Acta Bot. Neerl. 22(2) April 1973, p. 124–134.

THE RELATIONS BETWEEN VARIATION IN EDAPHIC FACTORS AND MICRO-DISTRIBUTION OF WINTER ANNUALS

J. G. M. JANSSEN

Botanisch Laboratorium, afd. Geobotanie, Nijmegen

SUMMARY

The variations in edaphic factors associated with the small scale pattern of distribution of some winter annuals in the coastal dunes near Oostvoorne have been studied. Analysis of the soil samples showed a wide variation in edaphic factors which may occur over short distances and which indicated an evident relationship between edaphic factors and the micropatterns within pioneer vegetation of dry, sandy soils. Also the microdistribution of winter annuals appeared to be related to these small scale variations in the edaphic factors. The most important factors appeared to be the nutrient status, the lime content and the shading of the soils. However, other factors, still unknown, must play an important role in controlling the micro-distribution of the annuals considered.

1. INTRODUCTION

In a previous paper (JANSSEN 1972) some micropatterns within pioneer communities of dry sandy soils in the coastal dunes of north-western Voorne were described. Seventeen clusters were distinguished, which showed a considerable variation in their winter annual composition. These open communities, belonging to the class Koelerio-Corynephoretea and especially to its association Tortulo-Phleetum, can be found all over the investigated dune area, forming mosaics with dune grasslands and dune scrubs (VAN DER MAAREL & WESTHOFF 1964).

In recent studies concerning winter annuals these species are mostly considered as members of the same ecological group, having in common the ability to persist on open dry sandy soils (HAJKOVA & KREKULÉ 1972; KREKULÉ & HAJKOVA 1972; NEWMAN 1963, 1967; RATCLIFFE 1961). The main causes of this ability seem to be the presence of seed dormancy, adjusting the plants to unfavourable summer conditions, as well as the presence of vernalisation and photoperiodic reaction related to the hibernation and early spring flowering. The studies mentioned above are related to the large-scale distribution of the winter annuals. This study is concerned with the differences in the small-scale distribution patterns of some winter annuals and their relation to environmental factors, especially edaphic ones. It has been found that edaphic factors, particularly the concentration of certain cations and anions or their combinations, may have great importance in controlling the distribution of species whilst at the same time they often show considerable variation along short distances (AYYAD & EL-GHAREEB 1972; VAN DEN BERGH 1969; CLAPHAM 1969; CHAPMAN 1966; SNAYDON 1962; RORISON 1960a, 1960b). However, little research has been done on the direct relation between short distance soil variations and species micropatterns. In the areas studied the winter annuals often showed low degrees of cover percentages and were apparently non-random in distribution. Under these conditions, i.e. at the limit of the distribution of the annuals, small variations in individual soil factors might be expected to have the maximum effect upon performance. The present study aims at establishing the magnitude and significance of the variations in some of these factors in relation to the variation in clusters described (JANSSEN 1972) and to the microdistribution of some winter annuals.

2. METHODS

From 176 stands (JANSSEN 1972) soil samples were collected from the upper 0–3 cm layer. The samples were stored in closed tubes at 5 °C and dried at the air some days previous to the analysis. Soil: water extracts at 1:3 were prepared for the determination of soil reaction and the concentrations of water soluble Na, K, Ca, Mg, Fe, Cl, PO_4, NO_2 and NO_3. Soil reaction was measured with a glass electrode pH-meter with calomel reference electrode.

Soil: ammonium-lactate-acetic acid (AL) extracts at 1:3 were prepared for the determination of the concentrations of the above mentioned ions in this acid extract. No determination of the minor elements except Fe has been made, since in dune soils no symptoms of deficiency of the minor nutrients may be expected (WILLIS & YEMM 1961). All ions were determined with an auto-analyser. Sodium and potassium were estimated by a flame photometer. All other ions were estimated by colorimetric standard procedures (VAN DER GAAG 1972). Organic matter was estimated by oxidation with potassium bichromate by the method of Walkley and Black (FIEDLER 1965; SPITHORST 1932). The cation exchange capacity was estimated by the methylene blue method (PETER et al. 1959; HOFFMAN 1962; FIEDLER 1965).

Total carbonate was determined by displacement of carbon dioxide with hydrochloric acid. After incubation of the samples for 10 weeks at 25 °C under moist conditions NO_2 and NO_3 were determined again, together with NH_4, in order to obtain an idea of the mineralisation rate of the organic matter and the subsequent N-delivery of the soil (GÉHU & GHESTEM 1965). The cation exchange capacity was expressed in mval/100 gram soil. Total carbonate and organic matter were expressed in percentages. PO_4, NO_2, NO_3 and NH_3 were expressed in μ gram P resp. μ gram N per gram soil. All other ions were expressed as μ gram/gram soil. In addition some other environmental characteristics have been estimated. The mass cover, the herb cover as well as the total cover were expressed in percentages. The inclination was expressed in degrees, whilst the exposition was evaluated by using a 1–9 scale; a north exposition was evaluated by the lowest value, a south exposition by the highest value. Furthermore, a global estimation was made of the shading of the soils by using a 1–4 scale; the value four indicated the unshaded soils, the value one the deeply shaded soils.

The analysis of variance was applied and the value of "F" calculated in order to assess the significance of variations in soil characters with the 17 clusters, distinguished on the basis of the floristic composition of the relevés (JANSSEN 1972). For each annual a t-test was applied in order to assess the significance of the difference between the mean value of each factor in the relevés containing that annual and the relevés not containing that annual. In order to ascertain the degree of correlation between the cover percentage of each winter annual and each of the soil factors, Spearman's rank correlation coefficients were calculated on the basis of the relevés containing that winter annual. A Kaiser-Caffrey alpha factor analysis followed by a varimax rotation (HARMAN 1967; HORST 1965) which is part of a "factor analysis package" of the Nijmegen computing centre, has been applied to explore the patterns of relationships among the various factors and to obtain an idea of the ecological significance of these factors in respect of the winter annuals. With respect to each factor the stands were divided into 8 classes, each class containing c. 22 stands. On the basis of the frequency distribution of each annual in the different classes of that factor the mutual information between the annuals and the factors was determined (GUILLERM 1971). The probability of chance variation of the frequency distribution of each annual in the different classes of that factor is calculated with a chi-square test. All computations were carried out on the IBM 370/155 at the Nijmegen computing centre.

3. RESULTS

For a listing of the winter annuals considered in this study see *table 1*. Some main statistics of the soil characters involved, such as mean, standard deviation and minimum and maximum value, are summarised in *table 2*. A general idea about the magnitude of variation in each of the soil parameters between the 17 clusters (JANSSEN 1972) may be gained by examining *table 3*. This table presents the value of "F" related to the probability of chance variation. The values for most soil parameters agree reasonably well with other data (cf. FREYSEN 1967; WILLIS et al. 1957). The values found after 10 weeks incubation for NO_3 appeared to be high, those for NH_4 low compared with values found in comparable Tortulo-Phleetum arenarii samples (GÉHU & GHESTEM 1965). With respect to the significance of the variation in the values for $NO_2 + NO_3$ the considerable daily variations which these parameters may show have to be taken into

Table 1. List of winter annuals considered in this study.

1. *Aira praecox L.*	7. *Phleum arenarium* L.
2. *Arenaria serpyllifolia* L.	8. *Saxifraga tridactylites* L.
3. *Cardamine hirsuta* L.	9. *Silene conica* L.
4. *Cerastium semidecandrum* L.	10. *Veronica arvensis* L.
5. *Erophila verna* (L.) Chevallier	11. *Vicia lathyroides* L.
6. *Myosotis ramosissima* Rochel ex Schult.	

Table 2. Some main statistics of the soil characters. The units of the various characters are percentages (total carbonate and organic matter), μ gram N per gram soil (NO_2, NO_3 and NH_3), μ gram P per gram soil (PO_4), mVal per 100 gram soil (cation exchange capacity) and μ gram per gram soil (all other ions).

Soil factors	Mean	Stand. dev.	Minimum	Maximum
1. $NO_2 + NO_3$	3.2	3.4	0.0	14.3
2. NO_2	0.69	1.1	0.02	5.4
3. $NO_2 + NO_3$ after inc.	92	75	3	495
4. NO_2 after inc.	0.5	0.8	0.08	5.5
5. NH_3 after inc.	2.4	1.8	0.7	20.5
6. PO_4-water	1.5	2.1	0.1	16
7. PO_4-AL	16.1	52.6	1.8	622
8. Cl	14	8	6	79
9. Fe-water	0.18	0.20	0.04	2.0
10. Fe-AL	21.3	17.5	2.4	81
11. K-water	10.6	4.6	3.8	33.3
12. K-AL	30.3	17.5	9.3	118
13. Na	29	6	15	61
14. Mg-water	3.8	1.8	0.7	13.7
15. Mg-AL	60	39	7	209
16. Ca-water	16	7	4	44
17. Ca-AL	3204	2670	190	13440
18. $CaCO_3$	2.0	2.7	0.0	30.6
19. pH	7.3	0.5	4.7	7.9
20. organic matter	3.6	2.5	0.6	14.4
21. cat. exch. cap.	8.5	7.7	0.0	44.6

account. The value of the fraction Ca-water/Mg-water lies within the "most desirable" range for most species (BLACK 1965). It may be noticed that chance variation of all characters except the ammonification, NO_2, Na and $CaCO_3$ is less than 0.1 per cent. This indicates that intercluster variations for these characters are significant. Since the clusters are distinguished on the basis of the floristic composition of the relevés, an evident relationship between soil parameters and total floristic composition may be concluded. Thus, the variability of the vegetation appears to be, at least in part, related to differences in local edaphic conditions. We will now compare the soil characters of two clusters showing a great difference in their floristic composition, viz. cluster 13 and cluster 3. Cluster 13 is characterised by the presence of *Cardamine hirsuta, Arenaria serpyllifolia, Erodium spec., Cerastium semidecandrum, Veronica arvensis, Poa annua, Bromus mollis, Galium verum, Hypochaeris radicata, Crepis capillaris* and *Trifolium dubium* and by the absence of *Myosotis ramosissima, Erophila verna, Sedum acre* and *Tortula ruraliformis*; cluster 3 is characterised by the presence of *Myosotis ramosissima, Tortula ruraliformis, Cerastium semidecandrum, Sedum acre, Hypnum cupressiforme* and/or *Brachythecium albicans* and by the absence of *Arenaria serpyllifolia, Vicia lathyroides, Cladonia rangiformis* and/or *Cladonia furcata* (cf. JANSSEN 1972). We find the greatest amount of organic matter, favouring the origin of a slightly higher

Table 3. "F"-values related to the probability of chance variation.

Soil factors	"F"-value	Soil-factors	"F"-value
1. $NO_2 + NO_3$	3.4	12. K-AL	10.3
2. NO_2	2.5	13. Na	6.0
3. $NO_2 + NO_3$ after inc.	9.6	14. Mg-water	5.5
4. NO_2 after inc.	4.4	15. Mg-AL	13.7
5. NH_3 after inc.	0.8	16. Ca-water	3.8
6. PO_4-water	6.9	17. Ca-AL	10.8
7. PO_4-AL	3.7	18. $CaCO_3$	2.6
8. Cl	8.4	19. pH	7.1
9. Fe-water	1.8	20. organic matter	13.6
10. Fe-AL	11.5	21. cat. exch. cap.	11.2
11. K-water	5.4		

Table 4. Probabilities of chance variation between the values of the soil characters of the samples containing and not containing a certain annual.

a. positive: significant higher level of soil character in samples containing that annual (+: $P \leqslant 5\%$; ++: $P \leqslant 1\%$).

b. negative: significant lower level of soil character in samples containing that annual (−: $P \leqslant 5\%$; −−: $P \leqslant 1\%$).

Soil factors	Annuals										
	1	2	3	4	5	6	7	8	9	10	11
1. $NO_2 + NO_3$			+	−						+	
2. NO_2	++										
3. $NO_2 + NO_3$ after inc.		++	++		−−		−−			+	++
4. NO_2 after inc.			++				−−				
5. NH_3 after inc.				−							+
6. PO_4-water		++	++		−		−−				+
7. PO_4-AL		++	++								+
8. Cl		+	++		−		−−			+	+
9. Fe-water							−	−			
10. Fe-AL	−	−	−			−		−−	−	−−	−−
11. K-water		++	++				−−		++	++	
12. K-AL		++	++		−		−−			+	++
13. Na		++	++					++		++	++
14. Mg-water			++				−−			+	
15. Mg-AL		+	++	−−	−−		−−	−		+	+
16. Ca-water	−	++	++					+		++	
17. Ca-AL	−−					+			−−		−−
18. $CaCO_3$	−										−−
19. pH	−−			++	+		++	++			−−
20. organic matter		++	++		−−		−−			++	++
21. cat. exch. cap.		++	++		−−		−−			++	++

nutrient status, cf. PO_4, Mg and K-AL, in cluster 13; cluster 3 shows the greatest amount of $CaCO_3$, Ca-AL and Fe-AL and the highest pH. Cluster 13 seems to prefer the more stable and favourable soil conditions associated with considerable accumulation of organic matter in the upper layers.

Table 4 indicates for each annual the significance of the differences between the mean value of each soil character of the samples with and without that species. The distribution of *Cardamine hirsuta, Arenaria serpyllifolia* and, to a lesser extent, that of *Veronica arvensis* and *Vicia lathyroides* seems to depend on the presence of a slightly higher amount of organic matter and a higher nutrient status. *Phleum arenarium* and *Erophila verna,* however, seem to prefer a lower nutrient status and a lower amount of organic matter associated with a higher value of the pH. *Aira praecox* seems to avoid conditions with a high value of the pH and high values for $CaCO_3$, Ca and Fe-AL. Except in the case of *Myosotis ramosissima* these results are in good agreement with the Spearman's rank correlations calculated on the basis of the relevés containing that annual. The stands with and without *Myosotis ramosissima* do not differ significantly in most soil parameters; the cover percentage of this annual, however, shows significant rank correlations with various soil factors; at the 1% level this annual shows a significant positive rank correlation with PO_4-water, K-water, K-AL, Mg-water, organic matter and cation exchange capacity and a significant negative rank correlation with Fe-AL and $CaCO_3$. This means that when the species is present its performance is influenced by these factors. This can be understood by assuming that another factor, e.g. seed dispersal, is the major limiting factor with respect to the distribution of this species. The correlation between presence of a certain annual and significantly higher or lower levels of various soil factors might be brought about by several mechanisms. The correlation might be causal, i.e. the soil factor may directly influence the presence or absence of that annual. Another possibility is that both the soil factor and the annual distribution are similarly influenced by a third factor. By the adsorption of nutrient ions at the soil particles and the influence of the mobility of the sand on the annuals both the annuals and various nutrient ions might be found correlated with the organic matter content.

The same complexity might exist between carbonate, Ca, Fe and the pH. A factor analytical approach seems to be suited to get a better insight into this problem. Some results of the Kaiser-Caffrey alpha factor analysis followed by a varimax rotation are presented in *table 5*. This table presents the loadings of the variables involved, viz. soil factors, winter annuals as well as inclination, local radiation, moss cover, herb cover, total cover and exposition, on the first four "aspects" (FERRARI et al. 1957) and the communality of each variable, i.e. the part of the variance of each variable explained by the first four aspects. The first 4 aspects explained only 47% of the total variance, whilst the first 11 and 23 aspects explained only 61 resp. 77% of the total variance. The resulting varimax criterion after 5 iterative rotations had the value of 0.35, i.e. the structure of this solution is satisfying.

Table 5: Correlation coefficients between aspects and variables. The last column presents the communalities.

Variables	Aspects I	II	III	IV	Communalities
1. $NO_2 + NO_3$	0.05	–0.31	0.58	0.04	0.44
2. NO_2	–0.03	–0.16	0.09	–0.00	0.03
3. $NO_2 + NO_3$ after inc.	0.76	–0.26	0.15	–0.20	0.71
4. NO_2 after inc.	0.31	0.04	0.39	0.05	0.25
5. NH_3 after inc.	0.33	–0.14	0.02	–0.10	0.14
6. PO_4-water	0.81	–0.01	0.08	–0.15	0.69
7. PO_4-AL	0.57	0.11	–0.02	0.02	0.34
8. Cl	0.82	0.12	–0.04	–0.01	0.69
9. Fe-water	0.46	0.17	–0.15	–0.18	0.29
10. Fe-AL	–0.46	0.55	–0.00	–0.18	0.54
11. K-water	0.74	–0.07	0.14	0.12	0.59
12. K-AL	0.85	–0.21	0.02	–0.08	0.78
13. Na	0.71	–0.05	0.12	0.15	0.55
14. Mg-water	0.57	0.10	0.55	0.17	0.66
15. Mg-AL	0.78	0.07	0.29	–0.32	0.79
16. Ca-water	0.61	0.46	0.51	0.25	0.90
17. Ca-AL	–0.28	0.90	0.33	0.01	1.00
18. $CaCO_3$	–0.16	0.74	0.18	0.00	0.60
19. pH	–0.50	0.63	0.14	0.51	0.93
20. organic matter	0.90	–0.22	0.10	–0.18	0.90
21. cat. exch. cap.	0.90	–0.17	0.17	–0.19	0.91
22. *Aira praecox*	–0.10	–0.32	0.05	–0.08	0.12
23. *Arenaria serpyllifolia*	0.42	0.05	–0.20	0.06	0.22
24. *Cardamine hirsuta*	0.38	0.09	0.38	–0.12	0.31
25. *Cerastium semidecandrum*	0.24	0.02	–0.38	0.43	0.38
26. *Erophila verna*	–0.19	–0.02	–0.09	0.48	0.28
27. *Myosotis ramosissima*	–0.02	–0.01	0.35	–0.04	0.12
28. *Phleum arenarium*	–0.26	0.04	–0.25	0.45	0.34
29. *Saxifraga tridactylites*	0.10	–0.07	–0.06	0.86	0.76
30. *Silene conica*	0.02	–0.06	–0.20	0.10	0.05
31. *Veronica arvensis*	0.32	–0.17	0.04	0.35	0.25
32. *Vicia lathyroides*	0.29	–0.22	–0.13	0.05	0.15
33. exposition	–0.07	0.10	–0.20	0.09	0.07
34. inclination	–0.12	–0.07	0.16	0.26	0.11
35. total cover	0.21	0.50	0.10	0.12	0.32
36. moss cover	–0.11	–0.37	0.08	0.13	0.17
37. herb cover	0.76	–0.12	–0.01	0.12	0.61
38. light intensity	–0.00	0.00	–0.70	–0.03	0.49

The first aspect explaining 27% of the total variance may be interpreted as representing the nutrient status of the soil, indicated by high loadings of organic matter, cation exchange capacity, potassium, magnesium, phosphate and nitrate and nitrite after 10 weeks incubation. This aspect has also high loadings of natrium and chloride. The high loading of the herb cover on this aspect indicates that the sparse growth and open character of many of the stands may be mainly attributable to the low level of the nutrient status. The second aspect explaining 8% of the total variance has been characterised by high loadings of Ca, $CaCO_3$ and Fe-AL as well as of the pH and may be interpreted as representing the lime content of the soil.

The third aspect explaining 6% of the total variance has been characterised by a high negative loading of the local radiation estimation, associated by relatively high loadings of $NO_2 + NO_3$. This aspect appears to represent the shading of the stands. This shading results in a longer daily period suited for nitrification in the soils with respect to the moisture content of these soils and thus in a higher content of $NO_2 + NO_3$ in the soils. Moreover, at the sunnier sites the daily temperature will reach higher values, the loss of NH_3 into the air will be more important and the bulk of NH_4 in the soil needed for nitrification will disappear. The low loadings of $NO_2 + NO_3$ on the first aspect indicates that not the organic matter content but rather the moisture content of the soil is the major limiting factor for the daily nitrification in these soils in spring.

The ecological meaning of the fourth aspect with only high loadings of some annuals, particularly *Saxifraga tridactylites* and, to a lesser extent, of the pH, cannot be interpreted.

Although none of the winter annuals have very high loadings on the first three aspects, it may be supposed that the annuals *Arenaria serpyllifolia*, *Cardamine hirsuta*, *Veronica arvensis* and *Vicia lathyroides* prefer the more stable soils with a relatively high nutrient status, whilst on the contrary *Phleum arenarium* and *Erophila verna* avoid these soils. The negative correlation of *Aira praecox* with the second aspect is also evident. The negative correlation of *Cerastium semidecandrum* and *Phleum arenarium* with the third aspect indicates that these annuals prefer the sunnier and drier sites. The opposite preference is indicated for *Cardamine hirsuta* and *Myosotis ramosissima*.

The absence of significant correlations between some annuals and soil factors with the above-mentioned methods only means that no "linear" correlation exist between these annuals and soil factors. In order to obtain an idea of other than linear correlations between annuals and soil factors the frequency distribution of some annuals in the different classes of some soil factors are presented in *fig. 1*. Also presented in this figure are the values of the mutual information and the chi-square values. It is clear that various annuals, especially *Aira praecox*, show other than linear relations with various factors.

4. DISCUSSION

The present study indicates that microvariations in some edaphic characters are significant. The relationship between these microvariations and the clusters, distinguished on the basis of the floristic composition of the relevés and reflecting the micropatterns within the pioneer communities of the dry sandy soils of the coastal dunes of Voorne, has also been demonstrated. These microvariations may be reduced, at least partly, to variations in the organic

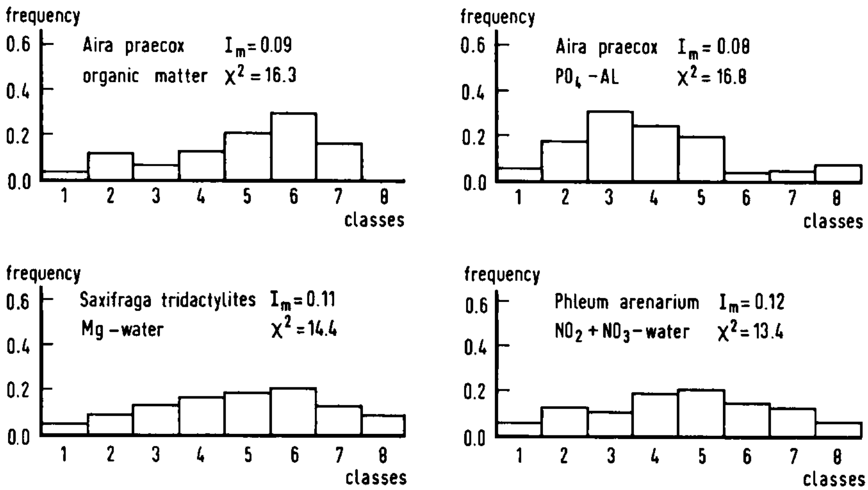

Fig. 1. Frequency distribution of some annuals in the different classes of some factors. Also presented are the values of the mutual information and the chi-square values.

matter content, the lime content and the shading intensity of the soils. Topographical features and surrounding vegetation might be greatly responsible for these microvariations. The most obvious effects of changes in topography and surrounding vegetation with respect to these variations are those displayed by wind, shading and accumulation of organic matter. By action of the wind sand containing much lime may be transferred and accumulated around mound-forming species or deposited on the leeward side of slopes. As pointed out before, the shading may effect the daily changes in the temperature and the moisture content of the soil and the resulting changes in the nitrification rate of the soil. The accumulation of organic matter results in changes in soil texture and structure, obviously affecting the relative amounts of water soluble salts due to changes in leaching capacity. Of course, these microvariations may be controlled by other factors, e.g. the nature of the dominating species and the stability of the soil.

In analysing the relationship between the microdistribution of various winter annuals and the edaphic factors, none of the simple linear correlations was found to be especially high. When the behaviour of the annuals was correlated with aspects which may be considered as special combinations of interrelated factors, somewhat higher values were obtained. The most important aspects may be interpreted as representing the nutrients status, the lime content and the shading of the soils. However, the percentage of variation explained by these aspects remained low. It may therefore be concluded that micro-variations in the edaphic factors involved can only explain a small part of the variation in the microdistribution of the annuals. To relate these field results to real nutritional requirements of the annuals, experiments are needed under relatively controlled conditions. Such experiments are now in progress. Moreover, the relationships often appeared to be non-linear; analysis of curvilinear correlations may throw more light upon this subject. It may be possible that the microdistribution of the annuals follows Boyko's Geo-ecological Law of Distribution. This Law reads in its shortened form: micro-distribution of plants is a parallel function of their macrodistribution, since both are dependent upon the same ecological amplitudo (BOYKO 1947, 1955). This would mean that the specific properties of the winter annuals, which enable them to persist on open dry sandy soils, e.g. seed dormancy, and in this way partly determine their macrodistribution, are also of great importance with respect to the microdistribution of the annuals. Because of the importance of the interaction between environmental factors, such as temperature, moisture content and local radiation, and these specific properties with respect to the macrodistribution of the annuals, microclimatological factors may be of great importance with respect to the microdistribution of the annuals. Further investigations with respect to this view are needed.

ACKNOWLEDGEMENTS

The author is very grateful to Prof. Dr. V. Westhoff and Dr. E. van der Maarel for their stimulating interest and to H. Claessen and P. Sluypers for their preliminary work on this subject during their M.Sc. research project at the Geobotany Division. This study was made possible by a grant of the Netherlands Organisation for the Advancement of Pure Research (Z.W.O.).

REFERENCES

AYYAD, M. A. & R. EL-GHAREEB (1972): Microvariations in edaphic factors and species distribution in a Mediterranean salt desert. *Oikos* **23**: 125–131.

BERGH, J. P. VAN DEN (1969): Distribution of pasture plants in relation to chemical properties of the soil. In: I. H. RORISON (Ed.), *Ecological aspects of the mineral nutrition of plants.* Oxford.

BLACK, C. A. (1965): *Methods of soil analysis: II. Chemical and microbiological properties.* American Society of Agronomy, Inc., Madison, Wis.

BOYKO, H. (1947): On the role of plants as quantitative climate indicators and the geo-ecological law of distribution. *J. Ecol.* **35**: 138–157.

— (1955): Climatic, ecoclimatic and hydrological influence on vegetation. *UNESCO Series Arid Zone Research* V: 41–48.

CHAPMAN, V. J. (1966): Vegetation and salinity. In: H. BOYKO (Ed.), *Salinity and aridity-New approaches to old problems.* Mon. Biol. XVI: 23–42.

CLAPHAM, A. P. (1969): Introduction. In: I. H. RORISON (Ed.), *Ecological aspects of the mineral nutrition of plants.* Oxford.

FERRARI, Th. J., H. PIJL & J. T. N. VENEKAMP (1957): Factor analysis in agricultural research. *Neth. J. Agr. Sci.* **5**: 211–221.

FIEDLER, H. J. (1965): *Die Untersuchung der Böden II.* Dresden & Leipzig.

FREYSEN, A. H. J. (1967): *A field study on ecology of Centaurium vulgare Rafn.* Thesis, Utrecht.

GAAG, M. VAN DE (1972): *Water analyses met de autoanalysor.* Nijmegen.

GÉHU, J. M. & A. GHESTEM (1965): La mineralisation expérimentale de l'azote organique de deux systèmes pédobiologiques littoraux naturels (dunes et prés salés). *Ann. Inst. Past. Suppl.* **109**: 135–152.

GUILLERM, J. L. (1971): Calcul de l'information fournie par un profil écologique et valeur indicatrice des espèces. *Oecol. Plant.* **6**: 209–225.

HAJKOVA, L. & J. KREKULÉ (1972): The developmental pattern in a group of therophytes: I. Seed dormancy. *Flora* **161**: 111–120.

HARMAN, H. H. (1967): *Modern Factor Analysis.* The University of Chicago Press, Chicago & London.

HOFFMAN, F. (1962): Beitrag zur Bestimmung der K.U.K. des Bodens. *Arch. Forstwesen* **11**: 1319–1331.

HORST, P. (1965): *Factor analysis of data matrices.* Holt, Rinehart & Winston, Inc. London.

JANSSEN, J. G. M. (1972): Detection of some micropatterns of winter annuals in pioneer communities of dry sandy soils. *Acta Bot. Neerl.* **21**: 609–616.

KREKULÉ, J. & L. HAJKOVA (1972): The developmental pattern in a group of therophytes: II. Vernalisation and photoperiodic induction. *Flora* **161**: 121–128.

MAAREL, E. VAN DER & V. WESTHOFF (1964): The vegetation of the dunes near Oostvoorne. *Wentia* **12**: 1–61.

NEWMAN, E. I. (1963): Factors controlling the germination date of winter annuals. *J. Ecol.* **51**: 625–638.

– (1967): Response of Aira praecox to weather conditions. I. Response to drought in spring. *J. Ecol.* **55**: 539–566.

PETER, H., S. MARKERT & G. GERICKE (1959): Die Bestimmung der Sorptionseigenschaften von Böden mit Methylenblau. *Z. Landw. Versuchs- & Untersuchungswesen* **5**: 165–172.

RATCLIFFE, D. (1961): Adaptation to habitat in a group of annual plants. *J. Ecol.* **49**: 187–203.

RORISON, I. H. (1960a): Some experimental aspects of the calcicole-calcifuge problem. I. The effects of competition and mineral nutrition upon seedling growth in the field. *J. Ecol.* **48**: 585–599.

– (1960b): The calcicole-calcifuge problem. II. The effects of mineral nutrition on seedling growth in solution cultures. *J. Ecol.* **48**: 679–688.

SNAYDON, R. W. (1962): Microdistribution of Trifolium repens and its relation to soil factors. *J. Ecol.* **50**: 133–143.

SPITHORST, C. (1932): De methodiek van de humusbepaling. *Versl. v. Landbk. Onderz.* **38**: 65–104.

WILLIS, A. J., B. F. FOLKES, J. F. HOPE-SIMPSON & E. W. YEMM (1957): Braunton Burrows: The dune system and its vegetation. I. *J. Ecol.* **47**: 1–24.

– & E. W. YEMM (1961): Braunton Burrows: Mineral nutrient status of the dune soils. *J. Ecol.* **49**: 377–390.