DET KONGELIGE DANSKE VIDENSKABERNES SELSKAB
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A METHOD OF ESTABLISHING GROUPS OF EQUAL AMPLITUDE IN PLANT SOCIOLOGY BASED ON SIMILARITY OF SPECIES CONTENT

AND

ITS APPLICATION TO ANALYSES OF THE VEGETATION ON DANISH COMMONS

BY

THORVALD SØRENSEN

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I KOMMISSION HOS EJNAR MUNKSGAARD
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CONTENTS

		Page
1.	Introduction and Survey of Problems Involved	3
2.	Description of a Method for Classification of Population Analyses in Groups of Equal Amplitude Based on Similarity of Species Content	6
3.	Application of the Method to GRÖNTVED's Population Analyses from Danish Commons	17
4.	Discussion	29
5.	Summary	33
6.	Literature Quoted	34

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1. Introduction and Survey of Problems Involved.

It is well known that certain combinations of species occur more frequently in nature than others, and it is natural that plant sociology has to a material extent focussed its attention on such combinations of species as are more or less favoured by nature itself. These combinations have come to figure as a permanent skeleton in the systematics of plant sociology as the "pure" units. Partly through abstraction and partly through generalisation, generally accepted concepts, sociations, associations, etc., have been arrived at, according to which rank has been assigned to them.

When making analyses of vegetations the requirement is generally made that "pure" populations be selected, i. e. the most frequently occurring combinations of species that are recognizable with more or less certainty. Such a procedure undeniably facilitates arrangement of the material, which, by the way, may be considered an important reason for adopting it. It cannot be denied, however, that the less frequent combinations of species, too, constitute an exponent of the vegetation of a district, and of the reaction of the species mutually and to life conditions. Only one demand may justly be made on the nature of the vegetation in the limited area under investigation, namely that it be homogeneous with as much approximation to that mathematical concept as nature can offer, and as at any rate becomes apparent to the plant sociologist during the analysis itself in the field.

If an attempt is made to procure, with the demand for homogeneity as sole assumption, and as far as is possible, a comprehensive and exhaustive material of population analyses within a certain area, difficulties arise afterwards, during the arrangement of the material. The various types of vegetation often are so insensibly merged as to form a sliding scale.

Danish plant sociologists, who have most often based their work on RAUNKIÆR's method (determination of frequency), (RAUNKIÆR 1909, 1913, 1934), have shown little interest in a definitive arrangement of the material analyzed into groups corresponding to the sociations of the Uppsala School (DU RIEZ 1930) or the associations of the Zurich School (BRAUN-BLANQUET 1928). Even in cases where a division of this nature might have been possible, Danish plant sociologists have been content with placing populations

in a line with the dominating (high frequency) species in a sloping line showing their gliding reaction towards some ecological factor, such as humidity or p_H.

A strictly objective and numerically supported development of this sloping line principle was made recently by TUOMIKOSKI (1942), who arranged the species in correlative sequence. Instead of RAUNKIÆR's frequency percentages he employed degree of coverage as expressed in percentages of the total area, drawing the borderlines between groups where the sloping line displays a greater or lesser degree of discontinuity.

When attempting to classify analyses of vegetations from two geographically separate areas within one system—even when selected "pure" populations are present in both cases—we meet with the same difficulties as when classifying "impure" material from one area only: groups overlap, or we find a continuous, sliding variation. Even with, in some measure, identical floristic content in the two areas, borderlines between the individual species, and so also the borderlines of the units of vegetation, will not conform in the two areas.

These difficulties give rise to two questions: 1) How great is the mutual similarity between populations within a group recognized as a sociation or an association respectively, and 2) how great a similarity to already established groups must a population exhibit to permit it to be classified as belonging to one such group? The physiognomical-ecological method of the Uppsala School teaches nothing about this, nor does the floristic method of the Zurich School, just to mention the best known leading sociological schools. Nor does TUOMIKOSKI take decided ground on the issue, even though his numerical method should provide an indication in this direction.

However, we find a suggestion of the problems outlined above in NORDHAGEN's (1934) outstanding attempt at combining the Uppsala Sociations with Zurich Associations. Where indicative species are partially or totally absent he employs the total floristic similarity between each pair of sociations, placing doubtful sociations where similarity of species is greatest as expressed by JACCARD's coefficient de communauté $\frac{c}{a+b-c}$ (JACCARD 1901 a, 1901 b, 1908), where a and b mean the respective numbers of species in the two sociations (A and B) with a percentage of constancy $\geqq 50$, and c the number of species occurring in both sociations with the aforesaid degree of constancy.

A numerical establishment of difference or similarity between associations already defined according to other points of view has already been made by KULCZYŃSKI (1928) on a basis of total content of species and degree of constancy, the latter expressed in a scale with five steps. The floristic similarity between two associations is expressed here by the Verwandtschaftskoeffizient $V = \frac{\left(\frac{c}{a}+\frac{c}{b}\right)\cdot 100}{2}$. The calculation of V is illustrated most easily by stating KULCZYŃSKI's example (l. c. p. 181):

Species	Ass. A Degree of Constancy	Ass. B Degree of Constancy	Common
N	5	3	3
O	2	4	2
P	1	—	—
Q	2	2	2
R	—	3	—
S	—	1	—
Sum	$a = 10$	$b = 13$	$c = 7$

$$V = \left(\frac{7}{10} + \frac{7}{13}\right) \cdot \frac{100}{2} = 61.92.$$

With V as a basis, associations are classified in floristic groups. KULCZYŃSKI, therefore, does not use V for marking the bounds of associations but applies it to making an estimate of the influence of various independent factors upon the floristic composition of associations: adaphic factors, neighbour effect, the mutual competition of species, succession.

Similar methods have subsequently been employed by RENKONEN (1938) and AGRELL (1941, 1945) in dealing with invertebrate communities. However, RENKONEN does not employ constancy, but the relative percentage of dominance. AGRELL (1941, p. 70 et seq.) employs both dominance numbers (quantitative properties) and constancy numbers (qualitative properties). According to AGRELL the two methods produce essentially consistent results. However, AGRELL's calculation formulae, which are different in principle in the two cases, seem, strictly speaking, hardly to permit of a direct comparison.

In conjunction with the works quoted in the foregoing it should only be pointed out here that AGRELL (1944) has indicated "An objective method for characterization of animal and plant communities", based on the quantitative and qualitative characteristics of communities. However, his method provides no objective basis for marking the bounds between communities, which, on the other hand, evidently was not the author's intention (cfr. the author's remark to that effect l. c. p. 14).

One feature still seems to be common to hitherto known statistical methods of treatment: that a statistical treatment is made of already defined groups of populations arranged according to subjective points of view. Hence these methods provide no satisfactory answer to the questions outlined above concerning the actual amplitude of the units. So long as the basis of an objective appreciation of the interdependence of a number of populations that have been included in one group, does not exist, any comparison between individual groups made on a statistical basis must in reality become deceptive to a certain extent.

2. Description of a Method for Classification of Population Analyses in Groups of Equal Amplitude Based on Similarity of Species Content.

During my endeavours to arrive at a consistent grouping of an extensive material of polulation analyses from North East Greenland I have developed a method of classification which seems to realize satisfactory results. The method is an objective one, it being based solely on the similarity of individual populations as expressed by the community of species.

The method is based on the following fundamental principles:

The plant sociological unit is the population analyzed. The unit employed in the statistic treatment is one species in one population, respectively each species in each population. The similarity between two populations is expressed by the quotient of similarity, $qs = \frac{c}{\left(\frac{a+b}{2}\right)} = \frac{2c}{a+b}$, where a means the number of species within the one population, A; b the number of species within the other population, B; c the number of species common to the two populations.

In principle, of course, it may be discussed[1] whether this formula is preferable to JACCARD-NORDHAGEN's $\frac{c}{a+b-c}$, or to KULCZYŃSKI's $\frac{\frac{c}{a}+\frac{c}{b}}{2}$. The former formula might perhaps seem the more logical one, inasmuch as it expresses the ratio between the species common to the two populations and all (different) species occurring in them. Actually, however, this means that we consider the two populations as one unit, which is confusing seeing that two separate populations were the starting point. When making a graphical representation of $\frac{c}{a+b-c}$ we have another difficulty to cope with, namely that both numerator and denominator change simultaneously—in other words that the number of species for two given populations decreases with increasing community of species. It is not possible to represent this function as a straight line. This difficulty is not involved by the two other formulas. If we assume that $a = b$, which, however, will rarely happen in practice, KULCZYŃSKI's formula and mine will produce identical results. In cases where a and b differ, KULCZYŃSKI's formula will produce the higher values, relatively higher the greater the difference.

It is appropriate at this stage to look a bit more closely at the formula $\frac{c}{\left(\frac{a+b}{2}\right)}$ and its application. For this purpose we shall use a theoretical example (cfr. table 1).

[1] I should like to give my thanks to Professor K. GRAM, Ph. D., for instructive discussion of, and good advice on, the formulae discussed here.

Let us figure to ourselves two populations, A and B, comprising the species N — T. Presence of a species is indicated by 1, absence by —. By substitution in the formula $\frac{2c}{a+b}$ we have $\frac{2 \cdot 4}{5+6} = \frac{8}{11} = 0.73 = qs.$ (1)

Table 1.
Determination of Quotient of Similarity between two individual populations, A and B.

	A	B	
N	1	1	1
O	1	1	1
P	1	1	1
Q	1	1	1
R	—	1	0
S	1	—	0
T	—	1	0
	$a = 5$	$b = 6$	$c = 4$

$$qs = \frac{2c}{a+b} = \frac{2 \cdot 4}{5+6} = \frac{8}{11} = 0.73.$$

The numerator, c, expresses the number of cases in which the individual species occur in both populations. With regard to the denominator it should be noted: Theoretically, each species in population A possesses 1 chance of coinciding with the same species in population B, and likewise each species in B has 1 chance of finding a partner in population A. Thus $a + b$ expresses the sum of the chances of the individual species of coincidence in the two populations separately. Every time 1 chance is made use of by a species in the one population the partner in the other population loses its individual chance, or, in other words, the two partners must share it. This means that $\frac{a+b}{2}$ expresses the sum of all theoretically realizable chances of coincidence of species in the two populations under comparison. Thus $\frac{c}{\left(\frac{a+b}{2}\right)} = \frac{2c}{a+b}$ expresses the number of actually realized coincidences divided by the number of possibilities theoretically inherent in the two populations of coincidence of species. This must be a perfectly valid expression of the degree of similarity of species between two populations. $QS = \frac{2c}{a+b} \cdot 100$, which expression will for practical reasons be used in the following instead of qs, then represents the percentagewise similarity of species between two populations in proportion to the similarity that is theoretically possible according to the number of species present.

When making a comparison between two individual populations the coincidence —or non-coincidence—of the individual species denotes a case of either-or. It will be obvious, however, that the chance of coincidence in a comparison of groups of

populations, each group comprising several individual populations, must be graduated. I have tried to illustrate this by an example (cfr. Table 2).

Table 2.
Determination of Quotient of Similarity between two groups of populations, A, comprising populations No. 1, 2, and 3, and B, comprising populations No. 4 and 5.

Population No. ...	A				B			
	1	2	3		4	5		
N	—	—	—	0	1	1	2	0
O	—	—	—	0	1	1	2	0
P	1	1	—	2	1	1	2	4
Q	1	—	—	1	1	1	2	2
R	1	1	1	3	—	1	1	3
S	1	1	1	3	1	—	1	3
T	—	1	1	2	—	1	1	2
U	1	1	1	3	—	—	0	0
				$a = \frac{14}{3}$			$b = \frac{11}{2}$	$c = \frac{14}{6}$

$$qs = \frac{2c}{a+b} = \frac{2 \cdot {}^{14}/_{6}}{{}^{14}/_{3} + {}^{11}/_{2}} = \frac{2 \cdot 14}{2 \cdot 14 + 3 \cdot 11} = \frac{28}{61} = 0.46.$$

In this example A comprises 3 populations marked 1, 2, 3; B 2 populations marked 4, 5. Compared with the example given above, one species in one population then represents ${}^{1}/_{3}$ in A, in B ${}^{1}/_{2}$. A species occurring in all 3 populations in A and in both populations in B will then have a chance of coincidence of ${}^{3}/_{3} \cdot {}^{2}/_{2} = {}^{6}/_{6}$. For instance, a species occurring in 2 of the A populations and in 1 of the B populations will have a chance of ${}^{2}/_{3} \cdot {}^{1}/_{2} = {}^{2}/_{6}$. In the example, the sum of coincidences realized is ${}^{14}/_{6} = c$. a is the sum of individual species of the individual populations in A divided by the number of populations, expressed in figures ${}^{14}/_{3}$; b, therefore, ${}^{11}/_{2}$. qs for the two groups of populations thus is $\frac{2 \cdot {}^{14}/_{6}}{{}^{14}/_{3} + {}^{11}/_{2}} = \frac{2 \cdot 14}{2 \cdot 14 + 3 \cdot 11} = \frac{28}{61} = 0.46$ (2), or, expressed percentagewise: $QS = 46$. In other words: In practice we have for c: the sum of the products of the numerical presence numbers for all coinciding species; for a: the sum of all individual species in all individual populations in A multiplied with the number of populations in B, and, likewise, for b: the sum of all individual species in all B-populations multiplied with the number of populations in A.

By way of illustration of the procedure of an objective division into groups of a heterogeneous (unclassified) material I shall now go through a simple fictitious example. We imagine the groups A and B in table 2 put into one group, in other words that the 5 populations are unclassified. We calculate the quotients of similarity for the populations in twos: 1,2: $QS = 80$; 1,3: $QS = 67$; 1,4: $QS = 60$; 1,5: $QS = 55$; 2,3: $QS = 89$, and so forth, and arrange the values in a square (cfr. Fig. 1) with the popula-

tion numbers along the sides of the square. The values are noted both horizontally and vertically (the figure is symmetrical around the diagonal). The columns are added together and divided by the number of values (here 4). We have now an expression of the average *QS* of each population with all the others. It follows from this that populations 1 and 2 occupy a central position in the material, while population 4 is the "poorest". The average of the bottom series of figures provides a summary expression of the mutual similarity existing within the material, the *QS* of the entire

1	2	3	4	5	
	80	67	60	55	1
80		89	40	55	2
67	89		22	40	3
60	40	22		73	4
55	55	40	73		5
262	264	218	195	223	
66	66	55	49	56	

Average: 58

Fig. 1.

a	b	c	
	39	74	a = 2, 3
39		58	b = 4, 5
74	58		c = 1
113	97	132	
57	49	66	

Average: 57

Fig. 2.

A	B	
	49	A = a, c
49		B = b

Fig. 3.

material considered as a group. This quantity is in itself of no value if the variation of the individual values in the square is great.

There now remains the task of arranging the material in groups. For this purpose we select a limit value for *QS*, below which no individual value within a group may fall. The position of this limit is chosen arbitrarily and must depend on how high values are at all represented in the material. To illustrate the importance of the position of the limit I shall now go through three cases in which the limit is placed, respectively, at $QS > 70$, $QS > 60$, $QS > 50$.

I. $QS > 70$: In the square (Fig. 1) all values above 70 are marked, and the possible combinations constructed on a basis of the *QS* of each individual population as compared with each of the other populations, the material (the square) being gone through, series after series:

Population 1 can only be combined with population 2 and hence gives the combination 1,2, $QS = 80$.

Population 2 can be combined with populations 1 and 3. From the first series it follows that the combination 1,3 is inapplicable ($QS = 67$, which is below the minimum limit), for which reason 1 is left out. There remains the combination 2,3, $QS = 89$.

Population 3 can only be combined with 2 and likewise gives the combination 2,3.

Population 4 can only be combined with 5 and therefore gives the combination 4,5, $QS = 73$.

Population 5 can only be combined with 4; this combination consequently is identical with the preceding one.

From a restricted material, as illustrated by the example selected, it follows directly which population or populations must be left out in each series. In the case of an extensive material, however, it may become necessary to construct the complete square and then strike out the longitudinal and transversal series containing the inapplicable value or values. After this, the series containing the greatest number of inapplicable values are crossed out in turn. This procedure also facilitates the determination of the average *QS* of the final combination (cfr. Fig. 1).

All combinations possible are arranged in tabular form, identical combinations of course only being put down once, and combinations merely representing a part of another, more comprehensive combination, are left out.

The practical arrangement is as follows:

Populations	1	2	3	4	5	Average *QS* of Combination
Combination I	80	80	..	..	..	80
Combination II	..	89	89	..	..	89
Combination III	..	..	..	73	73	73

As some of the combinations generally overlap, it is necessary to provide a system for making the final grouping. As guide therefor the following requirements must be complied with in sequence as set forth below:

1) The groups must in turn be made as comprehensive as possible, that is, the combination comprising the greatest number of populations must be preferred.

2) There must be as few groups as possible, or, in other words, the greatest possible number of the other combinations must be rendered superfluous through the consecutive establishment of groups. This will mean that out of two or more combinations that are equal with regard to 1), the one is to be preferred that "covers" the greatest number of places in the vertical columns of the table.

3) The groups must in turn become as good as possible. This means that out of two or more combinations that are equal with regard to 1) and 2), the one having the greatest *QS* is to be preferred.

That the requirement of *QS* is placed last is due to the fact that already through establishment of a minimum limit for *QS* provision was made that any possible combination is good enough in itself.

The first group selected in this way must, within the selected interval of similarity, be considered as the central group around which the rest occupy positions as secondary groups. These latter are selected in turn from the remaining material according to the same principles.

Theoretically, of course, a grouping after the principles outlined here may be rendered impossible if two or more combinations must be considered equal, even after trial in the three consecutive instances. In practice, at any rate, this will occur very rarely.

In our simple demonstration the result becomes the following grouping:

Group 2,3 *QS* = 89, hereafter designated as a
Group 4,5 *QS* = 73, hereafter designated as b
Group 1 , hereafter designated as c.

Next the primary groups (a, b, and c) must be arranged in secondary groups. In establishing the secondary groups we demand a certain minimum value of *QS* for each pair of primary groups entered. As arbitrary minimum value we chose $QS > 60$.

A second square is constructed for the primary groups (Fig. 2), similar to the original one for the individual populations, and *QS* for the groups are inserted. These *QS* values are determined as the average value of all *QS* values of the populations of each established group. For instance, the *QS* of a, b = $(40 + 55 + 22 + 40)/4 = 39$.

The establishment of secondary groups is now made on the same principle as that used in the first grouping. Combinations possible in this case are:

Primary groups	a	b	c	Average *QS* of combination
Combination I	74		74	74

The result is:

Group a, c *QS* = 74, hereafter designated as A
Group b hereafter designated as B.

For the sake of completeness the operation is continued with construction of the following square (Fig. 3), which constitutes the last phase. We have obtained a division of the material into two groups, the similarity of which is expressed through the quotient of similarity *QS* = 49.

II. $QS > 60$. Combinations possible in this case are (cfr. Fig. 1):

Populations	1	2	3	4	5	Average *QS* of combination
Combination I	74	85	78	..	..	79
Combination II	..	..	..	73	73	73

which results directly in group 1,2,3 $QS = 79$, hereafter designated as a
group 4,5 $QS = 73$, hereafter designated as b.

The final result has already been reached here as illustrated in figures 4 and 5.

QS for a,b is found to be 48.

III. $QS > 50$. Combinations possible are the following:

Populations	1	2	3	4	5	Average QS of Combination
Combination I	74	85	78	..	..	79
Combination II	58	..	..	67	64	63
Combination III.....	68	68	..	..	55	64

According to the rules set forth above, combination III must be considered a central group, since it "covers" 7 places, while neither of the two other ones "covers" more than 6, and we get this result:

Group 1,2,5 $QS = 64$, hereafter designated as a
Group 3 hereafter designated as b
Group 4 hereafter designated as c.

After this, the establishment of groups of the second order is made with regard to the minimum limit of $QS > 40$.

Combinations possible for secondary groups are:

Primary Groups	a	b	c	Average QS of Combination
Combination I	65	65	..	65
Combination II ...	58	..	58	58

which gives the groups of the third order:

Group a,b $QS = 65$, hereafter designated as A
Group c hereafter designated as B.

Here, the QS of A,B is 35.

The gradual comprehension into groups of the material on hand in the three cases is presented in schematic form in figures 4 and 5. With regard to the linear sequence of the groups and the populations respectively it should be pointed out that it has been based on the mutual QS of the groups and the populations respectively. For instance, in case *I* it will be seen (cfr. Fig. 2) that c must be placed in the middle inasmuch as c displays a greater similarity to a and b than the mutual similarity of a and b, and, similarly, for the populations: (cfr. Fig. 1) 1 displays a greater similarity to 2

and 4 than, respectively, to 3 and 5. Hence the linear sequence must become 3, 2, 1, 4, 5.

The two cases first treated, *I*, minimum limit $QS > 70$, and, *II*, minimum limit $QS > 60$, produce an identical grouping already at the limit of $QS > 60$, *I*, however, producing a finer division at the "top" end. *III*, on the other hand, produces

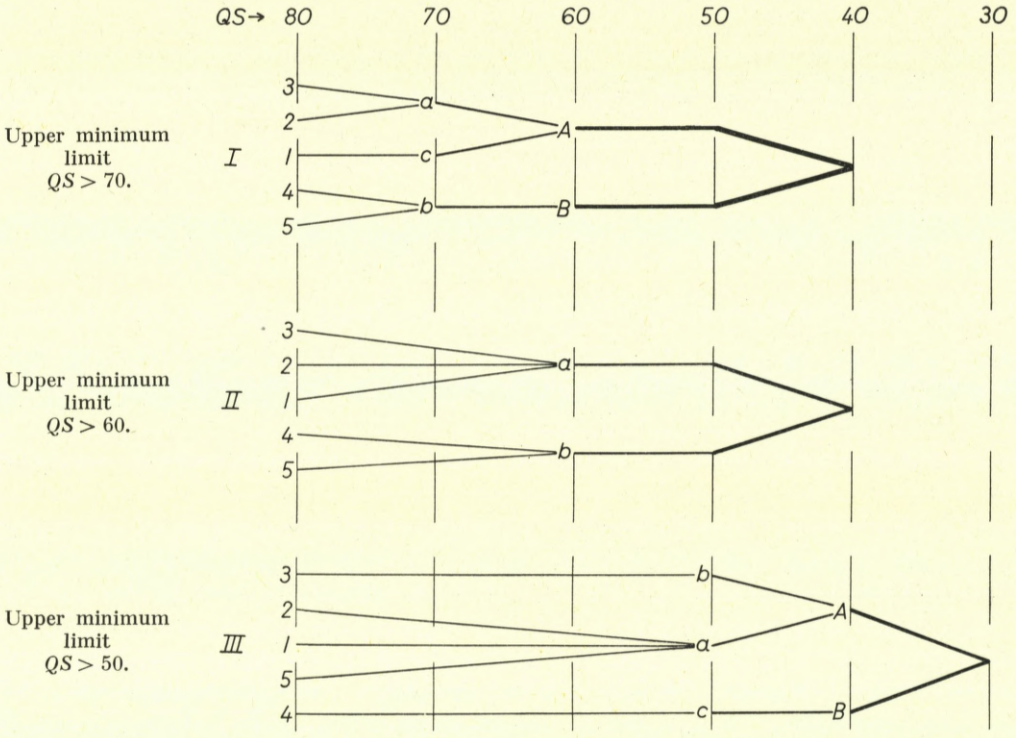


Fig. 4. Schematic representation of grouping at three different upper minimum limits. Only stepwise limits are given.

a rather meaningless grouping, which, at any rate, follows directly from Fig. 5. Now, a glance at Table 2 will at once show that *I* and *II* will give the most natural grouping, and from the combinations possible in *III* it will likevise be seen that combination I would have been preferable. This might be interpreted to mean that the principles applied to the grouping described on p. 10 are wrong. This is not the case, however. The poor result in *III* is due to the fact that the distance between two consecutive groupings was not made sufficiently small (that combination III was in reality not good enough). As a matter of fact, in this case we covered the interval between $QS = 89$ and $QS = 50$ at one stretch. The consequence is that the result obtained in this case was no better than that which would have been obtained by an immediate isolation, of

population 4 as being the poorest, as is apparent from Fig. 1. In fact, in *III* we have placed population 4 against all the other populations as a separate unit.

A strictly schematic use of the method on the principles outlined above can be made only by selecting not too great distances between the consecutive groupings.

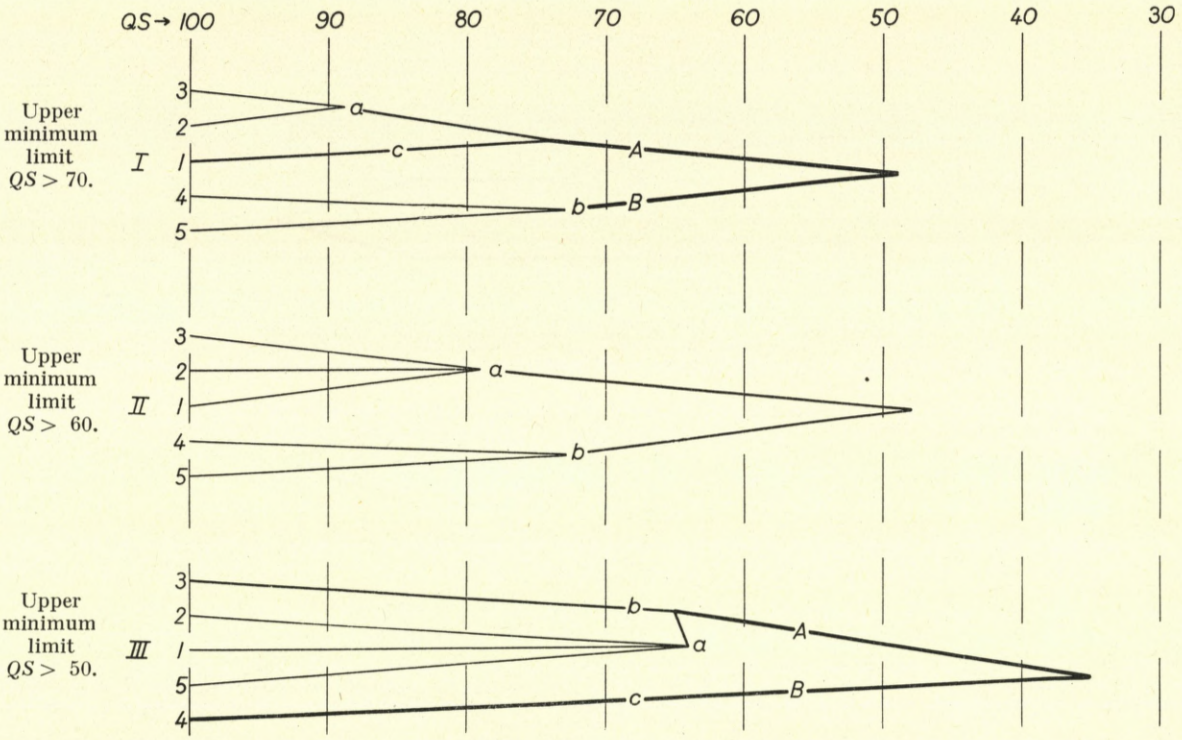


Fig. 5. Schematic representation of grouping at three different upper minimum limits. On the *QS* scale, exact expression of the degree of connexion (average *QS*) within the individual groups is illustrated through the points of confluence of the units.

The limits in the case described were chosen arbitrarily with intervals of 10 as expressed in terms of *QS*. The smaller intervals one selects the better is the guarantee of uniformity within the groups established, and the better is the guarantee that the final seriate arrangement of populations and groups (see Fig. 5) becomes absolutely unassailable. The width of the intervals must be left to individual judgment, as is depends on the use it is desired to make of the result, and on the amount of work that can be expended on the arrangement of the material.

In certain cases, of course, a consideration of the combinations possible will be sufficient to provide an indication as to where it is reasonable to place the limits. If an extensive material is on hand, however, it will often be possible to make such a

variety of combinations that the surveyableness is lost, which absolutely necessitates a procedure based on definite principles. The concrete material submitted in the following section will serve as a demonstration that a treatment made in strict accordance with the rules given can lead to a useful result. I wish to point out, moreover, that after training in the use of the method, an ordinary office staff will be able to make the grouping and the seriate arrangement of the groups quite mechanically from the first phase to the last and even to the least details.

However, in the case of an extensive material the calculation of *QS* for all pairs of populations will be a time-consuming task. For n populations, the number of individual values of *QS* becomes $n \cdot (n-1)/2$. In practice, therefore, it may be a good plan first to arrange the material roughly into preliminary groups and then to check the mutual interdependence within each individual group. This can be done in two ways: 1) The groups are treated according to (1) (see p. 7), that is, as in the example described above (Fig. 1). The primary groups must be made approximately equally "good"; in other words: they must respect the same minimum limit. 2) The second procedure assumes that the rough grouping of the material was made with relative care, and that we desist in advance from a strict compliance with the requirement of a minimum limit for the individual values within the square (cfr. e. g. Fig. 1). It is then possible to avoid the inconvenience of calculating each *QS* and so reduce the task to calculating, within the individual groups, the *QS* of each population against the sum of the others according to (2) (see p. 8). This reduces the number of separate calculations from $n \cdot (n-1)/2$ to n. A practical arrangement for calculating these *QS* values is shown in Table 3 for the same material as that dealt with in the foregoing, from which it follows that the *QS* values of the individual population against the sum of the others practically do not differ from the mean values found by the square method (cfr. the bottom series of figures in Fig. 1). The poorest populations of the group will then produce the lowest *QS* values and may be removed or transferred to another group. The width of variation in the *QS* values thus found reflects the variation in the material. When establishing co-ordinated groups by this method it is necessary to observe that the variation within each group be slight, also that the groups be approximately at the same *QS* level. The observance of any definite minimum value is of minor interest in this case.

A drawback of this method is that after removal of the "poor" populations one has no longer any concise expression of the similarity within the group, whereas the square method very easily provides an expression of the uniformity of the improved group after rejection of the inapplicable series in the square. The method is less exclusive than the one first described but may be useful for establishing the "quality" of groups arranged discretionally.

An extensive raw material of population analyses will as a rule be so heterogeneous that it does not pay to calculate each *QS* of all the populations. Hence the calculation of *QS* for the various pairs of groups of the first order must be made direct, which is

Table 3.

Table for determination of the Quotient of Similarity between the individual populations in a discretionarily composed group (Average designated the *QS* of the group) on comparison of each population with the sum of the others.

Population No.	1	2	3	4	5		1	2	3	4	5
N	—	—	—	1	1	2	—	—	—	2	2
O	—	—	—	1	1	2	—	—	—	2	2
P	1	1	—	1	1	4	4	4	—	4	4
Q	1	—	—	1	1	3	3	—	—	3	3
R	1	1	1	—	1	4	4	4	4	—	4
S	1	1	1	1	—	4	4	4	4	4	—
T	—	1	1	—	1	3	—	3	3	—	3
U	1	1	1	—	—	3	3	3	3	—	—
	5	5	4	5	6	25	18	18	14	15	18

Example: Population No. 1 (A) against Populations No. 2—5 (B). (Cfr. Table 2, p. 8).

$$
\begin{aligned}
c &= 1 \cdot (4 - 1)/4 \\
&+ 1 \cdot (3 - 1)/4 \\
&+ 1 \cdot (4 - 1)/4 \\
&+ 1 \cdot (4 - 1)/4 \\
&+ 1 \cdot (3 - 1)/4
\end{aligned}
$$

$$c = 1 \cdot (18 - 5)/4 = \frac{13}{4}, \qquad a = \frac{5}{1}, \qquad b = \frac{25 - 5}{4} = \frac{20}{4}.$$

$$qs = \frac{2 \cdot c}{a + b} = \frac{2 \cdot {}^{13}/_{4}}{{}^{5}/_{1} + {}^{20}/_{4}} = \frac{2 \cdot 13}{20 + 20} = \frac{26}{40} = 0.65; \quad QS = 65.$$

QS 1 against 2, 3, 4, 5: 65
QS 2 against 1, 3, 4, 5: 65
QS 3 against 1, 2, 4, 5: 54
QS 4 against 1, 2, 3, 5: 50
QS 5 against 1, 2, 3, 4: 56

Average: 58

From the example the following general mode of calculation is derived:

c denotes the presence sum of the entire group for species present in the individual population (A)[1] less the presence sum of the individual population.

a denotes the presence sum of the individual population multiplied by the number of populations of the entire group less 1 (i. e. number of B populations).

b denotes the presence sum of the entire group less the presence sum of the individual population.

done according to (2). The groups are arranged in random sequence in only one table with the number of populations noted for each group. The presence number (constancy number) is put against each species, the sum of the presence numbers being placed at the bottom of each column. Then a direct comparison is made between each pair of groups (cfr. Table 2). The result is arranged in a square and treated according to the method outlined above, until the entire material comes within one group.

[1] Right columns in the Table.

3. Application of the Method to GRÖNTVED's Population Analyses from Danish Commons.

The following is an account of the application of the method to a concrete, already existing material, namely 50 population analyses of the vegetation on Danish commons, published by JOHS. GRÖNTVED in Dansk Botanisk Tidsskrift, vol. 40, p. 1—71 (1927). These analyses were made according to the circling method by RAUNKIÆR, each analysis comprising 25 elementary areas of $^1/_{10}$ m^2 each. My choice of this material for purposes of illustration instead of that from Greenland, on basis of which the method was developed, has been dictated by several reasons: 1) that the relatively small number of analyses makes the material easily surveyable as a whole, 2) that the material comprises types of vegetation that are not easily divisible into a) Uppsala-sociations, since they do not contain any single dominating species, b) Zurich-associations based on the principle of indicative species, the vegetation being essentially composed by the most common species of this country,—as GRÖNTVED puts it: "The outcome is not encouraging as seen from a purely floristic point of view" (l. c. p. 1). 3) A demonstration by means of a Danish material instead of a high-arctic one will make it possible to form an objective estimate of the method in wider circles of Scandinavian and Central European plant sociologists of whom it must be presumed that only few are just as conversant with the arctic as with the temperate flora and vegetation.

The analyses are listed in Table 4,[1] and the same numbering system is used as that of the original paper, in which the material is grouped on the following principles:

Group I, nos. 1—12. Most frequent type of vegetation on commons in dry inland areas. *Festuca ovina* and *Agrostis tenuis* occur rather constantly as dominants, i. e. with a high degree of frequency.

Group II, nos. 13—21. Is distinct from Group I by being in a more favourable position as regards water supply. *Poa pratensis* and *Agrostis tenuis* occur as dominants.

Group III, nos. 22—29. No proper group. Is stated to lack any closer relation to the other groups, both as far as soil and vegetation are concerned. The 8 populations are said to represent just as many "formations".

Group IV, nos. 30—44. Soil as Groups I and II, exposition 20°—45°: Nos. 30—36 N-E exposed, nos. 37—44 S-W exposed.

Group V, nos. 45—50. Comprises the vegetation on commons near sea-shores. Low-lying areas exposed to the influence of sea or brackish water, at any rate during the winter season.

The numerical values of the table designate RAUNKIÆR's percentages of frequency.

The arrangement is made consistently according to the method described in the foregoing. The primary groups (a—r) are each established after the square method (1)

[1] For Table 4 and Fig. 10 see the accompanying loose sheets.

j	r	f	g	m	p	o	c	i	a	d	b	q	e	k	l	h	n	
	31	41	26	35	25	30	33	41	41	45	33	19	36	26	16	11	6	j
31		44	39	32	38	21	17	19	29	17	16	7	13	14	20	6	3	r
41	44		36	41	36	29	35	44	45	37	32	23	30	28	27	16	7	f
26	39	36		47	40	29	32	33	41	27	22	17	31	20	26	20	6	g
35	32	41	47		39	28	40	45	41	41	26	29	29	24	22	19	6	m
25	38	36	40	39		41	42	24	37	24	31	26	22	19	25	30	6	p
30	21	29	29	28	41		43	27	44	27	41	20	31	30	24	26	7	o
33	17	35	32	40	42	43		44	42	38	39	38	31	27	19	19	4	c
41	19	44	33	45	24	27	44		49	49	43	43	40	28	18	17	1	i
41	29	45	41	41	37	44	42	49		47	47	30	44	43	37	26	7	a
45	17	37	27	41	24	27	38	49	47		42	37	47	31	17	12	3	d
33	16	32	22	26	31	41	39	43	47	42		43	46	47	30	27	11	b
19	7	23	17	29	26	20	38	43	30	37	43		35	27	13	18	7	q
36	13	30	31	29	22	31	31	40	44	47	46	35		47	28	19	12	e
26	14	28	20	24	19	30	27	28	43	31	47	27	47		43	34	27	k
16	20	27	26	22	25	24	19	18	37	17	30	13	28	43		39	20	l
11	6	16	20	19	30	26	19	17	26	12	27	18	19	34	39		27	h
6	3	7	6	6	6	7	4	1	7	3	11	7	12	27	20	27		n

Fig. 6.

(cfr. p. 7). Owing to the heterogeneousness of the material the minimum limit in the first grouping is not chosen higher than $QS = 50$, so as to avoid getting absurdly many meaningless groups. The central group, *a*, could of course have been divided more finely (and subsequently united) by placing the minimum limit at a higher value.

After placing of the minimum limit of $QS = 50$, the 50 populations are divided into 18 primary groups, designated *a*—*r*, each group comprising from 1 to 12 populations. All mutual *QS* values of these groups (cfr. Fig. 6) are calculated according to (2) (cfr. p. 8). After this, the groups of higher orders have been established in close

F	E	D	B	A	G	C	I	H	J	
	36	31	33	30	19	31	16	11	6	F=j
36		37	29	30	15	22	24	11	5	E=fr
31	37		35	35	23	26	24	20	6	D=gm
33	29	35		35	28	27	23	25	6	B=cop
30	30	35	35		38	41	26	21	6	A=abdi
19	15	23	28	38		31	13	18	7	G=q
31	22	26	27	41	31		36	27	20	C=ek
16	24	24	23	26	13	36		39	20	I=l
11	11	20	25	21	18	27	39		27	H=h
6	5	6	6	6	7	20	20	27		J=n

Fig. 7.

III	I	IV	II	V	
	32	22	16	6	III=EF
32		31	23	6	I=ABD
22	31		24	14	IV=CG
16	23	24		24	II=HI
6	6	14	24		V=J

Fig. 8.

α	β	
	15	α=IIIIV
15		β=IIV

Fig. 9.

Figures 6—9 show the stepwise comprehension of the groups. The figures in the squares are *QS* values.

Fig. 6: The 18 groups of the 1st Order, combined into 10 groups of the 2nd Order, Limit $QS > 40$.
— 7: — 10 — - - 2nd — — — 5 — - - 3rd — — $QS > 30$.
— 8: — 5 — - - 3rd — — — 2 — - - 4th — — $QS > 20$.
— 9: — 2 — - - 4th — — — 1 — - - 5th — — $QS > 10$.

The *QS* values above the limit value of the new division are underlined in all figures.

consistency with the successive comprehension principle, employing limits of $QS > 40$, $QS > 30$, $QS > 20$, $QS > 10$.

The stepwise formed groups are the following:

Groups of the 1st order, minimum limit $QS = 50$, designated $a, b, c, \ldots$
Groups of the 2nd order, minimum limit $QS > 40$, designated $A, B, C, \ldots$
Groups of the 3rd order, minimum limit $QS > 30$, designated $I, II, III, \ldots$
Groups of the 4th order, minimum limit $QS > 20$, designated α, β.

The stepwise comprehension is illustrated by the squares Figs. 6—9. It is seen that at a minimum limit of $QS > 10$ the entire material constitutes one group. A schematic presentation of the entire "system" produced in this way is attempted in Fig. 10. With regard to the sequence of the individual groups of the 4 consecutive "ranks" the following should be noted (cfr. also p. 12—13):

The arrangement is made in sequence from the more comprehensive groups to the more elementary ones, that is, from α, β to a, b . . . . . : α and β are two co-ordinate

groups, hence they present no possibilities of further placement. When arranging the 5 groups, *I—V*, it should be observed that groups possessing the greatest similarity of species (*QS*) are placed closest to each other, and, similarly, that groups possessing the lowest similarity of species are placed farthest away from each other, on the wings[1].

From Fig. 8 it follows directly that within *α*, *I* is more closely "related" to both *III* and *IV* than these latter mutually; consequently *I* should be placed in the middle. Of the two groups within *β*, *II* and *V*, *II* is more similar to *IV*. The sequence, then, is *III, I, IV, II, V.*

The arrangement of the units at the preceding stage follows from Fig. 7. Here, it is not possible to observe directly the sequence of *D, B, A,* within *I,* as all *QS* values are equal in this case, 35. We must, as in other cases when a group consists only of two subordinate groups, make sidewise comparisons. *D* is most closely related to the co-ordinate groups within *III, A,* on the other hand, to the groups within *IV,* while *B* occupies an intermediary position. Hence the sequence and the orientation. Finally, the primary groups (*a, b, c* . . .) are arranged after the same principles (Fig. 6).

Of course one will sooner or later come across a case when no consistent linear arrangement of the groups is possible. For instance, *q* cannot be inserted anywhere in the sequence *a, b, c* . . . without causing a breach in the natural, numerically defined sequence. This only indicates that a natural arrangement would demand several dimensions. The distance (within one plane) between the individual groups should then be inversely proportional to *QS*. If we look at the scheme, Fig. 10, it would mean, expressed popularly, that instead of lying in the plane of the paper in a row with the other primary groups, *q* would rather have to point away from the paper at some angle. Several other units in the scheme, too, should have a direction diverging more or less from the plane of the paper.

Fig. 10 conveys a direct impression of a strictly hierarchical system. That a system of this nature would correspond exactly with plant communities in nature must *a priori* be considered out of the question. The system of superior and subordinate groups, as shown in the schematic figure, is a natural consequence of the stepwise grouping principle, which, however, is a necessity with a view to collecting at each stage of the grouping such units as evince a certain definable conformity in contents of species, and also with a view to establishing, as far as is possible, a consistent sequence of the groups of the first order. Moreover, the limits have been fixed quite arbitrarily. In several cases, sharp boundaries between communities seem not to occur in nature at all, and if they do occur they will hardly conform to any imaginable numerical system.

The only result that, on the face of it, can be said to have been achieved through the schema obtained is a division of the material into groups whose floristic composition displays conformity within a certain interval, the width of which has been defined

[1]) In the squares shown in the illustrations the views propounded here have already been applied in practice, and the arrangement already made in accordance therewith, which of course facilitates a direct view of the method. The original, arbitrary group designations have been retained to illustrate the method of grouping and the final placement of the groups within the "system".

by known, though arbitrary, limits. Only a closer contemplation of the result can afford countenance to a judgment of the justification of the method, i. e. its practical applicability.

In Table 4 all of the 50 analyses are listed in the sequence given by the scheme (Fig. 10). The numbering system of the original treatise has been retained. The group designations that were arbitrarily assigned during the numerical operations have been put at the top to facilitate the direct comparison between the Table and the numerical treatment of which a summary was given above. It should be pointed out only for completeness' sake that the scheme was constructed first and the species put in subsequently according to judgment. Species having great amplitudes are placed at the top: $\alpha + \beta$ first, then in turn e. g. *I*, *A*, *a*. Within each interval the species having the greatest constancy are as a rule put down first, the "accidental" ones last. An absolutely consistent sequence would demand a calculation of the ecological affinity (cfr. IVERSEN, 1936) or the correlative mutual connections between the species (cfr. TUOMIKOSKI, 1942). However, it would seem superfluous to point out that the sequence of the species has no bearing on the grouping as such. A more accurate determination of whether or no a certain species should belong to a certain subordinate group is in several cases rendered difficult or simply impossible, owing to the unequal representation of the material in the groups. The mathematical error for a group consisting of but one population is infinitely great, and hence it becomes so difficult to determine to which group the species in question should belong that no definite placement is possible. In practice it would presumably be a good plan to omit such units (e. g. *q*). The reason why I have retained them in the Table is that I have wished to demonstrate a complete treatment of an existing material. On the other hand, the example clearly shows the applicability of the method to a demonstration of rare combinations of species within a given material. Moreover, the relations of such units to the better founded groups follow clearly from the demonstration.

Since the method used here for defining and grouping of plant sociological units is based on purely floristic distinguishing marks—as is also that of the Zurich School—a certain conformity in results must be expected in advance. In the event that conformity exists we should at some stage or other arrive at a demonstration of indicative species specific for certain groups. This just proves to be the case.

The principles of the Zurich School have never been applied to the vegetation of Denmark in any consistent way. However, TÜXEN (1937) has given a survey on the Zurich School principle, of the vegetation of North West Germany, which is in both geographical and climatical proximity to Denmark. A comparison with TÜXEN's survey of the present, arranged material will be made below.

According to the present method of grouping, the material is divided into two main groups, α and β, which are connected through a number of the most common Danish plants, which no doubt appear as important constituents of several other types of vegetation than those dealt with here. A particularly great amplitude is displayed by

Taraxacum vulgare
Poa pratensis
Festuca rubra
Cerastium caespitosum
Agrostis tenuis.

It is commonly known that at any rate the three first-mentioned species are highly polymorphous and consist of a number of specialized biotypes (ecotypes), which clearly explains the great amplitude of these species (collective species). It follows from Table 4 that even though a greater number of species is found both in α and β these species are confined to certain subordinate groups. The two main groups α and β indicate distinctly the separation between such populations as are influenced by sea-water, β, and such as are not influenced by sea-water, α.

α comprises the major portion of the material. The following species occur with a fair degree of constancy within the three main divisions of α, *III*, *I*, and *IV*:

Achillea millefolium
Luzula campestris
Anthoxanthum odoratum.

I represents the central group within α and comprises no less than 31 out of the 43 populations of α, and it lies in the nature of things, that is, both in the limited extent of the entire material and in the method of arrangement employed (cfr. p. 11), that this group is more poorly floristically characterized than the groups at the wings. Hardly a single species occurs with full constancy within the entire group, at the same time being absent without it. On the one hand a number of species from *III* overlap with *I*, on the other hand a number of species from *IV* likewise overlap with *I*, but from the opposite direction.

The following species are common to *III* and *I*:

Plantago lanceolata
Festuca ovina
Hieracium pilosella
Galium verum.

On the other hand, they are not entirely absent in *IV*, in which group, however, they play no essential part, neither with regard to constancy nor to frequency within the individual populations.

A number of other species of the same "linear" amplitude are specialized around a few subordinate groups.

The following species are common to *IV* and *I*:

Lotus corniculatus (this species was stated to occur occasionally in sea shore habitats (β), but in such cases may have been *L. tenuis*, which, so the investigator kindly informs me, was in all probability not kept separate from *L. corniculatus*)

Trifolium repens
Potentilla reptans

and a number of less frequent species whose habitats, however, are most often either on the one or on the other side of the boundary line between *I* and *IV*.

In spite of the fact that a great many species are common to the subordinate groups within *I*, that group constitutes no plant sociological unit, however. Only at the preceding stage of the process of comprehension do communities become clearly defined.

I comprises *D*, *B*, and *A*.

A comprises 20 of the 31 populations within *I*. It is quite obvious that this represents Alliance *Arrhenatherion elatioris* Pawlowsky, which here, within the existing material examined, may be best characterized by

Cynosurus cristatus, and also by the following species, which do not keep so strictly within the boundaries:

Stellaria graminea (Tab. 4_1: III I)
Lolium perenne
Bellis perennis, the two last-mentioned also in beach habitats (Tab. 4_1: $\alpha\ \beta$)
Ranunculus bulbosus, which overlaps *III* (Tab. 4_1: III I).

It seems most reasonable to place this Danish vegetation in Association *Lolieto-Cynosuretum* (Br. Bl. & De Leeuw) Tx. within the alliance. Judging from the number of populations in the material *a* may presumably be classed as the most fully representative type of vegetation on Danish commons. *i* and *d* represent secondary types, *i* being a variety that is rather sparse and poor in species and hardly characterized by any particular species except perhaps by *Polygala vulgare*, but distinct from *a* through the absence of certain species, such as

Bellis perennis
Lolium perenne
Stellaria graminea,

which species may hence be designated as differential species for *a* with regard to *i*. *d* represents the opposite wing of our *Arrhenatherion*, characterized in particular by

Medicago lupulina
Potentilla erecta (Tab. 4_5: IV)
Galium hercynicum.

In this wing, on the other hand, there are absent a number of common species that display a high degree of constancy in *a*. *d* in reality forms a transition to *Ulicion* Malcuit, and the content of species is indicative of incipient formation of raw humus.

b, i. e. population no. 14 displays an atypic combination of species. In his description of localities Grøntved (l. c. p. 28) remarks about this locality: "This area was under cultivation for a couple of years twelve years ago and before then was

a heath". It is not stated about other localities within group *A* that they have been under cultivation.

Even though well separated, *D* and *B* possess certain common characteristics which are clearly expressed in the three common species,

Rumex acetosella
Aira praecox
Scleranthus annuus,

all of which, it is true, slightly overlap the boundaries of *DB* but nevertheless clearly occur most abundantly there. *D* and *B* are both Danish representatives of Order *Corynephoretalia* Tx.

D undoubtedly belongs to TÜXEN's Alliance *Koelerion albescentis.*

Our representative of that Alliance does not conform with any of its Tüxenian associations, however. It may be said to be characterized by

Trifolium striatum
Vicia lathyroides
Carex arenaria, and
Cerastium semidecandrum (Tab. 4_1: $\alpha\,\beta$), which last mentioned species, however, overlaps other groups perceptibly. Primary group *g* is richer in species than *m.* Here, for instance, we find *Myosotis micrantha* and *Armeria vulgaris* (Tab. 4_1: $\alpha\,\beta$), which also occurs in *Armerion* (see p. 27). All *D* populations were derived from dry, sandy habitats near beaches, except population no. 43, which was drawn from an inland locality in Jutland. The latter population is not quite typical and in certain respects approaches *Bromion* (see p. 25).

B clearly belongs to Alliance *Corynephorion canescentis* KLIKA and is almost identical with TÜXEN's Association *Corynephoretum canescentis,* even if *Corynephorus* is only sparsely represented. The vegetation is characterized particularly by

Hypochoeris radicata
Jasione montana.

Moreover

Teesdalea nudicaulis
Vulpia dertonensis
Alchemilla arvensis
Holcus mollis
Corynephorus canescens.

It may be mentioned that *Alchemilla arvensis* is considered an indicative species of *Secalinion medioeuropaea* (vegetation of weeds on lean arable land). Here, however, it is no doubt a case of *Alchemilla microcarpa* (*Aphanes m.* ROTHM.), which was but recently recognized as an independent species (cfr. GUÐJÓNSSON 1941).

It is of the greatest interest to note that our *Corynephoretum,* as represented in the present material examined, must be regarded as a type of vegetation the existence

of which is at any rate in some measure due to former cultivation of the areas in question. This is what GRÖNTVED observes on this point for each individual locality analyzed:

No. 22: ". . . . was formerly under cultivation".

No. 30: "According to statements by people well acquainted with it, this locality was cultivated about 50 years ago".

No. 21: "Fenced-in pasture land which was under cultivation many years ago".

No. 32: "The smooth level surface would seem to indicate that this area was cultivated formerly".

No. 37: "No boulders occur. It is possible that this area was under cultivation at some time though traces of furrows are no longer to be seen".

No. 11: "Former arable land . . . . . having exceedingly lean sandy topsoil".

(Apart from these six localities GRÖNTVED could establish the presence of traces of cultivation in only two cases out of the total number of localities investigated. These localities are No. 14 (see p. 23) and No. 29 (see p. 26), both of which occupy isolated positions according to the method employed and so prove to represent abnormal or at any rate unusual combinations of species.)

It is not surprising, therefore, that *B* dissolves into the subordinate groups *c*, *p*, and *o*, of which the two last-mentioned are units. These do not seem to have freed themselves as much from cultural influence as has *c*. Thus in *o* and *p* we find the following species which must undoubtedly be considered cultural relics in the light of the information that the soil is exceedingly lean, dry, and sandy:

Bellis perennis (Tab. 4_1: $\alpha\ \beta$)
Lolium perenne (Tab. 4_1: $\alpha\ \beta$)
Holcus lanatus (Tab. 4_5: C)
Ranunculus repens Tab. 4_5: C)
Medicago lupulina (Tab. 4_2: A).

This association is evidently bound up with so poor soil that it was not thought worth while to continue cultivation.

Group *III* clearly contains communities belonging to Alliance *Bromion erecti* (KOCH) BR. BL., characterized here by

Avena pratensis
Filipendula hexapetala
Pimpinella saxifraga
Viscaria viscosa.

The Alliance divides itself into two well-defined groups, *E* and *F*. As compared with the North West German associations, *E* most closely resembles a sub-atlantic variety, described by TÜXEN, of *Mesobrometum erecti* SCHERRER, Sub-Alliance *Mesobromion* BR. BL. & MOOR. On the other hand a remote resemblance is perceptible to

Braun-Blanquet's *Phleum phleoides — Potentilla argentea* Association of Sub-Alliance *Xerobromion* Br. Bl. & Moor (1938). — Our representative of *Mesobrometum*, *E*, is characterized by

Dianthus deltoides
Phleum Boehmeri
Artemisia campestris

besides a great number of species (see Table 4_4) which are no doubt just as characteristic of the association though being less amply represented in our not very comprehensive material. Gröntved states that all four populations are derived from areas sloping in a south-westerly direction. *r* is distinct from *f* essentially through its scarcity of species.

F, which comprises only two populations, both from sepulchral mounds (barrows) in Zealand (the only populations from sepulchral mounds in the entire material), represents a strongly divergent type of the Danish *Bromion*, characterized by

Solidago virga-aurea
Hieracium umbellatum
Lathyrus montanus,

which species are suggestive of Danish brushwood and heath vegetation. These populations clearly form a transition to *Ulicion* similarly to *d* within *Arrhenatherion* (cfr. p. 23).

IV consists of two groups, *C* and *G*.

Carex panicea

is the only representative of species that keep essentially within *IV* and are constant in *C* and *G*. The *QS* for *C*, *G* is also relatively low, only 31 (interval: $41 > QS > 30$). The isolated position of *G* (*q*) has already been pointed out (p. 20), and it may be said that as a group it is of no value, being based on only one population. The locality "is flat country at the bottom of a valley, surrounded by grassy and heathery hills that seem not to have been under cultivation, while traces of old furrows can be seen on the flat land between them" (Gröntved l. c. p. 38). Together with a number of plants generally occurring on commons, the plants of the moist moorland are represented here by

Salix repens
Calluna vulgaris
Erica tetralix
Pedicularis silvatica
Drosera rotundifolia.

The following two species also occur:

Radiola linoides
Gnaphalium uliginosum.

Application of the Zurich terminology leads to a confusing result: A kind of association *Callunetum* to Alliance *Ulicion* combined with an exceedingly fragmentary association *Cicendietum* ALLORGE to Alliance *Nanocyperion flavescentis.*

C belongs to Order *Molinietalia* KOCH, and our association must evidently be referred to Alliance *Caricion Davallianae* KLIKA (syn. *Schoenion ferrugineae* NORDH.) although it has no closer connection with any of the associations defined that belong to that alliance. It is primarily characterized by

Briza media,

further by

Deschampsia caespitosa
Cardamine pratensis
Achillea ptarmica
Sagina nodosa.

The two common species *Carex hirta* and *Ranunculus acer* are likewise to a material extent connected with Group *C* but are also found scattered in *Lolieto-Cynosuretum* (cfr. p. 23). The relation between the two primary groups, *e* and *k*, shall not be discussed further as the material is too insufficient.

All populations grew in moist soil, three of them (*e*) being from inland localities, two of them (*k*) from localities in some proximity to the beach though hardly influenced by sea-water.

β, i. e. *II* + *V*, all belong to order *Juncetalia maritimi* BR. BL., which is connected here by these salt marsh species:

Juncus Gerardi, and
Plantago maritima.

Agrostis alba and *Potentilla anserina* likewise occur most abundantly here even though they exceed the boundaries of *Juncetalia.* The scattered occurrences of *Agrostis alba* within *α* must, at any rate to some extent, be ascribed to a different species, *Agrostis gigantea* ROTH, which was not at the time of the investigation recognized as a good species distinct from *A. alba.* (It is a matter of course that the calculations were based on the species to the same extent as that in which they were given in the original work!)

I and *H* are both representatives of Alliance *Armerion maritimae* BR. BL. & DE LEEUW, in the present case chiefly characterized by

Bupleurum tenuissimum, and
Sagina maritima,

also by *Agropyrum repens,* which obviously displays no particular fidelity towards this community.

I is a typical *Armerietum* (WI. CHR.) BR. BL. & DE LEEUW, which is characterized here mainly by

Armeria vulgaris
Carex distans
Festuca arundinacea, and
Cerastium subtetrandrum.

The last-mentioned species indicates that the material is of a local character. Both populations are from the Sound area.

H, on the other hand, is rather atypical. In actual fact it represents an alien element in the *Juncetalia* (alternatively the *Armerion*), namely a fragmentarily developed Association *Centunculeto-Anthoceretum* (Koch) Moor (Alliance *Nanocyperion flavescentis,* Order *Isoetetalia* Br. Bl.), which is characterized here by the therophytes

Myosurus minimus
Montia minor
Polygonum aviculare,

and further by

Alopecurus geniculatus
Sagina procumbens.

V. The two populations represent the pure seaside meadow vegetation, a community belonging to the order *Juncetalia maritimi.* As compared with the preceding group, *II,* the vegetation here is characterized particularly by

Heleocharis uniglumis
Glaux maritima
Triglochin maritimum.

I desist from discussing what alliance this group should belong to. The alliances set up by Tüxen are insufficient in this case.

To sum up the attempt described above at inserting the separate groups in the Central European sociological system, the units established on a basis of the present material on Danish commons will be given below in schematic from. The primary groups I rank as sociations; the designations given to the latter must be taken only as orientating and purely preliminary ones. The appended literal notations refer to Table 4.

Order	Alliance	Association	Sociation	
Brometalia	*Bromion erecti*	*Mesobrometum*	*Dianthus deltoides-Phleum Boehmeri Soc.*	(*f*)
			Solidago virga-aur. Hierac. umbellat. Soc. (Transition to *Ulicion*)	(*j*)
Corynephoretalia	*Koelerion albescentis*	?	*Armeria-Cerastium semidecandrum Soc.*	(*g*)

Order	Alliance	Association	Sociation	
	Corynephorion canescentis	*Corynephoretum canescentis*	*Hypochoeris radicata-Jasione montana* Soc.	(*c*)
Arrhenatheretalia	*Arrhenatherion elatioris*	*Lolieto-Cynosuretum*	*Cynosurus cristatus-Ranunculus bulb.* Soc.	(*a*)
		?	*Medicago lupulina-Potentilla erecta* Soc. (Transition to *Ulicion*)	(*d*)
Molinietalia	*Caricion Davallianae*	?	*Ranunculus acer-Briza media* Soc.	(*e*)
Juncetalia maritimi	*Armerion maritimae*	*Armerietum maritimae*	*Armeria-Cerastium subtetrandrum* Soc.	(*l*)
		?	*Potentilla anserina-Heleocharis uniglumis* Soc.	(*n*)
Isoetetalia	*Nanocyperion flavescentis*	*Centunculeto-Anthoceretum*	*Polygonum aviculare-Myosurus minimus* Soc.	(*h*)

The five first orders, of which four comprise only one alliance each, while one, *Corynephoretalia*, comprises two, are clearly identified. The sixth order, *Isoetetalia*, must be accepted with some reservation, seeing that it is fragmentarily developed and occurs mingled with *Juncetalia maritimi* communities.

4. Discussion.

On the face of the matter it must seem surprising that Danish commons, which have thus far been considered more or less a unit—also phytogeographically—contain a vegetation spanning so great an amplitude, seen from a plant sociological point of view. The systematics and terminology of the floristic plant sociology is based essentially on the Central European vegetation, and it is possible that Central European plant sociologists would not immediately feel on sure ground if confronted with the vegetation of our commons. They would no doubt find the content of indivative species much too low. However, it is not strange that the Central European plant communities ebb out as we get farther away from the place of their establishment. There is a gradual decrease of the number of species concurrently with a decline in differentiation of life conditions, and the remaining species get compressed ecologically. There is a mingling of the remainders of the orders, alliances, and associations, that were so well defined in the original area, the clear groups are blurred so that at last the system with its ingeniously devised hierachical plan seems rather devoid of meaning. It is easily possible to point out cases of compression or displacement (cfr. also Du Riez 1924, Nordhagen 1940). By way of example, *Dianthus deltoides* is listed as Verbandscharakter-

art for *Corynephorion*. In this country it occurs, as we have seen, constantly in *Bromion*. *Ranunculus bulbosus* is given as Ordnungscharakterart for *Brometalia*. Here, it becomes one of the most constant species for *Arrhenatherion*. *Bromus hordeaceus* (*B. mollis*) is given as Ordnungscharakterart for *Arrhenatheretalia*, here, it is found mainly in *Bromion* and *Koelerion* (to *Corynephoretalia*). In spite of these discrepancies and several others besides, it is nevertheless possible to apply the Central European system to Danish conditions, but identification may be difficult for the very simple reason that no identity exists. Indicative species are much too scarce and sometimes misleading.

However, the method propounded here for arranging the sociological raw material, the population analyses, according to similarity and dissimilarity in the total composition of species, renders possible a rational arrangement even in cases when indicative species are absent. The material submitted in this paper shows that a similarity of species defined by $50\,(40) > QS > 40\,(30)$ ties populations into groups of such magnitude (wideness) as to correspond to a great extent to the alliances of the Zurich School. As order, alliance, and association often cover each other in the present material the latter hardly permits of further conclusions about the numerical limits of the sociological order of precedence. Only future, more comprehensive investigations conducted on the lines set forth here can provide information on the actual wideness of the sociological units already established.

Hence it is not possible to give any direct reply to the question thrown out in the introduction as to what wideness plant sociological units have or should have; but the method used here provides us with a means of practical determination of the amplitude of the units. An elementary demand for equality of amplitude for coordinate groups would seem an indispensable prerequisite in the case of a hierarchical system. It is rather odd that no such demand seems to have been formulated as yet.

When investigating the dependence of plant communities on ecological factors workers invariably attempt to make measurements increasingly accurate. Dispersion in the observatory series and standard error of arithmetic mean, are calculated. How natural would it not be to establish at the outset, or at any rate at the same time, a measure of the dispersion for the populations constituting as a unity the object of the exact investigations of life conditions. For this the present method affords a possibility. In Fig. 10 (first column) the average *QS* of anyone population against all the other populations of the group has been placed against each population, the "best" being for convenience placed at the top and the "poorest" at the bottom, in other words: the populations have been listed in sequence according to their mutual "quality" (actually the "best" should be put in the middle!). Provided the group does not comprise a too small number of populations the dispersion of the populations in the group may be made the subject of mathematical treatment.

It might perhaps be maintained that the very presence of a species is no sufficient measure of its importance in the population in question. It follows from Table 4, however, that the degree of frequency of a species in the individual populations is

often directly proportional to its degree of constancy within the group. Since the grouping, which is already based on presence and absence, so expresses to a certain extent, and reacts upon, the frequency of the species, the basis of arrangement used here must presumably be considered sufficient. An arrangement solely based upon the presence of the species also offers the advantage that populations may be compared direct regardless of whether the analysis was made with determination of frequency, of degree of coverage, or without either. In making this statement I do not wish to speak unfavourably of determinations of frequency, which, even though they may be unnecessary to the grouping as such, may be of the greatest interest in other respects. Determination of frequency, e. g. by RAUNKIÆR's circling method, moreover offers the great advantage that it exposes, already during the work in the field, pronounced cases of overdispersion for each individual species.

The object of the present work was not primarily to demonstrate which alliances and associations are represented in the vegetation on Danish commons. Still less was it intended as a proposal for a consistently hierarchical vegetation system, which perhaps the schematic arrangement in superior and subordinate groups might give reason to suppose. It would hardly be possible to maintain a strictly hierarchical system on idiobotanical patterns because a plant sociological unit, of whatever rank it might be, cannot be paralleled with the systematic concept of species and genera.

While a plant species (sub-species, variety) retains, to a more or less pronounced degree, its identity to its farthest geographical limit, this will never be the case with any plant community. For the plant species there exist diagnostic characters that apply throughout its area. A plant community, a population, remains always an aggregate of plants whose constituent parts are not organically connected, and whose closer identification, its diagnostication, is feasible only through analysis, consideration being taken of its total number of its constituent idiosystematic units. Whether or no it contains so-called diagnostically useful species, any homogeneous vegetation must *a priori* be of equal interest to plant sociology. There is no sense in speaking of "pure" and "impure" plant communities as soon as we move outside the type area. Seen from a Zurich point of view, of course, all Danish plant communities are impure or at any rate fragmentary.

It is a well-known fact that certain plant aggregates occur with greater frequency or over larger geographical areas than others; but this constitutes no proof of their integrity. The field of activities of plant sociology is not exclusively confined to these more or less recognizable units. Its object must be that of giving a perspicuous picture and an exact, and in related branches of research applicable measure of the distribution of plant species in nature. Ideologically, sociology and ecology must work independently on each other. The fact that this has far from always been the case has not contributed towards furthering and enriching collaboration between the two related branches of research.

It seems that originally the Zurich School worked on a purely floristic basis. Gradually, as it extended its geographical field of activities, it was found necessary

to give ecological content to the purely floristic sociological units so as to avoid working with purely imaginary concepts. This School clung to the "ökologische Zeigerwert" (BRAUN-BLANQUET 1928, p. 57) of the last remaining indicative species, or, in the last instance, to species that might serve as ecological substitutes. Thus the floristic system has developed into a camouflaged ecological system. Simply because the ideological potentialities of the system were insufficient.

A floristic sociological system ultimately depends on flora-lists. It would seem a prime condition to the consistency of the system that all species of the flora-list are taken into consideration; failure to observe this might cause the worker to become a victim to subjective points of view. A subjective estimation of the diagnostical value of a species does not even depend solely on the observer; it depends just as much on the object, that is, the vegetation present within a given area of investigation. Towards the limits of their area many species must be looked upon as good indicative species, whereas in the central portion of their area, where they most often figure most conspicuously, they would by the same subjective judgment be degraded into simple companions. By the method used in the present paper indicative species and companions simply do not exist as such, at any rate not until the result is to hand. Whether the species in question should be called one thing or another is unimportant in this connection.—It might be maintained that the groups are arbitrary. Yes, to a certain extent they are, but it is beyond discussion that in any case the resulting "linear" sequence is the natural one. The result is a "Slektskapskjede" (chain of affinity) (NORDHAGEN 1943, p. 56).

To some extent a floristic system is of purely local interest and application. Given equal or at any rate parallel life conditions the community of species must decline with an increase of geographical distance, or even completely disappear at last as a different floristic kingdom is reached. If we comprise all intermediate stages we may assume that the chain of affinity in which the floristic system results, is theoretically endless. In practice it proves a blind alley. There is of course no sense in speaking of a comparison, made on a floristic basis, of plant communities from different floral kingdoms. Here we must resort to other aids. A comparison of content of RAUNKIÆR's life forms would seem a proper course to pursue. It is relatively unimportant whether plant communities are established and arranged according to floristic or biological-morphological points of view. Within one floral kingdom the floristic method will provide the most detailed and concise arrangement which will be the more accurate the smaller the area under investigation. Where the floristic community fails for geographical reasons we have only life forms to resort to, no matter to what category they belong. These two methods are incommensurable, and they must in all cases be applied independently on each other (even when applied to the same material).

During its victorious northward advance the Zurich School, too, has become a victim to the same mingling of floristic and ecological points of view that was always

the Achilles' heel of the Uppsala School. This tendency will, if carried to extreme, cause the objective unambiguousness of the floristic method to fall to the ground.

A purely ecological system, towards which the Zurich School is now gradually approaching, might, at any rate theoretically, be a solution (cfr. also IVERSEN's "Biologische Pflanzentypen" 1936). Such a system would then have to be founded on an experimental basis, and its establishment evidently deferred till a distant future.

5. Summary.

This paper describes a method of grouping population analyses on a basis of similarity of species content without making any kind of subjective distinction between indicative species and companions, in other words: all species are being considered equally. During grouping, frequency and degree of coverage are disregarded. The similarity between two populations (or two groups of populations) is expressed by the Quotient of Similarity $QS = \frac{2c}{a+b} 100$, where a designates the number of species in one population (A), b the number of species in the other population (B), c the number of species common to the two populations. The individual population figures as the sociological basic unit. The unit used in calculating QS, therefore, is one species in one population, also in making comparisons of groups of populations mutually (cfr. Table 1 p. 7 and Table 2, p. 8). Groups of the lowest order are combined into groups of higher orders on a basis of the average QS of the primary groups mutually. This process of combining populations into increasingly more comprehensive groups is made stepwise, during which process such minimum values of QS are observed as guarantee minimum limits of mutual similarity between units within the consecutively established superior groups (cfr. Figs. 1—3, p. 9).

Table 3 (p. 16) illustrates a convenient application of QS to an objective determination of the mutual degree of conformity of populations within an arbitrary group composed according to other subjective points of view. Each population is in turn compared with the sum of the others.

A practical application of the method has been demonstrated on a material of 50 polulation analyses from Danish commons (J. GRÖNTVED, 1927) made according to RAUNKIÆR's circling method (determination of frequency). The stepwise grouping is illustrated in Figs. 6—9 (p. 18—19). The result is given in schematic form in Fig. 10 (on the accompanying loose sheet). In Table 4 the population analyses are listed in sequence in conformity with this scheme. The species are then listed in sequence according to judgment.

The groups established by this method may without difficulty be inserted in the Zurich System (cfr. p. 28—29).

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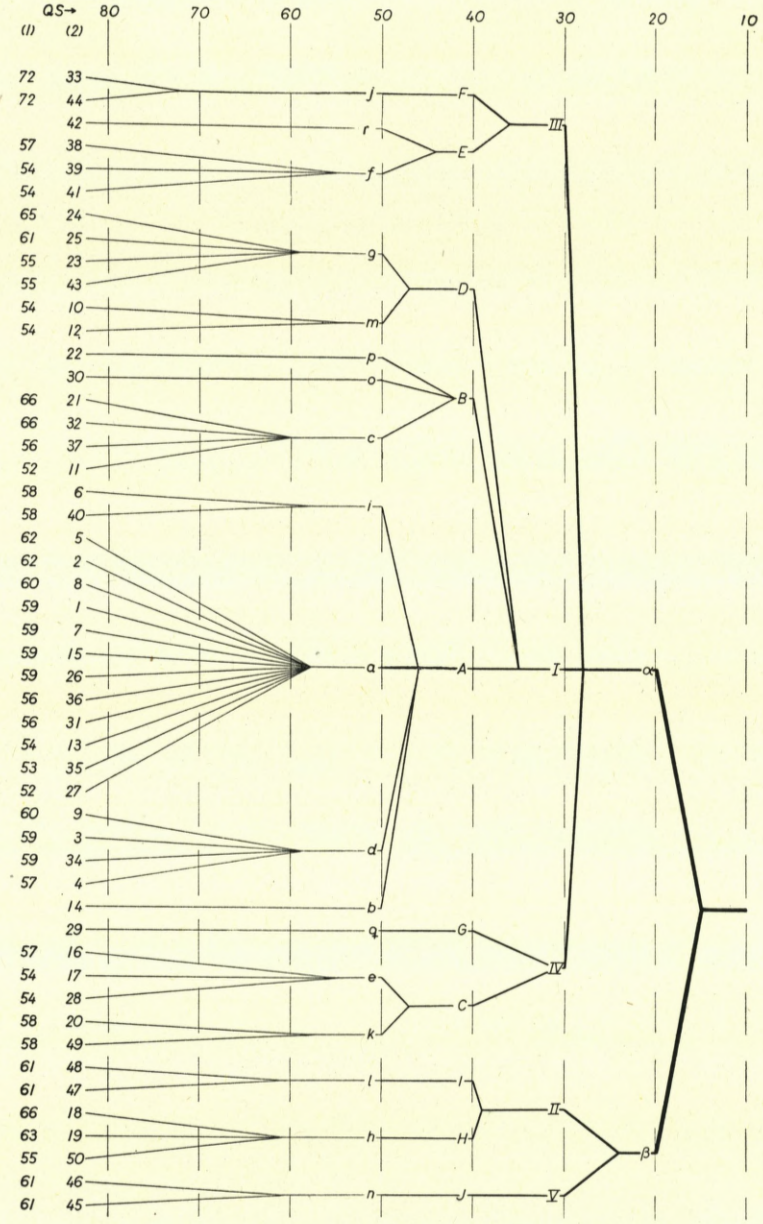


Fig. 10. A schematic presentation of the grouping of population analyses from Danish commons.

Groups of the 1st Order: Limit $QS > 50$, designated *a, b, c, ...*
— - - 2nd — — $QS > 40$, — *A, B, C .....*
— - - 3rd — — $QS > 30$, — *I, II, III .....*
— - - 4th — — $QS > 20$, — *α, β.*

Column (1): Average *QS* of population against the rest of the group.
Column (2): Number of the original paper.

	α																																											β						
	III						I																														IV						II					V	
	F		E				D						B						A																		G	C					I		H			J	
	j		r	f			g				m		p	o	c				i		a												d				b	q	e			k		l		h			n	
	33	44	42	38	39	41	24	25	23	43	10	12	22	30	21	32	37	11	6	40	5	2	8	1	7	15	26	36	31	13	35	27	9	3	34	4	14	29	16	17	28	20	49	48	47	18	19	50	46	45
α β																																																		
Poa pratensis	28	52	..	28	..	36	16	20	..	52	36	4	8	12	16	4	..	..	..	..	60	48	12	60	52	88	100	60	64	96	80	100	..	92	..	96	88	..	84	92	20	68	68	92	100	100	80	56	8	4
Festuca rubra	48	100	..	8	..	60	52	20	..	96	..	..	80	..	20	4	..	4	92	..	24	16	36	72	8	44	72	68	96	64	100	92	24	36	..	20	100	12	100	40	88	80	100	100	100	12	8	..	..	..
Agrostis tenuis	100	96	..	48	52	100	80	16	52	100	100	80	76	12	100	100	100	88	100	100	100	100	100	100	96	100	44	100	92	100	100	..	88	100	100	100	100	68	100	84	28	92	..	..	..	88	100	24	..	..
Taraxacum vulgare	12	8	4	..	32	16	8	20	12	..	..	..	..	96	..	8	..	..	4	..	44	16	60	20	64	84	100	100	..	16	..	72	..	..	..	..	32	..	..	..	4	24	16	56	16	..	..	..	16	..
Cerastium caespitosum	32	..	..	24	..	36	..	..	..	..	8	..	4	52	96	32	28	4	..	8	40	36	60	84	..	52	52	68	24	12	28	40	4	..	..	4	4	4	16	..	20	4	4	28	84	..	..	..	..	..
Cerastium semidecandrum	..	..	12	32	56	4	96	96	96	..	16	44	20	..	12	..	..	..	..	8	48	..	76	24	68	..	40	..	..	..	..	8	..	..	..	..	..	..	..	4	..	..	..	4	24	76	88	..	..	..
Myosotis micrantha	..	..	..	..	..	..	16	16	4	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	8	..	4	20	..	..	..
Armeria vulgaris	..	..	..	..	32	20	100	8	100	60	..	..	..	..	4	..	..	4	..	44	24	..	..	4	64	..	20	..	16	..	20	..	..	..	..	..	..	..	..	4	..	..	..	20	100	..	..	..	..	..
Agropyrum repens	..	..	..	..	..	8	28	16	..	4	4	..	8	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	36	80	..	..	..	..	..	..	..	40	..	4	60	64	100	72	100	76	..	..
Trifolium minus	..	..	..	..	..	..	..	..	..	4	..	..	84	80	..	..	4	..	4	..	64	..	12	20	92	..	..	..	..	..	24	12	..	..	..	..	8	..	..	..	..	4	..	..	..	12	12	4	..	..
Leontodon autumnalis	..	..	..	..	..	..	..	..	..	..	..	..	..	84	24	100	8	..	52	..	4	4	4	12	64	60	12	88	..	..	4	56	8	..	..	..	100	8	..	4	8	20	76	72	..	56	64	20	..	..
Bellis perennis	..	..	..	..	..	..	..	..	..	..	..	..	..	32	..	..	..	..	..	..	40	..	20	4	52	32	40	36	..	..	16	88	..	..	..	..	4	..	..	..	20	8	56	88	4	44	24	..	..	..
Lolium perenne	..	..	..	..	..	..	..	..	..	..	..	..	12	72	..	..	..	..	..	..	68	28	4	..	96	20	96	..	88	32	36	44	..	..	..	..	..	..	..	..	..	28	4	56	88	72	60	4	..	..
Sagina procumbens	..	..	..	..	..	..	..	..	..	..	..	..	4	16	..	4	8	..	..	..	20	4	..	..	..	12	..	..	..	..	8	8	..	..	..	..	72	4	..	..	..	..	16	..	..	16	12	44	8	..
α																																																		
Achillea millefolium	76	96	80	56	20	40	8	..	24	16	36	..	52	8	96	36	48	4	56	32	72	100	96	100	88	100	100	100	96	72	100	68	80	96	64	96	32	..	12	28	36	12	..	64	..	4	..	..	..	..
Luzula campestris	..	20	..	20	80	8	..	8	..	4	52	88	12	72	44	44	12	72	96	96	92	96	80	96	88	40	20	100	76	96	100	68	72	100	84	92	48	52	16	24	40	12	..	44	..	..	..	..	..	..
Anthoxanthum odoratum	40	8	..	96	84	4	..	..	..	20	..	4	..	..	72	8	12	100	64	4	88	100	16	72	40	68	..	64	44	84	44	..	20	92	52	32	84	56	52	44	52	32	8	..	..	..	..	..	..	..
Rumex acetosa	12	88	..	48	..	80	..	..	..	..	..	..	..	..	..	..	..	..	4	12	56	20	..	..	8	20	8	8	20	..	80	..	8	60	32	48	16	..	24	40	4	..	..	..	..	..	..	..	..	..
Equisetum arvense	4	24	..	..	..	..	..	..	..	..	..	..	..	28	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	20	..	4	..	..	20	..	20	..	..	..	..	..	..	..	..	..
III I																																																		
Plantago lanceolata	60	20	8	88	32	84	28	92	..	80	4	..	..	88	28	32	88	8	80	28	16	84	76	36	20	96	8	100	44	100	84	96	20	80	16	28	12	..	..	8	40	8	..	..	..	..	..	..	..	..
Festuca ovina	28	48	24	100	100	96	8	100	52	76	100	96	4	..	8	..	..	32	100	100	96	100	100	100	84	32	4	100	88	16	..	16	100	100	100	100	..	8	..	80	72	40	..	..	..	..	..	..	..	..
Hieracium pilosella	..	20	52	100	80	100	..	16	16	92	48	80	28	88	100	44	24	100	100	100	48	92	100	100	36	20	4	92	72	32	100	28	100	..	100	32	12	16	..	4	4	..	..	..	..	..	..	..	..	..
Galium verum	68	100	92	80	72	88	100	92	40	4	84	28	..	..	..	..	..	..	..	36	88	100	88	84	92	16	28	80	36	..	..	8	12	4	..	16	..	..	..	16	..	20	4	40	..	..	..	..	..	..
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Campanula rotundifolia	40	68	..	28	40	4	..	..	..	..	24	8	..	..	..	..	..	4	100	24	..	60	44	96	..	32	..	64	76	40	..	..	76	56	60	64	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Phleum pratense	44	16	..	36	..	32	..	..	..	4	..	..	..	92	..	..	..	..	..	..	20	8	..	..	4	..	76	..	4	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
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Ranunculus bulbosus	..	..	..	64	24	92	..	..	..	100	..	..	..	..	..	..	..	..	68	12	28	36	64	52	84	72	40	96	16	40	92	20	20	72	..	20	..	..	..	..	..	..	..	40	..	..	..	..	..	..
Saxifraga granulata	..	..	..	32	16	64	..	..	..	64	..	..	..	..	..	..	..	..	..	20	32	..	56	..	8	..	44	..	..	..	12	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..	..	..
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Table 4_3.

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Aira praecox	..	..	..	..	92	8	56	20	96	4	52	80	84	4	64	100	96	12	20	72	20	8	72	36	..	..	..	..	..	..	..	..	52	..	16	..	..	4	..	..	..	..	..	..	..	20	40	..	..	..
Rumex acetosella	..	..	..	4	16	8	32	8	68	100	60	16	..	28	64	80	80	64	4	24	12	12	36	52	8	8	..	8	..	..	8	..	24	..	..	24	..	..	..	8	..	..	..	..	..	..	..	..	..	..
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Lathyrus montanus	12	64	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	28	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	92	8	..	64	..	..	..	..	..	..	..	..	..	..	..
Solidago virga aurea	28	12	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
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Calluna vulgaris	..	..	..	4	16	..	..	..	..	..	..	68	..	..	..	..	..	20	12	..	..	..	..	8	..	..	..	..	..	..	..	..	..	..	..	24	16	100	..	..	..	..	..	..	..	..	..	..	..	..
Juncus squarrosus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	20	8	96	..	..	..	..	..	..	..	..	..	..	..	..
Salix repens	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	92	..	..	..	..	..	..	..	..	..	..	..	..
Erica tetralix	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	96	..	..	..	..	..	..	..	..	..	..	..	..
Pedicularis silvatica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	24	..	..	..	..	..	..	..	..	..	..	..	..
Drosera rotundifolia	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	84	..	..	..	..	..	..	..	..	..	..	..	..
Carex stellulata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	92	..	..	..	..	..	..	..	..	..	..	..	..
Pingvicula vulgaris	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	24	..	..	..	..	..	..	..	..	..	..	..	..
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Gnaphalium uliginosum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..	..	..	..	..	..	..
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Vicia cracca	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	8	12	..	..	12	..	12	20	..	24	..	8	40	..	12	..	..	..	..	..	..
Hieracium auricula	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	20	..	..	..	..	..	4	..	4	8	..	..	..	24	8	..	..	..	..	..	..	..	..
Ranunculus acer	..	..	..	..	..	..	..	..	..	..	..	..	..	8	..	..	..	..	..	..	..	..	..	..	..	4	..	..	44	..	..	4	..	4	..	..	28	..	96	60	88	32	40	49	..	4	..	..	..	..
Brunella vulgaris	..	..	..	..	..	..	..	..	..	..	..	..	..	64	8	20	4	..	..	..	..	..	..	..	..	..	..	24	12	..	84	4	32	..	..	..	100	..	8	..	84	8	68	..	..	..	..	..	..	..
Holcus lanatus	..	..	..	..	..	..	..	..	..	..	..	..	4	68	..	12	..	..	..	..	..	..	..	16	..	4	..	..	..	20	..	..	..	88	..	..	96	..	24	76	8	..	..	..	..	..	..	..	..	..
Ranunculus repens	..	..	..	..	..	..	..	..	..	..	..	..	..	20	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..	..	..	..	..
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Cardamine pratensis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	16	..	24	4	..	..	..	..	..	..	..	..
Achillea ptarmica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..	4	..	12	..	..	..	..	..	..	..	..
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Juncus conglomeratus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	20	..	..	..	..	..	..	..	..	..	..	..
Galium uliginosum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	32	..	8	..	..	..	..	..	..	..	..	..
Carex Goodenoughii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	40	48	..	..	20	..	..	4	..	4	..	4
Sagina nodosa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	16	..	16	72	..	..	..	..	..	..
Juncus compressus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	60	..	..	..	..	..	..	..	..	..
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Caltha palustris	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	16	..	..	..	..	..	..	..	..	..
Mentha aquatica-arvensis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	8	..	..	..	..	..	..	..	..	..
Ajuga reptans	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	48	..	..	..	..	..	..	..	..	..
Alchemilla minor	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	8	..	..	..	..	..	..	..	..	..
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Geum rivale	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	16	..	..	..	..	..	..	..	..	..	..	..

Table 4_6.

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	33	44	42	38	39	41	24	25	23	43	10	12	22	30	21	32	37	11	6	40	5	2	8	1	7	15	26	36	31	13	35	27	9	3	34	4	14	29	16	17	28	20	49	48	47	18	19	50	46	45
β																																																		
Agrostis alba	..	..	..	8	56	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	24	..	..	..	..	..	..	..	..	52	..	8	..	..	..	..	..	4	8	32	84	96	100	..	..	80	100	100
Potentilla anserina	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	32	16	60	..	72	..	..	32	100	100
Juncus Gerardi	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	16	8	24	36	20	32	100	100
Plantago maritima	..	..	..	..	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	60	..	44	12	56	52	16	12	16
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Erophila verna	..	..	..	..	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	56	..	..	8	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	36	12	..	..	..
Bupleurum tenuissimum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	20	20	4	..	4	..	..
Sagina maritima	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	16	76	..	..	..	..
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Cerastium subtetrandrum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	76	32	..	..	..	..	..
Festuca arundinacea	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	8	..	..	..	76	36	..	..	..	..	..
Carex distans	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	84	4	..	..	..	..	..
Lathyrus pratensis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..
Taraxacum balticum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..
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Poa annua	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..	4	..	..	..	..	..	..	..	4	4	..	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	16	..	24	..	..
Polygonum aviculare	..	..	..	..	..	..	..	..	..	..	..	..	20	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	12	24	56	..	..
Myosurus minimus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	36	16	68	..	..
Montia minor	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	20	8	..	..	..
Alopecurus geniculatus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	12	..	100	..	..
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Plantago major	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	8	..	..
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Glaux maritima	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	8	..	..	..	..	..	100	100
Triglochin maritimum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	8	..	..	..	..	..	100	84
Heleocharis uniglumis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	60	100
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Trifolium fragiferum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..	96
Scirpus compressus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	20	..	..	..	..	..	..	..	..	52
Suaeda maritima	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	12
Phragmites communis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	12

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