ACKNOWLEDGEMENTS

I would like to express my sincere thanks to Professor Dr. F. LeBlanc, Biology Department, University of Ottawa, for the constant interest which he has shown as a thesis advisor.

The helpful advice given by Dr. R. Reed, Professor of Forest Ecology with the same department is also greatly appreciated.

The field work was very much facilitated through the cooperation of the National Capital Commission in Ottawa, particularly Mr. F. Edey, Superintendent of the Gatineau Park, and Mr. E. Ross, District Forest Ranger.

My most grateful appreciation is expressed to the various members of the Civil Service of Canada for their expert advice in their respective fields of specialization. Dr. J. Maini, Program Coordinator-Tree Biology, Dr. J. Cayford, Program Coordinator-Silviculture and Dr. P.J. Rennie, Forest Soils, all employed with the Department of the Environment, Canadian Forestry Service. Mr. A.A. Buys, Mr. F. Everett and Mr. N. Lopoukhine with the Department of the Environment, Forest Management Branch.

The Multivariate Analysis, which required computer processing, was possible only through the most generous assistance given by Mr. L.P. Lefkovitch, Statistical Research Service of the Canada Department of Agriculture.

Special thanks also to Dr. A.W. Douglas, Biometrics and Computer Science Branch, Department of the Environment, for his expert advice concerning the Correlation Analysis.

The assistance given by Mr. H. Muhle, Ph.D. candidate with the Biology Department, University of Ottawa, in the identification of bryophytes and lichens is very much appreciated.

Many thanks also to Mr. G. Godbout, agronome et Chef du laboratoire des Sols in La Pocatiére, P.Q. for the chemical analysis of the soil samples.

My son George merits a very special acknowledgement for the many hours he has spent in the hemlock stands giving important technical assistance. Last, but surely not least, I would like to thank my wife Eva for her technical assistance in the field and her relentless effort in typing the manuscript and its proofreading.

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ABSTRACT

The main objective of this biometrical study was to investigate the possible existence of vegetational patterns along horizontal and vertical gradients in forests.

Three stands of hemlock in the Gatineau Park, P.Q. were selected for study. The tree, shrub and ground strata and soils were sampled along belt transects. The stands were chosen for low overall species diversity and dominance by a single tree species.

The statistical procedures were chosen to analyze quantitative interrelationships between tree height, diameter, age and ratio combinations thereof along linear transect gradients. It was found that tree shape or form, defined in terms of the diameter and height ratio, varies in a regular pattern along the vertical gradient.

Résumé

Le but principal de cette étude biométrique est d'étudier l'existence possible de patrons de végétation suivant des gradients horizontaux et verticaux dans les forêts.

Trois forêts de pruche du Parc de la Gatineau, P.Q. ont été sélectionnées pour étude. La strate arborescente, la strate arbustive, la strate herbacée ainsi que le sol ont été échantillonnés le long des courbes de niveau. Les lieux d'échantillonage furent choisis en raison de la diversité limitée des espèces présentes et de la dominance par une seule espèce d'arbre.

Les procédures statistiques ont pour but d'analyser les relations quantitatives existant entre la hauteur des arbres, le diamètre et l'âge le long des gradients sur les transects. On a trouvé que la forme des arbres définie en terme de diamètre et de hauteur varie selon un patron régulier.

I. INTRODUCTION

Investigations into spatial patterns of vegetation or gradient analysis have been conducted by Whittaker (1967) in order to determine gradient effects on population distributions. Similar ideas were expressed in the continuum concept of the Wisconsin school of thought which was mainly represented by Curtis (1959) and Bray and Curtis (1957).

The basic objective of gradient analysis as employed by these authors was to study the alternating succession of populations along linear gradients. The main interest, therefore, is of an inter- rather than intra-population nature.

This study attempts to determine changes of individual tree characteristics such as height, age and diameter representing the primary measurements, and two derived quantities in form of basal area and volume along horizontal and vertical transect distances. The statistical procedures employed in form of correlation and multivariate statistics will analyze in particular the variations of tree diameter and height and their ratio expression referred to as tree shape or form factor.

The pattern of quantitative change of individual or stand growth dynamical characteristics is used as an indicator of structural symmetry within as well as between the different stands.

The degree of deviation from absolute identity of spatial ordination measured in terms of pattern symmetry is considered as an expression of relative homogeneity along linear distance gradients.

PLATE I

Locations of the hemlock stands in the Gatineau Park

Stand	Latitude (N.)	Longitude (W.)
F	45°30 1/2'	75°50'
C	45°36 1/3'	75°56'
B	45°37 1/2'	45°56 1/6'

(By permission of the National Air Photo Library, Surveys and Mapping Branch, Department of Energy, Mines and Resources, Ottawa, Ont.)

II. GENERAL DESCRIPTION OF THE HEMLOCK STANDS

a) Stand selection and location

Three stands of hemlock were located from aerial photographs aided by field observation and were selected in conjunction with topographic interpretation techniques as suggested by Chevrier and Aitkens (1970).

These forest tracts are situated in the Gatineau Park, a nature conservation area northwest of Ottawa, Ontario and administered by the National Capital Commission (Plate I). The entire park area is located in the southern portions of Pontiac and Gatineau counties, both forming part of the extreme southern region of the Province of Québec. The stands subsequently referred to as Stand F (Camp Fortune), Stand B (Branch-off), and Stand C (Carman Lake) are found between 45°30' and 45°38' northern latitude and have a longitudinal range from 75°49' to 75°57' W.

b) Topography, physiography and geology

Topographical features of the stand areas are typically hilly to mountainous with north-westerly to northerly slope exposures having frequent cliff-like rock outcrops (Plate II), ranging up to 30 feet in height. The hills, physiographically speaking, form a part of the Canadian Shield referred to as the "Laurentians" with basic elevations ranging from approximately 400 feet to 1300 feet above mean sea level.[1]

The lowest transect elevations measured are 480 feet in stand B, 570 feet in stand C and 625 feet in stand F. The general drainage pattern is

---

[1] Topographic maps No.31G/12d, 31G/5e, 31G/5f Department of Energy, Mines and Resources, Survey and Mapping Branch.

TABLE I

Mean monthly and yearly temperature and precipitation as observed at the reference station in Chelsea, Québec (according to Lajoie, 1962)

Month	Temperature (^oF)	Precipitation (inches)
January	12	3.0
February	11	2.3
March	24	2.9
April	39	2.7
May	54	3.0
June	64	3.1
July	69	3.0
August	67	2.6
September	58	3.3
October	47	2.5
November	33	2.9
December	18	3.4
Yearly mean	41	--
Yearly total	--	34.7

PLATE II

Silica-rock cliffs are characteristic for all three stands of hemlock

PLATE II

Silica-rock cliffs are characteristic for all three stands of hemlock

characterized by the presence of numerous larger and smaller sized glacial lakes flanked in the north-east by the Gatineau river, a major tributary of the Ottawa river which flows through the lowlands framing the park along its south-western border.

As described by Wilson (1969) the first major geologic event in the area was the formation of the Gatineau hills in the Precambrian era, large portions of the rock stratum being of Grenville age. The invasion of glaciers from the north about a million years ago and their retreat from the area about 10,000 years ago is comparatively recent history. The main rock formations are classified as Proterozoic composed predominantly of granite and allied plutonic rocks, as well as metasedimentary rocks such as gneiss, quartzite, and schist, with inclusions of volcanic rocks and granitic materials as described by Hogarth (1962). All three stands of hemlock have almost exclusively outcroppings of silica rock with high SiO_2 content and iron-oxide products, presumably members of the plagioclase series (Plate II).

c) Climatology

According to Lajoie (1962) the following observations were made in Chelsea, Qué., a representative reference station: an average number of 154 frost-free days at 32°F with a mean date for the first frost on October 8 and the last frost on May 7. The recordings of monthly and yearly mean temperatures and precipitation are shown on Table I.

d) Forest classification

The forest classification of the general area under consideration is referred to by Braun (1950) as the Laurentian Section of the Hemlock-White Pine-Northern Hardwoods region and by Weaver and Clements (1938)

PLATE III

A cluster of red spruce in the Camp Fortune stand

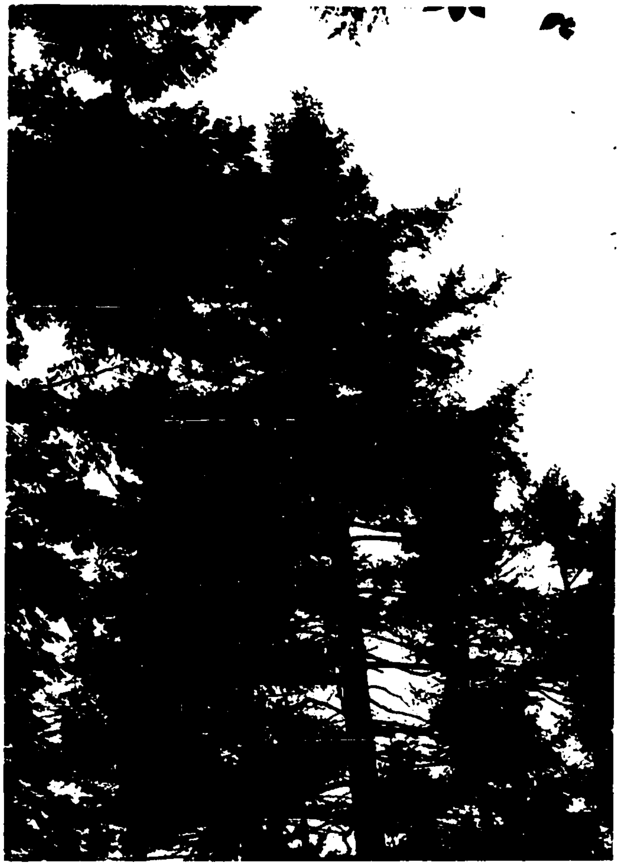


PLATE III

A cluster of red spruce in the Camp Fortune stand

as the Lake-Forest and by Halliday (1937) and Rowe (1959) as the Great-Lakes-St.Lawrence region. A thorough discussion of the major forest types has also been given by Nichols (1935) placing the centre of distribution of hemlock, white pine, yellow birch, Norway pine and red spruce within the region. According to Braun (1941) the Hemlock-White Pine-Northern Hardwoods type represents a phylogenetic variation and northern extension of the mixed mesophytic forest.

The region under discussion, however, which lies at the southern border of the Laurentian Upland or Canadian Shield, to the north of the Great Lakes and east of Lake Superior, is bordering on the Boreal forest formation as shown by Braun (1950) and could thus possibly be considered a transition zone between boreal and southern forest elements resulting in extreme interspecific tension and competition. The admixture of red spruce found in the hemlock stands could be considered an intrusion of boreal forest elements (Plate III).

e) Historical background

The forest history of the Gatineau Park is closely related to the early settlement pattern with forest exploitation being its main economic resource. The two principal tree species involved were white and red pine as described by Hughson and Courtney (1965).

According to early traveller reports, white pine specimens had reached 250 feet in height and 6 feet in diameter. The red pine was not quite as tall but obtained diameters similar to white pine in virgin forests. The Ottawa river system contained British North America's most important white pine sources of superior quality wood. With the arrival of Philemon Wright in 1796 a large scale forest exploitation began to satisfy the demands for squared timber of the British navy. The sawnlumber industry and potash production also took a heavy toll of forest species including maple, beech and birch. The exploitation of the forest within the present boundaries of the Gatineau Park came to an end in 1938, when the area came under the management of the National Capital Commission in Ottawa.

Several major forest fires have swept through parts of the park during the past. The evidence gained from observation shows very little or no indication of fire in the hemlock stands, possibly a result of their rather protected sites due to northerly exposure, high humidity and moisture.

Fig. I Generalized range of *Tsuga canadensis* (L.) Carr. (adapted from "Silvics of Forest Trees of U.S.", Agric. Handbook no. 271, U.S. Dept. Agric., For. Serv., 1965)

III. FOREST ECOLOGY OF HEMLOCK

The evolution of hemlock within the dominant forest types throughout its present range (Fig.1) is subject of considerable controversy. According to Braun (1950) hemlock has long been an essential constituent of the Mixed Mesophytic climax pattern which originated in Tertiary forest vegetation. The species therefore did not occupy its present range as a result of postglacial migration from the north and cannot be considered a typical "northern" species or member of the boreal forest formation. This hypothesis seems to be supported by the fact that the northern limit of distribution of eastern hemlock coincides with the southern boundary of the boreal forest formation (Fig.1).

Friesner and Potzger (1932) look upon hemlock consociations as "rearguards" or "relics" retreating from a "northern" centre of distribution during glacial periods which somewhat contradicts the "south"-centred theory as suggested by Braun (1950). A study conducted by Goder (1955) seems to indicate that important factors influencing the range of Tsuga canadensis are climatic conditions characterized by gradients of high rainfall and snowfall, low evaporation and cool temperatures.

In the general area studied, hemlock is found in association mainly with Pinus strobus, Picea rubens, Abies balsamea, Thuja occidentalis, Acer saccharum, Betula alleghaniensis, Fagus grandifolia, Quercus rubra, and Populus tremuloides in various degrees of admixture.

The formation of "pure" stands of hemlock, characterized by a 75% to 95% frequency representation of the species in the tree stratum, seems to be restricted to special microsites.

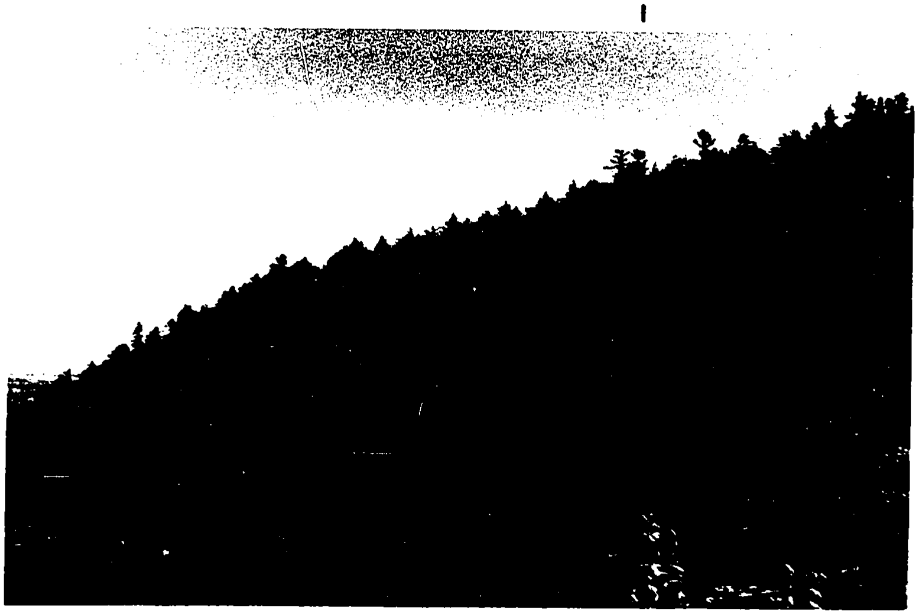
The microclimatic conditions as found in pure stands of hemlock

PLATE IV

Streamlined canopy integration of the hemlock stand in Camp Fortune with the surrounding hardwood forest

PLATE IV

Streamlined canopy integration of the hemlock stand in Camp Fortune with the surrounding hardwood forest



are characterized by relatively high moisture or local humidity and fresh, cool sites resulting in what might be referred to as a localized "coolhouse" habitat or "refrigerator" effect. Steepness of slope seems to be a more important factor in maintaining high humidity and cool temperatures than either proximity to lakes or interspersion with ravines. Other factors which are essential in maintaining a favourable microclimate are the usually very dense crown canopy and northerly exposure as well as the streamlined canopy integration with the surrounding hardwood forests (Plate IV) resulting in reduced "air-flow" and light intensities (Oosting and Hess 1956).

Several investigations by Weaver and Clements (1938), Kershaw (1964), Munns and Brown (1925), Curtis (1959), and Oosting (1942) have established the universality of the specific habitat. It was found that hemlock forests 300 miles apart were more closely related with respect to evaporation than hemlock and hardwood stands 300 yards apart (U.S. Dept. of Agric. Public. 1965). The phytosociology of areas of high concentration of hemlock or "consociations" as proposed by Weaver and Clements (1938) has been investigated by several authors such as Kershaw (1964), Martin (1959), McIntyre (1932), Munns and Brown (1925), and Friesner and Potzger (1932). As a result the nature of hemlock consociations and their rather sporadic distribution pattern has been explained as relic or physiographic and environmental climax. According to Weaver and Clements (1938) relic communities often display either preclimax or postclimax characteristics with respect to the surrounding vegetation criteria which apply to the relic stands of hemlock in the maple-beech forest of the Eastern United States. As observed by Friesner and Potzger (1932) the physiographic climax results in many cases in the virtual exclusion of other species and is characterized by a relatively sporadic distribution. The characteristic physiographic features include a northernly slope exposure, freshness and coolness of site and relatively steep rock outcroppings. Whether or not hemlock consociations are expanding as suggested by Martin (1959), retreating, or occupying a relatively constant area is a subject of considerable controversy.

The species of Tsuga canadensis is well known for its extreme tolerance of minimal light intensities enabling seedlings to survive with as little as 5 per cent of full sunlight intensities as shown by Bourdeau and Miriam (1958), Burns (1923), and Grasovsky (1929). The ability to recover from prolonged periods of suppression up to more than 200 years was shown by Hough and Forbes (1943) and Nichols (1918).

Another major aspect of the survival potential of the tree species is its overall competitive ability as investigated by Friesner and Potzger (1932), Grasovsky (1929), and Hough (1936), enabling hemlock to thrive successfully under more unfavourable conditions than hardwoods. Hemlock seems to be able to compete more successfully over time periods comprising several hundred years than any other associated tree species.

If we accept the basic theory as formulated by Nichols (1935) that the nature of the "rising" generation, i.e. the character of the immature trees can be considered to be a criterion of permanency, then the remarkable regenerative ability of hemlock is the fundamental criterion of its survival potential.

IV. SAMPLING PROCEDURES

a) Sampling objectives

The sampling technique used in this investigation helped to provide accurate, reliable and adequate data which could be used for subsequent statistical analysis. Main emphasis was placed on the sampling of growth-dynamic characteristics of each member of the tree stratum in form of height and diameter. If it can be assumed as suggested by Archibald (1949) that the dominant species in a plant community is the most important factor in determining community character, then the central objective would be to sample the arborescent stratum. Cooper (1926) has stressed the importance of measuring a change as the basic fact in vegetation studies, implying the use of "dynamic" rather than "static" criteria. It is expected that an analysis of growth-dynamic effects might reveal organizational or developmental stand patterns.

A numerical evaluation based largely on the presence, absence, or frequency distributions of stand members would have to be considered "static" in this sense and unsatisfactory for measuring biometrical characteristics of the dominant tree stratum. Dominance in forestry usually referred to as physiologic dominance would be measured in terms of crown class (dominant, codominant or suppressed) of the trees or as suggested by Cain (1932) expressed as total relative basal area occupied by each tree species/acre.

The extrapolation from the concrete community to the abstract association has been referred to by Ashby (1948) as one of the major problems of plant sociological investigations. One of the essential elements of statistical procedures used in this study is reference made to "ideal" population parameters such as the parametric correlation coefficient ρ and its corresponding z-transformation ξ used in the various statistical tests. In a strictly mathematical sense this approach might serve as a means of abstraction.

In order to qualify for the objectives and statistical analysis the final criterion in the selection of sampling technique must be the randomness of the sample as required by most statistical tests. The accuracy of the sample data obtained will be largely determined by the method used for placing the sampling units, their shape, size and numbers. This in turn directly influences the per cent of total stand area sampled which is an important factor in the assessment of sample variation.

b) Sampling forest vegetation

1. Plot-sampling

The belt-transect, a special form of rectangular quadrat, due to its extreme elongation decreases the variance/area if the long axis is run across the contour lines as has been shown by Bauer (1943). Bormann (1953) has obtained best estimates of tree populations in his investigations by using transect strips 12 x 420 feet and 30 x 420 feet whereby the long axis was crossing contours and vegetational banding. Cottam and Curtis (1956) have shown that traditional quadrat sampling is by no means a superior method for phytosociological sampling as indicated by the results obtained from measuring three forests and one artificial random population.

2. Plotless-sampling

Plotless techniques seem to have their best use in economic surveys or woodland management but not in phytosociological investigations.

Applications of the random-pair technique by Cottam (1947) tested in oak-hickory and maple-basswood forests to sampling spruce-fir and other dense forest types showed very unreliable estimates. Rice and Penfound (1955) arrived at similar conclusions about plotless sampling in general. In addition the variable radius method originally designed by Bitterlich (1948) and described by Grosenbaugh (1952), as well as the random pair technique, according to Shanks (1954) sample only inadequately the inferior layers or inferior size classes in forest stands.

c) Sampling the ground stratum

The results obtained from investigations by Bormann (1953) indicated the possibility of using the same sampling technique for both the dominant and the ground stratum when using transects. "Type" vegetation in this connection, at least with respect to forests would be determined mainly in terms of basal area dominance as described by Penfound (1945).

In measuring "low" herbaceous vegetation the results of statistical studies according to Clapham (1932) have clearly indicated that to obtain the same amount of information with squares as with strips nearly twice as large an area would have to be observed.

In addition, short strips (1:4) gave less variable data than squares but more variable than long strips. A combination of quadrat and transect sampling was used by Pechanec and Stewart (1940) concluding that lineplot sampling with subunits spaced at systematic intervals along a line was most efficient. Regarding the size of quadrats, the 1 meter x 1 meter plot for sampling herbaceous species has been used satisfactorily in sampling forest vegetation as shown by Oosting (1942, 1956).

d) Evaluating the adequacy of the sample

Archibald (1949) and Cain (1935) have both employed multiple quadrats and species-area curve techniques for recording the cumulative presence of each species within each area and taking a sufficient number of samples until the average number of species per unit area became constant. Raunkiaer's (1934) frequency distribution law of life-forms provides the criterion for sufficient sample intensity in each of the foregoing methods. As expressed by Goodall (1952), however, frequency does not provide a measure of the quantity of species present, and moreover accumulative and successive species counts become dependent on each other and repetitive.

The species-area curve originally used by European ecologists to determine the "minimal" area constituting a stand has subsequently been used as a panacea and "classical" model in an attempt to find the number and size of sampling units required. The number of species (absolute or per cent of total) accumulated in sampling is plotted on the y-axis against the number or size of samples on the x-axis. The characteristic curve therefore first rises abruptly because many species occur in the first few samples and then tends to level off (assuming complete random distribution of species) as no further species are added with increased sampling.

The crucial factor is the 10% increase point in sampling with various alterations thereof. However, the 10% point (or equivalents) is rather open to criticism for various reasons. According to Rice and Kelting (1955) the 10% point moves upward with an increase in the number of quadrats used and therefore has but little value as an indicator. Penfound (1945) claims that the number of quadrats used should be at least ten times as many as those indicated by the "break"-point on the curve.

The concept of minimal-area also has important implications regarding the species-area curve. According to Braun-Blanquet (1932) it is the size of sample area which, when increased, results in little if any change in the number of species encountered. Cain (1935, 1938, 1943) has defined it as the least area upon which a community can develop its typical structure and composition employing both multiple quadrat techniques and a differential coefficient of the species-area curve for its calculation.

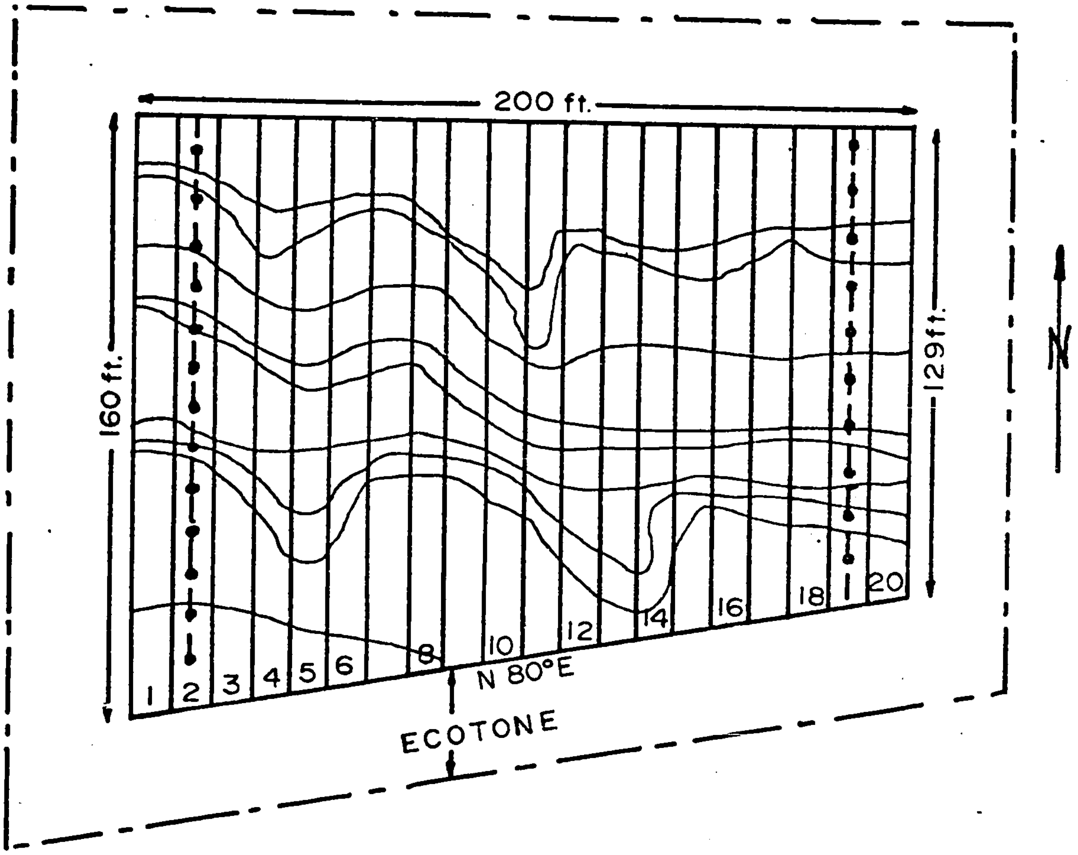
Ashby (1948) has expressed severe criticism of Cain's proposals stating that the differential coefficient of the curve depends on the asymptotic value which can only be guessed and the point of apparent flattening of the curve also depends on the scales used for y- and x-coordinates.

Rather than using the concept of minimal area as the basis in the determination of the degree of sampling intensity required, a percentage approach was used by Bormann (1953) in a study conducted in a relatively undisturbed, immature _Quercus-Carya_ climax forest sampling 14% of the selected area. A similar investigation conducted by Clapham (1932) in a forest study also gave optimum estimates when taking a 14% sample using transects.

e) Sampling procedures used in this investigation

The foregoing discussion indicates the use of belt-transects running across the contour lines appears to be most adequate for sampling the hemlock stands. The percentage approach as described in the previous section was adopted as the principal method of estimating the adequacy of sampling intensity, with approximately 10% of the total selected area sampled considered to be satisfactory.

The use of species-area curve centered techniques apart from theo-



• represent ground-stratum quadrat locations

Fig. 2. Generalized map showing design of transect grid pattern.

retical inadequacies of the model has been rejected because of the low degree of species diversity found in the hemlock stands which, particularly in the tree stratum, would lead to an undesirable "asymptotic" effect. It would also make plotting of the curve technically impossible for the tree stratum and very difficult for the ground stratum due to an insufficient number of coordinate points.

The comparative species poverty of the ground stratum,restricted essentially to a few members of the Bryophytes, Thallophytes and Pteridophytes, with no flowering plants present, by its very nature made the use of multiple quadrat techniques rather unreliable. Before determining the total stand area to be selected for sampling purposes the ecotonic "frame" or transition zone between the hardwood forest and the "pure" hemlock stand was marked off to eliminate possible "edge" effects.

The perimeter of the hemlock stand was next surveyed to find its dimensions and directions. The total area was then calculated on a horizontal projection basis and subsequently divided into a transect grid pattern (Fig.2). Transects to be sampled were located on the grid by using Tippett random number systems to ensure the random selection of sample areas. Depending on the overall size of the hemlock stand two or three transects were then selected in each stand the combined area of which amounted to approximately 10% of the total stand area, the desired level of sampling intensity. A sample calculation is given below:

Total hemlock stand area: $\frac{(a+b)}{2} \times h = \frac{(129+160)}{2} \times 200 \text{ ft.}^2 = 29,000 \text{ ft.}^2$

Transect No.19 area: $129 \times 10 \text{ ft.}^2 = 1,290 \text{ ft.}^2$

Transect No. 2 area: $155 \times 10 \text{ ft.}^2 = \underline{1,550 \text{ ft.}^2}$

Total transect area: $2,840 \text{ ft.}^2$

Per cent of total stand area sampled: $\frac{2,840}{29,000} \times 100 = 10\%$

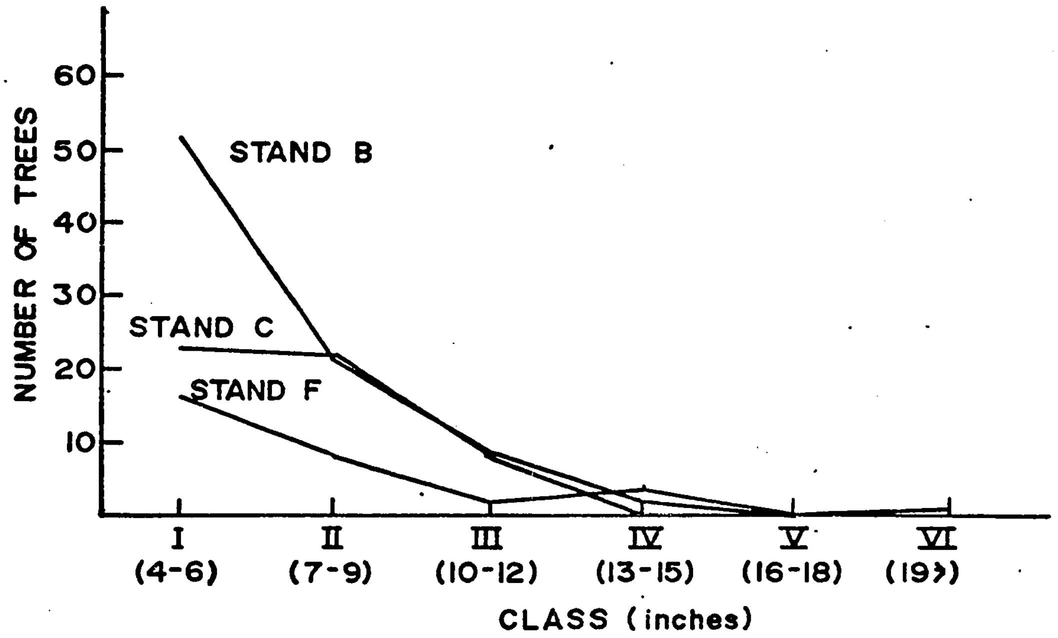


Fig. 3. Diameter class distribution.

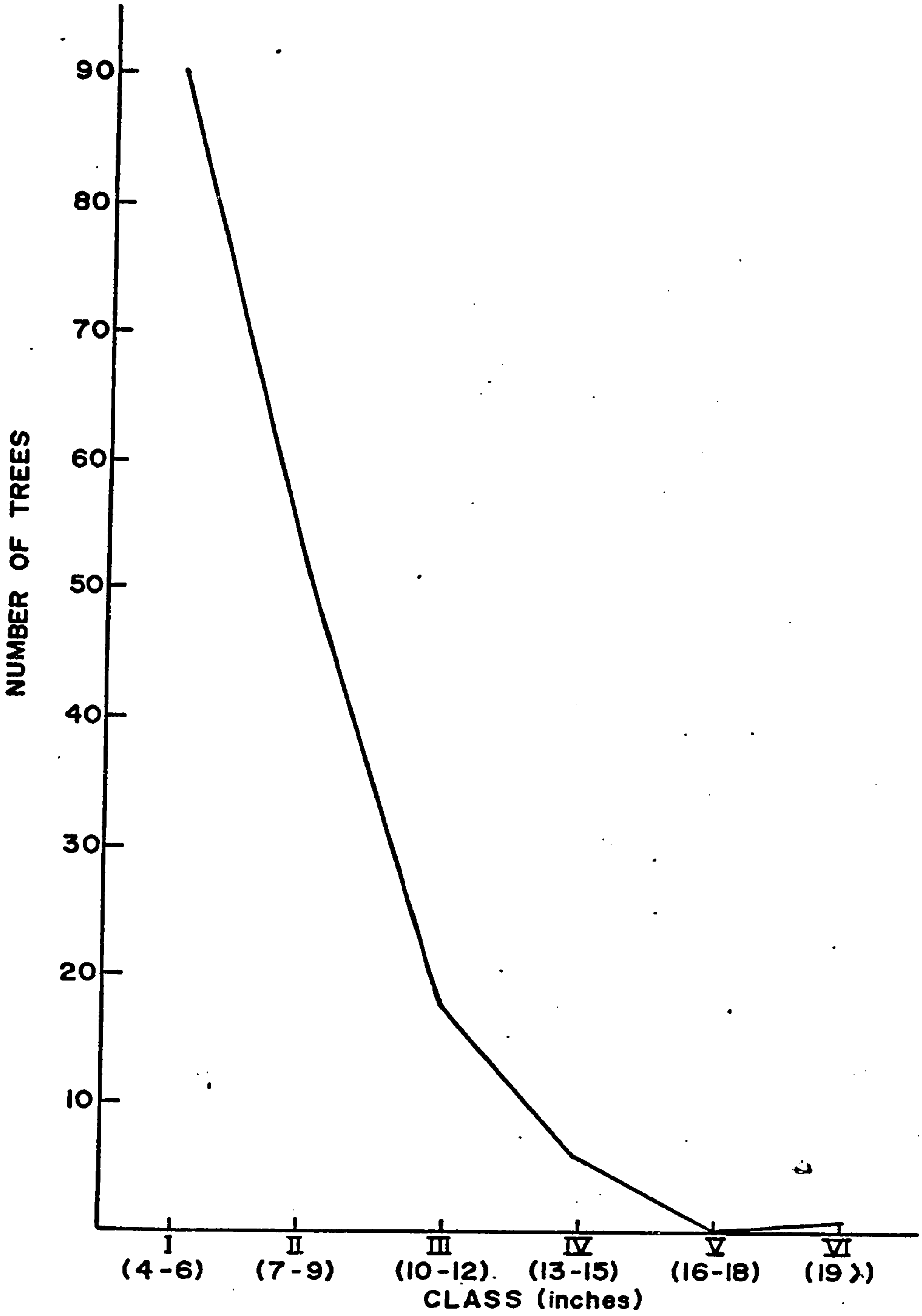


Fig.4. Accumulative diameter class distribution for all stands.

V. QUANTITATIVE RESULTS

a) Frequency-distributions

Figures 3-8 illustrate diameter-class, age-class and height-class frequency distributions for each stand separately, as well as for all stands combined. All live trees on the transects with a d.b.h. of 4" or larger were considered in the calculations.

The graphs illustrating the combined stand structure represent a hypothetical or parametric hemlock consociation which reflects the integration effects of all three stands. These effects are characterized in all cases by a highly regular and normal distribution pattern for the class intervals considered, which can be interpreted as an indication of a high degree of structural similarity between the individual stands.

Fig.3 shows a distinct skewing of the diameter-classes to the right. This pattern is obviously due to the fact that hemlock saplings between 1" d.b.h. and 4" d.b.h. were not taken into consideration. All three stands show the highest frequencies in the lowest diameter classes and a relatively balanced class distribution, starting with the minimum diameter as indicated by the absence of sharp and sudden breaks in the curve.[1]

In terms of European silvicultural practices and schools of thought, the hemlock stands may as a result represent a selection forest type characterized by an all-diameter tree structure.

The near plateau shown for stand C (Fig.3) does not seem to have a noticeable effect on the "projected" stand as shown in Fig.4.

[1]

Stand:	F	B	C
Maximum d.b.h. (inches)	19	15	11
Minimum d.b.h. (inches)	4	4	4

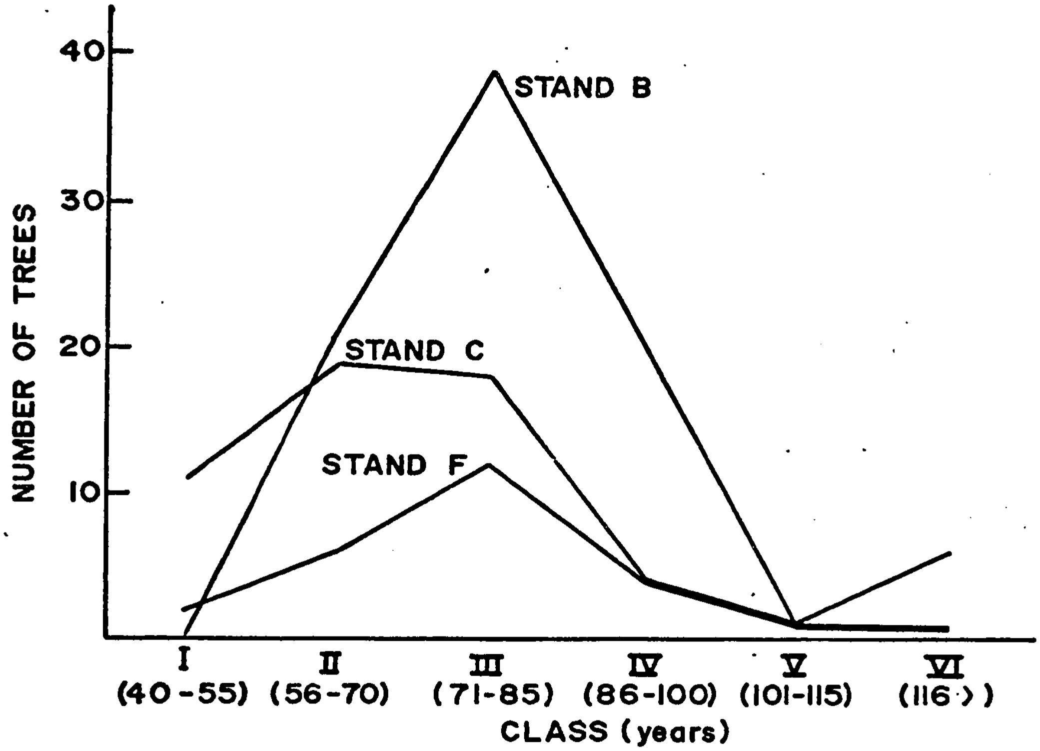


Fig. 5 Age-class distribution.

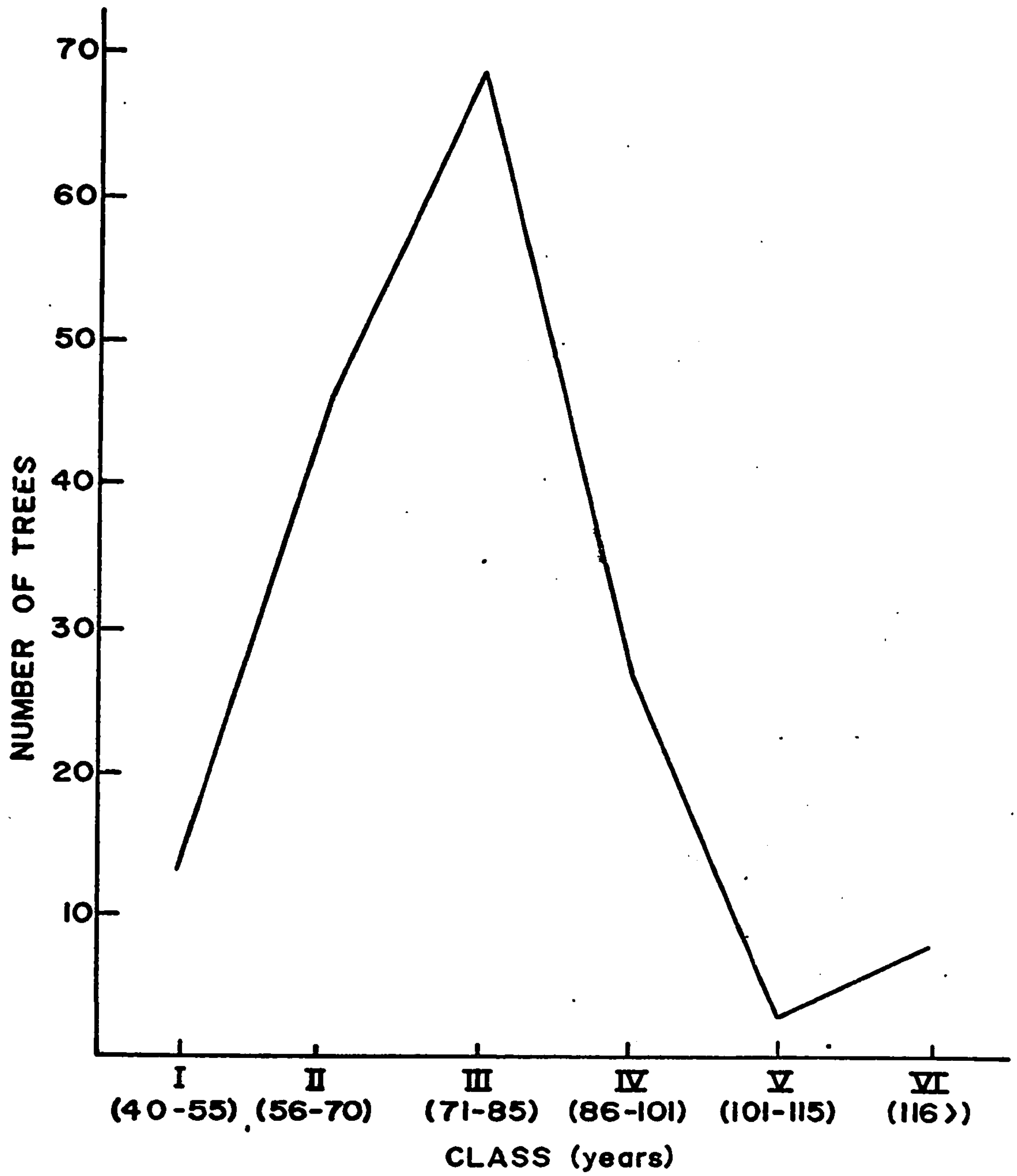


Fig. 6. Accumulative age-class distribution (all stands).

The age-class frequency distribution (Fig.5) reveals in each stand an uneven-aged structure within the age-class range represented which can be taken as a reliable indicator of the potential vegetation. The minimum age recorded for the smallest diameter-class is 40 yrs.[1]

All stands with the possible exception of stand C reach their peaks in the same age-class. It is also quite obvious that stand F and stand B show normal distribution approximations for the age-class range (Fig.5).

The plateau observed in diameter distribution of stand C (Fig.3) seems to repeat itself in age-class distribution for the same stand (Fig.5). A basically normal distribution pattern can also be observed for the combined stand graph (Fig.6). The height-class distribution in stand B (Fig.7) seems to display a pattern very similar to the age-class distribution in the same stand.[2]

A comparison between Fig.5 and Fig.7 will show an almost symmetrically reversed age-class and height-class frequency distribution for stand C. The same effect seems to be present in stand F, even though it is much less conspicuous.

As in the previous cases the combined stand illustration (Fig.8) shows a good approximation of a normal distribution type pattern.

In comparison with the maximum values of 19 inches for d.b.h., 243 years for age, and 70 feet for tree height obtained for each measured variable in this study, Kershaw (1964) describes a maximum recorded age

[1]

Stand:	F	B	C
Maximum age (years)	243	130	135
Minimum age (years)	53	60	40

[2]

Stand:	F	B	C
Maximum height (feet)	70	69	63
Minimum height (feet)	26	27	20

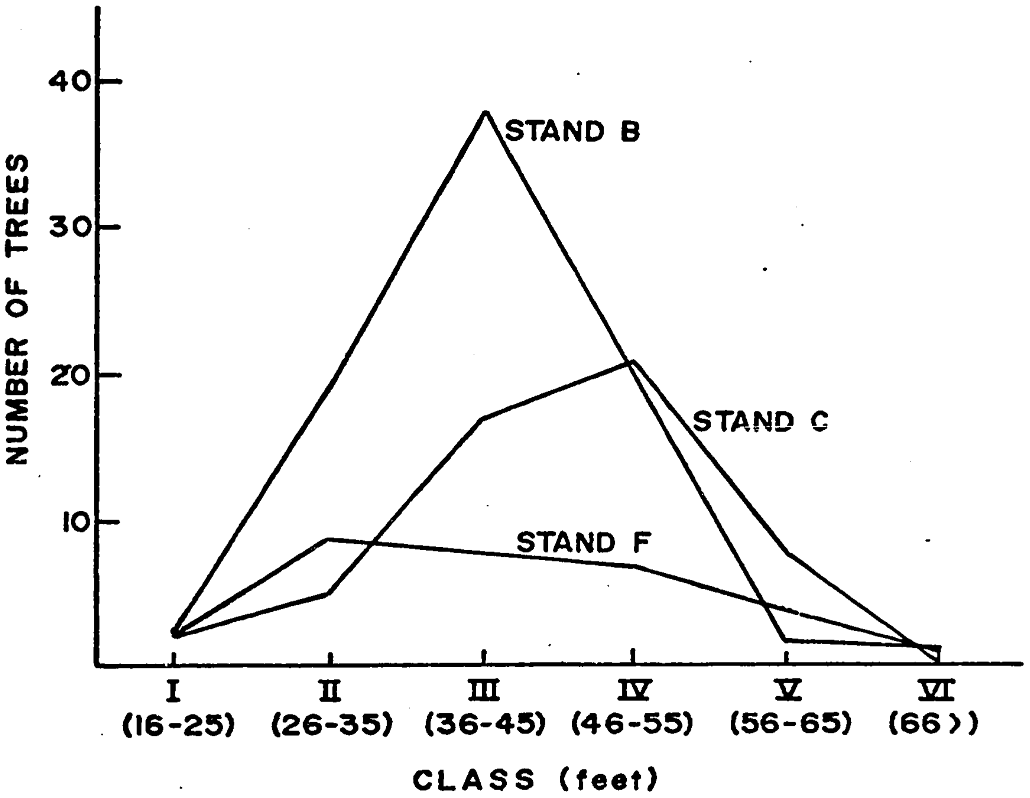


Fig. 7. Height-class distribution.

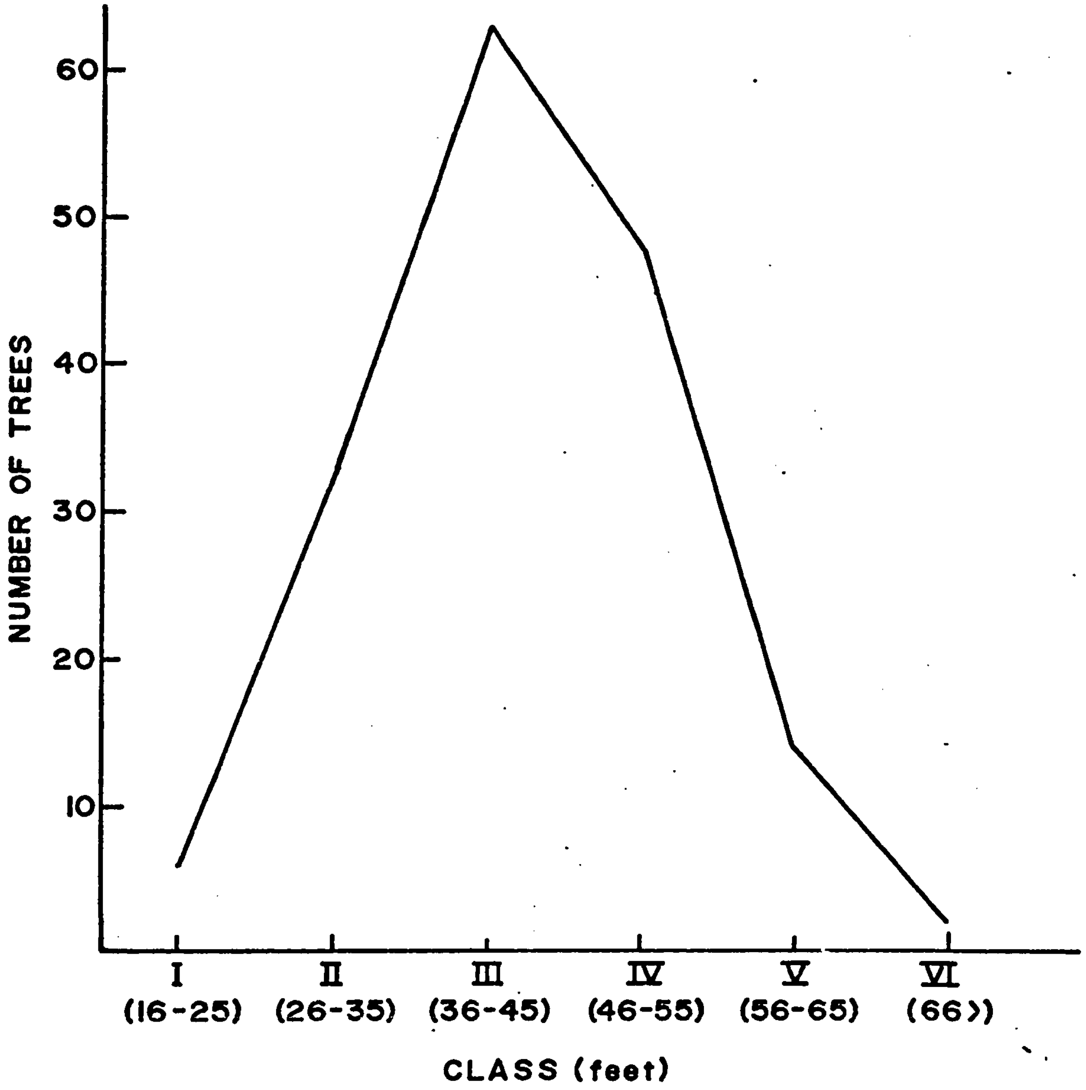


Fig. 8. Accumulative height-class distribution
(all stands).

TABLE II

Stand and transect survey data

Stand		F		B		C		
Transect No.		1	2	1	2	1	2	3
Stand-area	sq.feet	29000		45000		36000		
	acres	0.7		1.0		0.8		
Transect dist.	horiz.	155	129	206	224	129	106	117
	vert.	104	72	66	83	45	37	51
Transect area[1]	sq.feet	2840		4300		3520		
	acres	0.07		0.10		0.08		
Per cent of total stand area sampled[1]		10		9		10		
No.of ground quadrats		13[2]	10	15	17[2]	10	8	9
Total No. of trees		15	16	44	38	14	12	27
No.of trees other than hemlock		3	6	4	2	3	1	2
"Other" species		*Picea rubens* *Betula lutea*		*Pinus strobus* *Picea rubens* *Quercus borealis* *Populus tremuloides*		*Pinus strobus* *Picea rubens* *Quercus borealis* *Acer saccharum*		
Per cent of "other" tree species		20%	38%	9%	2%	21%	8%	7%
No.of dead trees		2	0	2	1	0	1	1
"Ideal" slope[3]		34°	30°	18°	20°	19°	19°	23°

[1] Combined and approximate values.

[2] Some quadrats were centred on bare rock outcroppings.

[3] Calculated from vertical and horizontal distances in each transect.

for hemlock of 490 yrs. and a maximum d.b.h. of more than 45 inches. Nichols (1918) reports a maximum d.b.h. of more than 48 inches with a somewhat lower maximum age of over 300 yrs. for trees exceeding heights of 100 feet. According to Kershaw (1964), hemlock at 100 yrs. is still comparatively young and this criterion would apply to the stands investigated as shown by the results obtained in Fig.5.

The main purpose of basic frequency distribution graphs is to indicate trends and reveal fundamental patterns. Causal relationship, however, between the various parameters of the population, if present at all, can only be demonstrated by means of statistical techniques such as ratio and correlation analysis or at a more advanced level in the form of multivariate analysis.

b) Derived quantities

Table II shows data obtained from direct measurements. Horizontal transect distances represent the maximum horizontal elongation and vertical distances the altitudinal change between the lowest and highest point of each transect.

The average per cent admixture of species other than hemlock in stand F is approximately 29%, in stand B 6%, and in stand C 12%, based entirely on numerical abundance. The maximum number of different species encountered in any of the three stands is five and the smallest is two. A hemlock consociation as studied by Lutz (1930) shows the following breakdown by species and relative numerical abundance:[1]

Tsuga canadensis	81.6
Fagus grandifolia	3.4

---

[1] Trees 10 inches d.b.h. and over.

TABLE III

Volume[1] and basal area[2] values per stand

Stand	Transect total volume (cu.ft.)	basal area (sq.ft.)	Conversion factor	Per acre total volume (cu.ft.)	basal area (sq.ft.)	Volume and basal area ratios
F	286.2	11.6	14.3	4089.7	165.8	24
B	427.7	18.5	10.0	4277.0	185.0	23
C	334.5	14.3	12.5	4181.3	178.1	23

---

[1] Honer (1967)

[2] Cross-section of tree at breast-height (4.5 ft. above ground level), subsequently referred to as B.A.

Pinus strobus	5.7
Acer rubrum	1.5
Betula lenta	2.7
Betula lutea	4.2
Fraxinus americana	.8

Stand F with a slightly higher admixture of "other" species than the other two stands of hemlock compares more favourably in terms of only two different species rather than six which could be considered a compensating factor.

Data obtained from investigations by Braun (1950) based on canopy composition of hemlock consociations show the following results:

Tsuga canadensis	95.8
Pinus strobus	2.1
Acer rubrum	2.1

Stands B and C seem to be very similar in terms of stand composition and "other" species diversity.

Per acre values, as shown in Table III, were computed by multiplying the combined B.A. and volume data for the transects in each stand with a conversion factor which is the mathematical expression of the ratio between transect area and unity.

Volume measurement (Table III) for each tree was obtained by using volume tables for eastern hemlock which take into consideration average-site conditions rather than individual site-classifications. Basal areas were determined by using mathematical tables listing circular cross-sections corresponding to definite radii or diameters. A comparable study conducted by Lutz (1930) records maximum basal areas in virgin hemlock forests of approximately 200 sq.ft./acre. This quantity seems to compare very favourably with the results obtained in this investigation, possibly indicating a relative constancy of basal area/acre regardless of age of the stand.

Munns and Brown (1925) reported a close relationship between volume and basal area values/acre. These ratios show a remarkable degree of constancy for the hemlock stands under consideration (Table III).

A high degree of similarity between basal area and volume is by no means an established fact, because of its dependence on the proportionate change between tree diameter and height. Tree height in turn is mainly influenced by site-qualities unless stoking and species variations are large.

Basal area and volume data likewise display a high degree of similarity in results obtained from gradient analysis as shown in section VIb.

c) Soil analysis

1. Methods

The soil samples were taken from the center of the 1m x 1m quadrats used for sampling the ground vegetation (Fig.2) over the entire depth of the organic soil material, on the average not more than about 15 - 20 cm deep.

Soil reaction was determined with a radiometer pH meter using a 1:1 soil-water ratio. The organic carbon analysis was done according to Walkley and Black (1946) using the potassium bichromate method (wet combustion) and soil nitrogen was determined by the Kjeldahl method.[1]

---

[1] a. A.O.A.C. - 1950.
b. Chemical Methods of Soil Analyses, Canada Department of Agriculture, Ottawa, 1958.

TABLE IV

Soil analysis results (Stand F)

Transect No.	Quadrat No.	% C	pH	% N	P_2O_5 (mg/100g)	C/N[1]	P[1] (mg/100g)
1	1	31.7	3.9	1.4	6.08	22.6	2.68
	2	52.5	4.1	1.6	5.54	32.8	2.46
	3	54.9	3.7	1.5	3.90	36.6	1.72
	4	50.7	3.8	1.4	3.68	36.2	1.62
	5	54.3	3.8	1.5	3.00	36.2	1.32
	6	56.1	4.4	1.5	3.14	37.4	1.38
	7	53.1	3.8	1.6	2.18	33.2	0.96
	8	- - - - - - - - - - cliff - - - - - - - - -					
	9	55.8	3.8	1.3	4.58	42.9	2.01
	10	53.0	4.1	1.5	4.80	35.3	2.12
	11	55.0	4.0	1.6	3.90	34.4	1.71
	12	55.0	4.0	1.8	1.34	30.5	0.59
	13	52.6	3.9	1.9	3.00	27.7	1.32
2	1	18.6	3.7	.7	1.88	26.6	0.83
	2	53.9	3.8	1.6	3.44	33.7	1.53
	3	55.2	3.6	1.6	2.54	34.5	1.12
	4	40.2	4.0	1.3	4.34	30.9	1.91
	5	55.8	3.5	1.4	1.72	39.9	.76
	6	54.2	3.5	1.6	4.12	33.9	1.81
	7	53.2	3.7	1.2	1.12	44.3	.49
	8	47.2	3.8	1.6	1.72	29.5	.76
	9	54.4	3.8	1.3	1.34	41.5	.59
	10	51.4	4.0	1.8	2.40	28.6	1.05

---

[1] Calculated and rounded off values.

TABLE V

Soil analysis results (Stand B)

Transect No.	Quadrat No.	% C	pH	% N	P_2O_5 (mg/100g)	C/N[1]	P[1] (mg/100g)
1	1	53.2	4.1	0.7	9.90	76.0	4.36
	2	53.7	4.2	1.7	8.32	31.6	3.66
	3	54.0	4.2	2.9	12.38	18.6	5.44
	4	55.5	4.1	1.4	5.54	39.6	2.44
	5	53.5	4.2	1.4	10.58	38.2	4.65
	6	52.3	4.4	1.7	17.70	30.8	7.78
	7	51.6	4.5	1.7	17.70	30.4	7.78
	8	55.5	4.0	1.4	11.62	39.6	5.11
	9	49.5	4.5	1.7	21.00	29.1	9.25
	10	51.9	4.2	1.7	18.74	30.5	8.24
	11	51.8	4.0	1.5	10.20	34.5	4.48
	12	39.3	4.1	1.1	15.30	35.7	6.74
	13	8.5	4.6	0.3	17.18	28.3	7.55
	14	51.9	4.0	1.6	10.94	32.4	4.82
	15	49.5	3.9	1.5	7.20	33.0	3.16
2	1	52.8	4.2	1.4	15.30	37.7	6.74
	2	52.3	4.3	1.7	9.90	30.8	4.34
	3	52.8	4.4	1.7	25.20	31.1	11.10
	4	50.3	4.2	1.7	10.58	29.6	4.66
	5	50.5	4.1	1.7	10.94	29.7	4.82
	6	58.4	4.5	1.2	5.54	48.7	2.44
	7	53.7	4.4	1.6	5.84	33.6	2.57
	8	- - - -	- - - - -	cliff	- -	- - - -	- - - - -
	9	49.9	4.3	1.6	15.74	31.2	6.92
	10	52.2	4.0	1.8	10.94	29.0	4.81
	11	47.2	4.2	1.3	21.68	36.3	9.54
	12	52.2	4.0	1.3	8.62	40.1	3.81
	13	45.5	4.1	1.4	7.20	32.5	3.16
	14	39.9	4.4	1.3	21.68	30.7	9.54
	15	51.4	4.3	1.4	16.64	36.7	7.32
	16	53.4	4.0	1.4	6.60	38.1	2.90
	17	43.2	4.1	1.2	12.38	36.0	5.44

---

[1] Calculated and rounded off values.

TABLE VI

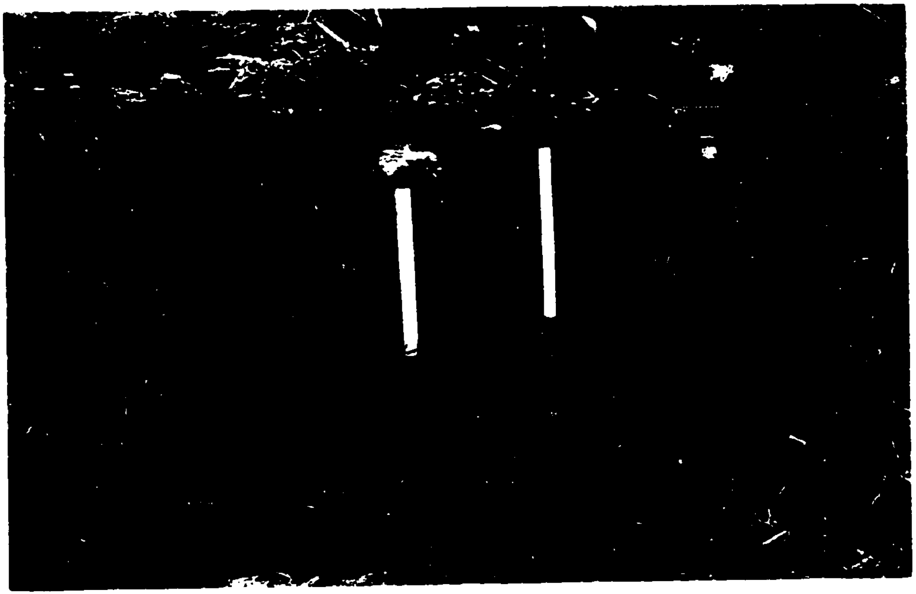
Soil analysis results (Stand C)

Transect No.	Quadrat No.	% C	pH	% N	P_2O_5 (mg/100g)	C/N[1]	P[1] (mg/100g)
1	1	52.5	4.0	1.4	8.32	37.5	3.66
	2	30.5	4.1	0.8	10.58	38.1	4.65
	3	32.6	4.1	0.9	12.00	36.2	5.28
	4	27.2	4.1	0.8	10.20	34.0	4.45
	5	37.4	4.1	0.6	10.58	62.3	4.65
	6	41.9	4.5	0.9	14.40	46.5	6.34
	7	29.3	4.3	0.9	17.18	32.5	7.55
	8	38.9	4.5	1.1	10.58	35.4	4.65
	9	50.3	3.8	1.3	11.24	38.7	4.95
	10	13.4	4.5	0.4	19.88	33.5	8.71
2	1	12.0	3.9	0.5	4.12	24.0	1.82
	2	33.5	4.1	1.5	6.08	22.3	2.67
	3	41.4	4.1	1.5	5.10	27.6	2.25
	4	43.3	4.3	1.6	12.00	27.1	5.28
	5	56.2	3.8	1.5	7.42	37.5	3.26
	6	32.0	4.2	1.1	21.68	29.1	9.54
	7	25.9	4.4	0.7	40.80	37.0	17.90
	8	16.8	4.5	0.5	31.84	33.6	13.90
3	1	30.2	4.3	1.2	8.62	25.2	3.80
	2	19.3	4.1	0.6	6.38	32.2	2.80
	3	55.3	3.8	1.1	8.32	50.3	3.66
	4	52.3	3.8	1.4	12.74	37.3	5.61
	5	53.6	4.0	1.5	18.22	35.7	8.00
	6	26.2	4.0	1.8	8.62	14.5	3.79
	7	42.9	4.2	1.5	12.38	28.6	5.45
	8	54.2	4.4	1.7	34.50	31.8	15.15
	9	39.2	4.0	1.0	6.90	39.2	3.20

[1] Calculated and rounded off values.

PLATE V

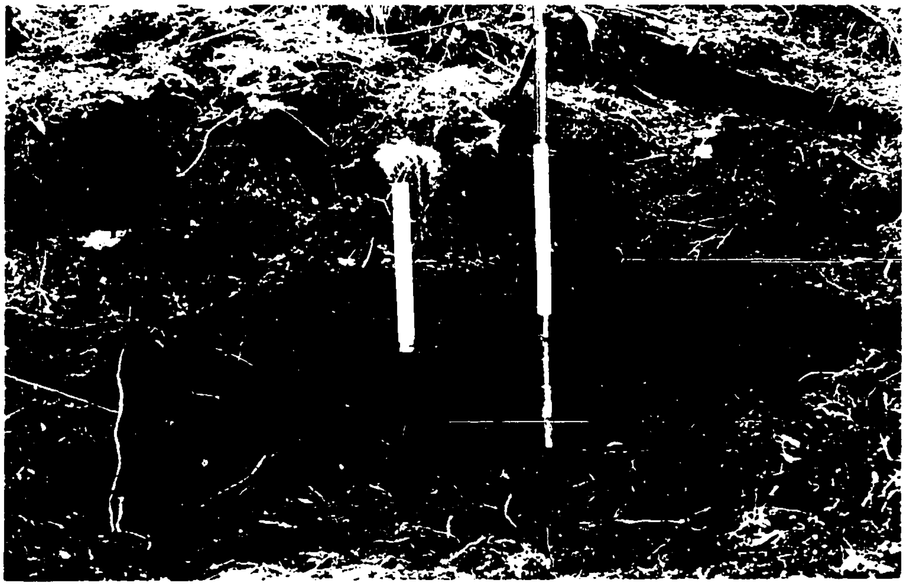
Matted mor-humus profile



Typical matted mor-humus consisting of largely unincorporated organic matter. Note the variation in texture from "greasy" (white ruler) to fibrous in the bottom layers. Munsell classification 5 Y R 2/1 black.

PLATE V

Matted mor-humus profile



Typical matted mor-humus consisting of largely unincorporated organic matter. Note the variation in texture from "greasy" (white ruler) to fibrous in the bottom layers. Munsell classification 5 Y R 2/1 black.

The analytical results of organic matter are expressed as per cent carbon and must be multiplied by a factor of 1.724 in order to obtain the percentage of organic matter.

The phosphorus content was measured in terms of milligrams per 100 grams of soil (phosphorus-V-oxide) which was then multiplied by a factor of 0.44 to obtain the total phosphorus content.

2. Results

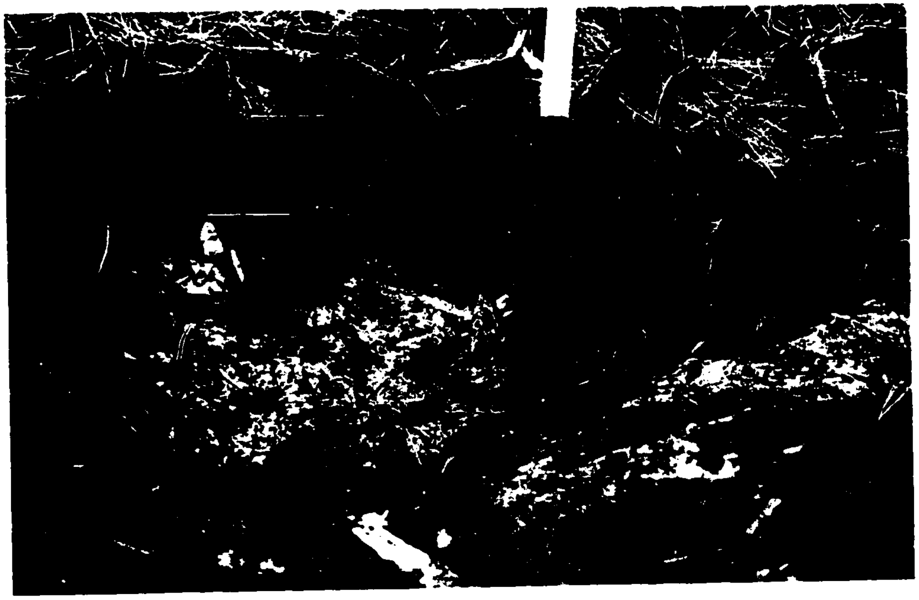
The predominant soil type in the hemlock stands is almost entirely composed of organic matter (Plate V) except for small coarse rock fragments which are found mainly in the contact areas with the parent rock material. The organic material seems to be only partially decomposed and ranges in thickness from about 2-5 centimeters to more than 40 centimeters with a representative Munsell classification code 5 YR 2/1 black.

The organic matter is entirely azonal with a matted or completely patternless structure interwoven with extremely dense and decaying root materials. Similar observations made by Goder (1955) in coniferous stands suggest the classification of the soil types in the hemlock stands investigated as matted mor-humus.

Zonal soil types in the form of podzols (Plate VI) are relatively infrequent and seem to occur mainly in small depression type pockets or level areas within the stands. They are characterized by a distinctly leached and greyish A_2 horizon with a uniformly brownish coloured B_2 horizon. In most cases the podzols are rather shallow and not more than about 10 to 30 centimeters deep. Their general characteristics seem to agree with observations made by Lajoie (1962) and

PLATE VI

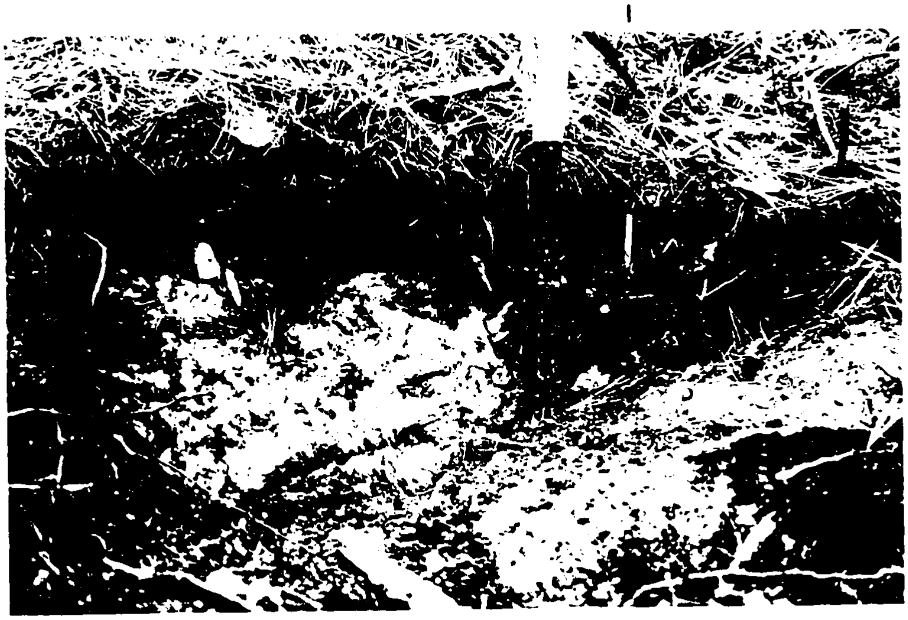
Podzolic profile



Munsell classification: 2.5 Y 3/2 very dark, grayish brown Podzolic profile on the right of the survey pole. Shallow layer of mor-humus to the left. The whitish materials in the middle and in the foreground of the picture are parent rock materials.

PLATE VI

Podzolic profile



Munsell classification: 2.5 Y 3/2 very dark, grayish brown Podzolic profile on the right of the survey pole. Shallow layer of mor-humus to the left. The whitish materials in the middle and in the foreground of the picture are parent rock materials.

TABLE VII

Soil analysis: Calculation of the standard error of the mean (Stand F)

Soil factor:	%C	pH	%N	P(mg/100g)
n	22	22	22	22
$\bar{x}$	50.4	3.9	1.5	1.41
$s = \sqrt{\frac{n \, . \, \Sigma x_i^2 - (\Sigma x_i)^2}{n \, . \, (n-1)}}$	8.9	0.2	0.2	0.61
$s_{\bar{x}} = \frac{s}{\sqrt{n}}$	1.9	0.04	0.04	0.13
$df = n-1$	21	21	21	21
$t_{.05}$	1.72	1.72	1.72	1.72
$\bar{x} + t_{.05} \cdot s_{\bar{x}}$	53.7	4.0	1.6	1.48
$\bar{x} - t_{.05} \cdot s_{\bar{x}}$	47.1	3.8	1.4	1.34
intervals for μ	47.1-53.7	3.8-4.0	1.4-1.6	1.34-1.48

TABLE VIII

Soil analysis: Calculation of the standard error of the mean (Stand B)

Soil factor:	%C	pH	%N	P(mg/100g)
n	31	31	31	31
$\bar{x}$	49.5	4.2	1.5	5.66
$s = \sqrt{\frac{n \cdot \Sigma x_i^2 - (\Sigma x_i)^2}{n \cdot (n-1)}}$	3.6	0.2	0.4	2.31
$s_{\bar{x}} = \frac{s}{\sqrt{n}}$	0.6	0.04	0.08	0.41
$df = n-1$	30	30	30	30
$t_{.05}$	1.31	1.31	1.31	1.31
$\bar{x} + t_{.05} \cdot s_{\bar{x}}$	50.3	4.3	1.6	6.20
$\bar{x} - t_{.05} \cdot s_{\bar{x}}$	48.7	4.2	1.4	5.12
intervals for μ	48.7-50.3	4.2-4.3	1.4-1.6	5.12-6.20

TABLE IX

Soil analysis: Calculation of the standard error of the mean (Stand C)

Soil factor:	%C	pH	%N	P(mg/100g)
n	27	27	27	27
$\bar{x}$	36.6	4.1	1.1	6.04
$s = \sqrt{\frac{n \cdot \Sigma x_i^2 - (\Sigma x_i)^2}{n \cdot (n-1)}}$	12.8	0.2	0.4	3.91
$s_{\bar{x}} = \frac{s}{\sqrt{n}}$	2.5	0.04	0.08	0.75
$df = n-1$	26	26	26	26
$t_{.05}$	1.7	1.7	1.7	1.7
$\bar{x} + t_{.05} \cdot s_{\bar{x}}$	40.9	4.2	1.2	7.31
$\bar{x} - t_{.05} \cdot s_{\bar{x}}$	32.4	4.0	1.0	4.77
intervals for μ	32.4-40.9	4.0-4.2	1.0-1.2	4.77-7.31

Lutz (1930).

With the exception of rather minor accumulations of coarse inorganic materials in rock fissures and crevices the main source of nutrient supply appears to be organic material. The very shallow and extremely dense root system showing extreme surface adaptation (Plate VII) suggests a form of "solid-phase" feeding as described by Wilde (1958).

A standard error of the mean of per cent carbon, pH, per cent nitrogen and phosphorus was calculated for each stand according to the formula:

$$s_{\bar{x}} = \frac{s}{\sqrt{n}}$$

whereby:

$$s = \sqrt{\frac{n \cdot \Sigma x_i^2 - (\Sigma x_i)^2}{n \cdot (n-1)}}$$

Subsequently a t-test was performed at the 95% probability level for

$$df = n - 1$$

in order to determine the intervals for μ, the parametric sample mean.

The results of the soil statistical analysis (Tables VII-X) seem to indicate a relatively high degree of similarity between the three stands of hemlock with respect to per cent carbon, pH, and per cent nitrogen.

A major discrepancy appears to exist regarding the phosphorus level in stand F as compared to both stand B and stand C.

PLATE VII

Characteristic plate-type root system

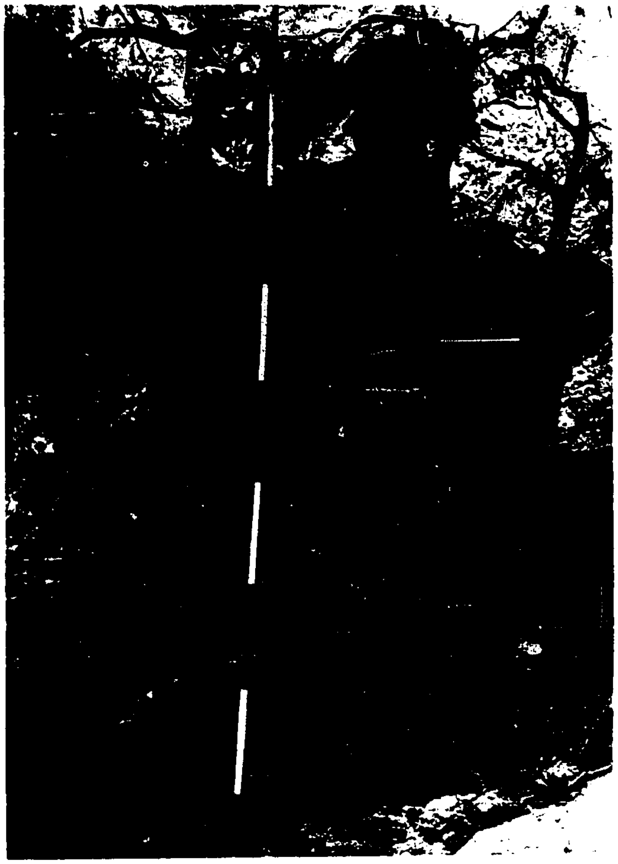


PLATE VII

Characteristic plate-type root system

TABLE X

Comparison of soil statistical testing results

Factor	Statistics	Stand F	B	C
%C	$\bar{x}$	50.4	49.5	36.6
	$\bar{x} + t_{.05} \cdot s_{\bar{x}}$	53.7	50.3	40.9
	$\bar{x} - t_{.05} \cdot s_{\bar{x}}$	47.1	48.7	32.4
pH	$\bar{x}$	3.9	4.2	4.1
	$\bar{x} + t_{.05} \cdot s_{\bar{x}}$	4.0	4.3	4.2
	$\bar{x} - t_{.05} \cdot s_{\bar{x}}$	3.8	4.2	4.0
%N	$\bar{x}$	1.5	1.5	1.1
	$\bar{x} + t_{.05} \cdot s_{\bar{x}}$	1.6	1.6	1.2
	$\bar{x} - t_{.05} \cdot s_{\bar{x}}$	1.4	1.4	1.0
P(mg/100g)	$\bar{x}$	1.41	5.66	6.04
	$\bar{x} + t_{.05} \cdot s_{\bar{x}}$	1.48	6.20	7.31
	$\bar{x} - t_{.05} \cdot s_{\bar{x}}$	1.34	5.12	4.77

Apparently no detailed analyses of soil chemistry for pure hemlock stands are available for comparison.

The following conclusions can be drawn from the observations made in the field and the results obtained from the chemical analysis:

i. The apparently slow rate of organic decomposition with the resulting excessive accumulation of organic debris may be due to the generally cool microclimate and the very acid soil conditions.

ii. The conspicuous absence of flowering plants may be due to possible growth inhibition and associated organic toxicity - effects resulting from the high percentage of organic carbon in the soil as suggested by Oosting (1956).

iii. The pH values are relatively low throughout the stands (Tables IV-VI). Comparable podzol profiles for the general area as found in coniferous stands and investigated by Rennie (1966) seem to display somewhat less acidic conditions in comparison with the hemlock stands.

d) Ground stratum

Members of the ground stratum as described by Curtis (1959) do not include seedlings and saplings of the overhead stratum unless used for regeneration studies, a method applied in this investigation.

Probably the most intriguing observation made is the fact that the ground stratum shows a complete absence of flowering plants (Table XI).

Many hardwood stands with full foliage cover seem to have com-

TABLE XI

List of ground species

1. MUSCI
    - Brotherella recurvans
    - Calliergon Schreberi
    - Dicranum flagellare
        - D. montanum
        - D. scoparium
    - Heterophyllium haldanianum
    - Hypnum imponens
        - H. pallescens
    - Leucobryum glaucum
    - Mnium spinulosum
    - Paraleucobryum longifolium
    - Plagiothecium spp.
    - Pohlia nutans
    - Polytrichum ohioense
    - Sphagnum capillaceum
    - Tetraphis pellucida
2. HEPATICAE
    - Bazzania trilobata
    - Blepharostoma trichophyllum
    - Jamesoniella autumnalis
    - Lepidozia reptans
    - Lophocolea heterophylla
    - Lophozia attenuata
    - Ptilidium pulcherrimum
3. THALLOPHYTA
    - Amanitopsis spp.
    - Cladonia spp.
        - C. chlorophaea
        - C. coniocraea
    - Clavaria botrytis
        - C. cinerea
        - C. flava
    - Cortinarius spp.
    - Flammula spumosa
    - Ganoderma tsugae
    - Laccaria amethystina
    - Lepraria spp.
    - Naematoloma sublateritium
    - Parmelia rudecta
    - Russula decolorans
        - R. fragilis
    - Tricholoma spp.
        - T. subacutum
4. PTERIDOPHYTA
    - Polypodium virginianum

PLATE VIII

The "indicator" fern Polypodium virginianum L.

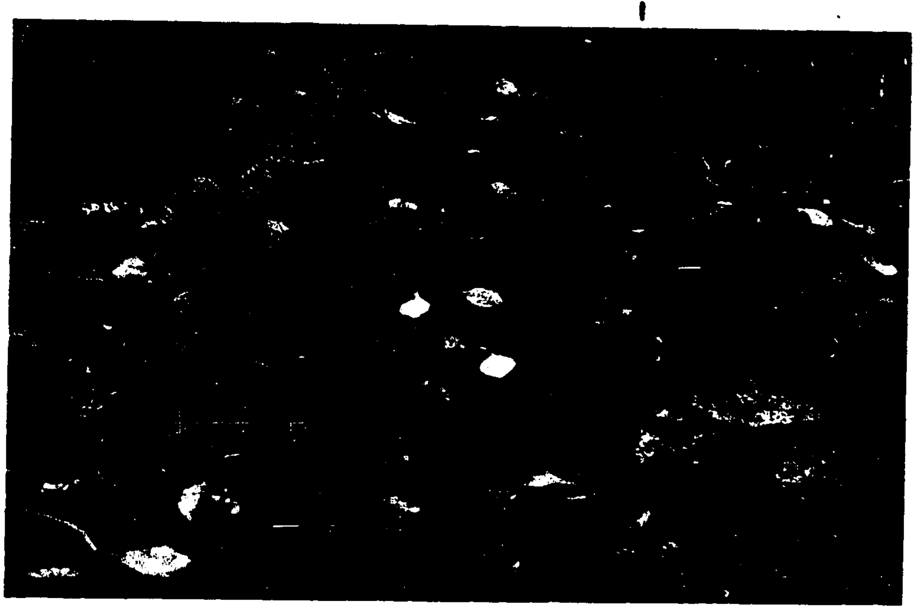


PLATE VIII

The "indicator" fern Polypodium virginianum L.

PLATE IX

A typical cluster of Bazzania trilobata (L.) S.F. Gray

PLATE IX

A typical cluster of Bazzania trilobata (L.) S.F. Gray

paratively lower light intensities at the ground level than hemlock stands, but a relatively large variety of flowering species. A possible limiting factor might be the high organic carbon content of the soil in conjunction with the matted structure of its largely undecomposed humus material.

The main authorities used for identification of ground species were Gillett (1958), Groves (1962), Brayshaw (1959), Durand (1949), Cody (1956) and Grout (1965). Only two members of the bryophyte vegetation, Mnium spinulosum and Plagiothecium spp., show a relatively high abundance index in all stands.

Of major mycological interest is the conspicuous presence of Ganoderma tsugae in all stands found mainly on decaying logs. An analysis of the ground stratum and soil pH has not shown any significant species/pH correlation.

Some plant species found in the transition zone between the surrounding hardwood forests and the hemlock stands are Aralia nudicaulis L. (Sarsaparilla), Maianthemum canadense Desf., Dryopteris spinulosa var. intermedia (Muhl.) Underw., the spinulose wood fern or florist's fern.

The following analytical quantities were used in the numerical analysis of the ground stratum:

1. Quadrat-presence:

   Number of quadrats in which a species occurred.

2. Per cent quadrat presence:

   $$\frac{\text{Number of quadrats in which a species occurred} \times 100\%}{\text{Total number of quadrats per stand}}$$

3. Subquadrat-frequency (based on 100 subquadrats per quadrat):

   Number of subquadrats per stand in which a species occurred.

TABLE XII

Numerical analysis of ground species occurring on all transects

	1			2			3			4		
	Quadrat presence			Per cent quadrat presence			Subquadrat frequency			Average subquadrat frequency		
Stand species	F	B	C	F	B	C	F	B	C	F	B	C
1. Musci:												
Brotherella recurvans	6	8	5	25	25	19	83	53	26	13.8	6.6	5.2
Dicranum spp.	1	3	3	4	9	11	8	99	32	8.0	33.0	10.7
D. flagellare	2	10	16	8	31	59	5	41	70	2.5	4.1	4.4
D. scoparium	3	8	1	13	25	4	11	70	4	3.7	8.8	4.0
Hypnum pallescens	1	15	4	4	47	15	2	86	17	2.0	5.7	4.3
Leucobryum glaucum	14	3	5	58	9	19	146	23	35	10.4	7.7	7.4
Mnium spinulosum	4	17	8	17	53	30	79	206	84	19.8	12.1	10.5
Plagiothecium spp.	14	6	21	58	19	78	95	40	264	6.8	6.7	12.6
Pohlia nutans	1	2	14	4	6	52	6	20	115	6.0	10.0	6.2
Polytrichum ohioense	6	3	4	25	9	15	41	10	21	6.8	3.3	5.3
Tetraphis pellucida	7	1	8	29	3	30	52	30	63	7.4	30.0	7.9
2. Hepaticae:												
Bazzania trilobata	12	11	8	50	34	30	208	168	61	17.3	15.3	7.6
3. Lichens:												
Cladonia coniocraea	3	6	4	13	19	15	7	47	20	2.3	7.8	5.0
C. spp.	1	4	5	4	13	19	6	13	28	6.0	3.3	5.6
4. Pteridophyta:												
Polypodium virginianum	8	4	6	33	13	22	63	50	19	8.0	12.5	3.2

TABLE XIII

Calculation of the abundance-index for jointly occurring ground species and their pH range

Stand species	Abundance-index F	B	C	Accumulative abundance indices	pH - range F	B	C
1. Musci:							
Brotherella recurvans	345	165	99	609	3.8-4.4	4.0-4.4	3.8-4.4
Dicranum spp.	32	307	118	457	4.0-4.1	4.5	3.8-4.4
D. flagellare	20	127	260	407	4.1	4.0-4.4	4.0-4.5
D. scoparium	48	220	16	284	3.8-4.1	3.9-4.6	4.0
Hypnum pallescens	8	268	65	341	3.7	3.9-4.6	4.0-4.5
Leucobryum glaucum	603	69	133	805	3.5-4.0	4.0-4.4	3.8-4.0
Mnium spinulosum	337	641	315	1293	3.8-4.0	4.0-4.5	3.8-4.5
Plagiothecium spp.	394	127	983	1504	3.5-4.0	3.9-4.5	3.8-4.5
Pohlia nutans	24	60	426	510	3.8	4.0-4.3	3.8-4.5
Polytrichum ohioense	170	30	80	280	3.8-4.1	4.1-4.2	4.0-4.5
Tetraphis pellucida	215	90	237	542	3.8-4.1	4.5	3.8-4.5
2. Hepaticae:							
Bazzania trilobata	865	520	228	1613	3.5-4.1	4.0-4.5	3.8-4.3
3. Lichens:							
Cladonia spp.	24	43	106	173	3.6-3.8	4.2-4.5	4.0-4.5
C. coniocraea	30	148	75	253	3.6-4.0	4.0-4.6	3.8-4.5
4. Pteridophyta:							
Polypodium virginianum	264	163	70	497	3.6-4.1	4.2-4.5	3.8-4.2

4. Average subquadrat-frequency:

Average number of subquadrats per quadrat in which the species occurred.

5. Abundance-index:

Per cent quadrat presence times average subquadrat frequency.

An abundance index was calculated for species occurring jointly in all stands (Tables XII and XIII). Species which are consistently found in hemlock stands are Plagiothecium spp. and Mnium spinulosum representing the mosses, the liverwort Bazzania trilobata, (Plate IX) and the pteridophyte Polypodium virginianum (Plate VIII).

VI. GRADIENT-ANALYSIS

a) Theory

As defined by Whittaker (1967), gradient analysis is a method of research which deals with vegetation in terms of continuity and gradient relationships which analyze spatial patterns of vegetation. According to the same author, neither elevation nor any other particular gradient can be accepted without experiment as "cause" of a population distribution. The fact is stressed that population distributions are the result of gradients of environmental complexities according to which a relative positioning of populations occurs. Distributional similarity of species taken from different samples can as a result be measured only with extreme difficulty.

The continuum idea of the Wisconsin school of thought mainly represented by Curtis (1959) and Bray and Curtis (1957) employs concepts of gradient analysis which are quite similar in nature, with the predominant idea to study the nature of successive alterations of different communities along a gradient and not possible changes within a specific and definite population.

An attempt was made in this study to analyze possible changes of individual tree characteristics, such as height, age, diameter, and two derived quantities in form of basal area and volume along horizontal and vertical transect distances. The results obtained from a study of this type reflect a cumulative rate of change effect for all the unit members of a specific community along linear gradients, and can be used as a measure of the degree of distributional symmetry or cause and effect interrelationships.

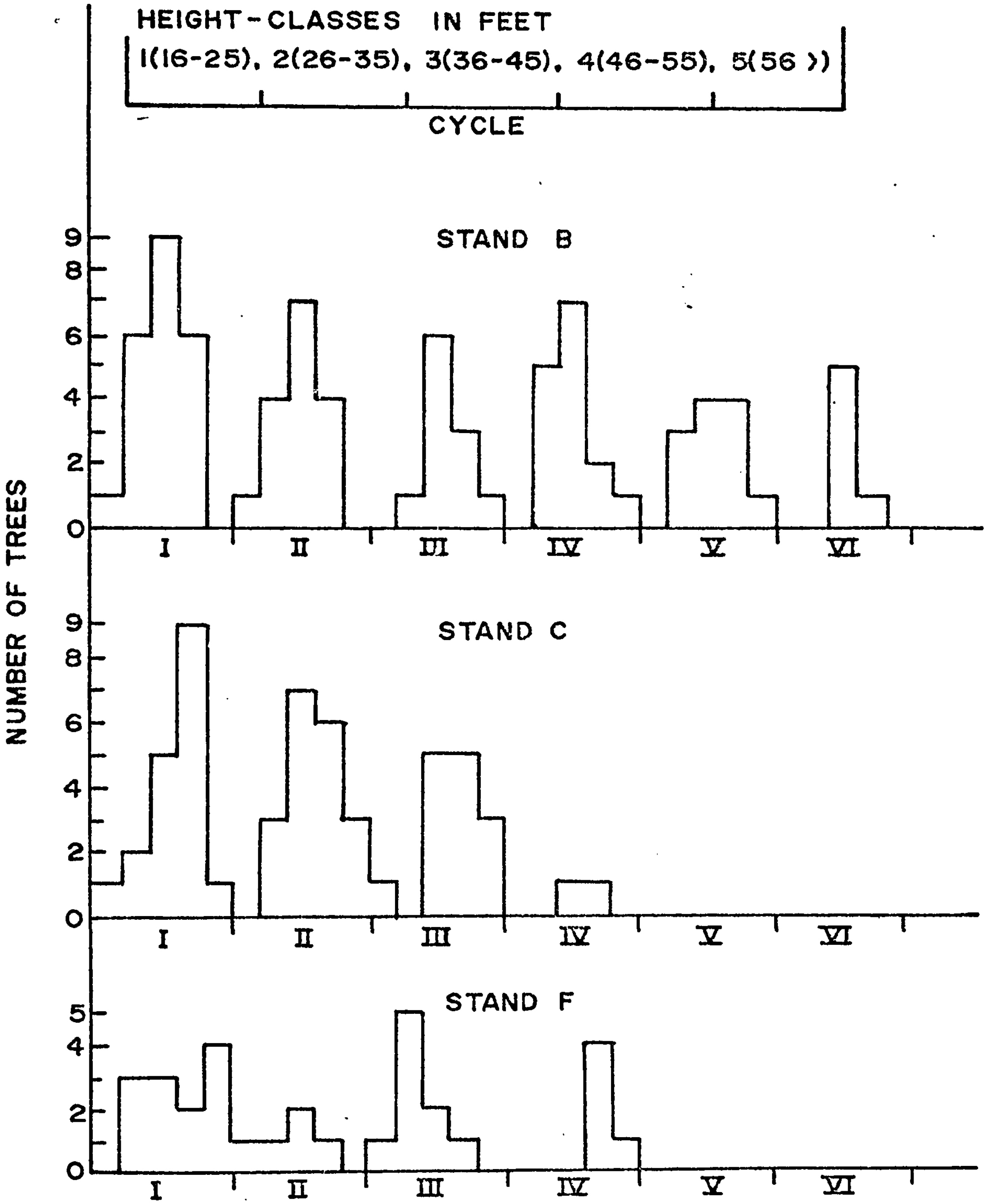


Fig. 9. Height-class frequency distribution per cycle (within 40 foot horizontal transect intervals).

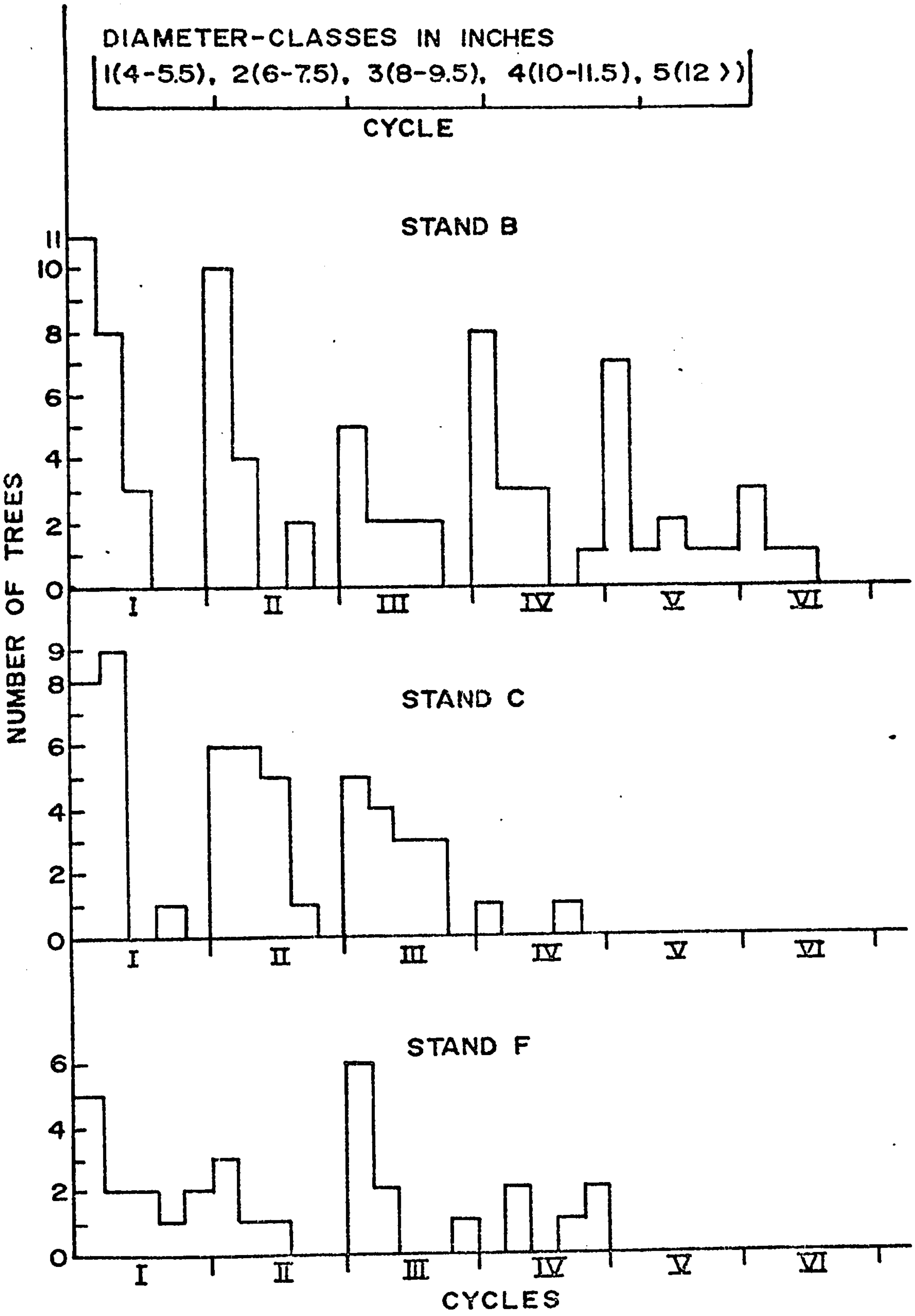


Fig.10 Diameter-class frequency distribution(per 40 foot horizontal transect distance intervals).

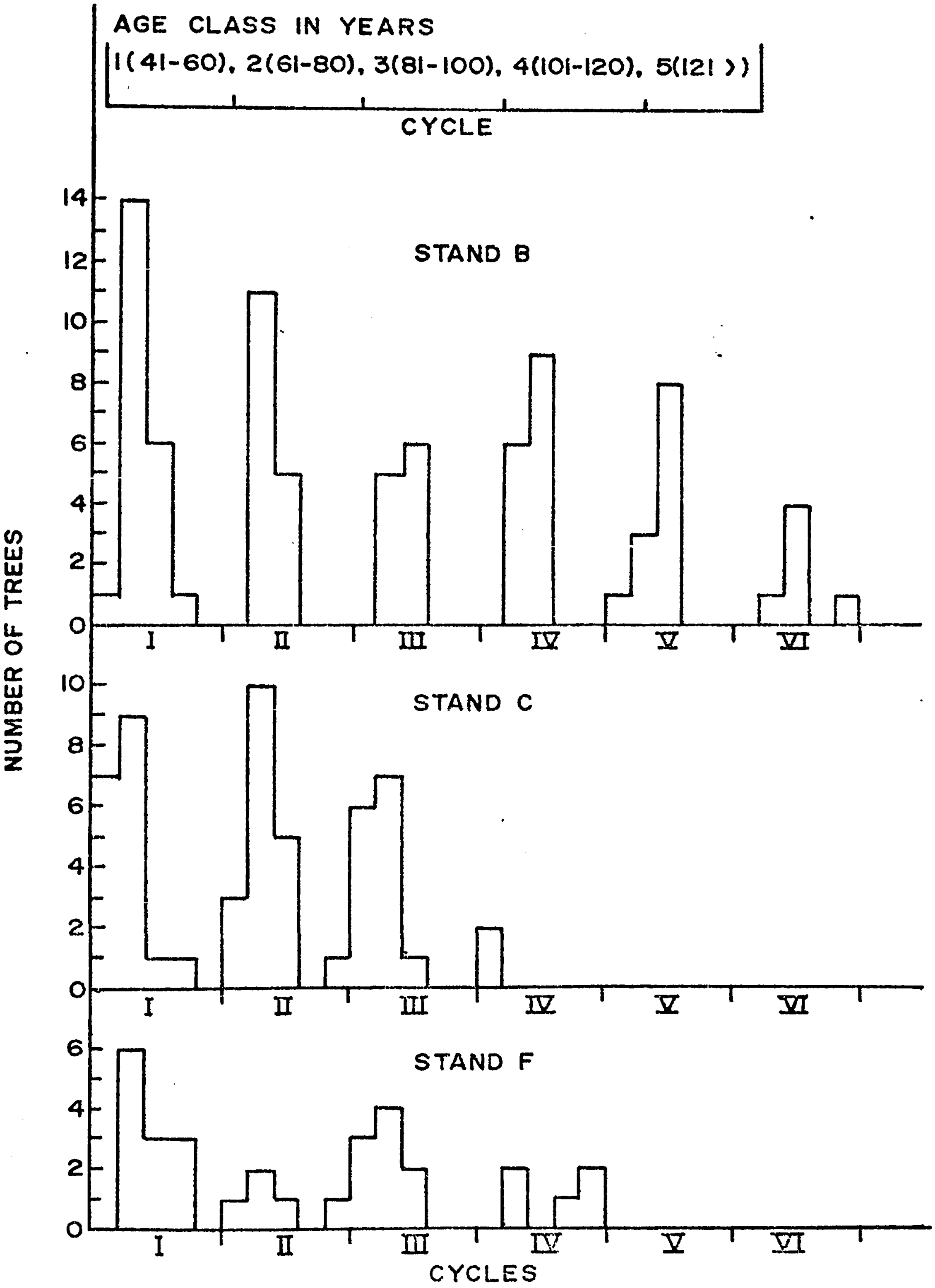


Fig.11. Age-class distribution per cycle (within 40 foot horizontal transect intervals).

b) Gradient-analysis data

Figs. 9-11 illustrate basic frequency distributions calculated for each successive 40 feet intervals of horizontal transect distance. The similarity of the patterns obtained seems to indicate a relatively high degree of distributional symmetry within as well as between the different stands. Absolute identity of the spatial ordination of stand members would be reflected by perfect geometrical superposition of the individual patterns. The degree of deviation thereof can be considered as a measure of asymmetry of distribution or non-homogeneity along a linear gradient. It could also be argued that horizontal transect distance is an environmental gradient along which there are no significant changes of the parametric characteristics of the unit members of the stand.

Table XIV shows the summation figures obtained for the direct and indirect measurements as well as the ratios of the primary measurements. These figures have subsequently been used to find the corresponding numerical values expressed in terms of per unit gradient distance as shown on Tables XV and XVI. The results obtained represent a rate of change of dynamic tree measurement data along a linear gradient in each of the hemlock stands. For this purpose individual tree data have not first been converted to the same measuring units, but the results are looked upon as absolute proportionality constants calculated for analytic purposes rather than subsequent mathematical use.

The results obtained from vertical and horizontal gradient analyses (Tables XV and XVI) indicate a nearly constant rate of change of basal area within and between transects and stands. The diameter-height and diameter-age ratios also display a high degree of similarity along the horizontal gradient (Table XV). The accumulative values seem to be the numerical expressions of a highly uniform net-distributional pattern

TABLE XIV

Basic data for gradient and ratio analysis (all species)

Stand	F		B		C		
Transect No.	1	2	1	2	1	2	3
Total volume (cu.ft.)	118.3	167.9	192.5	235.2	101.2	99.1	134.2
Total basal area (sq.ft.)	5.0	6.6	9.0	9.5	4.2	3.9	6.2
Accumulative tree heights (feet)	585	712	1777	1581	654	586	1143
Accumulative tree diameters (inches)	97.5	123.5	257.5	251.0	100.0	89.5	167.5
Accumulative tree ages (years)	1398	1628	3432	3159	993	937	1791
$\Sigma \frac{\text{Diameter}}{\text{Height}}$	2.8	2.7	6.3	6.1	2.1	1.8	4.0
$\Sigma \frac{\text{Diameter}}{\text{Age}}$	1.1	1.3	3.4	3.1	1.5	1.2	2.6
$\Sigma \frac{\text{Height}}{\text{Age}}$	6.5	8.3	23.0	19.3	8.8	7.9	17.9

TABLE XV

Vertical gradient and ratio analysis[1]

Stand	F		B		C		
Transect No.	1	2	1	2	1	2	3
Vertical dist. (ft.)	104	72	66	83	45	37	51
Total volume	1.1	2.3	2.9	2.8	2.2	2.7	2.6
Accumulative age	13.4	22.6	52.0	38.1	22.1	25.3	35.1
Total basal area	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Accumulative diameters	0.9	1.7	3.9	3.0	2.2	2.4	3.3
Accumulative heights	5.6	9.9	26.9	19.0	14.5	15.8	22.4
$\Sigma \frac{\text{Diameter}}{\text{Height}}$	0.03	0.04	0.10	0.07	0.05	0.05	0.08
$\Sigma \frac{\text{Diameter}}{\text{Age}}$	0.01	0.02	0.05	0.04	0.03	0.03	0.05
$\Sigma \frac{\text{Height}}{\text{Age}}$	0.06	0.12	0.35	0.23	0.19	0.21	0.35

---

[1] Values are rounded off and obtained as a result of dividing all measurements by the respective vertical transect distance.

TABLE XVI

Horizontal gradient and ratio analysis[1]

Stand	F		B		C		
Transect No.	1	2	1	2	1	2	3
Horizontal dist.(ft.)	155	129	206	224	129	106	117
Total volume	0.8	1.3	0.9	1.1	0.8	0.9	1.1
Accumulative ages	9.0	12.6	16.7	14.1	7.7	8.8	15.3
Total basal area	0.03	0.05	0.04	0.04	0.03	0.04	0.05
Accumulative diameters	0.6	1.0	1.3	1.1	0.8	0.8	0.8
Accumulative heights	3.8	5.5	8.6	7.1	5.1	5.5	9.8
$\Sigma \frac{\text{Diameter}}{\text{Height}}$	0.02	0.02	0.03	0.03	0.02	0.01	0.03
$\Sigma \frac{\text{Diameter}}{\text{Age}}$	0.01	0.01	0.02	0.01	0.01	0.01	0.02
$\Sigma \frac{\text{Height}}{\text{Age}}$	0.04	0.06	0.11	0.09	0.07	0.07	0.15

---

[1] Values are rounded off and obtained as a result of dividing all measurements by the respective horizontal transect distance.

of individual tree characteristics within and between areas.

A dominant causal factor in the formation of such a pattern might be the intense intraspecific competition in pure stands of hemlock magnified by the necessity for optimum adaptation to the environmental conditions of a very restricted and specific microhabitat. Any quantitative investigation attempting to interpret the cause-effect interrelationships underlying "quasi-constancy" patterns of this type should necessarily concentrate on the analysis of the predominant species in the stand. Before any further conclusions can be drawn concerning the conceptual quality and phytosociological applicability of the quasi-constants, their genuine existence must be verified by statistical tests. The set of data obtained so far can serve only as a preliminary tool of inquiry or simply a trend-setter.

VII. BIOSTATISTICS

1. Correlation Statistics

a) Objectives

The basic objective was to establish the degree of association between tree height and diameter. With special reference to the ecological characteristics of hemlock the assumption can be made that there is a greater proportionate relationship between tree height and diameter than there is between either diameter and height or age.

In this statistical analysis we are not interested in possible causation of changes in one variable by changes in the other but in the question whether or not the two variables are interdependent or covary. The strength of a linear relationship between the two principal variables which are tree diameter and tree height is measured by the sample correlation coefficient r representing an estimate of the theoretical population coefficient of correlation ρ. The main references used for the design of the statistical procedures are Sokal (1969a, 1969b), Spiegel (1961), Fisher and Yates (1963) and Freund (1960).

b) Testing for a bivariate normal distribution

If Y_1 = tree diameter and Y_2 = tree height then s_1 = standard deviation of Y_1 and s_{12} = covariance of Y_1 and Y_2 = $\frac{(1)}{n-1} \Sigma Y_1 Y_2$. In case of a bivariate normal distribution the correlation coefficient $r_{jk} = \frac{\Sigma Y_i Y_k}{(n-1) s_j s_k}$ will estimate a parameter of that distribution symbolized by ρ_{jk} . r_{jk} can range from +1 (perfect association) to -1 (no association).

A three dimensional realization of a normal distribution can be represented by mounds which assume different shapes depending on the degree of correlation. A 0-correlation is represented by a bell-shaped mound

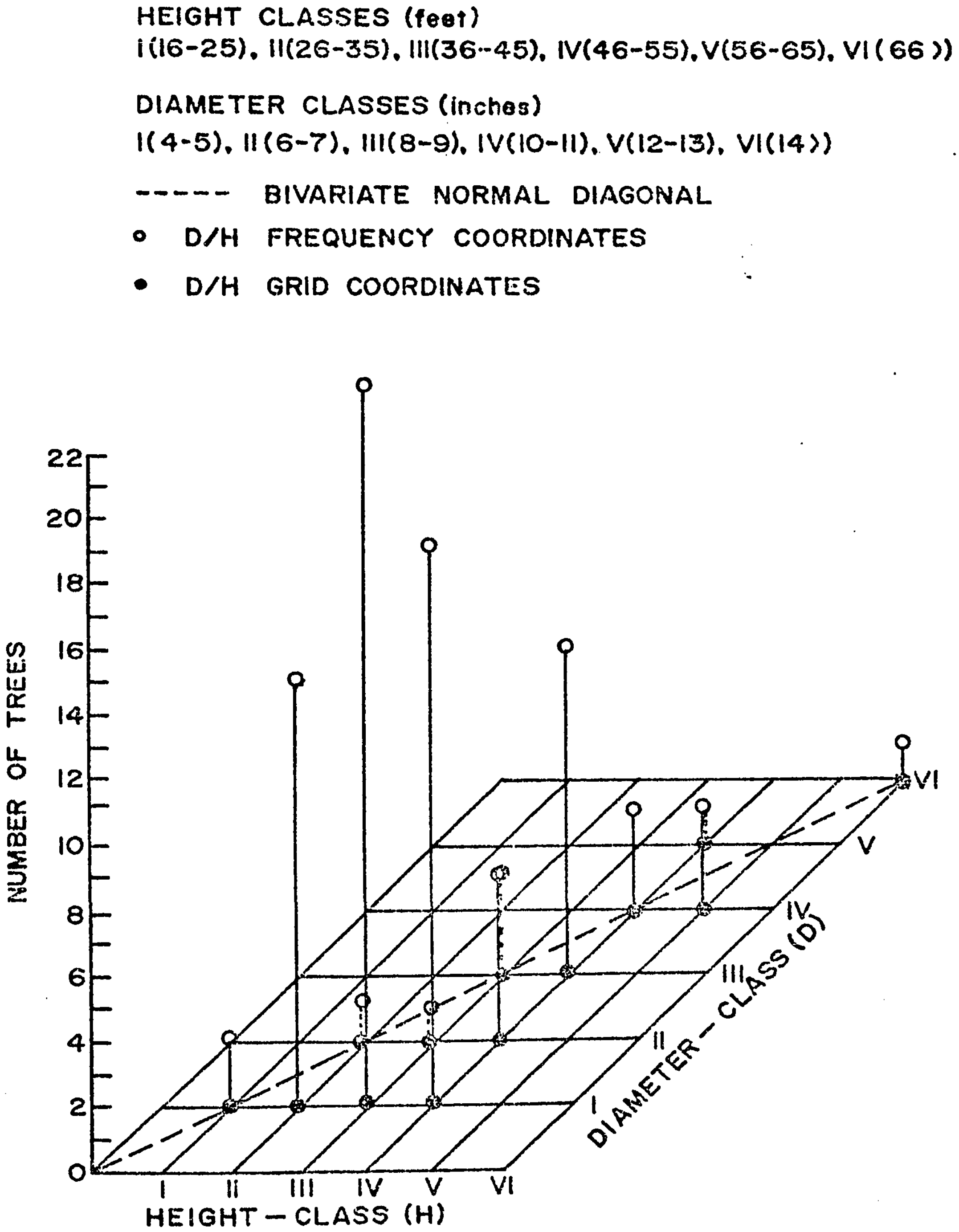


Fig.12 Diameter and height scattergram (Branch-off).

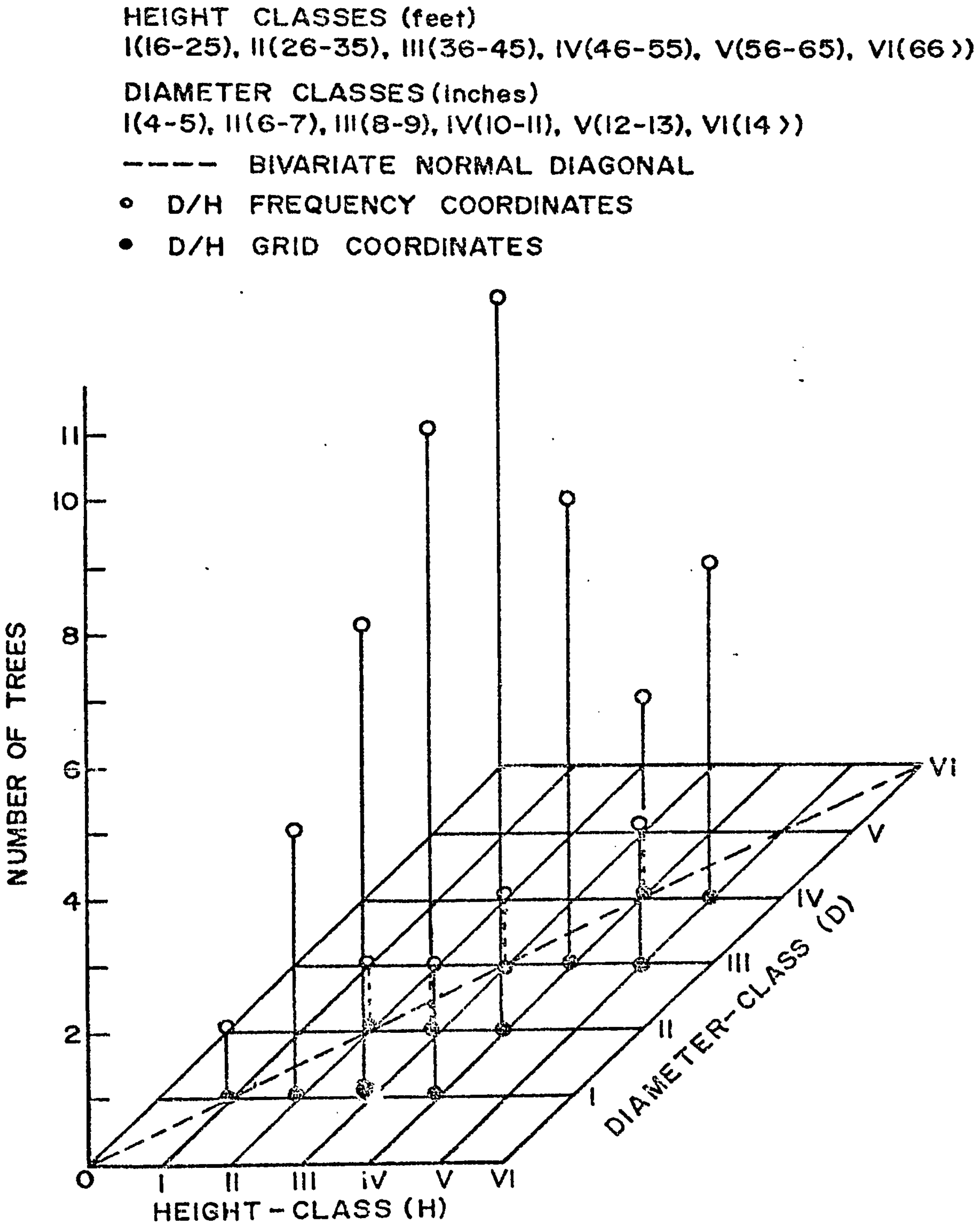


Fig.13. Diameter and height scattergram (Carman-Lake).

HEIGHT CLASSES (feet)
I(16-25), II(26-35), III(36-45), IV(46-55), V(56-65), VI(66>)

DIAMETER CLASSES (inches)
I(4-5), II(6-7), III(8-9), IV(10-11), V(12-13), VI(14>)

------ BIVARIATE NORMAL DIAGONAL

○ D/H FREQUENCY COORDINATES

● D/H GRID COORDINATES

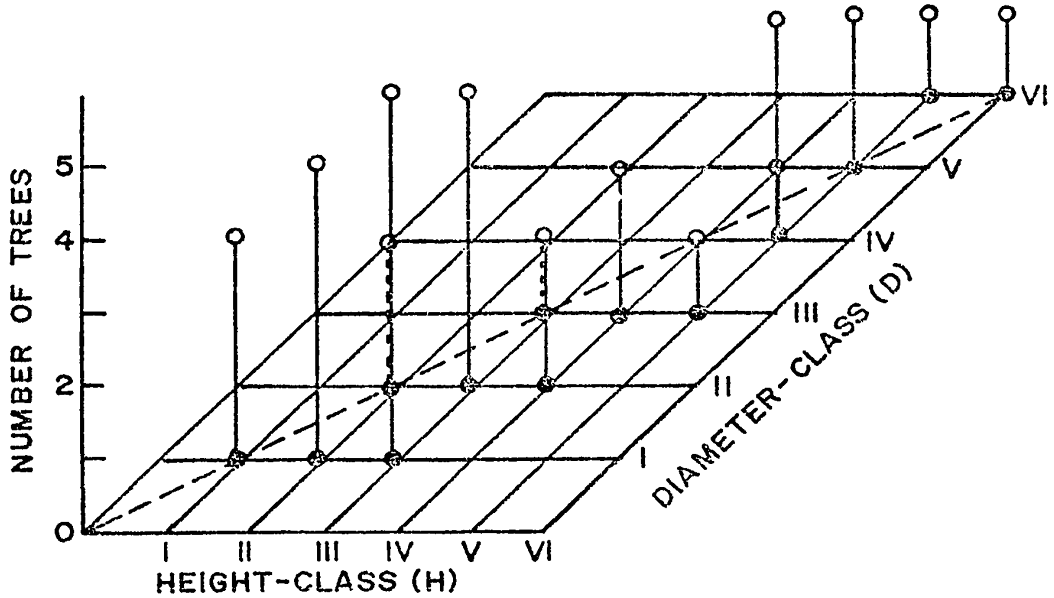


Fig. 14. Diameter and height scattergram
(Camp-Fortune).

which assumes elliptical shape for a correlation. In case of a perfect correlation all data fall along a single regression line and the corresponding three dimensional model would be a flat, essentially two dimensional curve lying on this line. The variations found in most instances range from circular patterns to elliptical shapes.

The bivariate scattergrams shown on figures 12-14 with their diagonal representing the single regression line show a slight skewing effect to the right. It should be kept in mind, however, that the tree measurements start at 16 feet of height (20 feet rounded off) and 4 inches in diameter which provides a partial explanation of this fact. The shape of the mound determined by the degree of correlation between the two variables is an expression of the parameter ρ_{jk} of the bivariate normal distribution and can be defined as $\rho_{jk} = \sigma_{jk}/\sigma_j\sigma_k$ whereby σ_{jk} = parametric covariance of Y_j and Y_k and σ_j and σ_k are the parametric standard deviations of variables Y_j and Y_k. When the two variables are distributed normally the sample correlation coefficient r_{jk} estimates the parametric correlation coefficient ρ_{jk}.

c) Calculation of the product moment correlation coefficient

The computations required for small and medium sized samples are shown on Table XVII. The diameter-height relationship could be considered to be a part-whole correlation since diameter distance represents a fractional expression of tree height. The correlation coefficients computed for the three stands indicate a high degree of linear relationship between tree diameter and tree height.

d) Significance testing

The question may be asked whether or not the sample correlation co-

TABLE XVII

Data for the calculation of the Product-Moment-Correlation-Coefficient

r_{12}

Stand Computations	F	B	C
1. ΣY_1	221	509	357
2. ΣY_1^2	2121	3537	2586
3. ΣY_2	1297	3358	2383
4. ΣY_2^2	61753	145977	111517
5. $\Sigma Y_1 . Y_2$	10868	22152	16710
6. $\Sigma Y_1^2 - \frac{(Y_1)^2}{n}$	545	377	181
7. $\Sigma Y_2^2 - \frac{(Y_2)^2}{n}$	7488	8463	4372
8. $\Sigma Y_1 . Y_2 - \frac{(Y_1 . Y_2)}{n}$	1622	1308	744
9. $r_{12} = \frac{\Sigma Y_1 . Y_2}{\sqrt{\Sigma Y_1^2 . \Sigma Y_2^2}}$	0.80	0.73	0.84
n	31	82	53

TABLE XVIII

Significance testing

$H_o : \rho = 0$ versus $H_1 : \rho \neq 0$[1]

Location	F	B	C
n	31	82	53
r_{12}	0.80	0.73	0.84
$\nu = (n-2)$	29	80	51
level of significance:			
0.05	0.36	0.22	0.27
0.01	0.46	0.28	0.35

---

[1] An additional test for the Camp Fortune stand with $n < 50$ using the z-transformation (Hotelling 1953) did not reject y-table values (see p.74) used in this calculation.

efficient could have come from a population with a parametric correlation coefficient of zero implying that the two variables are uncorrelated. Tests of significance concerning various values of ρ require a knowledge of the sampling distribution of r. For $\rho = 0$ this distribution is symmetric and a statistic involving the Student's distribution can be used. If $\rho = 0$ the distribution is skewed and a transformation according to Fisher (z-transformation) produces a statistic which is approximately normally distributed. It should be kept in mind, however, that the z-transformation for most practical applications produces only insignificant differences as compared to the results obtained from non-transformed computations.

The null hypothesis $H_o : \rho = 0$ being tested as a t-test with n-2 degrees of freedom whereby $t_s = (r-0)\sqrt{(1-r^2)/(n-2)} = r\sqrt{(n-2)/(1-r^2)}$ can be rejected at $P << 0.01$ according to the critical values as shown on Table Y (Sokal 1969b). The results obtained from the significance testing are shown on Table XVIII. Using a z-transformation for $n < 50$ an additional significance test was done for stand F. The computational steps required are as follows:

$$z^* = z - \frac{3z+r}{4n}$$

$$\sigma_z{}^* = \frac{1}{\sqrt{n-1}}$$

Test: $$H_o : \rho = 0 \text{ versus } H_1 : \rho = 0$$

$$\text{and } t_s = (z^* - \xi^*).\sqrt{n-1}$$

whereby ξ^* is the z^* transformation applied to ρ of H_o

$$\xi^* = \xi - \frac{(3\xi+\rho)}{4n}$$

which equals zero since ξ and ρ are both zero.

From Table N (Sokal 1969b) for $r = 0.80$ and $n = 31$ the value of $z = 1.10$ and as a result:

TABLE XIX

Testing the magnitude of the correlation coefficient for ρ = .60 and ρ = 0.50 at the 0.05 significance level

Location	F	B	C
for ρ = 0.60			
n	31	82	53
r	0.8	0.7	0.8
Z	0.9	0.9	1.2
μ_z	0.7	0.7	0.7
σ_z	0.2	0.1	0.1
z	1.1 2)	2.2 1)	3.8 1)
for ρ = 0.50			
n	30	82	53
r	0.8	0.7	0.8
Z	0.9	0.9	1.2
μ_z	0.6	0.6	0.6
σ_z	0.2	0.1	0.1
z	1.8 1)	3.4 1)	6.0 1)

1) Reject.

2) Cannot reject.

TABLE XX

Confidence limits at the 95% level

Location	F	B	C
n	31	82	53
r	0.80	0.73	0.84
z[1)]	1.07	0.93	1.22
α	0.05	0.05	0.05
L_1	0.71	0.71	0.94
L_2	1.15	1.15	1.50
retransformed L_1[2)]	0.61	0.61	0.72
retransformed L_2[2)]	0.82	0.82	0.91

1) Using z^* for F ($n < 50$).

2) Retransformed to r-scale.

$$z^* = z - \frac{(3z+r)}{4n} = 1.10 - \frac{(3.30+0.80)}{124} = 1.10 - 0.03 = 1.07$$

The difference between z and z* is very slight and for all practical purposes negligible. The acceptance of the table values therefore seems to be justified without requiring further t-tests. Since observed r is greater than the tabulated critical values at the 5% and 1% level of significance we can reject $H_o : \rho = 0$ at $P << 0.01$.

e) Testing the magnitude of the correlation coefficient

Can we reject the hypothesis that the population correlation coefficient is as small as $\rho = 0.60$ and $\rho = 0.50$ at the 0.05 significance level?

The calculations are based on Fisher's z-transformation:

whereby $$Z = 1.1515 \log_{10} \frac{(1+r)}{(1-r)}$$

standard deviation $$\sigma_z = \frac{1}{\sqrt{n-3}}$$

mean of normal distribution $$\mu_z = 1.1515 \log_{10} \frac{(1+\rho)}{(1-\rho)}$$

therefore $$z = \frac{(Z-\mu_z)}{\sigma_z}$$

Using a one tailed test for the normal distribution we reject the null hypothesis $\rho = \rho_o = 0$ at the 0.05 level only if $z > 1.64$ as shown on the Table of values for $t_{.05}$ (N) for df = ∞ . The results of the test are shown on Table XIX.

f) Confidence limits

Confidence limits are set to the correlation coefficients using the z-transformation.

The sample r's are first converted to z values, next confidence limits are set to this z and then the limits are retransformed to the

TABLE XXI

Test of homogeneity amongst the three correlation coefficients

Step No.	Location	F	B	C	Σ
1	n_i	31	82	53	166
2	n_i-3	28	79	50	157
3	r_i	0.80	0.73	0.84	
4	z_i	1.07	0.93	1.22	
5	weighted $z_n = (n_i-3).z_i$	29.9	73.5	61.0	164.4
6	weighted $z_i^2 = (n_i-3).z_i^2$	33.5	67.9	74.5	175.9

to the r-scale by referring to Table N (Sokal 1969b).

The lower limit:

$$L_1 = z - t_{\alpha(\infty)}\ s_z = z - \frac{t_{.05(\infty)}}{\sqrt{n-3}}$$

and the upper limit:

$$L_2 = z + \frac{t_{.05(\infty)}}{\sqrt{n-3}}$$

The results of the test shown on Table XX indicate that the correlation coefficients computed for the different stands fall well within the lower and upper limits.

g) Test for homogeneity amongst the correlation coefficients

The question can be asked whether or not the correlation coefficients might represent samples from a population exhibiting a common correlation among the variables. One way of stating the null hypothesis is to say that the sampled r's are homogeneous and estimate a common parameter or parametric value of ρ. The z* transformation has not been used since the calculated z and z* have yielded only insignificant differences in previous calculations.

The computational steps using the data shown on Table XXI are as follows:

I. Compute z:

$$\bar{z} = \frac{\Sigma(5)}{\Sigma(2)} = \frac{164.4}{157} = 1.05$$

II. To test whether or not the r's might have been taken from a common population:

$$\Sigma(6) = 175.9$$

compute a correction term by multiplying quantity I by $\Sigma(5)$

$$= 1.05 \times 164.4 = 172.62$$

compute χ^2 for n - 1 df

$$\chi^2 = 175.9 - 172.6 = 3.3$$

The value of χ^2 is smaller than the 5% and 10% critical values which are:

$$\chi^2_{.10(2)} = 4.6 \quad \chi^2_{.05(2)} = 6.0$$

in conclusion, the calculated correlation coefficients can be considered to be homogeneous.

III. Estimate of a common ρ:

from $\bar{z} = 1.05$ $\bar{r} = 0.78$

h) Conclusions

The high degree to which diameter and height are correlated can be considered as an indication of a high degree of stand structural or developmental homeostasis. This statistical result is a parametric expression of phytosociological and structural homogeneity. The high degree of correlation also indicates the possibility of a common environmental causation. To find out more about the nature of the morphogenetic forces, a multivariate statistic is applied in the following section.

2. Multivariate analysis

a) Objectives

The linear relationship between log diameter and tree height indicates a strong correlation between the two measures (Figs.15-17), here recorded. These variables, namely diameter and height, will therefore be used to define the tree shape and examined along with their relationship to vertical gradients in each transect. The data consist of 145 hemlock trees which were the phytosociologically dominant species.

The statistical procedures will be designed to test the effects of the independent variates, which are age, slope and elevation above mean sea level measured at the base of a tree, on the dependent variates represented by tree diameter and height. The slope at the base of a tree was determined by a numerical differentiation of the vertical and horizontal distances between successive trees along the transect. The Multivariate methods here used are given by Seal (1965).

b) Statistical design

The following model was constructed and subsequently subjected to significance tests:

$$z_1 = a_1 + b_1 z_2 + c_1 x_1 + d_1 x_2$$

$$y_2 = a_2 + b_2 z_2 + c_2 x_1 + d_2 x_2$$

The number and letter designations used are defined as indicated:

computer output number:	letter:	definition:
1	y_1	tree diameter (inches)
2	y_2	tree height (feet)
		variables 1 and 2 represent the dependent variates

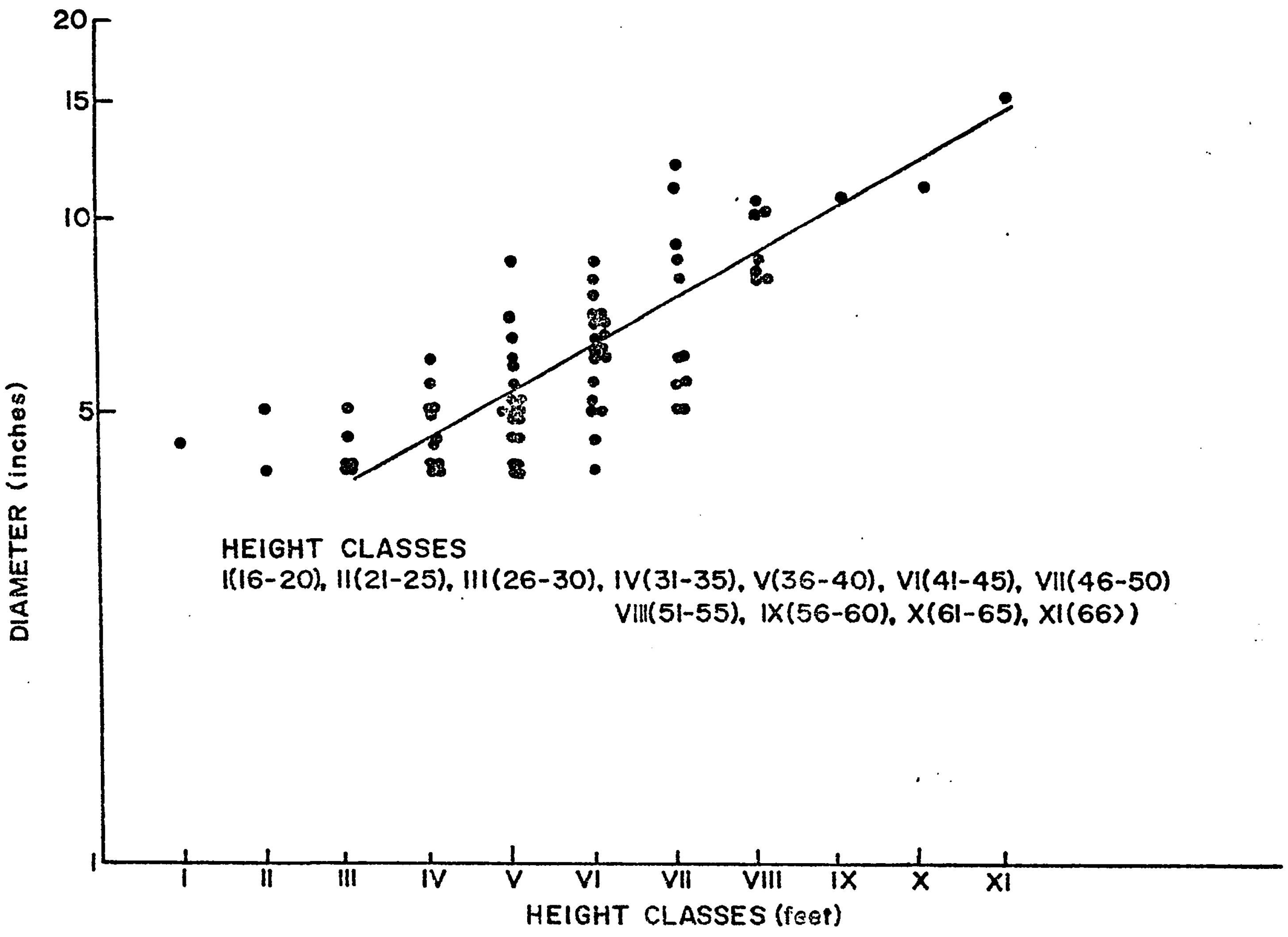


Fig. 15. Correlation between diameter and height. (Branch-off).

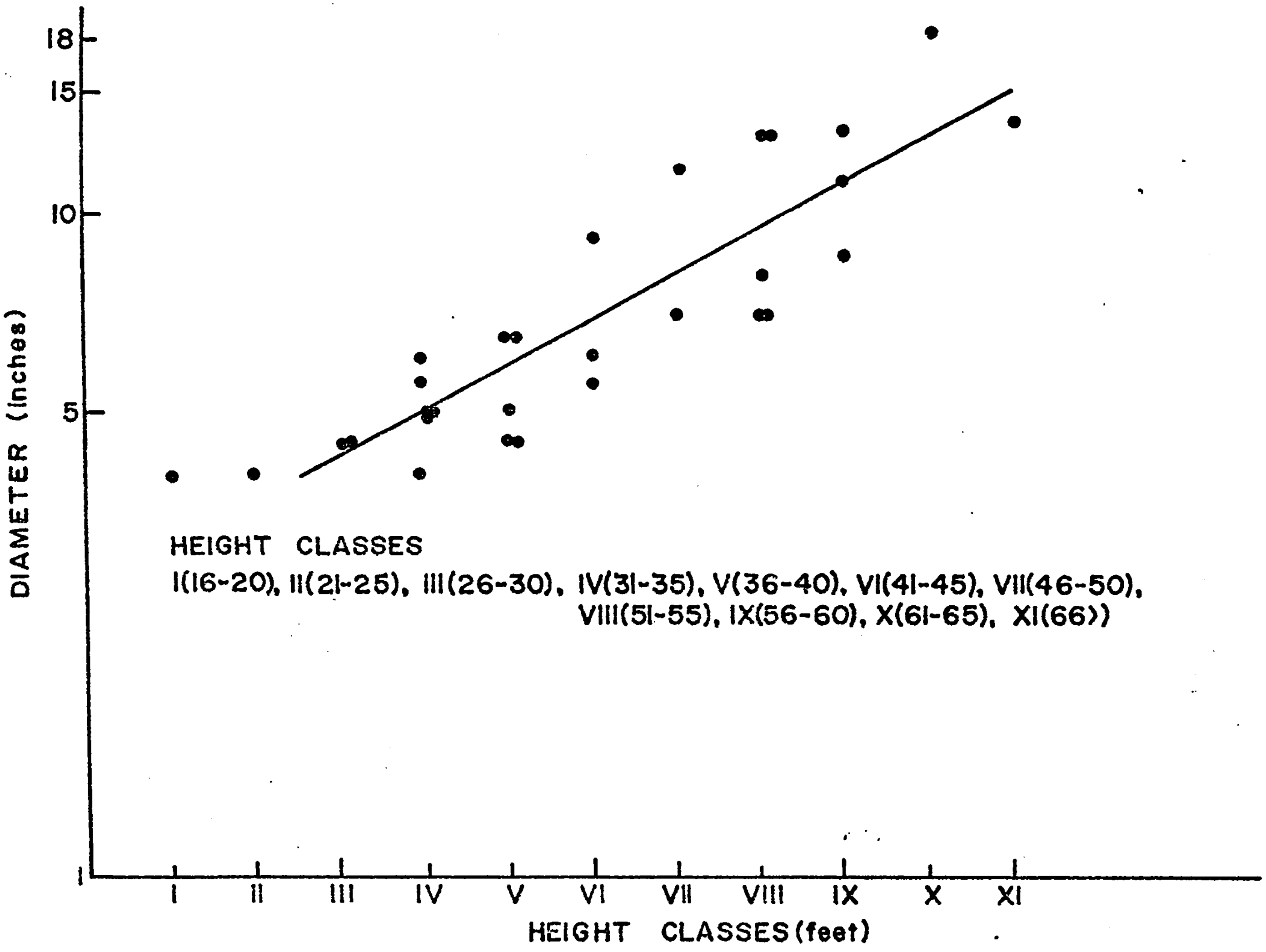


Fig. 16. Correlation between diameter and height (Camp Fortune).

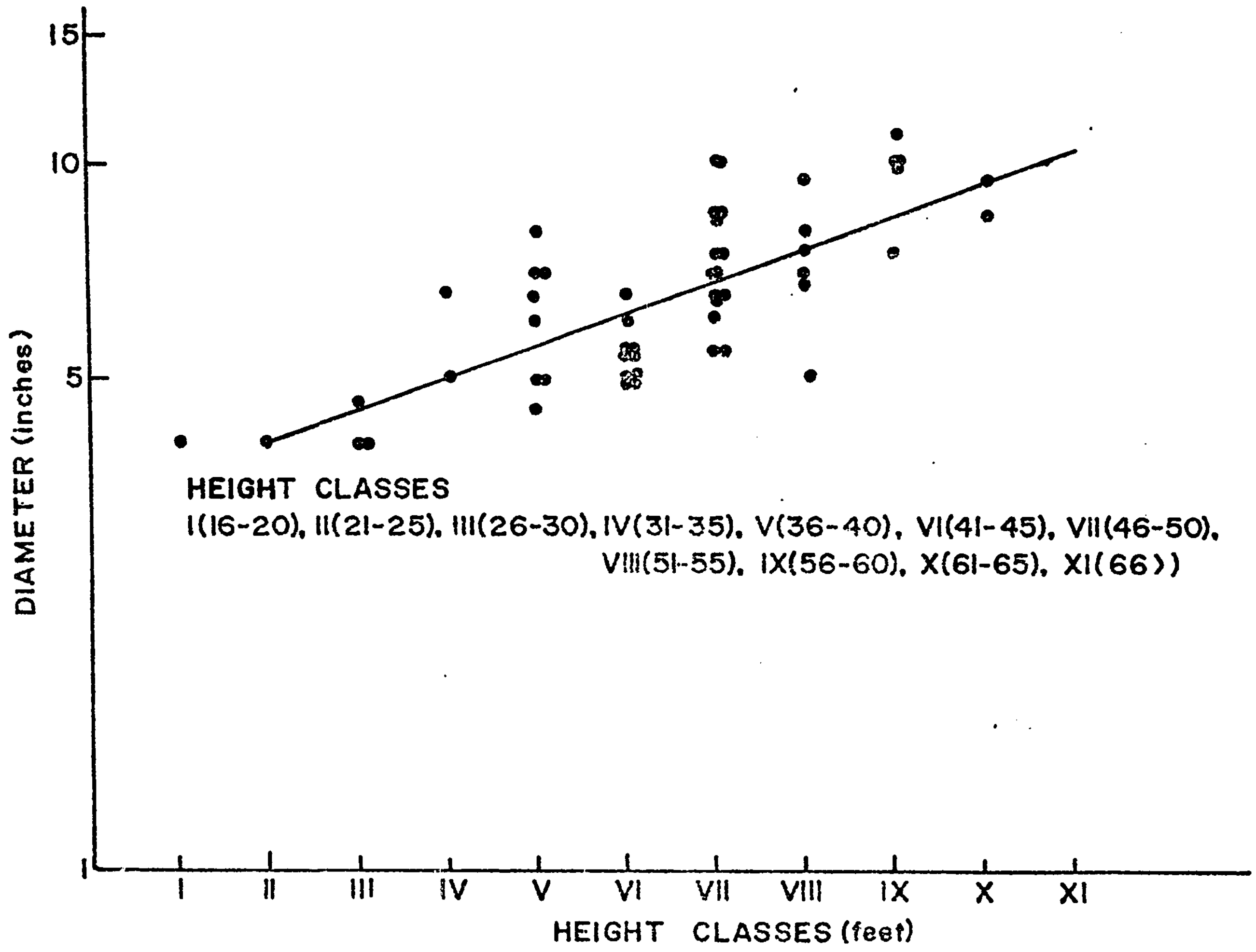


Fig. 17. Correlation between diameter and height (Carman Lake).

computer output number:	letter:	definition:
3	x_1	tree age
4	x_2	height at the base of a tree above mean sea level
-	x_3	accumulative horizontal distance from the lowest tree in each transect
-	z_1	log y_1
5	z_2	slope at the base of a tree (obtained by numerical differentiation)

The introduction of instrumental variables for the model analysis will permit the testing for general differences in stand localities as well as transect locations (see Appendix A).

c) Significance testing

The null hypotheses formulated for testing the theoretical multivariate programme are:

H_1 : b_1 and b_2 (simultaneously) = 0 versus b_1 and/or $b_2 \neq 0$
H_2 : c_1 and c_2 (simultaneously) = 0 versus c_1 and/or $c_2 \neq 0$
H_3 : d_1 and d_2 (simultaneously) = 0 versus d_1 and/or $d_2 \neq 0$

If the null hypotheses are disproved we can state that their associate variables affect tree shape.

The major model types used for the significance testing are as follows:

a. reduced model vs. no model
b. reduced model vs. full model

If a. is true then the variables currently included appear non-important by themselves (observed χ^2 < critical χ^2). If b. is true then the variates currently omitted appear non-important by themselves (observed χ^2 < critical χ^2).

d) Statistical results

Before fitting the model the log diameter and height are correlated by:

$$\frac{141.8224}{\sqrt{2.761932 \times 12127.06}} = 0.774927 \qquad \text{for 144 df}$$

After fitting the full model the correlation becomes:

$$\frac{.8059641}{\sqrt{.01548734 \times 72.40184}} = 0.761119 \qquad \text{for 139 df}$$

The interrelationships between log diameter and height are also given by the following expressions:

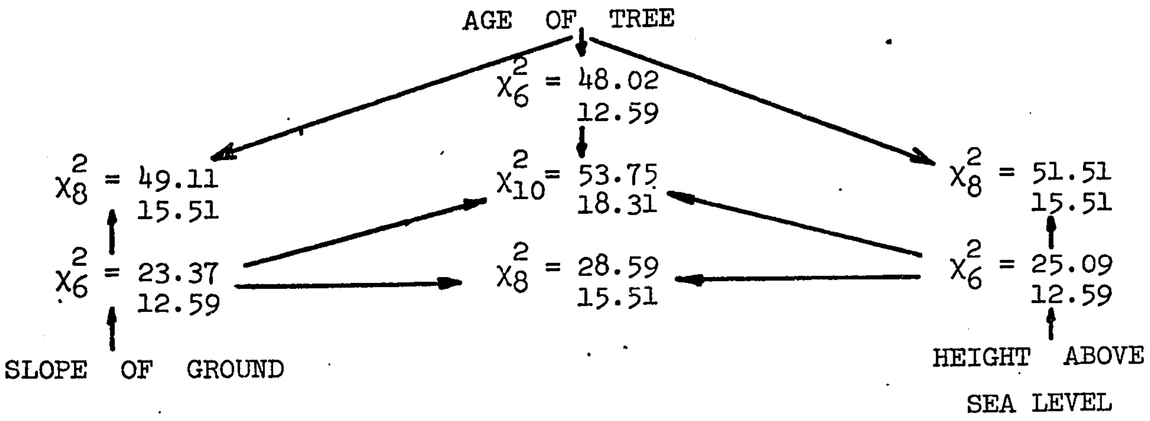
$$\text{log diameter} = \frac{.8059641}{72.40184} \times \text{height}$$

$$\text{or:} \quad \text{height} = \frac{.8059641}{0.0154873} \times \text{log diameter}$$

The results of the χ^2 tests are shown below:

(Observed values are shown above the critical values.)

(All tests are no model versus full model.)



The instrumental variables alone have a $\chi_4^2 = 20.57$ (no model versus reduced model) and variables 3,4 and 5 without the instrumental variables a $\chi_6^2 = 35.36$ (no model versus reduced model).

e) Biometrical evaluation

The estimates of the coefficients of the equations given at the beginning of section b) are:

log diameter (inch.) = $0.5175 + .3299 \times 10^{-2} \times$ age $+ .4807 \times 10^{-4} \times$ elevation at the base of tree $- .2708 \times 10^{-1} \times$ slope of ground + other locality factors;

height of tree (feet) = $0.5528 \times 10^{2} + .1730 \times$ age $- .4224 \times 10^{-1} \times$ elevation at the base of tree $- .4448 \times 10^{-1} \times$ slope of ground + other locality factors.

The results obtained from statistical analysis are interpreted as follows:

i diameter and height increase with age;

ii diameter and height decrease with increasing slope;

iii diameter increases with height above sea level whereas tree height decreases with increasing height above sea level.

It might therefore be concluded that hemlock trees in the stands investigated become shorter and stockier with increasing altitude and shorter and more slender with increasing steepness of slope. In summary, after allowing for age and some general differences between the three localities, the form factor varies in an orderly pattern along the vertical stand gradient. It also appears that differences among the transects in the three locations are non-important by themselves (see Appendix A) and, theoretically speaking, form part of a common hemlock stand.

In an attempt to assess the biological implications of the results, consideration should be given to the following criteria:

i the dependence of diameter and height growth on age is irrelevant in terms of gradient analysis;

ii the inverse relationship between tree diameter and height and steepness of slope can be understood as a function of the component forces of tree weight which can be supported along the slope;

iii the variation of tree shape along the slope cannot be explained as easily.

A vertical height difference between the lowest and heighest point of a transect which varies from 37 feet to a maximum of 104 feet can hardly by itself be considered a causal factor of the observed tree shape variation. Altitudinal gradient effects resulting in a proportionate form factor variation and associated with an alternating species sequence and vegetational zonation generally exist only over large distances. The difference could possibly be the integral expression of stand structural dynamics resulting mainly from a high degree of species interaction controlled by the intense environmental pressure exerted on the hemlock "enclaves".

If found in different stands of comparable nature, form variation can be used as an expression of structural similarity between stands. A numerical expression of the degree of structural similarity between hemlock stands in form of linear gradient constants is an essential step in the mathematical formulation of a homogeneity index.

VIII. HOMOGENEITY INDICES AND CONSTANTS OF SIMILARITY

As explained by Numata (1950), the concept of homogeneity, if equated with the degree of uniformity or similarity between population members, depends in its final interpretation on the specific objectives of a particular investigation. One of the objectives of phytosociological analysis, as conducted for this study, was to test the possible presence of mathematical patterns in the spatial ordination of tree characteristics in pure stands of hemlock.

The basic parameters of individual tree characteristics in form of height, diameter, age, and their derived quantities basal area and volume, are assumed to reflect the effects of intraspecific dynamic interaction as related to the total stand. Any patterns resulting from an interaction of this nature would necessarily be an expression of a specific aspect of community dynamics. It can be reasonably assumed that the complexities of population dynamics are considerably reduced or minimized in plant communities of low species diversity and single species predominance.

The statistical testing results obtained from the biometrical analysis of pure hemlock stands should accordingly be reliable, representative and accurate expressions of causal population dynamics. The definition of homogeneity could subsequently be based on the degree of measurable pattern similarity interpreted in a mathematical sense as a constant. The biological equivalent of such a constant would be a high degree of uniformity of tree characteristics as a direct result of homogeneous stand dynamics. If similar constants can be calculated for different stands of comparable phytosociological structure and environment, a hypothetical, parametric and common population denominator may be determined.

For purposes of ecological classification a mathematical expression based essentially on "dynamic" constants should be a much more valid and genuine analytical tool than most of the traditional systems depending almost entirely on "static" factors such as numerical abundance and absence or presence of population members.

The degree of population diversity as seen by Williams (1964) is determined by the ratio of groups (e.g. genera) and units (e.g. species). The same author however stresses the fact that identity of diversity does not necessarily imply identity of populations since obviously the same ratio can be obtained from different numerical combinations. Curtis (1959) distinguishes between homogeneity and distinctness of a community, the first being of an intra-communal and the second of extra-communal nature.

Various attempts have been made to find mathematical expressions for the measurement of homogeneity. A semi-quantitative definition of homogeneity was given by Braun-Blanquet (1932) in referring to an association as an abstraction based on the totality of more or less homogeneous releves (lists) which floristically correspond closely to each other.

Numata (1950) defines plant homogeneity in two major terms of reference:

1. individual homogeneity (h) and
2. communal homogeneity (H), which is determined by
   a) floristic homogeneity and
   b) vegetational homogeneity.

The corresponding interrelationships between members of a plant community are expressed by the following formula:

$$H = (h_a + h_b + \ldots\ldots h_k/k)$$

whereby h is measured preferably in terms of density. The same author discusses in great detail the possibility of applying the law of geometrical progression to plant communities for the purpose of measuring homogeneity. The applicability of the law to different types of plant communities apparently posed some serious problems.

The index of similarity as proposed by Bray and Curtis (1957) has the following mathematical form:

$$I.S. = \frac{2\,w}{a + b}$$

a = sum of all measures for one entity

b = sum of all measures for other entity

w = sum of lower values for each measure

The generic coefficient of Jaccard (1902, 1928) and its later modification by Gleason (1920) are dependent primarily on the number of individuals and species present in the communities to be compared.

The generic coefficient for a hemlock-beech consociation calculated from the formula

$$C = \frac{100 \times \text{No. of species common to two quadrats}}{\text{Tot. No. of species in the two quadrats}}$$

was 85%. An index figure of 100 in comparison would indicate absolute generic similarity.

It becomes quite obvious that most mathematical expressions designed to measure homogeneity are based in principle on "static" tree or population characteristics.

The concept of site in forest management, as described by Davis (1954), is basically a semi-quantitative measure and therefore not suitable for a quantitative analysis. Moreover, tree height and tree proportion expressed in terms of volume are relatively independent of site. To employ the concept of site as a technique of measuring homogeneity should prove extremely difficult.

From the results obtained in this investigation it is suggested to follow up with similar studies in forest stands containing a lower percentage admixture of hemlock and to establish the nature of "dynamic" constants. A subsequent statistical testing programme would have to establish the biological and mathematical validity of the proposed constant model on a proportionate scale. Any constant thus verified and calculated could be integrated into a mathematical index formula measuring comparative degrees of homogeneity in hemlock stands with possible adaptations and extrapolations for measuring other types of forest stands. If done successfully, the index would represent a sensitivity meter reflecting any changes in the dynamic expressions of forest trees and stands with possible applications for forest ecological studies concerning pollution effects. A reference stand selected within a certain climatic region for a specific forest type would be assigned a homogeneity index = 100 and the intensity of effects of air or water pollution on other stands would be assessed in terms of a sliding index scale.

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Appendix A

Differences among the transects in the three different locations.

```
X, THE INDEPENDENT VARIATES 10   11   12   13


 INVERTED SUM AND CROSS PRODUCT MATRIX OF THE INDEP ENDENT VARIATE

    X10       .4551435-001 X10       -.1509927-003 X11       -.1509927-003 X12

    X11      -.1509927-003 X10        .5403246-001 X11       -.3687663-001 X12

    X12      -.1509927-003 X10       -.3687663-001 X11        .5403246-001 X12

    X13       .3462614-004 X10       -.8741631-004 X11       -.8741631-004 X12


 UNBIASED MAXIMUM LIKELIHOOD ESTIMATE OF THE VARIANCE COVARIANCE MATRIX OF T

    Y 1        .1913038-01 Y 1        .9813693    Y 2

    Y 2        .9813693    Y 1       34.63727     Y 2


REGRESSION COEFFICIENTS

Y 1     =             .7850285     X 0      .1338401-001 X10       .1479995-001 X

Y 2     =            41.39798      X 0     -.6725437     X10       .8230336     X


                                                       TEST OF SIGNIFICANCE (REDUCED
                                                       -----------------------------

TESTING         NO OF VARIATES NO.S-1 LESS        DETERMINANT        U-RATIO
                  REMAINING    REMAINING           GEN.VAR                    COM

NO MODEL VS.          0           144               13380.5
REDUCED MODEL         4           140               12839.0         .959529      5.

REDUCED MODEL VS.     4           140               12839.0
FULL MODEL            9           135               8653.49         .674001      53
```

```
 12         .3462614-004 X13

 12        -.8741681-004 X13

 12        -.8741681-004 X13

 12         .1317794-001 X13


 OF THE DEPENDENT VARIATES





01 X11          .1592157-001 X12        -.2627324-001 X13

  X11            1.277629    X12         -1.363052    X13


UCED MODEL)
-----------

   CHI-SQUARE                DF. FOR
 COMPUTED CRITICAL(5%)  CHI-SQUARE


  5.804       15.51           8

  53.66       18.31          10
```