Technical Report No. 49

VEGETATION TYPES: A CONSIDERATION OF AVAILABLE METHODS AND THEIR SUITABILITY FOR VARIOUS PURPOSES

Dieter Mueller-Dombois

٦

Department of Botany University of Hawaii Honolulu, Hawaii 96822, USA

Heinz Ellenberg

Systematisch-Geobotan. Institut Universität Göttingen D-3400 Göttingen Untere Karspüle 2 West Germany

ISLAND ECOSYSTEMS IRP

U. S. International Biological Program

November 1974

PREFACE

The following manuscript is a draft chapter for an international synthesis volume (IBP/CT Synthesis Volume II). The acronym CT stands for Conservation of Terrestrial Ecosystems, an effort which formed a major activity-segment within IBP. The subject matter of this report is related to our program in that it ties our work into the worldwide activities of the International Biological Program.

ABSTRACT

The problem of classifying vegetation is discussed in relation to three general objectives: (1) inventorying existing vegetation types for conservation purposes, (2) providing a framework for biological field studies and local management, and (3) understanding plant and community distribution and dynamics in relation to the environment. It is shown that the map scale which is used imposes a set of constraints on the method of classification. Several different map scales are discussed in terms of these limitations. A number of well known structural and floristic classifying schemes are reviewed including a new scheme of world ecosystems. The IBP/CT (Conservation of Terrestrial Ecosystems) checksheet survey is evaluated in the light of these methods. The conclusion is made that Fosberg's structural scheme, which was adopted for the check-sheet survey, provided only a first approximation to the ultimate objective of inventorying existing vegetation types for conservation purposes. A recommendation for a next step is made, which involves a scheme of hierarchical mapping of world ecosystems.

It is anticipated that this activity will be carried out under the UNESCO Man-and-the-Biosphere (MAB) Project No. 8 (Conservation of Natural Areas and of the Genetic Materials they contain).

- ii -

TABLE OF CONTENTS

	Page
INTRODUCTION	1
GENERAL OBJECTIVES	2
Developing an inventory of existing types for conservation purposes	2
Providing a framework of reference for other biological field studies and for local management	3
Understanding plant and community distribution and dynamics in relation to environment	3
LEVELS OF SPATIAL GENERALIZATION	.4
Level 1: Very small-scale maps for global orientation, from 1:50 to 1:10 million	4
Level 2: Small-scale maps for overviewing individual continents or countries, from 1:10 to 1:1 million	5
Level 3: Intermediate-scale maps for closer regional or subregional orientation at state or provincial level, from approximately 1:1 million to 1:100,000	8
Level 4: Large-scale maps for research and management at county or national park level, from approximately 1:100,000 to 1:10,000	9
Level 5: Very large-scale maps for detailed local orientation from approximately 1:10,000 to 1:1,000	n, 12
SYSTEMS FOR CLASSIFYING VEGETATION	13
Structural vegetation type concepts and systems	13
The formation concept	13
The synusia concept	15
Dansereau's profile diagram scheme	16
Küchler's formula method	17
Fosberg's system	18
The Australian system for IBP/CT	21
The formation system of UNESCO	24

Page

Ellenberg's classification of world ecosystems: a functional scheme	27
Floristic vegetation units and systems	31
Species dominance community-type concepts: the sociation and consociation	31
The association concept	3,3
Braun-Blanquet's floristic association system	36
WALUATION	37
The check-sheet survey in relation to the stated methods and its specified objectives	37
Hierarchical mapping for conservation purposes: a recommendation	40

LITERATURE CITED

45

INTRODUCTION

The following section is concerned with the general problem of classifying vegetation. A few proven methods will be discussed. It will be shown how these methods are related to the geographic scale, the objectives of the classification and the nature of the vegetation itself. An attempt will be made to assess the check-sheet survey in view of these methods and its own specified objective, which was to provide a source of base-line data for conservation areas.

Vegetation can be defined as an assemblage of plants of one to many species growing in areas of different sizes. Classification requires an identification of geographic segments of vegetation that show a certain degree of homogeneity within each segment. Degrees of homogeneity can be recognized at different levels of generalization in the spatial sense. For example, one may recognize small patches of grass cover (a few square meters in size) as homogeneous segments among a stand of irregularly dispersed trees. One may also recognize the trees together with the grass patches as an open forest or woodland, which may form a more broadly defined homogeneous segment that may be separated from a closed forest or scrub vegetation. Moreover, one may view the open forest, the closed forest and scrub of an area together as woody vegetation that can be separated from an adjoining herbaceous vegetation such as a grassland. These are examples of separating vegetation segments by general life form and structural criteria. Vegetation segments may of course also be recognized by changes in species distribution, composition and quantities. For example, across a segment of a closed forest, one tree species may show a quantitative dominance in one area, while the rest of the forest may show a more uniform mixture of

several tree species, permitting the recognition of two floristically defined closed forest segments, a mono-dominant forest and a mixed-species forest. Where such variations are gradual, the boundary allocation may cause some difficulties. Undergrowth species distributions may permit further subsegmentation of the mixed forest.

The few examples may suffice to illustrate that vegetation segmentation can be done at different degrees of homogeneity and different geographic scale (or detail). All levels of vegetation segmentation can be useful. But their usefulness varies with the objectives. It is therefore of utmost importance in vegetation classification to specify and understand at least the broader objectives.

GENERAL OBJECTIVES

Since vegetation can be classified in so many ways, there is no single method of classification that can satisfy all purposes. The choice of a suitable method, however, is narrowed immediately by a statement of objectives.

Three general objectives may be stated as follows:

Developing an inventory of existing types for conservation purposes

This can be described as the major goal of the IBP/CT check-sheet survey, a relatively new objective. It is, however, closely related to the long-standing aim of the plant geographer and vegetation scientist, which is to comprehend and order the vegetation diversity of certain territories.

In this general objective, the main focus of attention is on the vegetation itself and not so much on the associated environments, which may be inferred from the vegetation or studied later in more detail.

- 2 -

An important question that may be asked immediately is, what is the size of the territory to be inventoried? The world, a continent, an individual country or state, a county or park? This leads to the specification of the geographic scale for classifying and mapping of vegetation.

Providing a framework of reference for other biological field studies and for local management

This general objective is rather pragmatic. It requires a relatively simple classification that can be agreed upon by non-specialists. The units must not be too many or too complex and yet must find considerable reality in the field to be useful. The types must show integrity only for the local territory since the objective does not include the need to integrate the units with the vegetation of other territories. The classification must be more than a description of types. It must at least be developed into a key. Preferably it should be portrayed in form of a map.

Understanding plant and community distribution and dynamics in relation to environment

This is a general and fundamental objective of the vegetation ecologist. It requires good floristic knowledge and a study of the environmental factors in different habitats or along gradients. An important methodological prerequisite is the laying out of sample plots or relevés, because vegetation samples form the basis for arranging the data, which may result in either a vegetation classification or ordination, or in both. If such studies are considered to be useful for providing an ecological basis for other field research or for natural area management, the resulting arrangements should also be portrayed on a map. Mapping removes some of the complexities of geometric models, dendrographs, or tabular arrangements. The latter are,

- 3 - .

however, needed for the proper documentation of such community ordinations and classifications.

These three broader objectives are related to the levels of spatial generalization of vegetation.

LEVELS OF SPATIAL GENERALIZATION

Vegetation is a geographical phenomenon. It cannot be understood without the space it occupies. The same applies to each vegetation segment or community. It must first be recognized in the field.

Vegetation can be mapped at all geographic scales. But different scale ranges give different information sets, and these in turn provide for different general objectives. In the following paragraphs, scale ranges used for vegetation mapping will be discussed briefly at five levels, from the most general to the most detailed:

Level 1: Very small-scale maps for global orientation, from 1:50 to 1:10 million

This scale range includes standard wall maps of the world and atlas maps of major world regions or continents. The most comprehensive recent world vegetation map in this category is that of Schmithüsen (1968) at the scale of 1:25 million (i.e., 1 cm on the map represents 250 km on the earth's surface). At this small scale, Schmithüsen was able to portray 143 world vegetation types on eleven pocket-sized map-sheets. The map units are shown by color and symbol combinations. (An improvement for greater clarity would be to print the vegetation type numbers, shown in the legend, also into their respective colored fields). Vegetation types projected include such concepts as tropical lowland rain forests, tropical evergreen dry-forests, thorn-scrub and succulent forests, summer-green conifer forests, alpine meadows, heath vegetation of the temperate zone, lichen- and mosstundras, shrub deserts, etc. The vegetation categories coincide approximately with the "biome" concept of IBP study groups, but many of Schmithüsen's units can even be considered as subdivisions of major biomes.

However, it is also apparent that Schmithüsen's vegetation units do not represent really existing vegetation, because much of the earth's surface is variously modified, i.e., converted into agricultural lands, into industrial or urban areas. The map units merely outline certain ecological zones of assumed homogeneous growth potential for the named vegetation types. There may be in these zones existing remnants of the kinds of vegetation for which the areas are named. For these remnant vegetations (provided they are still existing in their respective zones), the map establishes interesting differences and similarities (or equivalencies) across our planet. Therefore, the map can fulfill a useful purpose in an inventory of world vegetation.

Level 2: Small-scale maps for overviewing individual continents or countries, from 1:10 to 1:1 million

This scale is generally used for mapping vegetation zones, i.e., areas characterized by certain key species or areas of so-called "potential natural vegetation." A good example of the latter is Küchler's (1964, 1965) vegetation map of the United States at the scale of 1:7.5 million. The map shows 106 vegetation types with such names as spruce-cedar-hemlock forest, redwood forest, Douglas-fir forest, chaparral, sagebrush steppe, southern cordgrass prairie (<u>Sapartina</u>), cypress savanna , Great Lakes spruce-fir forest, oakhickory forest, etc. Thus, in contrast to Schmithüsen's world vegetation map which gives vegetation information only on the basis of physiognomy or

- 5 -

general structure, Küchler's U. S. vegetation map provides general floristic information by the citing of dominant species in his vegetation type names.

However, Küchler's map is similar to that of Schmithüsen's in one important aspect: it does not outline actually existing vegetations in the field. It only provides for the possibility that in the general outline of a map unit there may be one or more smaller tracts of vegetation remaining that may fit the type description given for the area. Apart from its general information value, such a map can become extremely useful for conservation purposes, because the actually existing remnants of the vegetation types can be located by points or asterisks directly on the map. In this way the representativeness of conservation areas or natural reserves can be evaluated across a large country. Wrongly handled, such a map can also be a dangerous tool, because it tends to overgeneralize vegetation type information. This overgeneralization can result in the omission of important variations in a regional vegetation for conservation purposes. Other good examples of vegetation maps in this category are the 1:1 million "International Vegetation Maps" for South Asia, e.g., for Sri Lanka, Ceylon prepared by Gaussen et al. (1964). In these maps, 1 cm represents 10 km in the field. A few actually existing, but very broadly defined vegetation types are outlined or marked by symbols on Gaussen's maps. Moreover, these existing types are shown within their respective ecological zones. The 1:1 million scale was chosen as a guide for the recently developed UNESCO classification of world vegetation types (UNESCO 1973).

However, in most situations, existing vegetation types can only be located by a symbol and not mapped directly on such small-scale maps. It is therefore less confusing to refer to these maps as vegetation zone maps or as ecological zonation maps depending on whether the main source of information

- 6 -

was obtained directly from the vegetation or from environmental parameters or from both. For example, Krajina's (1969, 1974) biogeoclimatic zonation map of British Columbia at 1:1.9 million, although couched in vegetation terms (by naming the map-units after dominant plant species), is what it says, a map of ecological zones and not one of vegetation types. Each of his zones contains a number of significant vegetation types, which however cannot be mapped with sufficient clarity at that small scale.

Such small-scale ecological zonation maps are usually derived from already existing information and they may not require any additional field work. One way of derivation is to assemble existing vegetation maps prepared at larger scales and to reduce these by carefully reasoned boundary elimination into more generalized units. However, larger-scale vegetation maps covering contiguous large areas are rarely available (only for a few intensively studied countries), and ecological zonation maps may then be derived from environmental data. Most important at the small-scale geographic level are climatic data, and there are several proven methods that can be employed for the derivation of bioclimatic maps [e.g. the Köppen (1936), Thornthwaite (1948) or the Gaussen (1957) method]. One of the simplest, easily understood and richly informative methods is Walter's climate diagram method (1957) explained briefly in Section 3.1.3 of this volume. At somewhat larger scales (approaching 1:1 million), topographic and soils data become important as additional environmental information for the delimitation of ecological zones. A good example of the latter kind of map, using climatic, topographic and soils data is the before mentioned biogeoclimatic zonation map of Krajina. The distribution of certain key species, for example, dominant trees, were used as another guiding parameter for the drawing of zonal boundaries. However, the mention of key species in the unit-name does not describe them

- 7 -

as vegetation types.

Level 3: Intermediate-scale maps for closer regional or subregional orientation at state or provincial level, from approximately 1:1 million to 1:100,000

Such maps may permit the mapping of structurally and broadly floristically defined vegetation units, such as alliances (<u>sensu</u> Braun-Blanquet 1964) or dominance communities (<u>sensu</u> Whittaker 1962). However, at this scale the vegetation is still often generalized into climax types or potential natural vegetation types. A good example of the latter is Küchler's (1974) map of the potential natural vegetation of Kansas at 1:800,000 (i.e., 1 cm on the map = 8 km in the field). It represents an enlargement of Kansas from Küchler's U. S. vegetation map by a factor of 10 (approx.). This enlargement permitted Küchler to recognize twice the number of potential vegetation types (14) to that on his U. S. map (7). In the text accompanying the 1:800,000 map, Küchler shows a photograph each of an example of still existing vegetation for the 14 mapped potential vegetation types. Yet it would probably be difficult to map these existing communities at this scale, because the landscape of Kansas is today dominated by man-introduced land modifications to agricultural and other uses.

From this point of view, Gaussen's 1:200,000 climax vegetation map of France (a section of which is shown in Küchler's 1967 book: 259) is particularly interesting. On this map, Gaussen shows several climax vegetation types by different colors. The climax types are not the existing vegetation types. They merely represent vegetation zones or belts established from existing remnant stands and from climatic and soil information.

For example, the beech climax zone may include meadows, apple orchards,

- 8 -

heaths, tall shrub formations and beech forests. But Gaussen shows the type of land use of the area on the same map by a system of overprinted symbols denoting various forms of agricultural land use, such as corn, potato, rye vineyards, plantation forests, etc. Totally man-modified or cultivated zones are shown without color (in white). Absence of land use symbols on the colored fields of the climax zones indicates the presence of less modified or near-natural vegetations. The occasional overprinting of a climax type symbol may denote the presence of a more typical remnant stand. It is evident that such a map carries a significant information value for the objective at hand, i.e., an inventory of natural areas.

Vegetation maps at this intermediate scale range can show the outline of existing vegetation types only in relatively undisturbed or undeveloped landscapes, e.g., for national parks or remote areas with low human populations. An example is Mueller-Dombois' (1972) "Generalized map of Ruhuna National Park, Ceylon," which was published at the scale of 1:140,000. The map shows the actual outline of 10 structural vegetation types, such as forest, scrub with scattered trees, scrub islands, short-grass cover, etc., which are based on Fosberg's (1967) system. This map was reduced from a large-scale map (at 1:31,680) with 28 structural vegetation types (Mueller-Dombois 1969), which were generalized by elimination of those vegetation boundaries that were less important at the smaller scale.

Level 4: Large-scale maps for research and management at county or national park level, from approximately 1:100,000 to 1:10,000 (i.e., 1 cm on map = 100 m in the field or 1 cm² = 1 hectare)

This scale range is commonly used for mapping the outlines of existing vegetation types or communities. Such maps can be considered factual, since

- 9 -

the hypothetical element of extending vegetation boundaries across manmodified terrain is avoidable at this level. Large-scale vegetation maps may require months or years for preparation, and when established may show the diversity and distribution of plant communities within specific nature reserves or natural areas.

The map units may be defined by all commonly used classification criteria, i.e., by structural vegetation criteria (<u>sensu</u> Dansereau 1957, Küchler 1967, Fosberg 1967 and others) by species dominance criteria (<u>sensu</u> Whittaker 1962 and other Anglo-American authors), by species association criteria (<u>sensu</u> Braun-Blanquet 1964 and other European authors) or by combined vegetation e.g., Eberhardt et al. 1967, and habitat criteria (<u>sensu</u> Kopp, / Mueller-Dombois 1965 and others). These classification criteria will be discussed in more detail in the next section.

Structural and species dominance criteria are often more practical at the upper range of this geographic level, i.e., on vegetation maps with scales of 1:50,000 to 1:100,000 while floristic association criteria permit the portrayal of more detail, and thus are often applied at the larger scale range of 1:10,000 to 1:50,000. However, there is no absolute or direct relationship of classification criteria and map scales within this geographic scale range. The criteria used depend on the nature of the vegetation itself, on the more specified objectives and on the viewpoint of the mapper. For example, in the international comparison of forest site mapping methods in Switzerland (Ellenberg 1967) which was carried out at the scale of 1:10,000, E. Schmid's species dominance and plant life form (= structural) criteria were applied to the same area as were the floristic association criteria of Braun-Blanquet. In this case, the authors' viewpoint entered strongly into the community classification and mapping schemes. On the other hand, areas with considerable species diversity may not permit recognition of species-

- 10 -

dominance communities even at large geographic scales. In such cases, structural criteria may offer a better tool for subdividing a regional vegetaion cover.

An example of a large-scale structural vegetation map is the before mentioned map of Ruhuna National Park in S. E. Ceylon (now Sri Lanka) by Mueller-Dombois (1969), which was prepared from air photo mosaics at the scale of 1:31,680. Fosberg's (1967) structural scheme was used in the preparation of this map. Yet the map scale was already so large that a number of additional units had to be established. This caused no difficulty in this tropical dryland region. Fosberg's scheme was flexible enough to permit establishment of additional map units along the same sort of criteria that are described in his system. For example, Fosberg (in Peterken 1967: 104) recognizes four seasonal short-grass vegetation types. Only one of these applies to the Ruhuna Park grasslands, namely 1 M2, 1 = <u>Seasonal orthophyll</u> <u>short-grass</u>. However, for mapping at this scale, 6 short-grass types were recognizable on the basis of structure:

- (1) short-grass cover without woody plants,
- (2) short-grass cover with scrub islands,
- (3) short-grass cover with forest-scrub islands,
- (4) short-grass cover with scattered trees,
- (5) short-grass cover with scrub islands and scattered trees
- (6) short-grass or graminoid cover with sections of sparse cover of barren areas near water.

Types 2 to 5 could, of course, also be treated as Fosberg's low savanna and shrub savanna types. They can be translated into the latter categories for regional comparisons between countries, but that was not the objective. Instead, the objective was to establish an integrity of map units for the dry zone in Ceylon. A similar structural vegetation map was prepared for Wilpattu National Park in the N. E. part of Ceylon's dry zone. The maps were used for periodic animal activity surveys (Mueller-Dombois 1972, Eisenberg and Lockhart 1972) for locating floristic and quantitative sample plots (Comanor 1971), for soil surveys, etc. The more immediate purpose of the map was to establish a framework of reference for a number of research activities and wildlife management objectives.

Level 5: Very large-scale maps for detailed local orientation, from approximately 1:10,000 to 1:1,000 (i.e., 1 cm on map = 10 m in the field, or 1 hectare = 1 dm² on the map)

Such detail-maps are not published very often, because they are usually prepared for rather special purposes of more local interest. A published example is the vegetation map of the Neeracher Riet by Ellenberg and Klötzli (967), which covers a wetland bird sanctuary in Switzerland of about 100 ha in size. The map shows 17 floristically defined communities, and the smallest variation recognized on the map is about 10 m^2 in the field. At this level it is sometimes possible to map individual species aggregations or even individual plants of larger life forms. The map was prepared for the conservation management of a unique ecological reserve, the largest existing low-moor habitat in northern Switzerland. Maps at such very large scales can be useful also for studies of vegetation development or succession, such as Pearsal's maps of a river-mouth habitat in England (Tansley 1939: 604-605).

Maps at scales larger than 1:1,000 are sometimes prepared for permanent research plots or sample quadrats. They are used as tools in the study of stand dynamics (e.g. the mapping of dynamic phases in a Yugoslavian climax forest, see Mueller-Dombois and Ellenberg 1974: 398), for the dynamic shifts of species in a community or for the location record of rare species and

- 12 -

individuals. Such maps are usually not included in the concept of vegetation maps, but they are rather thought of as individual stand or community sample maps.

SYSTEMS FOR CLASSIFYING VEGETATION

Structural vegetation type concepts and systems

The formation concept.--Nearly all earlier attempts in classifying vegetation were based on physiognomic criteria that were more or less closely associated with features of the environment. Plant communities that are dominated by one particular life form, and which recur on similar habitats, are called <u>formations</u> (in the physiognomic-ecological sense). Examples are the tropical rain forest, the mangrove swamp, the cacti desert, the grass steppe, the high moor and the dwarf-shrub heath. Recognition of such types serves for initial orientation in setting subsequent studies into the proper perspective.

Originally, the term formation was defined physiognomically; that is through structural properties of the vegetation itself. Environmental attributes were added for closer description only. A later tendency has been to define the same concept climatically or as a geographic area; that is, through properties outside the current vegetation cover. In the latter sense, the physiognomy of vegetation in certain areas of a macroclimatic or geographic zone was used only as a general indicator for the entire region. This has led to quite a different understanding of the same term. According to Clements (1928) a formation is the general plant cover of an area which may include several physiognomic variations. These variations are inferred to belong to the prevailing, climatically controlled, physiognomic type. For example the prevailing physiognomic type may be a grassland, though the area may show stands of scrub and open forest. These would still be part of the grassland formation if occurring in the same so-called grassland climate. The same idea in the original understanding is not a formation, but a vegetation zone or region. A vegetation region usually contains a mosaic of actual vegetation types. One of these vegetation types may prevail over larger areas in the zone, where it finds its most typical expression on nonextreme sites. Such vegetation was called zonal vegetation by Russian authors (Walter 1971), which is similar to the climatic climax concept of Anglo-American authors, but less ambiguous. The Russian concept refers to a specific formation type of actually existing vegetation and not to potential vegetation, which may not really be present in an area. The before discussed world vegetation types mapped by Schmithüsen (1968) should be called vegetation zones or regions. The zonal vegetation types, i.e., formations in the original sense could then be indicated by dots, where present, in the mapped zones.

Clements did recognize this zonal or regional vegetation mosaic, but he added to the confusion of the term formation, by interpreting this vegetation mosaic as consisting of different developmental stages of the same formation. Clements converted the spatial side-by-side variation of vegetation, i.e., the different vegetation types or stages, mentally into a successional series, i.e., a time sequence. He believed that the regional side-by-side variations would develop into the same climax formation given enough time. This has led to some erroneous assumptions. Such a system that links all vegetation units to the final stage in succession provides for a gigantic outline. However, it must resort to tenuous assumptions in many places. The system is inclined to force certain communities into preconceived positions. Such a system would be accompanied by many uncertainties in regions where the vegetation is almost everywhere modified by man. These uncertainties may be

- 14 -

sufficient to make the system of little scientific value.

The synusia concept.--A vegetation segment or plant community consists of plant species of different growth form and functions. For example, a grassland community may consist of scattered perennial bunch grasses, low-growing rhizomatous grasses and annuals. Each of these is a different type of life form and each life form type may be comprised of several species. The species of a life form type that grow together in the same habitat are referred to as <u>synusia</u> or "union." These have a certain individuality of their own in relation to the rest of the community. For this reason they were considered as the basic units of vegetation by some investigators, particularly by Gams (1918).

Very simple communities, such as annual grasslands may consist of only one plant synusia. More complex communities, such as forests may consist of 10 or more synusia. It is easiest to think of synusiae as layer communities (Lippma 1939), such as the moss, herb, shrub and tree layers in forests. But from a functional viewpoint, one may find more than one life form type in each layer, e.g. deciduous and evergreen trees in the upper tree layer, or geophytes annuals and hemicryptophytes in the herb layer.

Synusiae may be identified with the help of a life form classification such as the well known system of Raunkiaer (1937), which was developed into a key and further elaborated by Ellenberg and Mueller-Dombois (1967). Of course, synusiae may also be recognized less formally by broader life form classes. This depends on the specific objectives set for the investigation.

The advantages of the synusia concept are quite obvious: synusiae are easily recognized, even without knowledge of the species names. Descriptions of their combinations portray a clear picture of the communities and provide a certain idea of the habitat conditions. Synusial combinations can be

- 15 -

traced even across the limits of different floristic regions and permit recognition of ecological relationships. Therefore, they are useful for worldwide comparisons similarly as are the formations.

However, if they were used as basic units for classifying vegetation, one would arbitrarily separate the topographical and ecological unity of all those communities that consist of several synusiae, such as forest stands or heath communities. Synusiae should be treated as structurally definable subunits within a plant community.

Dansereau's profile diagram scheme. -- A well known structural scheme is that of Dansereau (1951, 1957). His scheme employs six categories: (1) plant life form, (2) plant size, (3) coverage, (4) function (in the sense of deciduousness or evergreenness), (5) leaf shape and size, (6) leaf texture. Each of these six categories contains a number of criteria that can be used to characterize a vegetation segment in the field. For example, his plant life form category includes six general life form groups: trees, shrubs, herbs, bryoids, epiphytes and lianas; his size category includes three height classes: tall, medium, and low, which are defined quantitatively for certain life forms (e.g. low trees range from 8-10 m in height); his coverage category includes four criteria: barren or very sparse, discontinuous, in tufts or groups, and continuous. Each criterion is designated by a letter symbol. The letter symbols can be combined to describe and differentiate formations as units in the field, on air photos or on a map. In addition, the map units can be further interpreted by schematic profile diagrams. These profile diagrams are established from a system of diagrammatic symbols, whereby each symbol denotes a structural criterion.

The method requires establishment of sample stands or relevés as is

- 16 -

necessary for detailed, floristic classification methods. Thus, Dansereau's method is more time consuming than other structural schemes. The profile method is very formalized and the coded symbols have to be learned. In spite of its worldwide applicability, Dansereau's scheme is particularly useful for more specific purposes, such as the evaluation of military terrain or the study of structural detail in tropical rain forests, where taxonomic complexity presents itself as a barrier to studies in vegetation ecology (Holdridge et al. 1971). The system may also be viewed as providing information complementary to the floristic association system of Braun-Blanquet (see below). Both systems work from below, i.e., from the detailed to the more general aspects.

<u>Küchler's formula method</u>.--Another well known structural system is that of Küchler (1967), which provides for a hierarchical approach. It begins with a separation into two broad vegetation categories: (1) basically woody vegetation (2) basically herbaceous vegetation. Within the first category, Küchler distinguishes seven woody vegetation types [B = broadleaf evergreen, D = broadleaf deciduous, E = needleleaf evergreen, N = needleleaf deciduous, A = aphyllous, S = semideciduous (B + D) and M = mixed (D + E)]. In the second category he distinguishes three herbaceous vegetation types (G = graminoids, H = forbs, and L = lichens and mosses). These 10 basic physiognomic categories can be further differentiated by whether they show a dominance of specialized life forms. The specialized life forms given in the system are five: climbers = C, stem-succulents = K, tuft plants = T, bamboos = V, and epiphytes = X. A third major distinction in Küchler's system is based on prevailing leaf characteristics in the vegetation segment [h = hard (sclerophyll), w = soft, k = succulent, 1 = large (> 400 cm²),

- 17 -

and s = small (< 4 cm²)]. Further structural separations are made on height (stratification) and coverage of the vegetation. For height Küchler gives eight classes (1 = < 0.1 m; 2 = 0.1 - 0.5 m; 3 = 0.5 - 2 m; 4 = 2 - 5 m; 5 = 5 - 10 m; 6 = 10 - 20 m; 7 = 20 - 35 m; 8 = > 35 m) and for coverage six [c = continuous (> 75%); i = interrupted (50-75%); p = parklike or in patches (25-50%); r = rare (6-25%); b = barely present or sporadic (1-5%); and a = almost absent or extremely scarce (< 1%)].

With this set of categories and criteria, any vegetation segment may be characterized structurally by a formula composed of the letter- and number-symbols given. Küchler gives various concrete examples and claims that the system can be applied to all map scales.

Fosberg's system.--Fosberg presented a first (1961) and later a second (1967) approximation of a general structural classification of vegetation, which was adopted as a guide to classifying vegetation for the International Biological Program (IBP). One of the main features of Fosberg's system is that it is based--as are the schemes of Dansereau and Küchler--strictly on existing vegetation and purposely avoids incorporation of environmental criteria. This has the advantage that the vegetation units, when portrayed on a map, can be objectively correlated to independently established environmental patterns, because the vegetation boundaries are not in part delimited by environmental features. Where vegetation units are delimited in part by environmental features, correlation of such a vegetation map to environmental maps of the same area becomes problematic as this may result in circular reasoning.

The objective of Fosberg's scheme is to subdivide the vegetation cover of the earth into units that are meaningful for a large number of purposes

- 18 -

by criteria that are applicable on a worldwide basis. These criteria cannot be floristic, because the distribution of plant species is geographically restricted. Therefore, they must be primarily structural.

Fosberg makes a distinction between physiognomy and structure. Physiognomy refers to the external appearance of vegetation and to its gross compositional features implying such broad units as forests, grasslands, savannas and deserts, among others. Structure relates more specifically to the arrangement in space of the plant biomass. In addition, Fosberg uses function in the sense of seasonal leaf shedding versus retention of leaves and specific aspects of growth or life form as important criteria for classifying the vegetation cover.

The vegetation is classified by use of keys. The first key begins with a breakdown into three alternatives--closed, open, or sparse vegetation. Thus, first consideration is given to spacing or cover of the plant biomass. Closed is defined as crowns or shoots interlocking, open as not touching, and sparse as separated by more than the plant's crown or shoot diameters on the average. Sparse vegetation is equated with the term desert, which is further. defined as vegetations where plants are so scattered that the substratum dominates the landscape.

This first separation results in the first rank of vegetation units, which are called the <u>primary structural groups</u> (namely closed, open, and sparse). Within each of these, the second rank of vegetation units--called <u>formation classes</u>--are separated.

For example, in the closed primary structural group, individual formation classes are distinguished as forest, tall savanna, low savanna (tall and low referring to height of grass layer), scrub, dwarf scrub, tall grass, short

- 19 -

grass, broad leaved herb vegetation, etc. Therefore, in the formation class breakdown, primary consideration is given to differences in the heights of vegetation layers and their continuity or discontinuity. But at least one of the layers in a vegetation unit must be continuous or closed to distinguish all of these formation classes from those in the open primary structural group.

Thirty-one formation classes are distinguishable in the first key. The individual formation classes are then further subdivided in separate keys. The first subdivision within each formation class key is by function, indicating if the foliage is evergreen or if there are leafless periods for the dominant layer. This functional separation distinguishes the third rank, called <u>formation group</u>. A further separation within the formation groups leads to the basic units, referred to as <u>formations</u>.

These are distinguished on the basis of dominant life form with emphasis on leaf texture (sclerophyllous, orthophyllous = ordinary leaf texture as opposed to sclerophyllous), leaf size (megaphyllous = at least 50 cm long and at least 5 cm wide, mesophyllous = leaves of ordinary size, and microphyllous = for trees 2.5 cm greatest dimension, for shrubs 1 cm or less), leaf shape (narrow versus broad), thorniness, and growth form (gnarled versus straight, succulence, graminoid, etc.).

Occasionally, the formations, which represent the fourth rank, are subdivided into <u>subformations</u>, the fifth and ultimate division. For example, the formation "gnarled evergreen forest" is subdivided into two subformations, "gnarled evergreen mossy forest" and "gnarled evergreen sclerophyll forest."

Each formation and subformation is supplied with at least one example of vegetation that fits the structural definition. A glossary defines all

- 20 -

technical terms.

The classification system is necessarily artificial because, for example, the primary criterion of spacing may separate some environmentally or floristically closely similar vegetations into different primary structural groups. Yet, it may serve as a practical tool for mapping and organizing vegetation data for general purposes. Floristic associations can be studied within and across the structural frame given by the units. The structural vegetation units, when mapped, can be compared to climate, soil, history and other environmental maps from which one can derive the major regional or zonal ecosystems.

The Australian system for IBP/CT.--It seems significant that the Australian CT Committee of the International Biological Program (Specht et al. 1974) opted not to use Fosberg's system that was suggested for the IBP/CT survey. Instead the committee used a similar system developed by Specht (1970), which is reproduced here as Table 1.

As is evident from Table 1, the two primary criteria for classification are spacing and height of the vegetation. In this respect there is no basic difference from Fosberg's system. However, the Australian system uses one more category for spacing, and its height divisions are more detailed for trees. Three divisions are given for the height of trees, where Fosberg's system gives only one, namely forest. The other main life forms, shrubs and herbaceous plants, are each separated into two height classes as in Fosberg's system. The Australian divisions are defined in quantitative terms, i.e., spacing in percent foliage cover and height in meters. Life form characteristics are used as an additional criterion in the height separations. For example, tall shrubs are defined as reaching from 2 m to

- 21 -

			1
 STRUCTURAL	FORMATIONS IN	AUSTRALIA	en en en alter en en en

[Reproduced from Specht et al. 1974:6]

Life form and height of tallest stratum*	Projective foliage cover of tallest stratum*			
	Dense (70–100%)	Mid-dense (30-70%)	Sparse (10-30%)	Very sparse† (< 10%)
Trees > 30 m ‡ Trees 10-30 m ‡ Trees 5-10 m ‡	Tall closed-forest * Closed-forest * Low closed-forest *	Tall open-forest Open-forest Low open-forest	Tall woodland Woodland Low woodland	Tall open-woodland Open-woodland Low open-woodland
Shrubs 2-8 m ‡ Shrubs 0-2 m ‡	Closed-scrub Closed-heath	Open-scrub Open-heath	Tall shrubland Low shrubland	Tall open-shrubland Low open-shrubland
Hummock grasses 0-2 m		_	Hummock grassland	Open-hummock grassland
Herbs (including moss, ferns, hemicryptophytes, geophytes, therophytes, hydrophytes, helophytes)	Closed-herbland § (1) Closed-tussock grassland (2) Closed-grassland (3) Closed-herbfield (4) Closed-sedgeland (5) Closed-fernland (6) Closed-mossland	Herbland § (1) Tussock grassland (2) Grassland (3) Herbfield (4) Sedgeland (5) Fernland (6) Mossland	Open-herbland § (1) Open-tussock grassland (2) Open-grassland (3) Open-herbfield (4) Open-sedgeland (5) Open-fernland (6) Open-mossland	Ephemeral herbland

22

* Isolated trees (emergents) may project from the canopy of some communities. In some closed-forests, emergent Araucaria, Acacia, or *Eucalyptus* species may be so frequent that the resultant structural form may be classified better as an open-forest.

† Some ecologists prefer to ignore scattered trees and shrubs, equivalent to emergents in a predominantly grassland, heath, or shrubland formation.

[‡] A tree is defined as a woody plant more than 5 m tall, usually with a single stem. A shrub is a woody plant less than 8 m tall, frequently with many stems arising at or near the base.

§ Appropriate names for the community will depend on the nature of the dominant herb.

Table 1.

8 m in height, while low stature trees are defined as reaching from 5 m to 10 m in height. In their overlapping height ranges the two kinds of woody plants are separated by presence or absence of basitonic branching. While it may work in Australia, this separation would probably cause difficulties on a worldwide vegetation basis.

The two-way breakdown by spacing (i.e., % cover) and height in Table 1 results in 26 structural <u>formations</u> for Australia, which can be compared to the 31 formation classes of Fosberg that were intended for worldwide application.

From this it can be inferred that a separation of forest vegetations into low stature, intermediate structure and tall forests is necessary for Australia, if a structural system is to make any sense there. Fosberg suspected the need for this height distinction. In his suggested refinement on p. 81 in Peterken (1967), he admits that his one height classification of forest may result in lumping rather unlike types, such as subarctic spruce taiga with giant Douglas-fir forests in northwest America. But Fosberg points out that his system is flexible enough to accomodate such refinement. Another point is the four-way breakdown of spacing by the Australian classification into, for example, closed-forest, open-forest, woodland and openwoodland as opposed to Fosberg's three-way breakdown into closed-forest, open-forest and savanna. It would seem that Fosberg's system provides the flexibility for refinement in recognizing, for example, two spacing subclasses in his open-forest category, so that the two systems are not incompatible. This means that the Australian spacing categories should be translatable into the Fosberg system if the need arises. It is interesting that the Australian system includes structural subformations under its three spatially defined

- 23 -

herbland formations, whereas none are shown for the woody formations. Most, if not all, of these herbland subformations can also be translated into Fosberg's herbaceous subformations. The absence of structural subformations for the Australian woody formations indicates a greater utility for using floristic subdivisions, although L. Webb shows (in the next Section) that a number of structural criteria were found useful in distinguishing tropical rain forest types in N. Queensland. No mention is made of seasonality in the Australian system--certainly a reflection of the near-absence of deciduous forests in Australia.

The formation system of UNESCO .-- This classification system was established by the UNESCO Committee on Classification and Mapping of the Worlds's Vegetation based on a list supplied by Schmithüsen and Ellenberg. The system was published initially by Ellenberg and Mueller-Dombois (1967) and then, in slightly modified form by UNESCO (1973). The latter version includes a color and symbol scheme for 225 vegetation types compiled by Gaussen. The purpose of this classification is to serve as a basis for mapping world vegetation at a scale of 1:1 million in terms of vegetation units that indicate parallel environments or habitats in different parts of the globe. Existing classifications were reviewed and these have influenced the thinking of the committee (notably Rübel's system). But none of the existing systems were found entirely suitable for the intended purpose. As in Fosberg's system, vegetation structure forms the main separating criterion. However, terms referring to climate, soil and landforms were included in the vegetation names and definitions, wherever they aided in the identification of the units. The reason for this is that significant ecological differences in habitat are not always reflected by easily definable structural or physiognomic vegetation responses. For example, tropical lowland rain forests differ ecologically from tropical

- 24 -

montane rain forests. Yet, their structural differences are apparent only in certain regions and not on a worldwide scale.

The vegetation units are listed in hierarchical order under each of five formation classes. The five formation classes are, I Closed forests, II Woodlands or open forests, III Scrub or shrubland, IV Dwarf-scrub and related units, and V Herbaceous communities. Thus, spacing and height of dominant growth forms are treated as parallel criteria in distinguishing formation classes. Each woody formation class is subdivided into formation subclasses on the basis of whether the vegetation is mainly evergreen, mainly deciduous, or xeromorphic. These are then further separated into formation groups by the macroclimate in which they occur. For example, distinguished among closed forests that are mainly evergreen are tropical ombrophilous (or rain) forests, tropical and subtropical seasonal forests, tropical and subtropical semi-deciduous forests, temperate rain forests, etc. The next lower subdivision is the formation. Formations in tropical rain forests are tropical lowland rain forests, submontane and montane rain forests, tropical cloud forests, tropical subalpine rain forests (usually transitory to woodlands), tropical alluvial forests, tropical swamp rain forests and torpical bog forests. The next lower level represents the subformation, which together with the formation is considered the main map unit. For example, the tropical cloud forest is subdivided into a broadleaved subformation (the most common form) and a needle-leaved or microphyllous subformation.

The classification gives an outline of all better known formations of the earth. The system is flexible and allows inclusion of additional units if this should become necessary. It provides a framework that permits

- 25 -

accommodating an unlimited number of floristically quite different units (that occur in various localities scattered over the earth's surface) into physiognomically and ecologically equivalent abstract categories.

Both the UNESCO classification and Fosberg's scheme can be applied to categorize vegetation in the field and on maps in comparative terms within each scheme and also between the two schemes.

Fosberg's scheme provides a ready field tool for mapping at large and intermediate map scales. It allows one to establish pure vegetation units for correlations with environmental units mapped independently at the same scale. Because of its strictly structural orientation it may group ecologically quite different vegetations into the same unit. For example, tropical lowland and montane rain forests may form one vegetation unit. However, the ecological difference would become apparent upon comparing the vegetation units to environmental maps of such an area, and there would be no danger of circular reasoning.

The UNESCO scheme gives some environmental-geographic information at the start and therefore conveys an immediate orientation that appears useful for a worldwide inventory. It provides for an outline of major vegetation types and a general overview that can serve for immediate statistical purposes. For example, endangered vegetation in different parts of the world may be singled out for conservation. Specific mapping criteria may have to be worked out regionally within this framework. These can then be conveniently based on a combination of regionally significant structural and floristic criteria.

All structural systems are artificial. For example, an open forest or woodland may differ from a closed forest only because of some disturbance.

- 26 -

However, the primary objective of these schemes is identification of given vegetations. An arrangement according to ecological, sociological or historical relationships would handicap the diagnostic value of such a classification. Moreover, it would hardly ever be completed, since ecological, sociological and historical relationships are the objects of continuing research and readjustment.

Ellenberg's classification of world ecosystems: a functional scheme

Recently, Ellenberg (1973) presented a scheme for classifying the world into a hierarchy of ecosystems from a functional viewpoint. The largest and all encompassing ecosystem is the "biosphere", i.e., the outer skin of our planet (soil, water and atmosphere) as far as it is the life medium of organisms. It includes the oceans to their maximal depths. The biosphere is subdivided into two main groups according to type of energy source: (1) <u>natural or</u> <u>predominantly natural ecosystems</u>, i.e., those whose functions depend directly on the sun as energy source, and (2) <u>urban-industrial ecosystems</u>, whose functions depend on reconstituted energy (fossil fuel and recently, also atomic energy).

Six main separating criteria are used at different levels in the hierarchy:

- (a) prevailing life-medium (air, water, soil, buildings)
- (b) biomass and productivity of the primary producers
- (c) factors limiting the activity of primary producers, consumers and decomposers
- (d) regulating mechanisms of matter- or nutrient-gain or -loss
- (e) relative role of secondary producers (i.e., of the herbivores, carnivores, parasites and other mineralizers)

- 27 -

3

(f) the role of man in the ecosystem (i.e., his role in the origin, development, energy flow and mineral cycling of the ecosystem, particularly his function in supplementing energy sources)

A hierarchical order is obtained by defining successively smaller ecosystems within larger ecosystems. Starting with the biosphere, the next lower size-level is referred to as <u>mega-ecosystems</u>. Five mega-ecosystems are recognized by the life-media (criterion a) that they represent (capital letters as used in Ellenberg's key):

M Marine ecosystems (saline water)

L Limnic ecosystems (fresh water)

S Semi-terrestrial ecosystems (wet-soil and air)

predominantly

T Terrestrial ecosystems (aerated soil and air)

U Urban-industrial ecosystems (the creations of man) - artificial <u>Macro-ecosystems</u> are the next lower size-level within each mega-ecosystem. The macro-ecosystems are still very broad or inclusive units that are separated mainly by the criteria b to d (e.g., forests).

<u>Meso-ecosystems</u> are considered the basic units of this scheme. They are the "ecosystems" in the most commonly understood sense. A meso-ecosystem is considered a relatively uniform or homogeneous system with respect to the abiotic conditions as well as the life forms of the prevailing primary and secondary producers (e.g., a cold-deciduous broadleaf forest with its animal life).

<u>Micro-ecosystems</u> are subdivisions of meso-ecosystems, which depart with respect to a certain component (e.g., a lowland, montane, or subalpine cold-deciduous broadleaf forest with its animal life).

<u>Nano-ecosystems</u> are considered to be small ecosystems that are spatially contained within larger ecosystems and that exhibit a certain individuality of their own (e.g., a wet depression in a montane deciduous broadleaf forest).

Within almost all ecosystems one can recognize strata or other <u>partial</u> <u>systems</u>, which can be analyzed individually. At least three partial systems can be recognized generally:

<u>Topo-partial system</u>, i.e., a layer or other topographically stratified segment within an ecosystem (e.g., the topsoil in a forest)

<u>Substrate-partial system</u>, i.e., a small island-like community within an ecosystem (e.g., a moss-covered log in a forest)

<u>Pheno-partial system</u>, i.e., a partial system that appears only during a certain time of the year (e.g., an algal bloom at the surface of a lake)

The classification scheme includes a special scale for defining the kind and degree of human influences for each ecosystem to be classified. Four kinds of human interferences are recognized:

- (a) <u>Harvesting</u> of organic materials and minerals, which are significant for the metabolism of an ecosystem
- (b) Adding of mineral or organic materials or organisms
- (c) <u>Toxification</u>, i.e., adding of substances which are abnormal for the metabolism of the ecosystem and which are detrimental to important organisms or organism groups
- (d) <u>Changing of the species composition</u>, i.e., by suppressing existing species or by introducing alien species into the ecosystem.

The degree for each of the types of human interferences is expressed by a scale of increasing severity from 1 (e.g., no harvesting) to 9 (e.g., destructive harvesting).

For worldwide comparisons of ecosystems the scheme also includes a biogeographic separation into nine regions, such as tropo-american, tropoafrican, tropo-asian, australian, etc. Each of these biogeographic regions can be further subdivided into biogeographic subregions or provinces.

All criteria are identified in the scheme by letter symbols and a decimal system. These provide for classifying any ecosystem by a short formula on a worldwide basis.

An overview, in form of a key, shows the four predominantly natural mega-ecosystem types (M, L, S and T) subdivided to meso-ecosystems and in some examples to the level of nano-ecosystem and partial system (where well known). The scheme can be completed with derivation of further knowledge.

The key makes a major division between aquatic (M + L) and land ecosystems (S + T) on the basis of structure. The vertical extent of predominantly natural land ecosystems (in contrast to aquatic ecosystems) is not determined by their life medium (soil and air) and the availability of light, but by the height growth of the dominant vascular plants. It follows that the terrestrial ecosystems are defined primarily by vegetation structural criteria, and their classification is based on the UNESCO formation system. Therefore, meso- and micro-ecosystems are divisions somewhat parallel to formation and subformation types, but they are described in functional terms (criteria b to f as far as these are known). It may also be noted that the second structural unit-concept of synusia has given rise to the functional concept of partial system as used in this ecosystem scheme.

While the scheme is based entirely on structural-functional criteria, it is also clear that any exact investigation of ecosystems cannot ignore the species composition that forms the living matrix of the system. On the contrary, for any detailed investigation of ecosystems it is desirable to derive as complete as possible a species list of the participating plants and animals. Moreover, abundance determinations should be made for at least those species of plants and animals that are significant for the productivity

- 30 -

and maintenance of the ecosystem. These lists are then usefully ordered or classified according to animal- and plant-sociological viewpoints.

Floristic vegetation units and systems

Species dominance community-type concepts: the sociation and consociation.---Single, easily noticed plant species provide the simplest floristic tool for attaining relatively fast a certain order in the great variability of plant communities. These have always been used even by untrained persons, for example, in differentiating forest stands (beech forest, pine forest, etc.). Such a simple classification can also be very satisfactory for scientific purposes, if the area is floristically poor. In Scandinavian countries the most abundant or the most dominant species are used for distinguishing the so-called sociations.

Du Rietz (1921) considered the <u>sociation</u> the basic unit of vegetation classification and defined it as a recurring plant community of essentially homogenous species composition with at least certain dominant species in <u>each</u> layer. For example, the East German pine-heath communities form a <u>Pinus</u> <u>sylvestris-Calluna vulgaris-Cladonia</u> sociation, certain beech forests a <u>Fagus sylvatica-Allium ursinum</u> sociation, etc.

Du Rietz speaks of a <u>consociation</u> if only the <u>upper stratum</u> of a severallayered community is dominated by one species. As a type concept, a consociation can also be understood as a class composed of individual concrete sociations, whose upper strata are dominated by the same species, while the lower strata may be dominated by different species in each vegetation sample. The term consociation was used also by Clements, Tansley and Rübel in a very similar way. Consociations are more common than sociations particualrly in species-rich areas. An example is the oak forests of England, which, according to Tansley,

- 31 -

represent a consociation with very variable undergrowth. Few oak forests have the same dominants in the herb layer; one example is the <u>Vaccinium</u>-oak forests on acid soils.

Petersen (1927) tried to apply the consociation concept to the classification of meadow communities in Central Europe. He distinguished meadow types by the dominance of certain grass species, one dominant species characterizing a meadow type. However, because of the great number of species in Central and South Europe, there are rarely meadows with only one dominant species. Therefore, it would be necessary to consider most communities as mixed types or they would not fit into Petersen's system at all.

This difficulty with regard to the sociation and consociation concepts exists in all regions with large numbers of species, where many species compete for the same habitat. A good example is the tropical rain forest in continental lowland areas. Therefore, sociations and consociations have no universal applicability as units in vegetation classification.

However, even in such communities where single plant species have become dominant it is often not satisfactory to classify them as belonging to a certain consociation type. It was found that the same species may become dominant under diferent habitat conditions, whereby the associated flora may differ considerably in response to the differences in environment. For example, the tall reed grass <u>Phragmites communis</u> may grow in pure stands at the margin of larger lakes with occasional admixture of <u>Scirpus lacustris</u> or other tall semi-aquatic plants. <u>Phragmites</u> is found to also form vigorous stands at river margins in the tidal ranges, in habitats with considerable daily and annual fluctuations in water level. The associated plants named above cannot grow under these conditions. Instead, a more or less rich geophyte-flora is found growing there in the spring especially the yellowflowering <u>Ranunculus ficaria</u> and <u>Caltha palustris</u>. It is obvious that the two <u>Phragmites</u> consociations can be considered one unit only for very superficial reasons.

Thus, community types defined by a single dominant species (consociations) may lump together very different habitats. Moreover, the single dominant species concept cannot be applied in many regions. It is better to use a more flexible concept of floristic dominance types, where community types can be recognized by one or more dominant species in the prevailing synusia. This in fact, is the most widely used community-type concept in North American vegetation studies (Whittaker 1962), and in Australian studies (Specht et al. 1974). It lends itself to a relatively easy and informal system of classifying communities in many parts outside the continental tropics. In such floristically simpler areas, dominance-community types may be used effectively as the first floristic subdivisions of formations. They correspond approximately to the European type concept of alliance (Ellenberg 1959), which in the more formalized system of Braun-Blanquet, forms the floristic unit above the level of association.

Because more than one dominant species are often used to designate these dominance-community types, they have been called "associations" by Clements. These so-called "associations" are usually very large and heterogeneous in habitat conditions and they differ entirely from the European association concept, which is discussed in the next section.

The association concept.--It is quite possible in the above cited examples to differentiate several vegetation units if one considers the associated, as well as the dominant species. Units that are floristically defined in this manner are called associations. In contrast to a sociation, an association does not have to show a single dominant species in each layer. Instead more

- 33 -

than one species per layer may be used to define an association.

Following a resolution of the International Botanical Congress in Brussels in 1910, it was agreed to apply the term association only to communities "of definite floristic composition, uniform physiognomy and when occurring in uniform habitat conditions." In the continental European understanding, an association refers to a relatively small vegetation unit, a unit below the level of consociation. The 1910 International definition of the term association was rather strictly interpreted in continental Europe. However, an exact fulfillment of the three requirements (definite flora, uniform habitat, and physiognomy) is not always possible.

The requirement referring to a "uniform" habitat is particularly difficult to fulfill. A uniform habitat may be found in several field situations, but the vegetation samples to be grouped into an association-type can never have identical habitats, because no two places on the earth's surface have exactly the same combinations of site factors. Likewise, the criterion of definite flora needs closer definition. In classifying, it is impossible, even though ideal, to consider all species to be of equal significance. Because of the great variability of communities, one would have to distinguish as many "units" as there are plant communities. Even two closely similar vegetation samples will not have identical species lists. Yet, closely similar vegetation samples will have a certain proportion of species in common. Therefore, it is possible only to emphasize certain groups of species, namely those that recur commonly in different locations of a region. Only those communities are put into a type that show the same groups of species. Such groups can be distinguished either by comparing a large number of vegetation samples (i.e., by tabular comparison) or in other ways. An association-type therefore can be defined as a unit of vegetation derived from a number of vegetation samples or relevés that have a

- 34 -

certain number of their total species in common. An individual association member, i.e., a concrete community, can be recognized in the field by the presence of certain species of a diagnostic group.

Unfortunately, the Brussels definition does not really specify the criteria that were meant to be applied in the distinction of an association. As a result, two entirely different association concepts evolved in continental Europe and North America. The only criterion common to both these different interpretations is that an association name is made up of a combination of species names. In North America, Clements (1928) interpreted the term association very broadly to refer to the first subdivision of a formation. This broad association concept is still widely used in the United States and in Australia. Since Clements' "formation" was actually the general plant cover in a given macroclimatic region (i.e., a vegetation mosaic), his association concept was more or less a climatic subregion of which a selected vegetation cover was used as an indicator. For the whole of North America Clements recognized three so-called climaxes--a grassland, a scrub, and a forest climax. Each climax was subdivided into a few "formations" (= regions) and each "formation" was subdivided into two or more "associations." For example, in the forest climax, the Pacific coastal forest (region) was called the Thuja-Tsuga formation. This formation was subdivided into two associations, the Thuja-Tsuga association and the Larix-Pinus association. Clements defined an association floristically by joining the names of two regionally dominant species and then implied that an association was a grouping of two or more consociations. The term consociation was understood sensu Du Rietz. Thus, Clements' association concept was even more inclusive than the consociation concept, which defines community types by single dominant species.

- 35 -

<u>Braun-Blanquet's floristic association system</u>.--In brief, the system consists of preparing species lists in relevés* and then processing these lists in synthesis tables. In these tables, the species common to several relevés are identified and emphasized. This process has recently been automated by computer programs (Spatz 1972, Ceska and Roemer 1971). The species unique to each relevé are not ignored, but they are not given the same value as the species that recur together in a number of relevés. These common species groups are the key to the identification and mapping of vegetation units.

The association, as previously defined in the continental European sense, is considered the basic unit in Braun-Blanquet's (1928, 1951, 1964) system. Therefore, his system can be called a floristic association system. Other vegetation units are recognized by the same tabulation technique, but as units above or below the rank of association. In this way all units are interconnected in form of a hierarchy, but each unit is identified by certain common groups of species.

The different ranks are usually designated by a particular ending added to the root of the scientific genus name of an especially characteristic species. The following summary gives a general outline:

Rank	Ending	Example
class	~etea	Molinio-Arrhenatheretea
order	-etalia	Arrhenatheretalia
alliance	-ion	Arrhenatherion
association	-etum	Arrhenatheretum
subassociation	~etosum	Arrhenatheretum brizetosum
variant	no ending	Salvia variant of the Arrhenatheretum brizetosum
facies	-osum	Arrhenatheretum brizetosum bromosum erecti

* relevés = vegetation samples in plots large enough to contain at least 90-95% of the species of a vegetation segment or community.

- 36 -

The lowest unit in this system, the facies, is no longer characterized by exclusive species (i.e., "character species"), but merely by dominance of a certain (or several) species. Therefore, it corresponds in some respects to the consociation or sociation. However, it is viewed here in relation to the other ranked units, whose geographic coverage is progressively larger.

Recently, the tendency has developed to distinguish associations merely by differentiating species. This implies dispensing with the requirement of character species for an association. This development results from the experience that there are only/few character species in the strict sense. However, the alliances retain their own character species, while orders and classes usually show numerous character species.

The segregation of different vegetation units by differential species is based on tabular comparison of vegetation relevés. Therefore, it is based on a purely inductive method. However, ranking of the units into the previously discussed system, that is, in particular the solving of the question as to which of the units can be considered associations, depends on the personal judgment of the investigator.

EVALUATION

The check-sheet survey in relation to the stated methods and its specified objectives

The general objective of the CT check-sheet survey was to obtain in a relatively short period a description of natural areas and research sites with their vegetation types in internationally comparable terms. The specific purposes were (1) to find out which major vegetation types or ecosystems are receiving conservation status and (2) to determine how representative these vegetation types are on a worldwide basis. It is clear that this survey had

- 37 -

to be based on a structural system, because species distributions are by nature provincial, i.e., confined to floristic provinces.

It may be said that the general objective has been met most efficiently by the adoption of Fosberg's system. The reason is that of the structural systems this method is the easiest to apply; and it carries the most universal meaning. Dansereau's and Küchler's systems appear to be equally universal in application, but they require more detailed observations in sample plots. Küchler's formula method may take an intermediate position as far as time investment is concerned. Its unit hierarchy is not so formalized and resulting structural formulae may permit too many combinations to achieve a ready overview of parallel types. But this is again a matter entirely of purpose. Dansereau's profile method is the most detailed and time-consuming. It is probably most useful at large scales to very large scales, and is almost comparable in detail of unit-separation to the floristic association system of Braun-Blanquet.

The Australian system can be considered a regional refinement of Fosberg's system in so far as it leaves out (for Australia) unnecessary units, (for example, all deciduous woody vegetation types), while it incorporates refinement in forest height classes and plant cover density units. The latter are quantified. This makes the Australian types more objectively assessible. But the Australian system is not fundamentally different from Fosberg's scheme, and the Australian formations and subformations can probably all be translated into Fosberg types, should the need arise.

The UNESCO system is more specialized than Fosberg's in the sense that its application requires more experience to yield good results. A person with a good knowledge of world vegetation types may be able to translate all of Fosberg's types into the UNESCO system, should that become necessary during the planned UNESCO mapping project.

- 38 -

A word of caution may be added regarding the proposed 1:1 million map scale for the UNESCO units. The scale rarely allows mapping the outline of existing structurally defined formation types. Therefore, it would be more appropriate to call the UNESCO units "formation zones." For an inventory of conservation areas it would be necessary to locate the existing remnant formation types in their respective zones and to mark these by shading or with asterisks on the proposed 1:1 million International vegetation maps.

The first of the two specific CT check-sheet purposes--to find out which of the major vegetation types or ecosystems are receiving conservation status and which not--poses a more complex problem. Of course, the conservation status itself may be readily established from the check-sheets. But the problem of vegetation type diversity of an area can only be resolved in reference to a specified geographic scale range, because Fosberg's structural categories can be identified at different levels of homogeneity. For example, the concept of a "gnarled evergreen mossy forest" (Fosberg unit 1A1, 3) may be interpreted as a cloud forest belt (at the scale of 1:1 million) in one surveyor's mind, while it may be rather exactingly interpreted (at the scale of 1:10,000) by another.

It must be remembered that classification of vegetation usually involves two levels of abstraction. The first level is introduced in the segmentation or subdividing of a vegetation cover by the homogeneity concept of the investigator. One must decide what range of variation in the vegetation cover one can reasonably recognize as a vegetation segment or unit. The second level of abstraction is introduced in the grouping of similar segments into vegetation categories or classes. This part of the classification process depends on the similarity concept of the investigator.

When vegetation has been abstracted twice in this fashion the established

- 39 -

categories may or may not have much reality in nature. The classification itself gives very little information on this question unless it is well documented by vegetation samples (i.e., relevés). But even then the validity of the classification is not always easy to interpret. The test of validity of a vegetation classification comes when the established categories are projected on a map. Therefore, a vegetation classification cannot really be considered complete until it is supplied with a vegetation map.

This means that the check-sheet survey may only give a first approximation of the diversity of structural vegetation types in the areas surveyed. A more definite answer can only be obtained through a map application of Fosberg's system in the check-sheet sites.

The second specific purpose of the IBP/CT survey--to establish what sort of representation the check-sheet areas give on a worldwide basis--can hardly be answered with this survey. This is so because there is generally not enough knowledge on the vegetation types outside the surveyed areas. This information can only be achieved through a worldwide effort to map vegetation types. This leads to the following recommendation.

Hierarchical mapping for conservation purposes: a recommendation

The insufficient cover of the IBP/CT check-sheet survey in terms of world distribution of available areas has been brought out in previous sections of this book. But even if the distribution of check-sheet returns have approached a more complete global coverage, the survey can only be viewed as a first approximation. As such it has established a momentum now, at the end of IBP, that should be utilized and developed further through the next internationally coordinated research programs, notably by the UNESCO MAB 8 Project.

One cannot reasonably expect that a complete survey of globally available

- 40 -

vegetation types at the previously discussed large geographic scale of level 4 can be made within the time contraints of even a 10-year program. However, it is at this large map-scale of 1:10,000 to 1:100,000 that ecological field research and natural area management has to operate in order to be locally meaningful and effective. For one thing, conservation of biological resources becomes meaningful only when we begin to take stock of the species in the communities and ecosystems. We must further understand their quantitative relationships, their dynamic tendencies, and the ecological roles of at least the more important species, whether they be dominant or rare and endangered.

A global survey for conservation of species and ecosystems would best be approached through a program of hierarchical mapping. A world inventory of conservation sites or ecological reserves should relate all sites to a <u>system</u> <u>of ecological zones</u>. Furthermore, because of the provincial nature of species distributions, it is of utmost importance that superimposed on the system of ecological zones is a <u>system of biogeographical provinces</u>. These provinces will serve to emphasize the uniqueness of the biological populations that comprise ecosystems occurring in otherwise structurally and environmentally similar vegetations in different parts of the world.

It is important that a global survey of this sort uses all existing information. At the broadest level of generalization (Level 1), Schmithüsen's 1:25 million world vegetation map can be adapted with relatively little extra work. Firstly, the world vegetation formation zones indicated on that map may be used to search for existing remnants of real vegetation types of world formations (to be located by dots on the same map). The same map should also be supplied with the boundaries of world biogeographic provinces of such categories as suggested by Ellenberg (1973; i.e., tropo-american, tropo-asian, australian, etc.). Secondly, a search should be made for Level 2 vegetation

- 41 -

and ecological zonation maps, e.g., Küchler's map of the U.S.A. or Krajina's map of British Columbia. On these maps also, the still existing remnant vegetation types of zonal significance should be located by asterisks. Wherever possible, biogeographic boundaries should be indicated. The UNESCO plan of generating a comparable set of international vegetation maps (UNESCO 1973) at the scale of 1:1 million deserves the greatest support in this respect: once put into action, the mapping project can supply reliable information on the status of world ecosystems. The 1:1 million mapping project should make full use of the tremendous advances recently made in remote sensing technology. In this way a real breakthrough could be achieved by mapping world ecosystems in considerable detail.

Any important individual area should then be enlarged to Level 4 map scales (ranging from 1:100,000 to 1:1 million) for an inventory of major ecosystems within states, provinces, or island groups. The next enlargement to Level 5 maps then becomes very meaningful in the global network of ecological reserves.

The large geographic scale range at Level 5 (1:10,000 to 1:100,000) is the one that forms the underpinning of the various vegetation type concepts and classification systems discussed above, because all of these are based on experience gained in the field with real (in contrast to potential) vegetation.

Recall the previously mentioned ambiguity of the homogeneity concept relating to segmentation of a vegetation cover into communities. This ambiguity can be minimized by specifying the geographic scale. For example, if an area is to be classified into communities at the scale of 1:10,000, different investigators are likely to stress similar subunits, particularly if the classification system is specified also. Ambiguity at the second level of abstraction in classification--the similarity concept of the investigator-would likewise be minimized by specifying geographic scale and classification

- 42 -

system. The similarity concept can even be objectified to some extent by using similarity indices.

It must be understood clearly that the task of surveying the biological resources on our planet is not complete until we produce an inventory of species populations with information on their grouping, quantities, and dynamic status in their respective communities. This task can only be accomplished through intensive local area studies involving the establishment of a large number of sample stands or relevés. There is little doubt that the most successful method for this purpose is the relevé method of Braun-Blanquet. It must be emphasized that the method cannot serve to establish a worldwide hierarchy of floristically defined communities, because species ranges differ from area to area. However, the sampling of species lists in the field, with indications of their quantities in a series of relevés or sample stands, can be done in all vegetation areas of the world. It is the most thorough and the most rapid community analysis method for this specific purpose. Moreover, there are a number of relatively simple, rapid, and meaningful data processing methods available, ranging from the two-way table technique to the dendrogram method of cluster analysis (Mueller-Dombois and Ellenberg 1974).

In the establishment of a global network of ecological reserves, it would seem appropriate that first urgency is put on the development of the 1:1 million International Vegetation Maps. Second priority should be given to the more detailed floristic and faunistic local area surveys. For the specified purpose at hand it would seem appropriate to promote the relevé method as the best formal inventory technique for local area research and management. Depending on the nature of the regional vegetation, the relevé method can be employed in connection with large-scale structural vegetation maps established through Fosberg's classification criteria, or it can be used in connection with any

- 43 -

other large-scale existing vegetation map (e.g., one based on speciesdominance criteria). Moreover, the method itself may supply the criteria for mapping floristically defined finer subdivisions by yielding--in most situations--diagnostic or key species through the two-way table technique. These key species in turn can serve as the basis for mapping floristically defined community types--community types useful as a framework for natural area research and management.

- 44 -

LITERATURE CITED

- Braun-Blanquet, J. 1928. Pflanzensoziologie. Springer-Verlag, 1st ed., Berlin, 1928, 2nd ed., Vienna, 1951. 631 p. 3rd ed., Vienna, New York, 1964.
- Ceska, A., and H. Roemer. 1971. A computer program for identifying speciesrelevé groups in vegetation studies. Vegetatio 23:255-277.
- Clements, F. E. 1928. Plant succession and indicators. H. W. Wilson Co., New York. 453 p.
- Comanor, P. L. 1971. An analysis of the woody scrub vegetation of Ruhuna National Park, Ceylon. Trop. Ecol. 12:209-222.
- Dansereau, P. 1951. Description and recording of vegetation upon a structural basis. Ecology 32:172-229.
- Dansereau, P. 1957. Biogeography, an ecological perspective. The Ronald Press, New York. 394 p.
- Du Rietz, G. E. 1921. Zur methodologischen Grundlage der modernen Pflanzensoziologie. Akadem. Abh. Wien. A. Holzhausen. 272 p.
- Eberhardt, E., D. Kopp, and H. Passarge. 1967. Standorte und Vegetation des Kirchleerauer Waldes im Schweizerischen Mitteland [with English summary]. p. 13-134 in H. Ellenberg, ed. Ecological and pedological methods of forest site mapping. Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich. Heft 39. 298 p. with 5 maps.
- Eisenberg, J. F., and M. Lockhart. 1972. An ecological reconnaissance of Wilpattu National Park, Ceylon. Smithsonian Contr. Zoology. Washington, D. C. No. 101, 118 p.
- Ellenberg, H. 1959. Können wir eine Gemeinsame Plattform für die verschiedenen Schulen in der Waldtypenklassifikation finden? Silva Fennica, Helsinki 105:26-32.
- Ellenberg, H. 1967. Ecological and pedological methods of forest site mapping [in German, English summaries]. Veröff. Geobot. Inst. ETH Stiftung Rübel Zürich, No. 39. 298 p. With six maps at 1:10,000.
- Ellenberg, H. 1973. Die Ökosysteme der Erde: Versuch einer Klassifikation der Ökosysteme nach funktionalen Gesichtspunkten. p. 235-265 in H. Ellenberg, ed. Ökosystemforschung. Springer-Verlag, Berlin, Heidelberg, New York. 280 p.
- Ellenberg, H., and F. Klötzli. 1967. Vegetation und Bewirtschaftung des Vogelreservates Neeracher Riet. Ber. Geobot. Inst. ETH, Stiftung Rübel, Zürich, 37:88-103. With 1:2,500 map.
- Ellenberg, H., and D. Mueller-Dombois. 1967. Tentative physiognomic-ecological classification of plant formations of the earth. Ber. Geobot. Inst. ETH, Stiftung Rübel, Zürich, 37:21-55.

- Ellenberg, H., and D. Mueller-Dombois. 1967. A key to Raunkiaer plant life forms with revised subdivisions. Ber. Geobot. Inst. ETH, Stiftung Rübel, Zürich, 37:56-73.
- Fosberg, F. R. 1961. A classification of vegetation for general purposes. Trop. Ecol. 2:1-28. [Republished in modified form in G. F. Peterken. 1967. Guide to the check sheet for IBP areas. IBP Handbook No. 4. Blackwell Scientific Publications, Oxford and Edinburgh, p. 73-120.]
- Gams, H. 1918. Prinzipienfragen der Vegetationsforschung. Ein Beitrag zur Begriffsklärung und Methodik der Biocoenologie. Vierteljahrsschr. Naturforsch. Ges. Zürich, 63:293-493.
- Gaussen, H. 1957. Interpretation of data by means of vegetation maps. Proceed. 9th Pacific Sci. Congress, Bangkok.
- Gaussen, H., P. Legris, M. Viart, and L. Labroue. 1964. International map of vegetation, Ceylon. Special sheet, Survey Dept. of Ceylon (Sri Lanka).
- Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi, Jr. 1971. Forest environments in a tropical life zone: A pilot study. Pergamon Press, Oxford, New York. 747 p.
- Köppen, W. 1936. Das geographische System der Klimate. Vol. 1, Part C <u>in</u> W. Köppen and R. Geiger, Handbuch der Klimatologie. Gebr. Borntraeger, Berlin.
- Krajina, V. J. 1969. Ecology of forest trees in British Columbia. Ecology of Western North America [Published by the Dept. of Botany, Univ. of British Columbia] 2:1-147. With map of "Biogeoclimatic Zones."
- Krajina, V. J. 1974. Biogeoclimatic zones of British Columbia. Map at 1:1.9 million published by Brit. Columbia Ecological Reserves Committee, Dept. of Lands, Forests and Water Resources, Victoria, B.C.
- Kuchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Manual to accompany the map. Am. Geogr. Soc., Special Publication No. 36. 116 p. Revised ed. of map, 1965.
- Kuchler, A. W. 1967. Vegetation mapping. The Ronald Press Co., New York. 472 p.
- Küchler, A. W. 1974. A new vegetation map of Kansas. Ecology 55:586-604.
- Lippma, T. 1939. The unistratal concept of plant communities [the unions]. Amer. Midl. Naturalist 21:111-145.

Mueller-Dombois, D. 1965. Eco-geographic criteria for mapping forest habitats in southeastern Manitoba. Forest. Chron. [Vancouver, B.C.] 41:188-206.

- Mueller-Dombois, D. 1972. Crown distortion and elephant distribution in the woody vegetations of Ruhuna National Park, Ceylon. Ecology 53:208-226.
- Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York [in press].
- Peterken, G. F. 1967. Guide to check sheet for IBP areas. IBP Handbook No. 4. Blackwell Scientific Publications, Oxford and Edinburgh. 133 p.
- Petersen, A. 1927. Die Taxation der Wiesenländereien auf Grund des Pflanzenbestandes. Berlin.

Raunkiaer, C. 1937. Plant life forms. Clarendon, Oxford. 104 p.

- Schmithüsen, J. 1968. Vegetation maps at 1:25 million of Europe, North Asia, South Asia, SW Asia, Australia, N Africa, S Africa, N America, Central America, South America (north part), South America (south part). XVIII: 321-346 in Grosses Duden-Lexikon [Bibliographisches Institut A. G., Mannheim].
- Spatz, G. 1972. Eine Möglichkeit zum Einsatz der elektronischen Datenverarbeitung bei der pflanzensoziologischen Tabellenarbeit. p. 251-261 in E. van der Maarel and R. Tüxen, eds. Ber. Intern. Vereinigung f. Vegetationskunde 1970 [Basic problems and methods in phytosociology]. W. Junk, The Hague.
- Specht, R. L. 1970. Vegetation. p. 44-67 in G. W. Leeper, ed. The Australian environment. 4th ed. CSIRO-Melbourne Univ. Press, Melbourne.
- Specht, R. L., E. M. Roe, and V. H. Boughton, eds. 1974. Conservation of major plant communities in Australia and Papua, New Guinea. Austral. J. Bot., Supp. Ser. Supp. No. 7. CSIRO, Melbourne. 666 p.
- Tansley, A. G. 1939. The British Islands and their vegetation. 2nd ed. 1953. Univ. Press, Cambridge, Vol. I:1-484, Vol. II:487-930.
- Thornthwaite, C. W. 1948. An approach toward a rational classification of climate. Geogr. Rev. 38:55-94.
- UNESCO. 1973. International classification and mapping of vegetation. UNESCO Ecology and Conservation series No. 6, 93 p. and chart with map symbols.
- Walter, H. 1957. Wie kann man den Klimatypus anschaulich darstellen? Die Umschau in Wissenschaft und Technik, Heft 24:751-753.
- Walter, H. 1971. Ecology of tropical and subtropical vegetation. [Transl. by D. Mueller-Dombois, ed. by J. H. Burnett]. Oliver and Boyd, Edinburgh. 539 p.
- Whittaker, R. H. 1962. Classification of natural communities. Botan. Rev. 28:1-239.

TECHNICAL REFORTS OF THE US/IBP ISLAND ECOSYSTEMS IRP

(Integrated Research Program)

- *No. 1 Hawaii Terrestrial Biology Subprogram. First Progress Report and Second-Year Budget. D. Mueller-Dombois, ed. December 1970. 144 p.
- *No. 2 Island Ecosystems Stability and Evolution Subprogram. Second Progress Report and Third-Year Budget. D. Mueller-Dombois, ed. January 1972. 290 p.
- *No. 3 The influence of feral goats on koa (<u>Acacia koa</u> Gray) reproduction in Hawaii Volcanoes National Park. G. Spatz and D. Mueller-Dombois. February 1972. 16 p.
- *No. 4 A non-adapted vegetation interferes with soil water removal in a tropical rain forest area in Hawaii. D. Mueller-Dombois. March 1972. 25 p.
- *No. 5 Seasonal occurrence and host-lists of Hawaiian Cerambycidae. J. L. Gressitt and C. J. Davis. April 1972. 34 p.
- *No. 6 Seed dispersal methods in Hawaiian <u>Metrosideros</u>. Carolyn Corn. August 1972. 19 p.
- *No. 7 Ecological studies of <u>Ctenosciara hawaiiensis</u> (Hardy) (Diptera: Sciaridae). W. A. Steffan. August 1972. 7 p.
- *No. 8 Birds of Hawaii Volcanoes National Park. A. J. Berger. August 1972. 49 p.
- *No. 9 Bioenergetics of Hawaiian honeycreepers: the Amakihi (Loxops virens) and the Anianiau (L. parva). R. E. MacMillen. August 1972. 14 p.
- *No. 10 Invasion and recovery of vegetation after a volcanic eruption in Hawaii. G. A. Smathers and D. Mueller-Dombois. September 1972. 172 p.
- *No. 11 Birds in the Kilauea Forest Reserve, a progress report. A. J. Berger. September 1972. 22 p.
- No. 12 Ecogeographical variations of chromosomal polymorphism in Hawaiian populations of <u>Drosophila immigrans</u>. Y. K. Paik and K. C. Sung. February 1973. 25 p.
- *No. 13 The influence of feral goats on the lowland vegetation in Hawaii Volcanoes National Park. D. Mueller-Dombois and G. Spatz. October 1972. 46 p.
- *No. 14 The influence of SO₂ fuming on the vegetation surrounding the Kahe Power Plant on Oahu, Hawaii. D. Mueller-Dombois and G. Spatz. October 1972. 12 p.
- No. 15 Succession patterns after pig digging in grassland communities on Mauna Loa, Hawaii. G. Spatz and D. Mueller-Dombois. November 1972. 44 p.
- No. 16 Ecological studies on Hawaiian lava tubes. F. G. Howarth. December 1972. 20 p.
- No. 17 Some findings on vegetative and sexual reproduction of koa. Günter 0. Spatz. February 1973. 45 p.
- No. 18 Altitudinal ecotypes in Hawaiian <u>Metrosideros</u>. Carolyn Corn and William Hiesey. February 1973. 19 p.
- No. 19 Some aspects of island ecosystems analysis. Dieter Mueller-Dombois. February 1973. 26 p.
- No. 20 Flightless Dolichopodidae (Diptera) in Hawaii. D. Elmo Hardy and Mercedes D. Delfinado. February 1973. 8 p.

* out of print

- No. 21 Third Progress Report and Budget Proposal for FY 74 and FY 75. D. Mueller-Dombois and K. Bridges, eds. March 1973. 153 p.
- No. 22 Supplement 1. The climate of the IBP sites on Mauna Loa, Hawaii. Kent W. Bridges and G. Virginia Carey. April 1973. 141 p.
- No. 23 The bioecology of <u>Psylla uncatoides</u> in the Hawaii Volcanoes National Park and the <u>Acacia koaia</u> Sanctuary. John R. Leeper and J. W. Beardsley. April 1973. 13 p.
- No. 24 Phenology and growth of Hawaiian plants, a preliminary report. Charles H. Lamoureux. June 1973. 62 p.
- No. 25 Laboratory studies of Hawaiian Sciaridae (Diptera). Wallace A. Steffan. June 1973. 17 p.
- No. 26 Natural area system development for the Pacific region, a concept and symposium. Dieter Mueller-Dombois. June 1973. 55 p.
- No. 27 The growth and phenology of <u>Metrosideros</u> in Hawaii. John R. Porter. August 1973. 62 p.
- *No. 28 EZPLOT: A computer program which allows easy use of a line plotter. Kent W. Bridges. August 1973. 39 p.

No. 29 A reproductive biology and natural history of the Japanese white-eye (Zosterops japonica japonica) in urban Oahu. Sandra J. Guest. September 1973. 95 p.

- No. 30 Techniques for electrophoresis of Hawaiian Drosophila. W. W. M. Steiner and W. E. Johnson. November 1973. 21 p.
- No. 31 A mathematical approach to defining spatially recurring species groups in a montane rain forest on Mauna Loa, Hawaii. Jean E. Maka. December 1973. 112 p.
- *No. 32 The interception of fog and cloud water on windward Mauna Loa, Hawaii. James O. Juvik and Douglas J. Perreira. December 1973. 11 p.
- No. 33 Interactions between Hawaiian honeycreepers and <u>Metrosideros collina</u> on the island of Hawaii. F. Lynn Carpenter and Richard E. MacMillen. December 1973. 23 p.
- No. 34 Floristic and structural development of native dry forest stands at Mokuleia, N.W. Oahu. Nengah Wirawan. January 1974. 49 p.
- No. 35 Genecological studies of Hawaiian ferns: reproductive biology of pioneer and non-pioneer species on the island of Hawaii. Robert M. Lloyd. February 1974. 29 p.
- No. 36 Fourth Progress Report and Budget Proposal for FY 1975. D. Mueller-Dombois and K. Bridges, eds. March 1974. 44 p.
- No. 37 A survey of internal parasites of birds on the western slopes of Diamond Head, Oahu, Hawaii 1972-1973. H. Eddie Smith and Sandra J. Guest. April 1974. 18 p.
- No. 38 Climate data for the IBP sites on Mauna Loa, Hawaii. Kent W. Bridges and G. Virginia Carey. May 1974. 97 p.
- No. 39 Effects of microclimatic changes on oogenesis of <u>Drosophila mimica</u>. Michael P. Kambysellis. May 1974. 58 p.
- No. 40 The cavernicolous fauna of Hawaiian lava tubes, Part VI. Mesoveliidae or water treaders (Heteroptera). Wayne C. Gagné and Francis G. Howarth. May 1974. 22 p.

* out of print

- No. 41 Shade adaptation of the Hawaiian tree-fern (<u>Cibotium glaucum</u> (Sm.) H. & A.). D. J. C. Friend. June 1974. 39 p.
- No. 42 The roles of fungi in Hawaiian Island ecosystems.I. Fungal communities associated with leaf surfaces of three endemic vascular plants in Kilauea Forest Reserve and Hawaii Volcanoes National Park, Hawaii. Gladys E. Baker, Paul H. Dunn and William A. Sakai. July 1974. 46 p.
- No. 43 The cavernicolous fauna of Hawaiian lava tubes, Part VII. Emesinae or thread-legged bugs (Heteroptera: Redvuiidae). Wayne C. Gagné and Francis G. Howarth. July 1974. 18 p.
- No. 44 Stand structure of a montane rain forest on Mauna Loa, Hawaii. Ranjit G. Cooray. August 1974. 98 p.
- No. 45 Genetic variability in the Kilauea Forest population of <u>Drosophila</u> silvestris. E. M. Craddock and W. E. Johnson. September 1974. 39 p.
- No. 46 Linnet breeding biology on Hawaii. Charles van Riper III. October 1974. 19 p.
- No. 47 The nesting biology of the House Finch, <u>Carpodacus mexicanus frontalis</u> (Say), in Honolulu, Hawaii. Lawrence T. Hirai. November 1974. 105 p.
- No. 48 A vegetational description of the IBP small mammal trapline transects -Mauna Loa Transect. James D. Jacobi. November 1974. 19 p.
- No. 49 Vegetation types: a consideration of available methods and their suitability for various purposes. Dieter Mueller-Dombois and Heinz Ellenberg. November 1974. 47 p.