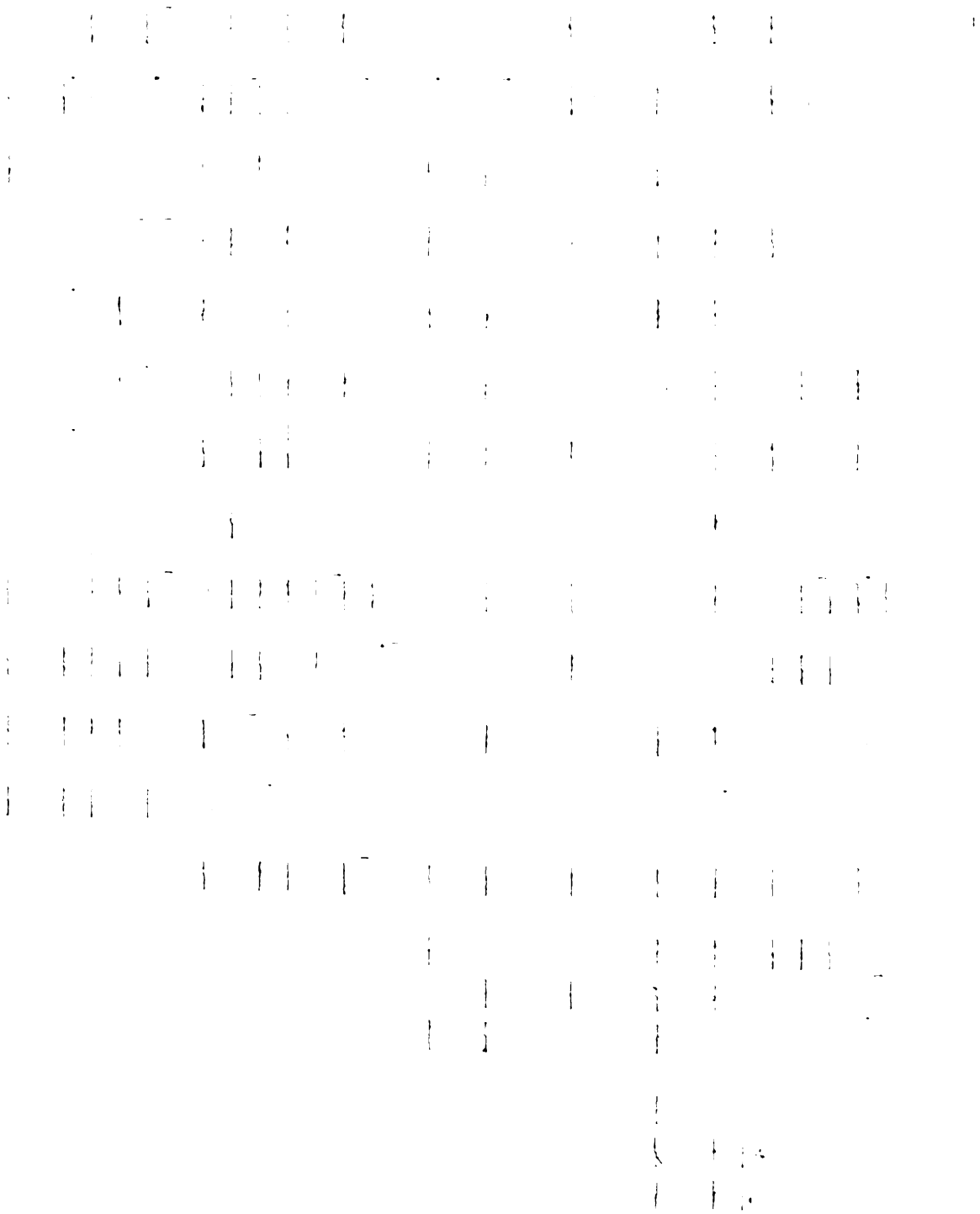
TABLE VII, cont.

		46 VOX 1	4	H	47 VIP 1	4	H	48 TRE 4	49 SHR 4	50 HRB 4	51 MOS 4	52 LCN 4	53 TOT 4	54 LIT 4	55 BAR 4	56 LIP 4	57 AOL 4	58 AOM 4	59 AOH 4	60 A-1 4	61 A-2 4	62 BEE 4
	O G				03																	
32	R				01	03	04	07	49#	02	01	06		05	02	02	08	04	07	15	02	03
	S WC				13	43#		13	36#	16	05	05		08	02	05	02	16	10	07	07	13
	AS				10	04		05	08	11	11	04		13	06	11	09	08	09	20	10	20
	P R																					
33	O DG		08					42#														
	S		42#			05																
	G				02																	
	P				00	04		03	41#	01	08	08		05	02	07	02	07	07	04	14	08
34	R WC																					
	U				05	01		06	20'	11	02	05		07	03	00	06	02	05	06	03	08
	AS																					
					05	04	00	02	09	20	13	06		14	11	15	14	20	21	06	16	15
	G				18	04					01	10										
	P				03	10	19'	11	09	48#	05	17		06	12	18	01	23"	01	18	07	01
35	T WC					04	06				06	17										
	R				13	03	07	24"	03	60#	02	05		11	23"	09	07	17	12	01	05	02
	AS																					
					08	11	16	05	29	70#	27	11		07	17	29	10	08	27	10	13	07
	WC				16						10	16										
	R				01	00	35#	13	05	15	10	09		11	06	06	16	24"	09	08	25"	22"
36	H AS																					
	O				13	09	47"	01	10	49"	19	08		21	09	21	16	23	19	17	16	02
	R	09			17																	
	R G				14	02		14	07	08	02	06		08	03	04	02	11	11	08	09	02
37	U WC				07																	
	B AS				03																	


63 GLI 4
39 SPP H
40 SOL 1 4
41 TRI 1 4 H
42 VAM 1 4 H
43 VIB 1 4 H
44 VIG 1 4 H
45 VIO 1 4
46 VOX 1 4 H
O G
32 R
S WC
AS 28
S AS
38 P R 26
L DG 32"
05
06 30
04
01 40' 07
03
P R
33 O DG
S
S R
39 P DG
P
12
12
01 02
08
G
P
34 R WC
U
AS 26
S G
40 O WC 11
L
04
11 04 09
02 15
T WC
41 R
I AS
44#41#
10 09
21
37'06 07
20 16 06
17
12 01
13 23 21
G
P
35 T WC
R
AS 15
WC
R
36 H AS
O
R 34'
WC
V
42 A AS
M
R
24"
20'33#01
32 03 06
08 17
28 31 14
12 03 06
11 16
V AS
43 I R
B
29 18 08
07 04
12 12
R G
37 U WC
B AS

			1	47 VIP 4 H	48 TRE 4	49 SHR 4	50 HRB 4	51 MOS 4	52 LCH 4	53 TOT 4	54 LIT 4	55 BAR 4	56 LIP 4	57 AOL 4	58 AOM 4	59 AOH 4	60 A-1 4	61 A-2 4	62 BEE 4	63 GLI 4
38	S	AS		08																
	P	R		22																
	L	DG		18																
39	S	R		10																
	P	DG																		
	P			11																
40	S	G	06	05	12	04	03	03	07		12	03	06	03	10	11	03	02	17	
	O	WC	09																	
	L																			
41	T	WC		11				13	05											
	R		10	04	08	06	18	08	06		06	06	03	05	03	18	07	17	11	
	I	AS	43"	15 10	17	08	04	15	09		23	16	19	14	02	12	10	03	13	34'
42		WC		04				16	13											
	V		03	03 16	04	35#	04	06	08		04	06	05	06	01	05	08	16	06	
	A	AS																		
	M		14	12 11	15	01	09	13	05		13	05	08	02	33'	08	00	24	14	25
		R	47"	25 01	25	51"	57"	16	11	02	11	16	20	13	23	06	00	15		
43	V	AS	00	09 12	18	23	20	01	04		37'	07	09	18	02	02	10	24	02	08
	I	R	08	05	09	09	13	16	14	19	09	07	20	05	14	00	05	13		
	B																			

	45 VIO 1 4	46 VOX 1 4 H	47 VIP 1 4 H	48 TRE 4	49 SHR 4	50 HRB 4	51 MOS 4	52 LCH 4	53 TOT 4	54 LIT 4	55 RAR 4	56 LIP 4	57 AOL 4	58 AOM 4	59 AOH 4	60 A-1 4
G	07 09		45#30#01 25"19'18	05	54#	15	05 07	30# 25"		03	11	04	05	12	02	02
WC			32#11				08	23#								
V 44 I AS G R			09 14 14 17 05 11	08 00	57# 19	03 20	12 13	22' 25		09 18	07 10	04 14	09 10	07 04	18 15	01 03
DG		12 08	20 05 13	03	56"	01	31	01	02	18	18	31	18	22	31	17
		16 11 03	00 05 04	06	14	05	03	01		04	13	04	07	07	17	
V 45 I G O			02 05	06	02	09	06	06	10	05	05	10	11	01	14	
V R 46 O DG X	22 27			32	09	11	22	07	22	19	10	24	00	13	40'	37
	09 00 02			08	06	89#	15	26		15	11	16	08	03	28"	
G				20'	58#	15	25" 02	20" 23"		07	13	10	13	16	20'	03
V WC 47 Y P AS R DG				02 19 06 07	76# 43" 36 08	08 15 38' 02	22" 11 30 05	12 18 17 33#	36'	16 15 18 03	01 02 15 02	23" 10 17 04	11 14 10 06	04 24 17 06	04 01 39' 15	05 09 04
48 T WC R AS E R DG				G 11 03 28 13	05 07 02 20 02	09 13 06# 20	17 12 05# 25 07	18' 22 25 11		39# 54# 24 50" 43#	17 07 04 31 04	02 15 06 50" 53#	21' 21' 26 33 14	15 34# 22 21 08	29" 35# 11 49" 09	21' 01 20 04



		61 A-2 4	62 BEE 4	63 GLI 4
	G			
	WC	22"	02	
	V	21'	19'	
44	I AS	27	10	22
	G R			
	DG	20		
	V			
45	I G	15	07	
	O			
	V R	05		
46	O DG			
	X			
	G			
	V WC	18	04	
47	Y			
	P AS	01	00	
	R	21	08	09
	DG	17		
	G	02	06	
	T WC	03	23"	
48	R AS	15	16	04
	E R	27		
	DG			

		50 HRB 4	51 MOS 4	52 LCN 4	53 TOT 4	54 LIT 4	55 BAR 4	56 LIP 4	57 AOL 4	58 AOM 4	59 AOH 4	60 A-1 4	61 A-2 4	62 BEE 4	63 GLI 4
	G	05	00	31#		04	15	10	06	21'	09	10	17	00	
	S WC	01	06	18		09	07	12	07	01	06	08	15	11	
49	H AS	27	20	09		22	03	36'	29	32'	24	11	12	10	12
	R R	34	20	20	01	20	38'	30	30	29	02	01	09		
	DG	05	33#	01		22'	01	24"	21'	10	21'				
	G	10	06			23"	10	04	07	07	00	03	00	00	
	H WC	15	09			31#	15	03	06	12	07	07	10	22'	
50	R AS	41"	14			15	16	46"	14	30	38'	20	25	07	31
	B R	05	02	09		17	20	02	21	22	06	28	08		
	DG	20'	22'			21'	18	22'	11	02	20'				
	G	16													
	M WC	06				14	01	66#	07	07	24"	11	15	06	
51	O	08													
	S AS	09				14	02	74#	02	03	05	03	15	08	
	R	19				43"	05	92"	14	21	55"	28	37'	07	13
	DG	26	02			73#	40'	89#	44"	06	47"	12	20		
		02				78#	04	98#	31"	07	17				
	G														
						19'	69#	38#	22"	17	28"	08	10	09	
	L WC														
52	C														
	N AS					10	13	01	03	03	11	00	15	17	
	R	11				12	13	25	10	40"	14	11	30	01	14
	DG					03	19	26	03	20	05	04	19		
						06	07	03	05	04	13				
	T														
53	O R					15	17	13	11	14	11	21	83#		
	T														

CHAPTER IV

THE QUESTION OF GROUPING

In studying anything as complex as a biotic community, any opportunity to group variables such as species into conveniently handled subcategories is most welcome. Such groupings must, of course, reflect real properties of the variables and the community if they are to have any value. A sizable body of literature concerning grouping techniques has developed, but frequently the authors seem to have made one or more kinds of errors which have partially or completely negated the value of their efforts.

Such errors may be categorized as follows.

(1) There is a failure to realize that, more often than not, species are not classifiable either spatially or physioecologically into discreet units, but have various and complex interrelationships with one another (e.g. Hopkins, 1957, and Goodall, 1952, 1953). Only in relatively rare situations such as the polygonal patterns found in some tundra vegetations (cf. Wiggins 1951) are the methods thus developed liable to provide a close ap-

proach to reality, and in such cases the groupings are so obvious that the pains required to elaborate them statistically man be wasted.

(2) Originators of a method or other users may try to apply it to biota in which it has little use. Application of Hopkins' or Goodall's techniques to understory vegetation in a mesic forest would be an example. Their procedures at least partially reflect the natures of the communities composed of two or more heterogeneous elements in which they were developed, but could not cope with assemblages of species each having broad and non-coincident contours of probability of occurrence over the whole sample universe.

(3) One or two factors are assumed to be the dominant pattern-producing forces. Species are arranged in accordance with these factors without considering that other factors may be of prime importance for particular species, and that environment is multidimensional. The approaches which view vegetation not as discreet groups but as continuously varying between two or more extremes, though frequently more in conformity with reality than grouping, tend to err in this respect. We have for example De Vries (1953), De Vries et al. (1954) and even the classic contin-

uum work of Curtis and McIntosh (1951) on a larger scale, Bray and Curtis (1957) on a smaller one. Whittaker (1956) demonstrates that, on a continuum axis based on only two variables, a given species may have demonstrable associates which nonetheless fall at widely separated intervals along the axis.

(4) A technique may be used simply because it is empirically found to produce groupings, without taking adequate pains to ascertain whether or not these groupings really represent the natural situation. Most of the authors already cited are guilty of this in some degree.

(5) The fact that a number of different patterning tendencies may occur simultaneously and may require several different approaches for their elucidation, is not considered. McIntosh (1962) demonstrates empirically that different methods such as those of Hopkins, of Goodall and of Agnew (1957) yield quite different results, although there was more similarity between the groupings obtained than could reasonably be due to chance. These techniques provide essentially two-dimensional views of the existing multidimensional patterns, and in fact I earlier erred in the same direction (Byer 1960).

(6) The imposition of relatively simple mathematical

models upon complex vegetational structure may tend to link species which are neither distributionally nor physio-ecologically related (Hopkins 1957). Conversely, they may fail to reveal close associations between species (Goodall 1953, 1954). (This is discussed below).

Perhaps the temptation to allow calculations which provide a neat-looking classification of the community to substitute for sound judgement is too strong. We may unconciously attempt to squeeze everything into the framework of a method even when it should be obvious that it does not fit, so that so-called "objective" techniques deteriorate into a sort of ecological numerology. Meanwhile, our original objective of understanding the community goes begging for attainment. Statistics require competent interpreters just as machines, to accomplish useful work, require competent operators.

With reference to number 6 in the listing above, grouping procedures may fail because they link chains of vicariously correlated species. Thus A is placed with E because A is positively correlated with B, B with C, C with D and D with E when, in fact, A is circumneutrally or even negatively correlated with E. Vicarious correlation is, in fact, often lacking, and dozens of examples may be

found in the results of the present study (Table VII, pages 91 ff.). Aster "hairy ovate" (Ash, no. 5 in the table) and Melampyrum lineare (Mel, no. 29), for example, are high positive correlates on G (r = +0.37 and +0.51 on 1 m^2 and 1/4 m^2 scales, respectively, both with $P < .001$). Aster is significantly positively correlated with Prunus serotina (Pru, no. 34) and Solidago "lanceolate long petiole" (Sol, no. 40), whereas Melampyrum's coefficients with these two are circumneutral (very slightly positive). Melampyrum, on the other hand, has very high positive values of $P < .001$ with Rubus canadensis (Rub, no. 37) and Vaccinium angustifolium var. nigrum (Vig, no. 44), with both of which Aster is only slightly positively correlated. Only with Viola adunca (Vio, no. 45) are both Aster's and Melampyrum's coefficients significantly positive. An examination of Hopkins' data, moreover, reveals that the species within his "basic units" are by no means mutually intercorrelated, either.

To illustrate a situation where two species are negatively correlated, yet vicariously linked by positive r or ϕ coefficients, let us take a simplified hypothetical (albeit unrealistic) example of a universe containing only five species, whose distributions are absolutely controlled

by the presence or absence of only two factors. As illustrated in Figure 6 (page 127), a combination of shade (diagonal hatching) and a mycorrhizal soil fungus (stipples) is necessary for the survival of species "A". Now, species "B" requires the same mycorrhizal fungus but is indifferent to the amount of shade, so that it co-occurs with A and, since it is absent from a large part of the area where A is also absent (clear, cross-hatched only), is positively correlated with A. If species C is an obligate heliophyte but indifferent to the presence of the fungus then C and B could be positively correlated by virtue of their co-occurrence (stippled, non-hatched), mutual absence from shaded fungusless microsites (hatched, non-stippled). But each occurs in some microsites without the other. Species D, which is intolerant of both shade and the fungus is positively correlated with heliophyte C (co-occurrence in clear patches) just as A is correlated with B. Obviously A and D would be highly negatively correlated, yet by virtue of a fortuitous unbroken series of habitat overlaps these species of exactly opposite environmental and spatial requirements would be included in the same basic unit! To complete the absurdity, a species E, which requires both shade and absence of the fungus

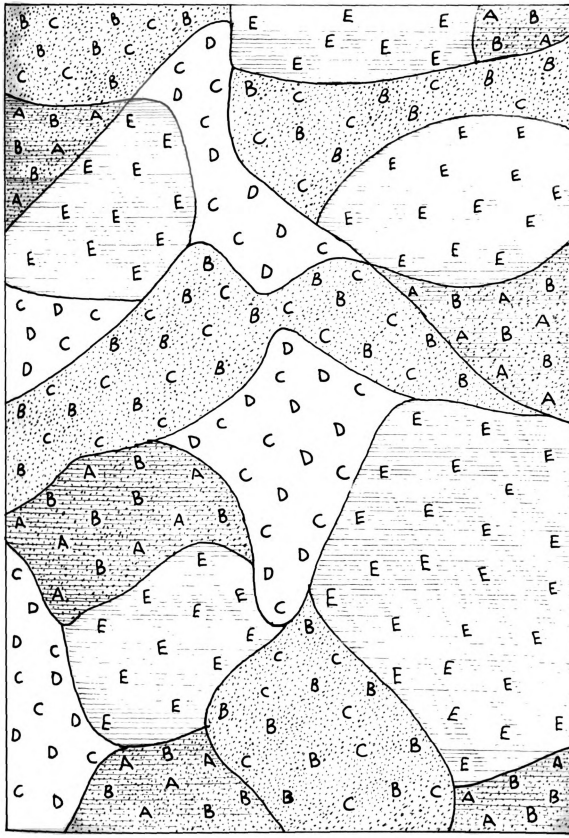
(hatched, non-stippled) will be excluded from the unit because it does not co-occur with A, B, C or D, although it has requirements in common with both A and D. In physio-ecological terms the two groupings, one containing A, B, C and D and the other E alone, are meaningless.

One other factor tends to produce improbable matchings in Hopkins' basic unit technique. Since roughly one correlation in twenty significant at the $P < .05$ level can be expected to be a random fluctuation, a few of the links in a long chain of vicarious correlations may be spurious. Especially where groups tend to be large to begin with, this error might tend to increase their size still further. But with small groups, with few species which could exhibit "random" correlations with others outside the group, this might be less serious. Since the chance of a random correlation decreases at the higher significance levels (only 1 in 1000 coefficients at $P < .001$), so also does the chance of this error.

Goodall (1953, 1954) perhaps errs in the opposite direction, in that his method divides the area into spatially mapable types, in each of which no significant positive correlations are found and which are therefore, presumably, homogeneous. The fact that this ignores inter-

FIGURE 6. Vicarious association of physioecologically dissimilar species

Shaded areas are cross-hatched, areas occupied by fungal mycelium stippled. Letters represent plant individuals. Explanation in text.



gradations even where they exist is not in its favor. Neither is the somewhat arbitrary way in which the area is divided and subdivided. Goodall always begins with the most frequent species showing one or more significant positive correlations and divides the quadrats into one group which contains it and another which does not. We could as well begin with the least frequent positively correlated species or with one showing negative correlations and separate out a different series of groups. Besides, as we break the quadrats into smaller and smaller groups, higher and higher correlation values are required for significance, so that one of our final groups might really be nearly as heterogeneous as the whole universe. In any event, since this method involves several calculations and recalculations of correlations it is most time consuming.

I wished to compare the results of one grouping or ordering technique as applied to the present study area with results obtainable without using such a procedure. Accordingly, I placed the species on each of the five gradient segments into Hopkinsian basic units. This technique was chosen both for convenience (i.e. the possibility of using the technique without calculating additional statistics) and because it does not seem quite so arbitrary as

Goodall's analysis. The results are presented in Figure 7 (page 137). The method used was essentially that of Hopkins (1957) as summarized by McIntosh (1962), and involves placing together those species which are positively correlated, or which are linked by a chain of positive correlations with other species. There are three modifications: (1) except in the cases of three species for which only ϕs had been calculated, correlations used were based upon cover (r) rather than upon presence (ϕ or chi square), (2) information obtained from different size quadrats was combined, so that species were considered significantly positively or negatively correlated if they were so on any of the three scales (in no case was a species significantly positively correlated on one scale, negatively on another), and (3) basic units were calculated at each of four levels of significance ($P < .001$, $P < .01$, $P < .025$, $P < .05$) instead of only at $P < .001$ as suggested by Hopkins.

Number 1 was largely a measure of convenience, for rs were available for a far greater number of species pairs than were ϕs, but I felt also that it might yield a result closer to reality. As explained in Chapter II, two species may frequently occur in close proximity to one another, and hence yield high positive correlations based

solely upon presence, even though each may produce its maximum cover in microsites spatially remote from the other's optimal spots. Thus, with the ϕs, it might be even easier to combine two groupings which had little in common with one another than with the rs.

McIntosh (1962), in addition to considerable difference, did discover considerable similarity between the results of various grouping and ordering techniques. It is not surprising, then, that the picture of the community which emerges from a non-grouping approach (Chapter III), or from an effort to group on the basis of macrodistribution rather than correlation (Chapter IX) is reflected in the basic units obtained here.

On G, WC and AS, for instance, there is a single large "core" unit at $P < .001$ including most of the species (Figure 7 A-C, page 137), which probably mirrors the mosaic of lush and sparse patches present on all three segments, and also the broad bands of lusher and sparser vegetation associated with drainage on these segments. The species remaining outside of these units, moreover, are among those which one might logically expect not to be included. Danthonia spicata (Dan) and Cladonia "cup" (Cup) on G (Figure 6 A) remain outside of the group even on the

$P < .05$ level and form a group of their own, joined by Oryzopsis pungens (Opu) at the $P < .01$ level. All of these species seem to occupy areas of hard-packed surface soil where other vegetation is sparse or absent. Carex pensylvanica (Car) patches are extensive and seem to leave no room for other species inside of them, except for Amelanchier oblongifolia (Amo) seedlings, which seem to germinate within them and join Carex at the $P < .01$ level. Comptonia perigrina (Com), a species observed to have few discernable microsite preferences, is not included in the large unit on G unless correlations significant at only the $P < .05$ level are considered.

Several of the small, non-clonal species (SS) included with the large group on G are "squeezed out" of it on WC (Figure 6 B), perhaps because they have low tolerance for excess moisture and/or for lush cover of other species, and so are scarce where the dominants produce maximum cover. In addition Pteridium aquilinum (Ptr), the large fern which seems to inhibit most other species here on WC where it reaches its highest cover, is included with the main "core" group only at the $P < .05$ level. On AS (Figure 6 C) both relative xerophytes and relative mesophytes are included in the main group, which is in harmony with field observa-

tions and other evaluations of the correlations. All members of the large "inner" unit calculated at $P < .001$ on R (Figure 6 D) are species having their greatest cover on AS. On DG (Figure 6 E) there are four rather distinct groupings which correspond fairly closely with what seems to be true on the basis of other criteria; (1) Chamaedaphne calyculata (Chm) by itself and seemingly inhibitory to most other species, (2) Polytrichum strictum (Pos) occurring in microsites less heavily covered by Chamaedaphne which also support Vaccinium oxycoccus (Vox) and Kalmia angustifolia (Kan), (3) Eriophorium spissum (Eri), growing with the lushest Sphagnum plumosum (Spl) in the interstices between Chamaedaphne hummocks which also support high cover of Vaccinium angustifolium var. nigrum (Vig) and, (4) Vaccinium boreale (Vyp) growing with Ledum groenlandicum (Led) in patches where the cover of all other species is low. Moreover, these four groupings show an unusually high number (five) of significant negative correlations (arrows) between them.

Negative correlations, as pointed out in Chapter III, are relatively uncommon. Of the nine from data for this gradient which are significant at the $P < .05$ level or higher, seven are between units and only two within

units. The latter, moreover, are found only within the "looser" units based upon $P < .05$ significance. Thus, although vicarious correlation is unreliable, at least the negatively correlated species tend not to be vicariously positively correlated here.

Noteworthy is the tendency exhibited by Vaccinium boreale (Vyp) to be associated with the large group while Vaccinium angustifolium var. nigrum (Vig) exhibits no strong associations on either AS or R. On DG they are members of different groupings. Although these two blueberries may be phyletically quite close and primarily by a ploidy difference (see Chapter IX, Section D), they would seem to be quite different in the roles which they play in the community.

Certain of the results of these groupings, however, are not so easily explicable on the basis of other available information. It is not startling that four of the six species on AS (Figure 6 C) which are not correlated with members of the "core" unit even at the $P < .05$ level are those whose optima are on the more poorly-drained Saugatuck Sand within this segment, most "core" members reaching their maxima for this segment on Au Gres sand. The two remaining Saugatuck "peakers", moreover, are ex-

cluded from the "core" unit of species based upon $P < .001$ significance. But why, then, is not one of these species characteristic of the more poorly drained soil significantly positively correlated with any of the others? Why, on R, are three bog species included with several upland species in the unit at $P < .05$, while the other two bog species are not included with the first three at this level?

Such results may, it is true, reveal things about the community which one might not have suspected otherwise, or might have by-passed in the complex matrix of coefficients. For example, the species which peak on Saugatuck may possess in common an intolerance of lush vegetation cover. It may be for this reason, rather than because of relatively great tolerance to poor drainage, that they produce their greatest cover on sparsely-vegetated Saugatuck, and this same intolerance of dense vegetation may even preclude positive correlation between themselves. Similarly, the apparent inconsistency of the groupings on R may reflect previously unsuspected qualities of species or environment, although at present it is difficult to say just what. An examination of all the correlations calculated with variables which could conceivably be influencing the

microdistributions on R reveals no consistent response on the part of the grouped species.

Other grouping and ordering techniques might reveal still other facets of community structure, precisely in their non-coincidence with the basic units and with each other discovered by McIntosh (1962). But in the paucity of our knowledge, we cannot know always which of these revelations may be the more valid nor, indeed, what each one really means.

I am convinced, however, that if used to the exclusion of painstaking examination and re-examination of the data, accompanied by intelligent interpretation and the tireless formulation and destruction of postulates, grouping devices based upon a single mathematical measure of association tend to obscure more relationships than they reveal. They oversimplify extremely complex situations, for it seems unlikely that grouping tendencies within a community conform to any single simple mathematical model. We might, thus wrongly conclude from the units on G that the small solitaries (SS) are physioecologically similar to, or occupy the same space as the more clonal (CX) and mesophytic (MD) and (MW). Representitives of all types are included in the same units and (SS) and (CX) both

have representatives outside of the unit. On AS we might conclude that xerophytic Carex (Car) and bog margin Cornus (Cor) are very similar in their moisture requirements or flooding tolerance, and so on.

I suggest the use of some fairly simple grouping or ordering technique when it is necessary to examine a great many stands within a short period, so that speed is at a higher premium than accuracy. Otherwise, they may be used as "scratch-work" to help visualize some order in a community or as a starting point in analysis in conjunction with other approaches. But, if only a single overly-simplified technique is relied upon to completely and accurately describe the existing patterns, it becomes merely an excuse to neglect one's responsibility to interpret.

FIGURE 7. Hopkins Basic Units on each Gradient Segment

Groups enclosed by the lines are the basic units. Species corresponding to the code symbols are listed in Appendix B, page 375. Code for the lines is as follows:

——— = united at the P<.001 level

- - - - - = united at the P<.01 level

—·—·— = united at the P<.025 level

····· = united at the P<.05 level.

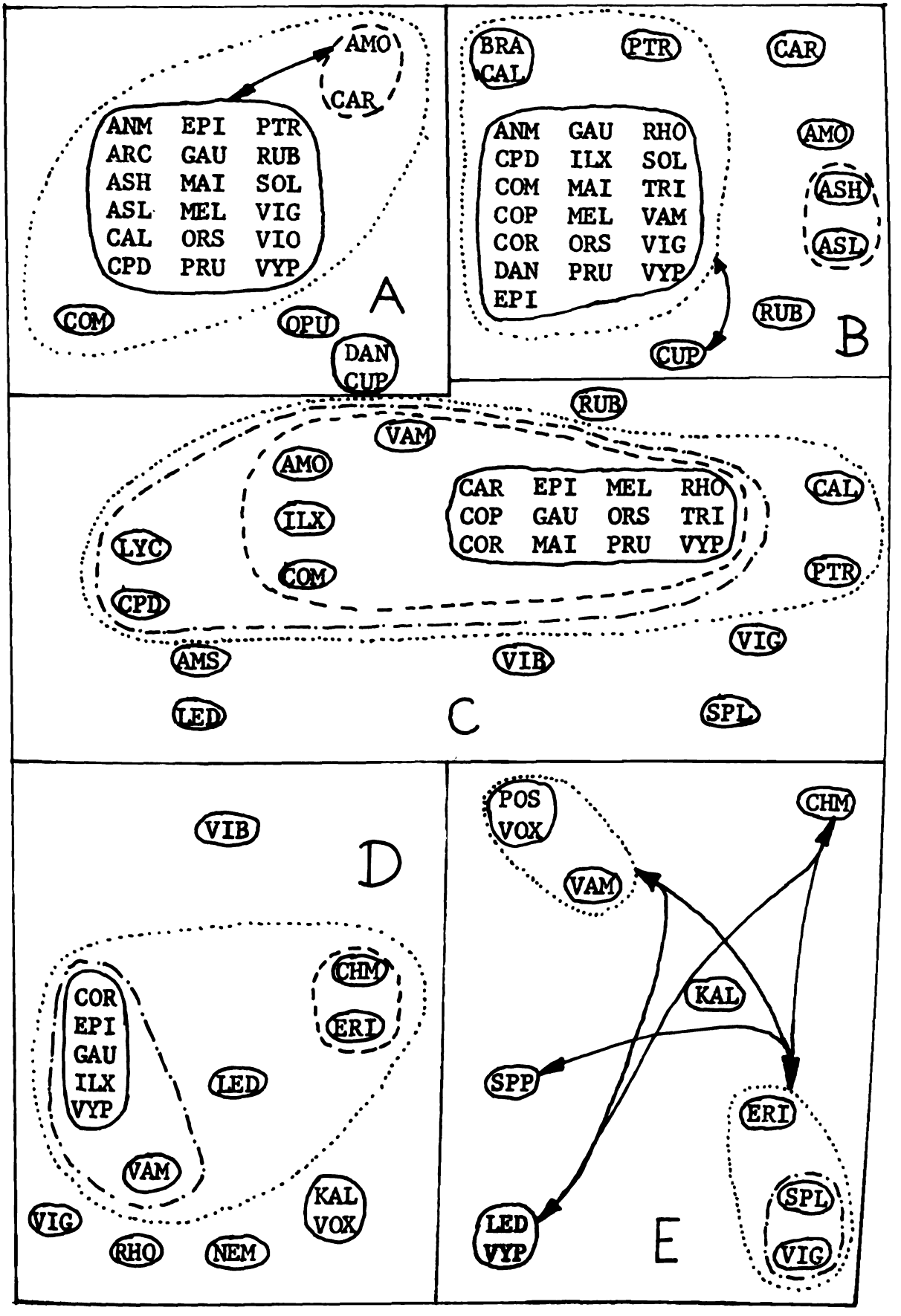
A. Basic units on Segment G.

B. Basic units on Segment WC.

C. Basic units on Segment AS.

D. Basic units on Segment R.

E. Basic units on Segment DG.


AMO
CAR
ANM EPI PTR
ARC GAU RUB
ASH MAI SOL
ASL MEL VIG
CAL ORS VIO
CPD PRU VYP
A
COM
OPU
DAN
CUP
BRA
CAL
PTR
CAR
ANM GAU RHO
CPD ILX SOL
COM MAI TRI
COP MEL VAM
COR ORS VIG
DAN PRU VYP
EPI
AMO
ASH
ASL
RUB
CUP
B
RUB
VAM
AMO
ILX
COM
CAR EPI MEL RHO
COP GAU ORS TRI
COR MAI PRU VYP
CAL
PTR
LYC
CPD
AMS
LED
VIB
VIG
SPL
C
VIB
D
CHM
ERI
COR
EPI
GAU
ILX
VYP
LED
VAM
KAL
VOX
VIG
RHO
NEM
POS
VOX
VAM
CHM
KAL
SPP
ERI
SPL
VIG
LED
VYP
E

CHAPTER V

PARTIAL CORRELATIONS

In the preceeding two chapters we have been dealing with the tendencies for pairs of species to occur in the same or in different microsites (ϕ coefficients) and for high cover of both members of such pairs or for generally high values of any two variables, to be present in the same or in different spots (r coefficients). In both cases we measure such correlation just as it is found in nature, thus obtaining the zero-order correlation between the pairs.

Now, in his search for the functional basis of the patterns, a worker may often wonder what the correlation between a pair x_1 and x_2 might be if a third variable, x_3, or a whole series of variables x_3, x_4, x_5,..., x_k were not influencing their co-occurrence or coincidence of high cover, great thickness, etc. in any way. Wright (1934), through his path coefficients, devised an excellent and precise way of measuring this, but unfortunately his techniques are difficult to use if we are dealing with the influences of large numbers of variables. Partial correlation analysis, on the other hand, is quite amenable to computer

programming, and provides a theoretical estimate of the influence of a large number of variables upon an association. In the words of Crow et al. (1960): "The sample partial correlation coefficient ($r_{yi.345...k}$)... estimates the correlation between y and x_i after the influences of (x_3, x_4, x_5,..., x_k), as estimated from the sample have been removed... The (partial correlation coefficient) systematically eliminates the variation caused by (x_3, x_4, x_5,..., x_k)".

This statement seems rather incautiously worded, however, for in practice we cannot know to what extent we are eliminating the influences of x_3, x_4, x_5,..., x_k themselves rather than that of other, perhaps unmeasured variables which concurrently influence the distribution of x_3, x_4, x_5,..., x_k along with those of x_1 and x_2. In reality the partial correlation coefficient merely measures the degree of co-occurrence of high and low values of x_1 and x_2 when the influence of x_3, x_4, x_5,..., x_k are removed from the correlation coefficient, but not necessarily from the correlated variables x_1 and x_2. Like other statistical techniques, partial correlation analysis is not a push button device for cranking out answers; as always we must process the results with other available information in order

to arive at "educated guesses" and eventually test these postulates experimentally. Kendall's (1952) explanation is therefore more accurate: "If a variate 1 is correlated with a variate 2, may this not be due to the fact that both are correlated with variate 3? The question may be decided by considering the correlation of 1 and 2 in the subpopulations for which variate 3 is constant".

Mathematical treatment of the partial correlations is presented in Kendall (1952). The majority of statistics texts seem to ignore them, or give them only passing mention.

In the present study, all possible combinations of the variables x_i and x_j, with all other variables x_k partialled out one at a time, were calculated to give all possible coefficients $r_{ij \cdot k}$ for each soil type and quadrat size.[7] Such coefficients are called <u>first order partial</u> correlations. Unless one can reasonably assume before hand that a group of variables all influence two other variables in approximately the same way, which is not true

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[7]Although many such combinations $r_{ij \cdot k}$ are meaningless or ridiculous, in terms of what we know about the particular variables, a computer routine which calculated matrices of all possibilities was easily devised.

for most cases in the present study, such first order partials yield the maximum amount of information in that they pinpoint the exact variables influencing a correlation. In partialling out more than one variable a time, moreover, the combined influences of several variables on a correlation may average out so that they cancel one another. The more variables we partial out at once, in fact, the smaller the difference between zero-order and partial coefficients is liable to be.

Table IX (page 154) presents, for each species treated all of its zero-order correlations which are over 0.2 in absolute value, and below these (indented) all the first-order partials which differ from them by more than 0.1. Zero-order coefficients of 0.15 or more are also included if and only if one or more of the partial correlations of the pair are over 0.25. A detailed analysis and discussion of every one of these coefficients would in itself fill a volume larger than this one. Here I am discussing only a few examples to illustrate the characteristics and use of these coefficients. Others are brought in where appropriate in other chapters.

Let us mention, at the outset, some types of situations in which partial correlations are ridiculous or

meaningless. A most common one in this study, because some variables are combinations of several others is that in which a variable partialled out from a pair is a major component of one of the pair members. For example, from page 11 of Table VII, the fall litter thickness (aol) - shrub cover (shr) correlation on DG, 1/4 m^2 is +0.21 ($P < .05$). But when Chamaedaphne calyculata (Chm), which constitutes about 80% of the shrub synusium, is partialled out the correlation is circumneutral (+0.07). If one member of the correlation pair is a major constituent of the one partialled out, we obtain similar results. Thus aol-Chamaedaphne (page157 of Table IX) has $r = +0.21$ ($< .05$) but with shrub cover (shr) partialled out it is only +0.07. A somewhat special case is that in which the variable partialled out is the sum of both correlated variables, giving a correlation of -1.00 as in the case on DG of Vaccinium oxycoccus (Vox) and Eriophorum spissum (Eri) with herb cover (hrb) partialled out. (If, on the other hand, the sum of the two is correlated with one and the other is partialled out, we obtain +1.00). In cases where the partialled-out variable could not reasonably be expected to influence the other two, e.g. moss cover partialled out of a tree-shrub correlation, we may

safely ignore them also.

As an illustration of a question which lends itself to analysis by partial correlation, we find that on the hingeline between upland and bog, the R segment, several species and synusia are substantially negatively correlated with tree cover (tre), although the small sample size on this segment precludes many significant coefficients there. Lichen cover (lcn), on the other hand, is positively correlated with tree cover here (Table VIII, page 151, top figure in each subcolumn headed $r_{t3.2}$). We would like to know whether it is the tree cover *per se* which brings about these correlations, *i.e.* whether tree shade itself inhibits survival and growth of vascular species while favoring lichens, or whether some other thing or things associated with the trees may be the controlling variables. Now, trees themselves produce litter. In this segment tree cover should also be highly correlated with soil horizon thickness since the great bulk of the trees are found on the portion of R bordering on AS, therefore more similar to the latter in its soil profile development than to DG. We see from column 1 of Table VIII that tree cover is indeed moderately to highly positively correlated with all litter parameters, most likely because the trees

produce most of the litter themselves. It is positively correlated also with the A_2 horizon (a-2) which is thicker on the AS side of R, and negatively with humus (aoh) which is much thicker on the less continuously tree-covered sites closer to the bog proper.

If now the thick litter and A_2 horizons associated with tree cover are responsible for the negative correlation coefficients of tre with species and synusia, we should find that these coefficients are less highly negative, i.e. shifted in a positive direction, when thickness of these horizons is partialled out. As it turns out, the mean correlation when these horizons are partialled out, -0.284, is only slightly lower in value than the mean of the corresponding zero-order coefficients, -0.317. (The figures averaged are, in the first instance, all those in the $r_{t3.2}$ subcolumns of Column 3, Table IV exclusive of the last subcolumn "lcn" and the top and bottom rows "zero" and "aoh"; in the second instance, the top or "zero" row exclusive of "lcn"). But individual cases are much more striking. Note, for example, the correlation of tree cover and moss cover (mos), (next to last variable to the right, Column 3) with litter cover (lip) and thickness (lit) partialled out. Other good examples are tree cover-

shrub cover (shr), tree cover-Vaccinium oxycoccus (Vox) and tree cover-Eriophorum spissum (Eri), all with litter cover (lip) partialled out.

In the r_{23} subcolumns of Column 3, Table VIII are presented the zero-order correlations of these species and synusia listed across the top with the litter and horizon variables of Column 2, which were partialled out in the calculations of $r_{t3.2}$. Each figure is the coefficient of the variables heading the row and column which cross at that point. Again excluding the last column (lcn) and row (aoh), most of them tend to be negative. Moreover, in general, the more highly negative the zero-order correlation of a Column 3 with a Column 2 variable, the more the former's negative correlation with tree cover ("A" subcolumns) is reduced, i.e. positively shifted, when the Column 2 litter or horizon parameter is partialled out. Now, we see from Column 1 that tree cover is positively correlated with all Column 2 parameters but A_{OH}, and negatively (top row across) with all Column 3 variables but lcn. But as just discussed, the Column 3 species and synusia are also negatively correlated with Column 2 variables. Thus, part of the negative Column 3 tree correlations are due to these negative correlations of Column 3

with Column 2 litter and horizon thicknesses, for the latter are positive correlates of tree cover. A negative correlation with them will "coincidentally" predispose towards a negative one with tree cover which has its high values where they do (cf. Crow et al. 1960).

To illustrate, Eriophorum spissum (Eri) has a zero-order correlation of -0.22 with tree cover, which becomes -0.12 when litter cover is partialled out. So about 0.10 (that is, (-0.22) - (-0.12)) of Eriophorum's correlation with tree cover is due to this species' coefficient of -0.25 with litter cover, itself a positive correlate of tree cover at +0.50. This does not necessarily mean, let us emphasize once more, that Eriophorum is sparse under heavy tree cover partly because this species is inhibited by litter. Still another factor may coincidentally preclude Eriophorum's growing with heavy litter. It does suggest such litter inhibition as a possibility to be tested.

A_{OH}, the one soil horizon with which tree cover is significantly negatively correlated, is highly positively correlated with two of the Column 3 bog species and with moss cover (mos). We might guess, then, that part of the negative correlations of Chamaedaphne, Vaccinium oxycoccus

and moss cover with tree cover is due to their affinity for areas of relatively thick A_{OH}, since tree cover here demmonstrates an "aversion" for microsites with thick humus. Indeed the partial correlation of tree cover with Chamaedaphne, V. oxycoccus and moss cover, A_{OH} partialled out is substantially less negative than the corresponding zero-order coefficients in all three cases. This is simply a modification of the preceeding case, with the difference that here Column 3 species and synusia occur with high, tree cover with low values of a third variable instead of vice versa.

Lichen cover (len), which is positively correlated with tree cover, fits into the developing picture. It is also positively correlated with bare ground cover (bar), litter cover and A_2, just as is tree cover. Now when these three variables are partialled out of the positive lichen-tree correlation, the value of that correlation is substantially reduced, or shifted in a negative direction. Not only, then, may a negative correlation be brought about by correlations of opposite sign of each member of a pair with a third variable, thus suggesting differing reactions of each to that variable. A positive correlation of a pair may result from their correlations of like sign with, or

similar reactions to, such a third variable. In the first case, partialling out the third variable will shift the correlation in a positive, in the second case in a negative direction.

Now, in general, part of the Column 3 tree cover correlations, which we shall designate r_{t3}, are due to the similar or different correlations of tree cover and Column 3 with Column 2 variables (r_{t2} and r_{23}, respectively). If r_{t2} is substantially positive (ignoring its magnitude for the moment), then the more positive is r_{23}, the more the correlation of the Column 3 variable with tree, r_{t3}, is likely to be due to its positive correlation with the trees' close spatial associate from Column 2. Consequently, the more positive r_{23}, the more in general will the partial correlation, which we shall designate $r_{t3.2}$, differ in a negative direction from the corresponding zero-order coefficient r_{t3}. Conversely, the more negative r_{23}, the more should $r_{t3.2}$ shift in a positive direction from r_{t3}. By an extension of the same line of reasoning we can also show that the opposite relations hold for the case where r_{t2} is substantially negative. In other words:

$$(r_{t3.2} - r_{t3}) = -f(r_{23}),$$

if r_{t2} is positive and

$$(\underline{r}_{t3\cdot 2} - \underline{r}_{t3}) = +f\ (\underline{r}_{23}),$$

if $\underline{r}_{t2}$ is negative, all other things being equal.

A number of things are not equal, however, one being the magnitude of $\underline{r}_{t2}$, and others being the degree to which all variables included in the calculations are influenced by still other variables. Nonetheless, the quantity $(\underline{r}_{t3\cdot 2} - \underline{r}_{t3})$ should at least be positively correlated with $-\underline{r}_{23}$, or with $+\underline{r}_{23}$ when $\underline{r}_{t2}$ is negative. The value of this correlation coefficient for the present data, appropriately changing the sign of $\underline{r}_{23}$ where A_{OH} is the Column 2 variable, in fact comes out to be +0.93, for above the $P < .001$ level of significance. This forcefully corroborates the suspected influence of litter and soil parameters upon species and synusia correlations with tree cover.

But is it not equally possible that tree cover influences correlations of Column 3 variables with the litter and soil variables of Column 2? If so, to what extent? As a test of these questions, partial correlations of each Column 3 with each Column 2 variable, tree cover partialled out were arranged in Column 3, $(\underline{r}_{23\cdot t})$. Substituting in the above equations, we now have, assuming hypothetical constancy of all other factors:

$$(\underline{r}_{23\cdot t} - \underline{r}_{23}) = -f\ (\underline{r}_{t3}),$$

and

$$(\underline{r}_{23\cdot t} - \underline{r}_{23}) = +f\ (\underline{r}_{t3}),$$

for those cases where $\underline{r}_{t2}$ is positive or negative respectively. The corresponding correlation coefficient between $(\underline{r}_{23\cdot t} - \underline{r}_{23})$ and $\underline{r}_{t3}$ comes out to be +0.82, substantially lower than in the reciprocal case but still with a probability well below 0.001.

Hence, correlations with litter and soil horizons influence correlations with tree cover very markedly, while correlations with tree cover influence those with the litter and soil horizons substantially, but somewhat less so. As discussed above, these influences on the correlations suggest, but do not imply, a cause-effect relationship between the microdistribution of the two variables correlated and the one partialled out. Since this relationship exists between the partial correlation coefficient of a variable pair and the correlation of each member of this pair with the variable partialled out, all the information contained in the partials is in fact "hidden" in the zero-order correlations.

But the practical advantage of partial correlation actually lies in this fact; we can eliminate the several steps of looking at the correlation of x_1 with x_2, then

of several species and synusia with tree cover and the influence

Legend: $r_{+3.2}$, correlation

Species ...
are listed in Appendix B.

looking for other variables with which one or both are positively or negatively correlated. We went through these steps above by way of demonstrating the relationships, but if the computer program is so arranged that all possible first-order partial coefficients of a pair are arranged in a column below the zero-order we can simply look down this column and pick out those variables most influencing the correlation.

In addition to revealing the factors influencing a correlation, analysis by partials can bring to light patterns and trends not evident from the zero-order coefficients. For example, on page 176 of Table IX we see that Pteridium aquilinum (Ptr, no. 35 in the table) is positively, but not significantly, correlated with Carex pensylvanica (Car, no. 10) on AS, 1 m^2 (r_{AB} = +0.24). But with the shrub Prunus serotina (Pru, no 34) partialled out, this correlation is highly significant ($r_{AB \cdot C}$ = +0.43, $P < .01$). Pteridium, the bracken fern and Carex, a sedge, are both dominant and conspicuous species "peaking" on Croswell and Grayling, respectively. On the more poorly-drained Au Gres portion of AS both tend to drop slightly in mean cover but on still "wetter" Saugatuck both are nearly absent, as we might expect of relative xerophytes. The afore-

mentioned partial correlation suggests that they do tend to "stick together" on the better-drained soil and perhaps in better-drained microsites. But an apparent strong affinity of Carex for the ground under Prunus (for this pair on AS, 1 m^2 r_{BC} = +0.62, $P < .001$, page 156) perhaps connected with alterations of soil chemistry by this shrub's litter, contrasts with an indifference or slight aversion to it on Pteridium's part (r_{AC} = -0.16, -0.21 and -0.11 in 1 m^2, 1/4 m^2 and 1/100 m^2 quadrats respectively). These differing reactions to a third species may thus tend to keep Carex and Pteridium apart in nature, masking their similarities in microsite preferences.

A somewhat different example is provided by the pair Rubus hispidus var. obovalis (Rho, no. 36), a creeping blackberry, and Oryzopsis asperifolia (Ors, no. 32), a broad-leaved caespitose grass, on AS, 1/4 m^2 (Table IX, page 178). Their zero-order correlation here is circumneutral (r_{AB} = -0.08), but with Prunus partialled out this becomes $r_{AB \cdot C}$ = -0.36 ($P < .05$). In this case an affinity for areas occupied by that shrub on the part of both species (r for Oryzopsis-Prunus and Rubus-Prunus +0.44 and +0.47, respectively, both with $P < .01$) apparently masks other differences in their microhabitat preferences.

TABLE IX

List of the more important first-order partial correlation coefficients.

The species abbreviation symbols are listed in alphabetical order at the headings of the columns (capitalized, underlined, numbered as in Appendix B, e.g. "1-AMO"). Below it are listed all those variables with which it exhibits "substantial" zero-order or partial correlation, whose abbreviations appear in capitals along the left side of the columns(e.g. "CAR"). All of the pertinent zero-order correlations of the variable heading the column with this latter variable are listed by gradient segment, in order of increasingly poorer drainage, and horizontally by quadrat size, beginning with the largest size at the left, and labeled 1, 4, H across the top of the column. Below the zero-order correlations for each segment labeled G, WC etc. at the left are listed all of those variables (indented, lower case, e.g. "Epi", "Car") which, when partialled out, change the correlation "substantially", along with the corresponding first-order partial correlations.

Decimal points are omitted and negative coefficients are underlined. Significance levels are indicated by symbols following the coefficients, as explained in the legend for Table I, preceding page 27.

For example, near the top of the left-hand column on the first page (154), the zero-order correlation between Amo and Car on Segment AS, 1/4 m^2, is +0.33, significant at $P < .05$. With Epi partialled out, this correlation becomes +0.19.

The criteria for "substantial" correlation and inclusion in this table are given on page 141. The legend for abbreviations of variable names, gradient segments, and quadrat sizes is given in Appendix B, pages 375-376, and within each category variables are listed in the same order given there.

TABLE IX, cont.

AMO, AMS, ANM

1-AMO

		1	4
CAR	G	17	24!!
	WC	05	07
	AS	22	33'
	Epi		19
COP	WC	00	01
	AS	42!!	07
	Cor	19	08
	Vam	52	
	a-2		17
COR	WC	00	00
	AS	38	19
	Cop	09	
	Rho		06
EPI	G	01	
	WC	03	04
	Gau	13	
	AS	11	33'
	Car	00	18
ILX	WC	02	03
	AS	02	08
	Cop	13	
	Cor	24	
LYC	AS	10	
	Cop	23	
	Cor	26	
MEL	G	05	05
	WC	06	05
	AS	10	01
	Cor	27	
	Rho	27	26
	hrb		14
ORS	G	02	00
	WC	01	01
	AS	04	05
	Car	14	26

		1	4
PTR	G	07	02
	hrb		10
	WC	13	03
	AS	01	05
	hrb		29
RHO	WC	01	01
	AS	19	32
	Cop	06	
	Cor	05	
	Mel	31	
TRI	WC	00	07
	AS	14	08
	Cop	30	
	gli		02
VAM	WC	03	03
	AS	10	08
	Cop	36	
VIB	AS	09	06
	Cop	21	
VIG	G	01	06
	WC	07	02
	shr		15
	AS	25	29
VYP	G	08	00
	WC	07	10
	shr		04
	AS	15	10
	Epi		25
HRB	G		22"
	Car		06
	WC		04
	AS		21
	Car		03
	Epi		03
	Ptr		35
	Rho		06

		4
A-1	G	09
	WC	05
	AS	24
	Car	13
GLI	AS	28

2-AMS

		1	4
CAR	AS	23	14
COM	AS	19	08
	Gau	30	
	a-1		18
COP	AS	16	12
	a-2		42
GAU	AS	23	14
	Com	33	
	Vyp	12	33
	a-1		00
	a-2		25
LED	AS	05	02
	aoh		22
MAI	AS	16	04
MEL	AS	26	12
PRU	AS	20	07
	Car	07	
TRI	AS	25	07
VYP	AS	21	17
	Gau		35
AOM	AS		07
	a-2		27
AOH	AS		23
	a-2		12

		4
A-1	AS	27
A-2	AS	40'
	Cop	54

3-ANM

		1	4
ARC	G	11	25!!
MAI	G	32#	
		05	02
	WC	13	08
	Rho	07	
ORS	G	34#	
		37#	02
	Pru	17	08
	shr		13
	WC	38#	02
PRU	G	21"	
		39#	22"
	Ors	22	
	WC	03	03
SOL	G	08	22"
	Ors	04	
	WC	33#	
VIG	G	20'	
		15	09
	shr		06
	WC	01	04
VYP	G	15	
		20'	31#
	shr		20
	WC	27!!	16
SHR	G		26!!
	Vyp		11
	WC		09
	Vyp		06
	lip		04

TABLE IX, cont.

ANM, ARC, ASH, ASL, CPD, CAR

3-ANM(Cont.)

		4
MOS	G	02
	WC	40#
	lip	13
LIP	G	02
	WC	43#
	mos	22

4-ARC

		1	4
ANM	G	11	25"
ORS	G	18"	02
	Prn	28	
PRN	G	05	03
	Ors	22	
SOL	G	31#	07

5-ASH

		1	4
ASL	G	03	03
	WC	27"	
MEL	G	37#	51#
	WC	03	
ORS	G	01	01
	Prn	22	
	WC	06	
PRN	G	25"	30#
	WC	03	
SOL	G	12	31#
	WC	00	
VIO	G	12	41#

6-ASL

		1	4
ASH	G	03	03
	WC	27"	
CPD	G	04	03
	Vio	23	
	WC	07	03
VIG	G	30#	17
	WC	01	03
VIO	G	33#	05
MOS	G		03
	WC		21'

9-CPD

		1	4	H
ASL	G	04	03	
	Vio	23		
	WC	07	03	
COM	G	04	03	02
	Vio	15		
	WC	08	02	
	Ilx		12	
	AS	41"		
COP	WC	04	03	
	Tri		24	
	AS	12		
EPI	G	03		
	WC	12	40#	
	Ilx		27	
	AS	07		
GAU	G	05	04	04
	WC	00	20'	
	AS	08		
	Com	26		

		1	4	H
ILX	WC	09	47#	
	Epi		37	
	Tri		37	
	AS	12		
MAI	G	05	04	
	WC	00	07	
	Epi		18	
	Ilx		22	
	Tri		18	
	AS	19		
ORS	G	04	02	02
	WC	23"	03	
	AS	05		
TRI	WC	09	40#	
	Epi		30	
	Ilx		26	
	AS	15		
	Com	27		
VIG	G	11	08	05
	WC	05	01	
	AS	15		
	Com	30		
VIO	G	45#	01	
HRB	G		08	
	Car		20	
	WC		10	
BEE	G		10	
	WC		31"	

10-CAR

		1	4
AMO	G	17	24#
	WC	05	07
	AS	22	33'
	Epi		19
AMS	AS	23	14

TABLE IX, cont.

CAR

10-CAR(Cont.)

	1	4	H
COM G	12	20'	21'
WC	10	15	16
shr		25	
AS	13	08	06
a-1		04	
COP WC	09	09	07
hrb		31	
AS	05	14	11
Amo	15		
Pru	19		
a-1		27	
a-2		04	
COR WC	09	09	
hrb		30	
AS	02	09	
Amo	08		
Cop		01	
Pru	15	19	
hrb		37	
a-1		20	
gli		14	
EPI G	00		
WC	11	12	10
AS	48"	55#	
Ors		67	
hrb		34	
bee		65	
GAU G	09	07	01
hrb		26	
WC			10
	19'	17	13
hrb		50	
AS	13	13	05
Epi	27	28	
Pru	00		
Vyp		24	
hrb		25	
a-1		08	

	1	4	H
ILX WC	06	04	
AS	18	15	
Epi	39		
bar		01	
aoh		04	
LYC AS	11		
Mel	21		
Pru	26		
MAI G	01	06	
hrb		37	
WC	20'	19'	12
AS	05	13	10
Epi	07	26	
Pru	11		
MEL G	07	08	
WC	04	04	06
hrb		07	
AS	15	15	04
Epi		02	
Pru		03	
Rho	05		
hrb		20	
ORS G	06	04	04
WC	03	10	
hrb		01	
AS	38"	49"	
Epi		63	
Pru	04		
PRU G	10	02	
WC	07	00	
AS	62#	28	08
Cor	33		
Epi		40	
Ors		08	

	1	4	H
PTR G	09	11	14
hrb		88	
WC			05
	15	09	05
hrb		71	
AS	24	15	31
Epi	14		
Ors		25	
Pru	43		
hrb		42	
RHO WC	16	15	11
Com			21
Mai	05		
hrb		31	
AS	19	13	01
Amo		02	
Epi		03	
Pru		00	
hrb		20	
TRI WC	15	13	
Mai	01		
hrb		30	
AS	05	05	08
Epi	05		
VIG G			04
	02	00	05
hrb		20	
WC			01
	22'	17	11
AS			32
	21	20	07
hrb		10	
VYP G			26#
	20'	27"	16
WC			14
	16	16	09
shr		04	
AS	11	08	07
Epi	08	16	
Gau	21	21	
Ptr		02	

TABLE IX, cont.

CAR, CHM

10-CAR(Cont.)

	4
TRE	G 19'
	lit 32
	WC 12
	lit 30
	AS 05
HRB	G 78#
	Ptr 96
	WC 61#
	Gau 72
	Ptr 83
	AS 56#
	Epi 36
MOS	G 08
	lip 23
	WC 11
	lip 23
	AS 30
	hrb 09
	lip 03
	aoh 14
LIT	G 25"
	tre 36
	hrb 12
	WC 23"
	tre 36
	hrb 05
	AS 00
	Epi 10
	hrb 10
	mos 15
	lip 15
LIP	G 14
	mos 26
	WC 07
	mos 22
	AS 31
	hrb 07
	mos 10
	aoh 16

	4
AOL	G 04
	lit 09
	WC 03
	lit 07
	AS 15
	a-1 26
AOM	G 06
	hrb 18
	WC 07
	hrb 19
	lit 20
	AS 08
	Epi 06
	hrb 11
	lip 02
AOH	G 01
	lit 10
	WC 11
	AS 34'
	hrb 17
	mos 22
	lip 22
A-1	G 14
	WC 10
	AS 38"
A-2	G 02
	WC 11
	hrb 22
	AS 21
	hrb 09
	mos 11
	lip 10
	aoh 11
BEE	G 00
	WC 08
	hrb 07
	AS 29
	Epi 49
	a-1 39

11-CHM

	1	4	H
CAL	R 31		
ERI	R 50"	51"	08
	shr	39	
	DG 17	20'	06
	shr	03	
GAU	R 14	10	
	19	14	04
	Eri 30	26	
	Vam	11	
	Vox	36	
	shr	01	
	hrb	04	
ILX	R 15	06	
	Eri 26		
	Gau 04		
KAL	R 20	16	
	Eri 09		
	Vox 17	01	
	DG 14	02	07
LED	R	17	
	14	13	01
	Vib 25		
	shr	45	
	lip	25	
	a-2	01	
	DG 44#	43#	30"
	shr	66	
SPL	R		13
	DG		25"
VAM	R 06	36	10
	Eri	19	
	Vox	68	
	shr	16	
VIB	R 27	21	

	1	4	H
VIG	R 07	01	06
	DG 18	15	14
	shr	48	
VOX	R 42'	70#	
	Eri 31		
	Vam	83	
	DG 08	11	03
	hrb	23	
VYP	R 03	11	16
	Vam	23	
	Vox	11	
	shr	35	
	tot	04	
	aoh	03	
	DG 29"	25"	21'
	Led 09	08	
	shr	56	
TRE	R	35	
	Vox	18	
	shr	25	
	DG	12	
	shr	01	
	mos	36	
	lip	31	
SHR	R	47"	
	Eri	34	
	Led	61	
	Vam	36	
	Vig	58	
	Vox	58	
	DG	83#	
HRB	R	14	
	Gau	04	
	Vam	09	
	Vox	30	
	shr	03	
	DG	01	
	Eri	11	
	Vox	20	

TABLE IX, cont.

CHM, COM

11-CHM(Cont.)

	4
MOS R	11
Eri	03
Vox	06
tre	13
lit	04
bar	03
lip	21
aoh	01
DG	35#
tre	47
shr	14
lip	46
TOT R	41'
BAR R	21
shr	04
DG	04
LIP R	22
Eri	12
Vam	32
Vox	08
tre	06
shr	10
DG	26"
tre	38
shr	10
mos	40
AOL R	11
DG	21'
shr	07
AOH R	21
Vox	11
tre	04
a-2	31
DG	32#
A-1 R	27
Vox	01

	4
A-2 R	22
Vox	36
tre	34
tot	24

12-COM

	1	4	H
AMS AS	19	08	
Gau	30		
CPD G	04	03	02
WC	08	02	
AS	41"		
CAR G	12	20'	21'
WC	10	15	16
shr		25	
AS	13	08	06
COP WC	00	07	04
Rho			20
AS	19		
	23	16	04
Cor	03	04	
Vam	33		
COR WC	03	03	
AS	17		
	26	19	
Cop	13		
Rho	38		
DAN G	15	08	02
WC	40#	00	
EPI G	04		
WC	19'	19'	
	20'	18	00
AS	06		
	04	13	

	1	4	H
GAU G	02		
	10	10	04
WC	19'	13	
	17	17	04
Rho			22
Vam		05	
shr		04	
AS	35'	38"	47"
a-1		26	
ILX WC	30"	19'	
AS	06	06	
MAI G	14		
	01	00	
WC	25"	11	
	06	03	08
AS	01	11	32
Gau			10
Pru			44
Tri			45
MEL G	12		
	15	08	
WC	25"	10	
	03	05	05
AS	19		
	13	08	15
Rho			28
ORS G	07		
	09	01	01
shr		21	
WC	05	08	
shr		25	
AS	06	07	
PRU G	03		
	03	04	
shr		20	
WC	09		
	11	01	
AS	42"		
	03	10	06
Mai			32

TABLE IX, cont.

COM, COP

12-COM(Cont.)

	1	4	H
RHO WC	41#	26#	
	28"	18	47#
AS	03		
	07	04	11
Cor	29		
Mel	19		26
TRI WC	29#	14	
	20'	05	
Rho	09		
AS	22	09	07
Cpd	32		
Mai			34
VAM WC	28#	26"	
	11	29"	12
Rho	00		
shr		19	
AS	04		
	11	06	12
Cop	26		
Vig	21		
VIG G	05		
	09	03	01
WC		10	
	09	05	03
AS	28	05	06
Cpd	38		
VIO G	20'	03	
VYP G	14		
	14	12	05
WC		20'	
	11	07	36#
Rho			23
AS	18	09	03
Gau	01	22	
TRE G		06	
WC		07	
lit		23	
AS		15	

4

SHR G	33#		
Vyp	50		
WC	38#		
Vyp	51		
AS	10		
HRB G	10		
WC	16		
AS	10		
Ptr	03		
lip	20		
MOS G	07		
WC	08		
	10		
AS	16		
lip	00		
aoh	06		
a-1	28		
LIT G	13		
WC	20'		
AS	07		
AOL G	08		
WC	04		
AS	24		
AOH G	04		
WC	07		
AS	22		
A-1 G	03		
WC	03		
AS	32		
Gau	16		
A-2 G	11		
WC	18		
AS	18		
BEE G	03		
WC	08		
AS	26		

13-COP

	1	4	H
AMO WC	00	01	
AS	42"	07	
Cor	19		
Vam	52		
CPD WC	04	03	
Tri		24	
AS	12		
CAR WC	09	09	07
hrb		31	
AS	05	14	11
a-1		27	
a-2		04	
COM WC	00	07	04
Rho			20
AS	19		
	23	16	04
Cor	03	04	
Vam	33		
COR WC	80#	74#	
AS	90#		
	81#	69#	
DAN WC	04	03	
Rho		21	
EPI WC	27"	11	05
Cor	16		
Rho	17		
Tri	14		
AS	25		
	03	09	
GAU WC	01	03	05
Cor	30	20	
Epi	13		
Tri	12		
AS	18	21	15
a-1		09	
a-2		10	

TABLE IX, cont.

COP, COR

13-COP(Cont.)

	1	4	H
ILX WC	03	02	
AS	23	15	
Cor		05	
LED AS	12	12	
aoh		26	
LYC AS	24		
Cor	06		
Rho	14		
MEL WC	16	30!!	65#
AS	12		
	17	18	20
Cor	20	03	
Lyc	09		
Rho	03	06	
a-2		31	
ORS WC	05	04	
AS	12	13	
Pru	29		
PRU WC	02	03	
AS	10		
	16	16	22
Cor	02		
Ors	31		
a-2		30	
PTR WC	22'	24"	04
hrb		13	
AS	36'		
	17	05	25
Vam	05		
RHO WC	42#	32#	29!!
Cor	26	18	
Dan	25		
AS	32		
	34'	22	15
Cor	30	11	
Mel			02
Pru		17	08

	1	4	H
TRI WC	30!!	43#	
Cor		33	
Epi	19		
Rho	14		
AS	29	01	25
Vam	14		
VAM WC	06	01	04
AS	40		
	47!!	37'	08
Cor	61		
VIB AS	23	08	08
Cor	34		
Tri	18		
Vam	09		
VIG WC	07	04	04
AS	14	17	12
Amo	28		
Vam	01	06	
a-2		03	
HRB WC		23"	
Car		36	
Cor		08	
Ptr		11	
AS		08	
Car		20	
Cor		23	
Rho		03	
a-2		26	
LCN WC		05	
AS		10	
a-2		32	
LIP WC		03	
AS		01	
mos		15	
a-2		28	

	4
AOM WC	19'
AS	06
Cor	19
Vam	07
a-2	20
AOH WC	24'
Cor	13
AS	09
Led	25
a-2	10
A-1 WC	11
AS	26
Cor	13
A-2 WC	14
AS	53#
Ams	63
GLI AS	06
Cor	32
Vam	04
a-1	17
a-2	10

14-COR

	1	4
AMO WC	00	00
AS	38"	19
Cop	09	
Rho		06
CAR WC	09	09
hrb		30
AS	02	09
Cop		01
Pru		19
hrb		37
a-1		20

TABLE IX, cont.

COR

14-COR(Cont.)

	1	4
COM WC	03	03
AS	17	
	26	19
Cop	13	
Rho	38	
COP WC	80#	74#
AS	90#	
	81#	69#
EPI WC	44#	19'
AS	25	
	15	03
Ilx	01	
Rho	01	
R	18	67#
Vam	30	
Vyp	06	
lcn		78
GAU WC	23"	14
Cop	37	24
Epi	04	
AS	14	14
Cop	02	00
Vyp		25
a-1		02
R	10	06
Epi		44
Vyp	27	
hrb		50
ILX WC	00	09
AS	46!'	26
R	09	09
KAL R	05	24
LED AS	11	12
hrb		02
aoh		30
R	17	18
Epi		05
Vig	38	

	1	4
LYC AS	34'	
Mel	21	
Rho	17	
MAI WC	22'	30!'
Epi	09	
Rho	03	
AS	09	27
MEL WC	10	22"
Cop		00
AS	14	
	35'	22
Lyc	22	
Pru		09
Rho	01	04
NEM R	12	29
Epi		50
Vyp	23	
lcn		04
ORS WC	05	04
AS	12	12
Pru	33	30
PRU WC	03	03
AS	10	
	21	31
Ors	37	41
Rho		14
PTR WC	17	14
Cop	01	
Epi	29	
AS	34'	25
	10	12
Cop	08	
Ilx	04	
Mai		22
Mel	23	
Rho	27	

	1	4
RHO WC	34#	28!'
Cop	01	07
Mai		18
AS	29	29
	59#	43!'
Pru		33
hrb		31
R	13	
TRI WC	22'	29!'
Cop	04	04
Epi	02	
Rho	07	
AS		12
	12	19
VAM WC	14	05
AS	49#	36'
	15	15
Cop	46	16
R	05	12
Epi	25	34
Vyp	26	
hrb		32
VIB AS	04	04
Cop	26	
Rho	14	
R	08	00
VIG WC	08	10
AS	09	02
Amo	20	
Cop	05	
Ilx	05	
Vib	08	
R	57!'	02
VYP WC	04	08
AS	00	08
Gau		23
R	35	15
Epi		05
Nem		26
hrb		07
lcn		25

	4
SHR WC	01
R	14
Vam	09
Vyp	21
hrb	23
lit	17
HRB WC	24"
Car	37
Cop	10
AS	35'
Car	48
Rho	18
R	23
Epi	17
Gau	54
Vam	37
LCN WC	05
AS	09
R	43'
Epi	65
Nem	33
TOT R	08
a-2	22
LIT WC	10
AS	26
R	14
AOM WC	11
AS	11
Cop	21
Rho	01
hrb	01
a-2	21
R	24
Epi	08

TABLE IX, cont.

COR, DAN, EPI

14-COR(Cont.)

		4
AOH	WC	21'
	Cop	05
	AS	13
	Led	31
	Rho	23
	hrb	30
	lip	19
	R	10
	Epi	20
A-1	WC	02
	AS	24
	Cop	09
	R	06
A-2	WC	09
	AS	18
	Cop	30
	Rho	28
	hrb	29
	R	05
	tot	21
BEE	WC	01
	AS	23
GLI	AS	24
	Cop	39
	Rho	11

18-DAN

		1	4	H
COM	G	15	08	02
	WC	40#	00	
COP	WC	04	03	
	Rho		21	
CUP	G	27#		
				30#

		1	4	H
EPI	G	03		
	WC	07	06	
	Rho		23	
GAU	G	20'		
		09	07	03
	WC	11	08	
	Rho		21	
MAI	G	09		
		07	05	
	WC	02	01	
	Rho	21	22	
OPU	G	01	27"	
ORS	G	02		
		01	02	02
	WC	02	28"	
RHO	WC	26"	45#	
TRI	WC	00	06	
	Rho		20	
MOS	G		04	
	lip		42	
	WC		03	
LCN	G		38#	
	bar		25	
	lip		27	
	WC		03	
BAR	G		73#	
	WC		11	
LIP	G		38#	
	mos		54	
	lcn		27	
	bar		09	
	WC		04	
AOL	G		21"	
	bar		02	
	WC		16	

		4
AOH	G	12
	lcn	01
	lip	20
	WC	08
A-2	G	10
	WC	10
	Rho	25

20-EPI

		1	4	H
AMO	G	01		
	WC	03	04	
	AS	11	33'	
	Car		18	
CPD	G	03		
	WC	12	40#	
	Ilx		27	
CAR	G	00		
	WC	11	12	10
	AS	48"	55#	
	Ors		67	
	hrb		34	
	bee		65	
COM	G	04		
	WC	19'	19'	
		20'	18	00
	AS	06		
		04	13	
COP	WC	27"	11	05
	Cor	16		
	Rho	17		
	Tri	14		
	AS	25		
		03	09	

TABLE IX, cont.

EPI

20-EPI(Cont.)

	1	4	H
COR WC	44#	19'	
AS	25		
	15	03	
Ilx	01		
Rho	01		
R	18	67#	
Vam	30		
Vyp	06		
lcn		78	
DAN G	03		
WC	07	06	
Rho		23	
ERI R	16	12	
Vam	35	22	
GAU G	17		
WC	23"	25"	
	45#	25"	06
Tri	32		
AS	21	19	
Car	31	31	
Vyp	02	07	
a-1		33	
R	32	37'	
Cor		55	
Ilx	55		
Vam	13		
Vyp	21		
hrb		15	
ILX WC	17	39#	
Cpd		25	
AS	31	03	
Car	45		
R	08	01	
Gau	48		
Led		10	
Vam	09		
hrb		29	
LED AS	10	10	
R	24	22	
Vam	13		
aom		12	
LYC AS	11		
Rho	21		
MAI G	58#		
WC	40#	32#	
	31#	23"	11
Gau	17		
Rho	20	12	
Tri	10		
MEL G	04		
WC	29#	15	
	36#	08	06
AS	03		
	14	24	
Rho	01		
Vyp		34	
hrb		07	
NEM R	11	12	
Cor		44	
ORS G	01		
WC	03	04	
AS	04	07	
Car		46	
PRU G	04		
WC	16		
	03	03	
AS	10		
	18	11	
Car	17	32	
Mel		26	
Rho		23	
hrb		27	
PTR G	13		
WC	25"	14	
	20'	20'	11
Cor	31		
Gau	34		
hrb		30	
AS	12		
	25	17	
hrb		40	
RHO WC	53#	53#	
	27"	30"	18
Mai	12		
Tri	05		
AS	29		
	23	19	
Amo		09	
Mel		06	
hrb		13	
R	03		
TRI WC	48#	51#	
	52#	35#	
Cpd		22	
Gau	42		
Ilx		23	
AS	19	03	
Vam	30		
Vyp	04		
VAM WC	45#	36#	
	12	06	03
AS	17		
	22	17	
Tri	32		
R	69#	19	
Cor		37	
Gau		04	
shr		24	
VIB AS	05	09	
R	09	13	
Vam	21		

TABLE IX, cont.

EPI, ERI

20-EPI(Cont.)

		1	4	H
VYP	G	00		
	WC		11	
		21'	13	17
	AS	37'	36'	
	R	38'	28	
	Gau		17	
	Vam	09		
	hrb		10	
SHR	WC		12	
	AS		01	
	R		03	
	Cor		08	
	Gau		17	
	Led		08	
	Vam		15	
	Vyp		15	
	hrb		26	
	bar		08	
HRB	WC		06	
	Car		17	
	Ptr		23	
	AS		57#	
	Car		38	
	R		51"	
	Gau		40	
LCN	WC		17	
			09	
	AS		07	
	R		08	
	Cor		54	
	Vyp		03	
AOM	WC		09	
	AS		24	
	hrb		09	
	R		27	
	Cor		16	

		4
AOH	WC	05
	AS	07
	R	08
	Cor	19
	Vyp	21
A-1	WC	07
	AS	17
	Car	05
	Gau	32
	hrb	07
	R	18
	hrb	05
A-2	WC	26"
	AS	19
	Car	09
	hrb	06
	R	03
	hrb	08
BEE	WC	27"
	Cpd	17
	AS	20
	Car	45
	hrb	30
GLI	AS	01
	Amo	09
	Car	10
	hrb	22
	aom	09

21-ERI

		1	4	H
CHM	R	50"	51"	08
	shr		39	
	DG	17	20'	06
	shr		03	
EPI	R	16	12	

		1	4	H
GAU	R	15	16	14
	Chm	28	27	
	shr		32	
	hrb		29	
ILX	R	13	10	
	Chm	24		
	Gau	01		
	shr		21	
KAL	R	25	02	
	Vox	00		
	DG	12	09	
		05	05	02
LED	R	02	02	27
	Spl			17
	shr		26	
	mos		15	
	lip		15	
	DG	13	18	
		00	05	03
SPL	R			36
	DG			23"
VAM	R	13	42"	03
	Chm		30	
	Epi	34		
	Gau		65	
	Vyp	27		
	shr		27	
	hrb		52	
VIG	R	05	15	25
	Spl			13
	shr		10	
	DG	11		
		21'	11	04
VOX	R	35	18	
	Chm	18	28	
	Kal	25		
	Vam		28	
	DG			03
		02	03	06

TABLE IX, cont.

ERI, GAU

21-ERI(Cont.)

	1	4	H
VYP R	21	18	16
Vam	31	32	
shr		38	
DG	04	05	08
TRE R		22	
Chm		06	
shr		12	
mos		08	
lip		12	
DG		04	
		04	
SHR R		40'	
Chm		21	
Vam		24	
Vyp		51	
DG		22'	
Chm		10	
HRB R		01	
Gau		25	
Vam		34	
shr		17	
DG		43#	
Vox		10	
MOS R		27	
Vam		37	
tre		17	
lip		10	
DG		13	
TOT R		05	
Chm		32	
LIP R		25	
Vam		37	
shr		15	
mos		02	
DG		15	
shr		10	
hrb		07	
lit		07	

	4
AOH R	06
DG	12
hrb	23
A-1 R	05
Chm	22
A-2 R	07
Chm	22

22-GAU

	1	4	H
AMS AS	23	14	
Com	33		
Vyp	42	33	
a-1		00	
a-2		25	
CAL G	20'	18	
			35#
WC	01	16	
			04
AS			10
R	03		
			13
CPD G	05	04	04
WC	00	20'	
AS	08		
Com	26		
CAR G	09	07	01
hrb		26	
WC			10
	19'	17	13
hrb		50	
AS	13	13	05
Epi	27	28	
Pru	00		
Vyp		24	
hrb		25	
a-1		08	

	1	4	H
CHM R	14	10	
	19	14	04
Eri	30	26	
Vam		11	
Vox		36	
shr		01	
hrb		04	
COM G	02		
	10	10	04
WC	19'	13	
	17	17	04
Rho			22
Vam		05	
shr		04	
AS	35'	38"	47"
a-1		26	
COP WC	01	03	05
Cor	30	20	
Epi	13		
Mai		08	
Tri	12	08	
hrb		11	
AS	18	21	15
a-1		09	
a-2		10	
COR WC	23"	14	
Cop	37	24	
Epi	04		
AS	14	14	
Cop	02	00	
Vyp		25	
a-1		02	
R	10	06	
Epi		44	
Vyp	27		
hrb		50	

TABLE IX, cont.

22-GAU(Cont.)

	1	4	H
EPI G	17		
WC	23"	25!	
	45#	25!	06
Tri	32		
AS	21	19	
Car	31	31	
Vyp	02	07	
a-l		33	
R	32	37'	
Cor		55	
Ilx	55		
Vam	13		
Vyp	21		
hrb		15	
ERI R	15	16	14
Chm	28	27	
Vam		57	
shr		32	
hrb		29	
ILX WC	12	15	
AS	13	11	
Vig	23		
Vyp	01		
R	89#	46"	
hrb		20	
LED AS	21	16	
a-l		26	
R		09	
	13	02	14
Ilx		27	
Vam		09	
shr		19	
MAI G	24!	21"	
	43#	30!	
WC	27#	18	
	38#	29!	22"
Epi	25		
Tri	25		
Vam		18	
AS	11	13	52#
Pru			67
Vyp		01	
tre		23	
MEL G	21"	20'	
	04	03	
WC	13	00	05
AS	11	12	13
Rho			27
Vyp		00	
hrb		23	
ORS G	07		
	02	02	03
WC	05	06	
shr		20	
AS	11	01	
PRU G	10		
	06	05	
WC	18		
	22"	37#	
AS	20	08	05
Mai			50
PTR G	29#	32#	
	22"	18'	24!
WC	13	05	06
	22'	16	01
Epi	35		
hrb		04	
AS	04	06	11
hrb		22	
RHO WC	32#	35#	
	20'	23"	31#
Epi	09		
Mai	02	12	
Tri	04		
AS	06	08	12
Mai			29
Mel			27
R	05		
Ilx	49		
TRI WC	32#	30#	
	38#	10	
Epi	19		
Mai	25		
AS	15	04	10
Mai			30
Vyp	11		
VAM WC	24!	32#	
	13	42#	29!
AS	00	06	14
R	34	60#	08
Epi	17		
Eri		74	
Vyp	20		
hrb		26	
VIB AS	17	14	06
R	06	16	
Ilx	24		
VIG G	24!	30#	
	11	07	15
WC		52#	10
	21'	22"	06
Vam		10	
shr		04	
AS	30	10	11
R	03	10	17
shr		34	
VOX R	14	16	
Chm	25	37	

TABLE IX, cont.

GAU, ILX

22-GAU(Cont.)

	1	4	H
VYP G	23"	16	
	20'	21'	16
WC		27#	05
	16	08	10
shr		29	
AS	53#	65#	09
R	38'	36	62#
Ilx	48		
Vam	26		
tot		48	
hrb		06	
TRE G		09	
WC		02	
AS		24	
R		10	
Vam		07	
hrb		15	
mos		24	
SHR G		10	
WC		33#	
Vam		22	
Vyp		43	
AS		16	
Vyp		18	
aom		30	
R		31	
Eri		41	
Vam		00	
Vyp		20	
hrb		03	
HRB G		12	
Car		28	
WC		33#	
Car		56	
AS		14	
Car		26	
Epi		04	
Ptr		25	
aom		04	
a-1		29	
R		85#	

	4
MOS G	17
	13
WC	13
	10
AS	06
Led	05
lit	20
lip	13
a-1	24
R	16
Vyp	05
tre	27
lit	34
LCN G	17
	14
WC	37#
	16
AS	12
Vyp	01
aom	02
R	10
Nem	03
hrb	22
TOT R	22
Vyp	40
a-2	10
LIT G	13
WC	05
AS	27
R	10
Vam	22
hrb	08
mos	32
lip	28

	4
LIP G	11
WC	08
AS	11
lit	25
aom	00
a-1	25
R	06
shr	17
mos	17
lit	27
AOL G	20'
WC	08
AS	18
Vyp	36
R	13
hrb	10
AOM G	08
WC	06
AS	34'
R	12
Epi	02
Vam	03
shr	23
hrb	14
AOH G	28"
WC	15
AS	11
R	03
Ilx	15
Vyp	20
A-1 G	16
WC	13
AS	51"
R	18
Ilx	04
A-2 G	18'
WC	17
AS	23
Vyp	13
aom	11
R	20
tot	04

	4
BEE G	02
WC	20'
AS	01
GLI AS	09
Vyp	20
a-1	36

23-ILX

	1	4
AMO WC	02	03
AS	02	08
Cop	13	
Cor	24	
CPD WC	09	47#
Epi		37
Tri		37
AS	12	
CAR WC	06	04
AS	18	15
Epi	39	
bar		01
aoh		04
CHI R	15	06
Eri	25	
Gau	04	
COM WC	30"	19'
AS	06	06
COP WC	03	02
AS	23	15
Cor	28	05
COR WC	00	09
AS	46"	26
R	09	09

TABLE IX, cont.

ILX, KAL

23-ILX(Cont.)

	1	4
EPI	WC 17	39#
	Cpd	25
	AS 31	03
	Car 45	
	R 08	01
	Gau 48	
	Led	10
	Vam 09	
	hrb	29
ERI	R 13	10
	Chm 24	
	shr	21
GAU	WC 12	15
	AS 13	11
	Vig 23	
	Vyp 01	
	R 89#	46"
	hrb	20
LED	AS 05	07
	aoh	46
	R 12	44'
MAI	WC 31#	25"
	Vam 21	
	a-2	20
	AS 27	16
	bar	00
PRU	WC 03	04
	AS 05	10
	Car 20	
	Cor 06	20
	Ors 16	
RHO	WC 14	04
	AS 21	10
	Cor 08	24
	R 29	
	Gau 55	

	1	4
TRI	WC 26"	38#
	Cpd	24
	Mai 14	
	AS 15	15
	bar	03
VAM	WC 24"	16
	Mai 06	
	AS 06	05
	R 21	16
	Gau 21	17
	shr	05
	hrb	13
VIB	AS 00	08
	R 05	12
	Gau 24	
VIG	WC 04	02
	AS 28	04
	R 06	03
	Led	21
	shr	12
VOX	R 10	10
	a-1	25
VYP	WC 07	18
	shr	02
	AS 22	12
	Epi 12	
	bar	22
	R 19	07
	Gau 36	11
	hrb	11
TRE	WC	16
	lit	26
	AS	01
	R	12
	aoh	25

	4
SHR	WC 22"
	AS 01
	R 22
	Gau 09
	Led 02
	hrb 09
HRB	WC 04
	AS 04
	R 43"
	Gau 08
MOS	WC 01
	AS 04
	bar 14
	aoh 28
	R 10
	Gau 20
	Led 09
	lit 02
	aoh 23
LCN	WC 05
	AS 06
	bar 27
	R 07
LIT	WC 10
	tre 23
	aom 20
	AS 13
	R 16
	Led 04
BAR	WC 03
	AS 80#
	R 10
LIP	WC 02
	AS 03
	bar 22
	aoh 25
	R 11

	4
AOM	WC 19
	AS 04
	bar 20
	R 02
	Led 27
	hrb 08
AOH	WC 00
	AS 33'
	Led 54
	bar 18
	R 20
	tre 30
A-1	WC 08
	AS 03
	bar 20
	R 32
A-2	WC 21'
	AS 02
	R 10
	Led 20

24-KAL

	1	4	H
CHM	R 20	16	
	Eri 09		
	Vox 17	01	
	DG 14	02	07
COR	R 05	24	
ERI	R 25	02	
	Vox 00		
	DG 12	09	
	05	05	02
LED	R 05	04	
	mos	20	
	lip	18	
	DG 13	07	
	03	05	08

TABLE IX, cont.

KAL, KAN, LED

24-KAL(Cont.)

		1	4	H
VIB	R	20	14	
VOX	R	73#	23	
	DG	12	01	09
SHR	R		04	
	DG		10	
	Chm		21	
MOS	R		34	
	lip		20	
	DG		12	
LCN	R		08	
	Cor		21	
	DG		06	
LIT	R		22	
	mos		04	
	lip		02	
	DG		09	
LIP	R		28	
	mos		04	
	lit		17	
	DG		11	
AOM	R		14	
	lip		27	
	DG		08	
A-1	R		17	
A-2	R		20	

25-KAN

		1	4	H
VOX	DG	20'	15	03
TRE	DG		29"	

		4		
MOS	DG	03		
	tre	21		
LIP	DG	02		
	tre	21		

26-LED

		1	4	H
AMS	AS	05	02	
	aoh		22	
CHM	R		17	
		14	13	01
	Vib	25		
	shr		45	
	lip		25	
	a-2		01	
	DG	44#	43#	30"
	shr		66	
COP	AS	12	12	
	aoh		26	
COR	AS	11	12	
	hrb		02	
	aoh		30	
	R	17	18	
	Epi		05	
	Vig	38		
EPI	AS	10	10	
	R	24	22	
	Vam	13		
	aom		12	
ERI	R	02	02	27
	Spl			17
	shr		26	
	mos		15	
	lip		15	
	DG	13	18	
		00	05	03

		1	4	H
GAU	AS	21	16	
	a-1		26	
	R		09	
		13	02	14
	Ilx		27	
	Vam		09	
	shr		19	
ILX	AS	05	07	
	aoh		46	
	R	12	44'	
KAL	R	05	04	
	mos		20	
	lip		18	
	DG	13	07	
		03	05	08
MAI	AS	20	18	
	aoh		39	
SPL	R			33
	DG			07
SPP	R			22
	DG			17
VAM	AS	12	08	
	mos		20	
	R	22	14	11
	Epi	07		
	Ilx		24	
	shr		51	
VIB	AS	08	05	
	R	31	23	
VIG	AS	10	01	
	R	23	45"	08
	Cor	40		
	shr		26	
	DG	18		
		07	03	07

TABLE IX, cont.

LED, LYC, MAI

26-LED(Cont.)

	1	4	H
VOX	R 12	10	
	mos	21	
	lip	24	
	DG 17	17	09
	hrb	03	
VYP	AS 20	17	
	shr	28	
	R 20	04	20
	shr	26	
	mos	10	
	DG 50#	42#	10
TRE	AS	21	
	mos	09	
	R	15	
	shr	03	
	mos	12	
	lit	01	
	lip	08	
	aom	28	
	DG	06	
		05	
SHR	AS	18	
	Vyp	28	
	mos	08	
	lip	01	
	aoh	01	
	R	47"	
	Chm	61	
	Vam	65	
	Vig	30	
	DG	07	
	Chm	55	
	Vyp	12	

	4
HRB	AS 28
	mos 04
	lip 06
	aoh 02
	R 04
	Epi 08
	Ilx 28
	shr 25
	aom 06
	DG 17
	Vox 05
MOS	AS 60#
	lip 38
	aoh 36
	R 41'
	Vig 31
	lit 30
	lip 07
	DG 10
	lit 27
LCN	AS 21
	lip 11
	R 13
	DG 08
	Vox 03
	Vyp 25
LIT	AS 25
	mos 02
	lip 05
	aoh 12
	R 29
	mos 02
	lip 14
	DG 09
	mos 27
	lip 22
BAR	AS 02
	lip 10
	aoh 32
	R 14
	DG 02

	4
AOM	AS 23
	lip 07
	R 44"
	lip 34
	DG 01
AOH	AS 72#
	mos 58
	lip 61
	R 00
	Ilx 10
	Vig 16
	mos 23
	lit 10
	lip 15
	aom 17
	DG 18
	Chm 05
A-1	AS 11
	Gau 23
	mos 07
	R 07
	Ilx 25
	aom 06
A-2	AS 06
	mos 22
	lip 18
	aom 04
	aoh 27
	R 17

27-LYC

	1
AMO	AS 10
	Cop 23
	Cor 26
CAR	AS 11
	Mel 21
	Pru 26

	1
COP	AS 24
	Cor 06
	Rho 14
COR	AS 34'
	Mel 21
	Rho 17
EPI	AS 11
	Rho 21
MEL	AS 48"
	Rho 36
ORS	AS 06
	Pru 20
PRU	AS 14
	Car 27
PTR	AS 05
	Mel 24
RHO	AS 36'
	Cor 21
	Mel 11
VYP	AS 09
	Gau 20

28-MAI

	1	4	H
CPD	G 05	04	
	WC 00	07	
	Epi	18	
	Ilx	22	
	Tri	18	
	AS 19		
CAR	G 01	06	
	hrb	37	
	WC 20'	19'	12
	AS 05	13	10
	Epi	26	

TABLE IX, cont.

MAI

28-MAI(Cont.)

	1	4	H
COM G	14		
	01	00	
WC	25"	11	
	06	03	08
AS	01	11	32
Gau			10
Pru			44
Tri			45
COR WC	22'	30"	
Epi	09		
Rho	03		
AS	09	27	
DAN G	09		
	07	05	
WC	02	01	
Rho	21	22	
EPI G	58#		
WC	40#	32#	
	31#	23"	11
Gau	17		
Rho	20	12	
Tri	10		
AS	23	15	
Car		27	
Ptr	31		
Vyp		08	
bee		10	
GAU G	24"	21"	
	43#	30"	
WC	27#	18	
	38#	29"	22"
Epi	25		
Tri	25		
Vam		18	
AS	11	13	52#
Pru			67
Vyp		01	
tre		23	

	1	4	H
ILX WC	31#	25"	
Vam	21		
AS	27	16	
bar		00	
LED AS	20	18	
aoh		39	
MEL G	14	08	
	09	08	
WC	24"	05	
	16	03	04
Epi	05		
AS	01	25	09
shr		36	
ORS G	24"		
	05	03	
WC	06	07	
AS	24	02	
Pru	14		
PRU G	18'		
	04	05	
WC	01		
	11	07	
Gau	21	20	
AS	21	09	59#
Gau			71
Ors	08		
PTR G	15	20"	
	23"	35#	
WC	08	13	
	13	13	15
Gau	24		
AS	23	31	18
Tri			31
shr		41	

	1	4	H
RHO WC	52#	55#	
	57#	42#	32#
Tri	45		
Vam	45		
AS	09	00	24
Gau			35
Pru			06
TRI WC	48#	32#	
	46#	23"	
Rho	29		
AS	20	04	60#
VAM WC	34#	36#	
	62#	33#	33#
AS	03	05	00
VIG G	25"	29#	
	20'	06	
WC		14	
	19'	06	04
Vam	09		
AS	14	20	07
VYP G	19'	13	
	13	10	
WC		09	
	07	13	13
AS	10	21	03
shr		36	
TRE G		17	
WC		10	
AS		34'	
SHR G		06	
WC		16	
Vam		05	
AS		25	
Mel		36	
Ptr		38	
Vyp		39	

TABLE IX, cont.

MAI, MEL

28-MAI(Cont.)

	4
	4
HRB G	21'
Car	42
Ptr	05
WC	05
Car	21
Gau	06
Ptr	15
AS	09
Cor	20
Epi	21
Mel	05
Ptr	19
MOS G	19
	12
WC	08
	09
AS	14
Led	04
Ptr	24
aoh	25
BAR G	05
WC	06
AS	20
LIP G	04
WC	02
AS	13
Ptr	24
mos	00
aoh	23
AOL G	04
WC	06
AS	14
tre	25
AOM G	11
WC	08
AS	15
bar	07
lip	22

	4
AOH G	06
WC	14
AS	12
Led	37
mos	24
A-2 G	07
WC	36#
AS	08
BEE G	03
WC	16
a-2	04
AS	26

29-MEL

	1	4	H
AMO G	05	05	
WC	06	05	
AS	10	01	
Rho	27	26	
hrb		14	
AMS AS	26	12	
ASH G	37#	51#	
WC	03		
CAR G	07	08	
WC	04	04	06
AS	15	15	04
Epi		02	
Pru		03	
Rho	05		
hrb		20	
COM G	12		
	15	08	
WC	25"	10	
	03	05	05
AS	19		
	13	08	15
Rho			28

	1	4	H
COP WC	16	30"	65#
AS	12		
	17	18	20
Cor	20	03	
Lyc	07		
Rho	03	06	
a-2		31	
COR WC	10	22"	
Cop		00	
AS	14		
	35'	22	
Lyc	22		
Pru		09	
Rho	01	04	
hrb		06	
EPI G	04		
WC	29#	15	
	36#	08	06
AS	03		
	14	24	
Rho	01		
Vyp		34	
hrb		07	
GAU G	21"	20'	
	04	03	
WC	29#	20'	
	13	00	05
AS	11	12	13
Rho			27
Vyp		00	
hrb		23	
LYC AS	48#		
Rho	36		
MAI G	14	08	
	09	08	
WC	24"	05	
	16	03	04
Epi	05		
AS	01	25	09
shr		36	

TABLE IX, cont.

MEL, NEM

29-MEL(Cont.)

		1	4	H
ORS	G	16		
		06	01	
	WC	03	06	
	AS	12	11	
		Car	21	
		Pru 27	40	
PRU	G	24"		
		07	09	
	WC	19		
		14	11	
	AS	12		
		14	47"	02
		Ors 28	58	
		Ptr	58	
		Rho	26	26
PTR	G	00	20'	
		01	05	
	WC	11	08	
		12	06	00
	AS	17#		
		32'	32'	11
		Pru	48	
		hrb	07	
RHO	WC	33#	12	
		08	10	06
	AS	12		
		58#	60#	63#
		Pru	48	
		Vyp		51
		hrb	46	
RUB	G	42#	45#	
	WC	00		
	AS	17		
		Rho 29		
TRI	WC	29#	10	
		14	14	
	AS	29	04	05
		Rho		22

		1	4	H
VIG	G	37#	34#	
		31#	20'	
	WC	02	19'	
		02	02	08
	AS	23	10	02
		Rho	26	
		hrb	24	
VIO	G	19'	26"	
		Ash	07	
VYP	G	25"	28#	
		22'	10	
	WC		09	
		01	07	07
	AS	00	19	56#
		Epi	31	
		Rho		38
		shr	06	
		hrb	32	
SHR	G		09	
	WC		02	
	AS		32	
		hrb	22	
HRB	G		03	
	WC		15	
	AS		52	
		Rho	32	
MOS	G		10	
			07	
	WC		10	
			04	
	AS		23	
		hrb	02	
		lip	00	
		aoh	09	
LIT	G		07	
	WC		12	
	AS		09	
		Rho	04	
		mos	21	
		lip	21	

		4
LIP	G	10
	WC	03
	AS	24
		shr 14
		hrb 01
		mos 09
		aoh 11
AOM	G	04
	WC	11
	AS	22
		Rho 11
		hrb 08
AOH	G	06
	WC	10
	AS	28
		hrb 11
A-2	G	12
	WC	02
	AS	16
		Cop 30
		hrb 04
		gli 11
GLI	AS	22
		Pru 12
		Rho 02
		hrb 08

30-NEM

		1	4
CHM	R	12	17
		Vox	25
		tot	26
COR	R	12	29
		Epi	50
		Vyp 23	
		lcn	04
EPI	R	11	12
		Cor	44

TABLE IX, cont.

NEM, OPU, ORS

30-NEM(Cont.)

	1	4
VIB R	05	27
VIG R	04	32
shr		44
lcn		48
VYP R	24	28
TRE R		00
lcn		29
aoh		10
SHR R		07
Vig		32
Vyp		03
lcn		11
HRB R		04
Gau		21
Vam		07
Vyp		08
MOS R		01
Vig		12
Vyp		11
lcn		28
lit		18
LCN R		74#
LIT R		15
lcn		25
lip		32
LIP R		04
Vig		15
lcn		25
lit		29
aom		06
AOM R		26
Vig		36
AOH R		17
Vyp		06
lcn		31

31-OPU

	1	4	
DAN G	01	27"	
PTR G	15	14	
BAR G		04	
Dan		23	
CPD G	04	02	02
WC	23"	03	
AS	05		
CAR G	06	04	04
WC	03	10	
AS	38"	49"	
Epi		63	
Pru	04		
COM G	07		
	09	01	01
shr		21	
WC	05	08	
shr		25	
AS	06	07	

32-ORS

	1	4	H
AMO G	02	00	
WC	01	01	
AS	04	05	
Car		26	
ORS G	34#		
	37#	02	
Pru	17		
WC	38#	02	
ARC G	18'	02	
Pru	28		
ASH G	01	01	
Pru	22		
WC	06		

	1	4	H
COP WC	05	04	
AS	12	13	
Pru	29		
COR WC	05	04	
AS	12	12	
Pru	33	30	
DAN G	02		
	01	02	02
WC	02	28"	
EPI G	01		
WC	03	04	
AS	04	07	
Car		46	
GAU G	07		
	02	02	03
WC	05	06	
shr		20	
AS	11	01	
LYC AS	06		
Pru	20		
MAI G	24"		
WC	06	07	
AS	24	02	
Pru	14		
MEL G	16		
	06	01	
WC	03	06	
AS	12	11	
Car		21	
Pru	27	40	
hrb		20	
PRU G	28#		
	63#	42#	
shr		28	
WC	02	03	
AS	64#	44"	
Mel		56	
Rho		54	

TABLE IX, cont. ORS, PRU

32-ORS(Cont.)

	1	4	H
PTR G	05		
	12	06	04
WC	04	11	
AS	13	14	
Car	24	25	
hrb		31	
RHO WC	02	04	
AS	08	08	
Pru	24	36	
gli		19	
SOL G	31#	03	
WC	06		
Anm	21		
TRI WC	10	01	
AS	13	06	
Pru	26		
VIG G	18'		
	12	01	03
shr		34	
WC	01	24"	
shr		04	
AS	04	02	
VYP G	05		
	01	03	04
shr		44	
WC	13	43#	
shr		26	
AS	10	04	
SHR G		49#	
Pru		39	
Vyp		62	
WC		36#	
Vyp		05	
AS		08	

4

HRB G	02		
WC	16		
AS	11		
Car	22		
Ptr	30		
A-1 G	15		
WC	07		
AS	20		
Car	02		
BEE G	03		
WC	13		
AS	20		
Car	07		
GLI AS	28		

34-PRU

	1	4	H
AMS AS	20	07	
Car	07		
ANM G	21"		
	39#	22"	
Ors	22		
WC	03	03	
ARC G	05	03	
Ors	22		
ASH G	25"	30#	
WC	03		
CAR G	10	02	
WC	07	00	
AS	62#	28	08
Cor	33		
Epi		40	
Ors	53	08	

	1	4	H
COM G	03		
	03	04	
shr		20	
WC	09		
	11	01	
AS	42"		
	03	10	06
Mai			32
COP WC	02	03	
AS	10		
	16	16	22
Cor	02	08	
Ors	31		
a-2		30	
COR WC	03	03	
AS	10		
	21	31	
Cop	13		
Ors	37	41	
Rho		14	
EPI G	04		
WC	16		
	03	03	
AS	10		
	18	11	
Car	17	32	
Mel		26	
Rho		23	
hrb		27	
GAU G	10		
	06	05	
WC	18		
	22"	37#	
AS	20	08	05
Mai			50
ILX WC	03	04	
AS	05	10	
Car	20		
Cor	06	20	
Ors	16		

TABLE IX, cont.

PRU, PTR

34-PRU(Cont.)

	1	4	H
PTR G	04		
	11	09	
WC	10		
	03	05	
AS	04		
	16	21	11
Car	40		
Mel		43	
hrb		50	
RHO G	04		
	07	06	
WC	23		
	16	47"	33'
Car	05		
Cor	04		
Mel		27	
Ors	27		
SOL G	04	07	
Ors	21		
WC	06		
TRI WC	18		
	01	01	
AS	11	16	20
Mai			23
Ors	25		
VAM WC	09		
	05	03	
Gau		22	
AS	11		
	00	02	06
VYP G	02		
	00	04	
shr		26	
WC	05	01	
shr		25	
AS	05	04	00

	4
SHR G	41#
Ors	25
WC	20'
Gau	09
Vyp	32
AS	09
HRB G	01
WC	11
AS	20
Car	05
Epi	32
Mel	06
Ptr	50
Rho	04
AOM G	07
WC	02
AS	20
Rho	10
AOH G	07
WC	05
AS	21
Mel	09
A-2 G	14
WC	03
AS	16
Cop	29
GLI AS	26
Ors	16
Rho	12

35-PTR

	1	4
AMO G	07	02
WC	13	03
AS	01	05
hrb		29

	1	4	H
CAR G	09	11	14
hrb		88	
WC			05
	15	09	05
hrb		71	
AS	24	15	31
Epi	14		
Ors		25	
Pru	43		
hrb		42	
COP WC	22'	24"	04
hrb		13	
AS	36'		
	17	05	25
Vam	05		
COR WC	17	14	
Cop	01		
Epi	29		
AS	34'	25	
	10	12	
Cop	08		
Mai		22	
Mel	23		
Rho	27		
hrb		19	
EPI G	13		
WC	25"	14	
	20'	20'	11
Cor	31		
Gau	34		
hrb		30	
AS	12		
	25	17	
hrb		40	
GAU G	29#	32#	
	22"	18'	24"
WC	13	05	06
	22'	16	01
Epi	35		
hrb		04	
AS	04	06	11
hrb		22	

TABLE IX, cont.

PTR

35-PTR(Cont.)

	1	4	H
LYC	AS 05		
	Mel 24		
MAI	G 15	20"	
	23"	35#	
	WC 08	13	
	13	13	15
	Gau 24		
	AS 23	31	18
	Tri		31
	shr	41	
MEL	G 00	20'	
	01	05	
	WC 11	08	
	12	06	00
	AS 47#		
	32'	32'	11
	Pru	48	
	hrb	07	
ORS	G 05		
	12	06	04
	WC 04	11	
	AS 13	14	
	Car 24	25	
	hrb	31	
PRU	G 04		
	11	09	
	WC 10		
	03	05	
	AS 04		
	16	21	11
	Car 40		
	Mel	43	
	hrb	50	

	1	4	H
RHO	WC 16	17	
	05	03	13
	AS 07	14	
	20	08	06
	Cor 32		
	Mel 02	14	
	Pru	21	
	hrb	42	
TRI	WC 11	04	
	04	13	
	Cop	03	
	hrb	03	
	AS	06	
	20	00	10
	Mai		27
	Mel 32		
VAM	WC 22"	10	
	10	04	06
	AS 41"	34'	
	28	07	16
VIG	G 27#	35#	
	37#	26"	00
	WC	05	10
	20'	16	01
	AS 10	08	08
VYP	G 18	04	
	03	09	19'
	WC	04	06
	13	03	07
	AS 08	11	16
	shr	01	
	hrb	31	
TRE	G	11	
	WC	24"	
	AS	05	
SHR	G	09	
	WC	03	
	AS	29	
	Mai	40	
	hrb	15	

	4
HRB	G 48#
	Car 91
	WC 60#
	Car 82
	AS 70#
MOS	G 01
	05
	WC 06
	02
	AS 27
	hrb 02
	lip 01
	aoh 16
LIT	G 06
	WC 11
	AS 07
	hrb 25
	mos 06
	lip 06
BAR	G 12
	WC 23"
	AS 17
LIP	G 18
	WC 09
	AS 29
	hrb 05
	mos 11
	aoh 18
AOL	G 01
	WC 07
	AS 10
	shr 21
	hrb 29
AOM	G 23"
	WC 17
	AS 08

	4
AOH	G 01
	WC 12
	tre 22
	AS 27
	hrb 01
	mos 15
	lip 14

TABLE IX, cont.

RHO

36-RHO

	1	4	H
AMO WC	01	01	
AS	19	32	
Cop	06		
Cor	05		
Mel	31		
CAR WC	16	15	11
Com			21
Mai	05		
hrb		31	
AS	19	13	01
Amo		02	
Epi		03	
Pru		00	
hrb		20	
COM WC	41#	26#	
	28!!	18	47#
AS	03		
	07	04	11
Cor	29		
Mel	19		26
COP WC	42#	32#	29!!
Cor	26	18	
Dan	25		
AS	32		
	34'	22	15
Cor	30	11	
Mel			02
a-2		37	
COR WC	34#	28!!	
Cop	01	07	
Mai		18	
AS	29	29	
	59#	43!!	
Pru		33	
hrb		31	
R	13		
DAN WC	26!!	45#	

	1	4	H
EPI WC	53#	53#	
	27!!	30!!	18
Mai	12		
Tri	05		
AS	29		
	23	19	
Amo		09	
Mel		06	
hrb		13	
R	03		
GAU WC	32#	35#	
	20'	23''	31#
Epi	09		
Mai	02	12	
Tri	04		
AS	06	08	12
Mai			29
Mel			27
R	05		
Ilx	49		
ILX WC	14	04	
AS	21	10	
Cor	08	24	
R	29		
Gau	55		
LYC AS	36'		
Cor	21		
Mel	11		
MAI WC	52#	55#	
	57#	42#	32#
Tri	45		
Vam	45		
AS	09	00	24
Gau			35
Pru			06
MEL WC	33#	12	
	08	10	06
AS	12		
	58#	60#	63#
Pru		48	
Vyp			51
hrb		46	

	1	4	H
ORS WC	02	04	
AS	08	08	
Pru	24	36	
PRU WC	04		
	07	06	
AS	23		
	16	47!!	33'
Car	05		
Cor	04		
Mel		27	
Ors	27	56	
PTR WC	16	17	
	05	03	13
AS	07	14	
	20	08	06
Cor	32		
Mel	02	14	
Pru		21	
hrb		42	
RUB WC	05		
AS	11		
Mel	26		
TRI WC	64#	59#	
	45#	24''	
Cop		12	
Mai	25		
AS		15	
	09	04	18
Mai			05
Mel			28
VAM WC	63#	60#	
	39#	12	11
Mai	06		
AS	31'	20	
	10	02	11
R	01		
VIB AS	13	08	09
Cop	22		
Mel	02		
R	06		

TABLE IX, cont.

RHO, RUB, SPP, SOL, TRI

36-RHO(Cont.)

	1	4	H
VIG WC		21'	
	06	01	03
AS	04	19	15
Mel	23	31	
R	17		
VYP WC		16	
	01	00	35#
Com			22
AS	13	09	47"
Epi	23		
Mel			17
R	17		
HRB WC		15	
Car		32	
AS		49"	
Mel		26	
Ptr		60	
MOS WC		10	
		10	
AS		19	
Mel		08	
hrb		01	
lit		32	
lip		01	
LIT WC		11	
AS		21	
Cor		11	
mos		33	
lip		33	
LIP WC		06	
AS		21	
Mel		08	
hrb		02	
mos		07	
lit		32	

4

AOM WC	24"
AS	23
Mel	13
hrb	11
gli	12
A-2 WC	25"
Mai	12
AS	16
Cop	34
Cor	27
hrb	05
BEE WC	23"
AS	02
GLI AS	34'
hrb	23

37-RUB

	1	4
MEL G	42#	45#
WC	00	
AS	17	
Rho	29	
RUB WC	05	
AS	11	
Mel	26	
TRI WC	04	
AS	26	
VAM WC	06	
AS	14	
Tri	26	
VIG G	21'	12
Mel	10	
WC	04	
AS	03	

39-SPP

	H
LED R	22
DG	17
SPL R	26
DG	32"
VIG R	12
Spl	25
DG	08

40-SOL

	1	4
ANM G	08	22"
WC	33#	
ARC G	31#	07
ASH G	12	31#
WC	00	
ORS G	31#	03
WC	06	
Anm	21	
PRU G	04	07
Ors	21	
WC	06	

41-TRI

	1	4
AMO WC	00	07
AS	14	08
Cop	30	
AMS AS	25	07

TABLE IX, cont.

TRI

41-TRI(Cont.)

	1	4	H
CPD WC	09	40#	
Epi		30	
Ilx		26	
AS	15		
Com	27		
CAR WC	15	13	
Mai	01		
hrb		30	
AS	05	05	08
COM WC	29#	14	
	20'	05	
Rho	09		
AS	22	09	07
Cpd	32		
Mai			34
COP WC	30"	43#	
Cor		33	
Epi	19		
Rho	14		
AS	29	01	25
Vam	14		
COR WC	22'	29"	
Cop	04	04	
Epi	02		
Mai		24	
Rho	07		
AS		12	
	12	19	
Cop	20		
DAN WC	00	06	
Rho		20	
EPI WC	48#	51#	
	52#	35#	
Cpd		22	
Gau	42		
Ilx		23	
AS	19	03	
Vam	30		
Vyp	04		
GAU WC	32#	30#	
	38#	10	
Epi	19		
Mai	25		
AS	15	04	10
Mai			30
Vyp	11		
ILX WC	26"	38#	
Cpd		24	
Mai	14		
AS	15	15	
bar		03	
MAI WC	48#	32#	
	46#	23"	
Rho	29		
AS	20	04	60#
MEL WC	29#	10	
	14	14	
AS	29	04	05
Rho			22
ORS WC	10	01	
AS	13	06	
Pru	26		
PRU WC	18		
	01	01	
AS	11	16	20
Mai			23
Ors	25		
PTR WC	11	04	
	04	13	
Cop		03	
hrb		03	
AS		06	
	20	00	10
Mai			27
Mel	32		
RHO WC	64#	59#	
	45#	24"	
Cop		12	
Mai	25		
AS		15	
	09	04	18
Mai			05
Mel			28
RUB WC	04		
AS	26		
VAM WC	44#	41#	
	10	09	
Mai	27		
Rho	09		
AS		21	
	37'	06	07
Vyp	48		
VIB AS	20	16	06
Vam	09		
VIG WC		17	
	12	01	
AS	13	23	21
Vam	03		
Vib	03		
VYP WC		11	
	10	04	
AS	43"	15	10
Rho			21
Vam	53		
HRB WC		18	
Car		32	
AS		04	
LIT WC		06	
AS		23	

TABLE IX, cont.

VAM

42-VAM

	1	4	H
AMO WC	03	03	
AS	10	08	
Cop	36		
CHM R	06	36	10
Eri		19	
Vox		68	
shr		16	
COM WC	28#	26"	
	11	29"	12
shr		19	
AS	04		
	11	06	12
Cop	26		
Vig	21		
COP WC	06	01	04
AS	40		
	47"	37'	08
Cor	61		
COR WC	14	05	
AS	49#	36'	
	15	15	
Cop	46	16	
R	05	12	
Epi	25	34	
Vyp	26		
hrb		32	
EPI WC	45#	36#	
	12	06	03
AS	17		
	02	17	
Tri	32		
R	69#	19	
Cor		37	
Gau		04	

	1	4	H
ERI R	13	42"	03
Chm		30	
Epi	34		
Gau		65	
Vyp	27		
shr		27	
hrb		52	
GAU WC	24"	32#	
	13	42#	29"
AS	00	06	14
R	34	60#	08
Epi	17		
Eri		74	
Vyp	20		
hrb		26	
ILX WC	24"	16	
Mai	06		
AS	06	05	
R	21	16	
Gau	21	17	
shr		05	
hrb		13	
LED AS	12	08	
mos		20	
R	22	14	11
Epi	07		
Ilx		24	
shr		51	
MAI WC	34#	36#	
	62#	33#	33#
AS	03	05	00
NEM R	07	17	
aom		24	
PRU WC	09		
	05	03	
Gau		22	
AS	11		
	00	02	06

	1	4	H
PTR WC	22"	10	
	10	04	06
AS	41"	34'	
	28	07	16
RHO WC	63#	60#	
	39#	12	11
Mai	06		
AS	31'	20	
	10	02	11
R	01		
RUB WC	06		
AS	14		
Tri	26		
TRI WC	44"	41"	
	10	09	
Mai	27		
Rho	09		
AS		21	
	37'	06	07
Vyp	48		
VIB AS	32	03	06
R	08	17	
Epi	20		
VIG WC		24"	
	20'	33#	01
shr		17	
AS	28	31	14
R	12	03	06
Vyp	24		
VOX R	11	16	
Chm		62	
Eri		26	
tre		26	

TABLE IX, cont.

VAM, VIB

42-VAM(Cont.)

	1	4	H
VYP WC		04	
	03	03	16
AS	14	12	11
Tri	36		
R	47"	25	01
Epi	31		
Eri		36	
Gau		05	
shr		08	
hrb		04	
TRE WC		04	
AS		15	
R		25	
Chm		14	
shr		13	
mos		43	
lit		35	
lip		41	
SHR WC		35#	
Com		21	
Gau		24	
Vig		20	
Vyp		57	
AS		01	
R		51"	
Chm		41	
Eri		41	
Led		67	
Vig		64	
hrb		41	
lip		61	
aom		62	
HRB WC		04	
AS		09	
R		57"	
Gau		15	

	4
MOS WC	16
	06
AS	13
Led	23
R	16
Eri	32
tre	40
shr	31
lip	03
LCN WC	13
	08
AS	05
aom	21
R	11
LIT WC	04
AS	13
R	11
Eri	21
Gau	22
tre	28
shr	26
hrb	26
mos	01
lip	10
BAR WC	06
AS	05
R	16
shr	04
hrb	06
lip	28
LIP WC	05
AS	08
R	20
Chm	31
Eri	35
tre	39
shr	43
bar	30

	4
AOL WC	06
AS	02
R	13
shr	02
hrb	02
mos	23
lip	24
AOM WC	01
AS	33'
R	23
shr	47
hrb	13
AOH WC	05
AS	08
R	06
Vyp	04
tre	21
A-1 WC	08
AS	00
R	00
Chm	11
Gau	14
hrb	20
A-2 WC	16
Mai	05
AS	24
Cop	06
aom	12
R	15
Gau	03
GLI AS	25

43-VIB

	1	4
AMO AS	09	06
Cop	21	
CHM R	27	21

TABLE IX, cont.

VIB, VIG

43-VIB(Cont.)

	1	4	H
COP AS	23	08	08
Cor	34		
Vam	09		
COR AS	04	04	
Cop	26		
Rho	14		
R	08	00	
EPI AS	05	09	
R	09	13	
Vam	21		
GAU AS	17	14	06
R	06	16	
Ilx	24		
ILX AS	00	08	
R	05	12	
Gau	24		
KAL R	20	14	
LED AS	08	05	
R	31	23	
NEM R	05	27	
RHO AS	13	08	09
Cop	22		
Mel	02		
R	06		
TRI AS	20	16	06
Vam	09		
VAM AS	32	03	06
R	08	17	
Epi	20		
VIG AS	29	18	08
R	07	04	

	1	4	H
VYP AS	00	09	12
Gau		01	
shr		21	
R	08	05	
TRE AS		18	
lit		30	
R		09	
SHR AS		23	
lit		34	
R		09	
HRB AS		20	
R		13	
MOS AS		01	
hrb		09	
lit		20	
lip		22	
a-2		09	
R		16	
lip		05	
LIT AS		37'	
R		09	
LIP AS		09	
shr		19	
hrb		21	
mos		24	
lit		07	
a-2		20	
R		20	
AOL AS		18	
lit		30	
R		05	
A-2 AS		24	
lit		34	
R		13	

44-VIG

	1	4	H
AMO G	01	06	
WC	07	02	
AS	25	29	
ASL G	30#	17	
WC	01	03	
CAL G	32#	20'	
			11
WC		06	
			07
AS			11
R			22
CPD G	11	08	05
WC	05	01	
AS	15		
Com	30		
CAR G			04
	02	00	05
hrb		20	
WC			01
	22'	17	11
AS			32
	21	20	07
hrb		10	
CHM R	07	01	06
DG	18	15	14
shr		48	
COM G	05		
	09	03	01
WC		10	
	09	05	03
AS	28	05	06
Cpd	38		
COP WC	07	04	04
AS	14	17	12
Amo	28		
Vam	01	06	
a-2		03	

TABLE IX, cont.

VIG

44-VIG(Cont.)

	1	4	H
COR WC	08	10	
AS	09	02	
Amo	20		
Cop	05		
Ilx	05		
Vib	08		
R	57"	02	
ERI R	05	15	25
Spl			13
shr		10	
DG	11		
	21'	11	04
GAU G	24"	30#	
	11	07	15
WC		52#	10
	21'	22"	06
Vam		10	
shr		04	
AS	30	10	11
R	03	10	17
shr		34	
ILX WC	04	02	
AS	28	04	
R	06	03	
Led		21	
shr		12	
LED AS	10	01	
R	23	45"	08
Cor	40		
shr		26	
DG	18		
	07	03	07
MAI G	25"	29"	
	20'	06	
WC		14	
	19'	06	04
Vam	09		
AS	14	20	07

	1	4	H
MEL G	37#	34#	
	31#	20'	
WC		19'	
	02	02	08
AS	23	10	02
Rho		26	
hrb		24	
NEM R	04	32	
shr		44	
lcn		48	
ORS G	18'		
	12	01	03
shr		34	
WC	01	24"	
shr		04	
AS	04	02	
PTR G	27#	35#	
	37#	26"	00
WC		05	10
	20'	16	01
AS	10	08	08
RHO WC		21'	
	06	01	03
AS	04	19	15
Mel	23	31	
R	17		
RUB G	21'	12	
Mel	10		
WC	04		
AS	03		
SPL AS			01
R			40'
DG			07
SPP R	12		
Spl	25		
DG	08		

	1	4	H
TRI WC		17	
	12	01	
AS	13	23	21
Vam	03		
Vib	03		
Vyp	23		
VAM WC		24#	
	20'	33#	01
shr		17	
AS	28	31	14
R	12	03	06
Vyp	24		
VIB AS	29	18	08
R	07	04	
VOX R	12	08	
aoh		23	
DG	16	11	03
VYP G	49#	38#	01
	25"	19'	18
shr		17	
WC		32#	11
	09	14	14
AS	17	05	11
Gau	01		
Rho			21
R	20	05	13
Cor	00		
DG	00	05	04
TRE G		05	
WC		08	
AS		00	
R		03	
shr		16	
mos		20	
lip		15	
aom		08	
aoh		15	
DG		06	

TABLE IX, cont.

VIG, VIO, VOX

44-VIG(Cont.)

	4
SHR	G 54#
	WC 57#
	Vyp 73
	AS 19
	R 56"
	Led 45
	Vam 67
	DG 14
	Chm 48
HRB	G 15
	Car 25
	Ptr 03
	WC 03
	AS 20
	Mel 30
	R 01
	DG 05
MOS	G 05
	07
	WC 08
	12
	AS 13
	lit 23
	lip 00
	a-2 03
	R 31
	Led 15
	lip 09
	aoh 20
	DG 03
LCN	G 30#
	25"
	shr 10
	WC 38#
	22'
	AS 25
	a-2 36
	R 01
	Nem 38
	shr 13
	DG 01

	4
TOT	R 02
	a-2 28
LIP	G 04
	WC 04
	AS 14
	a-2 04
	R 31
	Led 14
	shr 17
	mos 09
	DG 04
AOM	G 12
	WC 07
	AS 04
	R 22
	Led 03
	Nem 33
	shr 07
	aoh 36
	DG 07
AOH	G 02
	WC 18
	AS 15
	R 31
	mos 19
	aom 41
	DG 17
A-2	G 22"
	shr 16
	WC 21'
	AS 27
	lcn 37
	R 20
	tot 34
GLI	AS 22

45-VIO

	1	4	
ASH	G 12	41#	
ASL	G 33#	05	
CPD	G 45#	01	
COM	G 20'	03	
MEL	G 19'	26"	
	Ash	07	

46-VOX

	1	4	H
CHM	R 42'	70#	
	Eri 31		
	Vam	83	
	DG 08	11	03
	hrb	23	
ERI	R 35	18	
	Chm 18	28	
	Kal 25		
	Vam	28	
	DG		03
	02	03	06
GAU	R 14	16	
	Chm 25	37	
ILX	R 10	10	
	a-1	25	
KAL	R 73#	23	
	DG 12	01	09
KAN	DG 20'	15	03

	1	4	H
LED	R 12	10	
	mos	21	
	lip	24	
	DG 17	17	09
	hrb	03	
POS	DG		08
			42#
VAM	R 11	16	
	Chm	62	
	Eri	26	
	tre	26	
VIG	R 12	08	
	aoh	23	
	DG 16	11	03
VYP	R 22	27	
	aoh	14	
	DG 09	00	02
TRE	R	32	
	Chm	11	
	aoh	15	
	DG	08	
SHR	R	09	
	Chm	39	
	Vam	20	
	Vyp	21	
	DG	06	
	Chm	06	
	hrb	22	
HRB	R	11	
	Chm	29	
	Gau	06	
	Vyp	00	
	a-1	23	
	DG	89#	
	Eri	100	

TABLE IX, cont.

VOX, VYP

46-VOX(Cont.)

	4
MOS R	22
tre	04
lit	12
lip	00
aoh	04
DG	15
hrb	05
lit	05
lip	02
LCN R	07
DG	26
hrb	16
TOT R	22
Chm	11
a-2	47
LIP R	04
tre	10
aoh	14
DG	16
hrb	07
lit	06
AOM R	13
lip	24
aoh	00
a-1	03
DG	03
AOH R	40'
tre	29
DG	28"
A-1 R	37
Chm	26
A-2 R	05
Chm	30
tot	43
aoh	10

47-VYP

	1	4	H
AMO G	08	00	
WC	07	10	
AS	15	10	
Epi		25	
AMS AS	21	17	
Gau		35	
ANM G	15		
	20'	31#	
shr		20	
WC	27"	16	
CAR G			26#
	20'	27"	16
WC			14
	16	16	09
AS	11	08	07
Epi	08	16	
Gau	21	21	
Ptr		02	
CHM R	03	11	16
Vam		23	
Vox		11	
shr		35	
tot		04	
DG	29"	25"	21'
Led	09	08	
shr		56	
COM G	14		
	14	12	05
WC		20'	
	11	07	36#
Rho			23
AS	18	09	03
Gau	01	22	

	1	4	H
COR WC	04	08	
AS	00	08	
Gau		23	
R	35	15	
Epi		05	
Nem		26	
lcn		25	
EPI G	00		
WC		11	
	21'	13	17
AS	37'	36'	
R	38'	28	
Gau		17	
Vam	09		
hrb		10	
ERI R	21	18	16
Vam	31	32	
shr		38	
DG	04	05	08
GAU G	23"	16	
	20'	21'	16
WC		27#	05
	16	08	10
shr		29	
AS	53#	65#	09
R	38'	36	62#
Ilx	48		
Vam	26		
tot		48	
hrb		06	
ILX WC	07	18	
shr		02	
AS	22	12	
Epi	12		
bar		22	
R	19	07	
Gau	36	11	
Vam	10		
hrb		11	

TABLE IX, cont.

VYP

47-VYP(Cont.)

	1	4	H
LED	AS 20	17	
	shr	28	
	R 20	04	20
	shr	26	
	mos	10	
	DG 50#	42#	10
	Chm 43	36	
LYC	AS 09		
	Gau 20		
MAI	G 19'	13	
	13	10	
	WC	09	
	07	13	13
	AS 10	21	03
	shr	36	
MEL	G 25!!	28#	
	22'	10	
	WC	09	
	01	07	07
	AS 00	19	56#
	Epi	31	
	Rho		38
	shr	06	
	hrb	32	
NEM	R 24	28	
ORS	G 05		
	01	03	04
	shr	44	
	WC 13	43#	
	shr	26	
	AS 10	04	
PRU	G 02		
	00	04	
	shr	26	
	WC 05	01	
	shr	25	
	AS 05	04	00
PTR	G 18	04	
	03	09	19'
	WC 13	03	07
	AS	04	06
	08	11	16
	shr	01	
	hrb	31	
RHO	WC	16	
	01	00	35#
	Com		22
	AS 13	09	47!!
	Epi 23		
	Mel		17
	R 17		
SPL	AS		08
	R		22
	DG		18
TRI	WC	11	
	10	04	
	AS 43!!	15	10
	Rho		21
	Vam 53		
VAM	WC	04	
	03	03	16
	AS 14	12	11
	Tri 36		
	R 47"	25	01
	Epi 31		
	Eri	36	
	Gau	05	
	shr	08	
	hrb	04	
VIB	AS 00	09	12
	Gau	01	
	shr	21	
	R 08	05	
VIG	G 49#	38#	01
	25!!	19'	18
	shr	17	
	WC	32#	11
	09	14	14
	AS 17	05	11
	Gau 01		
	Rho		21
	R 20	05	13
	Cor 00		
	DG 00	05	04
VOX	R 22	27	
	aoh	14	
	DG 09	00	02
TRE	G	20'	
	WC	02	
	AS	19	
	Gau	04	
	R	07	
SHR	G	58#	
	Ors	68	
	WC	76#	
	AS	43!!	
	aom	55	
	R	36	
	Chm	48	
	Eri	48	
	Vig	47	
	DG	08	
	Chm	53	
HRB	G	15	
	Car	09	
	WC	08	
	AS	15	
	Epi	07	
	Mel	30	
	Ptr	33	
	shr	31	
	R	38'	
	Gau	16	
	DG	02	

TABLE IX, cont.

VYP

47-VYP(Cont.)

4

MOS G 25"
02
WC 03
22"
lip 08
AS 11
Led 01
shr 22
R 30
shr 41
bar 40
DG 05

LCN G 20"
23"
shr 06
WC 21'
12
AS 18
R 17
Nem 07
mos 27
DG 33

TOT R 36
Gau 48

LIT G 07
WC 16
AS 15
Gau 04
R 18
shr 28
mos 06
lip 08
aoh 07
DG 03

4

BAR G 13
WC 01
AS 02
R 15
shr 01
mos 31
lip 25
aoh 25
DG 02

LIP G 10
WC 23"
mos 10
AS 10
shr 30
mos 02
R 17
shr 31
mos 23
lit 03
aoh 06
DG 04

AOL G 13
WC 11
AS 14
Gau 34
shr 01
R 10
shr 02
mos 27
DG 06

AOM G 16
WC 04
AS 24
Gau 02
shr 44
R 17
Epi 27
shr 07
hrb 28
aoh 05
DG 06

4

AOH G 20'
WC 04
AS 01
R 39'
a-2 49
DG 15

A-1 G 03
WC 05
AS 09
Gau 38
R 04

A-2 G 18
WC 01
AS 21
Gau 08
R 17
Gau 27
tot 24
aoh 36

GLI AS 09
Gau 20
aom 20
a-2 16

CHAPTER VI

HIGHER POWER REGRESSIONS

From Chapter III, we know that the zero-order correlation coefficient indicates by its sign whether or not the species or variables in question tend to co-occur, i.e. whether high values of both are found in the same or different places. By the magnitude and significance level of these coefficients we get an idea of how rigorous and sharply defined this relationship is, and what the probability is of its being due simply to chance. With partial correlations (Chapter V) we can examine the correlation of one pair in the light of other variables, thus discovering to what extent a given correlation is influenced by correlations of each pair member with these variables. This suggests possible causative agents of the correlation.

But it became increasingly evident during the course of the study that there may be certain subtleties in the physioecological relationship between two species which are obscured by simple correlations. Even straight line regressions which show the magnitude of a relationship and not just its consistency, are not always adequate. As

a simple illustration, let us imagine a case in which values of the dependent variable, y, are relatively low at both low and high values of the independent variable x, but high at intermediate values of the latter (Figure 11 C, page 198d). Now, a simple regression which best fits these points is a nearly flat line, and the correlation is circumneutral (-0.06) which might cause us to pass over the codistribution of such a pair as indistinguishable from random. But now, if we calculate the quadratic regression of the pair (see equation 2 below) the resulting parabola fits the points much better (correlation +0.80), and is certainly a much closer approximation to the curve which we could fit "by eye". This is similar to several examples from my actual data for the DG gradient segment, of which the pair Vaccinium angustifolium var. nigrum (Vig, no. 44 in Table VII) plotted upon Ledum groenlandicum (Led, no. 26) has a nearly flat linear regression with correlation +0.03 (Figure 14 C, page 209). Now, both these species seem to produce little cover where the dominant shrub Chamaedaphne calyculata (Chm, no. 11) is lush, Ledum (correlation with Chamaedaphne -0.43) perhaps somewhat more so than the Vaccinium taxon (-0.15 with Chamaedaphne). In areas which are relatively free of the near-ubiquitous Chamaedaphne

perhaps both Vaccinium and Ledum can thrive, hence the initial rise in the cubic regression line (equation 3) of the first as the second increases. But as Ledum clones become established and grow lusher, they may exclude Vaccinium (by competition, antibiosis or both) as effectively as Chamaedaphne does, so Vaccinium decreases with further increasing Ledum. The correlation corresponding to this cubic regression is +0.25, significant at $P < .02$, but when we "average" the two tendencies with a linear regression neither of them comes to light.

Ideally, we should examine scatter diagrams of individual points in order to view all possible subtleties in the correlation between two variables. But in a study of the magnitude of this one, such a thing is simply not possible. Even when we are dealing with a relatively few variable pairs, moreover, such misplaced thoroughness might lead us to place undue importance on a few eratic and aberrant points, whose positions may be due only to random fluctuations, unique local conditions, or even measurement error. The present chapter is, therefore, a search for a workable solution to the problem of the insensitivity of straight-line regression, and for a method which yields valuable additional information within a realistic period

of time, while avoiding the pitfalls of overly detailed examination.

Accordingly, I first plotted several hypothetical sets of points designed to illustrate all imaginable situations. Because these points were purposely chosen to fit certain kinds of curves, their mean distances from those curves are considerably less than one would generally find in a natural situation and the correlations are extremely high, but most of the information derived from them should be applicable to real data. Linear, quadratic and cubic regressions, actually multiple regressions of the forms:

$$(1) \quad y = a + b_1x,$$

$$(2) \quad y = a + b_1x + b_2x^2,$$

$$(3) \quad y = a + b_1x + b_2x^2 + b_3x^3,$$

respectively, were calculated for each of these sets of points, and the resultant curves plotted (Figures 8-12, pages 198a-198e). For convenience the zero-order correlation between the two variables and the values for b_1 of equation 1, b_2 of equation 2 and b_3 of equation 3, are given with their significance levels beside each figure. The quadratic will always be a parabola or a part thereof, while the cubic regression will be all or part of a symmetrical curve in the form of an S turned on its side; the first may

be concave downward or upward and the second may have either its right-hand or left-hand branch concave down, and apices may be located anywhere (see illustrations). Regressions of still higher power would be nearly impossible to prove significantly different from their lower-powered counterparts, because of the rapid increase in standard error as one adds more parameters (cf. Ezekiel 1930). Moreover, I felt that curves of the fourth power or higher would generally be meaningless biologically, or else hopelessly difficult to interpret.

The results and conclusions of this hypothetical study were then applied to data for the DG (Dawson-Greenwood peat) gradiant segment. This segment was chosen because it is the lowest of all in number of species and consequently, for an exploratory study, the least complex. Data only from quadrats of intermediate size (1/4 m^2), were used so that environmental variables could be included.

In deciding which regressions to calculate and plot, all those possible combinations which would logically seem to be meaningless were first eliminated. For example, it is unlikely that the small, relatively ephemeral Vaccinium oxycoccus (Vox) appreciably influences the distribution of the large robust clones of Chamaedaphne caly-

culata (Chm). V. oxycoccus might conceivably influence seedling germination of the Chamaedaphne but, by the time the latter matured, would likely have shifted in its own distribution). The reciprocal regression on the other hand, might be meaningful. For those variable pairs not eliminated, quadratic and/or cubic regressions were plotted only if the coefficients of x^2 or x^3, respectively, were significantly different from zero at a level of $P < .05$ or higher (t-test). This level was judged, on the basis of experience with the hypothetical data, to be about that at which the quadratic was sufficiently different from the linear, or the cubic from the quadratic, to yield unique information of possible importance.

In several cases, reciprocal regressions are plotted for the DG data, i.e., Species B on Species A as well as A on B. Although the reciprocal of a linear regression is merely the same line rotated through 90 degrees, this is not true of the higher power curves. This can easily be demonstrated by plotting a series of points on two axes which would be well fitted by a concave-downward or concave-upward parabola, then actually rotating the paper through 90 degrees. It will be seen that if the former x-axis were now allowed to be the y-axis and vice

versa and Equation 2 above were again applied, the resulting parabolic fit to the points would be close to a straight horizontal line. The biological significance of this is that each such curve of a reciprocal pair may reveal aspects of the relationship between two variables which the other does not, e.g. the nature of the dependence of the distribution of A on that of B as well as the converse.

A. THE HYPOTHETICAL DATA. If we are to recognize deviations from randomness in regressions, we should be aquainted with the approximate range of divergence from a flat line generally found in data obtained from randomly co-distributed populations. Accordingly, regressions, were calculated for three sets each of 20 pairs of random numbers (Figure 8, page 198a). As it happens, 8 C has a correlation for the straight line regression significant at $P < .05$ (we would expect this in about one of 20 cases of variables which are in fact co-distributed randomly). It is in 8 A and 8 B, however, that the higher power curves appear more interesting, and in 8 B the quadratic regression is, in fact, significantly different from the linear at $P < .02$. If we now look at the scatter diagram of Figure 8 B, we find a cluster of four points in the upper left and another four in the middle near the bottom.

Flukes of this sort can so easily occur, especially with a relatively small number of observations, that we should be forewarned not to treat any regression plot as if it were inviolable. This is especially true in the DG data to be discussed below, in the cases of those bog species which are present in relatively few quadrats. Just as with the correlation coefficients, however, it is unavoidable that we will observe a certain number of such flukes and perhaps try to rationalize them.

Figures 9 A and 9 B (page 198b) are, respectively, "near-perfect" positive and negative linear regressions. As one would expect, the quadratic and cubic curves do not differ appreciably from the line, the latter being for all practical purposes the best fit in these cases. In Figure 10 (page 198c), on the other hand, we have what is intended to be a geometrically increasing y. Here the quadratic and cubic curves reveal this feature where the line cannot. The cubic is probably the better fit but neither its downward bend to the left nor the quadratic's corresponding upward bend represent any real feature of the data.

The last points up another danger in these higher power regressions; that whatever subtleties they may reveal they are as inflexible as the line in having to assume a

particular shape. The entire curve on one side of the inflection point, probably generally the smaller half within the quadrat between x and y axes where the data lie, may be completely misleading. Still interpretation, in the light of field experience, other statistics, and logic are indispensible. In the case of Figure 10 (page 198c) and in some others, another curve could be drawn in, based on "the eye" as well as the other curves, which is probably a better fit than any of the computed regressions. In such cases the latter do, however, suggest where the "best fit" should lie. Figure 11 A (page 198d) is the reverse of Figure 10, where y decreases more steeply at higher values of x. Again the quadratic is necessary to reveal this.

Figure 11 C was mentioned in the introduction to this chapter as a case where the straight line regression shows no relationship, although the quadratic does. Figure 11 B is a similar case in which the parabola opens upward. Figure 12 A is intended to represent a hypothetical case in which there are two separate areas of increase in y. Although the linear regression reveals a general increase it does not distinguish between these two areas, which may reflect two separate thresholds of influence for variable x upon y, each representing a different aspect of x's na-

ture. This pattern might also result from the influence of two different variables, each correlated with x, upon y, or one of the steep rises might reflect the action of x itself while the other represents a third variable. Figure 12 B is similar but with a third variable, or excess of x itself, actually causing an inhibition of y before the latter begins to rise. This rise might reflect an inhibition of a competing species, which suppresses y, by x, or a change in x's character as it increases so that it becomes favorable to y. As curves become more complex one can imagine more and more possible situations to account for them.

Figure 12 C was intended to represent a "sigmoid curve", that is, a more rapid increase in y at intermediate than at either high or low values of x. But as the t-values as well as the eye reveal, the quadratic and cubic regressions are scarcely different from the line. Now, the quadratic and cubic equations used here always yield curves such that a line which is parallel to the y-axis through the parabola's vertex or the cubic's inflection point will cut the curve into two halves which are upright or inverted images of each other. Hence they may be more efficient at revealing certain types of peculiarities than others such

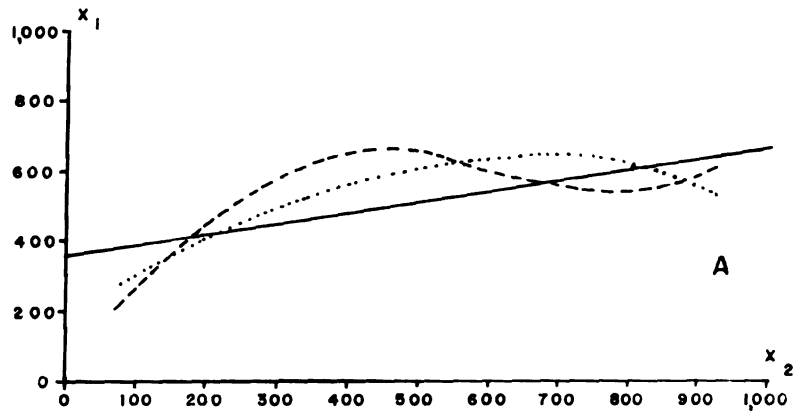
FIGURE 8. Hypothetical Linear, Quadratic, and Cubic Regression Curves

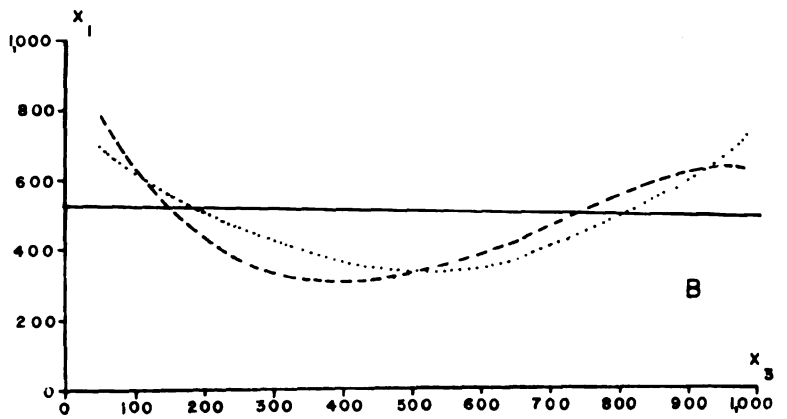
Code: solid line = linear, dotted line = quadratic, broken line = cubic.

A. Random numbers.

B. Random numbers.

C. Random numbers.


X1
1,000
800
600
400
200
0
A
X2
0
100
200
300
400
500
600
700
800
900
1,000


X1
1,000
800
600
400
200
0
B
X3
0
100
200
300
400
500
600
700
800
900
1,000

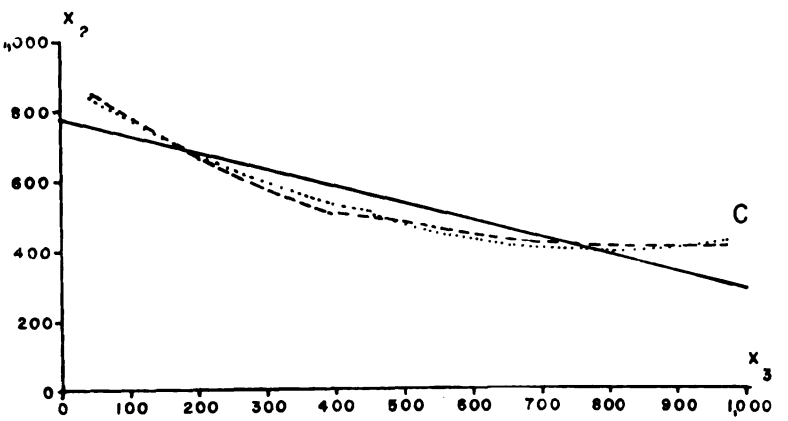
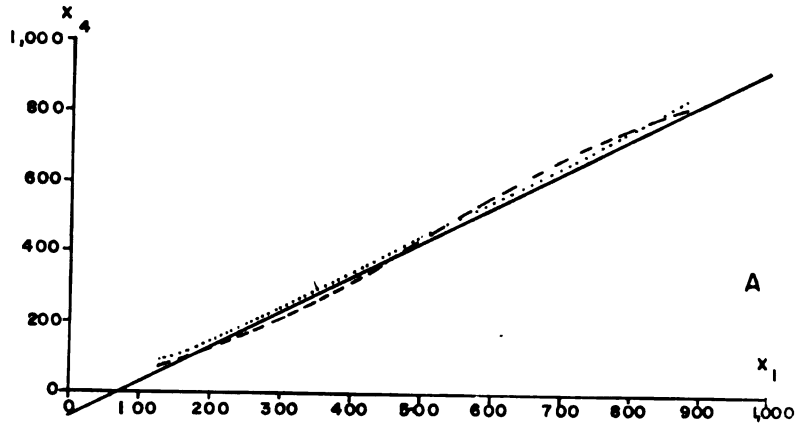

X2
1,000
800
600
400
200
0
C
X3
0
100
200
300
400
500
600
700
800
900
1,000

FIGURE 9. Hypothetical Linear, Quadratic, and Cubic Regression Curves, cont.

Code as for Figure 8, page 198a.

A. x_4 increasing arithmetically as x_1 increases.

B. x_5 decreasing arithmetically as x_3 increases.


x4
1,000
800
600
400
200
0
0
100
200
300
400
500
600
700
800
900
1,000
A
x1

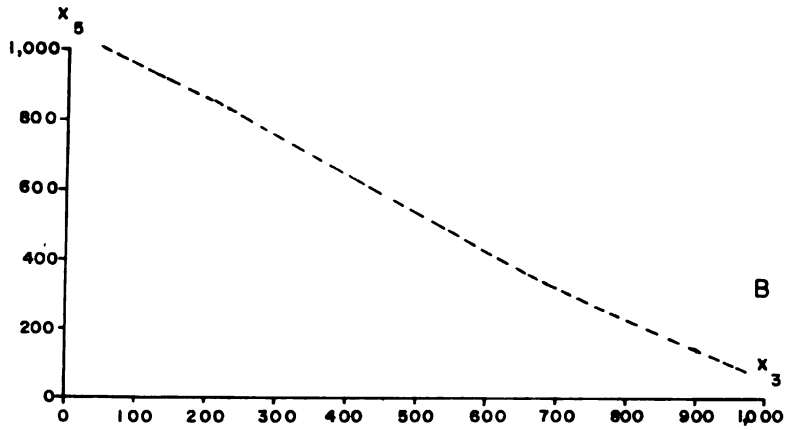

x5
1,000
800
600
400
200
0
0
100
200
300
400
500
600
700
800
900
1,000
B
x3

FIGURE 10. Hypothetical Linear, Quadratic, and Cubic Regression Curves, cont.

Code as for Figure 8, page 198a.

x_6 increasing geometrically as x_2 increases.

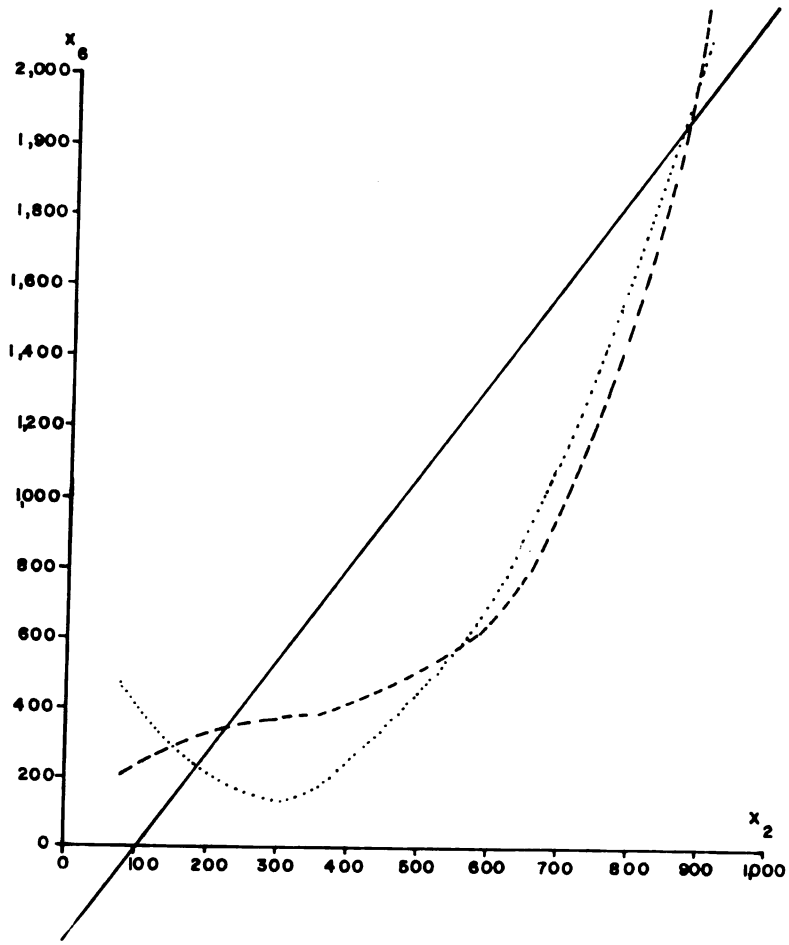

x_6
2,000
1,900
1,800
1,600
1,400
1,200
1000
800
600
400
200
0
0
100
200
300
400
500
600
700
800
900
1000
x_2

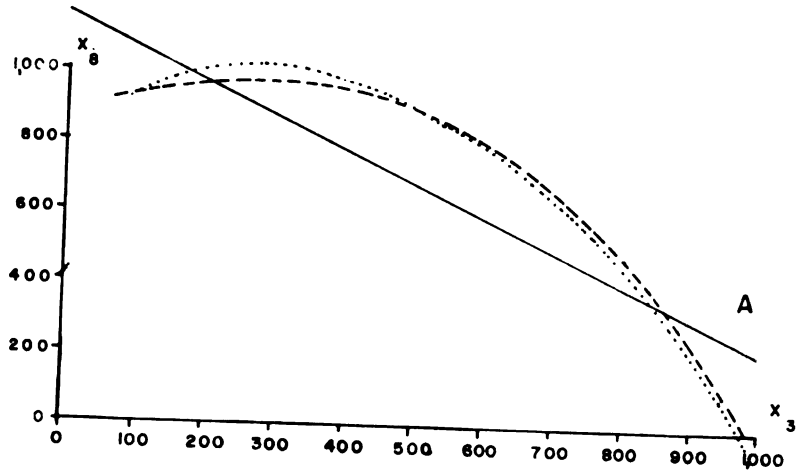
FIGURE 11. Hypothetical Linear, Quadratic, and Cubic Regression Curves, cont.

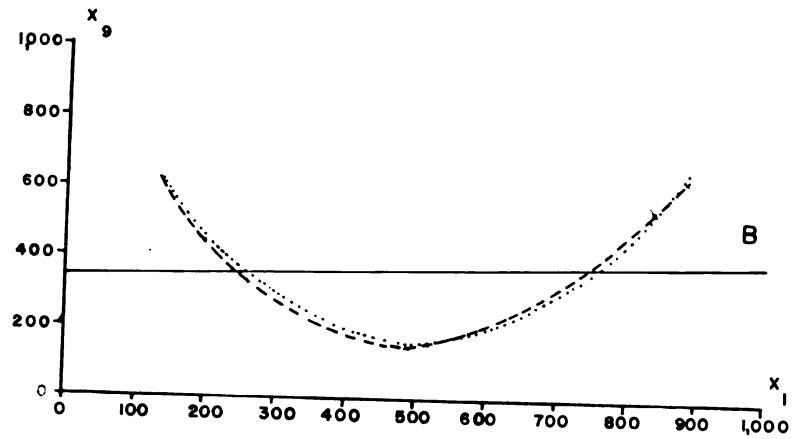
Code as for Figure 8, page 198a.

A. x_8 decreasing geometrically as x_3 increases.

B. Parabola opening upward.

C. Parabola opening downward.


X 8
1,000
800
600
400
200
0
0 100 200 300 400 500 600 700 800 900 1000
X 3
A


X 9
1000
800
600
400
200
0
0 100 200 300 400 500 600 700 800 900 1,000
X 1
B

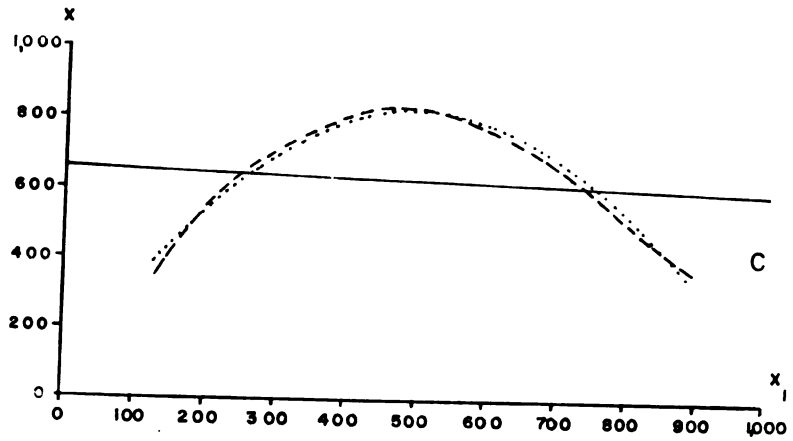

X
1,000
800
600
400
200
0
0 100 200 300 400 500 600 700 800 900 1000
X 1
C

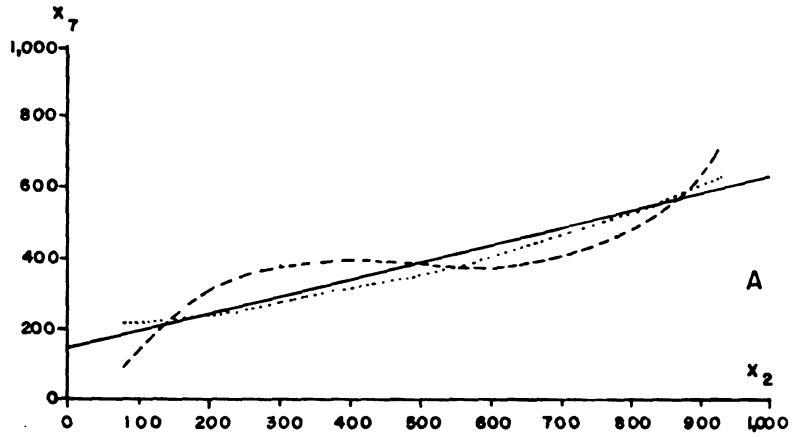
FIGURE 12. Hypothetical Linear, Quadratic, and Cubic Regression Curves, cont.

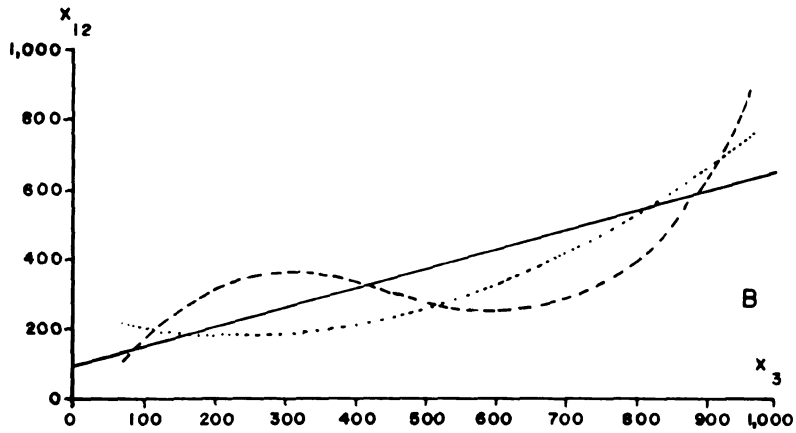
Code as for Figure 8, page 198a.

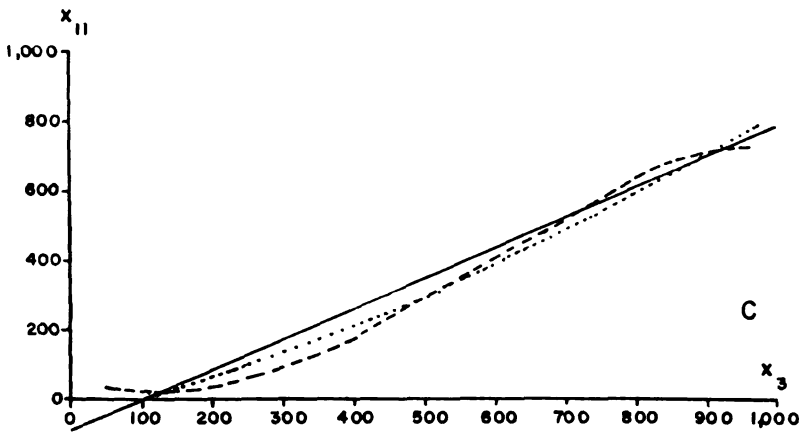
A. x_7 increasing rapidly at low and high values of x_2, more slowly at intermediate values.

B. x_{12} increasing at low and high values of x_3, decreasing at intermediate values.

C. Regression fits to data fitting a sigmoid curve; x_{11} increasing more rapidly at intermediate than at low or high values of x_3.


x_7
1,000
800
600
400
200
0
0 100 200 300 400 500 600 700 800 900 1,000
A
x_2


x_{12}
1,000
800
600
400
200
0
0 100 200 300 400 500 600 700 800 900 1,000
B
x_3


x_{11}
1,000
800
600
400
200
0
0 100 200 300 400 500 600 700 800 900 1,000
C
x_3

as this sigmoid curve.

B. DATA FROM DAWSON-GREENWOOD PEAT. Graphs for these regressions are presented in Figures 13-16 (pages 208-211).

Beginning with the shrubs we find that dominant Chamaedaphne calyculata appears to decrease somewhat more markedly at low than at high values of Ledum groenlandicum (Figure 13 A), according to its quadratic. If Chamaedaphne is responsible for the reduction in cover of Ledum as suggested by Figure 13 of the reciprocal plot, so the reverse may be true in microsites where Ledum has become established. If so, then the threshold for inhibition of Chamaedaphne would seem to be at lower values of Ledum, so that Chamaedaphne's cover is reduced to near zero where Ledum's cover is relatively low, and higher cover of the latter makes little difference. Perhaps the curve does not reach zero because parts of Ledum and Chamaedaphne clones, by chance, may sometimes be included in the same quadrat. It is suggested in Chapter IX that perhaps such inhibition is due to an antibiosis-like reaction between shrub species or their mycorrhizal symbionts, in addition to competition. On the other hand, Figure 13 A may merely reflect Figure 13 E (Ledum on Chamaedaphne).

Chamaedaphne plotted against tree cover Figure 13 B yields a quadratic similar to Figure 11 B, a parabola concave upward. On the basis of all other observations, however, tree cover simply inhibits Chamaedaphne in proportion to the former's cover, and in fact the mean of those values of Chamaedaphne to the right of the vertex (low point) of the parabola is considerably below the overall mean for the species. Therefore, in this instance, the upward-curving arm of the parabola would seem to reflect simply a decrease in the rate of decrease in Chamaedaphne cover with increasing tree cover, i.e., Chamaedaphne decreases most rapidly at lower values of tree cover and approaches a sort of lower asymplote at higher values, as represented by the heavy line in the figure. I mentioned in the preceeding discussion of hypothetical data that the higher power regressions are limited by the shapes of the curves, and throughout the curves of actual data one arm of a parabola frequently curves in a direction opposite the general trend of the variables. With care in interpretation, however, combination of such parabolas with the least square fitted line can still facilitate the plotting of a more realistic "fit".

Since shrub cover (shr) is composed of over 80%

Chamaedaphne, the regression of shrubs on tree (Figure 13 C) tells us no more than that of Chamaedaphne on tree cover. The regression of Chamaedaphne on peat (A_{OH}) thickness (Figure 13 D) is positive probably because of the former's partial replacement by Ledum on the shallow peat near the bog margin. In this case the downward-curving arm of the quadratic to the right must represent an upper asymptote (heavy line), i.e. the relative constancy of Chamaedaphne cover beyond a narrow marginal zone.

The negative correlation of Ledum on Chamaedaphne (Figure 13 E) probably reflects this also. The left hand positions of the quadratic and cubic curves are probably the meaningful ones since most of the points lie here, and they suggest that Ledum cover essentially goes down to zero in the lusher-than-average Chamaedaphne patches (heavy line). Vaccinium boreale on Chamaedaphne (Figure 14 A, page 209) is probably essentially the same story as Ledum on Chamaedaphne and like the latter presumably reflects essentially complete inhibition of other shrubs by lush Chamaedaphne or its mycorrhizae.

Vaccinium boreale on Ledum (Figure 14 B), since the upward-curving arm of the cubic curve to the right is much longer than the left branch, seems to indicate a strong

tendency for these to grow together, most especially where Ledum is relatively lush. But V. angustifolium var. nigrum (Vig) seems to have a tendency to be lush at low values of Ledum and to drop off at higher ones(Figure 14 C), as discussed in this chapter's introduction. Moreover, a check of the raw data, easy to do in this case since there are few observations beyond the means, reveals that all parts of the curves of both V. boreale and V. angustifolium var. nigrum on Ledum seem to follow real patterns.

The small ground shrub Vaccinium oxycoccus, a cranberry, seems on the basis of its quadratic regressions to rise to its lushest value at intermediate values of Chamaedaphne and to fall off at higher ones (Figure 14 D). Its regression upon shrub cover (Figure 14 E) is very similar and amounts to the same thing, since shrub cover is nearly synonymous with that of Chamaedaphne. Since this agrees with a visually evident pattern in the field, namely that V. oxycoccus occurs with medium lush younger Chamaedaphne clumps or only on slopes sorrounding older ones, it tells us nothing new.

V. oxycoccus and Eriophorum spissum are not present on the bare ground under trees or in the old patriarchal Chamaedaphne clones. On the other hand V. oxycoccus, with

about three times as much cover as Eriophorum is nearly absent from certain moss-covered microsites with little or no shrub cover or bare ground which are probably recently disturbed spots. Even Eriophorum is absent from the youngest of these. It is probably these peculiarities which make the cubic curve of herb cover, which is composed only of these two species, maximal at intermediate values of bare ground (Figure 14 F), reflecting the two species' occurrence near lush Chamaedaphne and other shrub patches but not directly in them.

The cubic of moss cover (mos) plotted on Chamaedaphne (Figure 15 A, page 210) suggests that at very low values of Chamaedaphne there is relatively little moss. A clue to the reason is found in the partial correlations between these two variables (Table IX, page 158), for we obtain values of -0.47 and -0.46 with per cents of tree cover and litter cover partialled out, respectively, as against a zero-order of only -0.35. Thus both mosses and Chamaedaphne are absent on the heavily litter-covered ground under scattered bog trees, tending to make their correlation less negative. Moss, by reason of this mutual aversion to tree cover, is present only where there is some Chamaedaphne (cubic peak), but it is also inhibited by the

shade or litter of Chamaedaphne as clumps of the latter grows older and denser. Hence, the decreasing curve to the right (the secondary slight rise is surely an artifact, like some discussed above). The lower asymptote of moss cover on spring litter thickness which one can infer from the linear and cubic curves (Figure 15 B) is not surprising, for a few milimeters of litter are probably as effective in inhibiting moss growth as a few dozen. The moss on A_{OL} (fall litter thickness) quadratic apparently reflects this (Figure 15 C).

Lichen cover (lcn) seems to be associated with high Vaccinium boreale, high V. oxycoccus and high herb covers, (the latter being over 75% V. oxycoccus (Figures 15 D-F). Moreover, if one supposes that the shorter left branches of the cubic regressions and the dips below the x-axis represent a slower rate of increase here than on the right, lichens must be more markedly favored where values of these variables are high (heavy lines), though it is difficult to suggest why. The cubic regression of lichen cover on bare ground (Figure 16 A, page 211) first goes up rapidly and then down. But here the linear regression is nearly flat ($r = +0.07$) so the cubic's down-curving arm to the right represents a real decrease, not a slowing up of

the increase rate. Thus lichens must be relatively abundant under the trees and senescent Chamaedaphne clones where most bare ground occurs, and where conditions are relatively xeric and similar to the upland. But even lichens may be inhibited where shade is extremly great. Alternatively, the most extensive bare spots represented on the right-hand side of the curve may occur in spots where litter has been present for so long as to kill both lichens and mosses. Heavily litter-covered, lichenless areas may result in such microsites, with many bare patches exposed by wind removing litter from the once moss-covered surfaces.

Figure 16 B probably represents a situation quite similar to that illustrated in 15 A for moss on Chamaedaphne. Per cent litter cover seems to be relatively high where there is no Chamaedaphne, i.e. under the trees, reaching a low where young Chamaedaphne is relatively sparse but increasing again in older, lusher patches, of this shrub , which produce their own litter. Here, too, the partial correlations seem to substantiate the hypothesis. Litter cover and Chamaedaphne are correlated at +0.26, ($P < .01$), zero-order, but this rises to +0.38 ($P < .001$) when tree cover is partialled out (Table IX,

page 158), so as to mathematically eliminate the contrast between microsites of high tree cover, no Chamaedaphne and of no tree cover, low Chamaedaphne.

In this connection, perhaps per cent litter cover on Ledum (Figure 16 C) reflects in the left, downward-curving arm of its quadratic a probable tendency for Ledum to become established where both trees and Chamaedaphne, hence litter, are sparse. The rise to the right then presumably reflects older, lusher Ledum's own litter production. A check of the raw data seems to bear this out.

In the regression of per cent litter cover on litter thickness (Figure 16 D), both the very steep upward slope of the linear curve and the raw data indicate that the cubic's slight decrease to the right represents an upper asymptote, a point beyond which there is little increase in per cent litter cover with increasing thickness. This stands to reason since 10 mm. or 100 mm. of litter will completely cover the ground beneath them whereas 1 or 2 mm. will cover but a thickness-related proportion, but this is merely a sidelight from our viewpoint and tells us nothing about the biology of the area.

Rounding out the group of curves which it seemed profitable to plot we have duff thickness on Chamaedaphne

(Figure 16 E) and on shrub cover (Figure 16 F), which is about 80% Chamaedaphne. The cubic suggests that two separate phenomena may be causing the positive correlation here, as in the hypothetical examples illustrated in Figures 12 A and 12 B (see Section A of the chapter). The nature of these forces is a mystery, however, for mean A_{OM} thickness on DG is about 60 mm., mostly dead Sphagnum. Since Chamaedaphne at best can produce but a minor fraction of that amount, its own contribution is probably not one such phenomenon.

If judiciously used in conjunction with other knowledge, higher power regressions do seem to reveal facts and details about the microdistributions and co-distributions unavailable from other sources. On the basis of this exploratory study they show promise as a tool in vegetation analysis.

FIGURE 13. Regression Curves, Segment DG.

Code: solid line = linear, broken line = quadratic, dotted line = cubic curve. The broad lines represent probable "best fits" to the biological situation.

A. Chamaedaphne calyculata on Ledum groenlandicum.

B. Chamaedaphne calyculata on per cent tree cover.

C. Per cent shrub cover on per cent tree cover.

D. Chamaedaphne calyculata on A_{OH} (peat) thickness.

E. Ledum groenlandicum on Chamaedaphne calyculata.

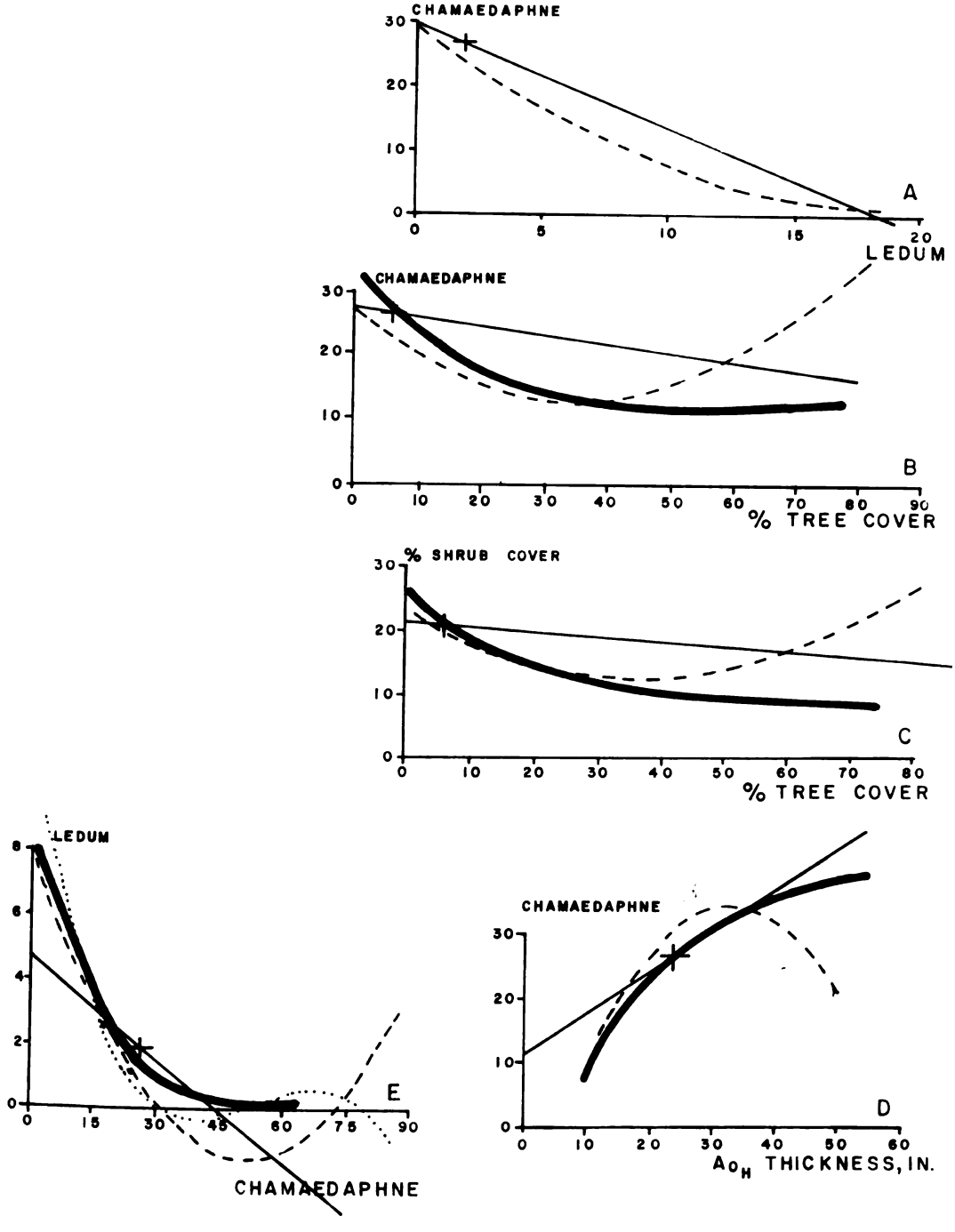

CHAMAEDAPHNE
A
LEDUM
CHAMAEDAPHNE
B
% TREE COVER
% SHRUB COVER
C
% TREE COVER
LEDUM
E
CHAMAEDAPHNE
CHAMAEDAPHNE
D
A_{0_H} THICKNESS, IN.

FIGURE 14. Regression Curves, Segment DG, cont.

Code as for Figure 13, page 208.

A. Vaccinium boreale on Chamaedaphne calyculata.

B. Vaccinium boreale on Ledum groenlandicum.

C. Vaccinium angustifolium var. nigrum on Ledum groenlandicum.

D. Vaccinium oxycoccus on Chamaedaphne calyculata.

E. Vaccinium oxycoccus on per cent shrub cover.

F. Per cent herb cover on per cent bare ground.

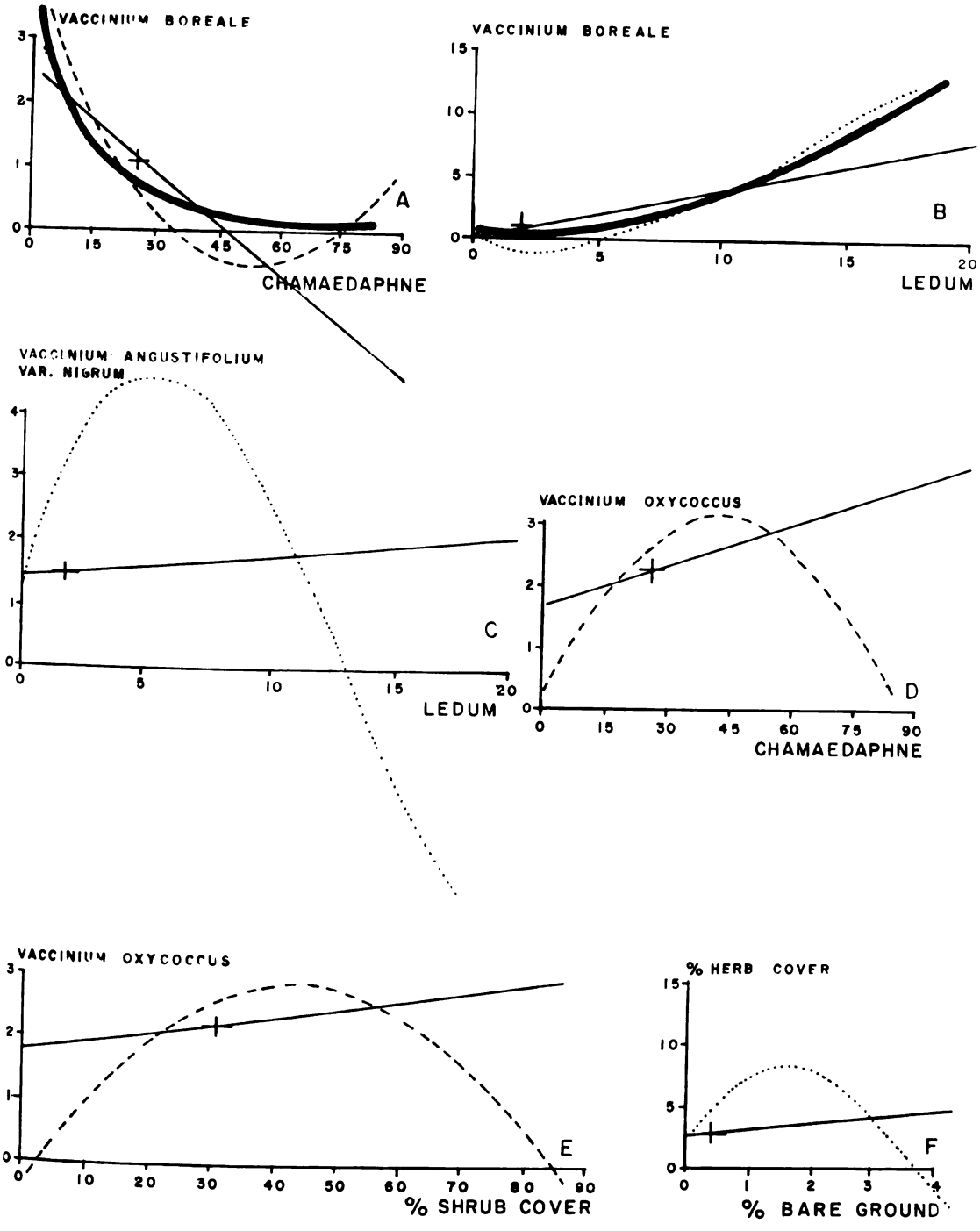

VACCINIUM BOREALE
A
CHAMAEDAPHNE
VACCINIUM BOREALE
B
LEDUM
VACCINIUM ANGUSTIFOLIUM
VAR. NIGRUM
C
LEDUM
VACCINIUM OXYCOCCUS
D
CHAMAEDAPHNE
VACCINIUM OXYCOCCUS
E
% SHRUB COVER
% HERB COVER
F
% BARE GROUND

FIGURE 15. Regression Curves, Segment DG, cont.

Code as for Figure 13, page 208.

A. Per cent moss cover on *Chamaedaphne calyculata*.

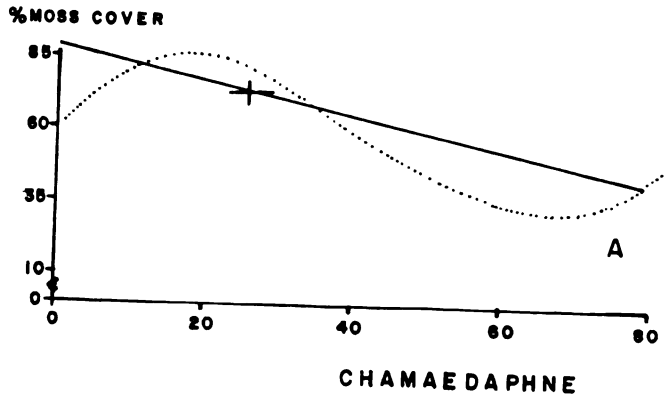
B. Per cent moss cover on litter thickness

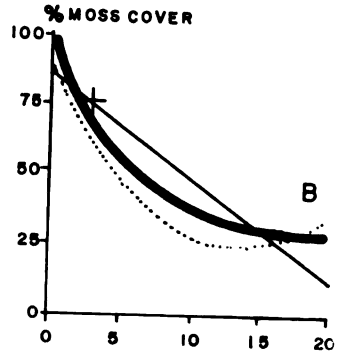
C. Per cent moss cover on A_{0L} thickness.

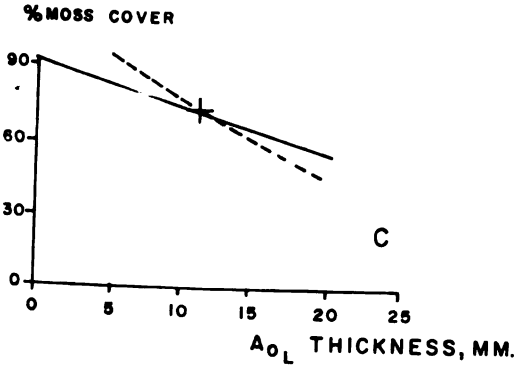
D. Per cent lichen cover on *Vaccinium boreale*.

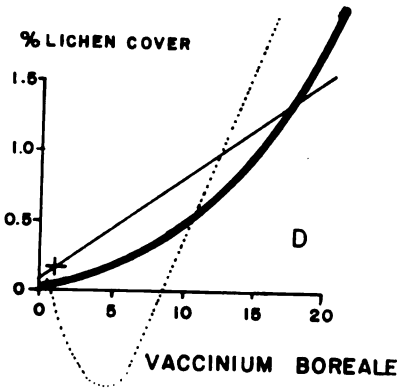
E. Per cent lichen cover on *Vaccinium oxycoccus*.

F. Per cent lichen cover on per cent herb cover.


%MOSS COVER
85
60
35
10
0
0
20
40
60
80
A
CHAMAEDAPHNE


%MOSS COVER
100
75
50
25
0
0
5
10
15
20
B
LITTER THICKNESS, MM.


%MOSS COVER
90
60
30
0
0
5
10
15
20
25
C
A_{0_L} THICKNESS, MM.


%LICHEN COVER
1.5
1.0
0.5
0
0
5
10
15
20
D
VACCINIUM BOREALE

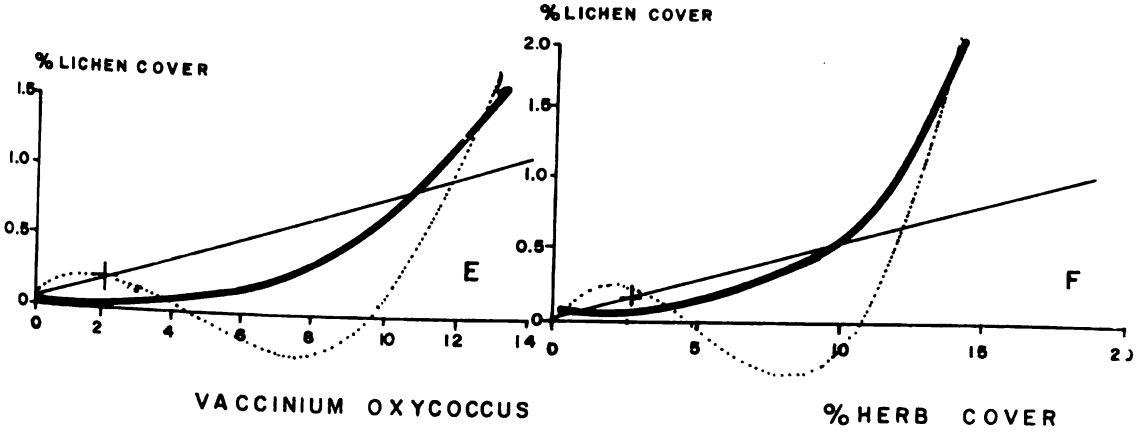

%LICHEN COVER
1.5
1.0
0.5
0
0
2
4
6
8
10
12
14
E
VACCINIUM OXYCOCCUS
%LICHEN COVER
2.0
1.5
1.0
0.5
0
0
5
10
15
20
F
%HERB COVER

FIGURE 16. Regression Curves, Segment DG, cont.

Code as for Figure 13, page 208.

A. Per cent lichen cover on per cent bare ground.

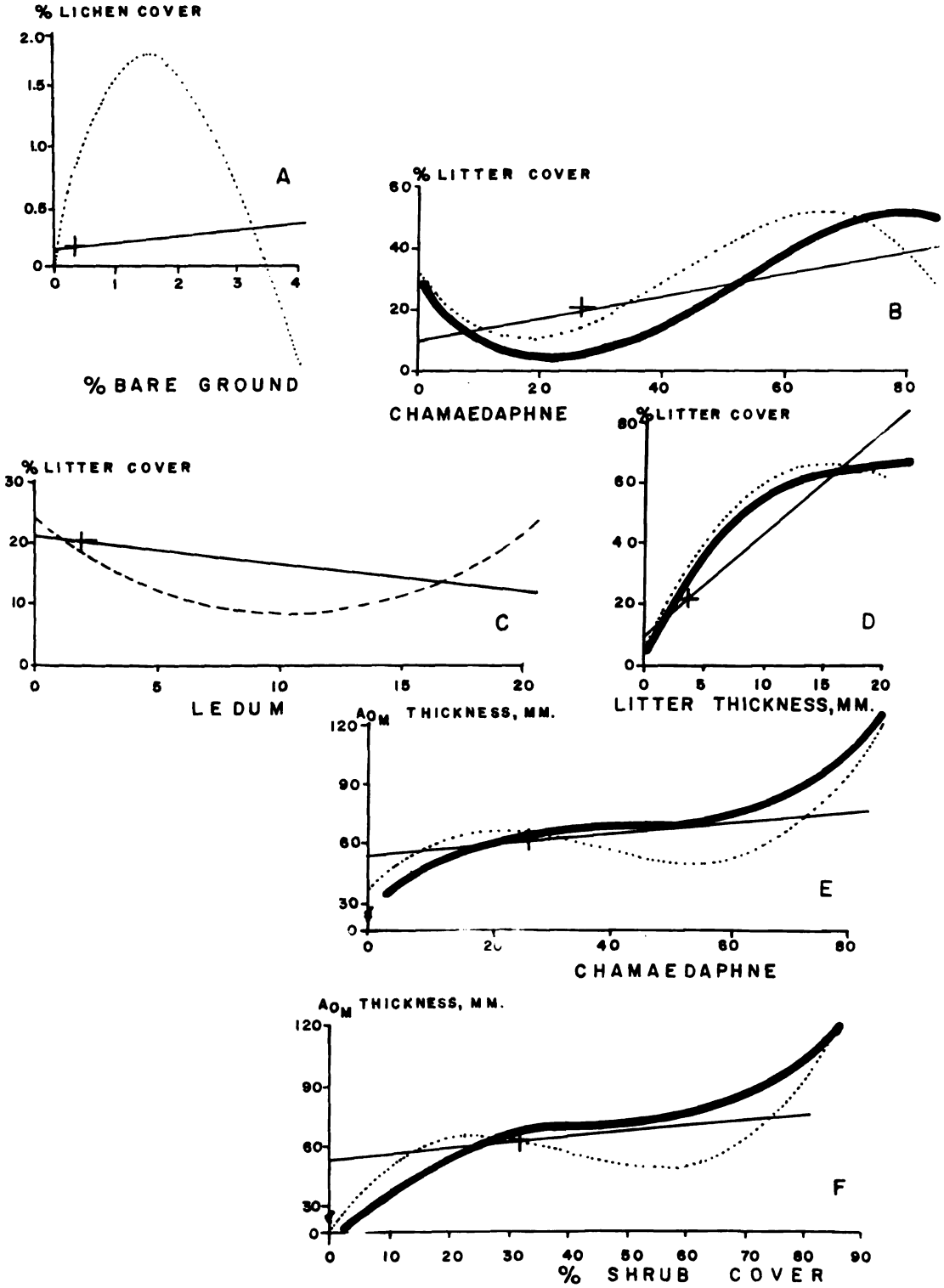
B. Per cent litter cover on Chamaedaphne calyculata.

C. Per cent litter cover on Ledum groenlandicum.

D. Per cent litter cover on litter thickness.

E. A_{OM} thickness on Chamaedaphne calyculata.

F. A_{OM} thickness on per cent shrub cover.


% LICHEN COVER
2.0
1.5
1.0
0.5
0
0 1 2 3 4
A
% BARE GROUND
% LITTER COVER
60
40
20
0
0 20 40 60 80
B
CHAMAEDAPHNE
% LITTER COVER
30
20
10
0
0 5 10 15 20
C
LE DU M
% LITTER COVER
80
60
40
20
0
0 5 10 15 20
D
LITTER THICKNESS, MM.
A_{0_M} THICKNESS, MM.
120
90
60
30
0
0 20 40 60 80
E
CHAMAEDAPHNE
A_{0_M} THICKNESS, MM.
120
90
60
30
0
0 10 20 30 40 50 60 70 80 90
F
% SHRUB COVER

CHAPTER VII

FIELD EXPERIMENTS

This phase of the study consists of two sets of experiments, one begun during the summer of 1960 and the other during the summer of 1961. Both were designed as tests of certain of the results of Byer (1960).

The earlier set consisted of transplants and seed plantings of some of the commoner species to all parts of the soil moisture gradient. The plots were kept free of natural plant encroachment during the course of subsequent observations. The species used were some which had showed relatively strong association patterns, and all but two were markedly restricted in nature to particular parts of the gradient. I felt that performance in the absence of natural interaction should yield clues to the causes of both macrodistributional (i.e. along the gradient) and microdistributional (i.e. association) patterns. The seed plantings were designed to demonstrate whether establishment (i.e. germination to maturation) was the same across the gradient as survivorship of transplanted, mature individuals.

The later set was designed to test whether interaction could account for the very strong correlations between certain pairs of species. Because of high transplant mortality, most experiments of this second set did not yield the hoped-for results, but survival and growth measurements from it were nonetheless useful in supplementing data from the earlier plots. Since the 1961 plots were located in a clearcut strip with or without artificial shade, it was possible to compare the performance of some species there and in the 1960 plots, which were located under the naturally-occurring tree cover.

A. METHODS. The same piece of land used for the 1958 sampling was employed. The dry to wet axis of the 100 meter long gradient was approximately North-South, the dry end to the North. The 1960 plots occupied the easternmost 15 X 100 meter strip, while the 1961 plots were located in the westernmost 30 X 100 meters. Both of these included all of the soil types encountered in 1958.

1960 Plots. For these experiments, the strip was divided lengthwise into ten 10 m X 15 m rectangles, so that there was a sequence of successively more poorly-drained blocks starting at the north end. The seven better-drained rectangles, representing the soil types Grayling through

Kinross sands, were located under a relatively open and uniform Pinus banksiana canopy. Data for relative light intensity from Byer (1960) however, show a steady rise from a mean of 12.6% of full sunlight intensity on well-drained Grayling sand through 33.4% on imperfectly-drained Au Gres sand (at noon on a late August day). This three-fold increase is no doubt due to an "edge effect", i.e. to infiltration of light from the nearly treeless bog to the south close to Au Gres. The difference is intensified by the fact that the open area is to the south and the slanting rays of the sun, coming from that direction at this latitude, can penetrate a considerable distance "up-gradient". This effect is reduced at midsummer but increased in the early spring (when most growth occurs) and late fall. On Saugatuck sand (about Block 7 from the north end) the next more poorly-drained soil adjacent to Au Gres, mean light intensity drops to 9.3% of full sunlight because of the heavy band of bog hingeline tree cover found there, but moving "down-gradient" to Kinross (Blocks 7 and 8) it rises to 76.3%. Although the latter segment contains much of the bog margin tree cover, the proximity of the open bog and the similar open character of the adjacent portions of Kinross itself apparently bring

about this relatively high figure. Bog intensity (Blocks 8-10) is 84.5% full sunlight. Thus, incident energy as well as drainage varied considerably across the gradient, as it did also locally within blocks due to the shadows cast by each tree.

The data from replicates from each rectangle or block were later treated as a unit. Ten randomly-located strip plots 15 m X 30 mm., with long axes perpendicular to the long axis of the 15 m X 100 m strip, were spaded up in each rectangle, turning the sod under and working it about with the spade until it could be manipulated easily with a rake.

In each spaded strip, there was room for 23 planting locations spaced 1/2 meter from one another. A strip 15 meters long can be marked off at 29 intervals of 1/2 m starting 1/2 m from one end, but in some strips as many as six such points were covered with tree bases or stumps. Each experiment was performed by locating one replicate at a randomly-chosen available position in each strip. Thus there were 10 replicates of each experiment in each rectangle, or ten groups of 10 total with each group representing a different "treatment".

Adults of 14 species and seeds of 9 species were

chosen for testing. The individuals to be transplanted were chosen from as restricted an area as possible, usually from what appeared to be a single clone, and as close as possible to that species' point of maximum cover along the gradient in order to increase the probability of selecting the "representative" ecotype. Individuals of as uniform a size and appearance as possible were afixed with randomly selected numbered tags, which made it possible to remove them and plant them in random order. The order in which the 100 positions in the rows were filled was also randomized, so that bias due both to selection of specimens and time of planting were minimized. Seeds, too, were always selected from as restricted an area as possible near the maximal cover of the species along the gradient. In these experiments also the positions were filled in random order. At each location, a given number of seeds or fruits, according to species, was chosen "blindly" from the container in order to eliminate unconcious bias as to seed color, size or appearance. Seeds or fruits were hand planted in "hills" like garden seeds. The area around each transplant or seed planting was weeded in the spring of each year during which readings were taken.

Survival of transplants or number of seedlings

present were recorded in Blocks 1-7 (numbering starting on the best drained segments or "dry end") in the spring and fall of 1961 and 1962 and in the spring of 1963. From the spring of 1962 onward, it was also noted whether the plants were flowering or fruiting. These data are presented in Table X (page 229). Since survival, flowering, and fruiting data had yielded almost no significant differences across the whole inorganic soil gradient by the spring of 1963, measurements were taken at that time of one or more parameters such as height, number of leaves, etc. of each transplanted species. One species grown from seeds was included; Toxicodendron radicans (L.) Kuntze, the only species studied not native to the 1958 sample area. It was planted in conjunction with the research of Mr. William T. Gillis of the Michigan State University Department of Botany and Plant Pathology, but was useful also in the present study. The characters measured for each species are listed and the results presented in Table XIII, page 242 , and in Figures 17-21 (pages 243-247).

Blocks 8-10, on the organic soil, were read at the same time and in the same fashion in the spring of 1961 and 1962. But the spaded peat had become compacted and settled about six inches below the overall bog surface, so

that in the fall of these years the strips on these blocks were flooded and impossible to read. In any case, it was evident after the spring of 1962 that all but a few individuals, all of species indiginous to the bog, had died in Blocks 8-10; accordingly they were abandoned.

1961 Plots. For the 1961 interaction experiments only the central 10 m. X 100 m. band of a 30 m. X 100 m. clearcut strip was used for planting, thus acheiving 10-meter-wide "buffer zones" on either side. This eliminated all natural shade during the growing season except for about one hour after sunrise and again before sunset, when only a small fraction of total daily incident energy falls on the earth's surface. The maximum variation in total insolation over the whole central strip, as checked by a foot candle meter, was less than 4%, so solar energy was presumably eliminated as a variable of any importance along with tree canopy-related differences in soil temperature, transpiration, rainwater reaching the surface and other factors.

This central 10 X 100 meter strip was divided into four segments by soil type according to a soil map plotted earlier (Byer 1960), transitional areas between them remaining unused. Experiments were located only on G, WC,

and AS. The plots for each experiment, 1/2 m. X 1/2 m. in size, were randomly located within the appropriate soil block. In some experiments, the plots were covered with saran plastic shade cloth, tacked to a frame above the plots.[8] The fabric used allowed light penetration of about 15% full sunlight, approximating the means found for the Jack pine forest in 1958 (Byer 1960). Each plot served as one replicate of an experiment.

These plots were not spaded, for it was desired to leave the soil as undisturbed as possible. Rather, the edges were cut down to a depth of about 25 cm. with a flat shovel, and then all visable plant parts carefully removed by hand in order to eliminate as much outside competition as possible while keeping the duff and humus layers fairly intact.

In planting, the model used by Sakai (1955) was utilized. The species whose performance was to be tested was located in the center of a plot, and it was surrounded in a hexagonal pattern by (A) six individuals of another species, (B) six of the same species, or (C) by nothing

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[8]Obtained from Lumite Division, Chicopee Manufacturing Corp., Cornelia, Ga. Fabric no. 1817-002.

(10 replicates of each treatment, 30 in all per experiment). (A) showed the reaction of the central plant to the proximity of a suspected interactant, as compared to the control (C). The (B) plots were designed to estimate how much of a reaction of the center plant might be attributable to intraespecific interaction, as compared to the interspecific interaction tested by the (A) plots. Surrounding plants were located 10 centimeters from the central individual and from each other. As in the case of the 1960 plots, plants were selected for uniformity of appearance and location, and the orders of planting and of filling spaces were randomized.

Survival was recorded for these plots in the fall of 1962 and the spring of 1963 (Table XIV, page 253). In the spring of 1963, the morphological features which were measured on the 1960 transplants were also measured on survivors in the interaction plots (Table XVI, page 259). The two species not included in the 1960 plots, Comptonia peregrina and Epigaea repens, did not survive in sufficient quantities to warrant such measurements.

Both survival readings and morphological parameter measurements were taken at times when mortality was not likely to be occurring, and after rapid spring growth had

ceased. Spot checks indicated that there was neither appreciable death nor appreciable growth during the several days required for the readings.

Analysis of Data. At the outset let us clarify a feature of the tables which could lead to confusion. If a transplanted individual in the 1960 plots gave evidence of life at any reading, and was definitely established as the specimen originally planted at that spot, it was counted as living for the reading in which it demonstrated life and for all previous readings (Table X, page 229). Individuals which were recorded as apparently dead in the spring following transplant (of which there were many) or even later (relatively few) sometimes gave rise to new shoots. Thus, this retroactive revision increased the accuracy of survival data, although undoubtedly a few short-term survivors escaped detection. The survival data for the 1961 plots were not summarized in this fashion, however, because I felt that the relatively short time elapsed did not permit the drawing of meaningful survival curves. Thus the figures in Table XIV (page 253) include only the number of individuals which appeared living at the time of the reading, not those demostrating life in any subsequent reading.

For the spring 1961 survival data from the 1960 plots, the data for Blocks 1 and 2 (dry end, Grayling sand) were treated as a unit, as were those for Blocks 6 and 7 (bog margin, Au Gres and Saugatuck sands) and Blocks 9 and 10 (bog, Dawson-Greenwood peat). Significance of difference in per cent survival between each pair of these units was determined by means of a chi-square test. For the seed plantings, differences between mean numbers of seedlings of each species per plot on Blocks 1-2 versus 6-7 were tested by calculating t-values. But here, fall 1961 data were used for all but Melampyrum lineare (Mel); the latter's spring 1961 data were used because this species is a winter germinating annual with a normally high mortality rate through the growing season (Cantlon and Curtis 1964). Since the seeds of many other species germinated during the 1961 summer and subsequent seedling mortality appeared relatively low, I felt that the fall readings would be more informative. Blocks 9-10 were not included in the germination calculations because here, in the bog, none of the planted seeds of any species germinated.

The significance tests were not repeated on data from later readings since there was little mortality any-

where on Blocks 1-7 (inorganic soil) after initial transplant loss. The number of seedlings did change appreciably from reading to reading but, with the exception of Toxicodendron, their proportions on different gradient segments apparently did not. Results of significance tests appear in Table XI (page 234).

For the measurements of morphological characters taken in the spring of 1963, the following comparisons were made by t-test: (1) for the 1960 plots, a comparison of Blocks 1-2 with Blocks 6-7, (2) a similar comparison between Blocks 1-2 and Block 7 alone (1 and 2, right-hand columns in Table XIII, page 242), (3) for the 1961 plots, comparisons between solitary central plants and those surrounded by individuals of the same or another species, for the only four experiments where survival was high enough to warrant it (Table XVII, page 264), (4) where the same interaction experiment was performed on two different soil types, differences between all plants (central and surrounders combined) on the two segments (Table XVI, page 259) and (5) differences between sun-grown and shade-grown plants (regardless of other treatment or position) of the one species (Vaccinium angustifolium var. nigrum) which was grown under both conditions, (Table XV, page 257).

In number (4) above, the comparisons should be valid because both soil types contain about the same proportions of individuals planted during any particular time interval. But the entire sets of sun-grown and shade-grown blueberries, number (5), were planted at different times, and while the former contains some central plants the latter does not. But all blueberries were planted within the same 4-day period about a month before first frost, and were thoroughly watered immediately after planting, then every three or four days (except when soaking rain made it unnecessary) for the next two weeks. Thus differences in dessication or recovery time before frost were not very great, and should have affected the results but little.

B. 1960 PLOTS: SURVIVAL, FLOWERING AND FRUITING. Data summaries for the different readings are given in Table X (page 229). In addition, the final (spring 1963) survival readings are graphed (solid lines) in Figures 17-21 (pages 244-248). Tests of significance of differences in survival and germination on different segments, based upon the 1961 data are given in Table XI (page 234). (Since the transplant survival data after 1961 show no more than what could easily be accidental changes, they are not

included here).

We see from Figures 17-21 that on the whole, transplant survival is not markedly different across the portion of the gradient on mineral soil, Blocks 1-7. The tests for significance (Table XI, page 234) show that only one of 14 species, Vaccinium angustifolium var. nigrum (Vig), has significantly different survival rates ($P < .05$) in Blocks 1-2 and 6-7. Out of 14 sets of data one would show differences significant at this level more often than not, even though the fluctuations were merely random, thus V. angustifolium var. nigrum's case is most probably a fluke. In fact, subsequent readings (Table X) revealed that most of the plants of this species apparently dead on Block 6-7 in 1961 were, in fact, alive, and the most recent reading shows equal numbers of living plants of this species on both blocks! Moreover, mortality since the initial transplant loss in Blocks 1-7 has been minimal. So it appears that most of the species tested, whose cover optima ranged from G to DG, have fairly uniform survival potential as adults in cultivated plots all the way across the non-organic soils of the soil moisture gradient. A comparison between either of the aforementioned blocks and Block 9-10, however, reveals much higher survival in the

"dry end" and "bog margin" blocks, most of the differences being significant at high levels (for 20 out of 28 $P < .001$). This merely confirms the obviously less favorable conditions for survival in the standing water in the spaded rows of the bog segments.

The results certainly do not mirror distributions observed in the 1958 study. Two Vaccinium taxa, which in nature are ubiquitous with high frequencies across the whole range of inorganic soil types and occur sporadically in the bog, reflect this in their transplant survival curves (Vig, Vvp, Figures 21 A, 21 B, page 248). But V. myrtilloides (Vam), in this study area a species of the bog margin exclusively, has a similar curve (Figure 20 C, page 247). Though it was not found at all in the bog proper in the 1958 study, it has a higher survival rate here than either of its gradient-spanning genus-fellows, and is, in fact, one of the few species showing no significant differences between Blocks 1-2 or 6-7 and Blocks 9-10. Chamaedaphne calyculata (Chm), a species naturally restricted to the bog, has a high survival rate there, but also survives at a rate not significantly different clear up to the excessively well drained Grayling sand. Another exclusively bog and bog margin species, Ledum groenlandicum

(Led) has high survival on the inorganic soil but extremely low survival in the bog, just the opposite of its natural distribution pattern. This low bog survival, suggesting flooding intolerance, may be reflected in Ledum's natural tendency to be concentrated on higher hummocks than is Chamaedaphne. Yet some of the most xerophytic species such as Danthonia spicata (Dan) and Carex pensylvanica (Car) have higher bog survival rates over the first fall, winter, and early spring than does Ledum. In general, in fact, the xerophytes were more tolerant of these extreme conditions than some slightly more mesophytic species (Pteridium aquilinum (Ptr), Gaultheria procumbens (Gau)), while three of four bog margin species (Coptis groenlandica (Cop), Cornus canadensis (Cor) and Rubus hispidus var. obovalis (Rho), the exception being Vaccinium myrtilloides discussed above) appeared to be the least tolerant of all.

Mere short-term tolerance ranges of mature plants to soil drainage, available nutrients, or other gradient-related environmental variables then, do not seem to be the primary factors responsible for the observed natural distribution of these species along the gradient. It could be that the block of native soil approximately 10 cm X 10 cm inserted with each transplanted individual has kept it a-

live. Yet there has been only token mortality since the first winter, and there should have been a second wave of mortality signaling exhaustion of this soil if this had been the case. Possibly such exhaustion had not occurred by the last reading. Probably, though, the species tested are prevented in nature from expanding up and down the gradient to the limits of their tolerance to the physical environment by various interactions with other species. The relative efficiency of species in occupying available niches surely changes along the gradient in response to physical factors, but such changes seem not to show up strongly under the relatively stress-free conditions of the cultivated strips. Failure of ecesis on certain soils, discussed in the following section, may be another natural distribution-limiting factor.

Flowering and fruiting (Figures in parentheses, Table X, page 229) were nowhere common enough for the testing of significance between segments. In most cases, in fact, they revealed or suggested nothing of the reasons for the natural distributions across the gradient which were found, for on the basis of limited data, margin-restricted and even bog species seemed to flower as well on the best-drained segment as elsewhere, while species na-

TABLE X

1960 plots; survival, flowering and fruiting. The non-parenthetical numbers under columns S 61 (spring 1961), F 62 (fall 1962), etc., indicate the numbers of survivors (out of 10 planted) in the corresponding blocks at the times indicated; the parenthetical numbers show the number flowering (first number) and fruiting (second number) at these times. The columns headed "M" show mortality between the two periods surrounding them (tplt. M = transplant mortality).

Block	tplt. M	S 61	M	F 61	M	S 62	M	F 62	M	S 63
					Carex pensylvanica					
1	0	10	0	10	1	9(0, 2)	0	9	0	9(0, 3)
2	0	10	0	10	0	10(0, 0)	0	10	0	10(0, 1)
3	0	10	0	10	0	10(0, 0)	2	8	0	8(0, 0)
4	0	10	1	9	1	8(0, 0)	1	7	0	7(0, 1)
5	0	10	0	10	0	10(0, 0)	1	9	0	9(0, 0)
6	0	10	0	10	0	10(0, 0)	1	9	0	9(0, 1)
7	0	10	0	10	0	10(0, 0)	0	10	0	10(0, 2)
1-7	0	70	1	69	2	67(0, 2)	5	62	0	62(0, 8)
8	8	2	1			1				
9	10	0	0			0				
10	10	0	0			0				
8-10	28	2	1			1(0, 0)				
					Chamaedaphne calyculata					
1	1	9	1	8	2	6	0	6	0	6
2	3	7	0	7	0	7	0	7	0	7
3	1	9	2	7	0	7	0	7	1	6
4	2	8	0	8	0	8	0	8	0	8
5	0	10	0	10	0	10	1	9	0	9
6	1	9	1	8	0	8	1	7	0	7
7	0	10	0	10	0	10	0	10	0	10
1-7	8	62	4	58	2	56	2	54	1	53
8	2	8	4			4				
9	4	6	5			1				
10	2	8	6			2				
8-10	8	22	15			7				

Table X, continued

Block	tplt. S M	61	M	F 61	M	S 62	M	F 62	M	S 63
						Coptis groenlandica				
1	0	10	0	10	0	10 (0, 1)	1	9 (0, 1)	0	9 (0, 2)
2	0	10	0	10	0	10 (0, 0)	0	10 (0, 0)	1	9 (0, 2)
3	0	10	0	10	1	9 (0, 0)	0	9 (0, 0)	0	9 (0, 4)
4	0	10	0	10	1	9 (0, 0)	0	9 (0, 0)	0	9 (0, 2)
5	0	10	0	10	0	10 (0, 0)	0	10 (0, 0)	0	10 (0, 0)
6	0	10	0	10	0	10 (0, 0)	0	10 (0, 0)	0	10 (0, 0)
7	0	10	0	10	0	10 (0, 0)	0	10 (0, 0)	0	10 (0, 1)
1-7	0	70	0	70	2	68 (0, 1)	1	67 (0, 1)	1	66 (0, 11)
8	9	1	0			1				
9	10	0	0			0				
10	9	1	1			0				
8-10	28	2	1			1 (0, 0)				
						Cornus canadensis				
1	2	8	1	7	1	6	0	6	1	5 (0, 0)
2	2	8	1	7	2	5	0	5	0	5 (0, 0)
3	1	9	1	8	1	7	1	6	1	5 (0, 0)
4	3	7	1	6	1	5	2	3	0	3 (0, 0)
5	2	8	2	6	0	6	2	4	0	4 (1, 0)
6	3	7	2	5	0	5	0	5	1	4 (1, 0)
7	2	8	0	8	1	7	1	6	0	6 (0, 0)
1-7	15	55	8	47	6	41 (0, 0)	6	35 (0, 0)	3	32 (2, 0)
8	9	1	1			0				
9	10	0	0			0				
10	10	0	0			0				
8-10	29	1	0			0 (0, 0)				
						Danthonia spicata				
1	0	10	0	10	0	10 (9, 0)	0	10 (0, 8)	0	10 (0, 0)
2	0	10	0	10	0	10 (9, 0)	0	10 (0, 10)	1	9 (1, 0)
3	0	10	0	10	1	9 (5, 0)	1	8 (0, 7)	1	7 (0, 0)
4	0	10	0	10	1	9 (5, 0)	0	9 (0, 9)	0	9 (0, 0)
5	0	10	0	10	0	10 (9, 0)	0	10 (0, 10)	0	10 (0, 0)
6	0	10	0	10	0	10 (8, 0)	0	10 (0, 9)	0	10 (0, 0)
7	1	9	0	9	1	8 (8, 0)	0	8 (0, 6)	0	8 (2, 0)
1-7	1	69	0	69	3	66 (53, 0)	1	65 (0, 59)	2	63 (3, 0)
8	5	5	4			1				
9	7	3	3			0				
10	6	4	4			0				
8-10	18	12	11			1 (0, 0)				

Table X, continued

Block	tplt. M	S 61	M	F 61	M	S 62	M	F 62	M	S 63
						Gaultheria procumbens*				
1	0	10	0	10	1	9 (2, 0)	1	8 (0, 1)	0	8
2	0	10	0	10	1	9 (1, 0)	1	8 (0, 0)	0	8
3	0	10	0	10	0	10 (0, 0)	2	8 (0, 0)	3	5
4	0	10	0	10	1	9 (0, 0)	1	8 (0, 0)	0	8
5	0	10	0	10	0	10 (0, 0)	0	10 (0, 0)	3	7
6	0	10	0	10	1	9 (0, 0)	0	9 (0, 0)	0	9
7	0	10	1	9	0	9 (0, 0)	0	9 (0, 0)	1	8
1-7	0	70	1	69	4	65 (3, 0)	5	60 (0, 1)	7	53 (0, 0)
8			9			1				
9			9			1				
10			10			0				
8-10			28			2 (0, 0)				
						Ledum groenlandicum				
1	1	9	0	9	0	9 (1, 0)	0	9 (0, 1)	1	8
2	1	9	0	9	2	7 (0, 0)	1	6 (0, 0)	0	6
3	1	9	0	9	1	8 (0, 0)	0	8 (0, 0)	1	7
4	0	10	0	10	0	10 (0, 0)	0	10 (0, 0)	0	10
5	4	6	0	6	0	6 (0, 0)	0	6 (0, 0)	0	6
6	3	7	0	7	1	6 (0, 0)	1	5 (0, 0)	0	5
7	1	9	1	8	0	8 (0, 0)	0	8 (0, 0)	0	8
1-7	11	59	1	58	4	54 (1, 0)	2	52 (0, 1)	2	50 (0, 0)
8	10	0	0			0				
9	9	1	1			0				
10	9	1	1			0				
8-10	28	2	2			0 (0, 0)				
						Maianthemum canadense				
1	0	10	1	9	2	7	0	7	0	7 (0, 0)
2	0	10	1	9	1	8	0	8	1	7 (0, 0)
3	1	9	0	9	0	9	0	9	0	9 (0, 0)
4	0	10	0	10	0	10	0	10	0	10 (1, 0)
5	0	10	1	9	0	9	0	9	0	9 (2, 0)
6	0	10	0	10	1	9	0	9	1	8 (0, 0)
7	1	9	0	9	1	8	0	8	0	8 (0, 0
1-7	2	68	3	65	5	60 (0, 0)	0	60 (0, 0)	2	58 (3, 0)
8	5	5	5			0				
9	7	3	3			0				
10	9	1	1			0				
8-10	21	9	9			0 (0, 0)				

*First reading on segments 8-10 in the spring of 1962.

Table X, continued

Block	tplt. M	S 61	M	F 61	M	S 62	M	F 62	M	S 63
Oryzopsis asperifolia										
1	0	10	0	10	0	10 (0, 0)	0	10	0	10 (0, 0)
2	0	10	0	10	0	10 (0, 1)	0	10	0	10 (0, 2)
3	0	10	0	10	0	10 (0, 0)	0	10	0	10 (0, 1)
4	0	10	0	10	0	10 (0, 0)	0	10	0	10 (0, 1)
5	0	10	0	10	0	10 (0, 0)	0	10	0	10 (0, 0)
6	0	10	0	10	1	9 (0, 0)	0	9	0	9 (0, 3)
7	0	10	0	10	1	9 (0, 0)	0	9	1	8 (0, 0
1-7	0	70	0	70	2	68 (0, 1)	0	68 (0. 0)	1	67 (0, 7)
8	8	2	2			0				
9	10	0	0			0				
10	10	0	0			0				
8-10	28	2	2			0 (0, 0)				
Pteridium aquilinum										
1	1	9	0	9	4	5	0	5	0	5
2	0	10	0	10	0	10	3	7	4	3
3	0	10	0	10	2	8	0	8	1	7
4	0	10	0	10	4	6	0	6	2	4
5	1	9	0	9	1	8	0	8	1	7
6	3	7	0	7	1	6	0	6	4	2
7	1	9	0	9	2	7	0	7	1	6
1-7	6	64	0	64	14	50	3	47	13	34
8	10	0	0			0				
9	10	0	0			0				
10	10	0	0			0				
8-10	10	0	0			0				
Rubus hispidus var. obovalis										
1	0	10	0	10	0	10	1	9	0	9 (1, 0)
2	2	8	0	8	0	8	1	7	1	6 (2, 0)
3	0	10	0	10	0	10	0	10	0	10 (3, 0)
4	0	10	0	10	1	9	0	9	0	9 (2, 0)
5	1	9	0	9	0	9	0	9	0	9 (2, 0)
6	0	10	0	10	1	9	0	9	0	9 (4, 0)
7	0	10	0	10	0	10	0	10	1	9 (6, 0)
1-7	3	67	0	67	2	65 (0, 0)	2	63 (0, 0)	2	61 (20, 0)
8	8	2	1			1				
9	10	0	0			0				
10	10	0	0			0				
8-10	28	2	1			1 (0, 0)				

Table X, continued

Block	tplt. M	S 61	M	F 61	M	S 62	M	F 62	M	S 63
Vaccinium myrtilloides										
1	2	8	0	8	0	8	1	7	0	7 (0, 0)
2	0	10	0	10	0	10	0	10	0	10 (0, 0)
3	1	9	0	9	1	8	0	8	0	8 (0, 0)
4	0	10	0	10	0	10	1	9	1	8 (0, 2)
5	1	9	0	9	1	8	0	8	0	8 (0, 0)
6	1	9	0	9	0	9	0	9	0	9 (0, 0)
7	1	9	0	9	1	8	0	8	0	8 (0, 1)
1-7	6	64	0	64	3	61 (0, 0)	2	59 (0, 0)	1	58 (0, 3)
8	6	4	4			0				
9	5	5	5			0				
10	7	3	3			0				
8-10	18	12	12			0 (0, 0)				
Vaccinium angustifolium var. nigrum										
1	2	8	0	8	0	8	0	8	0	8 (0, 0)
2	0	10	0	10	0	10	1	9	0	9 (0, 0)
3	2	8	0	8	0	8	0	8	0	8 (0, 0)
4	0	10	0	10	1	9	0	9	0	9 (0, 0)
5	0	10	0	10	0	10	0	10	0	10 (0, 1)
6	0	10	1	9	0	9	0	9	0	9 (0, 1)
7	0	10	1	9	0	9	1	8	0	8 (0, 0)
1-7	4	66	2	64	1	63 (0, 0)	2	61 (0, 0)	0	61 (0, 2)
8	9	1	1			0				
9	7	3	3			0				
10	9	1	1			0				
8-10	25	5	5			0 (0, 0)				
Vaccinium boreale										
1	0	10	0	10	1	9	1	8	2	6
2	0	10	0	10	0	10	0	10	1	9
3	0	10	0	10	1	9	1	8	2	6
4	2	8	0	8	0	8	0	8	1	7
5	0	10	1	9	0	9	0	9	0	9
6	2	8	1	7	0	7	0	7	1	6
7	0	10	0	10	0	10	2	8	0	8
1-7	4	66	2	64	2	62 (0, 0)	4	58 (0, 0)	7	51 (0, 0)
8	6	4	4			0				
9	5	5	5			0				
10	9	1	1			0				
8-10	20	10	10			0 (0, 0)				

TABLE XI

1960 transplant plots. Significance of differences between gradient segments, 1961 data. A dash (—) indicates absence of significance ($P > 0.05$).

A. CHI-SQUARE TESTS OF DIFFERENCES BETWEEN BLOCKS 1-2 (DRY END), 6-7 (BOG MARGIN) AND 9-10 (BOG), SURVIVAL.

Species*	Segments compared					
	1-2 vs 6-7		1-2 vs 9-10		6-7 vs 9-10	
	chi sq.	P<	chi sq.	P<	chi sq.	P<
CAR	0.00	—	36.10	0.001	36.10	0.001
CHM	2.29	—	0.00	—	1.40	—
COP	1.44	—	22.72	0.001	32 48	0.001
COR	0.00	—	16.41	0.001	18.57	0.001
DAN	0.00	—	16.41	0.001	13.29	0.001
GAU	0.91	—	0.52	—	0.91	—
LED	0.00	—	10.66	0.005	12.60	0.001
MAI	0.00	—	14.43	0.001	12.10	0.001
ORS	0.00	—	36.10	0.001	36.10	0.001
PTR	0.00	—	10.80	0.001	6.23	0.02
RHO	1.20	—	16.41	0.001	26.18	0.001
VAM	0.98	—	0.40	—	3.68	—
VIG	3.90	0.05	6.54	0.02	20.05	0.001
VYP	0.01	—	8.18	0.005	8.18	0.005

B. T-TESTS OF DIFFERENCES IN NUMBERS OF SEEDLINGS BETWEEN BLOCKS 1-2 AND 6-7.

Species*	t	P<	Species*	t	P<
CHM	2.000	—	TOX	2.154	—
COR	3.662	0.001	VAM	0.137	—
DAN	2.599	0.01	VIG	1.796	—
LED	0.000	—	VYP	0.000	—
MEL	0.271	—			

* Index to species abbreviation symbols in Appendix B.

tive to that segment showed no decrease in flowering on the margin. In only one or two cases, mentioned later where appropriate, were these data useful in interpreting the behavior of a species in nature.

C. 1960 PLOTS: SEED GERMINATION AND SEEDLING SURVIVAL. The results presented in Table XII (page 234) indicate that there was no apparent germination of any species in Blocks 8 through 10, in the bog. This is understandable, for the periodically flooded rows were probably not conclusive either to germination on seedling survival, even for normal bog species. These blocks were therefore of no use in analyzing natural distributions of species.

With the two bog species, Ledum groendandicum (Led) and Chamaedaphne calyculata (Chm), results do suggest that inability to germinate everywhere may impose a major restriction upon their gradient distribution. Ledum possibly produced seedlings (not confirmed) in strips 68 and 70 of block 7 only, while Chamaedaphne seedlings appeared in strips 69 and 70. These locations are on the Saugatuck soil type, very close to the bog hingeline. One of the locations is mossy (Polytrichum) and in all four moisture can be squeezed from the humus with the fingers during much

of the growing season. Thus all of them approximate the conditions upon which the seeds probably germinate in the natural course of events, on moist bog surface, probably on Sphagnum. The difference of Chamaedaphne's seedling number on Block 6-7 from total absence on Block 1-2 was not quite significant at the 5% level (Table XI, bottom), but this species continued to produce new seedlings in the bog margin locations every year up to the last reading (Table XII). The possible Ledum seedlings, on the other hand, did not appear until 1963.

In one other species, Cornus canadensis (Cor), special requirements for germination are by contrast evidently not responsible for the species' limited distribution. In fact in 1961, six seedlings were present in the most xeric Blocks 1-2, far removed from the species' normal habitat, and none in Blocks 6-7, where lush Cornus is ubiquitous between the planted strips. This difference was significant at $P < .001$, but since the time of this reading, as we see from Table XII, seedlings have appeared all over the inorganic gradient. It is questionable whether Cornus can really germinate more quickly on dry, sandy soil, as suggested by the earlier results, but at the least it is not prevented from germinating at all there. The

other bog margin-restricted species tested, Vaccinium myrtilloides (Vam), also continued to germinate across the whole gradient.

By the fall of 1961 fewer seeds of Danthonia spicata (Dan) had germinated in Blocks 1-2, on this species' native soil, than in much more poorly-drained Blocks 6-7, near its range margin (difference significant at $P < .01$, Table XI). This might suggest that Danthonia germinates best on fairly moist soil in the absence of competition from the lush vegetation of AS, but a glance at Table XII shows that in the spring of the same year the situation was reversed, and at the time of the last reading the differences had leveled off. With the other five taxa tested, germination was fairly uniform throughout Blocks 1-7.

With the three Vaccinium taxa (Vam, Vig and Vyp), seedling numbers seemed to reach a peak in the fall of 1961 and then decrease to only a few scattered individuals, but with no appreciable differences between segments, which in the case of the broad ranging V. angustifolium var. nigrum and V. boreale is not surprising. But Toxicodendron radicans (Tox) whose seeds continued to germinate throughout the period of the readings, shows increasingly lower

TABLE XII

1960 plots. Numbers of living seedlings present at each reading. "S 61" indicates spring reading, 1961, "F 62" indicates fall reading, 1962, etc.

Block	S 61	F 61	S 62	F 62	S 63	S 61	F 61	S 62	F 62	S 63	S 61	F 61	S 62	F 62	S 63
	Chamaedaphne calyculata					Cornus canadensis					Danthonia spicata				
1	0	0	0	0	0	0	3	1	0	0	24	31	15	16	15
2	0	0	0	0	0	0	4	4	3	5	25	33	14	17	18
3	0	0	0	0	0	0	1	0	0	1	10	16	12	13	16
4	0	0	0	0	0	0	1	0	0	0	24	24	12	31	23
5	0	0	0	0	0	0	3	1	2	2	26	23	11	13	12
6	0	0	0	0	0	0	0	0	0	0	38	21	9	13	12
7	0	4	14	13	20	0	0	0	0	1	22	27	12	22	18
tot	0	4	14	13	20	0	12	6	5	9	169	175	85	125	114
	Ledum groenlandicum					Melampyrum lineare					Toxicodendron radicans				
1	0	0	0	0	0	6	—	—	—	—	13	12	13	9	7
2	0	0	0	0	0	11	—	—	—	—	9	5	10	9	7
3	0	0	0	0	0	6	—	—	—	—	4	7	10	9	9
4	0	0	0	0	0	12	—	—	—	—	10	9	12	9	7
5	0	0	0	0	0	6	—	—	—	—	7	4	11	9	8
6	0	0	0	0	0	6	—	—	—	—	9	5	5	3	3
7	0	0	0	0	6	10	—	—	—	—	7	8	7	7	3
tot	0	0	0	0	6	57	—	—	—	—	59	50	68	55	44
	Vaccinium myrtilloides					Vaccinium angustifolium var. nigrum					Vaccinium boreale				
1	0	2	1	0	0	7	6	2	0	0	0	8	0	0	0
2	2	19	6	0	1	3	6	1	0	2	1	4	1	1	1
3	4	4	1	0	0	3	6	1	1	1	4	4	0	0	3
4	2	8	5	0	14+	7	18	4	1	4	1	3	2	0	1
5	3	6	1	0	10+	3	5	1	1	1	5	3	0	1	0
6	5	8	2	0	0	1	13	2	0	0	4	7	0	0	3
7	5	12	0	0	3	1	6	1	0	2	2	5	0	3	4
tot	21	59	16	0	28+	25	60	12	3	10	17	34	3	5	12

figures on the more poorly drained Blocks 6-7 from the first reading on, until in the final reading fourteen plants on 1-2 contrast with only six on 6-7. The random probability of a difference in the mean numbers per plot as great is slightly below 0.05. A check of the raw data shows that both delayed germination and survival were lower on the latter block. There is nothing in Toxicodendron's native habitats to suggest why, for in those few Pinus banksiana stands where it is present this species occurs only on the imperfectly to poorly-drained soils.

D. 1960 PLOTS: MORPHOLOGICAL MEASUREMENTS. The results are presented in Table XIII (page 242) and Figures 17-21, (pages 244-248).

The number of significant differences between the means of the characters measured on Block 1-2 and Block 6-7 significant at the $P < .05$ level or higher is only about what one would expect of randomly fluctuating variables. However, if we include the $P < .1$ level, about 21% of the differences have a random probability lower than this, about twice the proportion which we would encounter if in fact no real differences existed. Such measurements may, therefore, be somewhat more valuable indicators of diffential vigor, in cultivated plots such as these, than sur-

vival alone.

All of the criteria used were intended to reflect rapidity of growth and hence size of the photosynthetic surface, from which we may in some measure infer relative suitability of different physical environments along the gradient for a species. In areas where such measurements yield relatively low values in the cultivated plots, one might suspect the species of lower competitive ability in the adjacent natural habitat than in areas where the values are high. But it cannot be assumed, nor do the results indicate, that vigor as estimated from these measured values will predict natural distributions across the gradient. Ability to germinate, distribution of disseminating agents and other factors will enter the picture. In addition, relative competitive ability in an area itself depends not only upon reactions to physical factors, but also upon interactions with soil microbiota and other naturally-occurring species, some of which may enhance growth.

Among those differences which are significant, some do nonetheless reflect the natural gradient distribution of the species, suggesting reaction of adults to abiotic factors such as soil moisture or organic matter as at least major influences in this distribution. For in-

stance, mean clump size of Carex pensylvanica (Car) is smaller on the bog margin where cover of this species naturally begins to diminish rapidly (Figure 17 A, page 244). Similarly, the largest shoots of Cornus canadensis (Cor) reach maximum size on Blocks 6 and 7 where this species "peaks" (Figure 18 A, page 245). The bog margin blueberry, Vaccinium myrtilloides (Vam) also produces its longest shoots in the same area (Figure 20 C, page 247). On the other hand, the bog margin Coptis groenlandica (Cop) actually produces broader (though slightly fewer) leaves on the "dry end", so that with this species drought-related low vigor would not seem to be a cause of its exclusion from Grayling sand (Figure 19 B, page 246).

There is a general trend, evident from Figures 17-21 for values of all morphological characters to be lower on Blocks 2 and 3 than on the adjacent blocks on either side. The cause of this may be relatively heavy tree shade on these segments supressing growth, although shade actually causes greater shoot elongation and leaf expansion of most plants.

E. INTERACTION PLOTS: SURVIVAL AND GROWTH MEASUREMENTS. These results (Tables XIV for survival, page 253, and XVI for growth measurements, page 259) reveal few

TABLE XIII

1960 plots. Differences in growth measurements between dry end and bog margin, t-test. Linear measurements are in millimeters unless otherwise indicated.

Species	Character	Mean on blocks			Significance	
		1-2	7	6-7	1-2 vs 7 P< *	1-2 vs 6-7 P< *
Carex pensylvanica	bdth. clump	79.5	57.5	61.1	0.1	0.1
Chamaedaphne calyculata	no. of branches	8.2	9.1	7.4	—	-
	longest branch	114	111	114	—	
	avg. of all branches	77	82	75	—	—
Coptis groenlandica	no. of leaves	12.0	13.6	13.1	—	—
	bdth. largest lf.	33.8	26.1	28.1	0.1	0.1
Cornus canadensis	no. shoots	7.6	9.3	8.8	—	—
	bdth. broadest shoot	55.5	66.8	71 0	0.1	0.02
Danthonia spicata	bdth. clump	85 2	72.8	68.4	—	—
Gaultheria procumb.	no. of shoots	4.9	4.1	4.0	—	-
	hgt. lngst. sht.	34.2	39.8	33.4	—	—
	no of leaves, longest shoot	3.8	3.4	3.5	—	—

*A dash (—) indicates P > 0. 1.

Table XIII cont.

Species	Character	Mean on blocks			Significance 1-2 vs 7	Significance 1-2 vs 6-7
		1-2	7	6-7	P< *	P< *
Ledum groenlandicum	no. branches	5.6	7.1	6.2	–	–
	lngst. branches	69.1	63.0	64.5	–	–
	avg. of all branches	43.1	45.4	45.1	–	–
Maianthemum canadensis	no. shoots	3.9	8.0	6.8	0.05	0.1
	bdth. lngst. leaf	49.4	39.1	43.5	0.1	–
Oryzopsis asperifolia	no. of leaves	31.1	27.3	22.9	–	–
Pteridium aquilinum	no. of fronds	1.6	1.0	1.4	–	–
	lgth. lngst. frond	272	294	358	–	–
	bdth. " "	242	219	258	–	–
Rubus hispidus var. obovalis	no. of leaves	36.3	44.0	37.8	--	–
Toxicodendron radicans	hgt. plant	68.8	41.0	38.1	–	--
	no. of leaves	3.1	2.0	2.1	-	–
Vaccinium myrtilloides	no. of branches	19.1	21.9	18.2	–	–
	lngst. branch	58.7	87.1	74.0	0.1	--
Vaccinium ang. var. nigrum	no. of branches	28.5	34.1	31.8	--	
	lngst. branch	57.6	85.9	94.4	0.1	0.01
Vaccinium boreale	no. of branches	24.9	23.6	23.6	–	–
	lngst. branch	92.4	102.0	92.3	–	–

*A dash (–) indicates P > 0.1.

FIGURE 17. Survival and Growth, 1960 Plots

Code as indicated above the vertical axes. Block numbers along the horizontal axes.

A. Carex pensylvanica

B. Chamaedaphne calyculata

C. Coptis groenlandica

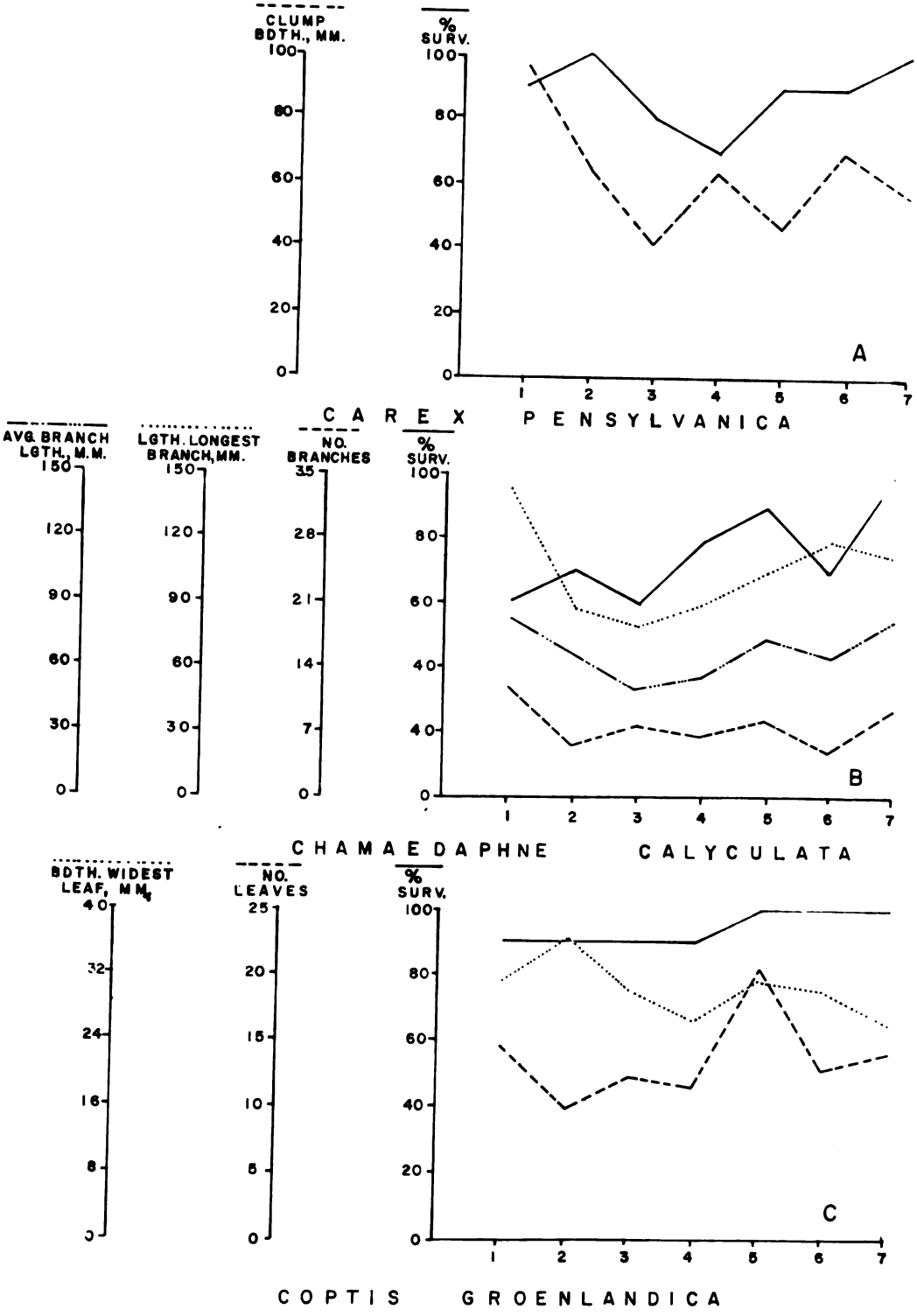

CLUMP BDTH., MM.
100
80
60
40
20
0
% SURV.
100
80
60
40
20
0
1 2 3 4 5 6 7
A
CAREX PENSYLVANICA
AVG. BRANCH LGTH., M.M.
150
120
90
60
30
0
LGTH. LONGEST BRANCH, MM.
150
120
90
60
30
0
NO. BRANCHES
35
28
21
14
7
0
% SURV.
100
80
60
40
40
0
1 2 3 4 5 6 7
B
CHAMAEDAPHNE CALYCULATA
BDTH. WIDEST LEAF, MM.
40
32
24
16
8
0
NO. LEAVES
25
20
15
10
5
0
% SURV.
100
80
60
40
20
0
1 2 3 4 5 6 7
C
COPTIS GROENLANDICA

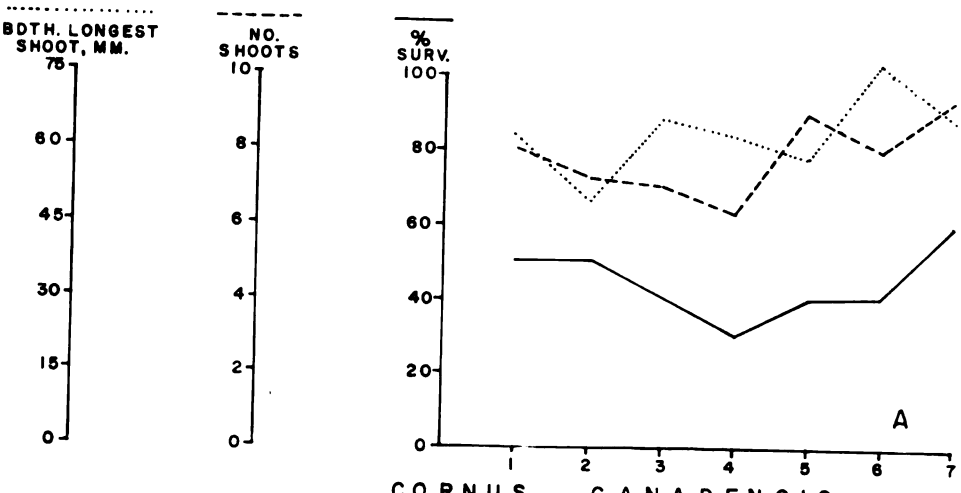
FIGURE 18. Survival and Growth, 1960 Plots, cont.

Code as indicated above the vertical axes. Block numbers along the horizontal axes.

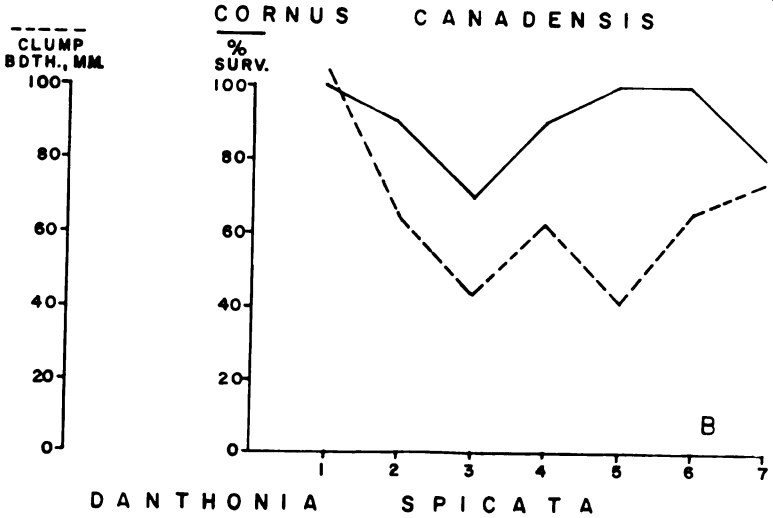
A. Cornus canadensis

B. Danthonia spicata

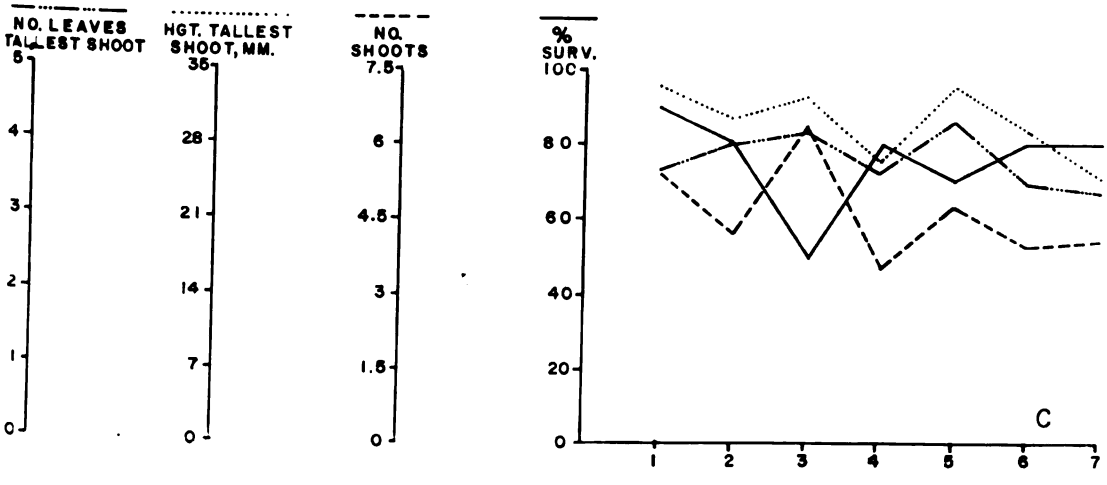
C. Gaultheria procumbens



CORNUS CANADENSIS



DANTHONIA SPICATA



GAULTHERIA PROCUMBENS

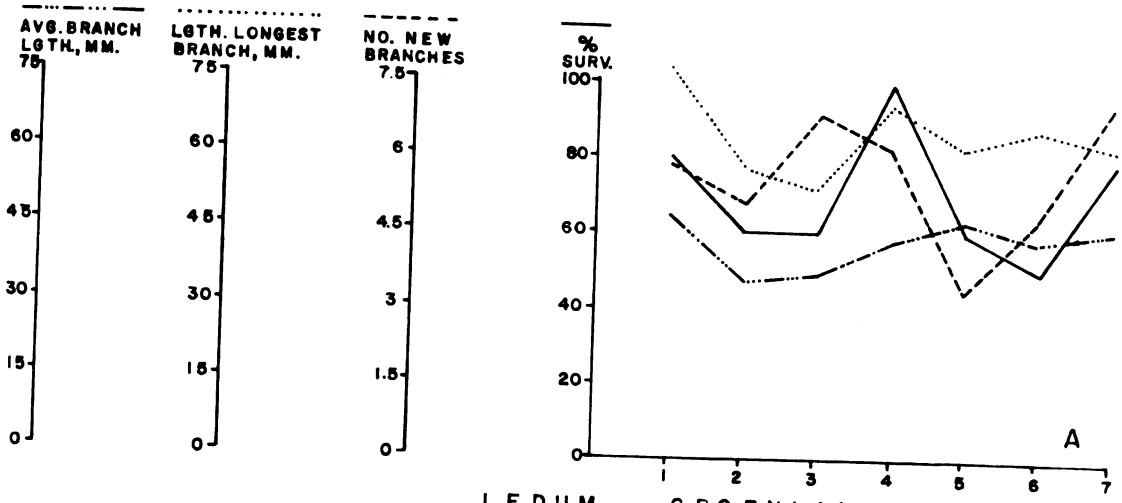
FIGURE 19. Survival and Growth, 1960 Plots, cont.

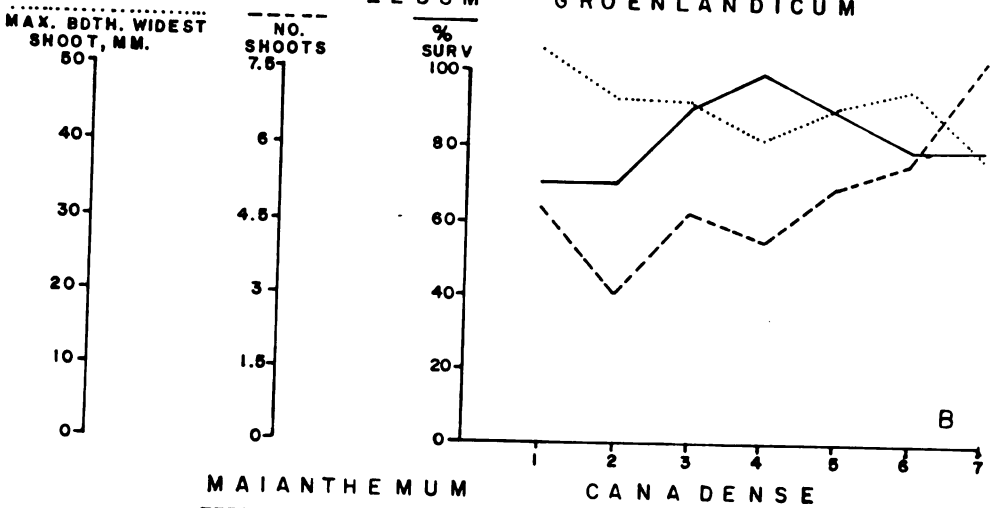
Code as indicated above the vertical axes. Block numbers along the horizontal axes.

A. Ledum groenlandicum

B. Maianthemum canadense

C. Oryzopsis asperifolia


AVG. BRANCH LGTH., MM.
LGTH. LONGEST BRANCH, MM.
NO. NEW BRANCHES
% SURV.
A
LEDUM GROENLANDICUM


MAX. BDTH. WIDEST SHOOT, MM.
NO. SHOOTS
% SURV
B
MAIANTHEMUM CANADENSE

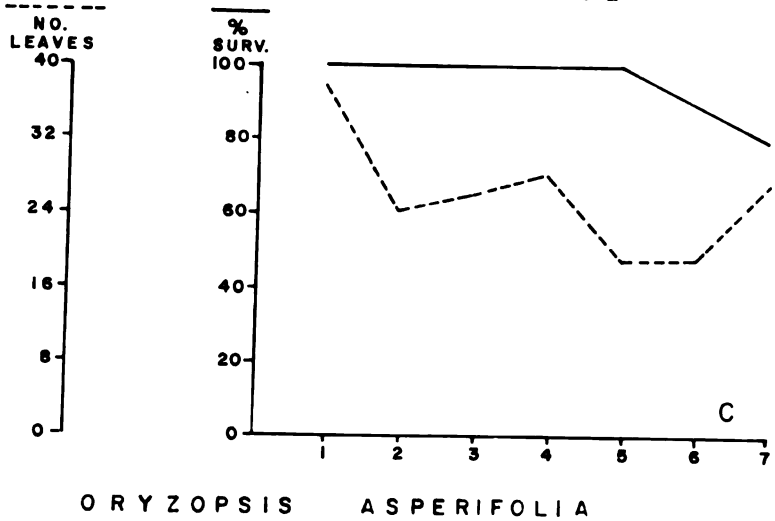

NO. LEAVES
% SURV.
C
ORYZOPSIS ASPERIFOLIA

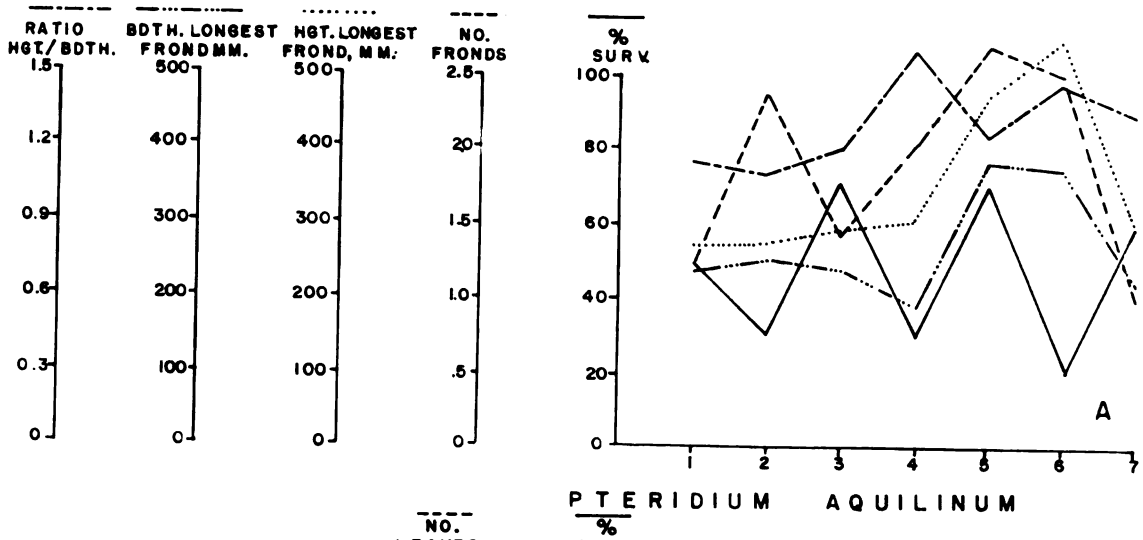
FIGURE 20. Survival and Growth, 1960 Plots, cont.

Code as indicated above the vertical axes. Block numbers along the horizontal axes.

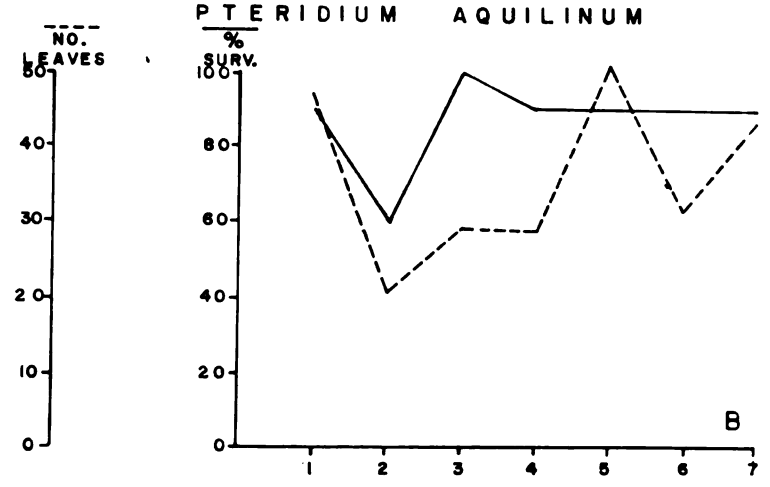
A. Pteridium aquilinum

B. Rubus hispidus var. obovalis

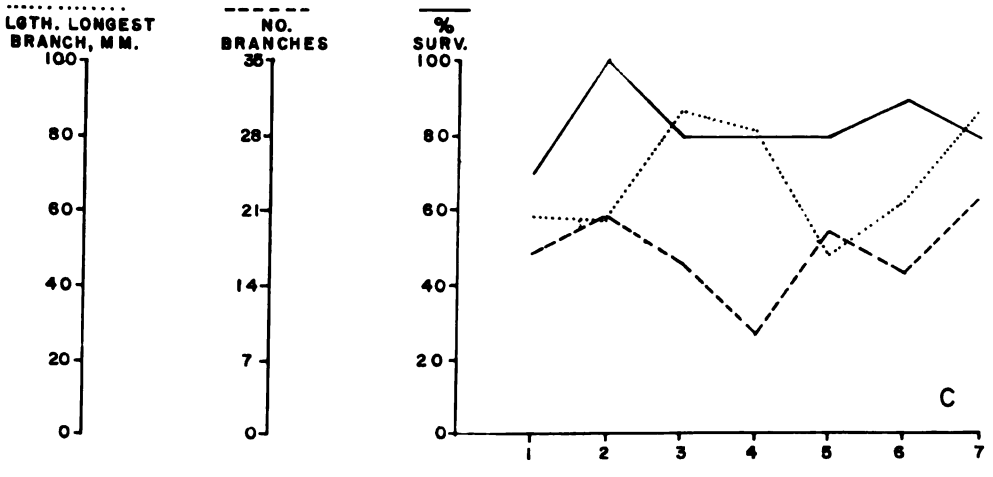
C. Vaccinium myrtilloides



PTERIDIUM AQUILINUM



RUBUS HISPIDUS VAR. OBOVALIS



VACCINIUM MYRTILLOIDES

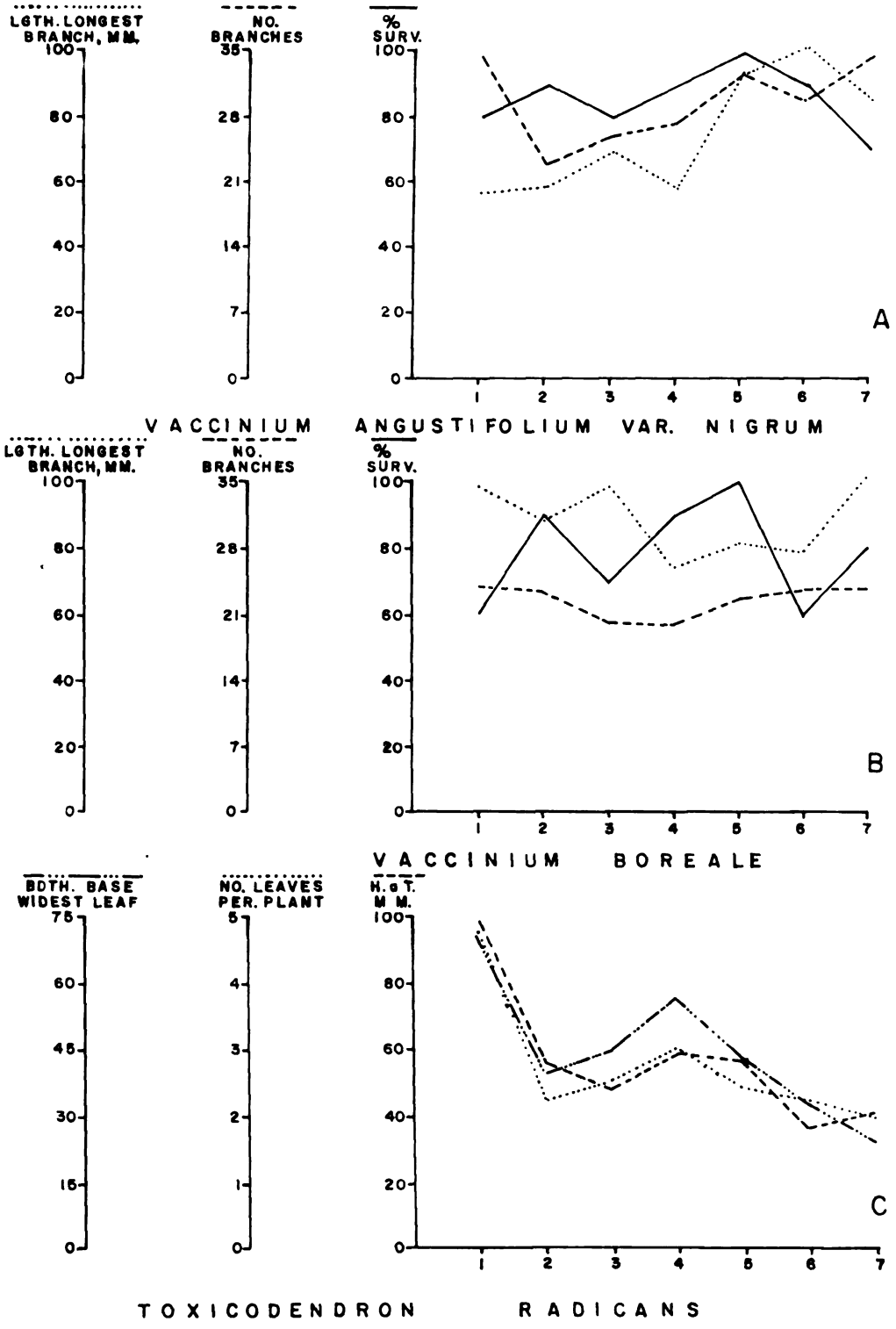
FIGURE 21. Survival and Growth, 1960 Plots, cont.

Code as indicated above the vertical axes. Block numbers along the horizontal axes.

A. Vaccinium angustifolium var. nigrum

B. Vaccinium boreale

C. Toxicodendron radicans


LGTH. LONGEST BRANCH, MM.
NO. BRANCHES
% SURV.
100
80
60
40
20
0
35
28
21
14
7
0
1 2 3 4 5 6 7
A
VACCINIUM ANGUSTIFOLIUM VAR. NIGRUM
LGTH. LONGEST BRANCH, MM.
NO. BRANCHES
% SURV.
B
VACCINIUM BOREALE
BDTH. BASE WIDEST LEAF
NO. LEAVES PER. PLANT
H. g T. M M.
75
60
45
30
15
5
4
3
2
1
C
TOXICODENDRON RADICANS

surprises. On the whole survival percentages, despite large differences due to the different sensitivities of species to transplanting, reflect the approximate scale of relative drought tolerances which one would postulate on the basis of distributions along the gradient and natural tendency to grow in open or shaded sites. In Table XIV we find the species which we would guess to be most xerophytic, Danthonia spicata (Dan) with by far the highest proportion of living plants (about 90%) in unshaded plots. Carex pensylvanica (Car), which also reaches its natural cover maximum on the best-drained soil, also survives fairly well (about 70-75%) in similar plots. Oryzopsis asperifolia (Ors), whose frequency and cover peak on Croswell and Au Gres sands respectively but which is only slightly below maximum abundance on best-drained Grayling sand, survived in about the same proportion as Carex, but in plots shaded after the first droughty spring following transplant. (Judging from the changes which have occurred in natural vegetation since clear-cutting, drainage differences made little difference in vegetation here between G and WC although they apparently did between the latter two and AS. It is therefore assumed in interpreting these results that such drainage-related differences on the two best-drained

segments, such as might occur between Carex on WC and Oryzopsis on G, are trivial compared to those related to presence or absence of transpiration-limiting shade cloth).

Omitting the three blueberries (Vaccinium spp.) for the moment, two other species have natural cover maxima on intermediate segment WC. They had quite low survival in unshaded plots on this segment, Pteridium aquilinum (Ptr) with but 15% and Comptonia peregrina (Com) with only one plant in 90. Evidently some transplanting intolerance is involved here, and in Pteridium's case this seems to be related to the exposure to full sunlight and/or the droughty spring following transplant since transplants of this species exhibited nearly 100% survival in the naturally-shaded 1960 plots. This is suprising, however, since local farmers complain that this species' rhizomes can produce new shoots even after cutting by farm implements, and Watt (1945) reports similar behavior for a closely related taxon, a rank weed in British pastures.

Moving to the presumably more mesophytic species (the foregoing are all classified in the xerophytic groupings (SS) and (CX) in Chapter IX), we have Maianthemum canadense (Mai) and Epigaea repens (Epi). Their natu-

ral maxima are on the bog margin but they are abundant on G (hence, (MD) in the Chapter IX grouping). Maianthemum in 1963 had 37% survival on well-drained G, actually somewhat better than more xerophytic Pteridium's 15%, but the shaded plots in which the first was grown probably contributed to this. Maianthemum was the only species tested to exhibit substantial transplant recovery between 1962 and 1963. But of 20 Epigaea individuals on the driest segment, also in shaded plots, none were able to survive, and even on much more poorly-drained sites only 1 of 20 lived out the first winter. Epigaea appears to be another case of a species difficult to move successfully; according to Parmelee (1965) this is consistent with its reputation. Finally, Coptis groenlandica (Cop) and Cornus canadensis (Cor), belonging to the (MW) grouping of "obligate" bog margin species which do not reach the "dry end", managed less than 25% survival under the most favorable moisture conditions (shaded, on AS).

As discussed above, the 1961 experiments were subjected to full sunlight at least through the first droughty spring, and for a longer period for those not shaded artificially. The moisture stress thus created probably revealed the rather great physiological differ-

ences between species which were not evident under the protective natural canopy over the 1960 plots. Pteridium is noteworthy in this respect; unfortunately there is no basis of comparison for two other very low survivors in the interaction plots, Comptonia and Epigaea. The much smaller block of native soil transferred with the 1961 as contrasted with the 1960 plants may also have contributed to the lower survival in the interaction plots.

The Vaccinium taxa do not behave as expected. Unshaded V. myrtilloides, the bog margin species, has higher survival on the xeric gradient segment than does unshaded V. angustifolium var. nigrum, the gradient spanner, while the latter fares better than the former on AS. One might expect the latter, abundant on the "dry end", to be hardier than the former, but the almost inevitable conclusion is that V. myrtilloides is the more desiccation-tolerant of the two, at least while they are recovering from transplanting. Yet the 1960 germination experiments indicated that it was not specialized germination requirements which in nature excluded V. myrtilloides from the "dry end". The present results, moreover, fairly safely preclude absence of humus or a specialized soil microbiota as this species' limiting factor, since the 1961 plants had little native

TABLE XIV

1961 competition plots. Survival of shaded (*) and unshaded individuals of all species tested, summaries for all experiments. F 62 = fall, 1962, S 63 = spring, 1963, N= number of original plants upon which figures are based (in parentheses).

Species	G living F 62	G living S 63	G N	WC living F 62	WC living S 63	WC N	AS living F 62	AS living S 63	AS N
Carex pensylvanica				75.0	71.3	(240)			
Comptonia perigrina				1.1	1.1	(60)			
*Coptis groenlandica							22.0		(150)
*Cornus canadensis							24.0		(150)
Danthonia spicata				95.3	89.7	(234)			
*Epigaea repens	0.0	0.0	(20)				5.0	0.0	(20)
*Maianthemum canadense	7.8	36.9	(103)						
*Oryzopsis asperifolia	73.3	70.0	(60)						
Pteridium aquilinum				22.8	15.0	(80)			
Vaccinium myrtilloides	21.3	21.3	(150)				40.7	45.3	(150)
Vaccinium angustifolium var. nigrum	14.7	15.3	(150)				64.0	64.0	(150)
*Vaccinium angustifolium var. nigrum	45.0	40.0	(60)				78.3	73.3	(60)

soil transferred with them. This leaves differential competitive ability of the two taxa as related to each other and to environment and other species as about the only feasible explanation, and indeed since V. myrtilloides' cover is much higher on relatively sparsely-vegetated Saugatuck than in the luxuriant vegetation on Au Gres it may be a poor competitor.

The morphological measurements for Vaccinium also yield somewhat puzzeling results. In the data for the 1960 plots, no change in numbers of blueberry shoots across the gradient could be detected (Figures 20 C, 21 B, pages 247, 248). In the 1961 plots, however, both shaded and unshaded V. angustifolium var. nigrum as well as V. myrtilloides produce many more shoots on more poorly-drained AS than on G, the differences being significant in all three cases (Table XV A, page 257). But again, as in survival, it is the seemingly drought-tolerant V. angustifolium var. nigrum which shows a stronger favorable response to increased soil moisture than the natural obligate mesophyte, V. myrtilloides. The former's shoot number differences are significant at $P < .01$, the latter's only at $P < .1$. V. myrtilloides, however, has longer shoots on the wet end, the difference being much more

highly significant than that for the 1960 plots. V. angustifolium var. nigrum, which in the 1960 plots exhibited a better-defined shoot length increase on the "wet end" than did V. myrtilloides, here shows only slightly, non-significantly longer shoots on AS than on excessively-drained G. By this criterion, then, it is the bog margin species which, under the relatively great moisture stress of the 1961 plots, seems to show the most striking moisture-related increase in vigor, in conformity with its distribution in the wild.

On both gradient segments, shading seems to stimulate production of longer shoots in V. angustifolium var. nigrum than does growth in the open (Table XV B), the difference being significant however only on AS (there was no evident difference in this character between the more and less heavily shaded blocks in the 1960 plots, incidentally). While this suggests that some shade is elongation-stimulatory, as does performance in nature, we must remember that increase in shoot length with reduced light is essentially universal among green plants. Number of shoots may be a better criterion of vigor. The 1960 and 1961 plots give somewhat conflicting results for this character in relation to shade, but in neither case are differences

significant.

For those species included in both 1960 and 1961 experiments, a comparison of morphological measurements between the two sets of plots is informative (Table XVI, page 259). The two sets of results are not truly comparable, for treatment of the soil, spacing, and time allowed for recovery from transplanting, just to name a few factors, are totally different in the two experimental series. Nonetheless, it is worth noting that all of the values are slightly to considerably smaller on the cutover (1961) area than they are on the same soil types in the naturally shaded (1960) plots. This indicates a slower growth rate in the open sunlight. Moreover, it is the apparent xerophytes which show the smallest, the more mesophytic species which show the greatest difference. Thus, for example, means for extreme xerophyte Danthonia from the 1961 plots are roughly comparable to 1960 plot values on the same or adjacent soils. Somewhat less xerophytic Carex' clumps average some 20% smaller in the cutover strip, although Oryzopsis, with its cover maximum "down-gradient" from Carex', (though with cover continuing near maximal up to the "dry end") shows as little difference as does Danthonia. More mesophytic Pteridium's various measurements are some

TABLE XV

1961 interaction plots. Differences between Vaccinium taxa grown under different conditions (significance by t-test). A dash (–) indicates P > .10.

A. A COMPARISON OF PLANTS GROWN ON G (GRAYLING) AND ON AS (AU GRES-SAUGATUCK) SEGMENTS.

Species and shading	Character	mean on G	mean on AS	t	P <
V. angustifolium var. nigrum, shaded	no. of branches	11.1	17.4	2.25	0.01
	longest branch, mm.	57.7	63.8	0.80	–
V. angustifolium var. nigrum, unshaded	no. of branches	9.9	16.4	2.25	0.01
	longest branch, mm.	44.5	51.0	1.21	–
V. myrtilloides, unshaded	no. of branches	12.3	17.2	1.91	0.1
	longest branch, mm.	33.4	45.2	2.37	0.02

B. A COMPARISON OF PLANTS OF VACCINIUM ANGUSTIFOLIUM VAR. NIGRUM GROWN IN SHADED AND UNSHADED PLOTS.

Soil type	Character	mean on Shaded	mean on Not Shaded	t	P <
Grayling	no. of branches	11.1	9.9	0.59	–
	longest branch, mm.	57.7	44.5	1.65	–
Au Gres-Saugatuck	no. of branches	17.4	16.4	0.43	–
	longest branch, mm.	63.8	51.0	2.78	0.01

30-50% smaller in the cutover strip, while margin-dwelling Maianthemum though artificially shaded in the cleared area, yields mean measurements there less than half those under natural canopy. The xerophytes predominate in clearings and savannas, and it is likely that they are better adapted to such sites and so less inhibited in them than are such species as Maianthemum.

Vaccinium myrtilloides shows about the same degree of growth supression in the cleared strip as does V. angustifolium var. nigrum, additional evidence that the first is not necessarily the less drought tolerant of the two as their macrodistributions would seem to indicate.

F. INTERACTION PLOTS: INTERACTION. The only interaction experiments in which survival was high enough to permit usage for their original purpose were those on WC involving Carex pensylvanica (Car), Danthonia spicata (Dan) and Pteridium aquilinum (Ptr) (Table XVII, page 264). Carex and Danthonia occupy obviously somewhat different microhabitats in nature, the latter being more abundant on much more xeric sites, yet the negative Cole coefficient[9]

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[9]A measure of association based upon presence or absence, similar in principle to the coefficient used here.

TABLE XVI

A comparison of the means of growth measurements for the same species in 1960 and 1961 plots, measurements June, 1963. All measurements of linear characters are expressed in milimeters.

		1960 plots segments		1961 interaction plots segments (s = shaded)				
Species*	Character	1-2	6-7	G	G^s	WC	AS	AS^s
CAR	bdth. clump	79.5	61.0	—	—	53.9	—	—
DAN	bdth. clump	85.2	68.4	—	—	64.2	—	—
MAI	no. shoots	3.9	6.8	—	1.2	—	—	—
	bdth. longest leaf	49.4	43.5	—	19.1	—	—	—
ORS	no. leaves	31.1	22.9	—	29.1	—	—	—
PTS	no. fronds	1.6	1.4	—	—	1.3	—	—
	hgt. longest frond	272	358	—	—	211	—	—
	bdth. longest frond	242	258	—	—	130	—	—
VAM	no. branches	19.1	18.2	12.3	—	—	17.2	—
	lgth. longest branch	58.7	74.0	33.4	—	—	45.2	—
VIG	no. branches	28.5	31.8	9.9	11.1	—	16.4	17.4
	lgth. longest branch	57.6	94.4	44.5	57.7	—	51.0	63.8

*Species names corresponding to these coded abbreviations are listed in Appendix B.

between them is not quite significant at $P < .05$. The pair Carex surrounded by Danthonia and its reciprocal were tested in order to see if there might be either positive interaction between them reducing the value of this negative coefficient, or a negative interaction not strikingly evident in nature because of habitat differences, but more dramatic when the species are forced together. An effort was made, in other words, to substantiate or reject a non-significant coefficient by experimental means.

Danthonia was found to be highly negatively correlated with Pteridium on G (Cole coefficient = -0.436, $P < .01$), so it was surrounded by Pteridium to see if the latter might inhibit it. Carex, which exhibited circum-neutral or only slight negative, non-significant correlation with Pteridium on G and WC, was also surrounded by Pteridium in order to compare its performance with that of Danthonia. In view of Carex' seemingly "indifferent" reaction to Pteridium in nature, it was supposed that whatever growth suppression it exhibited in contact with the latter might reflect ordinary interspecific interaction, not a specific inhibitory effect, and that such an effect could be postulated for Danthonia only if this grass showed substantially more growth suppression than

Carex.

Only two of twenty-four comparisons, unfortunately, yield differences significant at the $P < .1$ level or higher, which is slightly less than the expected number among randomly fluctuating variables. Nonetheless, it may be worthwhile to examine whatever trends are shown.

Carex, in sets A and B of Table XVII, is always by far the largest when grown alone. It is smallest when surrounded by Danthonia, intermediate in size when surrounded by Pteridium or by itself. But Danthonia in set C, and in sets C and D combined, is also smallest when surrounded by individuals of its own species. It is largest not when alone, but when surrounded either by Carex (set C) or by Pteridium (set D). Solitary plants are in one case larger, in one case smaller than those surrounded by Danthonia itself, and when the data are combined (C + D) there is little difference.

If these differences reflect real tendencies, the picture which begins to emerge is as follows. Carex seems to be a much poorer competitor than Danthonia, for it is strongly inhibited by this grass, and to a lesser extent by Pteridium. But Danthonia actually seems to thrive on competition with the other two species, and possibly cer-

tain interactions with these species are beneficial to it. It also appears to be a better competitor with itself than is Carex.

In comparing the experimental results with those of the present correlation analysis, we find that Carex (no. 10 in Table VII, page 97) actually has a moderate (though non-significant) positive r coefficient with Danthonia (no. 18) in 1 m^2 quadrats on WC, the soil type of the 1961 experiments. But we find that on a 1/4 m^2 scale the correlation of the two becomes slightly, non-significantly negative, in line with the somewhat negative Cole coefficient on 1 m^2. Thus the two xerophytes may have an affinity for the same or spatially close microsites, but on a smaller scale Danthonia may inhibit the Carex close to it. In any case the negative shift is not strong, and possibly any advantage Danthonia has over Carex is reduced under the more mesic conditions below the Pinus canopy, where Danthonia's natural cover is lower than in the open. On G, where perhaps more of the area is available to both species or their relative competitive ability is different, their correlation on all scales is circumneutral.

Carex with Pteridium exhibits non-significant though consistant slight to moderate negative correlation

on G and WC, as in the earlier Cole analysis. It does not seem as strongly inhibited by this fern when growing naturally under Jack pine canopy as in the environment of the interaction plots. Danthonia, which in the experiments does not seem to be inhibited by Pteridium, shows about the same degree of negativeness with it in the r coefficients on these two soil types. But the ϕ coefficient of the latter pair on G, 1 m^2, in common with the Cole value, is more highly negative than the rs and significant at $P < .001$. These coefficients based upon presence only thus suggest that Danthonia and Pteridium occur together rarely but, on the basis of the less negative r, they seem to have mutually high cover where they do. Thus, with a combination of experimental results and two correlation measures, we can suggest that the negative ϕ and Cole correlations are due not to an inhibition of one by the other, but to differing microsite preferences. An examination of partial correlations further shows that none of the other variables studied strongly affects the Danthonia-Pteridium correlations, and that the two species must differ in their preferences for some abiotic factor or a factor not studied.

G. COMMENTS ON INDIVIDUAL SPECIES. In this sec-

TABLE XVII

Results of interaction experiments, and tests of significance between the differences.

Experiment	Center species	treatment no.	surrounded by *	mean clump bdth. central plant, in mm.	Significance tests: between treatments	t	P< **
A	Carex	1	Dan	41.1	1 & 2	1.02	—
		2	Car	60.7	1 & 3	1.65	—
		3	—	89.1	2 & 3	0.77	—
B	Carex	1	Ptr	65.7	1 & 2	0.58	—
		2	Car	78.8	1 & 3	1.04	—
		3	—	93.8	2 & 3	0.55	—
C	Danthonia	1	Car	88.5	1 & 2	1.96	0.1
		2	Dan	57.8	1 & 3	0.55	—
		3	—	79.0	2 & 3	1.22	—
D	Danthonia	1	Ptr	87.5	1 & 2	0.61	—
		2	Dan	77.2	1 & 3	1.01	—
		3	—	67.3	2 & 3	0.55	—
A + B	Carex	1	Dan	41.1	1 & 2	1.65	—
		2	Ptr	65.7	1 & 3	1.70	—
		3	Car	70.3	1 & 4	2.02	0.1
		4	—	91.3	2 & 3	0.22	—
					2 & 4	0.87	—
					3 & 4	0.94	—
C + D	Danthonia	1	Car	88.5	1 & 2	0.06	—
		2	Ptr	87.5	1 & 3	1.63	—
		3	Dan	67.5	1 & 4	0.96	—
			—	73.2	2 & 3	1.42	—
					2 & 4	0.85	—
					3 & 4	0.45	

*Dan = Danthonia, Car = Carex, Ptr = Pteridium. A dash indicates that the central plants were surrounded by nothing.

**A dash indicates $P > 0.10$.

tion, the information available about each species from the several approaches is tied together. The species are treated in alphabetical order, Comptonia and Epigaea being omitted because they seemed to exhibit nothing but an intolerance to transplanting. In each instance the species name, its abbreviation symbol, and the grouping in which it is placed in Chapter IX are given in that order (the code for the last two is given in Appendix B, page 375).

Carex pensylvanica (Car) (CX) (Figure 17 A, page 244). The very large mean clump diameter in Block 1 is enough to cause differences between Blocks 1-2 and 6-7, and between the former and Block 7, both significant at the $P < .1$ level. This combined with an unusually sharp drop on shaded segments 2 and 3, suggests a competition-independent preference for fairly open "dry" sites. In such sites, however, Danthonia spicata may tend to outcompete it in nature, or so the results of interaction experiments (Section F) would suggest.

Chamaedaphne calyculata (Chm) (B). This bog species survived transplanting well in its native habitat, but neither survival nor morphological measurements indicated any diminution of vigor all the way "up-gradient" to the best drained soil (Figure 17 B). Inability of seeds

to germinate on such soil, on the other hand, could be a factor stopping Chamaedaphne at the bog margin, especially if vegetative expansion is relatively unsuccessful. Failure of flowering and fruiting may be another, since none was observed among the transplants while specimens in their natural habitat were doing so vigorously.

Coptis groenlandica (Cop) (MW). A narrow-ranging species absent from both "dry" and "wet ends", Coptis nonetheless survived nearly uniformly across the range of inorganic soils in cultivated plots (Figure 17 C). The greater mean breadth of largest leaves in Block 1-2 is different, at the $P < .1$ level, from the smaller values on 6-7 and 7 alone; thus Coptis in the absence of other green plants is perhaps less vigorous in its native habitat. Number of leaves shows no discernable trend, and both characters hold steady on heavily shaded Blocks 2-3 which corroborates a field-observed shade tolerance.

Cornus canadensis (Cor) (MW) (Figure 18 A, page 245). This species, whose gradient distribution curve nearly duplicates Coptis', has its shoots' maximum breadth increasing somewhat from the "dry end" to the bog margin (Block 1-2 vs. 6-7 significant at $P < .02$, 1-2 and 7 at $P < .1$). Number of shoots seems also to increase slightly

(non-significantly) and these differences may reflect a preference on the part of this species for its native Au Gres-Saugatuck soils with or without the usual vegetation.

Cornus shows a higher post-transplant mortality rate than most species, but no significant gradient-related differences in this (dieoff to 1963, 33% in Blocks 6-7, 42% in Blocks 1-5). Both Coptis and Cornus appeared relatively non-resistant to transplanting in the cleared strip, perhaps being more poorly fitted for withstanding the combination of drought and transplant shock than the xerophytes.

Special requirements for seed germination cannot be considered the decisive distribution-limiting factor for Cornus, either (see Section C), but there is a suggestion that inability of the plant to flower on drier sites may be limiting, for all of three plants which flowered in 1963 were in Block 5 or further "down-gradient" (Table X, page 230). Still, the fruits of this species are large, red, and fleshy, strongly suggesting that they may be bird-distributed. It is difficult to imagine any bird so limited in its distribution that it would not occasionally range 30 or 40 meters up the "dry end". Besides, the bare mineral soil of the spaded plots seems in every con-

ceivable respect more unlike Cornus' native soil environment than the undisturbed Grayling surface, so that occasional natural seedlings and sterile mature plants should occur on Grayling sand. Yet I know of no record of them on that soil in the study area or elsewhere. This would suggest that interspecific interactions plays a major role in this species' normal gradient position.

Cornus, like Coptis, seems to be uninhibited by the heavy shade on Blocks 2-3.

Danthonia spicata (Dan) (CX). Clump diameter for this species on Blocks 1-2 is not significantly different from that on Blocks 6-7, (Figure 18 B), although its natural habitat range suggests that it is more xerophytic than Carex, whose difference between these two sets of blocks is significant. A sharp dip in both clump size and survival on heavily shaded Block 2-3 is, however, in harmony with Danthonia's observed predominance in sunny spots, and the interaction experiments suggested a competitive advantage of Danthonia over Carex in such dry sites. Seed germination difficulty related to soil features (other than humus) is evidently not a limiting factor on the bog margin.

For no explicable reason, 80-90% of the transplants

flowered in 1962 but very few did so in 1963, although the wild plants flowered and fruited abundantly both years.

Gaultheria procumbens (Gau) (MD). This species, with its highest cover on the bog margin AS but presence on the "dry end", shows no discernible trends in the three morphological characters measured. Although survival decreases in Blocks 2-3, these characters remain constant even here, which agrees with Gaultheria's observed shade tolerance (Figure 18 C).

There has been a slow but steady dieoff in this species, on all parts of the gradient. If this trend continues, it will suggest that Gaultheria requires something in its native block of soil, possibly a suitable medium for its mycorrhizal fungus.

Ledum groenlandicum (Led) (B) (Figure 19 A, page 246). This bog-dweller, like Chamaedaphne, can evidently survive and grow about as well (morphological measurements) on the driest soils as on the bog margin in the absence of interaction with other vascular plants. Possibly, as discussed in Section C, inability of seeds to germinate or of seedlings to survive on dry, predominantly mineral soil may preclude its further advance upgradient. Suppression of vegetative expansion by interaction with other species may

also play a role in this restricted distribution, however, Ledum's distribution, unlike Chamaedaphne's, does not seem limited at the flowering-fruiting stage in the life cycle.

Maianthemum canadense (Mai) (MD). Increasingly moist conditions seem to make for much more abundant shoots of this species with slightly narrower leaves (Figure 19 B). The differences in mean shoot numbers between Blocks 1-2 versus 6-7 and 7 alone are significant at $P < .1$ and $P < .05$ respectively, while mean breadth of larger leaf in segment 7 differs at $P < .1$ from that in 1-2. This latter difference becomes more meaningful when we consider that on Block 6-7, there are about twice as many shoots per plot, and subjective observations there showed more leaves per shoot. The resultant increase in leaf number per plot probably increases the chance that an unusually broad one may be found.

Visual observations indicate that though the wet-end leaves are narrower than their dry-end counterparts, they are also longer. This, in conjunction with the far greater number of shoots and leaves on the wet end, probably makes for a much larger photosynthetic surface among the individuals located there, and suggests that the species is most vigorous on the bog margin. Yet the 1958

study revealed a cover peak for this species on soils intermediate between Blocks 1-2 and 6-7. Thus we may be dealing here with a species whose growth potential is greatest on the moistest inorganic soils, but which in nature is held in check on these soils by unfavorable interaction with other species.

Melampyrum lineare (Mel) (MD). Although it has a fairly strong cover peak on Au Gres, this chlorophyllous, annual root hemiparasite, in the absence of natural vascular plant interaction, germinated with seeming indifference over the entire spectrum of inorganic soils. So factors influencing seedling survival and growth subsequent to germination must be responsible for the cover maximum on imperfectly-drained soil. Now, frequency is fairly uniform across the three better-drained gradient segments, while cover changes. It is visually evident that individuals are markedly clumped; the results of Cantlon et al. (1963) suggest that this may be due to short dispersal distance from parent plants plus the storage of large batches of seed below the litter by ants or other animals. Hence the number of plants in a clump probably influences frequency but little. Cantlon and Curtis (1964) further report that germination rates are

apparently uniform on all inorganic soils in any given small area such as that occupied by the present study plots, which would account for the uniform frequency. But their seedling survival rates and size of individual plants vary such that maximum number and size of plants per clump would fall on about the part of the gradient containing maximum cover in my data.

Oryzopsis asperifolia (Ors) (SS). Slight decreases in numbers of leaves per plant and survival as the soils become moister (Figure 19 C) are non-significant. If they reflect a real natural "preference" for the drier soils in the absence of natural vegetation, then the observed slight cover maximum further down gradient may be interaction-related.

Pteridium aquilinum (Ptr) (CX). There is a marked increase in Blocks 5 and 6 in the combined criteria measured (number, length, and breadth of fronds) and then a sharp decrease in Block 7 (Figure 20 A, page 247). This peak may represent greater vigor in the area of the natural maximum, but is somewhat down gradient from the band of lush Pteridium found at about the lower Block 4 - Block 5 level in the 1958 sampling.

Almost all of the high post-transplant mortality

recorded for this species occurred during the winters. Pteridium, more than any of the other species tested, migrates long distances by rhizomes from year to year; the missing individuals may not have died but merely "escaped captivity".

Rubus hispidus var. obovalis (Rho) (MW). This bog margin species is absent in nature from best-drained Grayling sand, but as Figure 20 B shows its transplants survived and grew as vigorously there as elsewhere. Although transplants flowered in all blocks, the proportion was somewhat higher in Blocks 6 and 7, suggesting that these individuals transplanted into the species' natural habitat may be healthier. (Failure to flower in 1962 may probably be attributed to transplant recovery lag).

Vaccinium boreale (Vyp) (MD), V. angustifolium var. nigrum (Vig) (MD), and V. myrtilloides (Vam) (MW) (Figures 20 C, 21 A, 21 B, pages 247, 248). Of the two taxa tested in the 1961 plots, V. myrtilloides, which is restricted to the bog margin in the wild, seems to be more strongly favored in its shoot elongation under conditions of moisture stress than is the seemingly more drought-tolerant V. angustifolium var. nigrum, which spans the gradient. This is as one would expect. Yet in survival as well as in num-

ber of shoots produced it would seem to be the more xerophytic V. angustifolium var. nigrum which is more favored by greater soil moisture or more inhibited by its scarcity. Growth suppression of the two taxa in the cleared strip was about equal. Thus these closely related entities help to point out that physiological differences expressed in a "cultivated" situation may not predict performance within the context of the natural community.

Neither the 1960 nor 1961 plot results show statistically demonstrable shade-related differences in shoot numbers, but the 1961 plants of V. angustifolium var. nigrum produced significantly longer shoots in shaded plots on the more poorly-drained AS segment. V. boreale had much longer shoots in the 1960 plots than either of the others and, unlike the latter, did not have demonstrably longer ones on the "wet end".

Sporadic flowering, fruiting and seed germination showed no discernable soil moisture-related trends.

Toxicodendron radicans (Tox) (not indigenous to the study site). All of the measured characters (germination, seedling survival, height, number of leaves, breadth of largest leaf) seem to present a picture of increasing intolerance to more and more mesic conditions (Figure 21 C).

The majority of these criteria do not show significant difference between the xeric and mesic blocks, but the overall trend looks fairly convincing. Since the species is only rarely found in Jack pine forests and then usually on the more mesic Au Gres-Saugatuck sands, the results once more conflict with performance of the species in the wild.

CHAPTER VIII

ENVIRONMENTAL VARIABLES

A. SYNUSIA. In Chapter III we discovered that synusia as a whole seem to play a relatively minor role in species microdistribution, if indeed the low strength of species-synusia correlations reflects a low degree of influence of these vegetation layers. Significance proportions in species-synusia correlations are lowest on AS, where soil horizon thicknesses may play a more important role, and highest on R, where the tension-zone heterogeneity makes for marked synusium cover variation.

Correlation of species with tree cover (tre, variable no. 48 in the tables) must reflect almost entirely the influence of this synusium upon other species rather than the reverse. Most of the trees in the area are about 60 years old. Now, Watt (1947), among others, has demonstrated that clonal species migrate about, so that around 1900, when germination and seedling survival of the present trees could have been influenced by clones of Vaccinium, Carex, Gaultheria, etc., the positions of these clones probably bore little relationship to their present ones.

According to field observations supplemented by exact cover data (Table I, page 27) we have an open Pinus banksiana forest on the upland, a narrow band of dense, taller Pinus, Picea and Larix straddling parts of Saugatuck and Kinross on the bog hingeline, and scattered, somewhat stunted trees of these species in the bog. The heavy tree cover on the bog margin, as one might expect, seems to produce the largest number of high correlations with itself, mostly negative (though none are significant because N is small). But on the whole tree cover shows the lowest proportion of significant correlations of all the synusia. We must conclude, then, that degree of canopy closure, within the extremes found in this area, does not influence species microdistributions very greatly. This is not unexpected since, at these latitudes, light strikes the vegetation at a low angle. Hence the quantity of light striking a patch may depend upon the arrangement of trees or shrubs to the south which can block it, and bear little relation to the canopy directly overhead. In Chapter V, moreover, we showed that a large part of species correlation with tree cover might be vicarious and due to influence of the litter produced by trees, or to factors merely associated with the trees such as humus thickness.

In the bog, there is a positive correlation of tree cover with Kalmia angustifolia, and another shrub too rare here to have been included in the calculations (Nemopanthus mucronata) is definitely associated with the scattered trees here. In all likelihood these reflect the "bog margin-like" conditions, i.e. coniferous litter, low Sphagnum and somewhat more compact surface surrounding the isolated conifers here. On the inorganic soils, a weak tendency for other synusia to be negatively correlated with tree cover suggests a general shade inhibition of plant growth. This tendency might be more strongly evident in correlations with light intensity itself, for as indicated above the projection of tree canopy onto a quadrat gives but a poor estimate of the solar energy reaching the plants. Per cent of the ground covered by litter is not positively correlated with tree cover on the dry end. Bare patches may be as abundant in the deep litter beneath trees as in the relatively shallow litter between them, and as much ground may be covered by tufts of Carex and other plants which hide the litter (and prevent its being recorded) beneath trees as elsewhere. Conspicuous high positive correlations with humus thickness on G ($P < .01$) and WC ($P < .001$) may stem from the conspicuously much greater accumulation

of litter under trees than elsewhere, and a tendency for this litter to remain in place while decomposing. The circumneutrality of this correlation on AS may then result from the greater microrelief here, a tendency for redistributed litter to accumulate in the pits counter-balancing its tendency to rot where it first fell. A negative coefficient with aoh on R may reflect this same tendency on the even more severe microtopography here plus ecesis of trees only on the mineral matter of tipup mounds, or else concentration of the trees on the shallower organic matter nearer the hingeline.

Shrub cover (shr, no. 49) rises steadily from G through DG (Table I, page 36). Judging from its relatively high proportion of significant correlations even after we eliminate those with its own major components it is a somewhat better predictor of species microdistributions than is tree cover, although this need not necessarily imply that it exerts a greater influence. Indeed the distribution of this synusium could itself be influenced by members of the remaining synusia, especially tall ones like Pteridium which might cast a shadow over shrubs beneath them or species forming dense tufts (e.g. Carex, mosses) which could mechanically inhibit development of

shrub seedlings or young rhizome buds growing upward through them.

Most of shrub cover's correlations with individual species suggest nothing new and no general tendencies. However, shrub, herb, and moss cover's correlations on the bog margin, R, are mutually positive, probably arising from a visually evident mutual aversion to the areas beneath the hingeline trees. The non-significant negative shrub-herb correlation on AS, on the other hand, may reflect competition for light and moisture between the synusia here where both have lush cover.

Shrubs' positive correlations with A_{OL} (fall litter thickness) on AS and with A_{OM} thickness everywhere but on WC suggest that shrubs may act as collecting points for litter (a negative one with spring litter thickness (lit) on R then merely reflecting the absence of shrubs beneath litter-shedding trees). Or possibly most shrubs simply tend to grow in natural litter collection points (micro-depressions).

Herb cover (hrb, no. 50) is about even across the two best-drained segments and Au Gres sand; it goes down to about 1/3 of this value on Saugatuck and further decreases, less drastically, on R and DG (Table I, page 37).

After exclusion of correlations with those species which may themselves be an important part of the herb synusium, we are left with a possible trend towards positive correlation of this synusium with other species overall, but no discernible tendencies with individual species or groupings. Strong negative coefficients with spring litter thickness (lit) on G and WC may arise along with shrub cover's negative correlations with litter parameters, from a retardation of evaporation and thus of soil warming in the spring proportional to litter thickness. A consequent inhibition of spring rhizome buds and seedlings in the more thickly covered patches might result.

Herb cover has in addition several other significant correlations with litter parameters, other synusia, and soil horizon thicknesses. A negative correlation trend between herb cover and horizon thicknesses on AS suggests either a tendency for herbs to occur with younger, shallower and perhaps nutrient-richer profiles, or else simply greater herb cover in the shallow-profiled, better drained portion of AS which is less frequently saturated.

Throughout, moss cover's (mos, no. 51) correlation with per cent of litter cover (lip) is very highly and significantly negative. Now, mosses occur on quite different

kinds of microsites, patches of the same species being found on the high hummocks surrounding tree bases or on flat ground far below the mean level of the area. It may be that these seemingly quite different kinds of sites are similar in being so situated that they are exposed to relatively high wind currents, and so constantly cleaned of litter. Several milimeters' thickness of dead leaves would be enough to cover and exclude light from the small repent gametophyte stalks of these bryophytes. These different sorts of sites would also be relatively high in surface moisture which may favor mosses because of their shallowly situated rhizoids, the tree trunk bases because of stem flow and the low flat spots because of gravitational puddling of water in them.

Cover of the mosses exhibits a bimodal curve with maxima on the two extremes of the gradient and a low on Croswell sand (Table I, page 37). The maximum cover attained on DG is many times higher than the secondary high on G and represents the nearly solid cover of Sphagnum on the former. We might be inclined to assume that the decrease in moss cover from Grayling sand to Wet Grayling and the sharper one between the latter and Croswell was due to the existence of "dry end" and "wet end" moss species, with

no species having optima on the intermediate soil types. Yet all three of the inorganic soil mosses contributing appreciably to this synusium mirror this bimodality in their individual cover curves! Caliergonella schreberi (Cal, no. 8), constituting the majority of moss cover on all inorganic soils, is maximal on Grayling with a secondary high on Saugatuck, minimal on WC like moss cover generally. Brachythecium salebrosum (Bra, no. 7) "peaks" in cover on Wet Grayling and Au Gres, and Dicranum undulatum (Dic, no. 19) on Grayling and Kinross. Cantlon and Gillis (unpublished data), moreover, found the same to be true in several similar Pinus banksiana gradients within a 50-mile radius of the present one, so it does not seem to be an accidental peculiarity of this particular stand.

The causes of this distributional phenomenon may be related to the afore mentioned intolerance of mosses to litter. Pteridium aquilinum (Ptr) has a cover maximum nearly coinciding with moss' minimum and bare area (bar) is decidedly minimal in the same place. Possibly the luxuriant Pteridium here acts as a windbreak, reducing the velocity of air currents to the point where they can no longer clear many spots of litter. This would account for the scarceness beneath it of bare areas and consequently,

perhaps of mosses.

The moss cover-A_{OH} correlations are very positive on G and AS, not surprising in view of the visually conspicuous affinity of many mosses for organic matter. But this correlation is missing on intermediate WC, where the moss low occurs (Table VII, page 118). If this is related to the moss minimum on the latter segment it is not clear just how.

Since inorganic soil moss species and lichen taxa treated individually are so few in number, they will be discussed here rather than in Chapter IX. Sphagnum and Polytricum of the bog, however, fit in so naturally with the discussion of the assemblage native to DG that they are included with it (Chapter IX, Section F).

The three common inorganic soil mosses are decidedly positively correlated with each other on the two best-drained segments (the corresponding correlations were not calculated for AS). In the field it is evident that Brachythecium salebrosum (Bra, no. 7) and Dicranum undulatum (Dic, no. 19) patches occur inside of larger patches of Caliergonella schreberi (Cal, no. 8) or interdigitating with the latter, as if all three had similar requirements as suggested also by the aforementioned peculiar distribu-

tions. Or else a successional relationship exists with patches of pioneer Caliergonella once established, facilitating colonization by the other species.

With the xerophytic clonal vascular species on AS, mosses tend towards slight negative correlation, perhaps reflecting the greater moss cover on more poorly-drained Saugatuck. With the more mesophytic ones on G, the ϕ coefficients of the moss species are decidedly positive, suggesting moister microsite preferences on the part of the bryophytes, but this is only weakly reflected in the r coefficients with moss cover as a whole. So these tracheophytes apparently tend to occur with mossy patches but not to produce their best cover there. This is especially conspicuous with Melampyrum lineare. The number of both seeds and seedlings per unit area in moss patches tends to be higher than in non-mossy areas, but the larger plants are usually in non-mossy spots (Cantlon 1965).

The edges of Vaccinium patches on the dry end seem, on the basis of correlations, to be more conducive to moss growth than those of lush Carex. But this may be an artifact created by the spatial impossibility of other plant growth in the tight and extensive tufts of this sedge.

Negative correlations of moss (here mostly Sphagnum)

with both per cent and thickness of litter cover on the organic soil, DG, probably reflect the near-absence of mosses there under litter-shedding trees and old Chamaedaphne clones. Negative moss-tree and moss-shrub correlations seem to substantiate this interpretation.

Lichen cover (lcn, number 52) also has a decided bimodal distribution somewhat parallelling that of mos, with high points in this case on G and R and the low point on the Au Gres of AS (Table I, page 37). It is even clearer here than with mosses that this is not due to changes in species composition of the synusium along the gradient, for all three of the common lichen taxa have not only bimodal frequency curves but "highs" and "lows" in the same places as does lichen cover overall. In this case the peaks in the curves coincide with the areas of relatively sparse understory vegetation which these symbionts seem to find ideal. There is also an abundance of relatively xeric microsites on the two maximal segments, on G the whole excessively-drained segment itself and on R the tops of high tipup mounds. Their near-hiatus, moreover, corresponds to the soil type having by far the highest shrub-herb cover. The same lichen taxa continue into the bog, and in fact produce several times the cover

here which they do on AS. Here, though apparently on the surface, they are attached to abundant dying Chamaedaphne branches beneath the Sphagnum.

The lichen taxa have high positive ϕ correlations with each other leaving little doubt as to their high degree of physiological similarity suggested also by the frequency curves. With vascular plants generally, the lichen taxa collectivelly and individually exhibit an unusual negative correlation trend, very marked with the more mesophytic species found on G and WC. The trend is most marked on G; on this best-drained segment the best microsites for lichens are "drier" even than elsewhere and hence most unsuitable for mesophytic plants.

Moss and lichen cover tend to be circumneutrally, not negatively, correlated with each other even though the species of the former seem quite mesophytic. But there are some similarities besides the bimodal frequency or cover; both have a predeliction for ground bare or nearly so of light-eliminating litter. Lichen cover's relatively weak negative coefficients with per cent litter cover (lip) everywhere except on G can probably be attributed to the relatively small aereal extent of lichen patches relative to quadrat size except on the "dry end". On G, lichen

cover also has a high positive correlation with bare ground (bar) and a negative one with litter thickness (lit), both reflecting the intolerance of lichens to covering of their photosynthetic thalli.

Lichen correlations with A_{OM} and soil horizon thicknesses can probably be dismissed as macrodistributional coincidences, while a negative one with A_{OH} on G may be a reflection of lichens' association with bare, hard-packed soil there. Unlike mosses, lichens seem to avoid shrub and particularly Vaccinium cover, but are circumneutral with the dominant sedge Carex which mosses seem to shun.

B. LITTER PARAMETERS. It is the tree species rather than the shrubs and herbs which contribute the bulk of the litter, although Chamaedaphne contributes a great deal of the total on DG. Thus most correlations of species with these parameters do not reflect the species' contribution to them. But species may influence the litter patterns in other ways, such as the larger clonal species apparently acting as wind-reducing litter traps (Section A of this chapter). On the three best-drained segments the great bulk of the litter is of Pinus banksiana, but on R and DG Picea, Larix and Chamaedaphne play major roles and

thus differences in initial chemical composition of leaves could be related to changing species microdistributions.

On the whole spring-summer litter thickness (lit, no. 54), fall thickness (aol, no. 57), thickness of older compacted, fungus-impregnated litter, or duff (aom, no. 58) and per cent of the ground covered by litter (lip, no. 56) or by nothing (bar, no. 55) seem to be less important than the other "environmental" parameters as species patterning forces. This one can judge from the relatively low proportions of significant species-litter correlations ("LI" in Column 2 of Table II, page 55, as compared to "S-" and "HO" in adjacent sub-columns).

Lit and aol are measurements of the same parameter, litter thickness, not only at different times of year, but using quite different techniques. Therefore a comparison between their correlation tendencies will serve as an illustration of just how much difference such factors can make. Lit, recorded in the late spring through mid-summer (mid-June through late August), was measured by poking a ruler down through the litter at five points within the largest quadrats, namely the center and the four corners of the 1/4 m^2 quadrat, and averaging them. There was thus an unavoidable tendency to compact the litter slightly,

and thickness of the litter hidden within patches of tussocky graminoids such as Carex and Danthonia and of some mosses was not included, both leading to underestimation. In measuring aol (from mid to late September), a block of soil (used also in measuring soil profiles) was cut with a flat shovel in the center of the quadrat. This procedure tended to loosen the litter along the edge of the block slightly so that, in measuring each of the four block sides in order to obtain an average, over-estimates of thickness were made. Litter hidden within tussocks was also brought to light, further increasing the estimate of aol over that of lit. To be sure, we do find slightly higher mean thicknesses of aol than of lit on the three best drained segments, while on R and DG aol thickness is much the higher due to the inclusion in it of much litter hidden in the near-ubiquitous Sphagnum and not recorded in the lit measurements.

Also making for possible differences between the two measurements are the shedding of new Pinus banksiana leaves during the spring and summer and the decomposition of older ones during the same seasons. During the growing season also there may be a redistribution of litter by wind as postulated in Section A in connection with moss distri-

butions, and a differential accumulation related to tree trunks, shrub cover, and microrelief in the path of prevailing winds. This may lend to an overall leveling, whereas snow melt and emerging plants in the spring may lead to the heaping of litter in small piles. Coefficients of variation[10] (Clark 1961), which measure the absolute variability of factors regardless of means or units of measurement, range on different segments between 1-1/2 and 2-1/2 times as high for the spring-summer measurement lit as for the fall measurement aol. This seems to bear out the postulate of a leveling during the growing season, the higher spring variability reflecting the presence of thick heaps and thin patches between them. Corroborating the leveling postulate also are the correlations of both spring and fall thickness with per cent litter cover (lip) and per cent bare ground (bar) (Table VII, page 119). Spring thickness, lit, is circumneutrally correlated with both as would tend to be the case if thickness were highly variable and permitted extensive bare patches in the same quadrat with deep litter piles. Fall thickness, aol, is

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[10]These were not calculated for any species in Chapter IX because there the values would reflect primarily the proportion of quadrats in which a species is absent.

very negatively correlated with per cent bare ground, quite positively with per cent litter cover on G, the segment where the bare patches are most abundant and extensive. This suggests that here the litter patches are broad enough so that their thicker centers are far from the bare spots. Some of the higher variability of spring thickness, however, may originate in the failure to record thickness of litter hidden in graminoid tussocks at that time.

Both litter thickness measurements, especially the spring one lit, exhibit a decidedly negative trend in their correlations with synusia. This was attributed in Section A of this chapter to retardation of spring soil warming and consequent bud inhibition by thicker litter. Possibly, though, some of the larger species, especially the dense tussock-former Carex, mechanically exclude thick litter buildup.

Aol-species correlations are not nearly so high or significant as those with lit, very likely because the distribution of litter during the critical soil-warming period was more nearly reflected in the spring-summer lit measurement than in the fall reading, aol. This could, however, be due merely to the lower variability of aol.

The postulate changes in litter distribution during

the summer are really not suggested by the correlations between the spring-summer and fall measurements themselves, which are highly positive and significant everywhere but on AS. But on the basis of various other correlation patterns we can reconstruct something of the nature of such changes. Understandably very significant high positive correlations of litter with tree cover are considerably lower on G, WC, and DG when the fall measurement, aol, replaces spring-summer lit as the thickness criterion. On AS and R, on the other hand, there is a substantial increase in positiveness of this correlation in the fall, as if the sharper microrelief of these segments acted as a series of windbreaks allowing litter to remain in place where it falls below the trees. This conflicts, though, with the attempts to explain moss distribution patterns in Section A of this chapter, for the picture developed there suggested that the dense Pteridium cover on WC might be a more important wind-reducing factor than microtopography. There is also a suggestion discussed in Section A that dense shrubs on AS and R may act as important litter accumulation points.

Danthonia (Dan), to all appearances an extreme xerophyte among common dry-end species, is circumneutrally

correlated with spring lit but negatively with fall aol on G. Litter is probably easily blown off the dense clumps of this grass that tend to occupy xeric microprominences, hence the negative shift in correlation with it during the growing season. There is a corresponding change from positive with lit to circumneutral with aol in the correlation of hummock-dwelling Trientalis on AS, probably for similar reasons. On the other hand, correlation changes in the reverse direction of Carex and dry end mosses from negative with lit to circumneutral with aol seem attributable to the methods of measurement. These methods, as mentioned above, reveal litter hidden in tussocks of these plants.

Generally positive correlations of lit and aol with duff, or fungus-impregnated older litter (aom) and even with humus (aoh), which develops from litter, furnish evidence that litter falls and tends to decompose in place. This trend seems strongest on the "dry end" and is not evident on DG where aom represents primarily dead Sphagnum rather than leaves.

Species correlations with duff may reflect direct influence of this horizon upon species more than do those with litter thickness. Cycles of A_{OM} accumulation and decomposition are more nearly equal in length to 3-4 year

cycles of alternating occupancy of microsites by two or more species found by Watt (1945, 1947) and Kershaw (1958), among others. Also, most species' winter buds, as well as seeds of Melampyrum lineare (Cantlon et al. 1963) and probably of most species whose reproduction in the area is primarily sexual, are located at the juncture between the A_{OM} and A_{OH} horizons (Olsen 1963). Many have rhizomes and much of their absorptive surface in the A_{OM}. A thick duff mat might act as insulation, deterring both freezing and desiccation, and along with litter retarding soil warming in the spring.

A tendency towards moderate negative species-A_{OM} correlations on AS may be a consequence of the last, but it could also result from macrodistribution phenomena which place the lushest cover of most species on Au Gres rather than Saugatuck, where A_{OM} is decidedly thicker. (The only species significantly positively correlated with A_{OM} on this segment, Vaccinium myrtilloides, is in fact one of the few reaching maximum cover on Saugatuck). A slight positive correlation with moss cover and a surprising very highly positive one ($P < .02$) with lichen cover on AS suggests that while loose litter may inhibit these plants, a thick A_{OM} horizon is actually favorable to their growth and

that they grow on top of it.

Correlations with per cent of litter cover (lip) and of bare ground (bar) seem to yield little information not available from correlation with the other litter measurements. It would seem logical that they should be negatively correlated with each other but in fact they are so only on G, the lusher vegetation on less well-drained segments perhaps taking up most of the space not occupied by litter, or bare patches being small relative to quadrat size. A positive correlation on R results from relatively small quantities of both litter and bare patches on low, Sphagnum-covered areas here.

The cover of bare patches on WC is only a small fraction of that on the segments on either side of it. Bar is positively correlated on this segment with Pteridium (Ptr), the large conspicuous fern which reaches a maximum here. This plant may, though it is associated with the bare patches, cover most of them with its own litter.

Per cent litter cover exhibits an overall positive trend with other species, both xerophytes and mesophytes, on AS. It is difficult to explain why with our present knowledge, especially since plants occupy space which would otherwise be litter-covered. But a negative coefficient of

litter cover with shrub cover as a whole, on AS and R, is the only evidence here that plants might tend to exclude litter in this fashion. A decided negative correlation of the bog species with litter cover on R must surely reflect the near-absence of plant remains from the Sphagnum-covered portion of the segment, upon which these species grow.

C. SOIL HORIZONS. There is little evidence for species-soil interactions. Those high and significant coefficients which the horizons exhibit with species can mostly be explained simply by macrodistributional changes in species cover and horizon thickness within gradient segments. For example, we have the tendency discussed in Chapter III, Section H, for xerophytes to be negatively, and mesophytes positively correlated with horizon thicknesses. They tend to occur on better and more poorly-drained macro- or microsites, respectively, so the trend can be explained by horizon thickness' being generally inversely proportional to efficiency of drainage. The experimental studies (Chapter VII) did demostrate that at least one species (Chamaedaphne calyculata), may be limited in its macrodistribution by inability to germinate without sufficient organic material (aoh), but even in that case the requirement could be for increased moisture or some

other factor itself generally associated with thick humus.

Horizons are on the whole positively correlated with each other (although, strangely, not on WC), probably because of a tendency for the soil profile to develop as a whole. Therefore the soil on a recently created tipup mound will generally have all thin horizons, soil in a less recently disturbed spot thicker ones. The material leached from a thick A_2 horizon on more poorly-drained soil must form a relatively thick B, etc., other factors being equal.

Starting at the top of the soil profile, humus thickness (aoh, no. 59) may be important in that a concentration of winter buds, rhizomes, roots and seeds, and hence of plant activity, is found within it, as well as in the duff, or at the juncture between the two. The mean for A_{OH} thickness gradually doubles between Grayling and Saugatuck sand, then increases much more rapidly between Saugatuck and Kinross sand and also between the latter and Dawson-Greenwood peat, there becoming the peat itself.

Just how important is humus thickness, and at what point increasing thickness ceases to have much influence upon species macro-and microdistributions, are questions for future experimental testing. At any rate there are no particular trends in species-aoh correlations nor, for that

matter, an unusual proportion of significant correlations, so the simple amount of humus may be less important than some other characters of this horizon. Correlation trends with tree cover and litter parameters were discussed earlier in this chapter.

Mean organic-mineral or A_1 horizon thickness (a-1, no. 60) is nearly the same throughout the gradient although coefficients of variation (see Section B of this chapter) indicate that it is about as variable within each segment as the other horizons. Nonetheless, it exhibits a very low proportion of significant correlation with species.

The cause of a slight positive trend of all species with the leached horizon (a-2, no. 61) on G, may be that both plant cover and this leached horizon's thickness are increasing rapidly in the direction of moister WC. An unusual negative trend with somewhat mesophytic species (MD) on AS and a positive one on R seem to be macrodistributional also; patterns similar to these have been discussed.

Since the B horizon is relatively far below the surface, its thickness (bee, no. 62) in itself may have relatively little influence upon plant growth. Far more important may be the degree of cementing of the humus and sesquaoxides which the Bh contains, for the resultant range

in consolidation may run from slightly "crumbly" to literally rocklike. The B horizons of the study area represent the whole gamut, with no cementing on best-drained Grayling sand and a hardpan which must be chipped with a pickaxe on bog margin Saugatuck. This cemented B horizon, or ortstein, may tend to hold heavy rainfall in the horizons above, saturating the soil and plant roots until it finally seeps through or perhaps is removed by evapotranspiration! But it may also act as a barrier to root penetration, so that during droughts these organs cannot follow the downward retreat of the capillary fringe (cf. Joffe 1949).

Unfortunately, I had no objective way of measuring degree of cementing in the field, so measured only B thickness. There is no evidence that thickness and degree of cementing are related. For whatever reasons, there is a tendency on AS for xerophytes to be positively and mesophytes to be negatively correlated with this thickness.

Gley is orange motteling caused by local sesuquaoxide deposition in saturated soil. The highest level at which it is found (gli, number 63) is thus a "bench-mark" for the maximum level of persistent standing water in the soil. Gley was encountered above the B horizon consistently only on AS, and on that segment it was nearly always

visible at the juncture between A_1 and A_2 horizons; it could not be seen in the A_1 because of black organic staining in that horizon. Thus gli, in practice, is a total of the upper horizon thicknesses A_{OL}, A_{OM}, A_{OH} and A_1, and since correlations with it are thus correlations with the total upper part of the profile they are of limited value. A negative trend in gley-xerophyte correlations and a lesser one with species in general can be accounted for by thicker upper profiles, hence deeper gley on the moister, more sparsely-vegetated Saugatuck, but these are not unique revelations.

CHAPTER IX

CHARACTER OF THE VEGETATION

The preceeding chapters have examined the Pinus-Chamaedaphne transition in the light of various analysis techniques, discussing the more unusual or striking characteristics of species and community distribution patterns revealed by each one. We have thus been examining the vegetation structure from various angles as one might measure and describe various facets of a crystal, and it now behooves us to put these facets together so as to reconstruct the multidimensional ecological situation which exists.

In the discussion which follows, the species are placed into several convenient grouping which have been mentioned in previous chapters. These groupings are based primarily upon the part of the gradient where the species have their maximum cover, although in one case two groupings are also separated on the basis of presence or absence of strong clonality, and two taxa of Vaccinium which are abundant throughout the gradient are each included in two separate groupings.

These assemblages, let us emphasize, are visualized

here neither as "basic units" sensu Hopkins (1957) discussed in Chapter IV, nor as any other kinds of formally-derived groups, and indeed they resemble such units only remotely. The demarcations between the groupings discussed in the present chapter are arbitrary, like those between Hopkins' or Goodall's units. Moreover, it is extremely doubtful that there are in nature groupings of species all of whose probabilities of occurrence vary equally, or in the same direction, with all possible kinds of spatial or temporal changes. Nor is it likely that the same single dominant factor, such as soil drainage, is the predominating influence on these probabilities for all species involved. But the arrangements here are probably much more natural than those derived by the latter authors in that decisions are based upon information from several different sources, not just a single simplified formula. That reality is reflected in the present groupings is further suggested by the similarities evident among their members in respects not considered in the grouping procedure itself. This is particularly true of their interspecific associations.

A. SMALL SOLITARIES (SS). The species here included are characterized by:

1. highest cover on one of the best-

drained soil types, Grayling sand (including "Wet Grayling") or Croswell sand in all but two cases, Prunus serotina (Pru) reaching a cover maximum on Au Gres sand and Amelanchier sanguinea (Ams) on Saugatuck sand,

2. all but one, Amelanchier sanguinea, present on Grayling sand, the best-drained soil of the gradient and all absent from organic soil,
3. relative rarity,
4. relatively low cover even where they do occur,
5. all but one lacking in strong clonality in the study area; that one, Arctostaphylos uva-ursi (Arc), with only small, scattered clones here.

The (SS) are thus a rather heterogeneous assemblage of small, mostly non-clonal and non tussock-forming species whose areal extent is not great, which do not constitute a conspicuous part of the vegetation. Three tree seedlings are included, Amelanchier oblongifolia (Amo), Amelanchier senguinea (Ams), and Prunus serotina (Pru), one shrub,

Arctostaphylos uva-ursi (Arc), a small shrub Rubus canadensis (Rub), the five perennial dicotyledonous herbs Anemone quinquefolia (Anm), Viola adunca (Vio), Aster "hairy ovate" (Ash), Aster laevis (Asl), and Solidago "lanceolate long petiole" (Sol) (the last three are composites), and two grasses, Oryzopsis pungens (Opu) and O. asperifolia (Ors).[11]

On the basis of their "behavior" here and in sites somewhat different from the study area, many of these are dependent upon disturbance for their occurrence. The tree seedlings may tend to germinate anywhere there is a local disturbance in the soil. Composites which appear in pastures often require small openings in the sod for ecesis (Keever 1950, Caruso 1963). The three found here may have similar requirements, although they are growing under Pinus canopy. Rubus canadensis is a conspicuous denizen of burned or "brushed" areas and Arctostaphylos is a somewhat pioneer dune shrub along the Lake Michigan shore about 60 miles west of the study area. In this particular study area (though not necessarily in other communities where some of them occur) these species probably play the role

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[11]Life durations of species according to Fernald (1950).

of opportunists. They are mainly sexually reproducing here and probably seed in where other species, the real mainstays of the community which preempt most of the space in the models of Whittaker (1965), are by chance absent at a given moment.

It is probably because of this "semi-weedy" character, rather than physiologies which require perfectly drained conditions, that cover of most of these species "peaks" on the better-drained soils where vegetation cover as a whole is relatively light. The tendency to occupy sparsely vegetated spots, as well as the absence of large clones which in themselves would act as a strong pattern-inducing factor upon other species, may be responsible for the (SS)' exhibition of relatively few significant correlations (Chapter III). Since most significant correlations are positive, possibly because of an overall lush-sparse mosaic in the vegetation (see Chapter III), scarcity of significant coefficients among the (SS) may indicate that they produce high cover where cover of other species is low. Beaman and Andresen (1965) report that subalpine species, in the context of a true alpine community in Mexico, seem to play the role of opportunistic users of unoccupied space like that postulated for (SS) here. They

similarly exhibit the least positive or most negative correlation trends among the members of that community.

The dependence of the (SS) upon conditions favorable for germination and seedling survival in general may account for their overall more positive correlations among themselves than with members of other groupings, as well as their overall very high positive ones with Melampyrum lineare, (Mel, no. 29). The latter is an annual, and therefore perhaps also favored by such conditions.

From Table VII of the correlation coefficients (pages 91 ff.) we discover that there seem to be two sets of mutually positively correlated species among the (SS), one consisting of Anemone (no. 3 in the tables), Arctostaphylos (no. 4), Oryzopsis asperifolia (no. 32) and Solidago (no. 40), the other of Aster "hairy ovate" (no. 5), A. laevis (no. 6) and Viola (no. 45). Within the Anemone etc. set, all of six possible pairs are significantly positively correlated on G on either 1 m^2 or 1/4 m^2 scales, as are two of three on WC. Within Aster etc. all three pairs are significantly positively correlated on one of these two segments. The two sets are connected to one another by a strong positive correlation ($P < .001$) on G, 1 m^2 between Aster "hairy ovate" and Solidago. Prunus (no. 34) shows

affinities with both groupings, while the other four species, Amelanchier oblongifolia (no. 1), A. sanguinea (no. 2), Oryzopsis pungens (no. 31) and Rubus (no. 37) are essentially uncorrelated among themselves or with members of either set.

Correlations of the members of these two sets with other species and variables are of little help in suggesting causes of their apparent affinities for one another. Neither's members can be shown to be consistently mutually positively or negatively correlated with any other entity, so we must conclude tentatively that one or more unmeasured factors are responsible. Interactions between grouping members seems unlikely in this case, because the small sizes of these plants does not suggest a large or strong sphere of influence.

These correlation sets more likely result from several species' germination and seedling survival being favored by the same combination of conditions. Thus certain (SS), whose seeds were already present throughout the area, might quickly germinate where a tuft or part of a clone of one of the major species of the community had died. They could then thrive there for a year or two until another major species had found its way into the spot and displaced

them. The absence of other vegetation on the spot meanwhile would account for the generally circumneutral correlations which (SS) exhibit, tantamount in this area to negative correlations because of the overall positive trends. Or a very local disturbance phenomenon could be opening up microsites favorable for colonization by several (SS) species at once; a possible one in this study area is the paw marks made by deer in attempts to unearth fruiting bodies of the subterranean fungus Elaphomyces (Gillis 1959). Beaman and Andresen (1965) report ecesis of subalpine species, which seem to play a role similar to the (SS) in their study area, on the loose earth at the edges of rodent burrows. Or multispecific insect seed caches, much like the unispecific ones of Melampyrum reported by Cantlon et al. (1963), may serve as sources of clumps of several (SS).

In comparing these two sets of (SS) with the Hopkinsian basic units (Chapter IV), we find that on G, members of both are included within a single large basic unit along with many other species with which they have little affinity (Figure 7 A, page 137). On WC (Figure 7 B), Aster laevis and Viola of one set form a unit of their own at the $P < .01$ level, not connected to other

units. But here, too, members of the other set remain with their atrange bedfellows in the large basic unit. Some of the species not in either set are in the large unit on both soils, while others constitute unispecific units unto themselves or participate in small ones together with one or two non-(SS) species. We have a further demonstration, then, that a grouping technique based upon an oversimplification and vicarious correlation does not yield information comparable to that from one using information from several sources and involving "subjective" judgement.

On the "dry end" of the gradient there is a number of significant positive correlations of (SS) with both Vaccinium angustifolium var. nigrum and with shrub cover as a whole (no. 49). This could be a reflection of the field-observed affinity of these (SS) species for the more "hummocky" microtopography where Vaccinium is lushest, and also to a spatial exclusion from Carex pensylvanica (Car, no. 10) tussocks, for only one (SS), Amelanchier oblongifolia, is significantly positively correlated with Carex on G or WC and only at $P < .05$.

A tendency of the (SS) towards positive correlation not only with the clonal xerophytes (CX), but with the more mesophytic (MD) and (MW) as well on the more poorly drained

AS, may be the result of mutual exclusion of all of these species from the more poorly-drained portions of this soil type. This discussed in Chapter III.

Beginning with the individual species alphabetically, Amelanchier oblongifolia (Amo) is positively correlated with Carex (Car) on G. This suggests that germination or escape from seed predators of the former may be favored in heavy patches of that sedge, which seems inhibitory to other (SS). A. sanguinea's (Ams) positive correlations with soil horizons on AS and slight negative trend with other species do little but reflect its cover maximum on the more poorly-drained and poorly-vegetated Saugatuck sand of this segment. Anemone in the field seems to be favored in mossy areas of buried logs and stumps and sparse litter, along with such mesophytic species as Maianthenum canadense (Mai, no. 28) and Gaultheria procumbens (Gau, no. 22). But the general absence of positive rs with these same species must mean that Anemone grows best with sparse vegetation like other (SS).

Arctostaphylos and the two Aster species are fairly typical for the grouping in their correlations. Oryzopsis pungens (Opu), however, is somewhat unique in its positive and quite significant correlation with Danthonia spicata

(Dan, no. 18), a consequence perhaps of the extreme xerophytism of both. O. asperifolia (Ors), is peculiar in having cover "peaks" on both G and AS, with a low on the intermediate WC. This low represents a depauperateness of individual plants or small clones, since frequency was found not to diminish there. It seems not to be due to an intolerance to the heavy Pteridium cover on WC, for this Oryzopsis is not substantially negatively correlated with that fern. Nor, on the basis of available evidence, does it seem to be connected with the similar bimodal curves for moss and lichen cover (Chapter VIII, Section A). On G, the only segment where its correlations with the bryolichen species were calculated, O. asperifolia is circumneutral with all but one of them and negative with that. So causes of this peculiar distribution remain a mystery. Moreover, this rice grass, unlike a few (SS), is not positively correlated with the more moisture-tolerant mesophytes on AS and is highly negative with A_1 horizon thickness (no. 60) and gley depth (no. 63) there. Both of these suggest that, near the bog margin, it surely occupies the most xeric microsites and does not really have a broad tolerance with respect to soil moisture.

Much of Prunus' shrub and herb-sized cover on AS

actually represents root sprouts from larger and older tree sized plants. Thus this species' high correlations on that segment possibly reflect mostly the influence of these trees and their litter upon other species. Elsewhere, Prunus' negative correlations with several lichens on WC suggest either that it cannot ecese well on the hard packed, sparsely litter-covered soil favorable to these symbionts, or that lichens grow poorly under Prunus cover. Prunus litter, in fact, may contain inhibitory chemicals, since a number of vascular species also exhibit poor growth near these trees.

A very high positive correlation of Rubus with Melampyrum (Mel, no. 29) on G is noteworthy. Solidago's correlations are predominantly non-significantly negative, which suggests that its marked restriction to the sparsely vegetated "dry end" may be due to an even stronger intolerance of lush vegetation than that found in most (SS). Viola is also thus restricted, but its high positive correlations with Carex pedunculata (Cpd, no. 9) and Melampyrum suggest somewhat different reasons, possibly a selective relocation by insects of seeds of all three of these species in the same microsites (Cantlon 1965).

B. CLONAL XEROPHYTES (CX). All of these species

are characterized by the following:

1. maximum per cent cover found on one of the three best-drained soil types (Grayling, "Wet Grayling", or Croswell sands), although cover on Au Gres sand may nearly equal that on Croswell,
2. cover on the best-drained soil, Grayling, is at least more than half that on any other soil type,
3. all species are markedly and obviously clonal with large and extensive clones,
4. cover of all species exceeds 0.28% on the soil type where maximum and three of five have over 1.0%, the (SS), by contrast, never having over 0.48% (discounting Prunus' abundant root sprouts on AS), and half of the latter having less than 0.1%,
5. per cent frequency, on the segment where maximum, is on the whole much higher than for the (SS).

In short, then, these are the more common species having xerophytic microdistributions, generally more abun-

dant, clone-forming and conspicuous than the (SS). Two, Carex pensylvanica (Car, no. 10) and Pteridium aquilinum (Ptr, no. 35) are dominants in the herb layer on those soil types where they are most abundant. The criteria delineating the assemblage from the (SS) on the one hand and the "margin dry" (MD) species on the other are undeniably arbitrary, a species like Danthonia spicata (Dan, no. 18) approaching the former in its low cover and absence from AS, while Comptonia peregrina (Com, no. 12) approaches the latter in having close to maximal cover on Au Gres sand.

Of the five species included here, Carex pedunculata (Cpd, no. 9) is a tussock-forming sedge, C. pensylvanica a slightly smaller one which resembles it but contributes many times the amount of cover, Comptonia an odoriferous myricaceous shrub called "sweet fern", Danthonia the xerophytic "poverty oat grass" and Pteridium the large bracken fern.

Physio-ecological heterogeneity within the assemblage is suggested by the correlations between the included species themselves. Of ten possible pairs of species, only two, Carex pensylvanica-Comptonia and Comptonia-Danthonia, are significantly positively correlated with each other on

either G or WC, the grouping's optimal segments. In fact, the (CX) seem to have less in common than do the (SS). Throughout the various soil types and quadrat sizes, the former scarcely exhibit higher proportions of significant correlations than do the latter, in contrast to the groupings of more mesophytic species (see Table II, page 55).

In Chapter III, Section C, the predominant negative shifting between WC and AS of correlations between these (CX) and species reaching maximum cover on the bog margin was discussed. It was suggested that a positive trend on WC might result from members of both groupings here being near their range limits, therefore being mutually restricted to microsites in which neither competition nor abiotic conditions are severe, whereas on their optimal AS the mesophytes themselves act as a competitive restrictive force on the (CX). Now, for Carex pedunculata, Comptonia and Pteridium either all or most of these shifts are negative (in each case about half of them with (MD), half with (MW)). Carex pensylvanica, however, exhibits three positive shifts and no negatives, suggesting that this sedge may be more tolerant of soil saturation or of competition from the moderately mesophytic species than the other three. The latter seems more likely since C. pensylvanica decreases

sharply on the more frequently flooded part of AS. There are no correlations for Danthonia on AS.

On AS there is a tendency in the correlations of (CX) towards negativeness with A_{OH} (no. 59), A_2 (no. 61) and moss cover (no. 51). These variables exhibit higher values on the more poorly-drained Saugatuck part of AS, so this is compatible with the cover curves of these species and their postulated occupancy of the more xeric microsites. Perhaps for the same reason Carex and Comptonia are also quite positively correlated with thickness of the B horizon (no. 62), which becomes more compact and thinner in wet spots.

Carex pedunculata is positively correlated with B thickness on WC, however, which on that soil suggests a decided preference for the more poorly-drained portion. This is in harmony with the cover curve for this species, which is noteworthy for its puzzling secondary cover increase on Au Gres despite its primary maximum on G. As with Oryzopsis asperifolia of the (SS), the low of C. pedunculata on WC does not seem to be due to inhibition by Pteridium or connected with similar curves for mosses and lichens, and its causes remain obscure for the present.

Dominant Carex pensylvanica seems, to the eye, to constitute one of the primary components of the vegetation

on the "dry end", the blueberries Vaccinium angustifolium var. nigrum and V. boreale comprising the other. On each of the two best-drained segments, Carex is significantly negatively correlated with a different one of these two blueberries but not highly so. Evidently, then, the Carex and Vaccinium components are not arranged in a distinct mosaic, but blend and combine with one another almost imperceptibly.

Overall, Carex has a tendency towards slight (non-significant) negative correlation with most other species on these two soils, as if its large and extensive tussocks are inhibitory to their growth.

Comptonia has an ill-defined cover "peak" on Croswell, but its cover is relatively high from Grayling through Au Gres. In other areas it frequently colonizes disturbed microsites such as roadcuts, and in this it is capable of being a pioneer like some of the (SS). Of all the (CX) it exhibits the highest number of substantial positive correlations with other (CX) and with those (MD) which appear relatively drought tolerant on the imperfectly drained AS, suggesting some moisture intolerance and maximum growth on microhummocks. Comptonia's demonstrated intolerance to transplanting under full sunlight conditions (Chapter VII,

Section G) at present suggests little relating to its natural patterns.

The 1960 experiments showed that Danthonia, like most species, can both survive as an adult and germinate about as well on AS as on G, provided that natural interaction is eliminated (in fact a few plants survived transplanting in the bog!). On the basis of quadrat data, however, it is one of the species most restricted to the "dry end", and positive correlation with bare ground and lichens, slight negatives with litter cover and thickness are in line with a xerophytic microdistribution also. This must be due, then, not to simple moisture intolerance but rather to Danthonia's possession of the competitive edge over other species only in xeric situations. Such an edge was suggested, though indecisively, by the 1961 interaction experiments (Chapter VII, Section G). This grass' broad physiological amplitude in cultivation must therefore shrink remarkably under natural interactive stress. Probably its production of maximum cover in dry, open areas is, then, a result of inability to outcompete less drought tolerant species in the physically choicer microsites.

Pteridium is noteworthy on WC for its predisposition towards slight negative correlation with other species (see

Chapter III, Section I), contrasting with most species' positive trends. Watt (1945) found that the corresponding taxon in British pastures severely inhibited other species beneath or near it. Seemingly it produces an antibiotic substance which builds up slowly in the soil but remains for some time after the bracken clone has died in a spot and migrated elsewhere. As it happens, clones of Pteridium produce their densest, most extensive cover on WC (although overall per cent cover of this fern is not higher on this segment than elsewhere), and so this negative correlation pattern may stem from strong antibiotic inhibition here. It would almost surely be more marked if bracken cover of a year or two ago were correlated with present cover of other species in the same quadrats, for Watt found inhibition most apparent in spots where the bracken had recently died.

The Pteridium situation points up a need for temporal as well as spatial study of the present area, but in the absence of such a time dimension it is possible to detect some evidence of a cycle of bracken invasion, bracken death, inhibition, and gradual recolonization. For instance, the ϕ coefficient (based upon presence) of Pteridium-Danthonia on G is negative, significant at $P < .001$,

yet the r (based upon cover) is only slightly and non-significantly negative. Thus luxuraint Danthonia tussocks may be favorable new colonization ground for Pteridium, which would then move in vigorously and produce lush cover in the same spots with good growth of this grass. But later perhaps Pteridium kills this Danthonia, causing the negative ϕ and making r circumneutral rather than positive.

C. MARGIN DRY (MD). This grouping of six taxa is characterized as follows:

1. it is similar to the (CX) in being present on G,
2. but, unlike the latter, the cover maxima of its members occur on Au Gres sand or, if on Croswell sand, then their cover on Au Gres is only slightly lower,
3. cover of all species decreases between Au Gres and Saugatuck sand, appreciably so in all but Maianthemum canadense (Mai, no. 28), although it may rise again on Kinross,
4. all are markedly clonal, and
5. all are either dominants or conspicuous components of the vegetation, especially

near their cover optima.

Thus this assemblage is also one of clonal species, but with optima shifted "down-gradient" from those of (CX). They differ from the "margin wet" or (MW) species (Section E of this chapter) in at least being scattered throughout the best-drained soil type Grayling, not absent or merely sporadic.

Members of the grouping are Epigaea repens (Epi, no. 20) and Gaultheria procumbens (Gau, no. 22), both rhizomaceous ericaceous ground shrubs, Melampyrum lineare (Mel, no. 29), a delicate annual in the Scrophulariaceae, Maianthemum canadense (Mai, no. 28), a smallish liliaceous herb, and the low bush blueberries Vaccinium angustifolium var. nigrum (Vig, no. 44) and V. boreale (Vyp, no. 47).

In their negative trend with lichens and in their high positive correlations with other (MD) and (MW) on the "dry end" of their range, where they are probably mutually restricted to mesic or low-competition microsites, these species "behave" as expected for mesophytes. With soil horizons, which increase in thickness with poorer drainage, the (MD) are much more positively correlated on WC than are the (CX), but become negatively so on AS as befits species favored by moist, but not overly-saturated soils. Yet con-

sidering the relatively small changes between means of two of the horizons from Wet Grayling to Saugatuck, this pattern suggests a real preference for thick profiles on WC combined with an aversion to them on AS.

A count on G and WC of positive and negative coefficients with the two Vaccinium taxa and with Carex pensylvanica is revealing. About half of the coefficients of other (MD) with the two blueberries are positive (+0.1 or greater), the other half circumneutral (-0.09 to +0.09), with none more negative than -0.09. With Carex, on the other hand, the pattern is essentially reversed. No (MD) are more positive than +0.09 with it, and almost half are more negative than -0.09. The (MW), discussed in Section E, is another mesophytic grouping. With Vaccinium, seven of their eight coefficients which are 0.1 or over in absolute value are positive, the other only slightly negative. The pattern with Carex is negative, so the (MW)'s affinities seem similar to the (MD)'s. By contrast, the more xerophytic (CX) have slightly more negative (15) than positive (10) correlations with Vaccinium (32 circumneutral), if we use the same breaking points. With Carex they have 6 positive and only 3 negative (13 circumneutral). Thus on the well-drained end Carex and its associates seem in a

rough sort of way to represent the xerophytic element in a vegetational mosaic and Vaccinium the mesophytic one. (The aversion of the mostly xerophytic (SS) to Carex, discussed in Section A above, could stem either from supression of germination or low seedling survival of these species in the sedge tussocks.

All of this, incidentally, is only very slightly reflected in the Hopkins basic unit calculations of Chapter IV, yet another damaging bit of testimony against mathematical oversimplification.

Epigaea, of all the (MD), has the least of its total cover on G and WC (and thus comes closest to the (MW) grouping), but also is relatively low on fairly poorly-drained Saugatuck sand. This would suggest a rather narrow physiological amplitude for this species, except that its cover strangely rises again on R. Noteworthy among its individual correlations are a very highly positive one with Maianthemum on G, which is still quite high on WC. The latter is the other (MD) species most nearly absent on better drained soils, so both may be very severely restricted to the same mesic islands on those segments.

Gaultheria also has very low cover on G but, unlike Epigaea, much higher cover on Wet Grayling. On the "wet

end" of its range it also seems more tolerant than Epigaea by virtue of relatively high cover on Saugatuck, and is even found in one DG quadrat. Gaultheria's only slightly negative correlations with bog species on R are in line with this relative abundance unusually (for an inorganic soil species) far "down-gradient", and suggest relative saturation tolerance. This species is positively correlated with Epigaea and Maianthemum on the "dry end" except with Epigaea on G. It seems better able to withstand lush cover and possible antibiosis by Pteridium than some other species, and positive coefficients with thickness of A_{OH} (on G) and of A_1 (on AS) fit with an observed affinity for organic matter such as rotting logs. The latter is not likely macrodistributional in view of Gaultheria's nearly equal cover on both AS soils. Circumneutrality with both shrub and herb cover (nos. 49, 50) on AS, contrasted with high significant positive correlation with them both "up-gradient" and "down-gradient" from it, suggest that Gaultheria may be a relatively poor competitor in the closely-spaced vegetation of Au Gres and Saugatuck sands.

Maianthemum's cover curve looks like a combination of Epigaea's on the better-drained segments and Gaultheria's on the more poorly-drained ones, except that it is very low

on R; the species thus must tolerate moderate soil saturation better than drought. Some of Maianthemum's correlations seem contradictory. A positive one with tree cover (no. 48) on AS suggests that shade may be favorable but on G, where Maianthemum presumably would be even more in need of this transpiration-reducing factor, the correlation actually becomes non-significantly negative. Yet quite positive correlation with herb cover (no. 50) suggests that Maianthemum might be favored by the shading and wind-reduction benefits of this synusium. Significant positive

s with three of twelve (SS) are not necessarily in conflict with this, since the three are not the most xerophytic of the group, and the corresponding circumneutral rs indicate that Maianthemum's cover maxima are not with them. The same positive ϕ -circumneutral r pattern with mosses suggests similarly that Maianthemum is abundant in mossy patches but produces lower cover there than visual evidence would suggest.

Melampyrum produces relatively high cover on the well-drained soils. It is the only annual species among those regularly encountered in the study areas and probably the only one abundant in undisturbed areas in this vegetation type in general. It also has the distinction of being

a hemiparasite (Cantlon et al. 1963, Piehl 1962, Malcolm 1962). This last may not be particularly reflected in Melampyrum's correlations, however, since the roots of Pinus and other woody plants into which this annual sends haustoria could, as often as not, originate outside the quadrat containing the above-ground portion of this host plant. Melampyrum does, nonetheless, exhibit an unusual number of very highly positive ϕ coefficients, especially on the well-drained end of the gradient where vegetation is sparse. In interstices between lush patches of Vaccinium, Gaultheria, etc. the concentration of suitable host roots near enough the surface for this hemiparasite to attack would be relatively low, and desiccation-induced die off of fine mycorrhizal roots in these interstices may further reduce their number, resulting in low probability of Melampyrum occurrence.

Cantlon et al. (1963) and Curtis and Cantlon (1963) demonstrated that seeds of Melampyrum germinate in the mat, or duff, and Cantlon and Curtis (1964) found empirically that both seeds and potential host roots were sparse where the surface was nearly or quite bare of litter, duff, or humus and also in the 25-30 cm. circle around tree bases where litter is deep. It is not suprising, then, that

Melampyrum exhibits a slight but definite negative correlation trend with the measurements of litter and duff thickness (lit, no. 54, aol, no. 57, aom, no. 58) and also moderate negative correlation with A_{OH} (no. 59) on AS. Its moderate negative correlation with per cent of ground not covered (bar, no. 55) moderate positive one with per cent litter cover (lip, no. 53) are also as might be expected from these observations, as is a slight negative correlation with tree cover (no. 48), which may reflect the absence of seeds and host roots near the tree bases. On AS, moderate negative (though non-significant) correlations with shrub and moss cover (nos. 49, 51), on the other hand, do not corroborate the findings of the aformentioned workers that lush cover of these two synusia seems to reduce bird and insect predation on Mel seeds.

Mel's annual nature seems to show up in its many highly significant positive correlations with other species which also reproduce in this area mainly from seed, and may therefore have similar requirements for seedling survival (Section A of this chapter).

Vaccinium taxa, because of the peculiar taxonomic problem which they present and the desirability of discussing their taxonomy and ecology together, will be given a

section unto themselves.

D. VACCINIUM, AN ECOTAXONOMIC PROBLEM. The two distinguishable blueberry taxa which span the study gradient have recently been called two varieties of Vaccinium angustifolium (cf. Fernald 1950). The taxonomy, however, has been in a state of confusion, partly because both diploid and tetraploid forms of the blue-berried, non-glaucous leaved entity (abbreviation symbol, Vyp) seem to exist, while only tetraploid material of the black-berried, glaucous-leaved entity (Vig) has been found (Camp 1945, Hall and Aalders 1961, Aalders and Hall 1963). The two cytological conditions are apparently morphologically distinguishable in some areas, but unfortunately material from the study area has neither been examined cytologically nor compared with properly annotated herbarium specimens at the time of this writing. Nonetheless, the voucher specimens of the blue-berried form fit Camp's (1945) description for diploid material only, as most plants in the field appear to also. An occasional more robust, larger-leaved blueberried plant seems to vary in the direction not of tetraploid material, but of V. myrtilloides, which is also found in the area. These aberrant plants probably represent introgression with the latter such as seems to occur in other

regions (Camp 1945, Hall and Aalders 1961). The two papers just cited both report that V. myrtilloides is a diploid; if so then the gradient-spanning blue-berried form must also be diploid in order to readily exchange genes with it. This evidence strongly suggests that this blue-berried gradient spanner properly belongs to diploid V. boreale Hall & Aalders (the authors retaining V. angustifolium Ait. for tetraploid material since it matched the type specimen). The black-berried entity remains V. angustifolium var. nigrum (Wood) Dole. A comparison of recent nomenclature follows.

ABBREVIATION	2n	Camp 1945	Fernald 1950	Hall & Aalders 1961
Vyp	24	V. angustifolium Ait.	V. angustifolium Ait.	V. boreale Hall & Aalders
	48	V. lamarckii Camp	V. angustifolium var. laevifolium House	V. angustifolium Ait.
Vig	48	V. britonii Porter ex Bickn.	V. angustifolium var. nigrum (Wood) Dole	V. angustifolium var. nigrum (Wood) Dole
Vam	24	V. myrtilloides Michx.	V. myrtilloides Michx.	V. myrtilloides Michx.

Aalders and Hall (1963) furnish corroboration for the above postulates. They found that the "nigrum factor" segregated like a single dominant gene in crosses between V. angustifolium vars. nigrum and angustifolium from tetraploid populations of the Canadian Maritime Provinces. In both the laboratory and in the field the authors found occasional intermediates with only some characteristics of the nigrum form, such as might occur within a freely interbreeding population containing modifier genes. But they mention that such intermediates do not occur in the Lake States, and indeed I have encountered none during extensive field work in the study area and elsewhere in Michigan. The two entities thus appear to be reproductively isolated populations and hence separate species (cf. Davis and Haywood 1963), in this region, very possibly by virtue of the ploidy differences just postulated.

In the grosser aspects of their distributions, the two taxa which span the gradient in the study area do not violate one's expectations for a single species, for their frequency and cover curves (Table I, pages 35, 36) coincide almost exactly. In spanning the gradient, moreover, they differ from all other species save the three Pinus species found here. Yet if we examine their correlations, they do

not appear much more similar than any two phyletically remote species might.

To illustrate this last point, let us score each of the blueberries as positively associated with another species or other variable if it exhibits a positive correlation coefficient $r \geq 0.25$ with the variable, or an r smaller than this but significant at $P < .05$. Negative coefficients satisfying the same conditions will be accepted as evidence of negative association, and variables whose correlations with a Vaccinium taxon fall between these two limits will be considered unassociated with it. Then, of the 40 species and other variables with which at least one Vaccinium entity is positively or negatively associated, there are only 13% with which the other exhibits the same kind of association (on at least one of the same gradient segments, irrespective of quadrat size). With 77% the other is unassociated and with 10% it exhibits the opposite kind of association (i.e. negative as opposed to positive or vice-versa). The degree of similarity demonstrated is scarcely greater than, for example, that between the black-berried form and Cornus canadensis (Cor, no. 14, of the (MW)). Using the same criteria, these two phyletically remote taxa sxhibit 7% similar association with other

variables, 79% association of only one of the two with the variable and 14% dissimilar association. By contrast Cornus and Coptis groenlandica (Cop, no. 13, (MW)), taxonomically remote both from one another and from black-berried Vaccinium, but suspected of a positive interaction because of the inordinately high positive correlations between themselves, yield the respective percentages 50, 50 and 0. This is about four times the proportion of similarity exhibited by the two blueberries!

Thus, the two blueberries certainly show no more ecological similarity than can be found among separate species. At least, they exhibit more ecological difference than might normally be expected of two entities differing by a single gene, such as seems to separate two similar-appearing entities in Eastern Canada. Although the similar distributions of both across the gradient may reflect close phyletic relationship and recent isolation of the two populations, the demonstrable uniqueness of their microenvironmental relations is consonant with the taxonomic evidence that they must constitute two separate gene pools. Each may contain a fair number of alleles not possessed by the other, or, extrapolating from the findings of Löve and Löve (1943), a ploidy difference could itself account for the

observed ecological difference.

As for specific features of the two blueberries, their cover is maximal on Au Gres but is nowhere really low. They contribute sufficient cover in proportion to the total vegetation throughout the inorganic soils to be very decidedly the shrub dominants.

If we score each taxon according to whether it appears the more mesophytic or more xerophytic of the two on the basis of its correlations, we find V. angustifolium var. nigrum the most mesophytic-appearing on the "dry end" (G and WC) on the basis of four out of five correlation patterns. On AS, however, the two appear tied with three correlations or correlation groups each in the more mesophytic category. V. boreale seems to have much more aversion to the dominant shrub Chamaedaphne (Chm, no. 11) in the bog, and much more affinity for areas occupied by Eriophorum spissum (Eri, no. 21, "cotton grass") than does V. angustifolium var. nigrum. On R, V. boreale is quite positive with herb cover (no. 50) and seems to occur more on the open, "peat-like", non-litter-covered patches than does V. angustifolium var. nigrum.

E. MARGIN WET (MW). This assemblage includes nine clonal species of inorganic soils. They are the delicate

evergreen herbaceous goldthread, Coptis groenlandica (Cop, no. 13), the robust, codominant, herbaceous bunchberry, Cornus canadensis (Cor, no. 14), the large occasional shrubs Swamp holly, Ilex verticillata (Ilx, no. 23), nanyberry, Viburnum cassinoides (Vib, no. 43) and Mountain holly, Nemopanthus mucronata (Nem, no. 30), a lowbush blueberry, Vaccinium myrtilloides (Vam, no. 42), an occasional small herb, Trientalis borealis (Tri, no. 41), a repent blackberry, Rubus hispidus var. obovalis (Rho, no. 36), and the clubmoss Lycopodium obscurum (Lyc, no. 27).

In their maxima of cover as well as in their "dry end" range limits, the (MW) on the whole appear more mesophytic than the (MD). They are characterized by:

1. absence from G, or of too rare occurrence on this best-drained segment to have had correlations calculated for them there (thus distinguishing them from (MD)),
2. having their highest cover between Au Gres and Kinross, inclusive (whereas the (MD) sometimes peak on Croswell and never below Au Gres),
3. being otherwise like (MD), except that

some are not dominant or conspicuous.

Although (MW) are thus more mesophytic in distribution than (MD), some (MW) drop more drastically on Saugatuck and Kinross than some (MD). Although the groupings used in this chapter seem somewhat natural, they are nonetheless arbitrary, and in this case one could as well use "wet end" distribution to separate out two groupings of mesophytes about as physio-ecologically homogeneous as the (MD) and (MW).

Some overall correlation trends of the (MW) nonetheless do suggest that they have a general affinity for moister microsites than do the (MD). Unlike the latter, for example, (MW) tend to remain mutually positively correlated on AS as well as WC, perhaps tending to be unsuccessful in relatively xeric microsites even on their optimal segment and so being clustered where moisture is more plentiful. They are even more negatively correlated with lichens than are (MD) and even slightly so with mosses. Like the (MD) and to some extent the (CX), the (MW) are more abundant on those portions of WC with thicker profiles and more poorly-drained soils, and like them shun the heavily litter-covered areas shaded by dense tree canopy along the Saugatuck-Kinross border.

Those species which peak on Saugatuck and Kinross (Ilex, Nemopanthus, Viburnum, Vaccinium myrtilloides) are predictably much less highly positive in their coefficients with the (MD) and other (MW) on AS than are the remaining (MW) that reach cover maxima on Au Gres (Coptis, Cornus, Lycopodium, Rubus, Trientalis). Evidently the former must occupy less droughty and/or more frequently flooded microsites than either the latter or the (MD). The overall absence of high positive correlation between the (MW) themselves on R also fits the picture; these species are probably nearer their optima here and so not so mutually restricted to certain portions of the area as they are on AS, or as are the (MD) here on R.

Starting with those (MD) species having the most xeric gradient distributions, we have the codominant Rubus hispidus var. obovalis, maximal on Au Gres. Its cover is only about one-third less on Croswell, but drops to a small fraction of this on still better-drained soils. On the "wet end" its cover drops drastically also (relatively high frequency on Saugatuck, however, indicates abundance but depauperateness there). Significant positive correlations with Danthonia spicata and Prunus serotina, discussed respectively in Sections B and A of this chapter, suggest

that Rubus is a poor competitor, but responds favorably to the usually inhibitory litter of Prunus. Or possibly low competitive strength merely relegates high Rubus cover to relatively unfavorable sites like those under Prunus.

Trientalis, a very minor biomass component, also occurs on G and follows Rubus' general pattern on the better-drained segments, but its mean cover scarcely drops on Saugatuck and Kinross. Along with its positive correlation with gley depth, no. 63 (Rubus' is negative) this seems to mirror a prevalence on profiles developed under moister conditions than those most favorable to Rubus. It has relatively low (for (MW)) positive rs and ϕ s with other margin species on AS; whether as a result of encountering its optimal moisture regemin a bit farther "downgradient" than they or of poor competitive ability is a question.

Coptis and Cornus, with the very high positive correlation between them discussed in Section D of this chapter, reach up the "dry end" only as far as Croswell and reach their maximum in cover on Au Gres but in frequency on Saugatuck. Cover drops rather drastically on Saugatuck and Coptis' does not but otherwise their distributions are essentially the same, as are the majority of their corre-

lations with other variables. Evidence suggests that their coincidence in these respects may be a result of a positive interaction between them rather than a cause of their correlation, for the partialling out of other variables changes the high positive Coptis-Cornus coefficients but little, on the whole (Table IX, pages 159-162). On the other hand, the transplant experiments (Chapter VII) seemingly demonstrated that each could grow separately, but insufficient time may have elapsed for dispersal of metabolic byproducts in the soil blocks transferred with the plants. Cornus was shown to be independent of Coptis at the germination stage of the life cycle, but the converse was not tested. At the moment it is impossible to suggest, then, just what might be the mechanism of such an interaction if it exists.

Rounding out the species maximal on Au Gres is Lycopodium. It is relatively abundant on Croswell through Saugatuck and absent elsewhere. Correlations with this clubmoss were calculated only on AS, 1 m^2, which makes it difficult to say much except that it seems typical for the grouping.

Whether Vaccinium myrtilloides' high survival as transplants in the bog indicates a true flooding tolerance, masked in nature by competitve inferiority with Chamae-

daphne and other bog shrubs, or merely a greater ability to survive transplanting under more adverse conditions than most species, one cannot be sure. But positive correlations on R with Chamaedaphne (no. 11) and the bog grass Eriophorum (no. 21), are unique among the (MW) (even including Nemopanthus and Ilex which have their maxima farther downgradient) and certainly suggest the former. Yet to complicate the picture, V. myrtilloides on R also demonstrates greater affinities with the (MD) than with the other (MW), which one would interpret as an indication of some xerophytism or flooding intolerence (on optimal AS it is highly positive with (MW)). The 1961 experiments (Chapter VII, Section E) suggested that this Vaccinium is relatively drought-tolerant in the absence of competition, and now it appears that the same might be true for inundation tolerance. Possibly, then, V. myrtilloides has a wide moisture amplitude but is a poor competitor. Its relatively low cover in the lush vegetation of Au Gres sand is compatible with this interpretation.

Viburnum's cover curve is similar to Vaccinium myrtilloides', but the former first appears on Croswell, while the latter actually reaches Grayling. Viburnum exhibits a slightly negative trend with other species gen-

erally on AS, and is barely positively correlated even with other (MW), possibly a consequence of greater abundance on the more sparsely vegetated Saugatuck here. Yet V. myrtilloides, also with a maximum on Saugatuck, shows the usual overall positive correlation trend with other variables, and this continues even on R, where Viburnum's correlations are predominantly weakly negative. This leads one to suspect Viburnum of ability to take advantage of microsites unfavorable to most species, or possibly of some growth-inhibiting ability. It does not occur out on DG proper in any amount and would seem intolerant of "bog-like" conditions on the basis of its negative trend with organic soil species.

Nemopanthus first appears on Au Gres, going "downgradient", reaches a maximum on Saugatuck and Kinross and is present sporadically on the peat. In certain open bogs this species constitutes a distinct zone along the hingeline, and a very high positive correlation with lichen cover on R suggests an optimum on the relatively lichen-rich, better-drained side of this segment where such a zone would occur.

Ilex' maximum coincides with Nemopanthus' but the former has a broader amplitude on both sides though less

cover on Saugatuck. It, too, forms a bog margin zone in some areas and occurs in this bog on "high, dry" microsites near sporadic trees, associated with Ledum (with which its correlation is positive on R). On the better-drained side of its range, Ilex is astonishingly positive with Carex pedunculata (no. 9) and Comptonia peregrina (no. 12), two relatively quite xerophytic species. A high positive coefficient with herb cover, (no. 50), which predominates on inorganic soils, and a non-significant negative one with humus thickness (no. 59), which tends to be directly proportional to soil moisture, suggest that Ilex joins Nemopanthus in bordering the "dry side" of the hingeline. Yet the two would seem not be most luxuriant in the same microsites, for they are slightly negatively correlated with one another.

Ilex has a high positive correlation with bare ground (no. 55) on AS. Since this arborescent perennial's mature plant distribution could hardly be much influenced by small bare patches, and since the ones present when Ilex was a seedling have in all probability disappeared or shifted spatially, one wonders whether Ilex may not itself play a role in their production.

F. BOG SPECIES (B). The distinguishing features

of members of this grouping are:

1. sufficient abundance in the bog segment, DG, for correlation analyses (i.e. presence in 5 or more DG quadrats),
2. cover maxima on one of the two most poorly-drained segments, DG or R, or else present in at least 14 DG quadrats,
3. cover on each segment better drained than R characteristically (i.e. in all but two cases) only a small fraction of that on the adjacent, more poorly-drained one.

These are thus species characteristic of the bog, dominant or abundant there but usually not elsewhere on the gradient. All but the two gradient-spanning Vaccinium taxa decrease rapidly in abundance "up-gradient"; these last however span the whole gradient and thus are considered in both the (MD) and (B) groupings.

Here are included the unidominant bog shrub leatherleaf, Chamaedaphne calyculata (Chm, no. 11), the prominent cotton grass Eriophorum spissum (Eri, no. 21), the locally abundant shrub Labrador tea, Ledum groenlandicum (Led, no. 26), Bog laurel, Kalmia angustifolia (Kal, no. 25), the

blueberries Vaccinium angustifolium var. nigrum (Vig, no. 44) and V. boreale (Vyp, no. 47), the creeping cranberry Vaccinium oxycoccus (Vox, no. 46), and the inconspicuous small woody laurel, Kalmia polifolia (Kal, no. 24). Also included are the dominant moss Sphagnum plumosum (Spl, no. 38), other Sphagnum species (Spp, no. 39) and another moss, Polytrichum strictum (Pos, no. 33). These mosses together form the loose, fluffy upper substrate of dead moss known as "peat moss", which covers virtually the whole bog surface, and in which the roots, rhizomes, stolons and rhizoids of most bog species are found.

Affinity for "boggy" conditions among the (B) is seen in a decided aversion to the heavy tree cover and litter cover found on the portion of R resembling inorganic soil, and positive correlations with the high moss cover typical of the peat-like portion here. But a positive trend with A_{OH} thickness on this hingeline segment is relatively weak for some reason, although this horizon is decidedly thicker on the portion of R adjacent to DG.

With other species, the (B) show fairly simple, straight forward and predictable trends; a possible slight negative tendency with the (MD) and (MW) on R and AS, and mutual positiveness among themselves here near their "dry

end" range limits are traceable, probably, to mutual areal restriction. There is an unusual (for this gradient) number to high negative correlations between the (B) species on DG, where there is a wider variety of microhabitats open to them than on R so that interspecific physio-ecological differences are manifested. This is probably related to the strongly-developed hummock microtopography here, and an ecological differentiation among the species relative to it. It is precisely with this individuality that the part of Chapter IV dealing with these species was largely concerned, and for discussion of the bog community from the "basic unit" angle the reader is referred to that chapter. The distinct microtopography does induce a rather distinct mosaic patterning on the bog vegetation, so that this is the one segment where the Hopkins basic units seem to provide a reasonably accurate picture of nature.

The predominantly negative correlations between shrub species on DG, which cause them to form distinct basic units, may involve an amensal reaction between them. Such a reaction is suspected also from the appearance of clones of these species in the field, for these clones almost never interdigitate with one another. Possibly established clones or their mycorrhizal fungi liberate soil-

diffusible substances similar to antibiotics or auxins in their action; potential invader shoots from a neighboring clone of another species might then be inhibited if they began to grow against a gradient of such a substance. Such a mechanism would have a selective advantage, conserving the energy of the inhibitor-liberating plant which it might otherwise expend in mechanical stresses with shoots of other species, or lose by having its photosynthetic surface overshadowed by these shoots. Rhizome and fungal distribution maps of sectors might be helpful in corroborating or rejecting these postulates.

Kalmia polifolia is circumneutrally correlated with almost everything. This small shrub seems capable of sending up shoots within clones of other species, and it may be the only DG species here which is resistant to an amensal inhibition such as that just postulated.

Between Chapter IV on basic units and Chapter VI on higher power regressions, the patterns shown by the bog species have been fairly well documented. In addition to these an affinity of Chamaedaphne and Vaccinium oxycoccus for deeper peats, mentioned in Chapter VIII, must result from differences in peat age, distances to nutrients in the mineral soil, or thickness-related predisposition to

desiccation.

A possible temporal vegetational cycle in the bog is discussed by Byer (1960). At that time, I was too eager to speculate upon details on the basis of rather flimsy evidence, but it does seem clear that such a cycle is taking place. It consists in the buildup of hummocks either, in conjunction with or under the influence of maturing clones of Chamaedaphne or other shrubs, and appears to be a counterpart on non-permafrost soil of organic soil cycles described by Johnson and Billings (1962). These clones possibly become senescent upon death of areas of the clones; at any rate they are knocked over now and then by animals or frost action, possibly creating a new "microvalley" for lush growth of the ever-present Sphagnum and Eriophorum. Perhaps the shrub clones in time reinvade these and new hummocks form.

The bog moss taxa defined here reveal in their coefficients a fairly distinct ecological series coincident with the postulated bog cycle. Sphagnum plumosum predominates in the hollows, other Sphagnum species on the sides of hummocks, and Polytrichum on the tops with fairly luxuriant Chamaedaphne.

These mosses also find their way upland onto R and

AS, but their circumneutral correlations with species of inorganic soils suggest either that they do not occur in "boggy" or "peaty" pockets there, or that such pockets are very small relative to the size of sample units. Either Sphagnum must have some probability of occupying microsites also available to mosses such as Caliergonella and Brachythecium, or else rhizomaceous plants, solidly anchored in typical inorganic soil, can send shoots into the small pockets in which Sphagnum occurs.[12]

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[12]Moss species with cover maxima on inorganic soils and lichen species, because of their small numbers and because they do not readily fit into discussions of any of the above groupings, are included with the discussions of the synusia containing them in Chapter VIII, Section A.

CHAPTER X

SUMMARY AND CONCLUSIONS

1. This study, part of a projected continuing series on organization in biological communities, is an effort to describe the patterning of a vegetation by the use of correlation techniques, to put forth postulates concerning the causes and ramifications of this patterning, and to test a few of these postulates experimentally. The present paper is primarily concerned with the first of these, the descriptive phase, but attempts not to lose sight of the eventual goal of explaining biological organization on a functional basis.

2. A relatively undisturbed vegetation transition between Pinus banksiana forest and Chamaedaphne calyculata bog, located in northern "lower" Michigan, was used in the study. This vegetation occupied a drainage-related soil toposequence ranging from excessively dry Grayling sand to Dawson and Greenwood peats, and embracing several intermediate types. For analysis, this essentially continuous sequence was divided into five segments, each relatively homogeneous unto itself.

3. Observation of differences in the patterns ex-

hibited by species throughout their local ranges brought to light possible characteristics of species which study in a more homogeneous area would not have revealed. The same may be said for the examination of several quadrat sizes as opposed to only one.

4. The existence of small-scale, or microdistribution pattern is amply demonstrated by the proportions many times greater than expectation of both $\underline{r}$ and ϕ correlation coefficients. This is true of individual gradient segments and quadrat sizes as well as for the study area as a whole. It is hardly suprising, in view of the seeming universitality of non-random dispersion as inferred from diverse studies.

5. The more abundant, more clonal species, on the basis of the relatively high proportions of significant correlations which they exhibit, seem to be more strongly patterned than the more isolated, scattered species. On the same basis, mesophytes would seem more strongly patterned than xerophytes. Since most significant correlations are positive, this suggests that clonal species and mesophytes are relatively strongly clumped together with other species. In the case of the former, this may be a consequence of clonality itself acting as a patterning agent.

6. An exception to this trend (5), the distribution of the highest correlations primarily among the rarer species, suggests high specificity in the requirements of these species.

7. Species often exhibit stronger correlation, both positive and negative, at the margins of their ranges across the moisture gradient than on their optimal segments. Mesophytes, on the other hand, are more strongly mutually positively correlated on their optimal segments than elsewhere. Both trends may stem from restriction to certain portions of a segment and from greater susceptibility to microenvironmental differences near a species' tolerance limits. Mutual positive correlation among physio-ecologically similar species under relatively poor conditions, making for overall high correlation, is common, and probably a consequence of mutual restriction to similar more favorable microsites. The opposite tendency on the part of the mesophytes may reflect more unfavorable reaction to one another's competition on their part under adverse than under favorable conditions.

8. Judging from their relatively weak correlations where their values are low, certain species and other variables appear to have threshold values of cover, thickness,

etc., below which they do not greatly influence species microdistributions.

9. The two "wet-end" segments R and DG seem, inferring from their relatively high proportions of significant correlations, to be relatively heterogeneous, perhaps because of their hummock-hollow microtopography. WC, with more mesophytic elements, appears more heterogeneous than better-drained G.

10. Large changes in the correlations of variable pairs as quadrat size decreases are predominantly in a negative direction, and the proportion of highly positive coefficients decreases. Perhaps this is a consequence of increasing intensity of spatial exclusion and competition with decreasing spatial distance. But slight changes are most frequently positive, suggesting that some positive-association-producing phenomena themselves exhibit small-scale patterning.

11. High positive correlation greatly predominates over high negative correlation in the study area, but slight negative coefficients are more common than slight positive ones. The former may reflect the small-scale patterning forces, the latter the competition and spatial exclusion, both mentioned above.

12. The trend towards predominantly positive correlations (11) is most marked on the well-drained gradient segments, and modes of all coefficients are also least negative there. Probably these reflect respectively the large, visually evident, sparsely-vegetated patches on the better-drained soils, which are rare on the mesic to wet segments, and a reduction in the intensity of negative interspecific interactions among widely-spaced plants. Within-segment heterogeneity involving several ecologically different groupings on R may account for that segments' exhibiting the lowest proportion of positiveness among its significant correlations.

13. The more poorly-drained the soil where the maximum cover of a species is found, the greater in general seems to be the reduction in the proportion of its coefficients which are highly positive as quadrat size is reduced (10). No cause-effect relationship can be suggested at present. There is no consistency in the part of a species' range (optimal or marginal) where it exhibits its greatest quadrat size-related change in proportion of correlations which are highly positive.

14. A predominant lush-sparse patterning in the vegetation may account for the relatively high proportion

of significant and high value ϕ coefficients, which are based upon presence and absence alone. A more pronounced plastic response to interspecific interaction within the lush patches may offset the association tendencies resulting from co-occurrence, substantially reducing the magnitude and significance of the r coefficients which are based upon per cent cover.

15. But on DG there are similar proportions of significant ϕs and rs, perhaps resulting from a combination of strong inhibition by shrubs, ubiquitous presence of most species, and absence of extensive sparse patches on this segment.

16. A number of different sets of circumstances can be hypothesized to explain combinations of positive ϕ, less positive or negative r, or the inverse combination.

17. Parameters of thickness and distribution of litter cover, thickness of soil horizons and per cent cover of synusia, all arbitrarily designated "environmental" parameters, seem to exert somewhat less influence on species distributions than do other species. The litter parameters seem even less influential than the other two.

18. Strength of species correlations with "environmental" parameters often seems proportional to the local

variability of these parameters, as one might predict.

19. Since roots and rhizomes seldom penetrate the lower layers of peat, species-peat thickness correlations on DG may result not from any direct effect, but from distance to mineral nutrients, greater drought susceptibility of thin peat, or variation in recency of peat formation.

20. Correlations between "environmental" paramemeters themselves are quite strong, possibly as a result of strong responses of these parameters to relatively few other variables. In the case of synusia there is, then, an apparently stronger "environmental" influence upon synusia as a whole than upon their component species. Perhaps strong infrasynusial competitional and spatial stress tends to obscure strong "environmental" associations with these species.

21. In general, the more xerophytic, rarer and less clonal species are more weakly correlated with "environmental" parameters.

22. Trends among large numbers of non-significant correlations may be helpful in generalizing about microdistribution patterns, even though the small coefficients considered singly are not.

23. In attempting to group species within a com-

munity in order to arrive at useful generalizations, the desire for objectivity and simplicity has sometimes led biologists to use methods which do not accurately reflect biological situations. Theoretical objections to specific grouping techniques are discussed.

24. A particular grouping technique, the basic unit method of Hopkins (1957), was investigated, and was found to reflect the microdistributional patterns which had been brought to light by other methods very imperfectly. This is in accord with McIntosh (1957), who found marked inconsistencies among several methods. Therefore, grouping techniques which attempt to deal with complex natural situations solely in terms of a single exact formula might best be used only as guides.

25. Partial correlation analysis is used to determine which other variables may be responsible for correlations between particular variable pairs, and to what extent, and to infer the influence of these other variables upon members of the pairs. An example is given in which some species and synusial correlations with tree cover are shown to be largely due to their correlations with litter measurements, which depend upon the trees, and horizon thicknesses, which probably helped determine tree distribution.

26. Analysis by partial correlation can also reveal otherwise obscure patterning and association tendencies. As an example, both positive and negative correlations are revealed when, respectively, differences and similarities in strength of reaction to apparently inhibitory Prunus serotina litter are mathematically eliminated.

27. Plots of quadratic and cubic regression curves seem, for the poorly-drained DG segment, to reveal biologically consequential subtleties of physio-ecological relationships and patterns which linear regressions are too insensitive to bring to light. They show promise as a tool for pattern analysis, but are quite time-consuming, subject to larger random error than linear regressions, and like the latter are liable to be misleading owing to the limitations imposed by their mathematically simple form.

28. Fourteen species transplanted to all portions of the gradient having inorganic soils and subsequently cultivated fairly convincingly demonstrated that it is not differences in ability to survive as adults, flower and fruit, or grow vigorously under natural canopy, in the absence of natural vascular plant interaction which determines natural distribution limits and optima along this gradient. Seed plantings did clearly show, for one of

nine species and doubtfully for another, that specific germination requirements are a limiting factor in their spread to better-drained soils, but other species showed no clear-cut differences in germination or seedling survival in cultivated plots. Thus interaction between species, perhaps in combination with abiotic environmental influences, would seem to play the major role in their inorganic soil gradient distributions, although specialized germination requirements are a decisive factor in a few cases.

29. Measurements of morphological characters on transplanted species and seedlings, by means of which relative vigor may be inferred, do show somewhat greater differences between portions of the gradient than do simple survival counts. This suggests, then, that such measurements may be better indicators of the abiotic component in gradient distributions than is survival.

30. The frequent inundation of transplant and seed plots on the poorly-drained organic DG segment, due to faulty engineering, limited the usefulness of transplants on this segment. No seeds germinated, and all transplants died after a year or so. Noteworthy were the high short-term survival of one bog species as opposed to

that of the other one tested, the seeming independence of relative mesophytism-xerophytism in natural distributions and ability to withstand flooding, and the fact that Vaccinium myrtilloides, absent from the bog in nature, survived in these plots much more frequently than V. boreale and V. angustifolium var. nigrum, which are naturally abundant there.

31. Survival in the interaction plots, which were not covered by natural canopy nor artificially shaded during at least the first droughty spring following transplant, was considerably lower than the near 100% survival in the 1960 transplant plots (28). Under these conditions of moisture stress, the seemingly more xerophytic species were generally the best survivors, although species similar in their natural gradient distributions sometimes differed widely in transplant hardiness.

32. On the basis of survival data and morphological measurements for both transplant and interaction plots, gradient spanning Vaccinium angustifolium var. nigrum seems actually less able to withstand drought than bog margin-restricted V. myrtilloides. These two blueberries also performed contrary to expectation with regard to flooding (30), and they seem a good illustration of per-

formance under the influence of natural interaction being different from that in cultivated plots (28).

33. Interaction experiments suggest inconclusively that both Danthonia spicata and Pteridium aquilinum may be capable of outcompeting Carex pensylvanica in open (non-tree-covered) areas, and that Danthonia is not inhibited by Pteridium. The last seems reflected in the correlations under natural canopy, which suggests a propensity for high cover of these species to occur together, but Carex would not seem to be competitively inferior to the other two under this canopy. Naturally greater abundance of Danthonia in open and Carex in shaded areas may reflect these trends.

34. Correlations with tree cover suggest weak inhibition of other species by canopy shading, and both tree trunks and shrubs may act as litter collection points which in turn influence other species. There may be an inhibition of new spring buds of shrubs and herbs beneath heavy litter.

35. Moss and lichen cover are noteworthy for their bimodal distributions across the gradient, and each major component species of both synusia reflects the bimodality. In the case of mosses, no reasons can be suggested, but

the lichen minimum is coincident with a maximum of possibly inhibitory vascular vegetation. The common mosses of the study area are decidedly more mesophytic than the lichens, but both have in common a "preference" for microsites entirely free of litter or only sparsely covered and having a thick, partially decomposed mat (A_{0M} horizon), so their odd distributions may possibly be similarly caused. The physioecological similarity of species within each of these two synusia is suggested by their mutual positive correlations as well as their individual bimodality.

36. Correlations suggest that litter is redistributed, perhaps piled and puddled, over the winter. The spring measurement is more highly correlated with species than the fall one, possibly because thick litter, along with the partially decomposed organic mat (A_{0M}), retards spring soil warming or protects the surface from freezing and drying, thus influencing bud development. Yet positive correlations between litter thickness, A_{0M} thickness and humus (A_{0H}) thickness suggest at least some tendency for litter to decompose in place.

37. A_{0M} thickness may influence species somewhat more directly than does loose litter thickness, because A_{0M}

decomposition cycles more nearly correspond to life cycles of many perennial species and because many species are rooted in or just below this layer. At any rate, thickness of both loose litter and A_{0M} seem much better predictors of species microdistributions than are the proportions of the ground covered by litter.

38. Thickness of humus (A_{0H}) and mineral-organic (A_1) horizons seem less associated with species microdistributions than is thickness of the leached (A_2) horizon. This seems somewhat suprising, considering that A_2 is not in direct contact with many plant organs, but perhaps the leaching thickness is merely indicative of the completeness of drainage to which the species respond. Correlations with thickness of the deposition (B) horizon seem to reveal little of note; the degree of cementing of this horizon and its influence upon drainage and root penetration may be much more important biologically.

39. The species were separated into five convenient groupings for further study. These were based primarily upon macrodistribution across the soil moisture gradient but take into account all available information about the species. They are:

(SS) - small, relatively rare, solitary, predominantly

xerophytic, not markedly clonal species;

(CX) - species with maximal cover on better-drained soil, forming large clones, generally much more common than (SS);

(MD) - flourishing on the more poorly-drained inorganic soils, but occurring often on the best-drained segments;

(MW) - species similar to the (MD), which however seldom occur on the best-drained soils;

(B) - species native to the bog proper.

40. The relatively small physical size of the (SS) and their general non-correlation with more clonal species may result from their playing the role of temporary colonizers of unoccupied space in the study area. This role would imply that here they were primarily young plants growing from seed, not vegetatively reproducing ones; their positive correlations among themselves and with an annual, Melampyrum, do suggest that they have similar requirements which might indeed be sites generally favorable to germination and seedling survival. They seem to be favored by relatively hummocky microtopography, in shrubby patches and generally not with tussock-forming species which might inhibit normal seedling growth.

41. The (CX) are apparently relatively depauperate on the locally thicker-profiled soils and on mossy patches on the imperfectly-drained AS segment, which tends to corroborate the relative xerophytism of which their distributions across the gradient lead one to suspect them. Carex pensylvanica and C. pedunculata, however, seem able to coexist with mesophytic elements or mesic conditions better than other grouping members. Tussocks of these sedges seem to constitute a distinct element (not in the sense of a spatial mosaic) in the "dry-end" vegetation, one which is inhibitory to certain other species. Pteridium aquilinum is noteworthy for its apparent antibiotic inhibition of other species.

42. The more mesophytic (MD) seem to have a greater affinity for a vegetational element dominated by Vaccinium spp. than do the (CX), which appear more strongly associated with the aforementioned Carex element (41). Microdistributionally as well as macrodistributionally, the former are associated with the thicker inorganic soil profiles and therefore, seemingly, are favored by relatively imperfect drainage. Melampyrum lineare is unusual for its annual character and its hemiparasitism. The absence of reflection of this hemiparasitism in the correlations per-

haps results from generally large distances of both host and parasite aerial parts from the root connections between them.

43. Fairly great differences in microdistribution patterns corroborate morphological evidence that the two gradient-spanning Vaccinium taxa in the study area are tetraploid V. angustifolium var. nigrum and diploid V. boreale, for these differences suggest prior reproductive isolation of the two and evolution along different lines. The latter seems to exhibit occasional introgression with diploid V. myrtilloides.

44. The (MW) demonstrate an affinity for less complete drainage than do the (MD) not only in their near absence from the best-drained gradient segments, but also in an apparent restriction to the more imperfectly-drained microsites on the AS segment and in relative aggressiveness on still more poorly-drained R (where the (MD) seem at a disadvantage). Outstanding among them are the pair Coptis groenlandica and Cornus canadensis; the very high positive correlation between them and their similar correlations with many other variables suggest a positive interaction between them, although in cultivation adults of each survived without the other and Cornus seeds ger-

minated without Coptis.

45. The (B) species, on their native peat, demonstrate stronger patterning tendencies than are found on the better-drained segments. This may reflect partly an amensal reaction between shrub species, partly the heterogeneous hummock-hollow microtopography found here. There appears to be a cyclic pattern of buildup, breakdown and redevelopment of the bog hummocks in which all species participate. The native bog mosses, despite their sporadic occurrence on AS, seem to occupy the same microsites here as do the (MD) and (MW), the major components of that segment's vegetation. This suggests that the low probability of establishment, not a requirement for rare bog-like microsites, may cause the rarity of these species here.

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APPENDIX A

CRITERIA USED TO SEPARATE SOIL TYPES

Soil** type	Abbreviation symbol	Limits as here defined*
Grayling sand	G	A_2 thickness 0-14 mm., or A_2 thickness 15-19 mm., B horizon color 1-2 on an arbitrary scale, or A_2 thickness 20-24 mm., B color 1
"Wet Grayling" sand	WG	A_2 thickness 15-19 mm., B color 2.5-3, or A_2 thickness 20-24 mm., B color 2-3, or A_2 thickness 25-49 mm., B color 1-3
Croswell sand	C	A_{0L} + A_{0M} + A_{0H} thickness under 50 mm., and/or B texture "unconsolidated" A_2 thickness 25-49 mm., B color 3.5-5, or A_2 thickness 50 mm. or more
Au Gres sand	AG	B horizon texture "chunky", or B texture "crumbly", A_{0L} + A_{0M} + A_{0H} thickness 80 mm. or more
Saugatuck sand	S	B texture "cemented", A_{0H} thickness under 90 mm.

*B horizon color scale from 1 (lightest) to 5 (darkest)

**Soil "types" used here for convenience, not recognized by the Michigan Dept. of Agriculture, are placed in quotes.

Soil** type	Abbreviation symbol	Limits as here defined*
Kinross and "Wet Sauga-tuck" sands	R	B color 5, A_{OH} thickness under 12 inches B texture "crumbly", or B texture "unconsolidated" or "chunky", A_1 thickness 50 mm. or more, or B texture "cemented", A_{OH} thickness over 90 mm.
Dawson and Green-wood peat	DG	A_{OH} thickness 12 inches or more

*See page 373
**See page 373

APPENDIX B

ABBREVIATION SYMBOLS

Variables

no. in tables	symbol	name
		SPECIES
1	Amo	Amelanchier oblongifolia
2	Ams	Amelanchier sanguinea
3	Anm	Anemone quinquefolia
4	Arc	Arctostaphylos uva-ursi
5	Ash	Aster "hairy ovate"
6	Asl	Aster laevis
7	Bra	Brachythecium salebrosum
8	Cal	Caliergonella schreberi
9	Cpd	Carex pedunculata
10	Car	Carex pensylvanica
11	Chm	Chamaedaphne calyculata
12	Com	Comptonia peregrina
13	Cop	Coptis groenlandica
14	Cor	Cornus canadensis
15	Crn	Cladonia rangiferina
16	Crs	Cladonia cristatella
17	Cup	Cladonia "cup-shaped"
18	Dan	Danthonia spicata
19	Dic	Dicranum undulatum
20	Epi	Epigaea repens
21	Eri	Eriophorum spissum
22	Gau	Gaultheria procumbens
23	Ilx	Ilex verticillata
24	Kal	Kalmia polifolia
25	Kan	Kalmia angustifolia
26	Led	Ledum groenlandicum
27	Lyc	Lycopodium obscurum
28	Mai	Maianthemum canadense
29	Mel	Melampyrum lineare
30	Nem	Nemopanthus mucronata
31	Opu	Oryzopsis pungens
32	Ors	Oryzopsis asperifolia
33	Pos	Polytrichum strictum
34	Pru	Prunus serotina

no. in tables	symbol	name
35	Ptr	Pteridium aquilinum
36	Rho	Rubus hispidus var. obovalis
37	Rub	Rubus canadensis
38	Spl	Sphagnum plumosum
39	Spp	Sphagnum spp., other than S. plumosum
40	Sol	Solidago "lanceolate long petiole"
41	Tri	Trientalis borealis
42	Vam	Vaccinium myrtilloides
43	Vib	Viburnum cassinoides
44	Vig	Vaccinium angustifolium var. nigrum
45	Vio	Viola adunca
46	Vox	Vaccinium oxycoccus
47	Vyp	Vaccinium boreale
		"ENVIRONMENTAL" VARIABLES
48	tre	per cent tree cover
49	shr	per cent shrub cover
50	hrb	per cent herb cover
51	mos	per cent moss cover
52	lcn	per cent lichen cover
53	tot	total per cent cover, all synusia
54	lit	thickness of litter, spring-summer meas.
55	bar	per cent bare ground
56	lip	per cent litter cover
57	aol	thickness A_{0L} horizon (litter, fall meas.)
58	aom	thickness A_{0M} horizon (duff)
59	aoh	thickness A_{0H} horizon (humus)
60	a-1	thickness A_1 horizon (mineral-organic)
61	a-2	thickness A_2 horizon (leaching)
62	bee	thickness B horizon (deposition)
63	gli	depth to gley

Soil Types

ORIGINAL symbol	name	COMBINED, SEGMENTS symbol	name
G	Grayling sand	G	Grayling
WG	"Wet Grayling" sand	WC	Wet Grayling-Croswell
C	Croswell sand	AS	Au Gres-Saugatuck
AG	Au Gres sand	R	Kinross
S	Saugatuck sand	DG	Dawson-Greenwood
R	Kinross and "Wet Saugatuck" sands		
DG	Dawson and Greenwood peats		

Quadrat Sizes

symbol	size
1	1 m^2
4	1/4 m^2
H	1/100 m^2

Groupings of Variables

SPECIES		ENVIRONMENTAL	
symbol	name	symbol	name
(SS)	small solitary	(SY)	synusia
(CX)	clonal xerophytic	(S-)	synusia, excluding major components
(MD)	margin dry		
(MW)	margin wet	(LI)	litter parameters
(B)	bog species	(HO)	horizon thicknesses

(tot) total, all variables

APPENDIX C

SPECIES INCLUDED IN GROUPINGS

(SS) - Small Solitary

symbol	name
Amo	Amelanchier oblongifolia
Ams	Amelanchier sanguinea
Anm	Anemone quinquefolia
Arc	Arctostaphylos uva-ursi
Ash	Aster "hairy ovate"
Asl	Aster laevis
Rub	Rubus canadensis
Sol	Solidago "lanceolate long petiole"
Opu	Oryzopsis pungens
Ors	Oryzopsis asperifolia
Pru	Prunus serotina
Vio	Viola adunca

(CX) - Clonal Xerophytic

symbol	name
Cpd	Carex pedunculata
Car	Carex pensylvanica
Com	Comptonia peregrina
Dan	Danthonia spicata
Ptr	Pteridium aquilinum

(MD) - Margin Dry

symbol	name
Epi	Epigaea repens
Gau	Gaultheria procumbens
Mai	Maianthemum canadense
Mel	Melampyrum lineare
Vig	Vaccinium angustifolium var. nigrum
Vyp	Vaccinium boreale

(MW) - Margin Wet

symbol	name
Cop	Coptis groenlandica
Cor	Cornus canadensis
Ilx	Ilex verticillata
Lyc	Lycopodium obscurum
Nem	Nemopanthus mucronata
Rho	Rubus hispidus var. obovalis
Tri	Trientalis borealis
Vam	Vaccinium myrtilloides
Vib	Viburnum cassinoides

(B) - Bog Species

symbol	name
Chm	Chamaedaphne calyculata
Eri	Eriophorum spissum
Kal	Kalmia polifolia
Kan	Kalmia angustifolia
Led	Ledum groenlandicum
Pos	Polytrichum strictum
Spl	Sphagnum plumosum
Spp	Sphagnum spp., other than S. plumosum
Vig	Vaccinium angustifolium var. nigrum
Vox	Vaccinium oxycoccus
Vyp	Vaccinium boreale

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