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A preliminary ordination study of forest vegetation in the Kirchleerau area of the Swiss Midland

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Table of Contents

I. Introduction

At a meeting in 1959 of the working group on forest typology of the International Union of Forest Research Organizations (IUFRO), it was decided to make a comparative study using several different forest vegetation

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research and mapping methods. An area in Switzerland was then studied in the early 1960's using four methods, and the results were published as "Vegetations- und bodenkundliche Methoden der forstlichen Standortskartierung (Ecological and pedological methods of forest site mapping)", Veröff.Geobot. Inst.ETH, Stiftung Rübel, Vol. *39* (1967), H. Ellenberg, editor.

The four methods may be briefly described as follows (see references for titles of the individual papers):

1. The method of the Braun-Blanquet school as an example of a phytosociological method which considers combinations of species and leads to the naming and mapping of plant associations. This paper and the accompanying map will be cited as Frehner (1967).
2. The method of Aichinger which stresses the dynamics of plant associations and leads to the mapping of forest development types. Prof. Aichinger emphasized that he would have mapped this area by the Braun-Blanquet method if he had not been asked to apply his own method. The paper and map are cited as Aichinger (1967).
3. The combined method in which site and vegetational factors are equally considered, based on methods developed for forest site-mapping in the DDR. The paper is cited as Eberhardt et al. (1967) and accompanying maps are cited as Eberhardt.
4. The plant geographical method of Schmid in which regional and local phytocoenoses of the mapped area are related to the vegetation zones of Switzerland. The paper and map are cited as Saxer (1967).

The area studied was selected for its ecological diversity as will be described in more detail in the next section. Briefly, however, there are numerous combinations of exposures, soil parent materials and soil types. In addition, the area has a long history of forest management by man. Cutting and thinning of trees and saplings and planting of trees, primarily conifers exotic to the area, greatly enhance the complexity. Several areas within the forest were formerly used for agricultural purposes and have since been reforested which further modifies the sites. In short, the combinations of sites plus vegetation types approach the maximum possible diversity.

A. Purpose of study

The author of this paper was invited to study the area using methods of the so-called "Wisconsin school" which are summarized in a book (1959) by the late Prof. J. T. Curtis. The methods used in studying the forests of Wisconsin were developed for use in relatively large, homogeneous, natural forests (the antithesis of the Kirchleerau forests), and are not really applicable for mapping purposes. Actually, there is no "Wisconsin method". It is more a philosophy based on the individualistic interpretation of species behavior (GLEASON, 1926, 1939; RAMENSKY 1926, 1930) and the continuum concept of vegetation (McINTOSH, 1967).

It considers that there are no "typical examples", and that vegetation should be studied objectively, quantitatively, and comparatively for a relatively large number of stands within one community type or several closely related communities.

The purpose of my study then may be posed as a question: can a person having no previous knowledge of European ecological conditions (*i.e.*, not knowing which soil and geological conditions are important, not knowing the species, and not having any pre-knowledge of which understory species are associated with which trees and which environmental conditions) use quantitative methods and gain any understanding concerning Swiss forest vegetation in areas long and heavily modified by man?

Within this framework, the vegetation was sampled in May and June, 1968, using my modifications of "Wisconsin" field methods. Since FREHNER (1963) studied the vegetation in this region of the Midland in more detail than the other workers, his results may be more authoritative. I therefore placed my 25 study areas or stands in the associations as mapped by FREHNER (1967). Trees and understory species were studied quantitatively, an ordination of stands was made, and the results of my study were compared with the results of the other four methods.

In order to make these comparisons, the stands which I studied were located on the maps of the other workers and were assigned to the vegetation types as they had mapped them. It was sometimes necessary to group their stands in various ways using my interpretation of their data in order to determine what trends were represented. It is possible that errors have been made through misinterpretation of their data or through slight errors in the boundaries of vegetation types as drawn on their maps. I regret any errors, if such occur.

B. The study area

The following description of the area which was studied by the four methods plus mine is summarized in part from EBERHARDT et al. (1967). The study area is located in the Swiss Midland in Canton Aargau, approximately 35 km northwest of Luzern and 10 to 15 km south of Aarau on the east side of the Suhr Valley.

The forests are located on the western slopes of a ridge or plateau, the long axis of which runs in a north-northwest by south-southeast direction. The top of this ridge is mostly cultivated land. The drainage pattern toward the Suhr has dissected the western side of this ridge into many hilly areas. The forests consequently are on slopes which face north, west, and south, but seldom have an eastern exposure.

The village of Schöftland is at the northern end, Moosleerau is toward the southern end, and Kirchleerau is just south of the central part. The forests of the research area are owned by the above-mentioned communities, and extend about 5 km from north to south. The total forest area mapped by the various methods is approximately 415 to 420 hectares (*c.* 1030 acres).

Since the time available for field reconnaissance was limited, and also to minimize geographical differences, 23 of the 25 stands were placed in the southern half of the area in the Kirchleerau-Moosleerau vicinity. Stands 22 and 23 in the *Aceri-Fraxinetum* were at the northern end near Schöftland.

Elevations of forests in the total mapped area range from 460 to 713 meters above sea level. The macroclimate, averaged from a number of stations surrounding the research area, may be considered as relatively moist (1200 mm average annual precipitation) and relatively mild (8–9 °C. average annual temperature).

It would have been desirable to select my stands for study to include a variety of slopes and aspects, elevations, moisture conditions, etc. However, since I was unfamiliar with the area, several days were spent in exploring the area and selecting from FREHNER's mapped associations stands which were relatively as undisturbed as possible (*i.e.*, had not had recent cutting and planting), and that were large and homogeneous enough to be studied by my field methods. At that time plants were collected, and were identified with the help of Prof. E. LANDOLT and Mr. A. GIGON.

For analysis of stands by the ordination technique, it is desirable to have a minimum of perhaps 20 stands. Ultimately, 25 stands were studied belonging to seven different associations according to FREHNER. No stands were studied in FREHNER's association nine, *Carici remotae-Fraxinetum chrysosplenietosum* (he mapped only one tiny example of this association) or association four, *Querco-Abietetum* prov. (the areas mapped as such have received several diverse forestry treatments and from my standpoint were too small and heterogeneous). The listing of my 25 stands according to FREHNER's associations is shown in Table 1. As seen in Table 1, some of the associations have several subassociations, and the seven associations may be placed in three larger groups.

Table 1, Footnote 1.—Description of geological layers (soil parent material) from MÜHLBERG (1908) and SAXER (1967, p. 156). Numbers 1 to 6 indicate the relative geological age from oldest to youngest. The elevations listed are those for my stands in the various layers.

6. Würm moraine. 510–590 meters. Kalk-containing. Most of the "mixed deciduous forest" species of this region are on Würm moraine.
5. Riss gravel. 510 meters. "Kalk-reich" (rich in $CaCO_3$), often penetrated by sand and clay layers. At the boundary of the gravel on top of molasse, water seeps out in places which can lead to the formation of an *Aceri-Fraxinetum.*
4. Upper sweetwater molasse. 700 meters. Sandstone with marl and clay constituents which give a preference for *Abies.*
3. Upper marine molasse (Helvetien), Wienerstufe. 610–670 meters. Soft sandstone. A strong layer of "nagelfluh" (conglomerate), usually less than 1 m thick is in the lower part of this layer, normally at about 600 meters.
2. Upper marine molasse (Helvetien), musselsandstone. 540–610 meters. Somewhat softer sandstone. Water is conducted in the upper part of this layer just below a band of conglomerate, and trickles or seeps out in some places on the slope.
1. Lower marine molasse (Burdigalien) (upper marine molasse according to Saxer). 500 meters. Relatively hard sandstone makes possible steep slopes which make possible the entry of "Laubmischwald" (mixed deciduous forest) species into the beech forest.

Footnote 2.—Key to symbols for soil types and site factors from "Standortsformenkarte nach D. KOPP" by EBERHARDT.

Bodenformen – (soil types)

Mo Moosleerauer Schotter- und Moränen-Rendzina
Br Brönner – Lehm – Fahlerde
Gä Gänserain – Lehm – Fahlerde
Hi Hirschacker – Lehm – Braunerde
Rr Rossrücken – Lehm – Braunerde
Rö Rötler – Lehm – Braunerde
St Stolten – Lehm – Braunerde
Sö Schöftlander – Lehm – Hanggley

Kleinflächige Besonderheiten (small-surface peculiarities)

⇌ Kleinflächiger Wechsel von Bodenformen
V Kleinflächig nährstoffärmer

Reliefbedingte Wasserhaushaltsstufen (relief-caused moisture gradients)

1 Reliefbedingt frischer
2 Mittlere Stufe
3 Reliefbedingt trockener

Windausgesetzte und -geschützte Lagen (wind-exposed and -protected locations)

v Reliefbedingt windverhagert (relief-caused wind degradation)
| Reliefbedingt windgeschützt (relief-caused wind protection)
s Reliefbedingt warmbegünstigt (relief-caused warmth protection)

Hang- und Plateaulagen (slope and plateau locations)

p in Plateaulage

Weitere Besonderheiten (further peculiarities)

↓ Wuchsleistung ungewöhnlich gering (growth productivity especially small)

Table 1. Location and physical features of stands

Stand number	Forest communities (after Frehner, 1967): Group	Association	Sub-association	Location and elevation (Landeskarte, 1964): Location of stands Coordinates	Elevation in meters	Measured in field: Slope	Aspect	Estimated relative moisture	Geology and soils from maps: Soil parent material[1]	Soil types and site factors[2]
	A. Beech forests (Calcium-poor)									
1		Melico-Fagetum	asperuletosum	648550 - 235800	610	15°	NW	mesic	3	St 1
2		Melico-Fagetum	asperuletosum	648125 - 235400	640	5°	W	mesic	3	Rr 2
3		Melico-Fagetum	luzuletosum	647925 - 235500	620	5°	SW	dry	3	St 2p $\rightleftharpoons$ Rr 2p
4		Melico-Fagetum	luzuletosum	648600 - 235850	620	20°	W	dry	3	St 2
5		Melico-Fagetum	cornetosum	648425 - 237050	600	25°	S	dry-mesic	2	Br 2s
6		Milio-Fagetum(prov.)	dryopteridosum	647900 - 235725	570	20°	NE	mesic	2	St 1
7		Milio-Fagetum(prov.)	dryopteridosum	648475 - 235450	670	15°	NW	mesic	3	Rr 2 $\rightleftharpoons$ Hi 2
8		Milio-Fagetum(prov.)	dryopteridosum	648275 - 235425	640	25°	NW	dry-mesic	3	Rr 2
9		Milio-Fagetum(prov.)	luzuletosum	647925 - 235625	600	25°	N	dry	2	St 2v
10		Milio-Fagetum(prov.)	luzuletosum	648400 - 234875	610	20°	N	dry	2	St 1 $\rightleftharpoons$ St 2
11		Melampyro-Fagetum	typicum	648075 - 235225	630	20°	NW	dry	3	St 3v $\rightleftharpoons$ Rö 3v
12		Melampyro-Fagetum	typicum	648075 - 235175	630	15°	S	dry	3	St 3v $\rightleftharpoons$ Rö 3v
13		Melampyro-Fagetum	typicum	648100 - 236250	540	25°	SW	dry	2	St 2v
14		Melampyro-Fagetum	leucobryetosum	647875 - 235075	570	25°	W	dry	2	St 3v $\rightleftharpoons$ Rö 3v
15		Melampyro-Fagetum	leucobryetosum	647900 - 234625	600	15°	SW	dry	2	Br 3v
	B. Beech forests (Calcium-rich)									
16		Pulmonario-Fagetum(prov.)		648300 - 235175	640	20°	S	dry-mesic	3	Br 2s $\rightleftharpoons$ Gä 2s
17		Pulmonario-Fagetum(prov.)		647450 - 234625	530	10°	W	dry-mesic	6	Mo 2 $\rightleftharpoons$ Hi 2
18		Carici-Fagetum		648525 - 235350	700	25°	S	dry-mesic	4 $\rightarrow$ 6	Mo 3
19		Carici-Fagetum		648075 - 234350	590	10°	NE	dry-mesic	6	Mo 3
20		Carici-Fagetum		647675 - 234075	550	20°	W	dry-mesic	6	Mo 3
	C. Ash forests (Calcium-poor)									
21		Aceri-Fraxinetum		648275 - 235525	610	20°	NW	dry-mesic	3	Rö 1 | ∨
22		Aceri-Fraxinetum		646950 - 239025	510	15°	NE	moist	5 $\rightarrow$ 1	Rö 1 | $\rightleftharpoons$ Sö
23		Aceri-Fraxinetum		646725 - 239200	500	20°	N	moist	1	Mo 2 $\rightleftharpoons$ Sö
24		Pruno-Fraxinetum		648275 - 236550	580	5°	NW	dry-mesic	2	Rö 1 | $\rightleftharpoons$ Hi 1
25		Pruno-Fraxinetum		647400 - 234500	510	10°	W	moist	6	Sö $\rightleftharpoons$ Hi 1

Also shown in Table 1 are the locations of the stands and their approximate elevations as determined from maps. The precise location of my stands is not important for the purpose of this study, so no map of the forests is included. However, a map showing the location of the stands which were studied is on file at the Geobot. Institut in Zürich.

The degree and direction of slope were measured in the field. The moisture regime was estimated in the field, being reevaluated in the several visits to each stand. The listing in Table 1 is on no absolute scale, but is relative for the 25 stands studied. Note that there are five relative moisture classes: dry, *dry*-mesic, dry-*mesic*, mesic, and moist.

Underlying geology or soil parent material was determined from a map by Mühlberg (1908), and is correlated with a description of the various layers by Saxer (1967) in a footnote to Table 1. About 80% of the stands are on differing ages of Tertiary molasse deposits, primarily sandstone of various sorts. About 20% of the stands are on glacial deposits, mostly Würm moraine.

Soil types and site factors were determined from the site type map of Eberhardt. A key to the symbols is given in footnote 2 to Table 1. Since Eberhardt expresses many subtle differences, the descriptions are given in his German terms (with only the major categories also in English) to avoid mistranslations.

II. Field Methods

A. Selection of stands

As mentioned above, stands were selected from associations as mapped by Frehner (1967) with the ultimate aim of including several stands from each of his associations. The first criterion in choosing which stands to study was topographic homogeneity—approximately the same slope and aspect was required for the whole stand. The second criterion was "visual" vegetational homogeneity—approximately the same size classes and species were to be represented throughout the stand, *i.e.*, two halves of the stand could not have markedly different ages or composition. Stands which had had recent cutting were avoided, as were areas of pure conifers, in order to study vegetation as close to "natural" as possible. No two stands of the same association were placed adjacent to one another except for stands 11 and 12 which were located on opposite sides of a ridge.

The size of the stands had to be large enough to accommodate the plots used in sampling trees. The actual size of the stands sampled ranged from approximately 25 × 35 meters in stand 24 to 100 × 100 meters in stand 10. The average stand size was approximately 0.25 hectare or 0.6 acre.

The field methods used are designed to be rapid and to furnish the most information about the vegetation in the simplest way possible. A further aim is to use objective, quantitative measures rather than subjective estimates.

B. Sampling of trees

The trees and saplings of each stand were sampled using circular plots which had a radius of 26.3 feet and an area of $^1/_{20}$ acre (equivalent to a radius of 8 meters and an area of 2 ares). It was originally intended to use five plots per stand, but it was found necessary to use four plots in 14 of the stands in order to fit the plots into the stands without overlapping each other or the outer limits of the stand. The outer perimeter of a plot was determined using an Edscorp field rangefinder. Within a plot, all saplings were listed by species, and trees were listed by species and by size as measured with a basal area tape. Saplings and trees are defined by specific size limits. For this study, I have used the same size limits as used in studies of Wisconsin forests.

Saplings are small trees having a diameter at breast height (d.b.h.) of 1 to 4 inches (2.5 to 10 cm), with the d.b.h. measured at 4.5 feet or approximately 1.35 meters from the ground. Tree species less than 1 inch d.b.h. are considered as seedlings regardless of their height, and are listed in the small quadrats with herbs and shrubs.

Trees are those individuals over 4 inches d.b.h., *ie.* , having a basal area of more than 12 sq. in. (*c.* 77 cm^2), and are measured with a basal area tape giving readings in square inches. As a measure of size or importance of trees, such factors as height, spread of canopy, volume, etc., all play a part. However, basal area is more easily and objectively measured than the other factors and is often used as a quantitative approximation of relative size for trees.

C. Sampling of understory vegetation

Herbs, shrubs and tree seedlings were sampled in May and June using twenty-five 1 m^2 quadrats per stand. Shrubs are woody species which seldom or never attain tree size (4 in. d.b.h.). The presence of each species in a quadrat was recorded, and frequency was later determined for each species present in a stand. Understory species not found in any quadrats but seen in the stand were recorded in a "stand presence list". While sampling the trees in mid-June, the understory presence list was rechecked for corrections or additions. A few errors in identification of herbs have possibly been made, but these would not affect the overall trends or conclusions.

Bryophytes (mostly mosses) were collected if they occurred in the quadrats, and were later identified by Dr. F. Ochsner. They were not recorded by species in the quadrats for frequency purposes, however. Thus, presence in a stand by species and total Bryophyte frequency per stand were the only data determined. The presence of mosses in stands often seemed to be correlated with the presence of a certain substrate, *i.e.*, certain species seemed to be associated with rocks or with stumps, fallen branches, etc., rather than to occur on the soil where they would seemingly have closer correlation with certain vegetation types. The possibility of substrate specificity may therefore confuse the moss picture.

D. Other field methods

As mentioned earlier, slope and aspect were measured in each stand. Soil samples were collected from the A-1 horizon at three places in each stand and were combined into one sample for each stand. The soil samples were collected from all 25 stands in one day. Soil samples were later analyzed by technical staff members of the Geobot. Institut under the direction of Mrs. M. Siegl for pH, moisture, and various nutrient factors.

Relative moisture estimates were made over the period of three or more visits to each stand, and were made on the basis of the feel of the soil underfoot and between the fingers. Some soils were definitely spongy or soft, had water seeping out in places, etc., while others were obviously quite dry. However, it is difficult to avoid being influenced by such factors as herbaceous cover of certain species when making estimates such as these.

III. Analytic Methods

A. Understory species

Frequency was determined for each species of herb, shrub, or tree seedling in each stand on the basis of percentage occurrence in the 25 quadrats. Frequency is, of course, influenced by the size, shape, and number of quadrats used. It only indirectly reflects density, and gives diverse results for aggregated or clumped species as opposed to those which occur singly and more at random. It is, however, the most rapid method available to give a somewhat objective and relatively quantitative estimate of understory species present. Understory species checked as present in the stand but not found in any quadrat were assigned a frequency of 4% as if they had occurred in only one quadrat. Frequency for bare ground, a quadrat not containing a single individual of herbs, shrubs or tree seedlings, was also determined. The understory species plus bare ground were used as the basis of ordination of the stands as will be discussed below. The rationale for including tree seedlings in the ordination is that they seemingly had varying frequencies and presence in different stands just as the herbs and shrubs had. However, as part of the attempt to study "natural" vegetation, seedlings of conifers were not included.

B. Trees

When five $^1/_{20}$-acre plots were used, trees in a total of 0.25 acre were actually measured. Density per acre is therefore obtained by multiplying by four the number of each species recorded in the sample. When four plots totalling 0.2 acre were used, density is obtained by multiplying by five. The same procedure is used for sapling density. However, no conclusions (*e.g.*, as to potential successional trends in the stands) can be drawn from sapling figures because saplings have been drastically thinned in many stands.

Basal area was totalled for each species and likewise multiplied by four or five to give basal area per acre. An average size per species for each stand can be determined by dividing total basal area by the number of individuals of that species. Basal area measurements were taken in square inches because of the inability to obtain basal area tapes giving readings in square centimeters. Likewise, the rangefinder was calibrated in feet, and therefore, per acre figures were used. If the metric system were used, five 2-are plots would measure trees in a total of 10 ares. Number of trees per hectare would then be obtained by multiplying by 10 the number of each species recorded in the sample, or by multiplying by 12.5 if four plots were used. Although results for individual species are shown in square inches and numbers per acre, summary figures for each stand have been converted to approximate metric units. Numbers per acre are multiplied by 2.47 to give numbers per hectare. Square inch figures are multiplied by 6.45 to give readings in square centimeters.

It is desirable to have some measure of dominance or importance for the tree species, the dominant species being defined as those which exert the most influence on the environment. The distribution of individuals of a species throughout a stand (frequency), and the number (density), and size (dominance) of the individuals are perhaps the main aspects contributing toward which species are most important in a stand. A cumulative index combining these three measures (as relative frequency, density, and dominance) into an Importance Value is described by Curtis and McIntosh (1951) and Curtis (1959). However, the use of a composite, mixed quantitative measure such as this has been criticized by Anderson (1963), and Lambert and Dale (1964).

Frequency especially is a controversial measurement, and density alone does not adequately express the contribution of each species to a stand. However, numbers and size together contribute toward the importance of individual species in a stand. One method to determine basal area per acre is to multiply the average size of a species by the number per acre of that species. Basal area per acre therefore reflects both variables (numbers and size). Consequently, basal area per acre on a relative percentage basis is used as a measure of an "importance value" or of *relative importance* for the tree species in this study.

C. Ordination of the stands

1. Background

In the last two decades, ordination procedures have been much used with some of the pioneer studies being those of Curtis and McIntosh (1951), Whittaker (1951, 1952, 1956), and Bray and Curtis (1957). Ordination refers to the ordering or arrangement of stands (community samples) in relation to one or more environmental gradients or axes. An ordination technique is often used when vegetation is conceived as having a relatively continuous pattern, whereas classification procedures are often used when it is considered that sharper discontinuities exist in the vegetation. For the purposes of this study, the stands were ordinated on the basis of vegetation present and correlations were then made with abiotic environmental factors. An alternative method is the ordination of stands by environmental factors directly (direct gradient analysis of Whittaker, 1967). The paper by Loucks (1962) is an example of concurrent usage of environmental and phytosociological variables. The paper of van Groenewoud (1965) includes a comparison of ordination and classification methods.

Orloci (1966), and Austin and Orloci (1966) reviewed various ordination techniques and concluded that a principle component analysis gives the most accurate ordination. However, laborious calculations must be made using this method, and a computer is virtually necessary. Bannister (1968) found that with a relatively wide range of species-richness and abundance, the Bray and Curtis polar ordination method produces a more readily interpreted "simple ordination" than the method of perpendicular axes of Orloci (1966). (It is considered that the Kirchleerau stands exhibited a wide range of species and abundance.) Bannister concluded that "neither method is a substitute for more sophisticated techniques but both have the advantage that they can be computed by hand". For these reasons, the Bray and Curtis method, with modifications, was the ordination technique used, and the calculations were made by hand.

Yarranton (1967) points out that a simplification of the ordination is desirable if it is to be informative, for example by reduction of the number of axes. I have consequently used 2 rather than 3 axes as are often used in ordinations. Similarity of stands was considered concurrently with dissimilarity in an attempt to include more information than on the first 2 axes of a conventional dissimilarity ordination.

2. *Ordination procedure*

Ordination of vegetation is commonly done by comparison of the stands either on the basis of species present, or more accurately but also more time-consumingly, by using quantitative data such as frequency, density, etc., for the species present. Either all or only some of the species may be used, but the question may be raised as to how one should decide which species to use and which to ignore.

Two ordinations were performed for comparative purposes. One was based on the presence of all understory and tree species (herbs, shrubs, tree seedlings, bare ground treated as a species, and trees—with a total of 114 "species"). The second was based on frequency-classes of understory species only (herbs, shrubs, tree seedlings, and bare ground—with a total of 102 "species"). Stands were separated out in a similar manner by both methods. However, since the tree situation in the study area was somewhat unnatural due to the management practices of cutting and planting, it was decided to use the second method mentioned in which the stands are ordinated on the basis of the understory. The trees are thus omitted from the ordination procedure. When they are later correlated with the ordination, a better understanding of the relationship of the understory to the tree species is obtained. In addition, since use is made of the indicator value of certain understory species by some of the other workers in the Swiss study area, better comparisons could be made with their work. The ordination procedure will be described in a series of steps.

(1) When ordinating on the basis of "species present", it makes no difference whether a species is present in one quadrat or in 25 quadrats in a stand. In contrast, by the frequency technique, many diverse values are obtainable. If a species had a frequency of 36% in one stand for example, a frequency of 16% in a second stand, and of 84% in a third, this would mean that stands one and two had 16 of the 36% in common, stands one and three had 36 of the 84% in common, etc. (whereas by the "presence" method, there would be no

difference—the species was present in all three stands). It becomes extremely laborious to make comparisons of frequencies for all species in each stand.

As a compromise between the "species present" method in which much information is lost, and "frequency" method which is more time-consuming, frequency-classes were used. A species was assigned a value of "1" if it occurred in 1 to 8 quadrats (4 to 32% Frequency), a value of "2" for 9 to 16 quadrats (36 to 64% F.), and a value of "3" for 17 to 25 quadrats (68 to 100% F.). A fourth value or frequency-class is, of course, "0" if a species was not present in a stand. The number of frequency-class units in common therefore may range from 0 to 3 for each species (compared to 0 or 1 by the presence method and 0 to 100% by the frequency method). A slightly better comparison would have been achieved by using four or five frequency-classes rather than only three.

(2) The index of Czekanowski (1913) as discussed by Curtis (1959) was used to compare the similarity of each of the 25 stands with every other stand on the basis of understory-frequency-class units. The formula used is $\frac{2w}{a+b}$, where a is the total number of frequency-class units found in one stand, b is the total number of units in the other stand, and w is the number of units in common in the two stands. The percentage similarity of each stand with every other stand is shown in the upper right half of Table 2, and percentage dissimilarities are shown in the lower left half of the table. The order of the stands and the listing in four groups (A, B, C, and D) will be explained shortly.

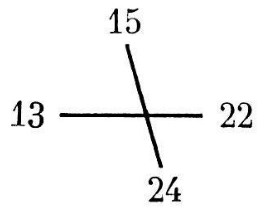
(3) In the right hand column of Table 2 is shown the total of the similarities for each stand when compared with every other stand; for example, stand 13 has a total of 491, stand 14 has a total of 588, etc., through stand 22 with a total of 733. Stand 13 has the least total similarity with every other stand and therefore becomes an end stand of the first axis. Stand 13 has least in common with stand 22 (100% dissimilarity, *i.e.*, no understory species or frequency-classes in common), so stand 22 is the other end stand of this axis and is placed 100 units from stand 13. To complete the first axis of the ordination, each of the other 23 stands is plotted graphically by its dissimilarity relationship to stands 13 and 22 by the method of Bray and Curtis (1957). Stand 15, for example, is 76 units from stand 13 and 83 units from stand 22, and so on for each of the stands. The placement of stands on the first axis is illustrated in Fig. 1 p. 44.

(4) Many stands which appear close together in the first axis are actually quite dissimilar, so a second axis is plotted. The second axis might be chosen as follows: all the stands could be projected directly onto the X (13–22) axis, thereby lining up the stands in the order 13–14–10, etc., through 25–23–22.

Table 2. The percentage similarity that each stand has with every other stand is shown in the upper right half of the table, and percentage dissimilarity in the lower left half. The comparisons were made on the basis of frequency-class units using 101 understory species plus bare ground treated as the 102nd species. The right-hand column shows a figure of total similarities for each stand (e.g., stand 13 compared with every other stand totals 491 etc.). The stands within each of the four groups (A, B, C, D) have most in common with the other stands in that group.

		Percentage Similarity																									Total
		Group A									B						C							D			
Percentage Dissimilarity	Stands	13	14	10	4	11	15	12	3	9	6	1	21	8	7	2	16	17	24	5	18	19	20	25	23	22	similarities
	13	X	48	35	43	37	24	41	43	33	23	8	26	20	4	19	13	6	16	20	5	13	7	3	4	0	491
	14	52	X	67	58	64	46	53	42	24	22	11	21	10	13	14	13	8	8	5	9	13	6	9	11	3	588
	10	65	33	X	60	42	36	38	29	29	24	12	23	11	14	10	7	6	4	13	5	7	3	6	8	3	492
	4	57	42	40	X	67	43	62	60	52	34	25	44	28	29	30	18	14	19	26	17	16	13	11	17	12	798
A	11	63	36	58	33	X	56	72	64	45	27	23	31	21	23	28	29	21	21	28	28	21	18	14	16	8	804
	15	76	54	64	67	44	X	47	33	28	24	28	19	18	10	21	18	21	15	29	21	31	21	17	23	17	646
	12	59	47	62	38	28	53	X	70	48	26	29	38	20	26	35	25	20	21	30	31	29	26	13	15	11	826
	3	57	58	71	40	36	67	30	X	54	43	37	47	32	39	47	38	32	30	35	37	31	26	17	19	20	925
	9	67	76	71	48	55	72	52	46	X	42	35	43	36	29	38	27	19	26	22	17	16	12	11	23	20	729
	6	77	78	76	66	73	76	74	57	58	X	60	68	62	58	60	46	40	44	43	24	33	21	31	35	40	930
	1	92	89	88	75	77	72	71	63	65	40	X	62	58	56	50	44	54	34	43	32	39	30	44	49	57	920
B	21	74	79	77	56	69	81	62	53	57	32	38	X	69	63	72	47	41	45	46	30	33	23	26	38	43	998
	8	80	90	89	72	79	82	80	68	64	38	42	31	X	65	54	46	51	58	51	32	37	30	34	45	47	935
	7	96	87	86	71	77	90	74	61	71	42	44	37	35	X	56	41	53	41	37	38	31	26	39	42	47	880
	2	81	86	90	70	72	79	65	53	62	40	50	28	46	44	X	60	47	53	57	42	51	33	27	30	34	968
	16	87	87	93	82	71	82	75	62	73	54	56	53	54	59	40	X	69	63	66	65	66	60	47	34	33	975
	17	94	92	94	86	79	79	80	68	81	60	46	59	49	47	53	31	X	61	61	58	60	54	56	45	50	947
	24	84	92	96	81	79	85	79	70	74	56	66	55	42	59	47	37	39	X	65	56	58	53	48	40	40	919
C	5	80	95	87	74	72	71	70	65	78	57	57	54	49	63	43	34	39	35	X	68	66	57	41	37	33	989
	18	95	91	95	83	72	79	69	63	83	76	68	70	68	62	58	35	42	44	32	X	65	67	49	33	30	859
	19	87	87	93	84	79	69	71	69	84	67	61	67	63	69	49	34	40	42	34	35	X	71	45	31	29	892
	20	93	94	97	87	82	79	74	74	88	79	70	77	70	74	67	40	46	47	43	33	29	X	56	33	30	766
	25	97	91	94	89	86	83	87	83	89	69	56	74	66	61	73	53	44	52	59	51	55	44	X	60	57	761
D	23	96	89	92	83	84	77	85	81	77	65	51	62	55	58	70	66	55	60	63	67	69	67	40	X	69	757
	22	100	97	97	88	92	83	89	80	80	60	43	57	53	53	66	67	50	60	67	70	71	70	43	31	X	733

From those in the central part of the axis could be selected the two most dissimilar stands. They could then be set opposite one another the proper number of units apart and in proper relationship to the end stands of the X axis. Stands 15 and 24 (with 85% dissimilarity) perhaps would have been chosen and placed thusly:



However, as is seen in Fig. 1, there is a gap in the central part of the axis between stands 15 and 5 of approximately 15 units. Choosing stands from the left and right sides of this gap would result in a very oblique relationship between the X and Y axes. Oblique axes have been criticized (Orloci, 1966), and an alternative method considering stand similarities was therefore used to construct the second axes.

Because of the gap between the left and right sides of the first axis, the similarity relationships of stands were investigated. Clustering of points or relatively large gaps between points may indicate some "association" of stands. Stands bear both a relative and an absolute similarity relationship to one another. For instance, on a relative basis we may consider which stands are mutually most similar, most similar, second most similar, etc., to which other stands. On an absolute basis, are they more than 70% similar, more than 60%, 50%, etc.? Stands most similar and most dissimilar to each other on absolute and relative bases were determined. Stands were then placed diagrammatically relative to one another to see if there were any self-contained groups. On the basis of absolute similarity at the 50% level (*i.e.*, stands which have more similarity than dissimilarity with each other), three groups were separated—groups B, C, and D containing the stands shown in Table 2. Every stand in each group has 50% or more similarity with every other stand in that group. There is some overlap among the three groups, however, with some stands from each group having more than 50% similarity with stands from another group. On the basis of relative similarity, the stands are restricted within the groups.

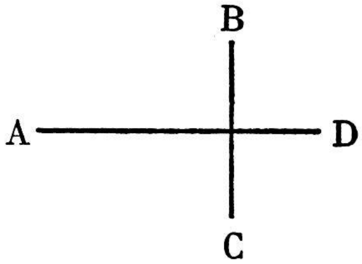
On the other hand, group A has no overlap at the 50% level with the other groups; in fact, not all stands within group A have 50% similarity with each other as is seen in Table 2. However, on the basis of relative similarities, group A may be separated although it is not as good a separation as were groups B, C, and D. (The relative relationships within all the groups will be shown later in Fig. 3.) One must in fact go to the 24% level before group A becomes an absolute group. On the other hand, certain stands of group A overlap some of group B at the 40% level, group C at the 30% level and group D at the 20% level as may be seen in Table 2.

In summary, four groups were separated using both a relative and an absolute similarity basis. There is no absolute level at which any significant number of stands may be completely separated without having some stands outside the group which are just as similar to some of those within the group. The average percentage similarity within and between each of the four groups is shown in Table 3.

Table 3.—Percentage similarity within and between each of the four groups of stands as averaged from Table 2.

	A	B	C	D
A	47	26	19	12
B		61	41	39
C			62	40
D				62

We may now think of group A as being at one end of the first axis of the ordination, and since group D is most dissimilar to it, it would be at the other end, with stands 13 and 22 still being the extreme end stands. Groups B and C lie between them, albeit closer to D than to A. The logical axes then are:



Therefore, the end stands of the second axis are not chosen in the conventional way using the most dissimilar stands from an arbitrarily-decided center section of the first axis, but are instead the two most dissimilar stands of groups B and C, *i.e.*, stands 6 and 20. Thus, relative and absolute similarities have been used to aid in the selection of the end stands of the second axis.

(5) The second axis is now plotted with stand 6 of group B being left at the same point as was shown in Fig. 1. Stand 20, the other end stand, is also located at the same point relative to stands 13 and 22, but is placed below the X-axis instead of above. Stands 6 and 20 are then moved toward each other until they are 79 units apart (they have 79% dissimilarity). They thus still bear the same relative relationship to stands 13 and 22 which are still 100

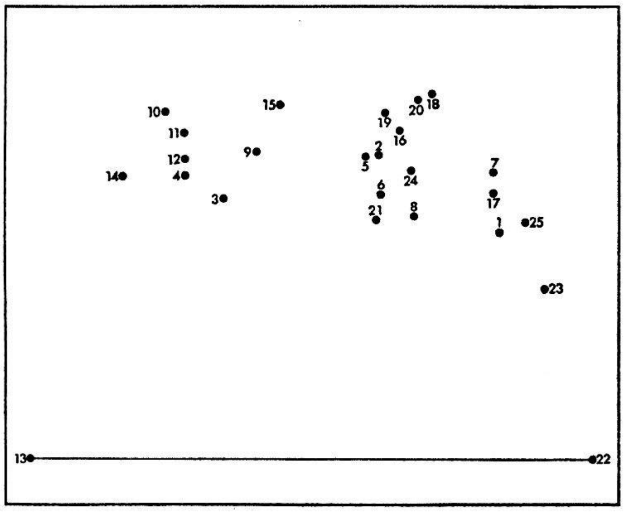


Fig. 1.—First axis dissimilarity ordination based on frequency classes of understory species. The ultimate placement of the stands in the 4 groups is indicated by the position of the stand numbers: A, to left of dot; B, above; C, below; D, right.

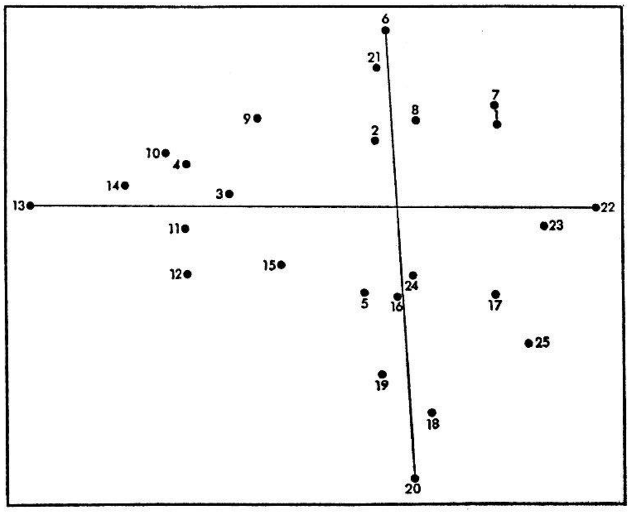


Fig. 2.—First and second axis dissimilarity/similarity ordination with stands projected in relation to the X axis (A13–D22) and Y axis (B6–C20).

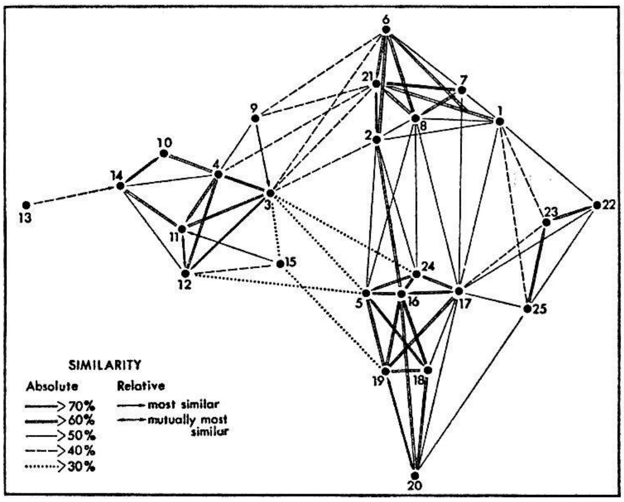


Fig. 3.—The final ordination. It is the same as Fig. 2, but with similarity readjustments of certain stands (A3,4; B7,21; C17,18; D25) to place them more accurately relative to intra- and intergroup similarity relationships. The key shows symbols for the absolute and relative similarity relationships. Not all of the lower similarity levels within and between groups are shown.

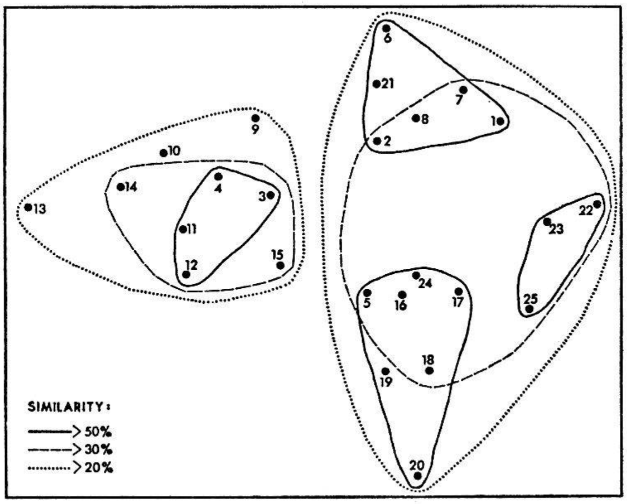


Fig. 4.—Same ordination as Fig. 3. All stands outlined have similarities with each other at the levels shown in the key. However, by excluding certain stands from any group, many other combinations would be possible within and between groups at several levels of similarity.

units apart, and the 6–20 axis is only slightly oblique to the 13–22 axis. Further, this B–C axis is closer to D than it is to A which is as it should be as mentioned above.

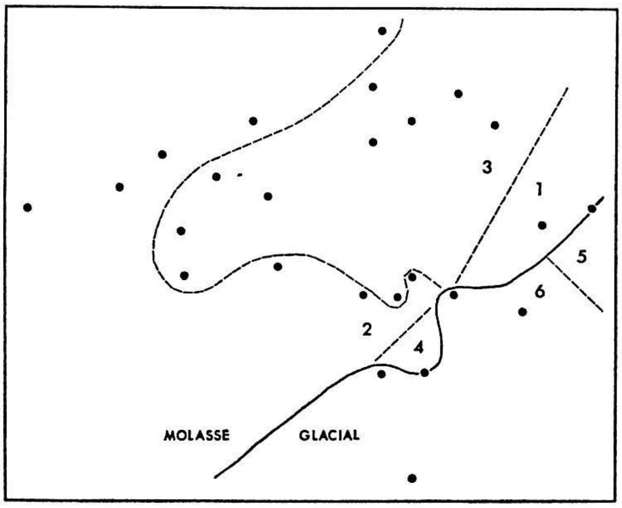
Each of the remaining 21 stands (all but the four end stands of the two axes) is now plotted in relationship to stands 6 and 20. Each of these 21 stands thus has two points: one in relationship to stands 13 and 22 (the X or A–D axis), and one in relationship to stands 6 and 20 (the Y or B–C axis). Each of the 21 stands is then projected to a position relative to the four end stands. This placement of stands is shown in Fig. 2.

(6) The final placement of stands on the ordination is shown in Fig. 3. The following stands were displaced slightly to better represent their relative distances: A 3, 4; B 7, 21; C 17, 18; D 25. Fig. 3, then, has been achieved by a two-dimensional dissimilarity ordination with similarity influencing the choice of the end stands for the second axis, and with a final similarity readjustment. The similarity modifications have been introduced as an alternative to a third dissimilarity ordination with the aim of presenting the stands in a more comprehensible two-dimensional plane. It is not denied, however, that a multi-dimensional relationship probably is the correct one.

Absolute and relative similarities among the stands are shown according to the key in Fig. 3. Note especially from the arrows indicative of relative similarities that the four groups appear as fairly distinct. On the basis of absolute similarities, however, there is some overlap between groups. Further details regarding overlap may be determined by consulting Table 2 in conjunction with Fig. 3. The position of the stands in the ordination shown in Fig. 3 is the basic diagram which will be used for the presentation of results for the understory and tree species and for the environmental factors.

Groups of stands are outlined on the basis of similarity in Fig. 4. Yarranton (1967) has noted that ordinations normally appear between a hypersphere (complete individuality) and definite clusters of points (associations). Whittaker (1967) has reviewed the concept of clustering of points in terms of hyperspace and plexuses. The conclusion may be drawn from examination of Figures 3 and 4 in conjunction with Table 2 that no sharply-defined non-overlapping groups appear at any similarity level. These results are consistent with the idea that the vegetation is a multi-dimensional pattern rather than a mosaic of clearly-bounded units.

Since the vegetation appears to be a multi-dimensional ordination, there is no "correct" way to line up the stands in one gradient or cline or continuum. However, for purposes of presenting species data in later tables, stands have been arranged across the top of Table 2 to reflect the general pattern across the ordination from A-13 through B and C to D-22.



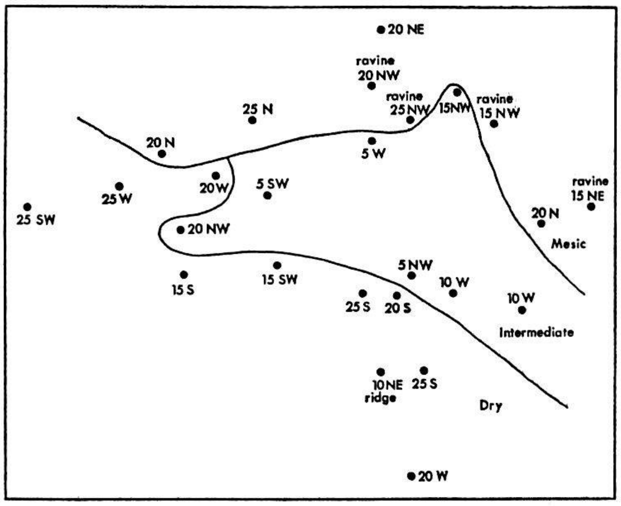
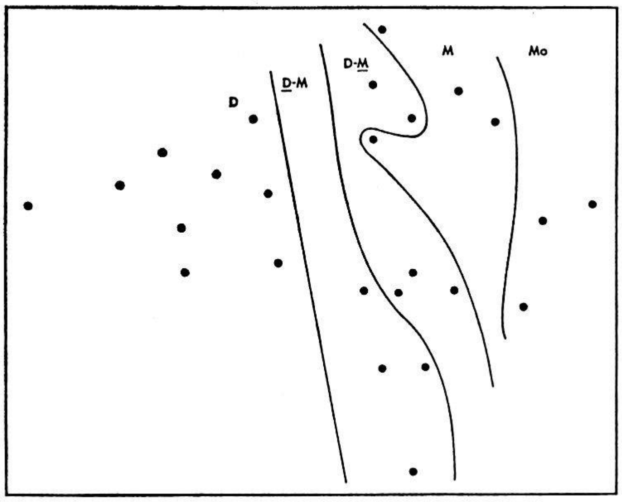


Fig. 5.—Soil parent materials: 1 to 4 are different types and ages of tertiary sandstone; 5 and 6 are glacial deposits. Relative geological age from oldest to youngest: 1. lower marine molasse; 2. upper marine molasse, musselsandstone; 3. upper marine molasse, Wienerstufe; 4. upper sweetwater molasse; 5. Riss gravel; 6. Würm moraine. See footnote 1 of Table 1 for description of the layers. No stand numbers will be listed from this figure on, as it is the relative trends which are of interest. Refer to Fig. 4 if information is desired regarding specific stand numbers.

Fig. 6.—Moisture relationships (mesic, intermediate, dry) that would be expected from the topographic situation of the sites. The numbers are slope °, and the letters are direction or aspects (North, South, East, West). Also shown are site influences such as ridge or ravine. These represent potential evaporation or runoff gradients.



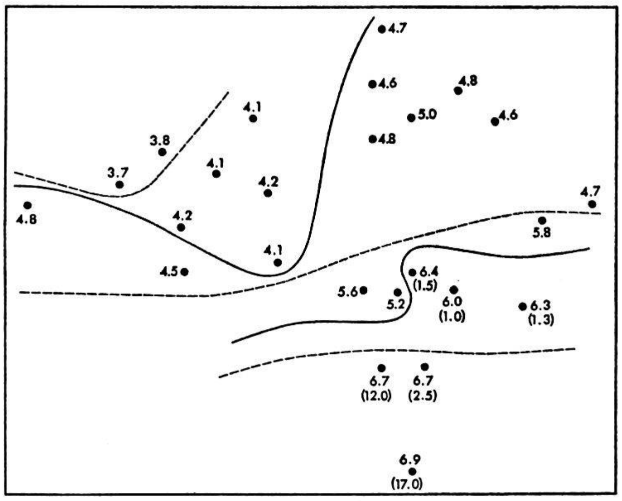


Fig. 7.—Relative soil moisture estimates as they were actually made at the time of sampling: D, dry; D-M, *dry*-mesic; D-M, dry-*mesic*; M, mesic; Mo, moist.

Fig. 8.—Soil pH and percentage $CaCO_3$. Lines are drawn separating 3 categories of pH from low to higher: 3.7–4.2; 4.5–5.8; 6.0–6.9. Further separation is shown by dashed lines. Percentage of $CaCO_3$ is shown in parentheses.

IV. Results and Discussion

The results of my study of forest vegetation in the Kirchleerau area are shown below in a series of figures and tables. The figures are all of data plotted on the ordination which was shown in Fig. 3. The fact that trends or patterns usually exist (rather than random plotting of data) assumes a 2- or 3-dimensional correlation with the patterns of stand placement. Since the ordination was done on the basis of understory species, it is natural that there will be patterns for the individual understory species. However, the patterns that are shown for environmental factors and tree species indicate that valid trends exist.

A. Environmental trends

In Fig. 5 is shown the pattern for the soil parent material as plotted on the ordination. It is logical that the understory species are influenced by soil parent material because this material helps determine the amount and type of nutrients present, soil pH, moisture relations, etc. Parent material group 2, musselsandstone, seems to have the poorest correlation pattern with the species-ordination. However, groups 2 and 3 are both upper marine molasse (Helvetien) so could nearly as well be treated as one group.

Fig. 6. illustrates the moisture conditions one would expect fromthe topographic relationship of the stands because of relatively more or less evaporation and runoff or percolation of water. It is expected that ravines and

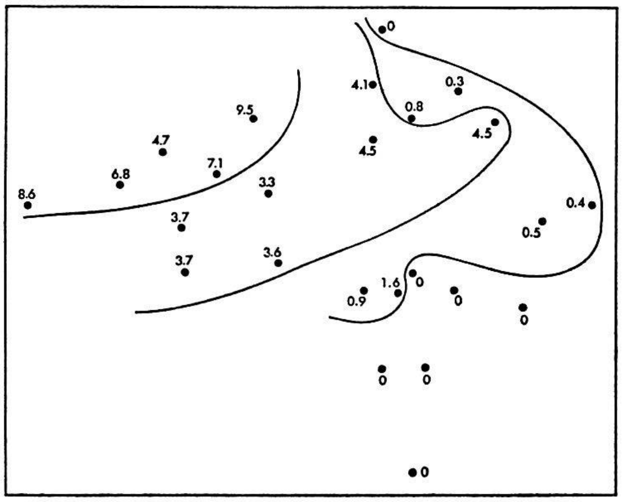


Fig. 9.—Soil analysis showing mg NH_4/100 g soil; analyzed 6 weeks after collection.

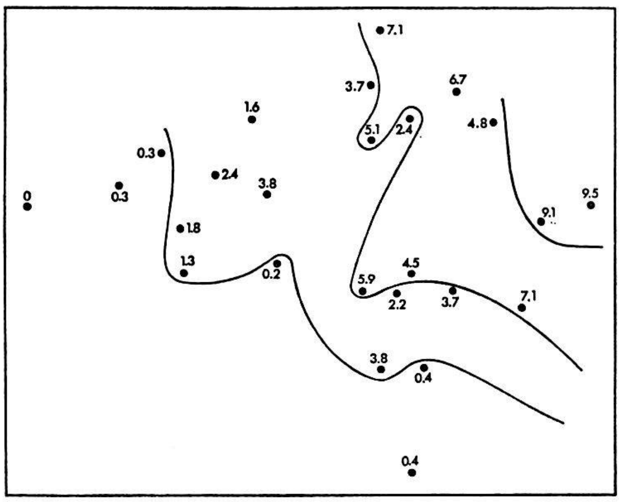


Fig. 10.—Soil analysis showing mg NO_3/100 g soil; analyzed 6 weeks after collection.

relatively steep north and east-facing slopes will be more mesic, and that ridgetops and south and west-facing slopes will be relatively more dry.

Fig. 7 illustrates the relative moisture conditions which were actually found. These are partly influenced by the potential evaporation, etc., shown in Fig. 6. The conditions are also influenced by moisture penetration or retention in the soil due to texture (clay, sand, humus, etc.), and by moisture movement toward the soil surface from underground sources in certain places. This moisture seepage or upward movement of water will be influenced not just by the soil parent materials in a given stand, but by the materials farther up a slope. A porous layer upslope underlain by a relatively impermeable layer may channel water toward the surface at a lower level.

As mentioned earlier, the actual soil moisture conditions were estimated for the 25 stands, relatively, over the course of several visits to each stand. Actual instrumented measurement of soil/moisture relationships in a comparative manner for the stands would be of interest. Correlation of a stand's topographic and parent material relationship with the conditions of stands upslope, and determination of the underground stratigraphical relationships would aid in clarifying the moisture situations I found.

Results of soil analyses are shown in Table 4 and in Fig. 8 to 10. Soil samples from each of the 25 stands were collected for analysis on one day. This was done in order to mitigate seasonal variation in the climate, plants, etc., which could influence the soils. Variation in soils occurs from place to place in a stand so a stand average must be determined. Three soil samples were collected in each stand and were mixed to form a composite sample for each stand. This technique is discussed by Cline (1944), and by Petersen and Calvin (1965). Composite samples are often used with the assumption that a valid estimate of the mean of several samples is thereby obtained. Soils were analysed for the factors shown in Table 4, and average results for each of the four groups of stands are indicated. These show only general trends, however, as the results for individual stands when plotted on the ordination usually cut across the various groups.

Fig. 8 shows the pattern which results when soil pH is plotted on the ordination. Soil pH is influenced by parent materials and moisture relations as well as by the presence of certain understory and tree species. The widespread planting of conifers may have influenced soil pH to the extent that pH conditions are not "natural" in many stands. Nevertheless, because of the quite well-defined patterns, it seems that the ordination based on the understory species is a fairly accurate reflection of the present soil pH. Most of the stands with relatively high amounts of $CaCO_3$ are seen to occur on Würm moraine when Fig. 8. is compared with Fig. 5.

Table 4.—Analysis of the soils, averaged by groups of stands.

Group	A	B	C	D
pH[1]	4.2	4.8	6.2	5.6
estimated moisture[2]	1.0	2.8	2.2	4.0
soil moisture %[3]	45.9	48.5	48.7	52.2
$CaCO_3$ corr. %	0.0	0.0	4.9	0.4
organic matter % (Glühverlust)	13.5	8.2	19.4	26.0
NO_3 fresh[4]	0.30	0.39	0.42	1.01
NO_3 6 weeks	1.30	4.96	2.97	8.57
NH_4 fresh	1.47	1.11	1.02	0.94
NH_4 6 weeks	5.65	2.37	0.34	0.27

Footnotes

1. Arithmetic average for pH; values for individual stands shown in Fig. 8.
2. Averaged by assigning values to the estimated relative moisture classes as follows: 1, dry; 2, *dry*-mesic; 2.5, dry-*mesic*; 3, mesic; 4, moist. Values for individual stands shown in Fig. 7.
3. Soil samples were collected from all stands on the same day, June 23.
4. Values for NO_3 and NH_4 are expressed as mg/100 g soil.

Individual stand results for estimated moisture were shown in Fig. 7. Actual percentage of moisture in the soil on the day of soil collection is somewhat correlated with the estimates of moisture for the stands as may be seen by comparing the group averages in Table 4. Soil moisture content is influenced by such factors as the amount and timing of precipitation, by the percolation and evaporation rate, and by the amount of organic matter and root mass in the soil. The estimates for stand soil moisture were made during several visits to each stand whereas the measurements of soil moisture % is from just one day. For these reasons, it is thought that the estimates give a more accurate total picture.

The results shown in Table 4 for Glühverlust % (loss on ignition) are an approximation of organic matter content of the soil. Soils of stands in group A were dry, sandy, and seemingly low in organic matter. However, a thin mat of tightly interwoven root material and possibly fungal hyphae occurred in some of the stands of group A, and probably raised the average organic matter % of this group.

The remaining factors in Table 4 are the ammonia and nitrate content of the soil. When plotted on the ordination, the analytic results show similar trends for fresh soils and for soils after six weeks for ammonia, and also for nitrate. However, the absolute values are more striking after six weeks. The rationale for a "six weeks" analysis is that under conditions in nature, ammonia and nitrate do not accumulate but are changed or taken up immediately after formation. If decomposition is allowed to proceed for six weeks in the laboratory soil sample, the nutrients accumulate and a better relative idea is gained concerning the amount of microbial activity and potential richness of the soil.

The six weeks soils analyses for ammonia and nitrate are shown in Figs. 9 and 10. If the results were to be interpreted in terms of one environmental factor, then ammonia may be correlated with soil pH (*cf.* Fig. 8)—high ammonia content in soils with low pH. Nitrate may be correlated with estimated soil moisture—high nitrates in moist stands and low nitrates in relatively dry stands. However, the nitrogen cycle is very complicated, and undoubtedly is influenced by a complex of factors. The amount and rate of production of ammonia and nitrates are influenced by temperature, moisture, soil pH, amount and type of organic matter and of decomposer organisms present, etc.

The ordination pattern therefore seems to reflect the several factors plotted in Figs. 5 to 10. Soil parent material, moisture relations due to topographic location and underlying material, soil pH and $CaCO_3$, soil nutrients, and no doubt additional environmental factors all play a part. Of all the factors which influence the ordination patterns of the stands, soil pH and soil moisture seem to be the two which bear the most direct relationship. Although the pattern is slightly oblique, soil moisture essentially increases from left to right, and soil pH increases from top to bottom on the ordination.

In Table 5 the stands are shown listed in relationship to these two factors. Plant communities are often delineated on the basis of soil moisture and soil pH/nutrients in what might be considered as 2-dimensional "subjective ordinations". The placement of the stands in Table 5 differs from that in the ordination, however, because the ordination reflects all the factors shown in Figs 5 to 10.

The pH and moisture gradients, then, are considered to be the major trends represented, but several other variables also influence the ordination. Various characteristics concerning the understory and tree species will next be shown followed by a comparison with the results of other workers. Bear in mind that the ordination technique is useful to point out trends and suggest correlation of various factors, but ordination will not prove these correlations.

B. Understory characteristics

In Table 6 (annex) are shown the understory species (and their frequencies) which were used as the basis of ordination. Before plotting the individual species on the ordination, some general trends for the understory as a whole

Table 5.—The stands are listed by soil pH and by relative soil moisture classes. These are the apparent major environmental gradients as shown in Figs. 7 and 8. The stands in each of the four groups are outlined.

pH	Dry	*Dry*-mesic	Dry-*mesic*	Mesic	Moist
3.7	14				
3.8	10				
3.9					
4.0					
4.1	4, 9, 15				
4.2	3, 11				
4.3					
4.4					
4.5	12				
4.6			21	1	
4.7				6	22
4.8	13			2, 7	
4.9					
5.0			8		
5.1					
5.2			16		
5.3					
5.4					
5.5					
5.6		5			
5.7					
5.8					23
5.9					
6.0			17		
6.1					
6.2					
6.3					25
6.4			24		
6.5					
6.6					
6.7		18, 19			
6.8					
6.9		20			
7.0					

will be discussed. These are *number of species*, and *frequency* which is a reflection of density or cover.

Fig. 11 shows the total number of understory species (herbs, shrubs, tree seedlings) per stand plotted on the ordination. Total understory frequencies, total number of herb species, total herb frequencies, and estimated herbaceous cover (all summarized in Table 6) likewise show this same pattern of increasing from upper left to lower right in the ordination. Note also in

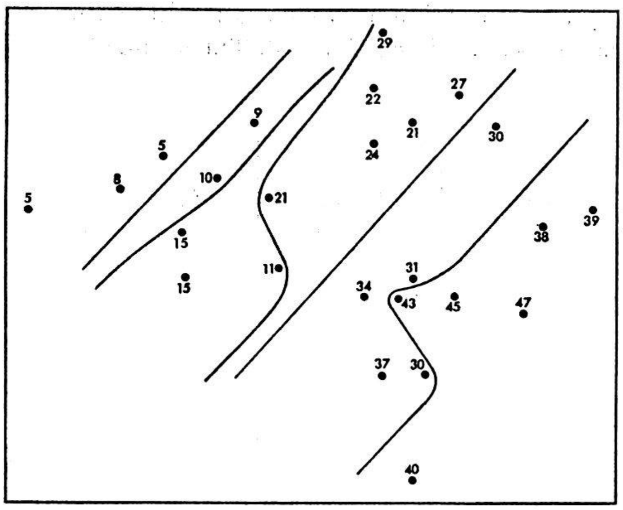


Fig. 11.—Total number of understory species (herbs, shrubs, tree seedlings) per stand. Total understory frequencies, total herb species and frequencies, and estimated herbaceous cover have a similar pattern.

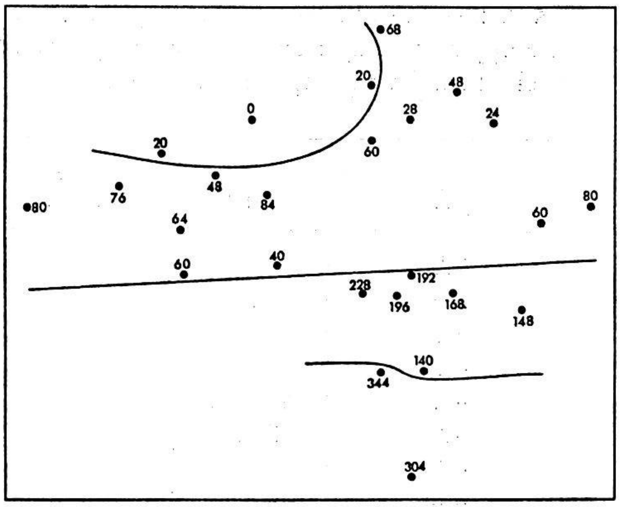


Fig. 12.—Total shrub frequency per stand. Number of shrub species per stand has a similar pattern. The stands above the long horizontal line have 0 to 8 shrub species per stand while those below the line have 10 to 14 species.

Table 6 that all bare-ground quadrats occurred in group A of the ordination. The general trend in Fig. 11 is from relatively drier and more acid soils in the upper left to relatively more moist soils with higher pH and nutrient levels in the lower right. The diversity response to these environmental axes is much like that of forests in Poland as plotted in Fig. 2 of Frydman and Whittaker (1968).

Fig. 12 illustrates the total shrub frequencies. A similar pattern exists for the number of shrub species per stand. Both number of species and total shrub frequencies are markedly higher in group C which includes stands that are dry-mesic with a high pH and much $CaCO_3$.

The Bryophyte species (mostly mosses) are listed in Table 7. When plotted on the ordination, the Bryophytes have a different pattern from the herbs and shrubs with the highest moss frequencies and numbers of species in group A and group D. Bryophyte distribution thus appears to be correlated with low pH and with moist soils. Note, however, in Table 7 that groups A and D have few species in common. No further discussion of Bryophytes will occur in this paper.

Table 7. Stands of occurrence for Bryophytes (four species of hepatics*; the others are mosses). Frequencies for total Bryophytes were recorded in the stands, but frequencies were not recorded for individual species. All species appearing in quadrats were collected and identified.

	Group A									B						C							D			Major
Species of Bryophyta Stand	13	14	10	4	11	15	12	3	9	6	1	21	8	7	2	16	17	24	5	18	19	20	25	23	22	group
Isopterygium elegans	X								X																	A
Hylocomium splendens			X																							A
Plagiothecium denticulatum			X																							A
Rhytidiadelphus triquetrus			X																							A
Dicranum scoparium			X	X		X																				A
Calypogeia fissa*					X																					A
Polytrichum formosum	X	X	X	X	X	X	X	X	X	X	X	X						X							X	A
Hypnum cupressiforme	X	X	X			X				X		X					X		X				X			A
Thuidium tamariscinum		X	X	X							X	X	X													B
Marchantia polymorpha*												X														B
Plagiochila asplenioides*													X													B
Atrichum undulatum									X	X	X	X	X	X					X					X	X	B
Isothecium myurum		X		X												X			X							C
Brachythecium rutabulum				X															X							C
B. velutinum										X						X	X	X	X			X		X		C
Scleropodium purum																						X				C
Eurhynchium striatum		X									X	X	X	X	X	X		X				X	X	X	X	D
Plagiothecium neglectum									X															X		A-D
Fissidens taxifolius												X	X	X		X	X			X			X	X		B-D
Mnium undulatum											X													X	X	D
Lophocolea heterophylla*																								X		D
Mnium punctatum																								X		D
Eurhynchium swartzii																								X	X	D
Acrocladium cuspidatum																									X	D
Cirriphyllum piliferum																									X	D
Total % frequency per stand	52	72	52	40	4	16	4	12	12	32	36	48	28	40	12	16	32	8	32	20	0	16	52	68	92	CABD
Ave. stand frequency per group	A = 29%									B = 33%						C = 18%							D = 71%			

C. *Results for the species*

1. *Understory species*

In Table 6, the understory species are listed in four categories: ferns and monocot herbs, dicot herbs, shrubs, and tree seedlings. The order in which the species are listed in each category corresponds to the group (A, B, C or D) in which the species attains its average highest frequency. The virtual lack of restriction of species to any "box" in Table 6 illustrates the individualistic behavior of the species and lack of clearly bounded "associations".

In Figs 13 to 17, the distributions of herb and shrub understory species are plotted on the ordination. Tree seedlings will be shown plotted in relation to the trees. It is not necessary to describe the pattern of each species. The main ordination trends were considered to be soil moisture and pH. Species patterns may be interpreted in terms of these and other environmental gradients. Knowledge of the precise environmental factors to which any species is responding is not claimed. Rather, the general trends are shown, the individualistic behavior of the species is noted, and the reader may draw his own conclusions for each species.

Note of explanation for Fig. 13 to 18 in which stands of occurrence of understory species are plotted on the ordination. Frequencies are usually listed and help to indicate trends or to contrast certain species. Where frequencies are shown for several overlapping species, the position of the numbers is constant for a given species and will thereby differentiate the species. When frequencies are listed for some stands but no numbers shown for others, a frequency of 4% is indicated. The groups in which the species attain average highest frequencies are underlined. These figures are constructed from Table 6 in which frequencies for all species are shown.

Fig. 13.—Distribution patterns for 4 species of ferns.

13a) *Pteridium aquilinum* and *Athyrium filixfemina*
13b) Two species of *Dryopteris*

Fig. 14.—Distribution patterns for 13 species of graminoids (grasses, sedges and wood rushes).

14a) Three species of *Carex* (sedge)
14b) One species of *Luzula* (wood rush) and two species of *Carex*
14c) Two species of *Luzula*
14d) Five species of grass distributed variously in groups B, C and D: *Milium effusum* (*B*C), *Brachypodium silvaticum* (*C*D), *Deschampsia caespitosa* (*C*D), *Festuca gigantea* (C), *Melica nutans* (C)

Fig. 15.—Distribution patterns for 8 species of monocot herbs.

15a) *Maianthemum bifolium* and *Polygonatum multiflorum*
15b) *Paris quadrifolia* and the orchid, *Neottia nidus-avis*
15c) *Allium ursinum*, *Arum maculatum* and the orchids, *Cephalanthera damasonium* and *C. longifolia*. Another orchid, *Platanthera bifolia* was found in stand 16 of group C.

Fig. 16.—Distribution patterns for 31 species of dicot herbs. Of the 45 species of dicot herbs sampled, 20 were restricted to 1 group (A, 2 species; B, 3 species; C, 4 species; D, 11 species). However, 14 of the 20 occurred in only 1 stand, and these 14are not diagrammed. The other 31 species are shown and their groups listed.

16a) *Ajuga reptans*, *Aegopodium podograria*, and *Melittis melissophyllum*, restricted to two groups.
16b) *Prenanthes purpurea*, *Primula elatior* and *Euphorbia dulcis* in 2 groups; *Lysimachia nemorum* and *Epilobium montanum* in 1 group.
16c) *Galeopsis tetrahit*, *Mercurialis perennis*, *Geum urbanum* and *Knautia silvatica* in 2 groups.
16d) *Vicia sepium*, *Fragaria vesca*, *Veronica montana* in 2 groups; *Crepis paludosa*, *Caltha palustris* and *Filipendula ulmaria* in 1 group.
16e) *Solidago virga-aurea* and *Lamium galeobdolon* in 3 groups; *Stachys silvatica* in 1 group.
16f) *Circaea lutetiana*, *Geranium robertianum* and *Mycelis muralis* in 3 groups.
16g) *Galium odoratum (Asperula odorata)* and *Hieracium murorum* in 4 groups; *Sanicula europaea* in 3 groups.
16h) *Viola silvestris* and *Phyteuma spicatum* in 4 groups.
16i) *Oxalis acetosella* and *Anemone nemorosa* in 4 groups.

Fig. 17.—Distribution patterns for 11 species of shrubs.

17a) *Ilex aquifolium* and *Hedera helix*. *Hedera* occurs in every stand of group C and D but has an average stand frequency of 73% for group C and 54% for group D.
17b) *Vaccinium myrtillus* is virtually restricted to group A. *Ligustrum vulgare*, *Crataegus monogyna/oxyacantha* and *Daphne mezereum* occur primarily in group C, but each has a slightly different pattern of distribution (no frequencies are shown for these 3 species).
17c) Partly overlapping distribution patterns for 3 species of *Rubus*. The use of frequencies helps to determine the primary patterns.
17d) Distribution patterns for 2 species of *Viburnum*.

The following species of shrubs are not shown:

Cornus sanguinea, *Corylus avellana*, *Lonicera xylosteum* and *Rosa canina* are nearly restricted to group C. *Berberis vulgaris*, *Evonymus europaea*, *Prunus padus*, *Rhamnus cathartica*, and *Ribes grossularia* each occured in 1 to 3 stands of group C or D. *Sambucus racemosa* was growing in two stands of group B, and *S. nigra* in group D and 2 stands of group B. Of 22 species of shrubs, no 2 species occur in the same combination of stands.

Fig. 18.—Distribution patterns of occurrence for trees and frequencies of tree seedlings are shown for 5 angiosperm tree species.

18a) Distribution of *Acer pseudoplatanus* trees and seedlings. (Distribution pattern and frequencies for *A. campestre* seedlings are also shown, but no trees occurred in the sample plots.)
18b) *Fraxinus excelsior:* occurrence of trees and frequencies of tree seedlings.
18c) *Prunus avium* trees and seedlings.
18d) *Quercus petraea* trees and seedlings.
18e) *Fagus silvatica* trees occurred in all 25 stands. In order to better understand the distribution of *Fagus*, the number of trees per acre are listed for each stand and higher numbers per acre are outlined. (compare also with Fig.19c for relative importance of *Fagus* trees.)
18f) *Fagus silvatica* seedlings were found in sample quadrats in all but 1 stand. Frequencies are listed, and stands having higher frequencies are outlined. (Compare with Fig. 18e and Fig. 19c.)

Fig. 19.—All stands of occurrence for the 5 most-widespread species of trees are out- lined and the relative Basal Area values (used as relative importance values) are listed. The stands in which the trees attain their maximum relative importance are outlined with a solid line.

19a) *Pinus silvestris*
19b) *Quercus petraea*
19c) *Fagus silvatica*
19d) *Picea abies*
19e) *Abies alba*
19f) The peak importance values for the 5 widespread trees are plotted on 1 ordination. In addition, *Acer pseudoplatanus* and *Fraxinus excelsior* are plotted for their stands of highest relative values.

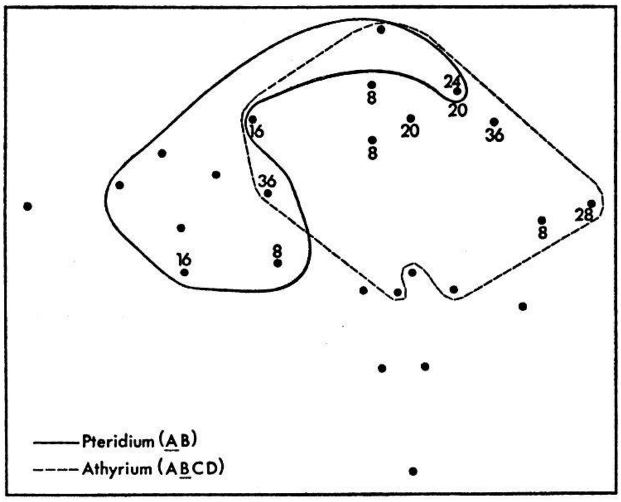


Fig. 13a

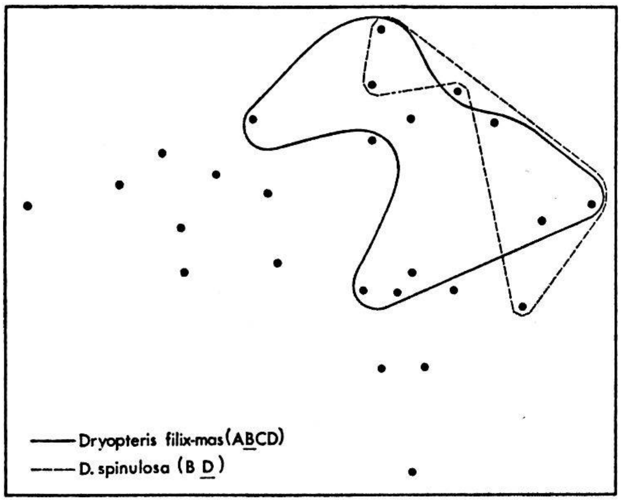


Fig. 13b

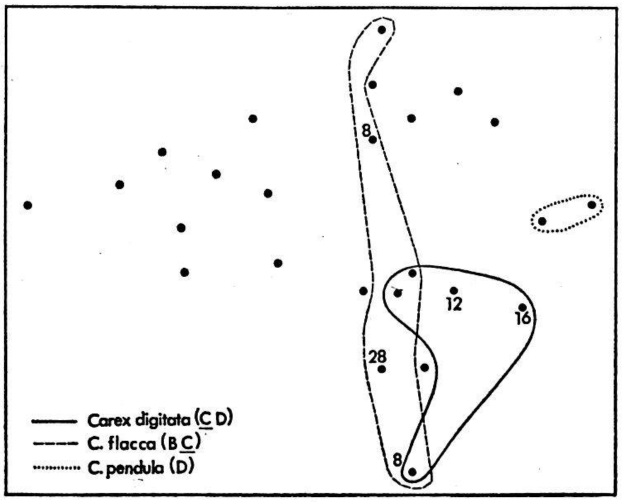


Fig. 14a

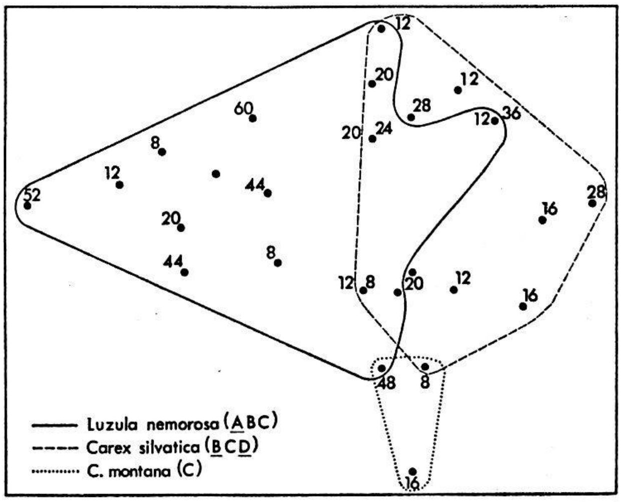


Fig. 14b

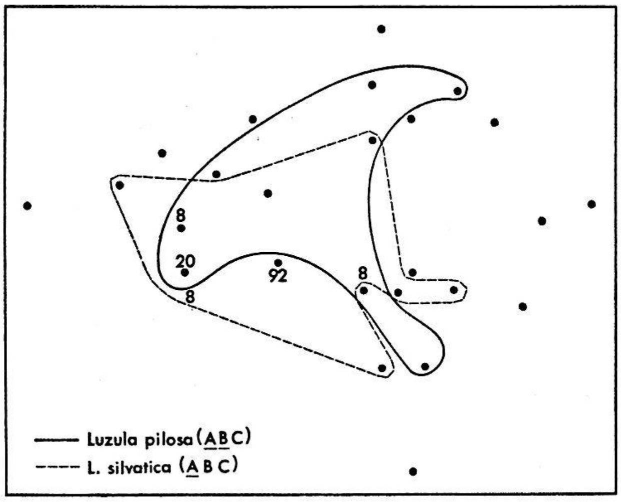


Fig. 14c

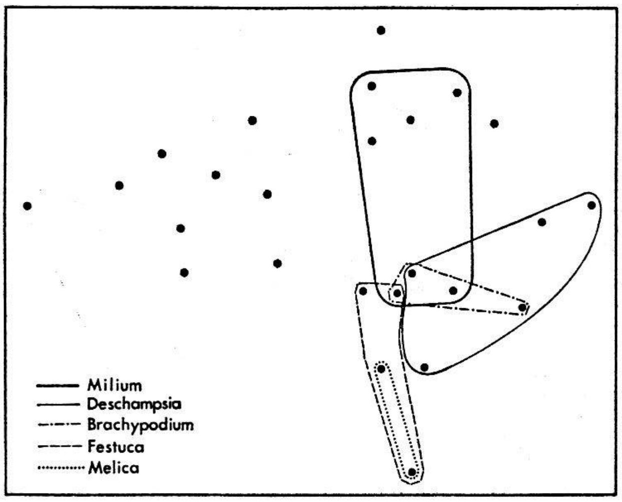


Fig. 14d

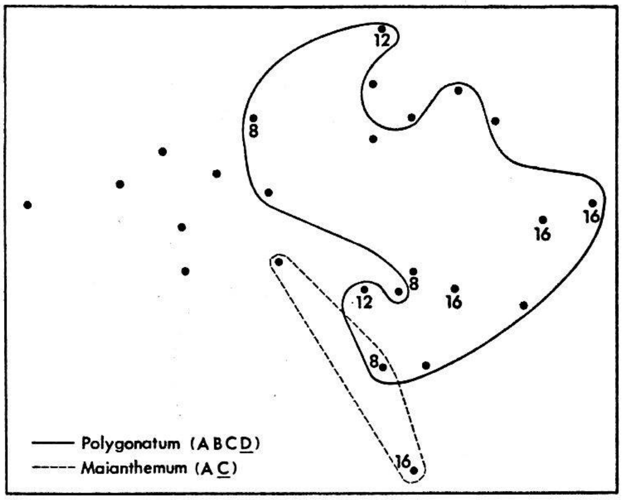


Fig. 15a

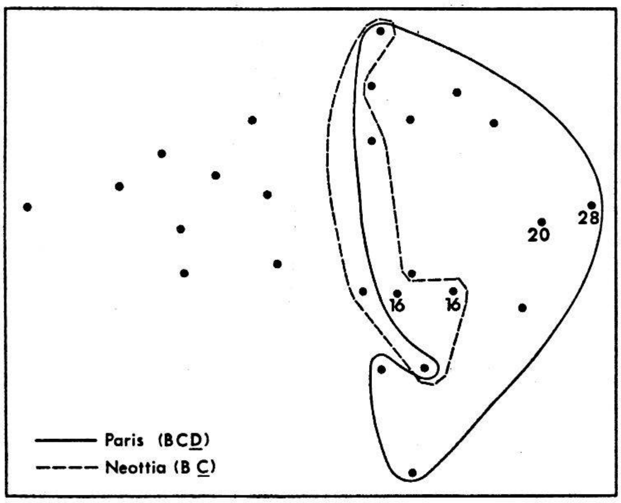


Fig. 15b

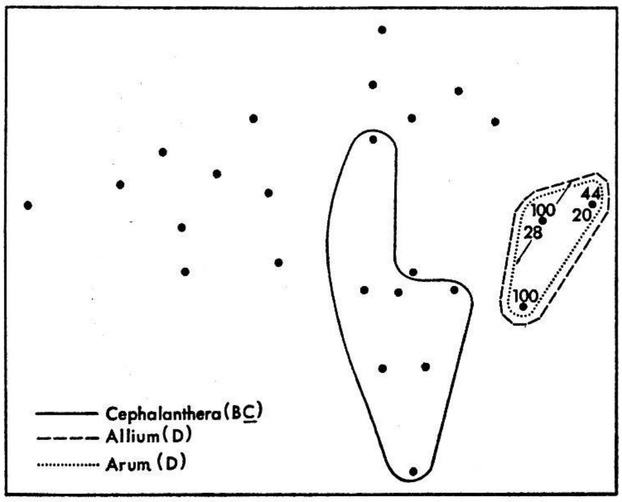


Fig. 15c

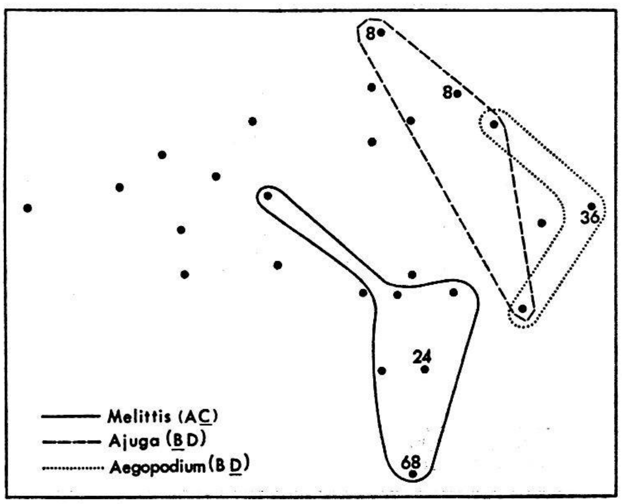


Fig. 16a

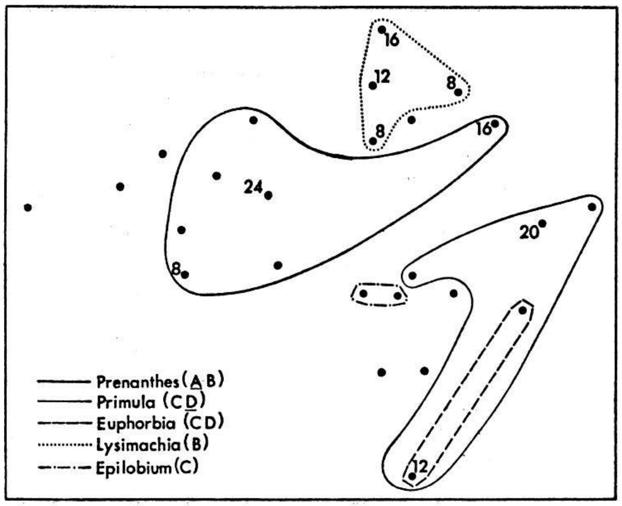


Fig. 16b

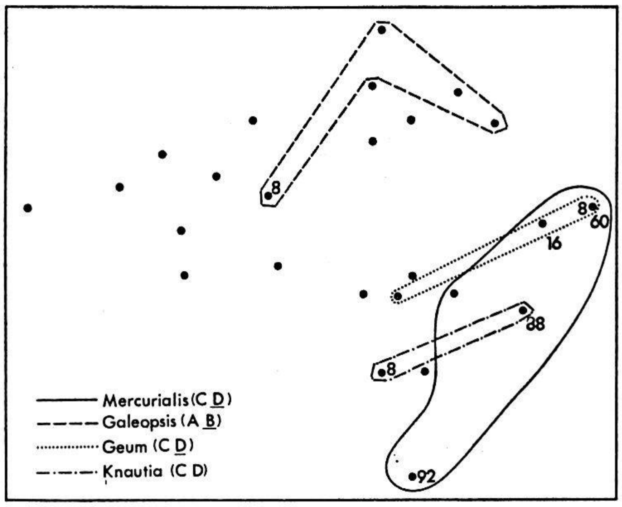


Fig. 16c

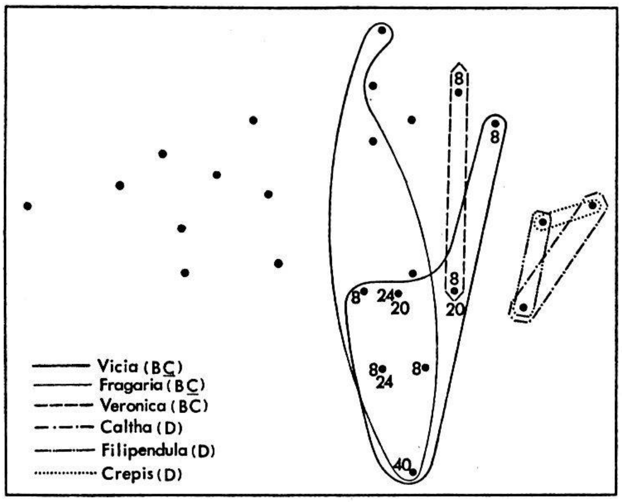


Fig. 16d

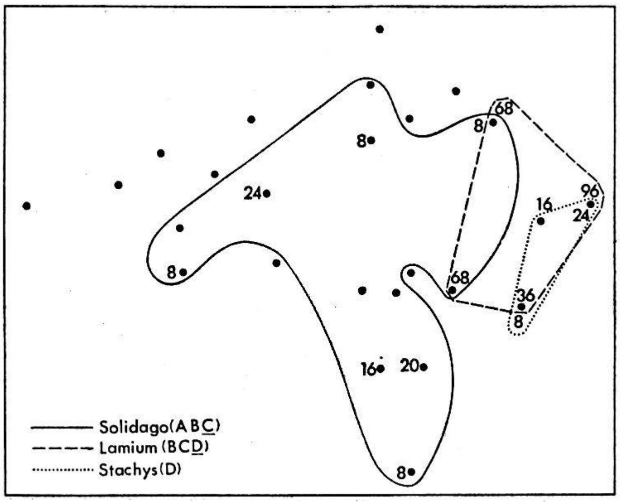


Fig. 16e

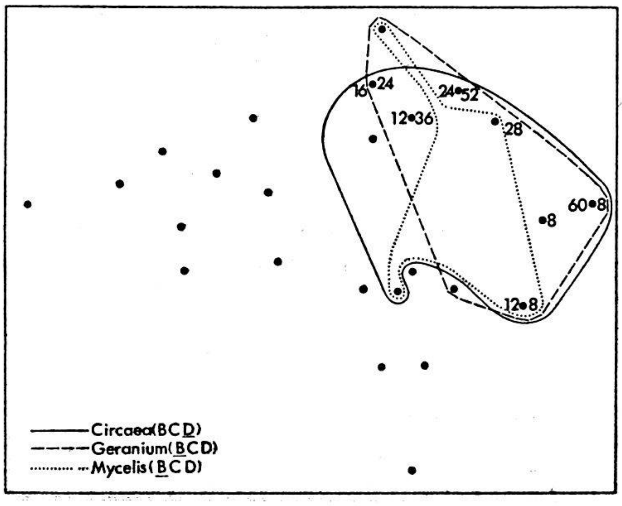


Fig. 16f

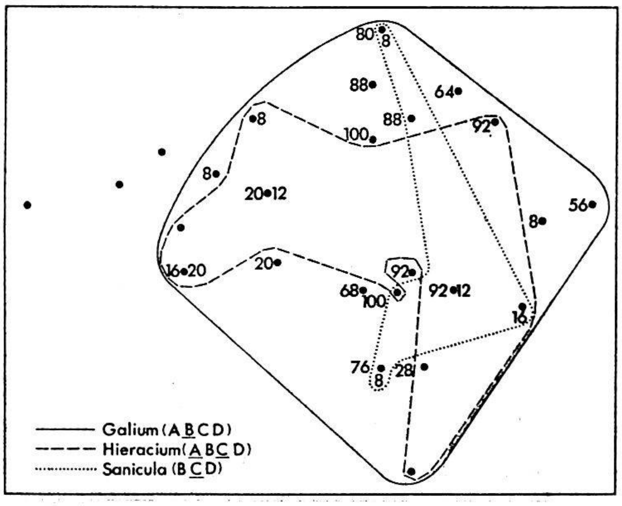


Fig. 16g

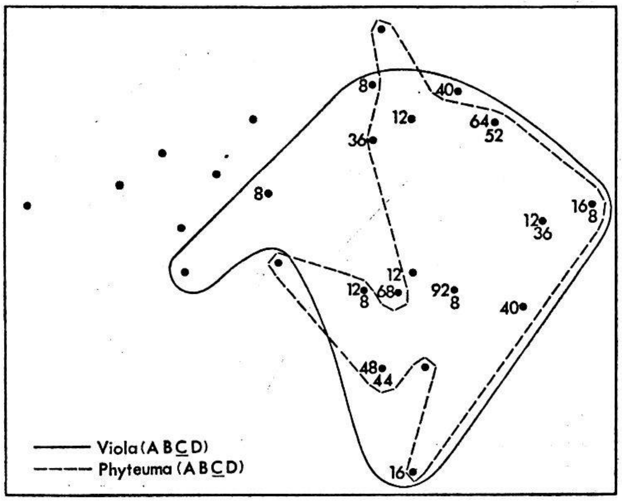


Fig. 16h

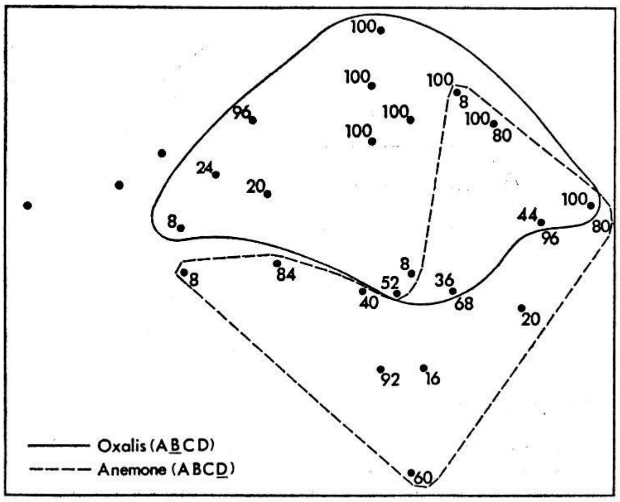


Fig. 16i

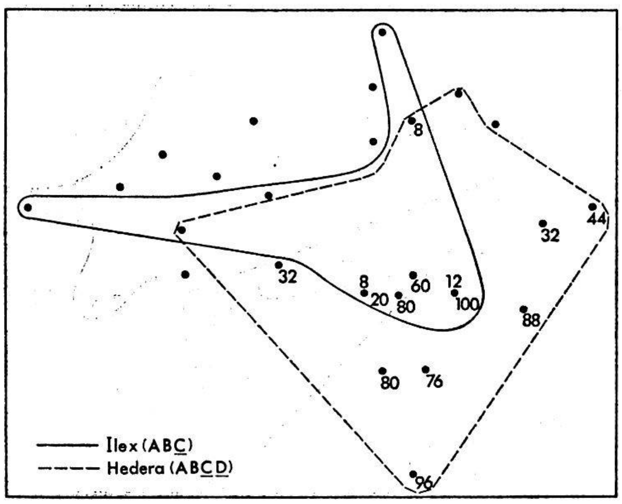


Fig. 17a

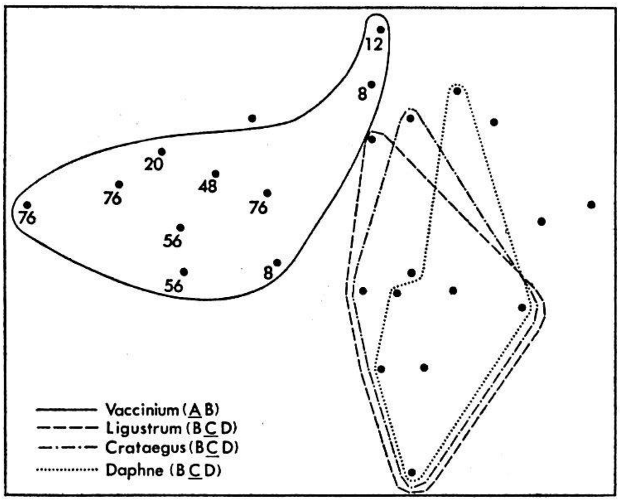


Fig. 17b

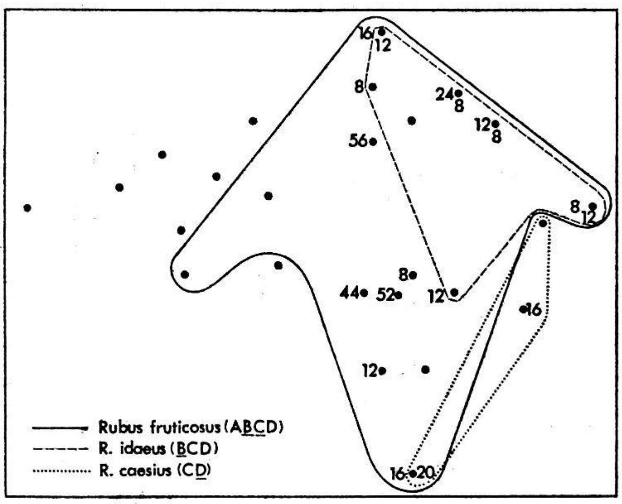


Fig. 17c

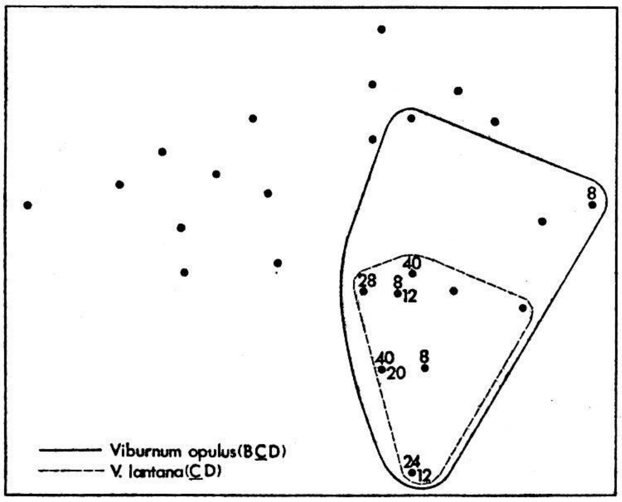


Fig. 17d

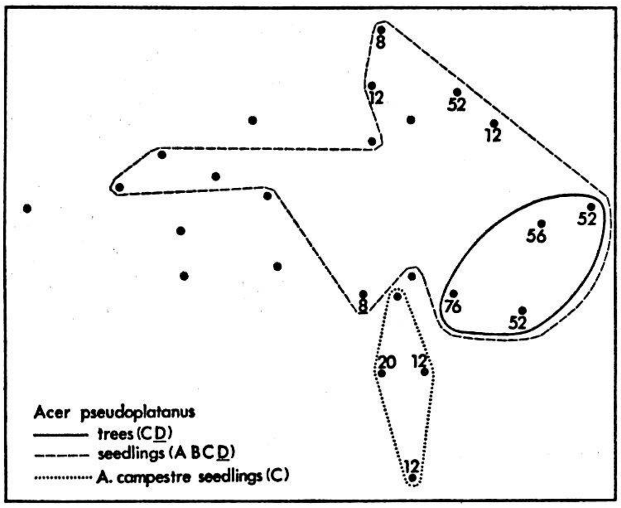


Fig. 18a

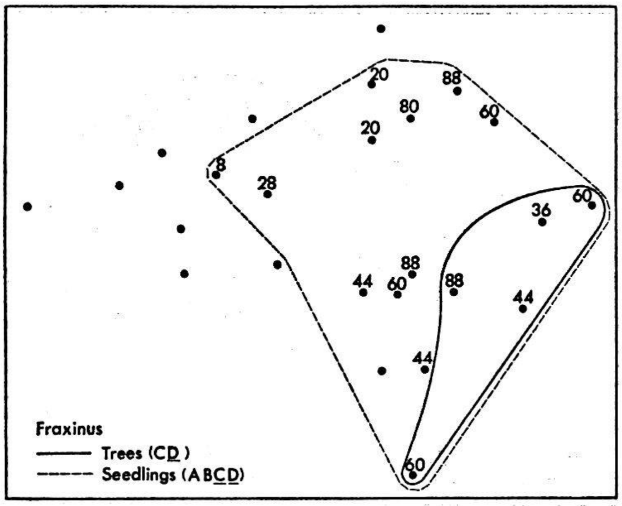


Fig. 18b

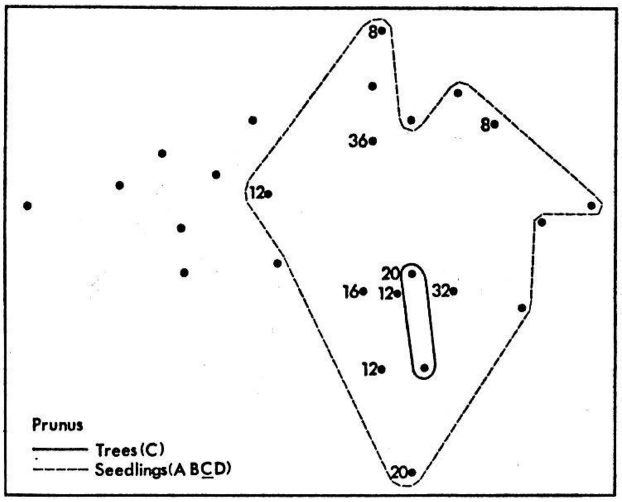


Fig. 18c

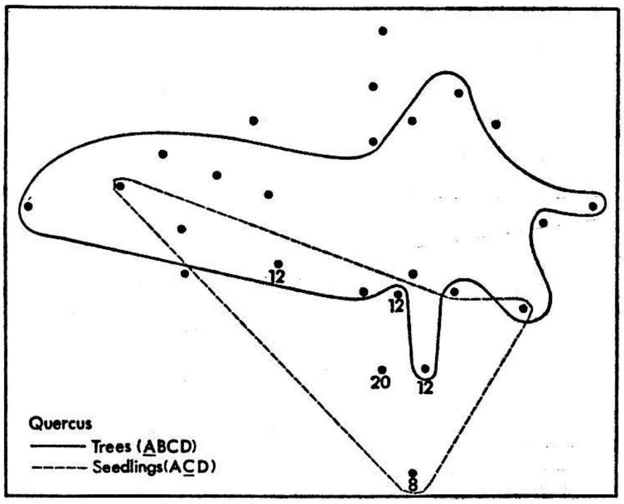


Fig. 18d

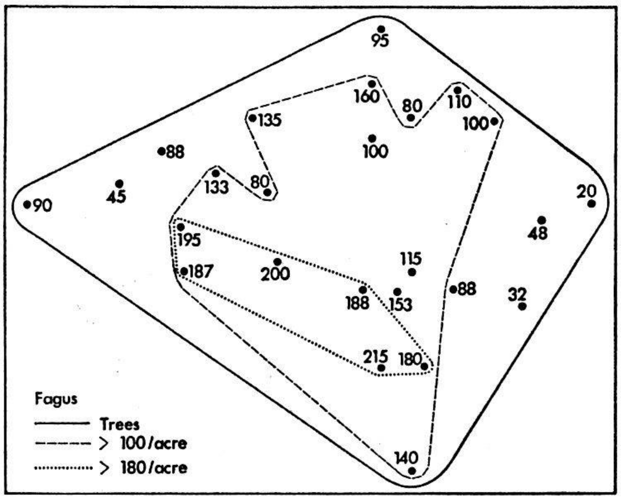


Fig. 18e

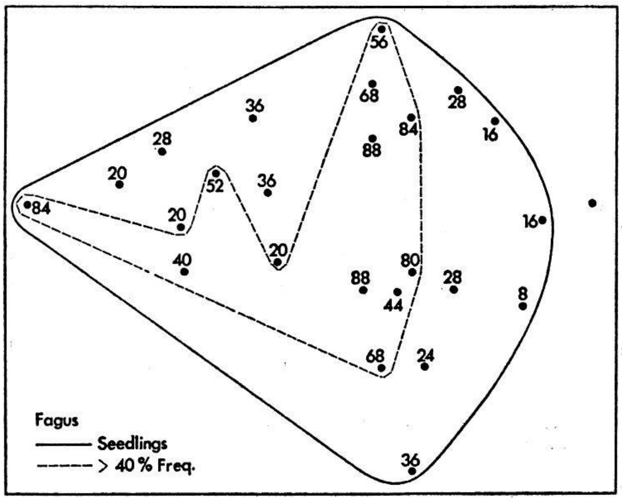


Fig. 18f

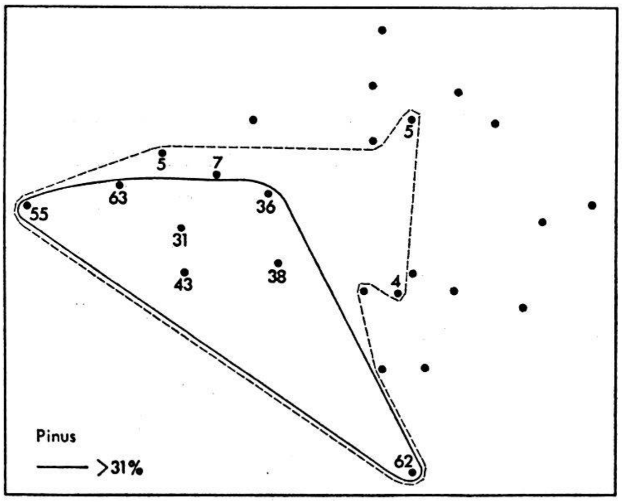


Fig. 19a

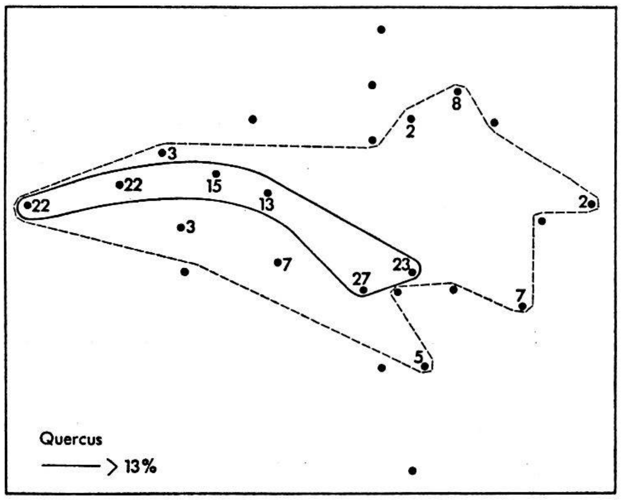


Fig. 19b

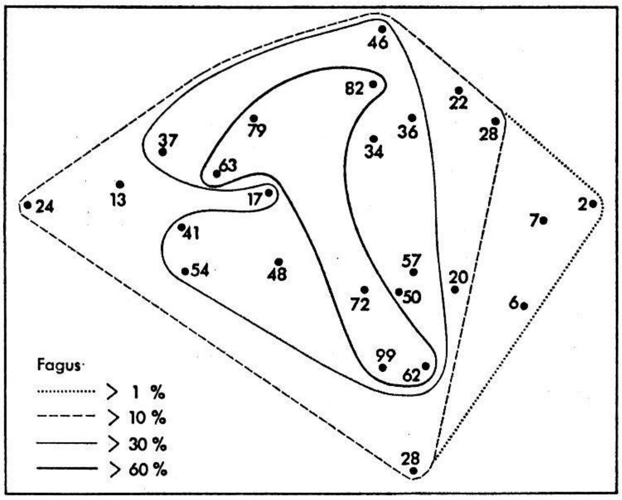


Fig. 19c

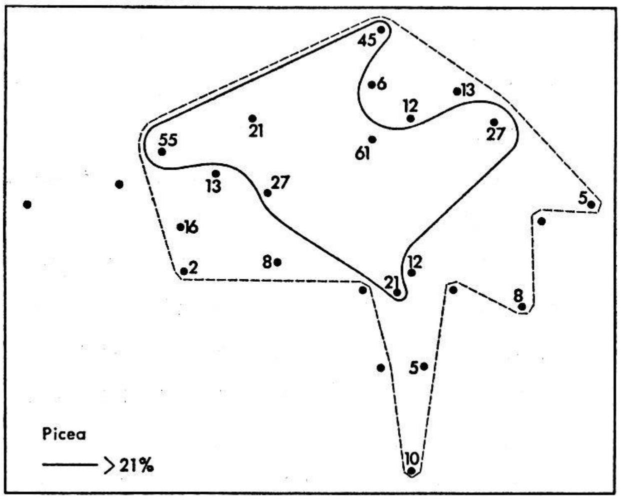


Fig. 19d

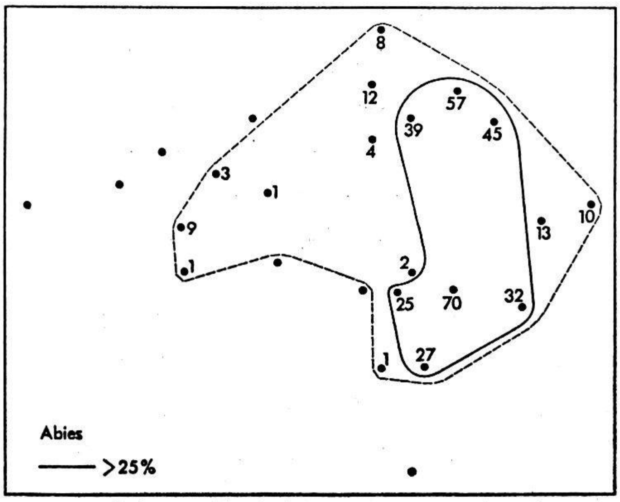


Fig. 19e

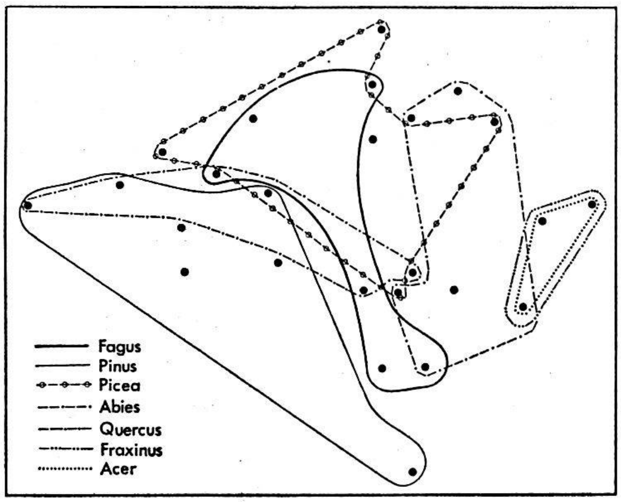


Fig. 19f

2. *Trees*

A discussion concerning the analytic methods used for the trees was given in part III-B of this paper. The two main measurements determined for the trees and used as a basis for comparison were density and basal area. The number of trees per acre per species for each stand is seen in Table 8. Various subtotals and totals are also shown. No ecological conclusions regarding dominance or importance are drawn from the density figures, *i.e.* high densities do not necessarily make a species dominant, as the trees may be very small. Forests of the Kirchleerau area are managed for cutting so density figures are strongly man-influenced and are quite variable in the study area. Thus, only a crude idea of relative importance or stand structure is gained from the density figures.

In Fig. 18, the distributions of the angiosperm trees are shown in relation to the tree seedlings. *Betula*, *Alnus* and *Carpinus* are not shown because they were rare in the stands studied. Coniferous seedlings were not evaluated as was mentioned earlier, so conifers likewise are not shown. Tree seedlings often have a wider ecological distribution than the trees of the same species. Examination of the frequencies of the tree seedlings in Fig. 18 aids in understanding the main ecological ranges of the species. *Acer* and *Fraxinus* seeds are wind-dispersed, and *Prunus* seeds probably are bird-dispersed so a wide distribution of seedlings would be expected. *Fagus* is present in nearly every forest type in the Kirchleerau region. Examination of density figures for trees and frequencies for seedlings as shown in Fig. 18-e and f helps to focus on the portion of the ecological community in which *Fagus* does best. The pattern for *Quercus* (Fig. 18-d) is somewhat puzzling—trees and seedlings have different distributions with little overlap. Perhaps where man allows *Quercus* to grow is not necessarily where it "prefers" to grow, or there may be some correlation with squirrels, insects or other factors. This pattern may be due only to chance because of a limited sample size. Because of cutting and other management practices, it is especially difficult to draw any firm conclusions regarding the trees. The trees are directly influenced by man, whereas the tree seedlings and other understory species are influenced only indirectly or secondarily.

In Table 9 (annex) are seen figures for basal area per acre (absolute and relative), and the most important species in each stand are noted. Recall from part III-B that basal area per acre is a reflection of both density and size, and is therefore used as the measure of relative importance. Total relative basal area or importance of conifers ranges from 0 to 70%, and the conifers are relatively more important in 12 of the 25 stands. Total relative im-

Table 8. Number of trees per acre is shown for each species in each stand. Subtotals are shown for number of conifers and angiosperms per acre. Total number of trees per acre and per hectare are also shown.

	Group A									B						C							D		
Tree species / Stand	13	14	10	4	11	15	12	3	9	6	1	21	8	7	2	16	17	24	5	18	19	20	25	23	22
Abies alba				20	25		7	5		30	50	20	40	90	15	40	148	5		55	5		72	40	40
Larix decidua								20					5												
Picea abies			80	20	30	12	20	55	20	35	35	5	15	35	95	27		25		10		24	16		36
Pinus silvestris	65	70	8	7	50	40	53	55					10			7						96			
Total conifers per acre	65	70	88	47	105	52	80	135	20	65	85	25	70	125	110	74	148	30	0	65	5	120	88	40	76
Fagus silvatica	90	45	88	133	195	200	187	80	135	95	100	160	80	110	100	153	88	115	188	180	215	140	32	48	20
Quercus petraea	30	65	4	33	4	8		40					5	10				40	32	15			8		4
Fraxinus excelsior																	16					4	84	108	44
Acer pseudoplatanus																	20						28	24	52
Carpinus betulus																		5					8	12	
Alnus glutinosa																							4		4
Betula pendula		5						5																	
Prunus avium																		15		5					
Total angiosperms per acre	120	115	92	166	199	208	187	125	135	95	100	160	85	120	100	153	124	175	220	200	215	144	164	192	124
Total trees per acre	185	185	180	213	304	260	267	260	155	160	185	185	155	245	210	227	272	205	220	265	220	264	252	232	200
Total trees per hectare	457	457	445	526	751	642	659	642	383	395	457	457	383	605	519	561	672	506	543	655	543	652	622	573	494

portance of the angiosperms ranges from 30 to 100%, and they likewise dominate 12 stands. The importance in stand 16 is evenly divided.

The relative basal area figures for individual species presumably bear a fairly direct relationship to the amount of light intercepted or shade cast, the amount of water and nutrients taken up, photosynthesis carried on, litter dropped, etc. Equating relative importance with factors such as these is the underlying reason for attempting to assess importance of the individual species.

Fagus is seen in Table 9 to be the first or second most-important tree in 20 of the 25 stands. Of the conifers, *Abies*, *Picea* and *Pinus* are each important in several of the stands. In an attempt to understand the relationship of the various species of trees to the ordination, these individually-important tree species are plotted in Fig. 19-a to e. When the stands of peak importance values for the various species are plotted together on one ordination (Fig. 19-f), an understanding can be achieved regarding the relationship of the species to one another, and to the environmental factors expressed on the ordination.

The "overlapping" relationship of the species to one another is similar to that of a continuum as originally shown by CURTIS and McINTOSH (1951). This "continuum" for the trees would be *Pinus-Quercus-Fagus-Picea-Abies-Fraxinus* and *Acer*. This is essentially a moisture gradient from dry to mesic to moist, and presumably could also approximate a successional gradient (from dry and from moist to mesic). The aspect of succession was not considered in this study because information on stand structure and reproduction is lost when cutting, thinning, planting, etc. occur. Nevertheless, it may be inferred from Fig. 19-f that *Fagus* is the mesic "climax" species.

Tree and understory species plotted on the ordination with some measure of importance (basal areas and frequencies in this case) show patterns with higher value stands grading to lower value stands in various directions. Patterns such as these have been discussed in terms of atmospheric distributions by BRAY and CURTIS (1957) and binomial solids by WHITTAKER (1967). Whittaker has further interpreted these distribution patterns in terms of the evolutionary history of species. The form of the pattern and location of the optimum express in part a species' genecology, *i.e.*, its adaptive center and range of genetic differentiation as expressed in the population distribution. Because of scattered centers and distributional overlap, the species populations form continua along the gradients. Groups of species whose population centers are close together form ecological groups.

Some indication of these groups for understory species may be gained by examination of Figs 13 to 18 and the "boxes" of Table 6. However, in forests such as those of the Kirchleerau area, unusual combinations of species likely occur in some stands because of past soil disturbance and canopy opening during cutting or thinning operations, or because of unusual soil conditions associated with the conifers which are probably exotic to the area. In addition, since the stands are relatively small, intrusion of species from one stand into geographically proximate but ecologically different stands has probably occurred.

D. Comparison with results of other workers

One of the reasons for my investigation of the forests of the Kirchleerau area was to make a comparison with the results of the four previous studies as published in the volume edited by Ellenberg (1967). This comparison is shown in Figs. 20 to 23 and Tables 10 to 13. The plant groups (associations, etc.) of the other workers are plotted on my ordination in the four figures. Conversely, my stands are plotted in relation to their plant groups in the four tables, and their groups are listed by the main environmental factors associated with the delimitation of these groups. It was necessary for me to construct these tables from the paper and map of each worker in order to make this comparison. Therefore, the tables become my interpretations of the other workers main environmental gradients. I may have oversimplified their results by the 2-dimensional tables, but trust I have not misinterpreted their results. Recall that I originally selected stands for study from the associations and sub-associations of Frehner (1967). My stand numbers are again shown on the ordination in Fig. 20, and these are the stand numbers referred to in Tables 10 to 13.

A moisture gradient and a soil pH/nutrient gradient were found to be the major environmental determinants in the associations of Frehner (1967), the phytocoenoses of Saxer (1967), and the site-type groups of Eberhardt et al. (1967). These were also the major gradients which appeared in my ordination. The ecological groups of Aichinger (1967) are based on soil moisture conditions; the species combinations are seen in his paper to be correlated with soil conditions which include nutrients and pH as major factors. Therefore, the papers of the other four workers as well as my paper all consider moisture and pH/nutrients as major environmental factors.

Despite the fact that the results of the five methods are associated with the same environmental factors, the stands appear on the ordination in different groupings. This may be partly due to erroneous interpretations of stand locations or boundaries—I equated my stands with their groups by plotting my stands on their maps. Certainly this type of error would affect the patterns

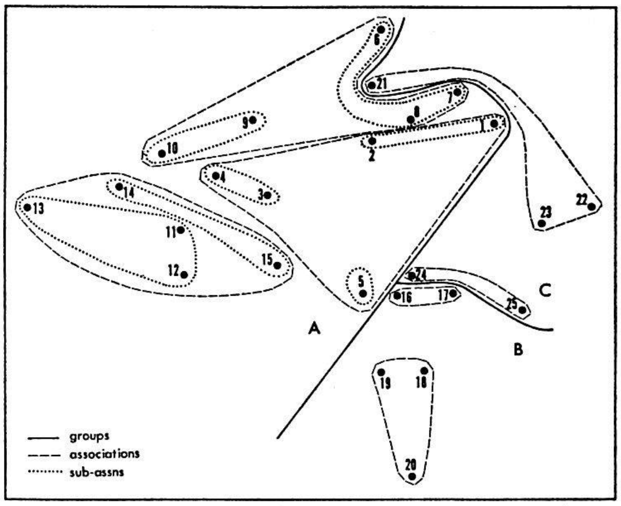


Fig. 20.—FREHNER's communities plotted on my ordination. See Table 10 for names of associations and Table 1 for names of his groups.

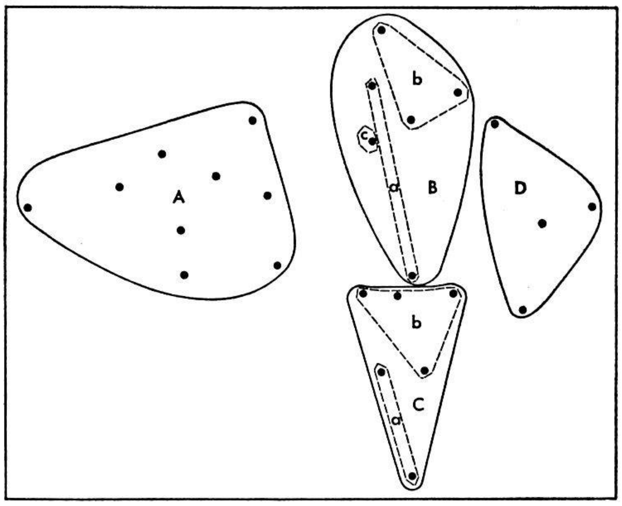


Fig. 21.—SAXER's phytocoenoses plotted on my ordination. See Table 11 for names and descriptions of the phytocoenoses.

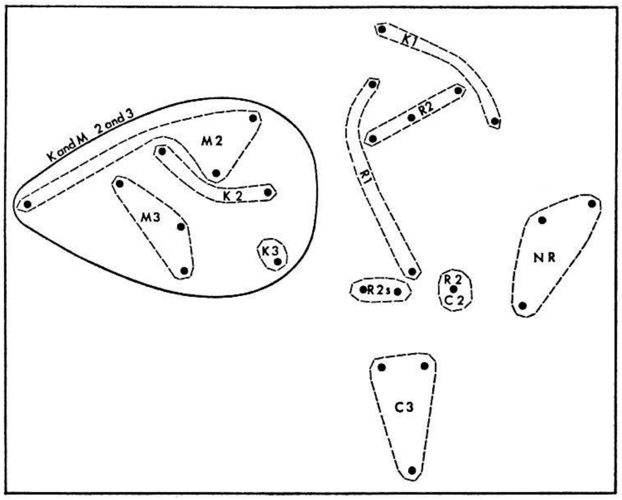


Fig. 22.—EBERHARDT's site-type groups plotted on my ordination. See Table 12 for description of these groups.

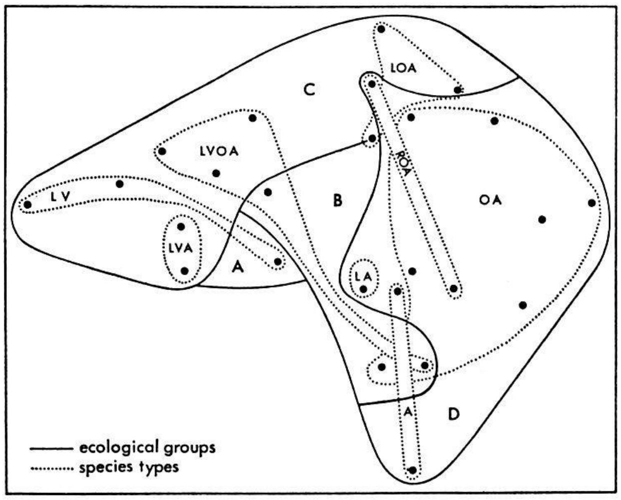


Fig. 23.—AICHINGER's species types and ecological groups plotted on my ordination. See Table 13 for names of these groups.

of groupings, so the groupings in Figs. 20 to 23 should not be taken literally. On the other hand, the plottings of most stands are probably accurate, in which case the differences would be primarily due to varying methods of grouping stands.

It can be seen that SAXER's phytocoenoses (plotted in Fig. 21) most closely resemble the four ecological groups which appeared on my ordination (see Fig. 4). It can also be seen that AICHINGER's groups (plotted in Fig. 23) show the least similarity with my ordination, and that the methods of FREHNER

Table 10.—Frehner's associations and my stands in relation to moisture and nutrient gradients. This table is adapted from a table of Frehner (1967, p. 147). By reference to his paper, I have placed his associations and sub-associations (and my stands) more precisely relative to one another and to the environmental gradients than is shown in his table.

Environmental Factors	Trockener (drier)	Frisch bis wechselfeucht (fresh to variably moist)		Feucht bis nass (moist to wet)
Basenarm (base-poor)	Melampyro-Fagetum			
Kalkarm, aber nicht basenarm (Ca-poor, but not base-poor)	14, 15 leucobryetosum typicum 11, 12, 13	Milio-Fagetum 9, 10 luzuletosum dryopteridosum 6, 7, 8	Melico-Fagetum 3, 4 luzuletosum asperuletosum 1, 2 5 cornetosum	Aceri-Fraxinetum 21, 22, 23
Kalkreich (rich in $CaCO_3$)	Carici-Fagetum 18, 19, 20		Pulmonario-Fagetum 16, 17	Pruno-Fraxinetum 24, 25

Table 11, Footnote 1.—Brief description of SAXER's phytocoenoses.

A. *Fagetum silvaticae* with *Quercus robur*, *Calluna*.

Regional phytocoenose on sour degraded sandstone molasse. These are the most acid soils of the research region; they are calcium-free, nutrient-poor and are dry. Tree growth is poor; there are few shrubs and herbs. Many acid-loving species of moss occur. SAXER found an average of 16 (12–20) vascular plant species per stand.

B. *Fagetum silvaticae.*

a) Local phytocoenose on moist gravel slopes or on moist molasse slopes with gravel which has rolled down. The soils are relatively nutrient-rich, calcium-containing and well-supplied with water. They are never on southfacing slopes and differ thus from phytocoenose C—b which has more warmth-loving "mixed deciduous forest species". This phytocoenose is very similar to the regional *Fagetum silvaticae typicum* (which is on sandstone, calcium-poor but nutrient-rich, and good water conditions). The shrub-layer is poorly developed, but the herb layer is rich in species and is well-developed. SAXER found 34 (22–45) species.

b) Local phytocoenose on oligotrophic molasse of steep slopes. The soils are drier and have less nutrients than the regional *Fagetum silvaticae typicum*, but are not as poor and dry as phytocoenose A. Less species than B—a. Found 24 (21–29) species.

c) Local phytocoenose on clay molasse. It is slightly more moist, but otherwise very similar to the regional *Fagetum silvaticae typicum*. Found 54 species.

C. *Fagetum silvaticae* with *Quercus*, *Tilia*, *Acer*.

a) Regional phytocoenose exclusively on Würm moraine. The soils are calcium-rich and relatively dry. It is in warm and low situations which lead to sites in which "mixed deciduous forest species" occur. The entry of these species is further enhanced by man's thinning of the forests which leads to the situation of this phytocoenose having the richest development of woody species (trees and shrubs) for the whole region. The herb layer is well-developed and covers the ground. Found 50 (43–55) species.

b) Local phytocoenose on sandstone with traces of calcareous-gravel, or on Würm moraine if it is relatively warm and dry. This phytocoenose stands between B—a and C—a. The soils are relatively nutrient-rich and contain $CaCO_3$. There are many woody species and the shrub layer is well-developed. The herb layer is rich in species, but the moss layer is virtually non-existent. Found 47 (42–52) species.

D. *Acereto-Fraxinetum.*

Local phytocoenose in basins or on slopes which are quite moist. The substratum does not contain much $CaCO_3$ but is relatively nutrient-rich. The shrub-layer is poorly-developed but the herb-layer is rich. Found 34 (25–46) species.

Table 11.—SAXER's phytocoenoses and my stands in relation to moisture and nutrient gradients. This table was constructed from what seemed to be the main evironmental gradients in SAXER's (1967) description of the phytocoenoses. The phytocoenoses are placed relative to one another on the basis of his descriptions which are summarized as a footnote[1].

Environmental Factors	Dry	(Dry-mesic)	(Mesic)	Moist
No $CaCO_3$, poor in nutrients, acid soil	A. Fagetum silvaticae with Qr-C 3, 4, 9, 10, 11, 12, 13, 14, 15			
No $CaCO_3$ but nutrients		B. Fagetum silvaticae (b) 6, 7, 8	(c) 2	D. Acereto-Fraxinetum 1, 22, 23, 25
Some $CaCO_3$ nutrient-rich		C. Fagetum silvaticae with Q-T-A (b) 5, 16, 17, 18	(a) 21, 24	
Rich in $CaCO_3$		(a) 19, 20		

Table 12.—EBERHARDT's site-type groups and my stands in relation to moisture and nutrient gradients. This table was constructed from the "Standortsformengruppen" map by EBERHARDT.

Environmental Factors	Unterdurchschittlich (3) wasserversorgt (below average water)	Durchschnittlich (2) wasserversorgt (average water)	Überdurchschnittlich (1) wasserversorgt (above average water)	Grundnass bis grundfeucht (N) (moist)
Mässig (M) (only moderate nutrients)	M3v 11, 12, 14 (v = moisture situation dry due to degradation)	M2v 4, 9, 13	—	—
Kräftig (K) (medium nutrients)	K3v 15	K2 10 (3)	K1 1, 6	—
Reich (R) (rich in nutrients)	—	R2 2, 7, 8, (3), (17) R2s 5, 16 (s = warmth protection)	R1 21, 24, (22), (25)	NR (22), (23), (25)
Kalkreich (C) (rich in $CaCO_3$)	C3 18, 19, 20	C2 (17), (23)	—	—

Table 13.—My stands plotted in relation to Aichinger's (1967) forest development types (species types by ecological groups). This table was constructed from the map by Dr. H. Bosse-Martin.

	A. Silicicolum (dry)	B. Agrum solum silicicolum (± dry)	C. Semi-superirrigatum (fresh)	D. Superirrigatum[1] (moist)
1. Luzula luzuloides-L. silvatica	15	—	—	—
2. L. luz.-Vaccinium	—	—	13	—
3. L. luz.-L. sil.-Vacc. (1–3: LV)	—	—	14	—
4. Luz.-Vacc.-Oxalis	—	18	9, 10 (→ C-5)	—
5. Luz.-Vacc.-Ox.-Asperula (4–5: LVOA)	—	3	4	—
6. Luz.-Vacc.-Asp. (LVA)	—		11, 12	—
7. Luz.-Ox.-Asp. (LOA)	—	2 (→ C-5)	6, 7	—
8. Luz.-Asp. (LA)	—	—	—	5
9. Ox.-Asp. (OA)	—	19	—	1, 8, 22, 23, 24, 25
10. Asp. (A)	—	—	—	16, 20
11. Rubus-Ox.-Asp. (ROA)	—	—	—	17, 21

Footnote 1.

A. Silicicolum: forests of dry-soil ridges and slopes.
B. A. s. silicicolum: forests on former agriculturally-used shallow soils of more-or-less dry plateaus with changeable subsoil moisture conditions.
C. Semi-superirrigatum: forests of more-or-less "fresh" slopes.
D. Superirrigatum: forests of more-or-less moist slopes with good subsoil water conditions.

(Fig. 20) and of EBERHARDT et al. (Fig. 22) give results between those of SAXER and AICHINGER. A complete analysis of the similarities and differences among the five methods could be the subject of another complete paper, so it is left to the reader to make as detailed a comparison as he wishes. In general, we may note that similar tree and understory species are associated with comparable environmental factors in the other four papers (ELLENBERG, 1967) and in my paper. The main differences are in the way in which the species groups are put together.

The basic difference between my interpretation and that in the other four papers is that the other workers seem to consider that groups (associations, phytocoenoses, etc.) exist, whereas I interpret my results to show relatively continuous variation. The "groups" which I recognized (A, B, C, D) are very loose (*cf.* Figs 3 and 4, and Table 6). When individual species are plotted on the ordination (Figs 13 to 18), no two species that are at all common have the same distribution or frequencies. Likewise, when species are placed in the "boxes" of their average highest frequency (Table 6), the lack of "associations" is indicated.

In Figs 5 to 10 it was illustrated that environmental groups are lacking as well as species groups. The several environmental factors each trend in different directions, and no two stands have similar combinations of environmental factors. Although definite groups do not appear to exist, this does not imply that environmental and species trends do not exist however. A series of gradients or clines has been illustrated for environmental factors and species in the figures throughout this paper. When several species and environmental factors trend in the same general direction, certain broad communities may be recognized while admitting that there is overlap between communities.

E. Conclusions

The results of the other four methods plus mine were fairly similar regarding the species distributions in relation to the environmental trends. The main differences among the methods were the ways in which the stands were grouped. Choices of different classificatory criteria lead to different groupings of community samples as has been pointed out by several workers (*e.g.*, WHITTAKER, 1962). The groupings of the other workers were based on correlation of environmental factors with species groups. By the ordination technique, stand similarities were determined, and ultimately four loose and overlapping groups were recognized. There appeared to be overlap of species between the groups of each of the other workers, so their classification groups likewise can not be interpreted in a completely rigid manner. Nevertheless, the differences between their methods and mine revolve around the concepts of classification vs. ordination. These concepts are not mutually exclusive and have been discussed at length elsewhere (*e.g.*, McIntosh, 1967).

My study was done partly as a comparison of methods. However, for my own interest another purpose was posed as a question in part I-A: is it possible for someone unfamiliar with European ecological conditions to apply quantitative methods (designed for use in relatively large natural forests) to small forests which have been heavily modified by man for a long period of time? One of my conclusions, then, is that I was able to study small disturbed areas of diverse ecological conditions and still get an indication of the main environmental trends and species behavior, as well as some quantitative description of the existing vegetation. I suggest that methods similar to those used in this study are useful for a preliminary rapid determination of the main environmental factors and species trends. The ordination technique is useful for suggesting correlation of various factors, but will not prove these correlations. The correlations could be considered as working hypotheses, and further detailed study could be designed to test these hypotheses.

Mapping was an important part of the methodological studies of the other workers. Mapping implies classification, and since the "Wisconsin" methods are not classificatory, no mapping was attempted in my study. Nevertheless, it might be possible to correlate vegetation (by plant community and by successional stage) with environmental or site factors and achieve ecological "groups" such as was done in this paper. From these groups, a map could be constructed, but it would probably take a study of greater detail than mine. Further, because of man's modification of the area, there is no way to determine in my study if the trees are where they "prefer" to be, or if they would do better in a different habitat. For a study such as the one under consideration, I believe the mapping should be done on the basis of tree-species potential for various site types. From the standpoint that Eberhardt et al. gathered the most detailed environmental information and attempted to correlate silvicultural relationships with the site types, I believe that their type of mapping is the most useful of those employed in this study.

I conclude, then, that an ordination study objectively gives good preliminary information regarding environmental and species trends. Quantitative data on vegetation can rapidly be obtained by the field and analytic methods described. The ordination technique could be adapted for mapping, but since classification is a prerequisite for mapping, it is better to do mapping after more detailed study and definitive correlation of the species with the environmental factors.

V. Summary

Forest vegetation of the Kirchleerau area of Switzerland was studied using field and analytic methods adapted from those of the so-called "Wisconsin school" of plant ecology. Results were compared with those of four European methods applied in the same area and which were compiled by Ellenberg (1967). The study area of *c.* 400 hectares had been selected for its ecological diversity. In order to insure a good range of vegetation types, areas to study were selected from seven associations of Frehner (1967); 25 stands were then sampled after on-site inspection. Quantitative information was gathered on size and number of trees in four $^1/_{20}$ acre (2 are) circular plots per stand. Frequency was determined for understory species (herbs, shrubs, tree seedlings) using 25 1 m^2 quadrats per stand. Various environmental data were also recorded for each stand.

A modification of the Bray and Curtis (1957) ordination was performed using a similarity index derived from frequency-classes of the understory species. On the basis of absolute and relative similarities, four groups of stands were recognized although these groups were somewhat overlapping. These four groups of stands were used in the selection of end stands of two axes. Vegetation and environmental data and correlations plotted on a two-dimensional ordination are more readily understood than data plotted on a multidimensional ordination. Since similarities and groups of stands as well as dissimilarities were used in achieving the ordination, it was considered that more information was expressed than in two axes of a conventional dissimilarity ordination.

Environmental data and data from the tree and understory species were plotted on the ordination. Several environmental trends were recognized on the ordination, but the main trends were considered to be soil moisture and soil pH. Patterns of individual species appear to show correlation with certain environmental trends. It is noted in the paper that the ordination technique is valuable for suggesting correlation, but that further study is necessary to determine if these correlations are valid or not.

Trees have been influenced by man for a long period of time in the Kirchleerau area by management practices of planting, thinning, and cutting, and this has influenced the understory species through opening the canopy, disturbing the soil, changing the soil characteristics by introduction of conifers, etc. Therefore, unusual (rather than "natural") combinations of understory species likely occur in stands. Considering that the ordination was based on understory species, it is of interest that good patterns appeared for the environmental factors and the tree species. No important understory or tree

species have identical distribution patterns, and an individualistic interpretation and lack of definitive groupings is indicated. No good environmental groupings appear either, as the various environmental factors trend in a number of directions. An individualistic interpretation and lack of species and environmental groups (*i.e.*, lack of "associations") does not mean that meaningful trends are absent, however. For example, relative basal area was used as a measure of relative importance for the trees, and when stands of peak importance values of different tree species are plotted on one ordination, a pattern resembling a continuum is achieved. Tree genera appear in the order of *Pinus-Quercus-Fagus-Picea-Abies-Fraxinus* and *Acer*, essentially a moisture gradient from dry to mesic to moist.

A comparison of my results with those achieved by the other four methods was made by plotting their groups (associations, phytocoenoses, etc.) on my ordination, and also by plotting my stands on tables based on their environmental groupings. When vegetation groupings of the other workers were plotted on my ordination, the major groups of SAXER were seen to be most similar to my ordination and those of AICHINGER were least similar. The groupings of FREHNER and of EBERHARDT et al. were intermediate. Species and environmental trends were found to be similar among all five methods, so the main difference seemed to be the method of grouping stands.

The differences between their methods and mine thus are mainly those of the concepts of classification vs. ordination.

Possible methods of mapping from ordinations are discussed, but it is concluded that classificatory methods lend themselves to mapping more readily than does ordination, especially in areas which have been long disturbed by man.

VI. Zusammenfassung

Die Waldvegetation der Gegend von Kirchleerau (Kt. Aargau, Schweiz) wurde im Feld aufgenommen und nach modifizierten Methoden der "Wisconsin"-Schule analysiert und anschliessend die Ergebnisse mit jenen von vier europäischen Methoden verglichen, nach denen in der gleichen Gegend bereits kartiert worden war (Zusammenstellung von ELLENBERG 1967). Das Untersuchungsgebiet von etwa 400 ha hatte man seinerzeit wegen der standörtlichen Vielfalt gewählt. Für die vorliegenden Untersuchungen wurden 25 Probeflächen aus 7 Assoziationen von FREHNER (1967) ausgesucht, um möglichst viele Vegetationstypen berücksichtigen zu können. In jedem Bestand wurden in vier Kreisflächen von 2 a Grösse und Anzahl der Bäume gemessen, ebenso auf 25 Quadratflächen von 1 m² die Frequenz der Untersuchsarten (Kräuter, Sträucher, Keimlinge) bestimmt und in jedem Bestand verschiedene Standortsfaktoren aufgezeichnet.

Die Unterwuchsarten wurden nach ihrer Frequenz klassiert und daraus ein Ähnlichkeitsindex bestimmt. Unter Anwendung dieses Indexes konnten die Bestände nach einer etwas abgeänderten Ordinationsmethode von BRAY und CURTIS aufgezeichnet werden.

Auf Grund der absoluten und relativen Ähnlichkeit zeigten sich vier Bestandesgruppen, die allerdings etwas überlappen. Diese vier Gruppen wurden für die Wahl der Endpunkte der beiden Ordinationsachsen herangezogen. Angaben und Korrelationen über Vegetation und Standortsfaktoren sind in zweidimensionaler Anordnung besser verständlich als in vieldimensionaler. Da sowohl die Ähnlichkeit wie auch die Unähnlichkeit der Bestandesgruppen für die Anordnung Verwendung fanden, kann auf diese Weise mehr Information geboten werden als bei konventioneller Anordnung nach der Unähnlichkeit.

Die Ergebnisse der Umwelts- und Bestandesanalysen wurden in die Ordination eingetragen, wodurch sich verschiedene Umweltsgradienten ergaben. Davon scheinen Feuchtigkeits- und pH-Gradient des Bodens am wichtigsten zu sein. Die Verteilung der einzelnen Arten zeigt offensichtlich eine gute Korrelation mit bestimmten Standortsfaktoren. Die Ordination erweist sich so als sehr wertvoll zu Erkennung von Korrelationen. Immerhin sind eingehende Untersuchungen notwendig, um abzuklären, wie weit diese Korrelationen gültig sind. Die Baumschicht der Wälder im Untersuchungsgebiet wurde durch die Bewirtschaftungsmassnahmen des Menschen (Anpflanzung, Durchforstung, Nutzung) seit langem beeinflusst. Dadurch haben sich auch die Lichtverhältnisse und die Eigenschaften des Oberbodens (durch Herausschlagen von Bäumen, Nadelholzanbau usw.) und damit auch der Unterwuchs verändert. Die Kombination der Unterwuchsarten dürfte deshalb kaum ganz den natürlichen Verhältnissen entsprechen. Wenn man berücksichtigt, dass die Ordination auf den Unterwuchsarten aufgebaut ist, so ist es aufschlussreich, dass die Standortsfaktoren und die Baumarten sinnvolle Verteilungsmuster zeigen. Keine Baumart und keine wichtige Unterwuchsart haben eine identische Verteilung; es fehlen gut umschriebene Artgruppierungen. Auch die Standortsfaktoren lassen sich nicht zu ähnlich verhaltenden Gruppen zusammenfassen, da sie sich nach verschiedenen Richtungen verändern. Dass jede Art und jeder Standortsfaktor einzeln interpretiert werden muss und keine Gruppierung (und damit auch keine «Assoziation») zu erkennen ist, bedeutet nicht, dass Zusammenhänge überhaupt fehlen. Wenn man die relative Stammgrundfläche (basal area) einer Art im Bestand misst und daraus einen relativen Bedeutungswert (importance value) berechnet (wobei die jeweiligen Gipfelwerte auf einer Achse der Ordination eingetragen werden), zeigt sich z.B. bei den Bäumen in der Ordination ein kontinuierliches Verteilungsmuster. Die Baumgattungen erscheinen in der Reihenfolge: *Pinus*, *Quercus*, *Fagus*, *Picea*, *Abies*, *Fraxinus*, *Acer*, was zur Hauptsache einem Feuchtigkeitsgradienten von trocken über frisch zu feucht entspricht.

Ein Vergleich der Resultate mit jenen der anderen 4 angewandten Methoden ergab sich durch Einordnen der dort erhaltenen Gruppierungen (Assoziationen, Phytozönosen) in die vorliegende Ordination und durch das Eintragen der hier untersuchten Bestände in die Tabellen der anderen, die auf den Standortsgruppierungen aufbauten. Wenn die Vegetationsgruppierungen der anderen Autoren in die Ordination übertragen wurden, erwiesen sich die wichtigsten Gruppen von Saxer (Phytozönosen) am meisten, jene von Aichinger am wenigsten mit den hier erhaltenen Resultaten in Übereinstimmung. Die Gruppierungen von Frehner und von Eberhardt et al. liegen dazwischen. Der grundlegende Unterschied in der Auswertung der Ergebnisse liegt darin, dass die anderen Autoren Artengruppierungen als gegeben annehmen, während die hier vertretenen Methoden hauptsächlich Gradienten aufzeigen, wobei nur lose und sich überschneidende Gruppierungen unterschieden werden können. Danach verhält sich jede Art verschieden und zwischen den Beständen treten kontinuierliche Veränderungen auf. Demgegenüber beruhen die Gruppierungen der anderen Autoren auf der Korrelation zwischen Standortsfaktoren und Artengruppen. Der Unterschied zu den anderen Methoden ist bedingt durch die verschiedene Auffassung: Klassifikation gegenüber Ordination.

Die Kartierungsmöglichkeiten anhand der Ordinationsresultate werden diskutiert. Klassifikationsmethoden sind für Kartierungen im allgemeinen besser geeignet, besonders in Gegenden, die schon lange durch den Menschen beeinflusst sind. Waldkartierungen sollten auf der Grundlage der Bonität der Baumarten an den einzelnen Standorten vorgenommen werden. Da Eberhardt et al. die ausführlichsten Umweltsstudien durchführten und versuchten, waldbauliche und standörtliche Eigenschaften miteinander in Beziehung zu bringen, dürften ihre Karten am nützlichsten sein. Die hier dargelegten Methoden erweisen sich dagegen auf eine andere Art als sehr nützlich. Die Probeflächenaufnahme gibt rasch Auskunft über die quantitative Zusammensetzung von Unterwuchs und Baumschicht. Die Ordinations-Technik deckt objektive Beziehungen zwischen den Beständen auf. Wenn die Arten und Standortsfaktoren in die Ordination eingetragen werden, können Gradienten und Korrelationen innert kurzer Zeit herausgelesen werden. Autökologische und experimentelle Untersuchungen sind daraufhin notwendig, um die Gültigkeit der angenommenen Korrelationen zu überprüfen. Ferner können die Bestände anhand der Ordination ungefähr gruppiert und die wichtigsten damit verknüpften Standortsfaktoren bestimmt werden. Zudem ist es möglich, waldbauliche Beziehungen und Sukzessionen der Bäume innerhalb der Gruppen sowie eingehende Untersuchungen der Standortsfaktoren durchzuführen. Anhand solcher eingehender Untersuchungen können die Gültigkeit der festgestellten Gruppen für die Kartierung geprüft und standortsabhängige Bonitätskartierungen der einzelnen Baumarten erstellt werden.

VII. Acknowledgements

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Table 6. The percent frequency is shown for 102 understory "species" (herbs, shrubs, tree seedlings, bare ground) based on 25 quadrats in each of 25 stands. Various totals and averages are shown at the bottom of the table. Frequency-class units were determined from this table and were the basis of the ordination.

Ferns, graminoids, monocot herbs	Group A									B						C							D			Group of ave. max. freq.[1]
Stand	13	14	10	4	11	15	12	3	9	6	1	21	8	7	2	16	17	24	5	18	19	20	25	23	22	
Pteridium aquilinum		4	4	4	4	8	16	36		4				24												A
Luzula nemorosa	52	12	8	4	20	8	44	44	60	4	12	4			20	4			12		4					A
L. silvatica		4			4	92	8	4							4	4	4				4					A
L. pilosa				4	8		20	4				4		4	4				8	4						A
Athyrium filix-femina								4	16	16	36	8	20	20	8	4	4							8	28	B
Dryopteris filix-mas									4	4	4	4	4			4		4	4					4	4	B
Carex silvatica										12	36	20	28	12	24	20	12	4	8	4			16	16	28	B
Maianthemum bifolium							4														8	16				C
Milium effusum												4		4	4	16	4	4								C
Carex flacca										4					8	4		4			28	8				C
Neottia nidus-avis										4					4	4	4		4	4						C
Cephalanthera damasonium/longifolia															4	4	4		4	4	4	4				C
Platanthera bifolia																4										C
Festuca gigantea																4			4		16	4				C
Carex montana																				8	48	16				C
Melica nutans																					4	4				C
Tamus communis																						8				C
Brachypodium silvaticum																4	4	8					4			C
Carex digitata																4	12	4				4	16			D
Polygonatum multiflorum								4	8	12				4	4		16	8	12	4	4		4	16	16	D
Paris quadrifolia										4	4	4	4	4	4	16	16	4			4	4	4	20	28	D
Dryopteris spinulosa										4	4	4											4	4	4	D
Deschampsia caespitosa																		4		4			4	4	4	D
Allium ursinum																							100	100	44	D
Arum maculatum																							4	28	20	D
Carex pendula																								4	4	D
Dicot herbs																										
Melampyrum pratense	8																									A
Teucrium scorodonia								4																		A
Prenanthes purpurea				4	4	4	8	24	4		16															A
Hieracium murorum					4		20	12	8		4					4	12			4		4	4			A
Galeopsis tetrahit								8		4	4			4												B
Oxalis acetosella				24	8			20	96	100	100	100	100	100	100	52	36	8						44	100	B
Galium odoratum				8	4	20	16	20	4	80	92	88	88	64	100	100	92	92	68	28	76	4	4	8	56	B
Cirsium oleraceum											4															B
Moehringia trinervia														4												B

Dicot herbs (cont.)	Group A									B						C							D			Group of ave. max. freq.
Stand	13	14	10	4	11	15	12	3	9	6	1	21	8	7	2	16	17	24	5	18	19	20	25	23	22	
Lysimachia nemorum										16		12		8	8											B
Veronica montana														8			8									B
Mycelis muralis										4	4					4							4			B
Geranium robertianum										4	28	24	36	52			4						8	8	8	B
Ajuga reptans										8	4		4	8									4			B
Melittis melissophyllum								4								4	4			24	4	68				C
Solidago virga-aurea					4		8	24			8	4			8	4	4		4	20	16	8				C
Viola silvestris							4	8			64	8	12	40	36	68	92	12	12	4	48	16	40	12	16	C
Fragaria vesca										4					4	24		4	8	8	8	40				C
Vicia sepium											8					20	20		4	4	24	4				C
Epilobium montanum																4			4							C
Actaea spicata																	4									C
Lathyrus montanus																	4									C
Aquilegia vulgaris																						8				C
Euphorbia dulcis																						12	4			C
Anemone nemorosa						84	8				80			8			68		40	16	92	60	20	96	80	D
Phyteuma spicatum						4				4	52		4		4		8	4	8		44	4	4	36	8	D
Aegopodium podograria											4												4		36	D
Circaea lutetiana											4	16	12	24	4	4							12	4	60	D
Sanicula europaea										8			4			4	4				8		16			D
Lamium galeobdolon											68						68						36	16	96	D
Geum urbanum																4								4	8	D
Mercurialis perennis																	4					92	88	16	60	D
Primula elatior																		4				4	4	20	4	D
Knautia silvatica																					8		4			D
Angelica silvestris																							4			D
Filipendula ulmaria																							4	4		D
Caltha palustris																							4		4	D
Stachys silvatica																							8	4	24	D
Cardamine pentaphylla																								4		D
Lathraea squamaria																								4		D
Crepis paludosa																								4	4	D
Aruncus silvester																									4	D
Impatiens noli-tangeri																									80	D
Ranunculus ficaria																									20	D
Silene dioeca																									4	D
Total frequencies of herb species	60	20	12	48	60	220	156	224	200	300	640	304	316	392	352	392	512	168	204	140	452	392	432	488	852	ACBD[2]

Shrubs	Group A									B						C							D			Group of ave. max. freq.
Stand	13	14	10	4	11	15	12	3	9	6	1	21	8	7	2	16	17	24	5	18	19	20	25	23	22	
Vaccinium myrtillus	76	76	20	48	56	8	56	76		12		8														A
Sambucus racemosa										8				8												B
Rubus idaeus										12	8	4	4	8			4								12	B
Ilex aquifolium	4				4			4		4			4			4	12	4	8							C
Rubus fruticosus							4	4		16	12	8	4	24	56	52	12	8	44	4	12	16			8	C
Hedera helix					4	32							8	4		80	100	60	20	76	80	96	88	32	44	C
Crataegus monogyna/oxyacantha													4			4	4	8	16	8	24	4	4			C
Daphne mezereum														4		4	4			4	8	24	4			C
Ligustrum vulgare															4	8	4	12	32	4	60	44	4			C
Viburnum opulus													4			8	4	40	28	8	40	24	4	4	8	C
Evonymus europaea																	4		4							C
Rhamnus cathartica																					28					C
Cornus sanguinea																4	4	4	8	4	8	28	4			C
Viburnum lantana																12	4	4	4	4	20	12	4			C
Corylus avellana																	4	8	16		4	16	4			C
Rosa canina																8	4	12	28	4	32	4		4		C
Lonicera xylosteum																12	4	32	20	24	28	8	4	4		C
Sambucus nigra										16	4												4	4	4	D
Berberis vulgaris																						8	4			D
Rubus caesius																						20	16	4		D
Prunus padus																							4	4	4	D
Ribes grossularia																								4		D
Total frequencies of shrub species	80	76	20	48	64	40	60	84	0	68	24	20	28	48	60	196	168	192	228	140	344	304	148	60	80	BADC[2]
Tree seedlings																										
Sorbus aucuparia		4			4		4											4						4		A
Fagus silvatica	84	20	28	52	20	20	40	36	36	56	16	68	84	28	88	44	28	80	88	24	68	36	8	16		B
Fraxinus excelsior				8				28			60	20	80	88	20	60	88	88	44	44	4	60	44	36	60	C
Prunus avium								12		8	8	4		4	36	12	32	20	16	4	12	20	4		4	C
Quercus petraea		4			4	12										12			4	12	20	8	4			C
Acer campestre																4				12	20	12				C
Carpinus betulus																	16	4	12						4	C
Acer pseudoplatanus		4	4	4						8	12	12	4	52			76		8				52	56	52	D
Total number of understory species	5	8	5	10	15	11	15	21	9	29	30	22	21	27	24	43	45	31	34	30	37	40	47	38	39	ABCD[3]
Average number of species per group	A = 11									B = 25.5						C = 37							D = 41			ABCD
Total frequencies of understory species	224	128	64	160	152	292	260	384	236	440	760	428	512	612	556	720	920	556	604	376	920	832	692	660	1052	ABCD
Average total frequency per group	A = 211									B = 551						C = 704							D = 801			ABCD
Total of frequency-class units[4]	10	10	5	12	16	15	18	26	13	34	43	28	30	35	33	53	60	39	41	33	50	51	57	46	55	ABCD
Bare ground (Freq.%, qdrts with no plants)		20	56	12	28		12	4	4																	(BCD)A
Estimated ground cover %[5]	2	1	1	2	1	2	2	2	1	4	5	3	4	4	5	4	4	3	3	2	3	4	5	5	5	ACBD

Table 6, Footnote 1. Total frequency of a group divided by number of stands in a group gives the group of average maximum frequency.
Footnote 2. Order of the groups from low to high average frequency is shown.
Footnote 3. Order of the groups from low to high totals, averages, etc. are shown.
Footnote 4. Frequency values were assigned for each species in each stand as follows: 1, 4-32% freq.; 2, 36-64%; 3, 68-100%. These frequency-class units were the basis of the similarity table (Table 2) and of the ordination (Figures 1-3).
Footnote 5. Estimates were made in the field by the following categories: 1, < 10% cover; 2, 10-25%; 3, 25-50%; 4, 50-75%; 5, > 75%.

Bericht Geobot. Institut ETH, Stiftung Rübel, Zürich, 40 (1970)

Table 9. Basal area (B.A.) in square inches per acre is shown for each species. The smaller fractional number below the B.A. for each species is relative B.A. (which sums to 100.0% for each stand). Relative B.A. is used as a measure of relative importance. For each stand, the most important or dominant tree species, and the second most important species on the basis of relative B.A. is shown (by underlining). Various totals and average sizes are also shown.

	Group A									B							C						D		
Tree species / Stand	13	14	10	4	11	15	12	3	9	6	1	21	8	7	2	16	17	24	5	18	19	20	25	23	22
Abies alba				447	1530		167	80		1645	9645	2020	11575	14480	885	570	13984	425		3350	115		7340	2484	2552
				3.0	8.8		1.0	0.4		8.4	44.9	11.7	39.4	56.9	4.3	25.	70.0	2.0		27.2	0.8		32.4	12.8	10.1
Larix decidua								1055					1700												
								4.7					5.8												
Picea abies			10520	1921	2735	1504	307	6100	3515	8900	5710	1025	3425	3345	12685	486		2470		590		1860	1720		1256
			55.0	12.7	15.7	7.5	1.9	27.4	21.3	45.5	26.6	5.9	11.7	13.1	61.2	21.		11.7		4.8		9.9	7.6		5.0
Pinus silvestris	13250	14275	900	1000	5470	7564	6997	7975					1600			83						11564			
	54.6	62.6	4.7	6.6	31.5	37.9	43.0	35.7					5.5			3.						61.8			
Total relative B.A. (conifers)	54.6	62.6	59.7	22.3	56.0	45.4	45.9	68.2	21.3	53.9	71.5	17.6	62.4	70.0	65.5	50.	70.0	13.7	0.0	32.0	0.8	71.7	40.0	12.8	15.1
Fagus silvatica	5725	2955	7092	9511	7140	9580	8811	3820	13020	9035	6085	14255	10570	5495	7150	1137	4008	12130	12328	7630	14455	5228	1332	1352	584
	23.7	13.0	37.1	62.9	41.1	47.9	54.1	17.2	78.7	46.1	28.5	82.4	36.0	21.7	34.5	50.	20.1	57.2	72.5	62.0	99.2	27.9	5.9	7.0	2.3
Quercus petraea	5265	5050	620	2241	510	1340		2850					475	2100				4760	4692	660			1500		520
	21.7	22.2	3.2	14.8	2.9	6.7		12.8					1.6	8.3				22.6	27.5	5.4			6.6		2.1
Fraxinus excelsior																	1104					60	7580	13388	12720
																	5.5					.4	33.4	69.2	50.5
Acer pseudoplatanus																	888						2560	1796	7204
																	4.4						11.3	9.3	28.6
Carpinus betulus																		185					240	320	
																		.9					1.1	1.7	
Alnus glutinosa																							380		364
																							1.7		1.4
Betula pendula		510						400																	
		2.2						1.8																	
Prunus avium																		1180		80					
																		5.6		0.6					
Total relative B.A. (angiosperms)	45.4	37.4	40.3	77.7	44.0	54.6	54.1	31.8	78.7	46.1	28.5	82.4	37.6	30.0	34.5	50.	30.0	86.3	100.0	68.0	99.2	28.3	60.0	87.2	84.9
Total B.A. per acre	24240	22790	19132	15120	17385	19988	16282	22280	16535	19580	21440	17300	29345	25420	20720	2278	19984	21150	17020	12310	14570	18712	22652	19340	25200
Average size tree (sq. in.)	131	123	106	71	56	77	61	86	107	122	116	94	189	104	99	10	73	103	77	46	66	71	90	83	126
Average size tree (sq. cm)	845	793	684	458	361	497	393	555	690	787	748	606	1219	671	639	64	471	664	497	297	426	458	580	535	813

Tab. I : Classi di presenza delle principali specie caratteristiche, differenziali e compagne delle associazioni seguenti.

1. Asplenieto-Primuletum hirsutae (Lüdi) Braun-Blanquet 1934 (Rilievi: 4 di Bertossi 1957, 1 di Lüdi 1952, 3 di Hofer 1967)
2. Andropogonetum grylli insubricum Koch 1943, variante acidofila
3.-9. Gryllo-Callunetum prov. con tre subassociazioni e sette varianti (successivamente: subass. a Allium senescens, var. a Aster Linosyris, var. a Andropogon contortus, var. tipica; subass. a Melampyrum pratense, var. a Hieracium Pilosella e var. tipica; subass. tipica, var. a Hieracium Pilosella e var. tipica)
10. Calluneto secondo Giacomini 1958 (Brughiera di Gallarate, Italia)
11. Associazione a Sarothamnus scoparius e Calluna vulgaris secondo Malcuit 1928 (Vosgi saonesi)
12. Calluneto-Genistetum secondo Quantin 1935 (Giura meridionale francese)
13. Calluno-Sarothamnetum Malc. 1929 secondo Oberdorfer 1957 (Foresta Nera centro-settentrionale)
14. Calluno-Genistetum typicum Tüxen 1937, var. tipica secondo Heinemann 1956 (Belgio centrale)
15. Calluno-Genistetum typicum Tüxen 1937 (Germania nord-occidentale)
16. Calluno-Sieglingietum secondo Heinemann 1956 (Belgio centrale)
17. Calluno-Antennarietum typicum Tüxen 1937 (Germania nord-occidentale)
18. Cytiso-Antennarietum Preising 1953, subass. a Carex ericetorum (Baviera occidentale)
19. Associazione a Sarothamnus scoparius e Prunella hastifolia secondo Susplugas 1942 (Pirenei orientali)
20. Callunetum secondo Aichinger 1956 (Carinzia)

Unità fitosoc.	Numero d'ordine	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
				Gryllo-Callunetum																	
Oberd. 62	Numero di rilievi	8	5	6	16	5	16	11	12	16	?	7	11	8	29	22	14	9	6	20	10
	B1 Andropogon Gryllus		5	5	4	2	2	4	5	3											
	Thymus Serpyllum coll.	5	5	5	5	2	3	3	3	2	3	3	2							4	1
(g+*q)	Peucedanum Oreoselinum	3	5	3	4	3	3	4	3	2									2	1	2
	Festuca varia	4		5	3	2	1	1	5	3											
(c)	Genista germanica			1	3	1	3	4	1	3	3		2					2	5		3
	Cistus salviifolius			3	3	2	2	4	2	3											
(g+B)	Galium lucidum	4	1	4	3	2	1	2	3	2											
l+(h)	Viola canina				2	2	3	3	3	1	(+)	1	2						1	2	
B+(V)	Dianthus Carthusianorum	2	4	4	3	3	2	1	1	1									1		1
FB	Carex humilis	1		2	3	3	1	2	2	1											
V+(x)	B2 Allium senescens	3		4	2	2				1											
(B+g)	Teucrium Chamaedrys	1	1	1	4			1	1		(+)										
g	Geranium sanguineum	1	2	2	3																
FB	Stachys recta	1		4	2		1	1		1											
FB+(l)	Euphorbia Cyparissias			2	3		1	1	1		(+)								1		1
FB	Andropogon Ischaemum		1	3	2																
TR	Rumex scutatus	1		2	2	1	1			1											
(S+FB)	Artemisia campestris	2		1	2	1					(+)									1	
(S+FB)	Phleum phleoides			1	2	1					(+)										
MA	Plantago lanceolata		3	3	1	2						3								4	1
(S)	Sedum Telephium ssp. maximum	3	3	5	3	4	1		1												1
SS	Sempervivum tectorum	2		4	3	1			1												
	Saxifraga Cotyledon	5		2	2																
AR	Asplenium trichomanes	4		2	2		1		1	1											
SS+(FB)	Sedum album			2	3																
AR+(T)	Sedum dasyphyllum	2		1	1	1			1												
S	Sedum rupestre	2		1	2															2	
V+B	B3 Veronica spicata	1		4	1					1											
FB	Aster Linosyris			3	1																
(FB)	Silene Otites			2	1																
P	Setaria viridis			3			1														
B+(A)	B4 Scabiosa Columbaria		4	1	4	1	1														
B	Bromus erectus		5	1	3	1							1								
	Andropogon contortus				2																
B	Hippocrepis comosa		2		2						(+)										
FB+(l)	Pimpinella saxifraga		3		2		1				(+)								3	1	
	B5 Erica arborea				3	4															
	Galium purpureum		1		2	3															
O	Origanum vulgare	1	1	1	3	1	1													1	
(*b)	Ligustrum vulgare			1	2	1															
*b	Coronilla Emerus				2	1		1													
n	B6 Phyteuma betonicifolium		4		1		3	3	1												
(*R+NC)	Melampyrum pratense				1		3	3		1											4
*QF	Hieracium silvaticum	1			1		3	2		1									2		
FB+(N)	B7 Brachypodium pinnatum		5	1	5	4	4	3			(+)		1								1
(A+h)	Lotus corniculatus		5		2	1	2	2			(+)	2					2		1	1	
	Galium rubrum				3	1	1	1													
	Galium vernum		2		1		2	1		1										2	1
O	Satureja vulgaris		4		2		1	2												4	
NC	B8 Hieracium Pilosella	1	4		1	1	5	1	5		3	1		4			3	4	4		1
l+(h)	Polygala vulgaris		4			1	2		3		(+)									2	
*E	Saponaria Ocymoides				1		2		2												
*R+(d)	S1 Pteridium aquilinum		2	1	2	3	5	5	4	5	1	3	5	3	1		1			4	3
*r	Teucrium Scorodonia			1	2	4	4	5	4	4	(+)	5	5	5			3			4	
NC	Potentilla erecta				2		4	5	3	3	4	5	4	5	+	2	3		1	1	2
NC	Carex pilulifera						3	3	3	1				1	2	2	4	2	1		2
(*r+c)	Frangula Alnus						2	1		5	2	5			1		2				2
(A+NC)	Agrostis tenuis	1	1		1		1	2		1		2	3	5	1	2	3	2	4		3
(MA+NC)	Anthoxanthum odoratum		5	1	1	1	1	1				3	3	3	+		1		1	4	1
(*r+NC)	Veronica officinalis				1		1		1					5			1		4	2	1
NC	S2 Calluna vulgaris		3	4	5	3	5	5	5	5	5	5	5	5	5	5	5	5	5	2	5
(d)	Sarothamnus scoparius			5	3	5	5	5	5	5	5	5	2	5	3		4			5	
(*r+NC)	Betula pendula				1		3	4	5	5	2			3	4	2	2	2	2	1	3
(FB+SS)	Festuca ovina	5	3	2	2	3	3	3	3	1	2	1	4		2	4	5	5	5	4	
NC	Sieglingia decumbens	1	3	1	2		3	3	3	2		3	2	1	1	3	4	5	3		2
(*r+U)	Hieracium umbellatum			1	2	4	2	3	2	2		1			1		5		5	+	2
(h+l+*b)	Juniperus communis			1	3	2	1	3	1	3		1	4	3		2			3		1
(x)	Anthericum Liliago		3	3	2	3	5	3	3	3									1		
*Q	Quercus pubescens		3	1	2	2	3	3	1	2											
T	Silene rupestris	2		3	1	2	2	1	2	2	2									+	1
(*e+c)	Cytisus nigricans	1		1			2	2	2	2	(+)								5		
m+(NC)	Genista tinctoria	1	2	1	1	1	2	1		1	3								5		2
(TG+*Q)	Silene nutans	1	4		1	1	2			1	(+)								1		
*E	Polygala Chamaebuxus						2		1	2									2		2
O+(h)	Viola hirta				1		1	1	1	1											
N	Dianthus Seguieri				1	1		1		1											
m+(A+N)	Succisa pratensis				1		1			1		3								+	
NC	Luzula campestris						2				1	1	1		2		5	4	3	+	
(g)	Cynanchum Vincetoxicum	3	5	4	5	3	4	5	5	5										2	1
(m)	Molinia coerulea		1	1	3	4	5	5	4	5	5		2		4		4				1
	Rubus sp.			4	3	3	4	3	5	4			5	5	1		4			3	
(O+NC)	Solidago Virgaurea			3	2	2	4	5	4	4				2	1		2		2	2	1
(*r+*Q)	Quercus petraea				1		1	1	1	3	3		3		+		1		2	+	
*r	Castanea sativa		2	1	2	1	3	4	3	4	2			1	+		1				
	Agrostis alba			3	2	1	2	2	1	1	2	2			1		1			1	
m+(NC)	Stachys officinalis	1	4	3	3	1	4	3	3	1		2	2						1		1
*P	Crataegus monogyna		1		2	1	2	1	2	1											
D	Asplenium septentrionale	2		3	1	1	1	1	1	2											
FB+(N)	Carex caryophyllea		4	1		2	2	2	1	2	(+)										
m+(h)	Serratula tinctoria				1		1	2	1	2											
(*q+*F)	Sorbus Aria				1	1		1	2	3				1							
FB	Prunella grandiflora		2	1	2		1	2	1												
*QF	Corylus Avellana		3		1	1	2	1	1												
(*c+*l)	Carex umbrosa				1		1	1	2	1											
(*b+*Q)	Amelanchier ovalis					2	1	1	1	1											
*P	Rosa cf. canina	1		2	2		1	1					1							1	
*c	Prunus avium			1	1	1		1	1	2											
(D+*r)	Asplenium Adiantum-nigrum	1	2		2		1		1	1											
	Phyteuma Scheuchzeri	3			1	2	1		1	1											
B+(l)	Helianthemum nummularium		5		2	1	1				(+)										1
*Q	Hypericum montanum		2		1	2	1	1													
MA	Holcus lanatus		2		1	1	1	1				3									
MA	Leontodon hispidus		3		1		1	1									1			2	
MA	Dactylis glomerata		3	1	2	1														2	
(h+g)	Silene Cucubalus		2			1	2													3	1
(h+m+l)	Hypochoeris maculata				1		1	1		1	1										
d	Orobanche Rapum-Genistae						1	1	1	1				3							
(NC+S)	Hypericum perforatum	2		2	1			1	1	1	2	2	1	3			2			3	
(A+m+l)	Hypochoeris radicata	1	4	1	1		1		1		(+)		2		+		3	2		2	
	Rumex Acetosella		3	1	1		1	1	1		2	1		4	2		3	2		3	
S	Jasione montana		4		1	1	1			1	4	1			+		2		1	1	1
(*b+d+c)	Populus tremula				1		1		1	1				2	+		1		1		1
A+(S+h)	Achillea Millefolium				1		1	1		1		2					2	2	1	4	1
(*p+*c)	Quercus Robur										2		2		4	3	3		4		5
(*e)	Pinus silvestris										5				1	3	1		5		4
(*r+NC)	Deschampsia flexuosa						2					2	5	3	5	3	1		4		2
(*VP+*r)	Sorbus aucuparia									1		2		2	2		2		1		2
(*V+d+c)	Vaccinium Myrtillus													3	3		3		1		4
(NC+FB)	Campanula rotundifolia				1							4	3	4	+			3	4	+	1
*r+(NC)	Holcus mollis												4	4	+		2		1	4	
c+(FB)	Genista pilosa											1	4		1	3		1			
N	Nardus stricta						1			1		2	4	1			1				1
N+(S)	Antennaria dioeca															+		4	5		1
l+(n)	Galium harcynicum											3		5			2				
	Agrostis canina											1			1		2				
*R+(d)	Hypericum pulchrum												1	1			1				
l+(h)	Cytisus sagittalis												2						3		4
*l	Luzula luzuloides										2								1		3
*r+N	Hieracium laevigatum								1	1					2				2		
l+(S)	Galium pumilum																		2	5	
	Prunella hastifolia																			4	
h	Ranunculus bulbosus		3																	4	
S	Trifolium campestre		3																	3	
FB	Sanguisorba minor		5	1	1															2	
S+(FB)	Sedum mite		5		1	1															
FB	Trifolium montanum		5																		
(h+N)	Briza media		4		1																1
(O+FB)	Galium verum		3		1							1									
FB	Anthyllis Vulneraria		3																		
FB	Salvia pratensis		3																		
(S+B)	Potentilla verna	2		1							2										
	Anarrhinum bellidifolium										2									1	
(h+g)	Hieracium piloselloides										2										
(P)	Crepis setosa										2										
NC	Cuscuta Epithymum													2		2					
(*v)	Betula pubescens														2		2				
(l+A)	Stellaria graminea											2		1							
l	Centaurea nigra											2		2							
	Carex praecox												2								
(*d+*e)	Carex ericetorum																		4		
*V+(c)	Vaccinium Vitis-idaea																				5

Classi di presenza: (+) = fuori rilievo ; + = 1-5% ; 1 = 6-20% ; 2 = 21-40% ; 3 = 41-60% ; 4 = 61-80% ; 5 = 81-100%

Abbreviazioni usate per indicare l'appartenenza fitosociologica secondo OBERDORFER (1962):

Due lettere maiuscole = Classe ; Una lettera maiuscola = Ordine ; Una lettera minuscola = Alleanza ;
* = Unità fitosociologica di vegetazione arborea ; ( ) = Specie soltanto frequente nella rispettiva unità

*b = Berberidion; *c = Carpinion betuli; *d = Dicrano-Pinion; *e = Erico-Pinion; *E = Erico-Pinetalia; *F = Fagetalia silvaticae; *l = Luzulo-Fagion; *p = Alno-Padion; *P = Prunetalia; *q = Quercion pubescenti-petraeae; *Q = Quercetalia pubescentis; *QF = Querco-Fagetea; *r = Quercion robori-petraeae; *R = Quercetalia robori-petraeae; *v = Vaccinio-Piceion; *V = Vaccinio-Piceetalia; *VP = Vaccinio-Piceetea

A = Arrhenatheretalia; AR = Asplenietea rupestris; B = Brometalia erecti; c = Calluno-Genistion; d = Sarothamnion; D = Androsacetalia vandellii; E = Epilobietalia angustifolii; FB = Festuco-Brometea; g = Geranion sanguinei; h = Mesobromion; l = Nardo-Galion; m = Molinion; MA = Molinio-Arrhenatheretea; n = Eu-Nardion; N = Nardetalia; NC = Nardo-Callunetea; O = Origanetalia; P = Polygono-Chenopodietalia; S = Festuco-Sedetalia; SS = Sedo-Scleranthetea; T = Sedo-Scleranthetalia; TG = Trifolio-Geranietea sanguinei; TR = Thlaspeetea rotundifolii; U = Calluno-Ulicetalia; V = Festucetalia vallesiacae; w = Sambuco-Salicion capreae; x = Xerobromion