Results and Discussion

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

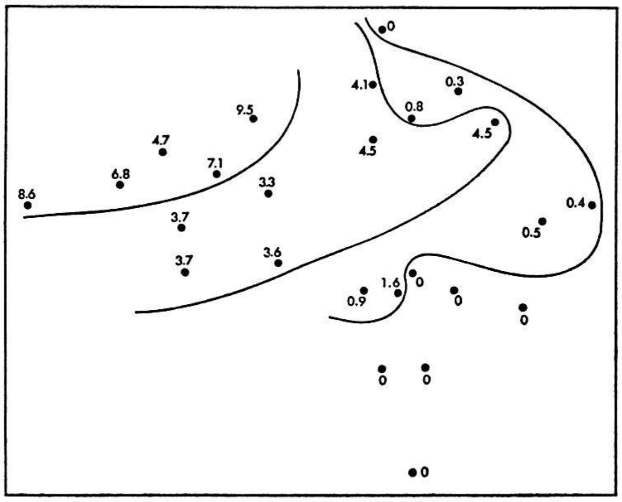

Fig. 9.—Soil analysis showing mg NH_4/100 g soil; analyzed 6 weeks after collection.

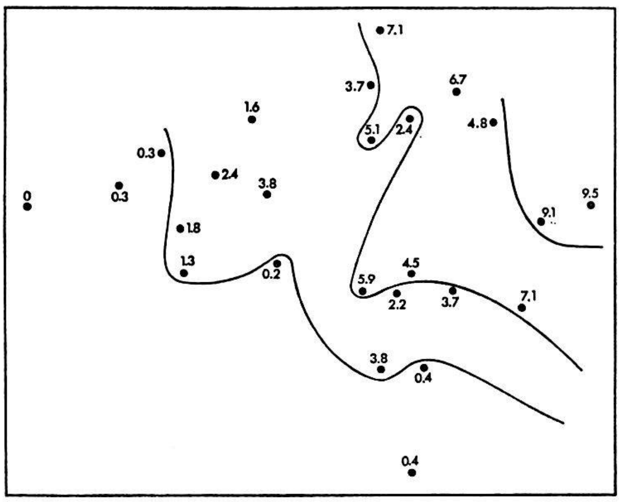

Fig. 10.—Soil analysis showing mg NO_3/100 g soil; analyzed 6 weeks after collection.

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

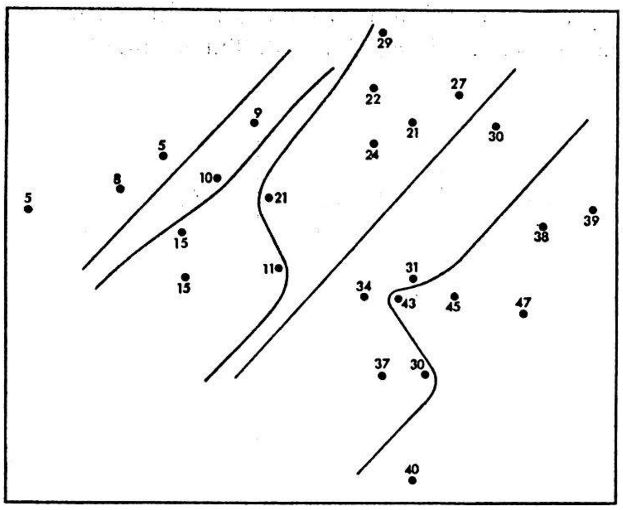

Fig. 11.—Total number of understory species (herbs, shrubs, tree seedlings) per stand. Total understory frequencies, total herb species and frequencies, and estimated herbaceous cover have a similar pattern.

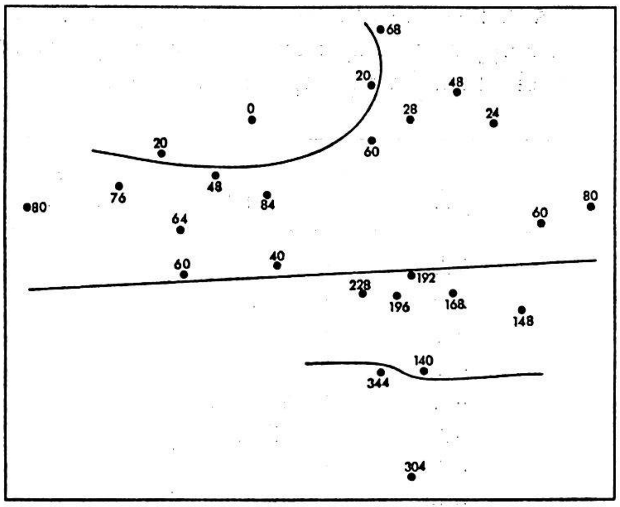

Fig. 12.—Total shrub frequency per stand. Number of shrub species per stand has a similar pattern. The stands above the long horizontal line have 0 to 8 shrub species per stand while those below the line have 10 to 14 species.

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. 19e.)

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.

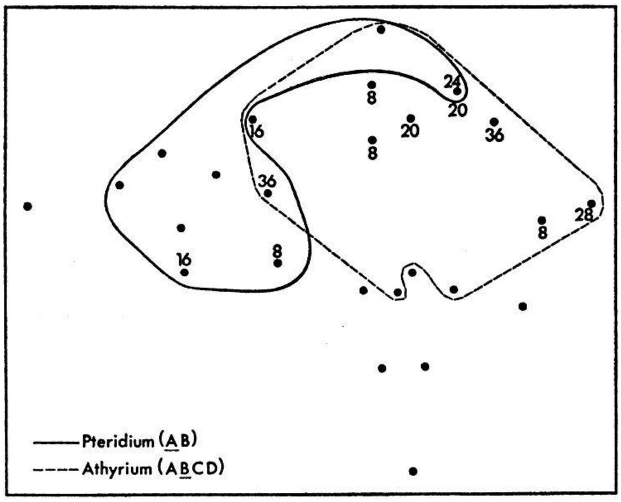

Fig. 13a

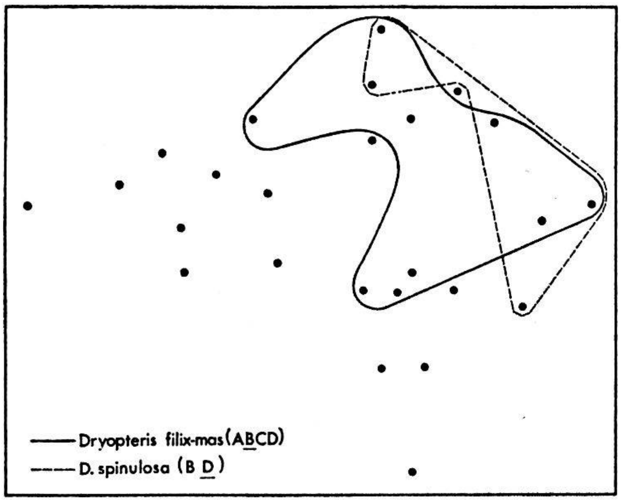

Fig. 13b

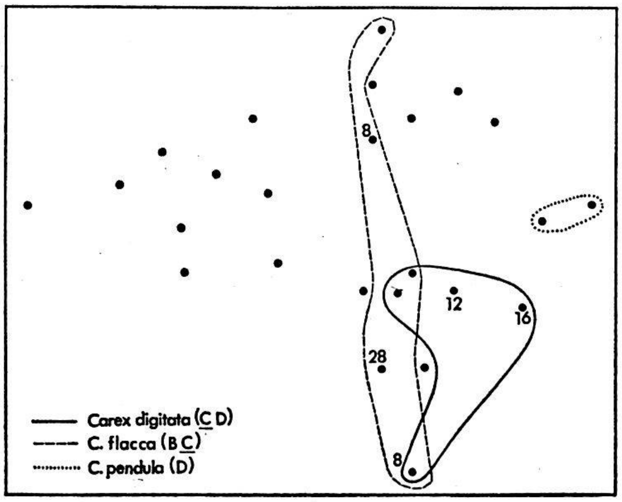

Fig. 14a

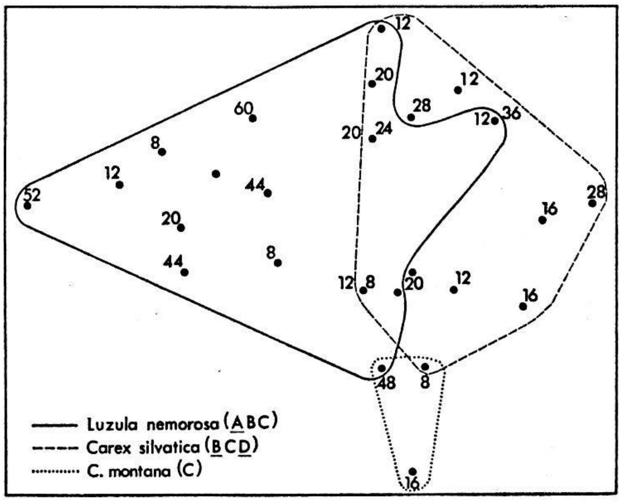

Fig. 14b

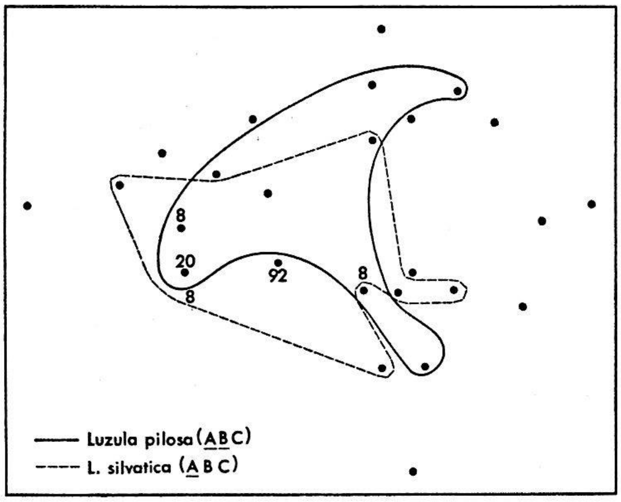

Fig. 14c

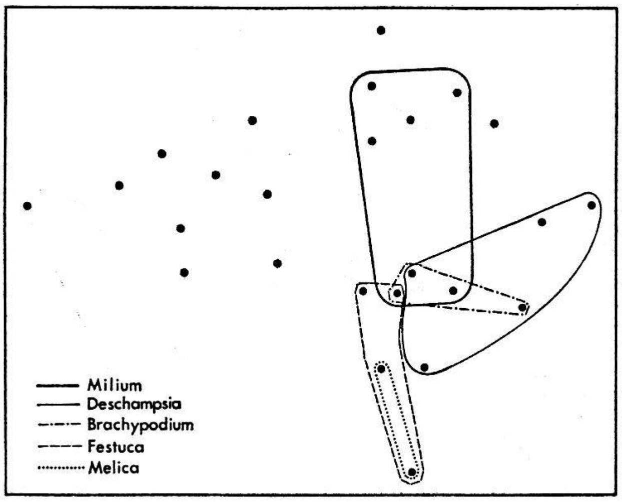

Fig. 14d

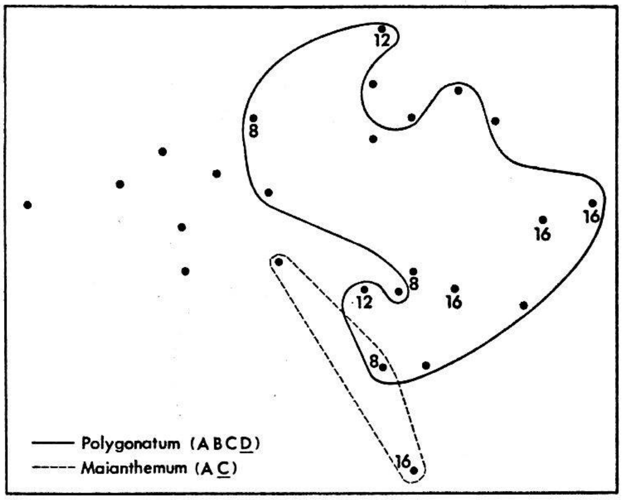

Fig. 15a

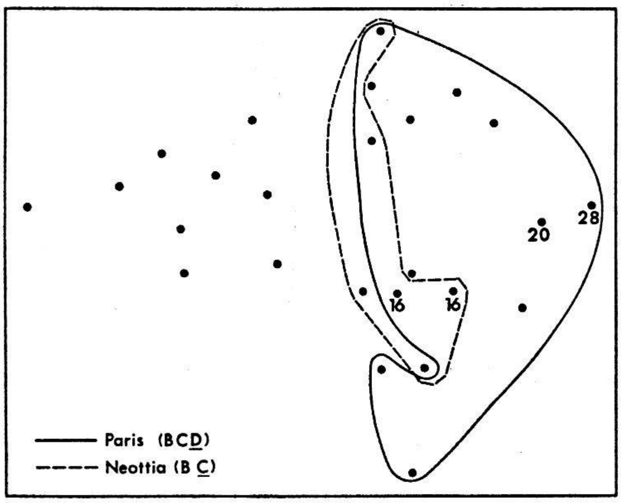

Fig. 15b

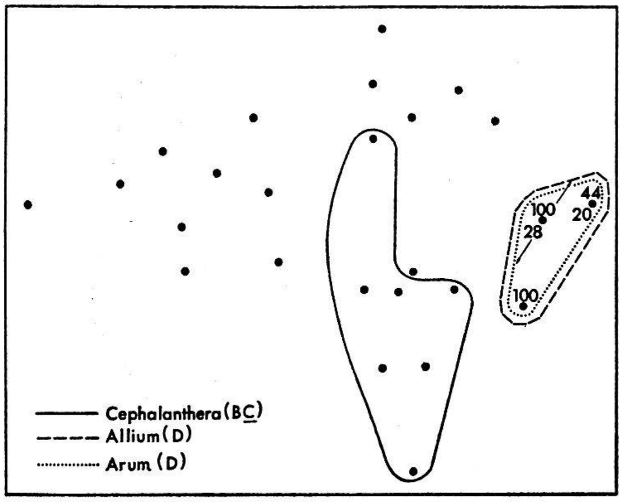

Fig. 15c

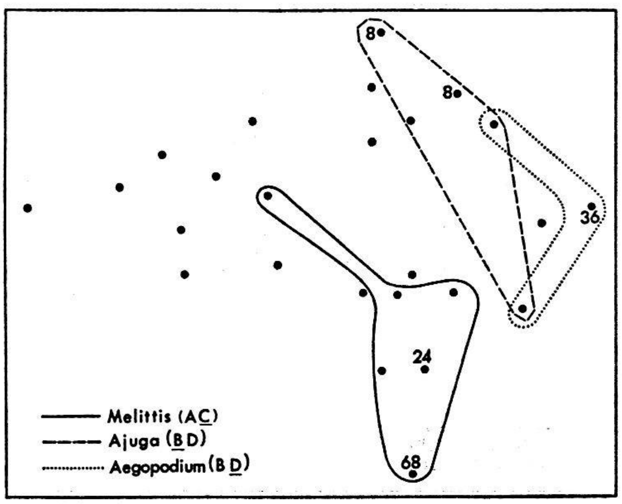

Fig. 16a

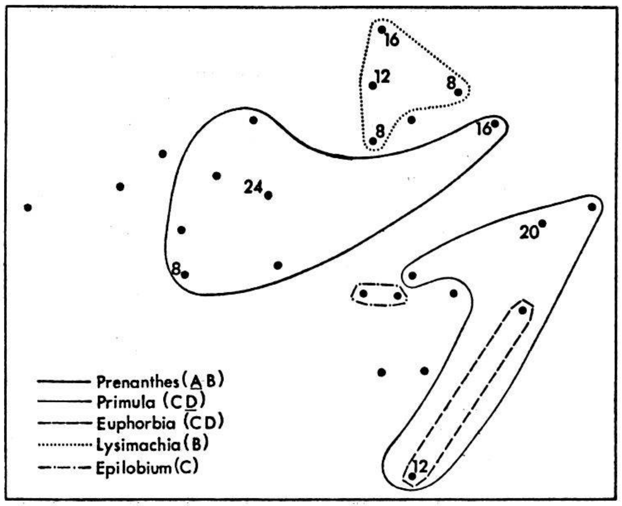

Fig. 16b

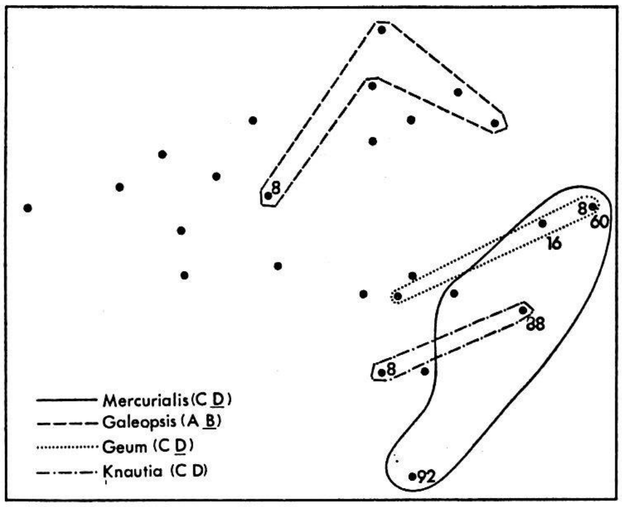

Fig. 16c

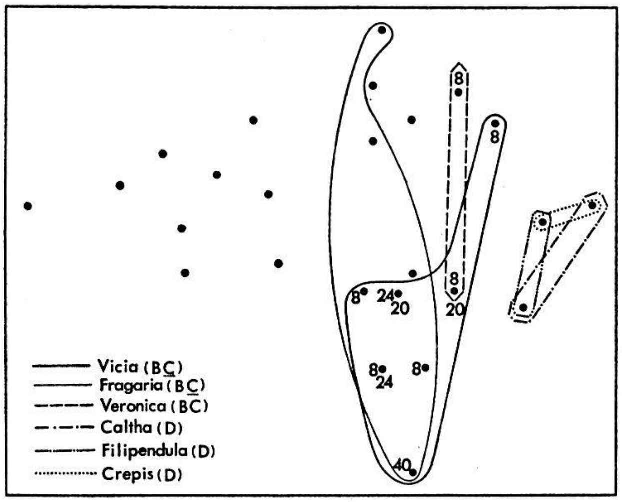

Fig. 16d

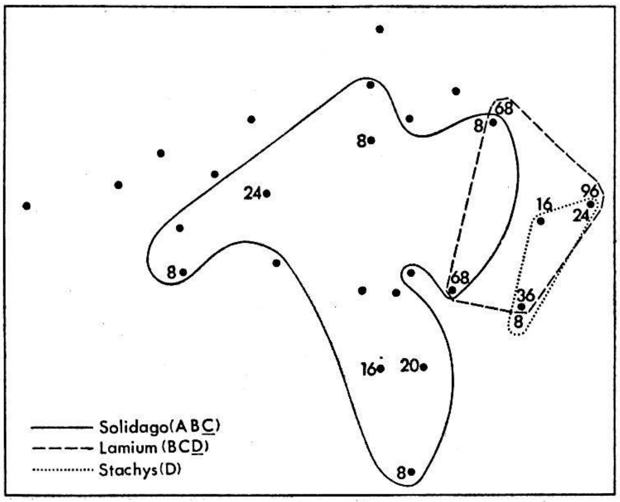

Fig. 16e

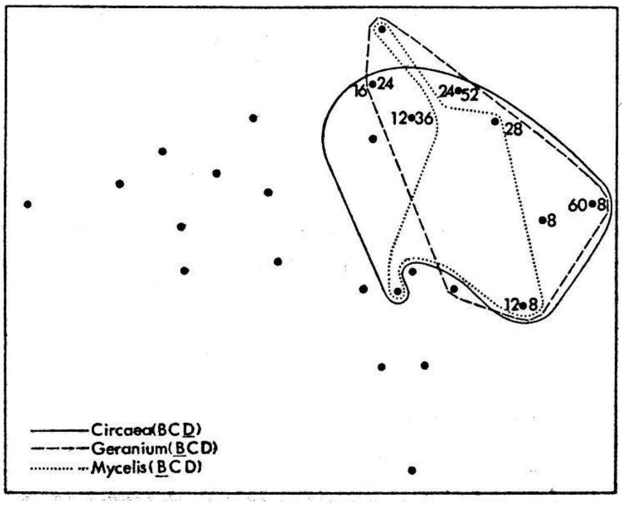

Fig. 16f

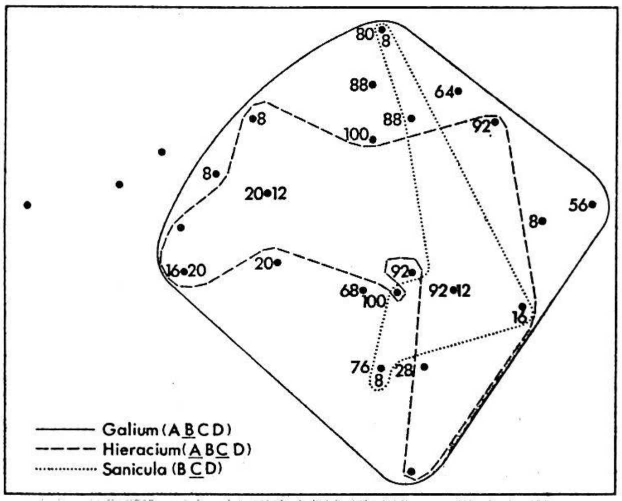

Fig. 16g

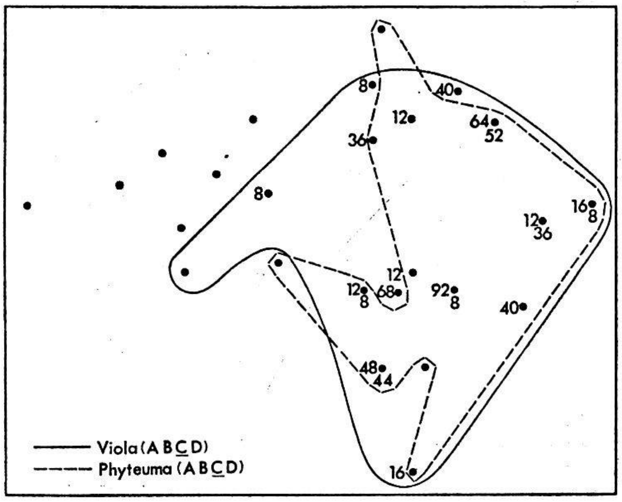

Fig. 16h

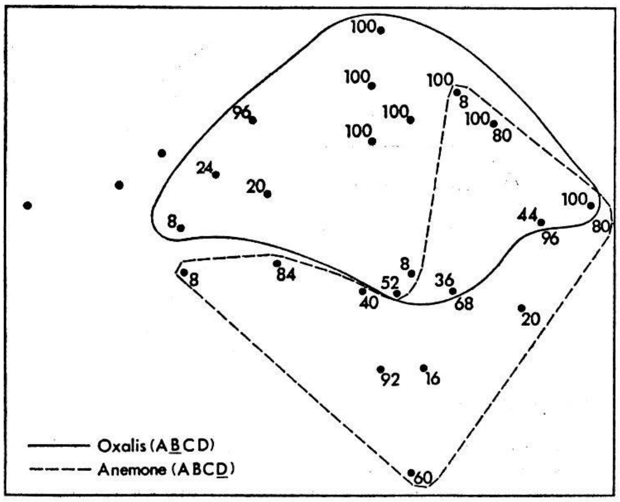

Fig. 16i

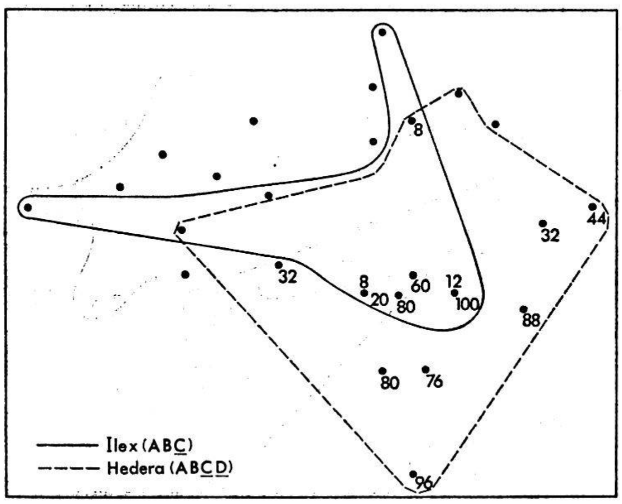

Fig. 17a

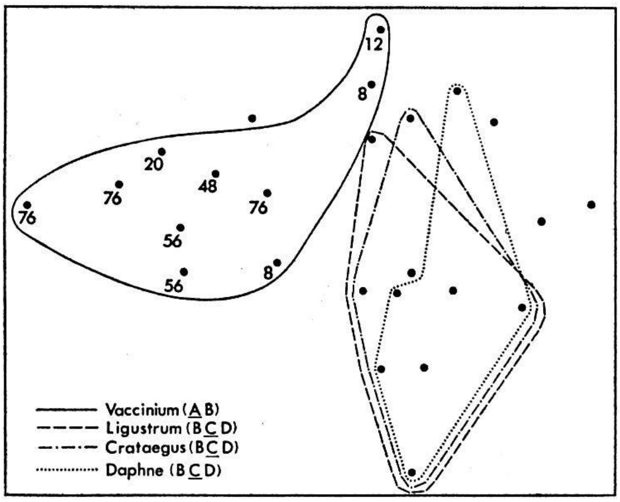

Fig. 17b

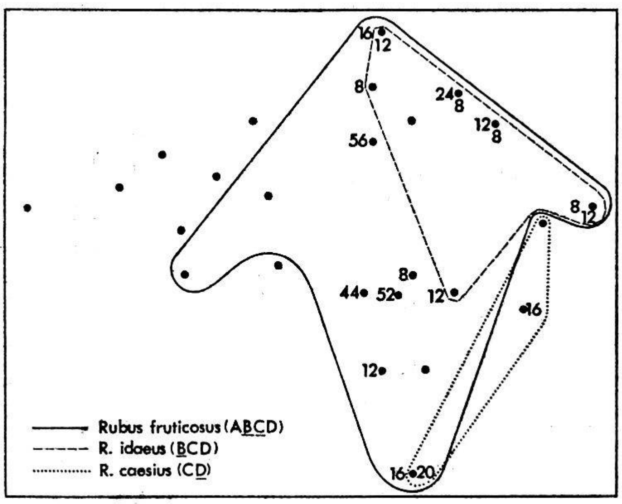

Fig. 17c

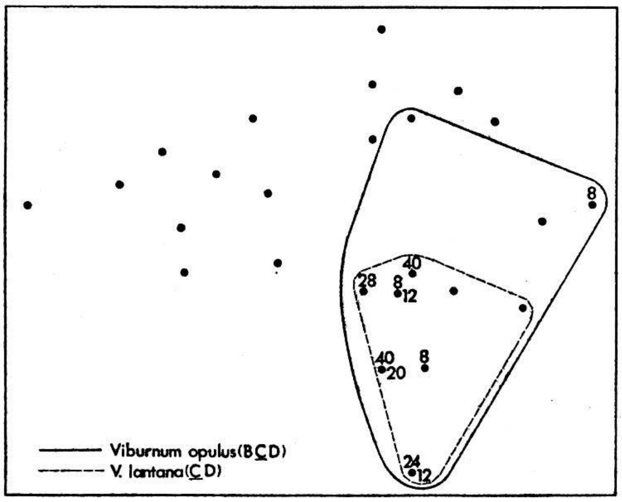

Fig. 17d

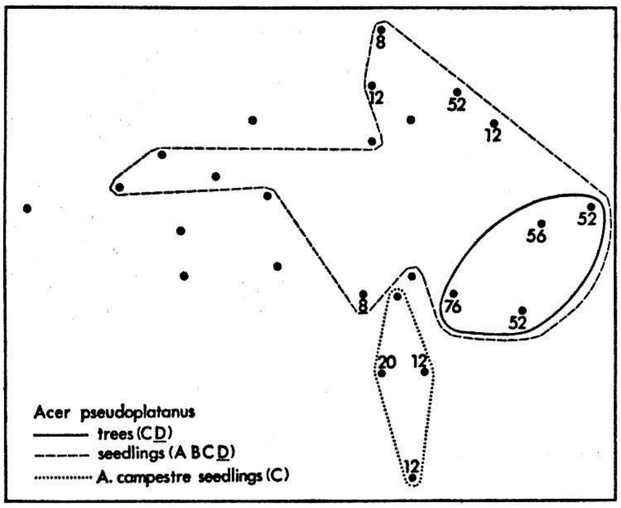

Fig. 18a

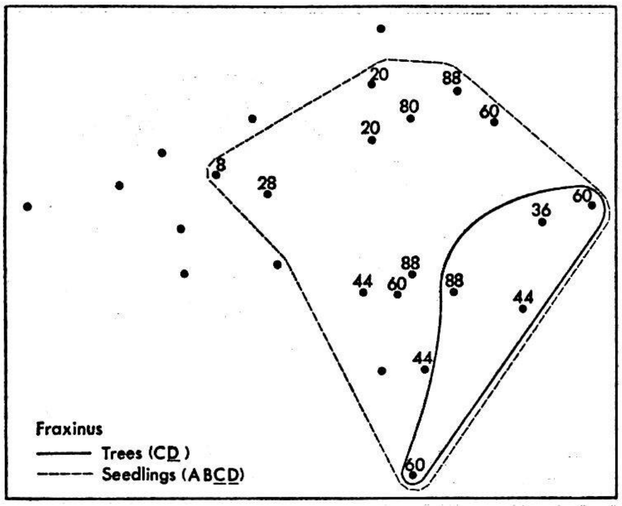

Fig. 18b

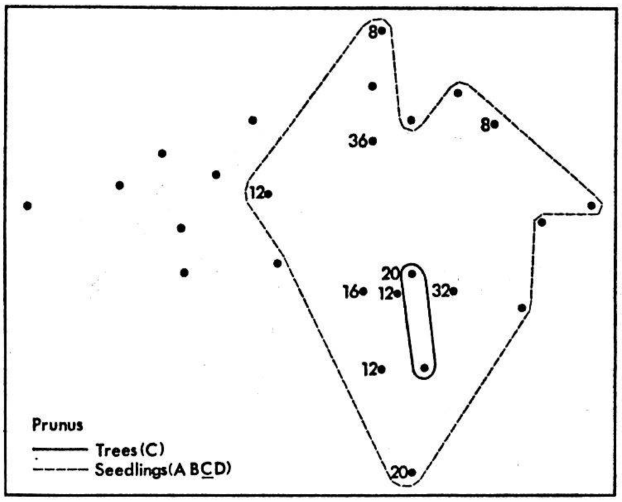

Fig. 18c

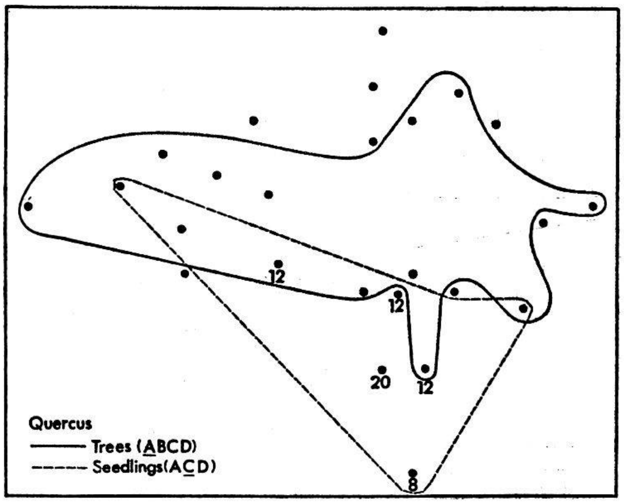

Fig. 18d

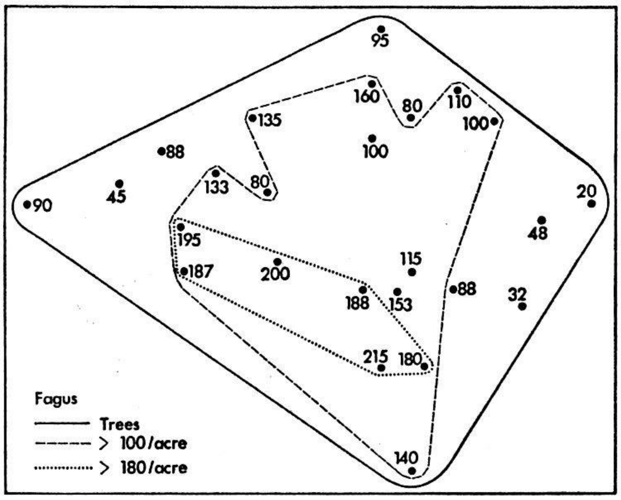

Fig. 18e

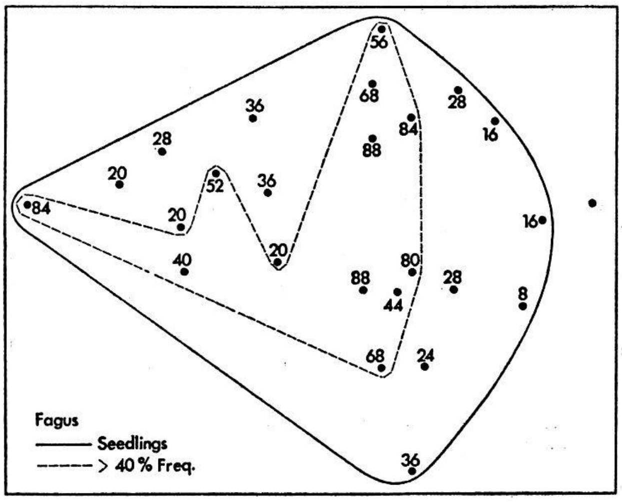

Fig. 18f

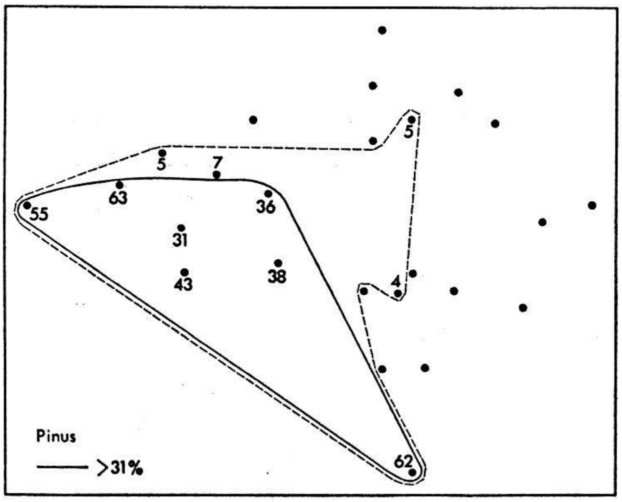

Fig. 19a

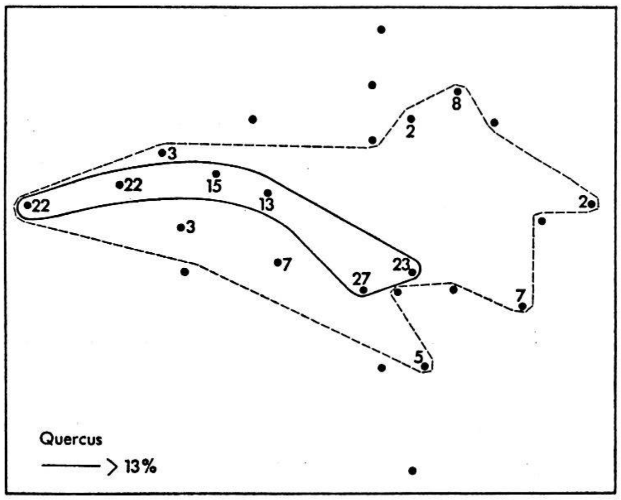

Fig. 19b

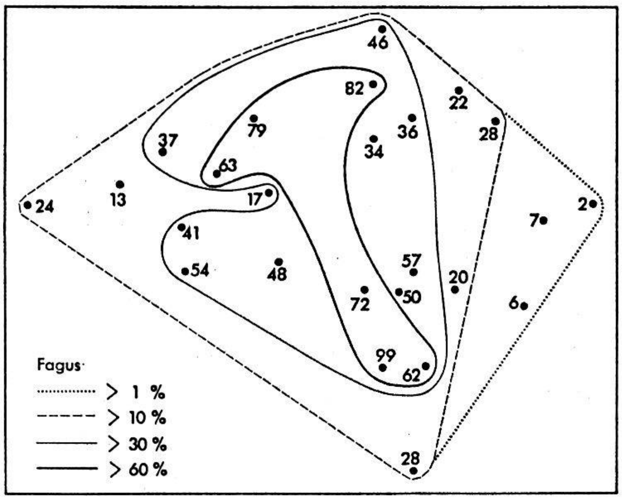

Fig. 19c

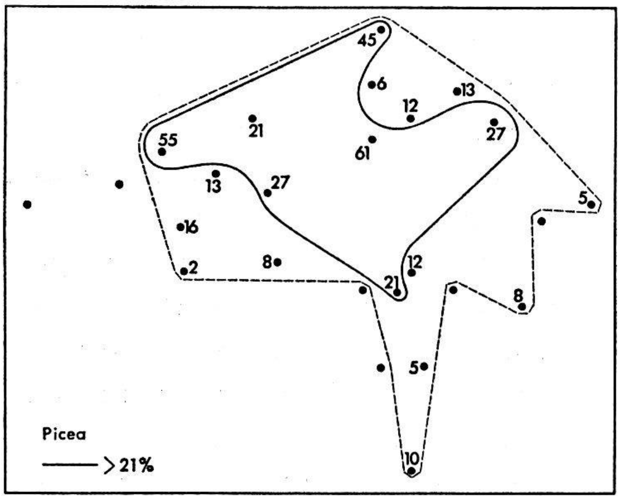

Fig. 19d

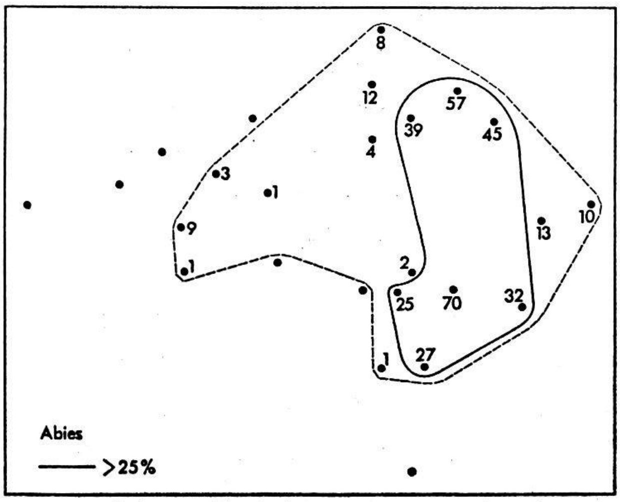

Fig. 19e

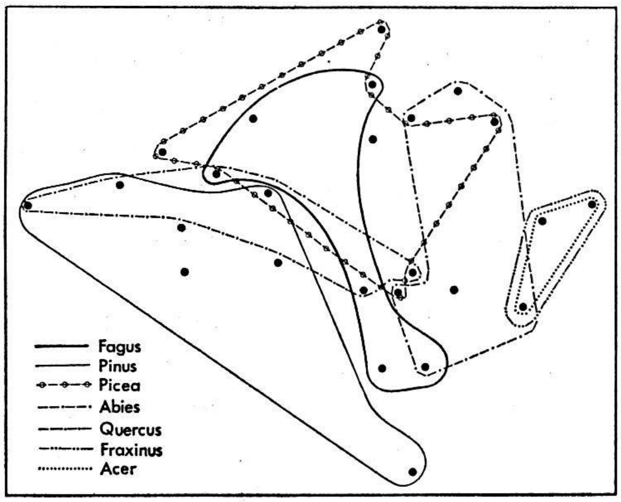

Fig. 19f

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

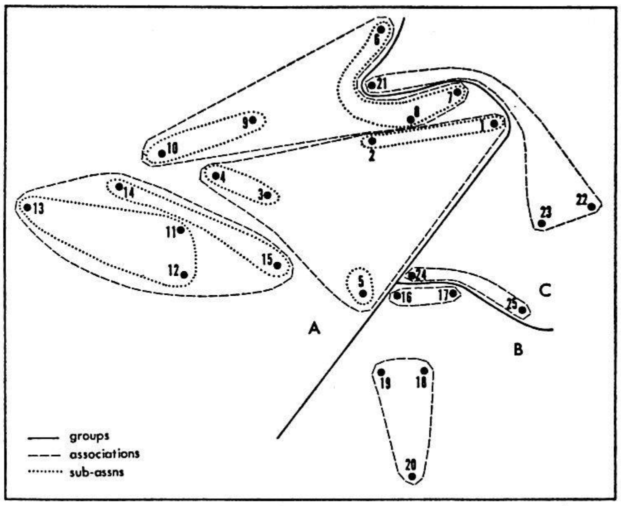

Fig. 20.—FREHNER's communities plotted on my ordination. See Table 10 for names of associations and Table 1 for names of his groups.

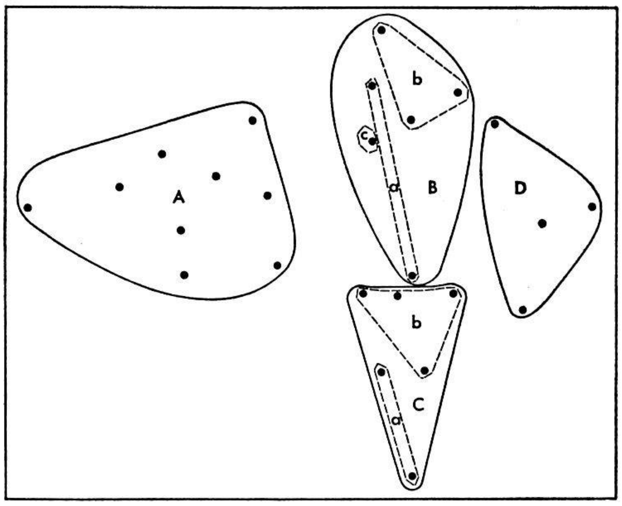

Fig. 21.—SAXER's phytocoenoses plotted on my ordination. See Table 11 for names and descriptions of the phytocoenoses.

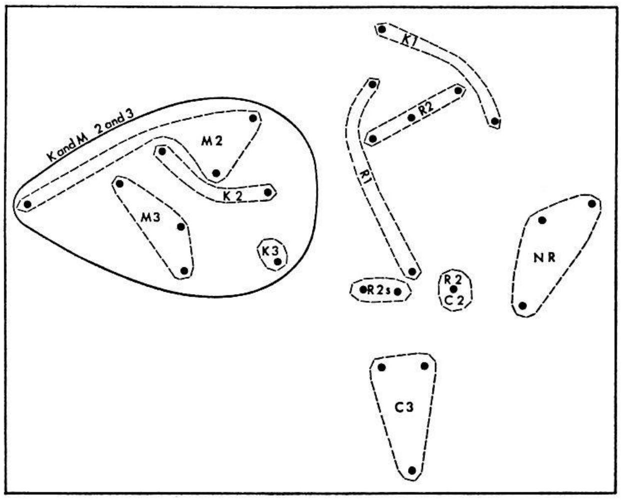

Fig. 22.—EBERHARDT's site-type groups plotted on my ordination. See Table 12 for description of these groups.

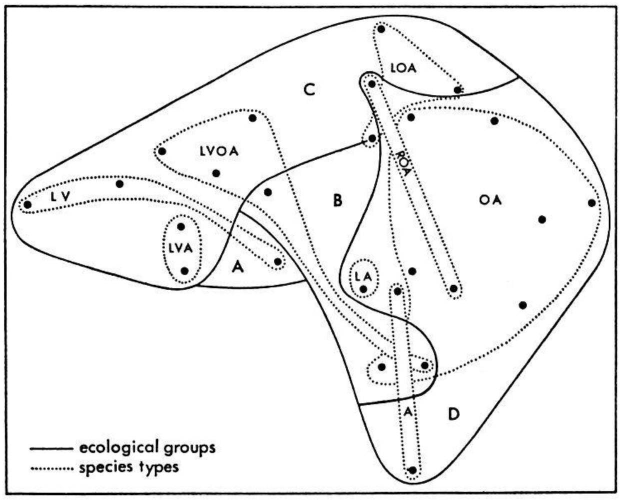

Fig. 23.—AICHINGER's species types and ecological groups plotted on my ordination. See Table 13 for names of these groups.

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 Pruno-Fraxinetum 24, 25
Kalkreich (rich in $CaCO_3$)	Carici-Fagetum 18, 19, 20		Pulmonario-Fagetum 16, 17	

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.