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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.

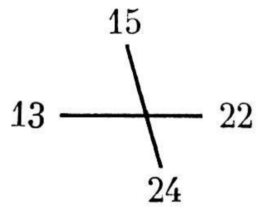
(3) In the right hand column of Table 2 is shown the total of the similarities for each stand when compared with every other stand; for example, stand 13 has a total of 491, stand 14 has a total of 588, etc., through stand 22 with a total of 733. Stand 13 has the least total similarity with every other 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																									
		Group A									B						C							D			Total
	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
Percentage Dissimilarity	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.

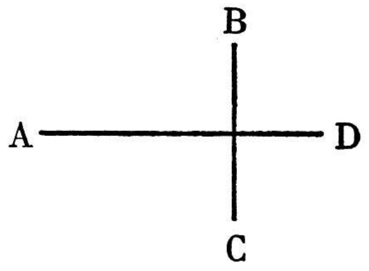
On the other hand, group A has no overlap at the 50% level with the other groups; in fact, not all stands within group A have 50% similarity with each other as is seen in Table 2. However, on the basis of relative similarities, group A may be separated although it is not as good a separation as were 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

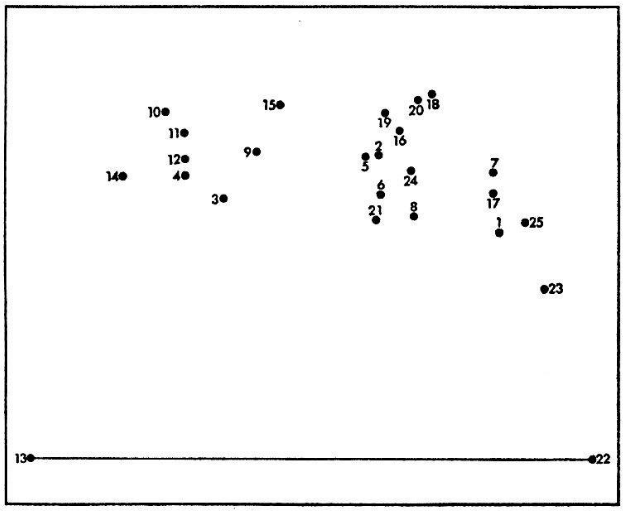


Fig. 1.—First axis dissimilarity ordination based on frequency classes of understory species. The ultimate placement of the stands in the 4 groups is indicated by the position of the stand numbers: A, to left of dot; B, above; C, below; D, right.

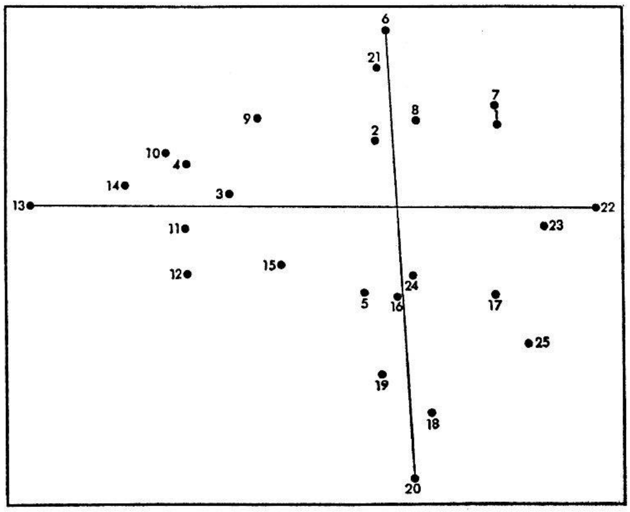


Fig. 2.—First and second axis dissimilarity/similarity ordination with stands projected in relation to the X axis (A13–D22) and Y axis (B6–C20).

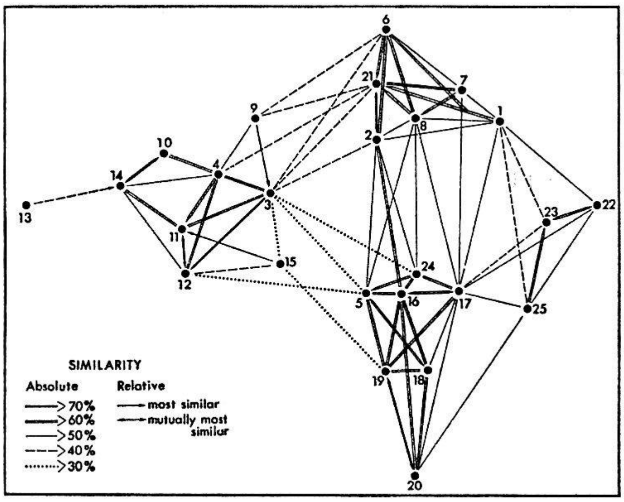


Fig. 3.—The final ordination. It is the same as Fig. 2, but with similarity readjustments of certain stands (A3,4; B7,21; C17,18; D25) to place them more accurately relative to intra- and intergroup similarity relationships. The key shows symbols for the absolute and relative similarity relationships.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

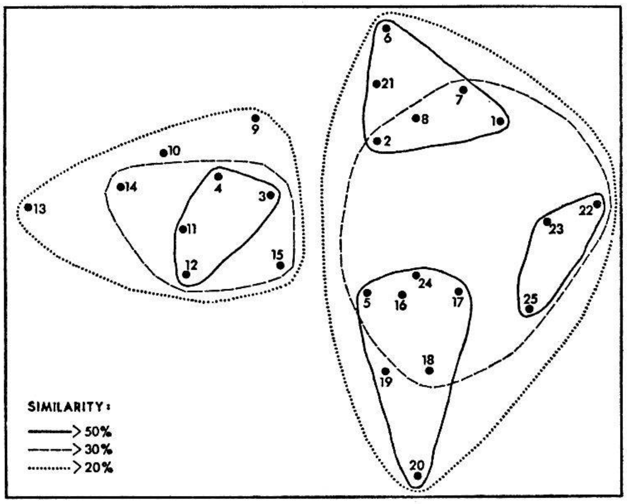


Fig. 4.—Same ordination as Fig. 3. All stands outlined have similarities with each other at the levels shown in the key. However, by excluding certain stands from any group, many other combinations would be possible within and between groups at several levels of similarity.

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.

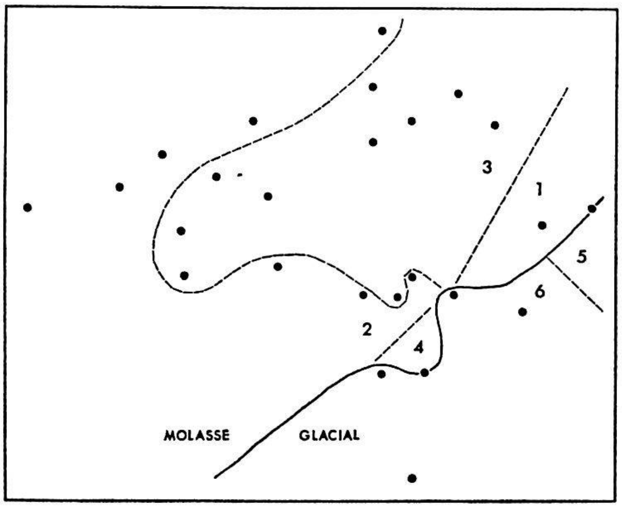


Fig. 5.—Soil parent materials: 1 to 4 are different types and ages of tertiary sandstone; 5 and 6 are glacial deposits. Relative geological age from oldest to youngest: 1. lower marine molasse; 2. upper marine molasse, musselsandstone; 3. upper marine molasse, Wienerstufe; 4. upper sweetwater molasse; 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.

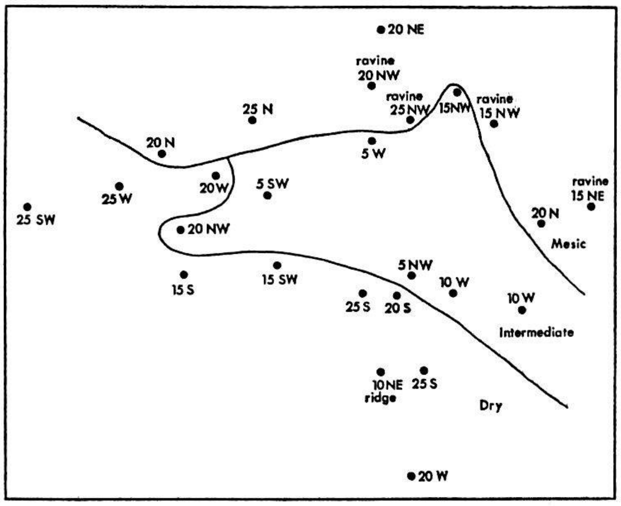


Fig. 6.—Moisture relationships (mesic, intermediate, dry) that would be expected from the topographic situation of the sites. The numbers are slope °, and the letters are direction or aspects (North, South, East, West). Also shown are site influences such as ridge or ravine. These represent potential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

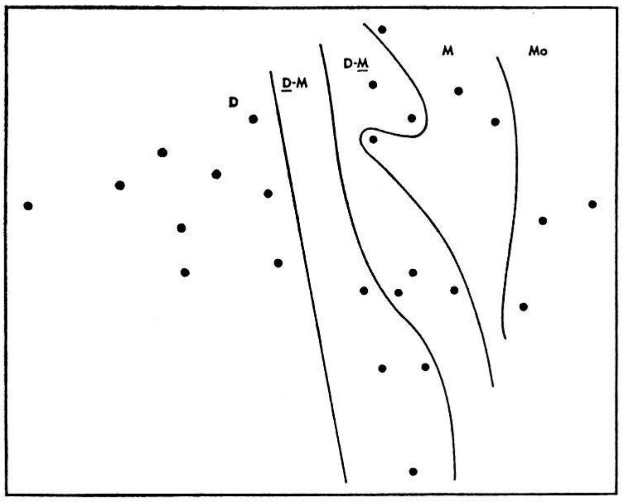


Fig. 7.—Relative soil moisture estimates as they were actually made at the time of sampling: D, dry; D-M, *dry*-mesic; D-M, dry-*mesic*; M, mesic; Mo, moist.

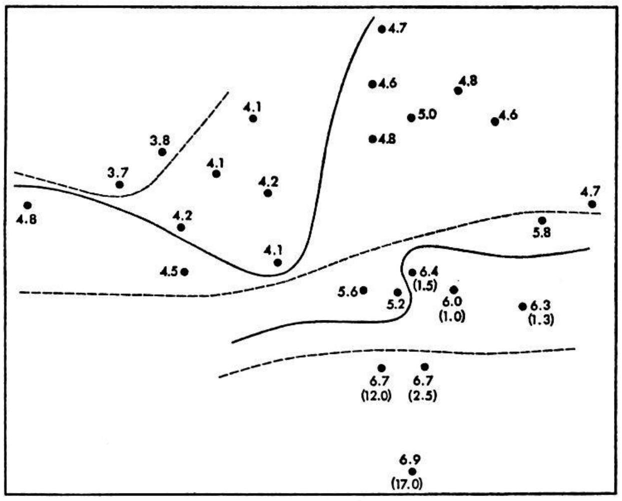


Fig. 8.—Soil pH and percentage $CaCO_3$. Lines are drawn separating 3 categories of pH from low to higher: 3.7–4.2; 4.5–5.8; 6.0–6.9. Further separation is shown by dashed lines. Percentage of $CaCO_3$ is shown in parentheses.