Bothalia 11,3: 365–367 (1974)

Improvement of association-analysis classification by Braun-Blanquet technique

B. J. COETZEE*

ABSTRACT

Normal association-analysis was carried out on data collected in the Jack Scott Nature Reserve in the Central Bankenveld of the Transvaal. As the method was found inadequate for obtaining optimal definition and arrangement of plant communities, it was supplemented by the Braun-Blanquet Table Method, which served as a substitute for inverse and nodal analyses. This led to a better understanding of the vegetation of the Reserve.

Because association-analysis is strictly hierarchical, presentation of inter-group relationships and interpretation of vegetation-habitat relationships are limited. It is argued that the monothetic character of normal and inverse association-analyses is a further limitation and although this is compensated for by nodal-analysis, valuable information is discarded as peripheral in the latter process.

A total of 229 4×4m, stratified, randomly-placed relevés were collected in the Jack Scott Nature Reserve, an area of 3 100 ha, 50 km west-north-west of Pretoria, in the Central Variation of Acocks's (1953) Bankenveld Veld Type. Relevés were classified by normal association-analysis (Williams & Lambert, 1959; 1960) to form a hierarchy with 49 final groups (Coetzee, 1972).

Each association-analysis final group could generally be distinguished from other final groups by the distinctive habitat features which its constituent relevés had in common. There were, however, a number of relevés which did not have the distinctive habitat features of the groups into which they had been classified. Furthermore, some groups, which were widely separated in the classification, appeared to be closely related because of their similarity in habitat features which were considered to be important for discerning inter-group relationships.

The Braun-Blanquet Technique, as described by Werger (1974), was employed as a means for possibly improving the classification. Floristic composition of all the relevés was presented in a two-way table, with relevés in columns and species in rows. Cover-abundance stimates were entered in the matrix. Species with similar distributions were grouped together in the table and association-analysis final groups were re-arranged to consolidate patterns in the Table as much as possible. This consolidation resulted in a major improvement in the interpretation of vegetation-habitat relationships. The association-analysis and semi-Braun-Blanquet classifications are compared in Figure 1.

The Braun-Blanquet classification excluded relevés which were classified by association-analysis into final groups which were very heterogeneous in floristic and habitat features. The classification accommodating 87 per cent of all relevés, comprised a total of 29 groups at various levels in the hierarchy. As indicated in Figure 1, 15 of these groups correspond to association-analysis groups without re-arrangement of the association-analysis hierarchy. Groups 4.1.2 and 4.2 in Figure 1 may be combined to form a group corresponding to association-analysis groups 36 to 41. Of the remaining 13 groups, another seven correspond approximately to association-analysis groups and six cannot be recognized in the association-analysis classification. These six are: 1.1, 2.1, 2.1(a), 2.2, 4.1.1 and 6.

A clearer concept of the plant communities and their floristic and habitat relationships was then obtained by arranging individual relevés completely according to the Braun-Blanquet Method (Coetzee, 1974). This classification is very similar to the re-arranged association-analysis hierarchy. Differences between the two are: (i) groups are more homogeneous in floristic composition and distinctive habitat features; (ii) the hierarchical arrangement of plant communities is slightly improved; (iii) the classification accommodates all but two of the 229 relevés, left out because they are obviously very heterogeneous in terms of floristic composition and habitat features.

Association-analysis and the Braun-Blanquet Method are similar in the following respects:

(i) both classificatory methods are intended to show discontinuities in the floristic response of vegetation to environment;

(ii) both methods take into account all species in order to establish which ones respond to environmental discontinuities by being non-randomly distributed and can therefore contribute to a meaningful classification of relevés;

(iii) both association-analysis and the Braun-Blanquet Method consider association between species as an indication of non-randomness of distribution; and

(iv) both methods then classify relevés primarily on their similarities with respect to groups of associated species.

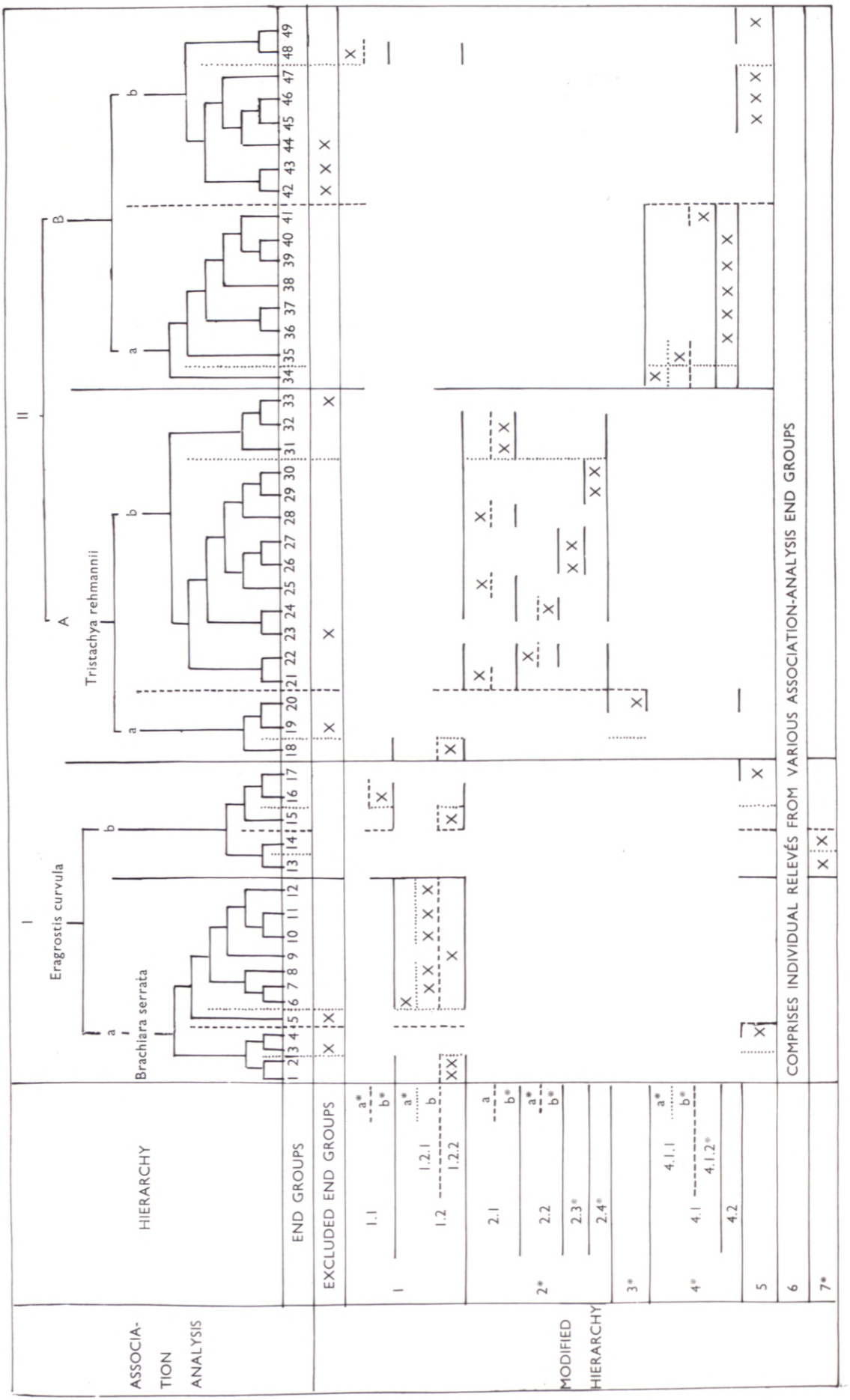
Despite these points of agreement, the Braun-Blanquet Method gave better results.

Where vegetation-habitat relationships are multi-dimensional, only very homogeneous groups and vegetation types at the most detailed level of classification have no equally or more plausible alternative classificatory possibilities. For more heterogeneous groups and vegetation types several classificatory possibilities may exist if the system is reticulate. A hierarchical arrangement merely draws attention to one such possibility, which has restricted value in interpreting vegetation-habitat relationships, as illustrated by the following example:

Relevés of the *Acacia caffra-Chrysopogon montanus* Savanna (group 1.1(a), Figure 1) and the *Acacia caffra-Ruellia cordata* Savanna (group 1.1(b), Figure 1) appear as two distinct groups in the association-analysis hierarchy, the hierarchy resulting from re-arranging association-analysis end groups, and the classification obtained by the Braun-Blanquet Method (Coetzee, 1974). Both savannas occur in sheltered valleys in dolomite and have in common a number of species which distinguish the sheltered valley vegetation from vegetation in the rest of the Reserve. The two savannas, therefore, belong to a single vegetation type with respect to a particular environmental discontinuity. In the association-analysis hierarchy, however, this relationship is obscured because the two communities are separated from one another by the

* Botanical Research Institute, Department of Agricultural Technical Services, Private Bag X101, Pretoria.

FIG. 1.—COMPARISON OF ASSOCIATION-ANALYSIS CLASSIFICATION WITH CLASSIFICATION RESULTING FROM RE-ARRANGEMENT OF ASSOCIATION-ANALYSIS GROUPS



* Floristically-defined and ecologically-interpreted communities that correspond to association-analysis groups at various levels of the hierarchy without rearrangement

first division separating different vegetation types following another environmental discontinuity. In the association-analysis hierarchy, the *Acacia caffra-Ruellia cordata* Savanna of mesic habitats in sheltered valleys is thus more closely related to dolomite communities exposed to cold weather than to the xeric *Acacia caffra-Chrysopogon montanus* Community of sheltered valleys. The summarizing Roman Table presented by Coetzee (1974) shows both discontinuities. Apart from its hierarchical arrangement, therefore, the Roman Table shows multidimensional relationships between plant communities. It presents the full floristic composition of each group of relevés as well as the overall distribution of all groups of species separating relevé-groups. Normal association-analysis is, as indicated by Lambert & Williams (1962), not a complete method for classifying vegetation. The method is intended as the first of three stages of a more complete method for studying community-habitat relationships. A two-way table representation of noda derived from normal and inverse association-analyses, also shows multidimensional classificatory relationships.

The nature of the vegetation types, apparent from a Braun-Blanquet Table, explains why sufficiently homogeneous groups cannot be obtained by association-analysis. Groups of relevés in a Braun-Blanquet table are each distinguised by a number of species. A single relevé need not contain a particular species or a particular combination (set) of species, but it must have a certain combination of species, which may be one of several sets of species, for it to be placed in a group (cf. Hull, 1964). For two distinct groups of relevés no single species need be, or usually is 100 per cent constant in and absolutely restricted to either of the two groups. Only approximations of such relevé groupings can be obtained with association-analysis, where one species is selected to represent a discontinuity in which two or more species are involved. Subsequent misclassifications make it difficult to relate groups to habitat and render them less suitable for describing plant communities. Inverse association-analysis by Williams & Lambert (1961), suffers from the same limitations as normal association-analysis. Although nodal analysis compensates for misclassifications of individual relevés and species, such relevés and species, which may be very typical of other groups, are discarded as being peripheral information (Lambert & Williams, 1962). The Braun-Blanquet Table Method provides a polythetic classification of species and relevés with no waste of information.

It is concluded that it would be desirable to classify relevés and species into fairly homogeneous groups by a polythetic method, to construct a two-way table for interpreting the reticulate vegetation-habitat relationships, and then to erect a hierarchical classification. Generally, for two-way table presentation of information, a hierarchy consolidating the distribution patterns in the table as much as possible is desirable.

ACKNOWLEDGEMENTS

The Department of Agricultural Technical Services made possible this study by seconding me to the University of Pretoria. The study was undertaken under supervision of Dr G. K. Theron of the University's Department of General Botany and Dr D. Edwards of the Botanical Research Institute.

I wish also to thank Dr M. J. A. Werger and Mr J. W. Morris for valuable comments.

OPSOMMING

Gegewens wat in die Jack Scott-natuurreservaat in die Sentrale Bankenveld van Transvaal versamel is, is met behulp van normale assosiasie-analise verwerk. Aangesien dit geblyk het dat die metode onvoldoende is om optimale definiëring en rangskikking van plantgemeenskappe te verkry, is dit aangevul deur die Braun-Blanquet-metode wat as plaasvervanger vir inverse- en nodale-analise gedien het. Dit het tot beter begrip van die plantegroei gelei. Die streng hiërargiese aard van assosiasie-analise verberg intergroepsverwantskappe en het beperkte waarde by die interpretasie van plantegroei-habitat-verhoudings. Die monotetiese aard van normale en inverse assosiasie-analise is 'n verdere beperking en alhoewel nodale-analise daarvoor kompenseer, word waardevolle inligting in laasgenoemde proses as perifeer verwerp.

REFERENCES

ACOCKS, J. P. H. 1953. Veld types of South Africa. *Mem. Bot. Surv. S. Afr.* 28: 1–192.

COETZEE, B. J. 1972. *'n Plantsosiologiese studie van die Jack Scott-natuurreservaat*. M.Sc. Thesis, University of Pretoria.

COETZEE, B. J. 1974. A phytosociological classification of the vegetation of the Jack Scott Nature Reserve. *Bothalia*, 11: 329–347.

HULL, D. L. 1964. The effect of essentialism on taxonomy—two thousand years of stasis (I). *Brit. J. Phil. Sc.* 15: 314–326.

LAMBERT, J. M. & WILLIAMS, W. T. 1962. Multivariate methods in plant ecology. IV. Nodal analysis. *J. Ecol.* 50: 775–802.

WERGER, M. J. A. 1974. On concepts and techniques applied in the Zürich-Montpellier method of vegetation study. *Bothalia* 11: 309–323.

WILLIAMS, W. T. & LAMBERT, J. M. 1959. Multivariate methods in plant ecology. I. Association-analysis in plant communities. *J. Ecol.* 47: 83–101.

WILLIAMS, W. T., & LAMBERT, J. M., 1960. Multivariate methods in plant ecology. II. The use of an electronic digital computer for association-analysis. *J. Ecol.* 48: 689–710.

WILLIAMS, W. T. & LAMBERT, J. M. 1961. Multivariate methods in plant ecology. III. Inverse association-analysis. *J. Ecol.* 49: 717–729.

Book Reviews

EPIPHYTIC ORCHIDS OF SOUTHERN AFRICA by E. R. HARRISON. *Durban: Natal Branch of the Wildlife Protection and Conservation Society of South Africa.* 1972. 107 pp. 48 black and white figures, 48 distribution maps. Price R4,50.

This is a field guide to the indigenous epiphytic orchids of Southern Africa. It is written and illustrated by Mr E. R. Harrison, farmer and well-known naturalist of Zululand. The 42 epiphytic orchids are distributed along the southern and eastern seaboard from Swellendam in the Cape through Natal and Swaziland to Messina in the Transvaal. The greatest concentration of species in South Africa is found in Zululand with 32 species. Mr Harrison was therefore ideally situated for his studies of this group of plants.

Apart from Bolus's monumental Orchids of South Africa (1893–1913), Rolfe's treatment in the Flora Capensis (1912, 1913) and Schelpe's recent semi-popular work, An introduction to the South African orchids (1966), there is very little information published on the epiphytic orchids of southern Africa. This book will serve to satisfy the demand for such information.

The author travelled many thousands of miles visiting known localities and collecting a vast amount of data. He soon found that photographing the plants was not satisfactory and so decided to illustrate the book himself.

The book starts off with "Hints for readers". Here the author explains, with the aid of figures, the vegetative and floral structure of epiphytic orchids. Then follows a mini-glossary of botanical terms and a vegetative key to the 18 groups which he recognizes.

For each species a distribution map, a brief non-technical description, a discussion of affinities, and a description of the habitat and origin of the specific epithet are given. In addition, there is a full-page plate in black and white made up of a habit sketch and drawings of the flower, fruit and sometimes portions of the leaf and root. The drawings are simple and unpretentious, but effective.

Mr Harrison obviously has a very intimate knowledge of the plants he is writing about. This book is recommended to all who are interested in orchids.

D. J. B. KILLICK

COMMON TREES OF THE HIGHVELD by R. B. DRUMMOND and KEITH COATES PALGRAVE. *Salisbury: Longman Rhodesia.* 1973. pp. 99, 54 black and white photographs, 54 colour plates. Price R2,50.

In a southern African context the choice of the title "Common Trees of the Highveld" for a book dealing only with the Rhodesian Highveld is perhaps unfortunate, because there is also a highveld in the Republic of South Africa where the name had its origin. Confusion could have been avoided by simply prefixing Highveld with Rhodesian.

In this book 54 trees are described and illustrated. The trees are arranged alphabetically according to family and then genus and species. The text for each species covers the common names in English and/or Afrikaans, Shona and Ndebele, distribution, habitat, a non-technical description and finally, considerable information about economic uses. It is rather a pity that these different aspects were not dealt with under separate headings. For reference purposes this would have been extremely useful. There is a black and white habit photograph of each species, also a colour plate by the second author's late mother. The colour plates were used in Palgrave's well-known "Trees of Central Africa" (1956).

This well-presented and reasonably-priced book will undoubtedly prove popular with tree enthusiasts. The A5 format, which is practically pocket-sized, and the serviceable cover, make it suitable for field use. One very minor criticism: on page 4 it is stated "This is a *synonym*, or a name which was applied to this tree in the past, but which is not now considered valid." Surely, in view of Article 6 of the International Code of Botanical Nomenclature (1972), "valid" should read "correct".

D. J. B. KILLICK

GEOBOTANICAL FOUNDATIONS OF THE MIDDLE EAST by MICHAEL ZOHARY. *Stuttgart: Gustav Fischer Verlag. Amsterdam: Swets & Zeitlinger.* 1973. 2 *vol., pp.* xxxi—738, 279 *fig.*, 8 *colour plates,* 7 *maps. Price* R106.

This monumental work in two volumes is published as part 3 in the series Geobotanica Selecta which is under the general editorship of R. Tüxen. In this book Zohary aims at pointing out the general and specific features and problems characteristic of the plant ecology and phytogeography of what he calls the Middle East. In this he has been particularly successful. Within the "Middle East", Zohary includes Turkey, Crete, Cyprus, Syria, Lebanon, Israel, Jordan, Egypt, the Arabian peninsula and Iran, but possibly it would have been more orthodox to call this the Near East. In this book an overall review of phytogeographical territories, vegetation units and the ecological relationships of these units, is given for the first time. In twenty chapters the author gives a comprehensive account of flora, habitats, plant geography, plant communities and plant utilization of the area, mainly based on his own investigations carried out during the last forty-five years. Information provided by his Israeli colleagues as well as data from the very scattered literature on this area has been integrated. The author carried out extensive field work in Israel, Jordan, Sinai, Turkey and Iran, whereas his studies in the rest of Egypt, Crete, Cyprus, Lebanon, Syria and Iraq were restricted to a limited length of time, and in some cases were performed more than thirty years ago. His knowledge of the Arabian peninsula is entirely based on literature.

In the first chapter the environmental features, geology, landforms, climates and soils, are outlined in an ecological perspective. Examples are frequently quoted to demonstrate a particular feature. Correctly, the author emphasizes that in the arid and semi-arid regions, which constitute by far the largest part of the area under discussion, not only the amount of precipitation, but particularly also the regularity and the seasonal distribution of the precipitation are extremely important ecological factors. Climatic diagrams of many localities (but not of Cyprus and Crete), illustrate the variety in climates in the area. A generalized climate map and also a generalized soils map for the entire area, would have been worthwhile additions to this chapter.

In Chapter 2 Zohary discusses the rich flora as well as the historical aspects connected with the botanical knowledge of the area. A chronological list of travellers, collectors and other contributors towards the botanical knowledge of the area is given. Important families and large genera (*Astragalus*) are briefly discussed. Then the composition of the floras of the individual countries is reviewed. It is interesting to learn how poor the Arabian peninsula is floristically when compared with the other areas, in particular Turkey and Iran, the two countries richest in flora.

The next chapter gives an outline of phytogeographical concepts such as the "phytogeographical region" and "speciation". A peculiar manner of expression is found in this section (p. 79), where it is stated that "phytogeographical regions are often speciation centres of certain taxonomic groups". Cause and effect seem to have been confused here.

Five phytogeographical regions meet in the area under discussion; the Euro-Siberian, the Mediterranean, the Irano-Turanian, the Saharo-Arabian and the Sudanian regions. A map shows their geographical positions. The regions and the subdivisions are each critically discussed, reviewing the literature concerned. Zohary differs from several other phytogeographers in his exclusion of the Sindian area from the Saharo-Sindian region and inclusion of it within the Sudanian Region. It is thus removed from the Holarctic Kingdom to Palaeotropis. Also, his inclusion of the North African Mauritanian Steppe province into the Irano-Turanian region is not conventional. Such decisions Zohary does not take lightly, but discusses critically. His arguments for the rejection of the Afro-alpine region in the mountains of the Arabian peninsula (p. 97) are, however, not convincing.

In the next five chapters (160 pages) the territories occupied by various phytogeographical regions are discussed in more detail. The most important communities in the different regions are mentioned, and their ecology is briefly outlined, sometimes illustrated by altitudinal transects. The statement in this section, that "one of the causes of the lack of a Saharo-Arabian Territory in Iran is that the local Irano-Turanian element displays an extremely wide ecological differentiation and is capable of populating the most desertic habitats by plants of its own" (p. 239), is perhaps too teleological. The five chapters are illustrated by nearly a hundred pen drawings as well as by eight colour plates of species mentioned in the text. The necessity for so many of these illustrations in a book like this is doubted by the reviewer.

The first volume concludes with a description of nine longitudinal and latitudinal, long-distance transects through the entire area, and a chapter on endemism, origin of the flora, and migration. An outline of concepts is given, and Zohary distinguishes between diffuse versus compact and neo- versus palaeo-endemism. Endemism in the various countries is discussed, from which it becomes apparent that endemics are not evenly distributed over the area, but that the Irano-Turanian group of species comprises by far the most endemics in all kinds of habitats in its territory. Many endemics also occur on isolated mountain peaks. The importance of the Arcto-Tertiary, the Indo-Malesian, the Palaeo-African and the Mesogean elements in the genesis of the present flora of the area is outlined, as well as floristic development since the Cretaceous.

Volume 2 opens with a discussion on trees and shrubs as "edificators" of the vegetal landscape. Distribution records, which are only accurate within the area under discussion, and the ecological preferences of most of the trees and shrubs are described. A table listing the altitudinal ranges of selected trees and shrubs is included here.

Chapter 12 follows, providing a short, general, theoretical introduction to the phytosociological description of the area. Zohary, who follows in general the principles of the Zürich-Montpellier School, states that although its methods "are very helpful as a general approach, (they are) delusive when applied to vegetation in arid zones" (p. 400). He deems modifications and deviations, mainly in the criteria of delimitation and characterization of the basic plant ecological units, the associations, a necessity. Because "the distribution ranges of species making up the associations are strikingly unequal in size, there will be a componental overlap between associations and the merging of communities into one another" (p. 400). Therefore, one of the modifications Zohary thought necessary is the application of dominance as the diagnostic marker of associations. As Zohary states, however, the vegetation in these Middle Eastern countries has been exposed to uncontrolled human interference for millennia, which in many cases will have led to selective eradication of several plant species. For this reason, and because facies often occur in the vegetation of arid and semi-arid regions, the application of dominance for the delimitation of plant communities is certainly not unequivocally desirable. It can easily lead to arbitrary decisions in recognizing the communities and to syntaxonomical difficulties. These recognized units would, perhaps, have better been called communities instead of associations, as long as they have not been delineated on the basis of comprehensive phytosociological tables. It is perhaps worth mentioning here, that several ecologists working in arid and semi-arid regions, including the reviewer, have experienced no particular difficulty in delineating associations, as meaningful floristic and ecological entities, on the basis of total floristic composition. It is, therefore, a puzzling statement which is made on page 400, saying, "to date, nobody established associations on the basis of floristic properties alone". Zohary possibly encountered difficulties owing to the long-term human disturbance of the vegetation and to the very application of the dominance criterion.

In seven chapters, altogether over 200 pages, the plant ecological units of the deserts, semi-deserts and steppes, the Mediterranean vegetation, the Euxino-Hyrcanian forests, the temperate steppe forests (both Euxinian and Irano-Turanian), the Sudanian vegetation and the hydrophytic vegetation are outlined. Notes on life and growth forms are also included. Phytosociological tables are omitted, but selected representative sample records are given. Most records are originally from Zohary himself, but those from some of his colleagues are also utilized. Many communities are illustrated by instructive photographs. The Arabian countries are, for understandable reasons, strikingly under-represented in sample records as well as photographs. Short remarks on the habitats of the communities are often added. Although Zohary expects his newly-described associations in the majority of cases to be affirmed by future phytosociological studies, he explicitly claims no nomenclatural validity for them. Minor points of criticism on his nomenclature include the following: he uses the suffix "-eto" after the first genus name, when an association is named after two species, instead of the use of binding vocal "o", which has already for more than ten years been the recognized practice in the Zürich-Montpellier tradition. He sometimes uses the phrase "association of . . . -etum", which is a pleonasm. Stipagrostetum should be Stipagrostietum. Sometimes authors are added to names of phytosociological units of higher rank, but more often they are omitted. It would acutally have been preferable to include them in all cases. Together these chapters represent a most valuable and useful account of the communities and their syntaxonomical and ecological interrelationships in the enormous area that is dealt with, and Zohary's statement, that "the Middle East as a whole is one of the most backward areas as far as botanical investigations is concerned" (p. 399), is certainly no longer true. The book concludes with a chapter on the interferences between man and plants through the ages. This section comprises short essays on the presegetal and the segetal eras as well as an anticipation on the neo-segetal and the near-future "era". Lists of plants used by man, grouped according to usage, are presented. The nature of the cultivated flora and of the segetal and ruderal flora and vegetation is outlined, and short notes on the syntaxonomy as well as some sample records of these vegetation types are included. The chapter also includes discussions on the origin of cultivated plants in the Middle East and on pastoralism and its selective effect on flora and vegetation.

A literature list of 22 pages, and two indices, a subject index and an index of plant and community names, of altogether 62 pages, are appended.

This work which comprises such an enormous wealth of information on plant ecology and phytogeography in general, as well as that of the area in particular, deserves a wide distribution and should be available in every library dealing with phytogeography or with plant ecology of arid and semi-arid areas. But also to other scientists, Zohary's book will prove to be extremely stimulating. As may be expected from the price, binding, paper quality, reproduction of photo's and lay-out are of a high quality. Printer's errors are few. Unfortunately the price (R106) will probably put this book beyond the reach of all but the larger libraries.

M. J. A. WERGER