The Role of Terrestrial Vegetation in the Global Carbon Cycle:
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CHAPTER 2
Classification and Mapping of Plant Communities: a Review with Emphasis on Tropical Vegetation

D. Mueller-Dombois
Deparrment of Botany, University of Hawaii at Manoa, Honolulu, Hawaii

ABSTRACT

Methods of classifying vegetation are reviewed. Classification is aimed at portraying either potential or existing vegetation. Potential vegetation is commonly mapped using bioclimatic classification schemes following scholars such as Holdridge or Walter or landscape classification schemes such as those of UNESCO and Ellenberg. Maps of potential vegetation obtained from bioclimatic parameters can be used as predictors of primary production. Existing vegetation is mapped by either a classification based on physiognomy or on floristics. The physiognomic method provides a better estimate of phytomass because it takes into account variations due to succession and habitat. Bioclimatic and landscape classifications work equally well in temperate and tropical zones when mapped at a small scale. Problems in large-scale mapping of the tropics arise from the diversity of the species, different patterns of distribution, and lack of field studies. The author suggests mapping the existing vegetation of the tropics by combining satellite imagery with ancillary information from large-scale maps. Satellite imagery can be used to monitor the rate of loss of tropical ecosystems by use of successive images.

2.1 INTRODUCTION

The general objectives for classifying and mapping vegetation are three:

(1) Recognition and outlining of vegetation patterns for purposes of overview or inventory.
(2) Extrapolation of field observations and measurements to an appropriate level of geographic and ecological generalization.
(3) Explanation of vegetation patterns in terms of environment, past as well as present.

2.2 CLASSIFICATION SYSTEMS: POSSIBILITIES AND LIMITATIONS

The classification and the mapping of vegetation are fundamental tools for obtaining knowledge about the earth's vegetation cover and its relationship to the earth's environment. Classification has a twofold purpose: to sort the various patterns of plant communities that form a matrix of global, regional and local vegetation covers, and to investigate and explain their ecological relationships.

Two basic aspects of vegetation require explanation. They are its variation in space and its variation in time. One of the important tools for determining vegetation's variation in space is mapping. One of the important tools for determining variation in time is repeated mapping. This latter approach to vegetation dynamics has not been used as widely as it could have been, but the approach will gain importance in the future because of developments in aerial photography. This approach will also be promoted through the increased use of remote sensing techniques.

In addition to mapping, there are many other traditional and modern tools for documenting spatial and temporal variations in vegetation. These include profile diagrams (Davis and Richards, 1933, 1934; Beard, 1946, 1978), ordination diagrams (Whittaker, 1978a), dendrographs, two-way tabulations (Braun-Blanquet, 1928, 1965; Mueller-Dombois and Ellenberg, 1974), and many other multivariate analysis techniques (Orloci, 1978). These data-display tools differ in their degree of abstraction and are often complementary. Maps and profile diagrams are perhaps the most fundamental and easy to understand.

Classification requires two levels of abstraction, which are also transferred to most vegetation maps. The first level occurs from the process of recording a vegetation sample (or relevé)* in the field. In a vegetation sample, the researcher 'abstracts' a number of characteristics from a segment of the plant community of which the sample should be representative. This first-level abstraction applies also to vegetation descriptions, which are done without taking formal samples. The second level of abstraction relates to the grouping of individual samples into community types.

Both levels of abstraction have received a great deal of attention, and disagreement over the second level caused a major schism. Gleason (1926) believed that community samples differ so much from place to place that it was not appropriate to group them into classes or types. Three decades later a multidimensional ordination technique was developed by Bray and Curtis (1957) which was believed to do more justice to the multivariate nature of vegetation than classification does. More recently, the two viewpoints have been reconciled (Mueller-Dombois and Ellenberg, 1974; Orloci, 1978;

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* The French word for 'abstract'.

Whittaker, 1978a), and the complementary aspects of the two techniques have been emphasized.

It is well to remember, however, that some detailed information is lost through the use of either process as certain generalizations are formulated. The value of a plant community classification lies in the formulation of generalizations which are the most appropriate ones for the purposes at hand. All classifications and all vegetation maps are purposive in nature, but they range from classifications and maps done for general ecological purposes to those done for very restricted purposes. In the latter group, for example, are many maps prepared for the exploitation of forests.

When existing maps and classifications are used for new purposes, such as answering questions about the global carbon dioxide cycle, they may not be adequate. New classifications or maps may have to be developed, or existing ones reinterpreted.

2.2.1 Criteria for Classifying Plant Communities

Vegetation is classified according to a number of criteria based on either the vegetation itself, the environment surrounding the vegetation or a combination of the vegetation and its environment.

Table 2.1 summarizes these criteria as physiognomic, floristic, environmental, geographic, successional and vegetation–environmental (two types).

The physiognomic criteria refer to the morphological patterns or form-variations of the vegetation cover. The basic plant community unit is therefore called a *formation*, and classification schemes using physiognomic criteria are often called formation systems. The subcriteria in Table 2.1 indicate that one can classify vegetation physiognomically by the dominant growth form or life form,* by a combination of life forms, by the characteristics of the vegetation layers (often easily distinguished by height stratification in forest communities) and by periodicity—for example, by the synchronized leaf fall and resprouting that occurs in certain forest and scrub communities. Analogous behaviour is the periodic dying of annuals in annual grasslands or the periodic drying and regreening of grass shoots in many perennial grasslands. The concept can be further extended to periodicity in flowering and fruiting and to the patterning of these phenomena within and between plant communities.

Floristic criteria are used for classifying and mapping variations in the distribution and composition of species in a vegetation cover. Depending on the vegetation and the purposes of the classification, one can use single

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* Some authors (e.g. Beard, 1978) prefer to apply the term 'growth form' to trees, shrubs, grasses, etc. and the term 'life form' to the Raunkiaerian life forms (Raunkiaer, 1937), such as phanerophytes, chamaephytes, hemicryptophytes, etc. The latter term has a more functional connotation, but the distinction is not important here.

Table 2.1 Criteria for classifying vegetation

Properties of the vegetation itself	Properties outside the vegetation	Properties combining vegetation and environment
1 Physiognomic Dominant growth form or life form Combination of growth or life forms Layers Periodicity 2 Floristic Dominant species Combination of dominants Certain groups of species: defined through tabulation techniques or numerical criteria (multi-variate analyses)	3 Environment (or habitat) By individual components Climate Topography Land form Soil Human influences By combination of site factors 4 Geographical location 5 Successional stage By presumed final stage (climax): defined by life-form combinations or floristic criteria or by environmental factors	6 By independent analysis of strictly vegetational criteria and independent analysis of environmental components and subsequent correlation (e.g. through map overlays) 7 By combined analysis of vegetation and environment into integrated units: Ecosystem classification Emphasis is on functional interrelationships

dominant species, combinations of dominants, or other groups of species. Community types classified through the use of a single dominant species or a combination of dominants have been distinguished by Whittaker (1962, 1978b) as *dominance types*. Communities classified through the use of species groups derived by means of the Braun-Blanquet tabulation technique, or species groups derived through mathematical multivariate techniques, have been distinguished as *association types* (Mueller-Dombois and Ellenberg, 1974; Whittaker, 1978b). Species or groups of species which are used to distinguish association types may also be dominant species, but the main criterion is that they must have restricted ranges or amplitudes within the vegetation cover to be analysed so that subdivisions or patterns can be distinguished. They can thus also be called differentiating (or differential) species.

Environmental criteria have been used for both formal and informal classification systems. Formal classification systems based on environmental criteria are, for example, the bioclimatic systems of Köppen (1936), Thornthwaite (1948) and Holdridge (1967). Walter (1955, 1971, 1973a) has demonstrated a more flexible approach through the use of climate diagrams, which do not necessarily prescribe the boundaries of the areas to be classified. Various landscape classifications have been developed through the use of one or more of the other environmental criteria listed in Table 2.1 with the aim of predicting the vegetation potential of different segments of land.

Geographic criteria are often used in comprehensive classifications of vegetation on whole continents, such as those for the forests of South America by Hueck (1966) or the vegetation of Africa by Knapp (1973). These treatments are informal and do not follow a prescribed scheme of classification.

A highly formalized scheme for classifying successional stages, based primarily on environmental criteria and dominant species, was developed by Clements (1916, 1928).

Schemes based on independent analysis of strictly vegetational criteria are those of Dansereau (1957), Fosberg (1961, 1967), Küchler (1964) and Specht (1970). The ecological meaning of these classifications is determined by matching them against independently derived environmental classifications or maps.

Criteria that involve the combination of information about vegetation and environment integrated into units include the ecological series approach of Sukachev (1928), the biogeoclimatic zonation scheme of Krajina (1965, 1969) and the world ecosystem classification of Ellenberg (1973).

2.2.2 The Classic Systems and Their Limitations

The best known classic systems are:

(1) The physiognomic classifications of Grisebach (1872) and Drude (1902), which use only vegetation form without reference to species.
(2) The environmentally oriented classifications of Warming (1909), Graebner (1925) and Sukachev (1932), which use environmental factors as the primary criteria for plant community recognition.
(3) The physiognomic–environmental classifications of Schimper (1898), Diels and Mattick (1908), Brockmann-Jerosch and Rübel (1912), Du Rietz (1921) and Rübel (1933). (Du Rietz also used dominant species.) These systems use physiognomic criteria mixed with environmental descriptors.
(4) The areal–geographic–floristic classification of Schmid (1963), which uses the geographic distribution of species to define floristic provinces at various levels of detail.
(5) The dynamic–floristic classifications of Clements (1916, 1928), Tansley and Chipp (1926) and other American and British ecologists, which are based mainly on the final stages of succession (climax). The detailed classification system proposed by Clements was based on a number of successional

stages inferred from environmental and dominant species criteria. This system, however, is no longer used as a formalized approach.

(6) The floristic–structural classifications of Cajander (1909) and Braun-Blanquet (1928). Both use species groups with restricted amplitudes for defining vegetation units. Cajander's method is oriented toward the identification of forest site types, whereas Braun-Blanquet's approach is oriented toward analysing all kinds of mosaic patterns of species distribution or composition in a regional or local vegetation cover.

The physiognomic–environmental concept, for example, provided the framework for the International Biological Program (IBP) Biome studies in the US, in which the focus of research was on the functional interrelationships of the components of ecosystems (criterion 7 in Table 2.1). The physiognomic–environmental concept also influenced a classification system (Mueller-Dombois and Ellenberg, 1974) developed for UNESCO (1973) for mapping the world's vegetation at a scale of 1:1 million. A further step toward a scheme for classifying ecosystems according to criterion 7 was provided by Ellenberg (1973).

The successional viewpoint (criterion 5) has given rise to studies of the long-term dynamics of vegetation. For example, it has inspired ecological approaches to analyses of stand structure for predicting the future development of forest stands (Leak, 1965; Goff and West, 1975). The environmental viewpoint (criterion 3) has spawned modern approaches to environmental, or 'direct', gradient analysis (Whittaker, 1978a). The floristic approach has given rise to new methods of mosaic analysis called 'indirect' gradient analysis by Whittaker (1978a). The physiognomic approach has been successfully subjected to detailed numerical analyses (Knight and Loucks, 1969; Webb *et al.*, 1970, 1976) and used to develop new approaches for classifying vegetation biomass (Fosberg, 1967; Specht, 1970; Specht *et al.*, 1974).

The six classic approaches and their contemporary modification all have certain limitations. The original physiognomic classifications, for example, gave only broad global overviews of the world's vegetation cover. When refined strictly by physiognomic–structural criteria—for example, by considering finer categories in stature and plant spacing—they become artificial. When a forest is distinguished from a woodland simply by the stature and spacing of trees, such categorization may separate units of vegetation that are closely related in ecological terms. They may differ only in the woodland being a recently disturbed portion of the forest.

One way out of this problem is the formation series approach of Beard (1978), which employs an ecological series (in this case, a climatic gradient) to portray physiognomic responses in the stature of certain types of formations through generalized profile diagrams.

Such generalized profile diagrams, which have been used by many authors, are useful tools for illustrating regional relationships between physiognomy and environment. It would be questionable, however, to try to draw a single generalized profile for all tropical plant formations regardless of regional variations, just as it would be questionable to try to draw a single generalized profile for all temperate plant formations. For example, the redwood (*Sequoia*) forests of northern California and the Douglas-fir (*Pseudotsuga menziesii*) forests of the Pacific Northwest form ecosystems whose physiognomy is unique to North America. The major physiognomic characteristics—i.e., stature, spacing, crown shapes, leaf characteristics (including deciduousness versus evergreeness), layering and plant biomass relationships—could hardly be presented on a single global profile diagram. The main reason for this is that stature, crown shape and leaf characteristics are not merely a function of the environment but also of the floristic history and plant types in a particular region (Walter, 1971, 1976). Any attempt at a globally integrated physiognomic–environmental classification scheme (classic or contemporary) cannot really do justice to the variability of the world's vegetation cover.

The environmentally oriented classifications give even less information about the vegetation itself. They only define certain climatically, topographically or edaphically homogeneous segments of land. They can broadly predict, however, what sort of vegetation formation—and, sometimes, species composition—will occur in a given area, provided there are no interfering factors. Environmental gradient analysis is a powerful ecological tool that evolved from this approach.

The areal–geographic–floristic approach is concerned with the provinciality of plant species and communities. It also includes historical investigations of plant species and communities, which are important in explaining the variability of the vegetation cover.

The provinciality of plant species becomes a problem in the five other approaches to classifying vegetation. This was first realized during work on the floristic schemes. The Braun-Blanquet association scheme, which dealt with vegetation in central Europe, was originally thought to be transferable to other continents. It was found, however, that the key species useful for determining association types in one region could not always be used when an attempt was made to extrapolate the scheme over a broader geographic range. Certain key species disappeared, while others lost their indicator value over larger areas.

The latter phenomenon is related to the frequently documented observation that widely distributed species have geographic varieties (ecotypes) which have evolved different adaptations to their environments. Thus, the floristic association system is useful only for intensive studies of regional vegetation covers, and the community types defined in these regional studies cannot be expected to be the same in other regions with similar environmental relationships. This does not mean, however, that the floristic association system does not work in regions outside central Europe. It has been found to work in many other regions, and has even wider applicability as a research tool than classifications based on dominance types.

Floristic dominance-type classifications are useful only where plant communities can be identified by dominant species. This restricts their application in regions where floristic diversity is great. That includes most tropical forests and many subtropical areas.

Another difficulty with the dominance-type concept in central Europe led to the association-type approach. This was the small number of dominant tree species and their indifference to changes in habitat. The few dominant tree species, such as the European beech (*Fagus sylvatica*) and pine (*Pinus sylvestris*), range over broad areas with considerable environmental heterogeneity. In these areas undergrowth species often show a much closer relationship to variations in habitat.

It is also important to realize, however, that dominance types can be found in some parts of the tropics—for example, the *Mora excelsa* forest in Trinidad, the *Metrosideros polymorpha* rain forest in Hawaii, and the teakwood (*Tectonoa grandis*) and sal (*Shorea robusta*) forests in India. Wherever the existence of such dominance types conveys useful ecological information, a dominance-type scheme is superior because of its simplicity.

Because of the limitations inherent in all of the major classifications so far devised, it is probably not possible to devise a general purpose classification of the world's vegetation.

Once the limitations in each system are realized, however, it is possible to combine the aspects of each system which are best suited for such new purposes as mapping the plant biomass and primary production of the globe.

2.3 VEGETATION MAPS

Vegetation has been mapped at all geographic scales, ranging from global overviews at very small scales (such as 1:100 million) to individual research plots and one-metre square quadrats at very large scales (such as 1:10, where 1 cm on the map corresponds to 1 dm on the ground). It is helpful to distinguish among three categories of vegetation maps: small scale, intermediate scale and large scale.

2.3.1 Small-scale Maps

Such maps may be defined as ranging from a scale of 1:1 million (where 1 cm on the map represents 10 km in the field) to scales of much smaller size, such as 1:100 million. It is useful to distinguish within this range the very small-scale maps (from 1:10 million to 1:100 million) which are commonly used for global overviews.

The Brockmann-Jerosch map reproduced by Woodwell (1978: 38–39) is a very small-scale vegetation map on which 1 cm corresponds to approximately 1000 km on the earth's surface (i.e., 1:100 million). The map shows 10 world vegetation types, from tropical rain forest to tundra. These 10 were supplied by Woodwell (1978) with plant biomass data in kg C/m^2. The map uses the physiognomic–environmental scheme of vegetation classification.

Whittaker (1970, 1975) recognized 25 such types for the world. To accommodate Whittaker's 25 types on a global map the scale would have to be enlarged, perhaps to twice that of the Brockmann-Jerosch map, i.e., to a scale of 1:50 million. At this scale a world map is approximately the size of two large atlas pages. Thus, 25 physiognomic–environmental types can still be accommodated on a very small-scale map.

Perhaps the best contemporary vegetation map in the very small-scale range is the 1:25 million map of Schmithüsen (1968), which shows 144 physiognomic–environmental types and includes such important types as mangrove forests and tropical swamp forests, which could not be shown on the Brockmann-Jerosch map. It is of interest to note that Schmithüsen's map includes some dominance types. These are indicated by printed symbols and include such species as *Quercus ilex*, *Q. suber* and some regionally dominant tree genera, such as *Pinus*, *Sequoia* and *Podocarpus*. The 1:25 million scale is about the same scale as that used in a standard wall map of the world. Schmithüsen's map is reproduced as a small pamphlet with 11 double pages.

The differences among these three maps can only be discussed in relation to particular objectives. As an overview of plant biomass relationships, the Brockmann-Jerosch map of 10 vegetation types serves very well. Greater detail and perhaps accuracy would be obtained, however, by supplying plant biomass values for the 144 vegetation types mapped by Schmithüsen and then calculating the surface area of each type. Such an approach was used by Rodin *et al.* (1975), who supplied plant biomass and productivity data for 106 terrestrial soil-plant formations. Since these Russian authors used a larger map-scale with many more vegetation types, one may conclude that their global estimates are more accurate than the values shown by Whittaker and Likens (cited in Lieth and Whittaker, 1975: 13). The latter based their global estimate of primary production on 15 terrestrial vegetation types and give 164×10^9 tons (t) of dry matter per year, while Rodin *et al.* give 172×10^9 t. Lieth (1973) estimated 100.2×10^9 t, based on 20 terrestrial vegetation types. For standing plant biomass (in dry weight), Whittaker and Likens (1975) give 1837×10^9 t. Rodin *et al.* (1975) give 2402.5×10^9 t. These two, and different, summation values were calculated for the same continental land area of 149×10^6 km^2.

Of course, the accuracy of these estimates is dependent not only on the map scale and number of vegetation types used but also on an estimate of the variation within each vegetation type and on the number of actual measurements. Both variables have to be considered in arriving at a best estimate, or properly balanced mean value, for each vegetation type.

A better estimate of structural variation can be made through the use of existing vegetation maps at successively larger scales. The next group larger in scale than global vegetation maps are maps of individual continents. These range in scale from 1:1 million to 1:10 million and are thus still small-scale vegetation maps. Two examples are the vegetation map of the United States by Küchler (1965) and the vegetation map of South American by Hueck and Seibert (1972).

Küchler's pocket map is at a scale of 1:7.5 million, i.e., 1 cm represents 75 km. A comparison of the information content of Küchler's map with that given for the conterminous United States on the Brockmann-Jerosch map is shown in Table 2.2. The global map of Brockmann-Jerosch shows seven

Table 2.2 Comparison of vegetation units within the small map-scale range for the US: temperature and subtropical

Global vegetation map of Brockmann-Jerosch (1:100 million)	Continental vegetation map of Küchler (1:7.5 million). Units grouped hierarchically	
1 Boreal and montane forest (in the Pacific NW)	1 Western needleleaf forests (21 types)	8 Central and eastern grasslands and forest combinations (12 types)
2 Evergreen hardwood forest (in parts of California)	2 Western broadleaf forests (2 types)	9 Eastern needleleaf forests (5 types)
3 Steppe and prairie (in central US)	3 Western mixed broadleaf/needleleaf forests (5 types)	10 Eastern broadleaf forests (8 types, including a mangrove type)
4 An undesignated unit (probably also grassland in south-central US)	4 Western shrubland (11 types, including a desert type)	11 Eastern mixed broadleaf/needleleaf forests (10 types)
5 Dry desert and semi-desert (in south and southwestern US)	5 Western grassland (9 types)	
6 Summer-green deciduous forest (for most of eastern US)	6 Western shrub- and grassland combinations (7 types)	Total 106 types
7 Temperate rain forest = Laurel forest (for Florida)	7 Central and eastern grassland (16 types)	

general physiognomic vegetation types for the conterminous United States, while Küchler's map shows 11 geographic–physiognomic units which serve as a broad framework for grouping the actual map units, which are 106 major types of vegetation. In most cases, these are recognized by a combination of physiognomic criteria and dominant species. Thus, by enlarging the map scale by a factor of approximately 10, the number of mappable vegetation types can be increased by a factor of about 10 to 20.

This illustrates an important point which is often overlooked. The definition of plant communities or vegetation types is strongly dependent on map scale. Another point, and one that is relevant to the carbon dioxide question, is this: hidden in the global physiognomic vegetation types, which are commonly called biome types (Whittaker, 1970, 1975), is a great deal of structural 'noise'. This 'noise', however, is not random. It is the product of the mosaic of vegetation types.

Table 2.3 presents a comparison of vegetation types for tropical South America. The increase in scale from the Brockmann-Jerosch map to the map

Table 2.3 Comparison of vegetation units within the small map-scale range for tropical South America. (Excluding Central America and Temperate South America)

Global vegetation Map of Brockmann-Jerosch (1:100 million)	Continental vegetation map of Hueck and Seibert (1:8 million). Units grouped hierarchically where possible	
1 Equatorial and tropical rain forest (Amazon area) 2 Raingreen forest, woodland scrub and savannah (N and S of Amazon area) 3 Temperate rain forest = Laurel forest (here seen as equivalent to tropical montane forest, Andes and parts of Brazil) 4 Steppe and prairie grasslands (Venezuela) 5 Dry desert and semi-desert (Peru, Equador) 6 Highland areas with alpine tundra (tropical part of Andean Mountains)	1 Evergreen tropical rain forests (13 types in Amazon and Orinoco areas) 2 Várzea swamp forest (Amazon River) 3 Campinas = grassland and open woodlands in rain forest area (Amazon) 4 Evergreen tropical montane forests (3 types in Andes, 2 types in Pacific and Caribbean region, 3 types in Atlantic region) 5 Mixed evergreen/raingreen tropical montane forests (3 types, Andes)	6 Tropical raingreen mesophytic forests (3 types) 7 Savannahs and palm savannahs (5 types) 8 Tropical dry forests (9 types) 9 Tropical scrub and grassland (6 types) 10 Desert and semi-deserts (4 types) 11 Tropical high-altitude vegetation (4 types) Total 57 types

of Hueck and Seibert (1972) is very similar to the previous comparison. The differentiation of vegetation types for tropical South America is increased by a factor of almost 10, i.e., from 6 to 57 types. If Central America had been included, the increased differentiation of vegetation types associated with the increase in map scale would have been even more comparable. The Hueck–Seibert map shows that tropical vegetation is just as varied as temperate vegetation, a point emphasized by Whitmore (1975) and Poore (1978). Many of the vegetation types on Hueck and Seibert's map are identified by colloquial names, such as Várzea forest, Alisio forest, Caatinga beixa, Campos Cerrados and Campos Limpos. These terms convey a particular physiognomy only to those familiar with South American tropical vegetation. It would not be difficult to translate them into internationally understandable terminology of vegetation structure for use in geographic calculations of plant biomass and primary production.

However, all small-scale vegetation maps have a major defect with respect to calculating plant biomass. They do not portray the outlines of existing vegetation. Küchler (1965) called his map a map of 'potential natural vegetation'. In other words, his map outlines certain areas where such vegetation could grow. Small-scale vegetation maps are not, strictly speaking, vegetation maps. They are site maps. They may be very useful for calculating primary production, which is more a function of site factors than plant biomass, but they may give erroneous values for biomass if an attempt is made to extrapolate real vegetation from potential vegetation.

2.3.2 Intermediate-scale Maps

These may be defined as ranging from 1:1 million to 1:100 000 in scale. The upper range of this scale accommodates 10 km, and the lower 1 km, on 1 cm of map. An example of an intermediate-scale map is Küchler's vegetation map of Kansas (1974). This map was published at a scale of 1:800 000 (1 cm = 8 km). It illustrates how much more information on vegetation can be displayed when a section of a continental map is enlarged by a factor of approximately 10. There is good similarity between the vegetation in the 4.5 × 9 cm rectangle that is Kansas on Küchler's map of the United States and the 40 × 80 cm vegetation map of Kansas alone. However, the number of vegetation types on the latter is 16, compared to 7 on the former.*

Another map in the same scale range is the vegetation map of the Hawaiian Islands prepared by Ripperton and Hosaka (1942). The island of Hawaii is portrayed in Figure 2.1 at a scale of 1:1.8 million (1 cm = 18 km). This map

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* Küchler's map of Kansas is called a map of potential natural vegetation. This map should not be confused with a map showing the outlines of existing vegetation types. One cannot deduce existing plant biomass easily from this map, but it may serve very well for providing indices of primary production.

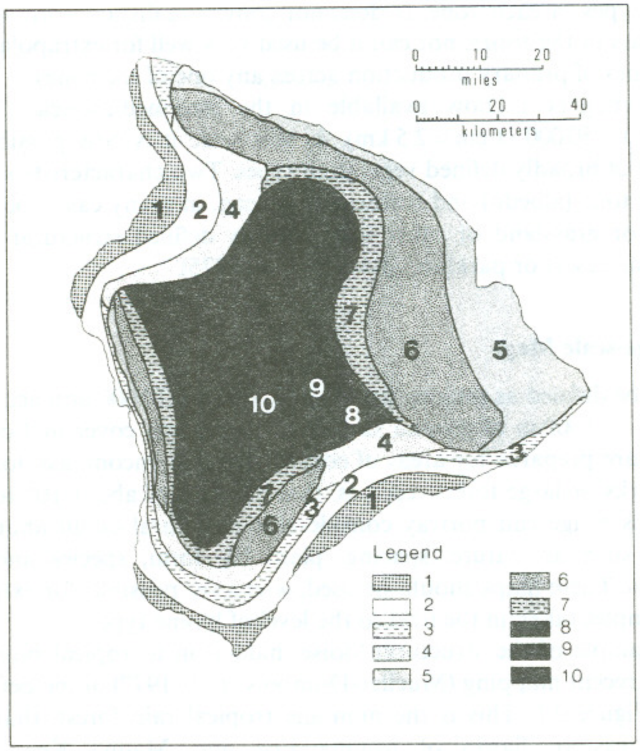


Figure 2.1 Vegetation zone map of the Island of Hawaii originally at 1:1 million (from Ripperton and Hosaka, 1942). Zone names modified: (1) Savannah and dry grassland, (2) Dry sclerophyll forest or scrub, (3) Mixed mesophytic woodland or scrub, (4) Mixed mesophytic forest and savannah, (5) Lowland rain forest, (6) Montane rain forest, (7) Upper montane rain forest, (8) Mountain parkland and savannah, (9) Subalpine forest and scrub, (10) Sparse alpine scrub and stone desert

shows 10 vegetation zones, rather than vegetation types, and that makes interpretation somewhat easier. The boundaries of the vegetation zones are the result of several factors, of which temperature and rainfall are the most important. Vegetation is also included as an indicator, but soil and substrate are largely ignored. This is apparent from the fact that there are a number of recent lava rock substrates that extend south and southeast from the top of Mauna Loa to the coast and northeast through the saddle between Mauna Loa and Mauna Kea toward Hilo. Many of the lava deposits to the south are practically devoid of vegetation, and it will take more than 2000 years for the deposits in the coastal lowland to become vegetated with anything resembling the plant biomass on adajacent soils. Thus, the map is not a map of potential vegetation. It is a bioclimatic map that includes a mosaic of different structural vegetation types in each zone. It does not convey realistic information about plant biomass in the zones, nor can it be used very well for extrapolating single average values of primary production across any one of the zones.

Satellite imagery is now available in the intermediate-scale range, for example at 1:250 000 (1 cm = 2.5 km). At this scale it is now possible to map the outlines of broadly defined vegetation types. Two characteristics which can be used are tone (albedo) and texture. These can, in many cases, be translated into forest or grassland or other very broadly defined structural vegetation units, such as desert or parkland (Reeves *et al.*, 1975).

2.3.3 Large-scale Maps

These may be defined as ranging from 1:100 000 to 1:10 000 and accommodate from 100 m to 1000 m of ground surface or vegetation cover in 1 cm of map. Such maps are prepared for areas of county size that encompass, for example, national parks or large forest reserves, that is, areas of about 10^2 to 10^4 km^2. Maps in this range can portray considerable structural detail about existing vegetation, such as stature, spacing, plant life form, species and biomass relationships. These maps should be used, whenever possible, for extrapolating biomass samples taken in the field to the level of biome type.

As an example of the structural 'noise' hidden in a tropical biome type, I refer to our recent mapping (Mueller-Dombois *et al.*, 1977) of the better part of zone 6 in Figure 2.1. This is the montane tropical rain forest, that stretches across the eastern flanks of Mauna Loa and Mauna Kea. The area encompassed by our large-scale map is approximately 80 000 ha (16 × 50 km). The map was prepared from colour aerial photographs at a scale of 1:12 000 and reduced to a scale of 1:48 000. On this map are shown five major structural types:

(1) Dense ’ōhi’a (*Metrosideros polymorpha*) forests with crown cover of more than 85 per cent	(2 subtypes)
(2) Closed ’ōhi’a forests with crown cover from 60 to 85 per cent	(5 subtypes)
(3) Open ’ōhi’a forests with crown cover from 15 to 60 per cent	(7 subtypes)
(4) Low-growing vegetation with scattered trees, less than 15 per cent cover	(5 subtypes)
(5) Low-growing vegetation with shrub-like trees under 5 m tall	(3 subtypes)
Total	22 subtypes

The subtypes here are the actual units on the map, and they are further distinguished by variations in stand stature, associated dominant species, and mappable characteristics of the undergrowth.

Large-scale vegetation maps have also been used as site indicator maps following research to establish correlations between certain vegetation patterns and the physical characteristics of the sites. Several examples are given in Mueller-Dombois and Ellenberg (1974: 411 ff.). Such maps can be used to project primary production values for local areas. Webb (1968) has worked out such site indicator properties for tropical rain forests in Queensland.

Unfortunately, published large-scale maps are few (Küchler, 1966, 1968, 1970; Küchler and McCormick, 1965). Some temperate areas, particularly western Europe, are well covered by published vegetation maps, but few maps of tropical vegetation exist. A number of such maps are in preparation for southeast Asia, according to de Rosayro (1974).

2.4 USE OF CONTEMPORARY CLASSIFICATION SYSTEMS IN VEGETATION MAPPING

Any ecologist who has done a certain amount of mapping of the vegetation will have made at least three observations relevant to mapping and classification of plant communities. The first is that certain vegetation boundaries are easy to draw because they are virtually self-evident on aerial photos or in the field, but that other boundaries must be drawn rather arbitrarily between two centres of structural or species compositional changes. The difficulty relates to the much-discussed continuum problem in vegetation (see Dansereau *et al.*, 1968). This problem is not unique to vegetation, however. It applies to all landscape components, such as topography, soils and geological formations.

A second observation is that difficulty is often encountered in integrating vegetation map units across a larger terrain. A new map unit may fall between two recognized unit categories. This is the problem of the classificatory continuum (McIntosh, 1967; Mueller-Dombois and Ellenberg, 1974), which usually requires repeated adjustment during the mapping process.

The third observation is that plant community definition, and therefore classification, is really a matter of geographic scale. One can argue a great deal about the merits of a particular classification scheme, but once the geographic scale is given the argument is narrowed substantially.

Related to the problem of scale is the question of whether one can really map the outlines of existing plant communities. This depends on the type of ground-surface imagery available from remote sensing.

It is useful to separate contemporary classification systems into two general categories: those capable of mapping the potential vegetation of an area, and those capable of mapping its existing vegetation.

2.4.1 Schemes for Mapping Potential Vegetation

Potential vegetation refers to the inherent capacity of a land area to support a particular kind of vegetation. In the small map-scale range, potential vegetation can usually be mapped only in physiognomic categories, but at the larger map-scales one may be able to predict general species and tree growth capacities through site or habitat mapping (Daubenmire, 1968; Mueller-Dombois and Ellenberg, 1974). The usefulness of these methods, however, also depends on the floristic complexity of a particular region. The importance of this can be seen by comparing Küchler's (1965) map of the potential vegetation of the conterminous United States with Hueck and Seibert's map of the potential vegetation of the South American tropics (Tables 2.2 and 2.3). Hueck and Seibert use mostly colloquial physiognomic terms, while Küchler uses dominant species combinations for designation. The difference is due to the greater diversity of species in tropical than in temperate America.

Two contemporary schemes are used for mapping potential vegetation: bioclimatic and landscape. *Bioclimatic mapping* is used in the small- and intermediate-scale map range. Analogous approaches useful for large-scale mapping are *environmental gradient analysis* in the sense of Whittaker (1967) and the *scalar approach* of Loucks (1962).

The large-scale version of the landscape approach is also known as *habitat-type mapping* (Daubenmire, 1968; Mueller-Dombois, 1964), or as the *ecological series approach* (Sukachev, 1928; Mueller-Dombois, 1965), or as the *biogeocoenotic approach* (Sukachev, 1945; Krajina, 1960; Sukachev and Dylis, 1974) or as *ecological land classification* (Mueller-Dombois and Ellenberg, 1974: 319).

2.4.1.1 Bioclimatic Methods

The better known bioclimatic methods for mapping zones of vegetation at global or regional levels are those of Köppen (1931, 1936), Thornthwaite (1948), Thornthwaite and Mather (1957), Holdridge (1947, 1967) and Walter (1955, 1957, 1971, 1973a, 1973b, 1976). All use selected climatic characteristics that outline zones within which a certain general level of vegetation homogeneity should be found. They also suggest a strong similarity of vegetation in equivalent bioclimatic zones in different parts of the globe.

Köppen's approach utilizes five broad zones identified by capital letters: A, humid tropical climates; B, arid and semi-arid climates; C, temperate climates; D, cold continental climates; and E, periglacial climates. These broad zones are further subdivided by rainfall and temperature threshold values. For example, the humid tropical A climates are all defined as having monthly mean temperatures over 18 °C. They are subdivided into four:

Af— tropical continuously wet (mean rainfall each month >60 mm)
Aw— tropical winter-dry (at least one month during the cooler season with rainfall under 60 mm)

As— tropical summer-dry (at least one month during the hotter season with rainfall under 60 mm)

Am—tropical monsoon (high annual rainfall with short dry season)

The method works very well as a first overview, but it includes such oddities as temperate-zone climates in tropical mountains. Apart from its rigidity, the system also suffers from a terminological problem.

Thornthwaite's system uses mean monthly rainfall and potential evapotranspiration. The latter value is derived through mean annual and monthly temperatures and a latitudinal correction factor, which takes seasonal changes in day length into consideration. The mean monthly potential evapotranspiration values, which are calculated from a formula, are plotted on a climate diagram together with the mean monthly rainfall values of a climatic station. The drying power of an environment is indicated on Thornthwaite's diagrams wherever the mean monthly rainfall curve falls below the potential evapotranspiration curve. The area on the diagram subtended by the two curves for the time period of such undercutting is subdivided into a period of soil water withdrawal, and the amount of this water is arbitrarily taken as 100 mm. When this storage water is used up, the remaining area between the curves is considered to reflect soil water deficiency or soil drought. The method makes it possible to estimate irrigation needs on arable cropland. It also works well to indicate the vegetation potential of an area through mapping of the diagrams and the use of certain threshold values for outlining bioclimatic zones. The method has not been tested widely in the tropics, where the calculation of potential evapotranspiration may require the incorporation of humidity in addition to temperature.

Holdridge's (1947, 1967) 'life zone' mapping method has become very popular in tropical America (Ewel and Whitmore, 1973; Barbour *et al.*, 1980). It employs two climatic characteristics, mean annual rainfall (or precipitation) and mean annual biotemperature. The latter is defined as the sum of mean monthly air temperatures (°C) divided by 12, with the provision that monthly temperatures of 0 °C and colder and those 30 °C or warmer are disregarded. For the tropics, mean annual biotemperatures are generally identical to mean annual air temperatures. A third characteristic, namely, a potential evapotranspiration ratio, is computed from the first two. Potential evapotranspiration is calculated from temperature by multiplying the annual biotemperature of a station (°C) by a factor of 58.93. A potential evapotranspiration ratio of one implies that water loss from evapotranspiration is equal to water gain from precipitation. These three climatic characteristics are worked into a triangular nomogram. Thirty world life zones are indicated in this triangular nomogram, each in form of a small hexagon. Life zones are outlined on maps simply by obtaining the mean annual precipitation and mean annual biotemperature from a number of climatic stations and by applying these data to the nomogram. One can also obtain the two characteristics from mean annual rainfall isohyets and calculation of the temperature lapse rate from stations at sea level. The nomogram informs the mapper of the threshold values for boundary interpolation and the life zone name.

Holdridge defines the tropical region as the global terrain with mean annual air temperatures of 24°C or greater. This is the narrowest proposed definition. Köppen's 18 °C is a more adequate index. Most authors, however, define the tropical belt as the geographical area between the Tropics of Cancer and Capricorn. Thus Holdridge's system, though providing an ingeniously derived climatic index, introduces a confusion in terminology. For example, according to Holdridge's system, Hawaii would be part of the subtropics because its mean annual temperature at sea level is near 23.5 °C. This delimitation is opposed to all conventional views. The natural lowland and lower montane vegetation in Hawaii is typically composed of tropical taxa and plant life forms. A second terminological problem is the naming of the life zones themselves. In his tropical belt (> 24 °C), for example, the sequence from wet to dry is rain forest, wet forest, moist forest, dry forest, very dry forest, thorn woodland, desert scrub and desert. These terms convey the impression of physiognomic vegetation units and thus prolong confusion between real vegetation and climate. It would be difficult, for example, to distinguish the rain forest category from the wet forest category physiognomically. None of the zones are physiognomic vegetation types. They are instead rigidly constructed bioclimatic zones. Beard (1978) has also commented on the rigidity and unfortunate terminology in the Holdridge system.

As a bioclimatic zonation scheme, however, Holdridge's system has an advantage in its simplicity of application. It may also be useful as a predictor of primary production. Since it is based on mean annual climatic characteristics, however, it lacks a clear definition of seasonality.

Walter's climate-diagram method has certain advantages over the preceding schemes even though, like them, it also uses only rainfall and temperature data. Like Thornthwaite's method, Walter's employs the annual sequence of mean monthly precipitation values of any given climatic station. These are plotted into the climate diagram.

In addition, Walter uses mean monthly temperature data without converting them into another form. The precipitation and temperature curves are plotted so that 10°C on the left-hand ordinate of each diagram corresponds to 20 mm of precipitation on the right-hand ordinate. The diagrams indicate a significant dry season (called drought season by Walter) wherever the precipitation curve falls below the temperature curve. The 10 °C/20 mm relationship is based on a suggestion by Gaussen and supported by empirical observations. It gives an index of environmental dryness, which is the third important characteristic in Walter's diagrams.

The method has been criticized because the mean monthly temperature curve does not take into account the varying relationship of potential evaporation to the temperature and humidity regime of a place. Of course, radiation and wind would be other important influences. A dry season in a tropical lowland environment as indicated on a climate diagram is, of course, drier in absolute terms than a similarly indicated dry season in a temperate climate. Moreover, a dry season in an arid tropical environment produces a proportionately greater evaporative power than a similar dry season in a humid tropical climate.

Walter answers this criticism with the equally logical observation that natural vegetation is acclimatized to the place in which it occurs. This implies that a short dry season in a humid tropical climate produces greater stress on indigenous vegetation than a short dry season on vegetation indigenious to a drier climate. Or, stated in the opposite way, a wet month (rainfall in excess of 100 mm) has a greater impact on dry-zone vegetation than it does on humid-zone vegetation. The 1/2 ratio of temperature to precipitation seems to have given a realistic drought index wherever the climate-diagram method has been tested, except in temperate climates with low winter precipitation. In these climates Walter has used as a second index a 1/3 relationship, which is indicated by a dashed line in the diagrams. The 1/3 ratio lowers the mean monthly rainfall curve relative to the temperature curve.

The climate-diagram method emphasizes many more climatic characteristics, where these are ecologically useful. In certain temperate environments, for example, the annual growing season is indicated by a line drawn at 10 °C, which makes it possible to estimate the average number of days above 10 °C. In some of the tropical climate diagrams the average day and night variations in temperature are shown. Each climate diagram also gives the annual mean precipitation and temperature at the station, which are the two basic kinds of data used in Holdridge's system. Thus, Walter's diagrams, though easy to understand, provide a great deal more climatic information than do other methods.

Walter's diagrams have been mapped by Walter and Lieth (1960) in a world atlas that shows climate diagrams for numerous places all over the globe. A more recent version in normal-sized book format (Walter *et al.*, 1975) contains eight maps, one for each continent or major world region. Each map is at the scale of 1:8 million and is filled with climate diagrams. These allow the user to appraise climatic variations over each continent and between continents with little effort. (The use of this method for identification of forest types on satellite imagery is discussed below.)

Unlike the other bioclimatic schemes discussed, Walter *et al.* (1975) do not prescribe boundaries for bioclimatic zones on the continental maps. Boundary designation is left to the user, who can quickly determine the climatic variation related to a distribution problem, for example, forest distribution on satellite imagery.

On a global map which accompanies the eight continental maps in the 1975 atlas, Walter outlines 10 world climatic zones. These correspond to traditional biome concepts, such as equatorial rain forest, tropical deciduous forest, boreal forest, etc., but it should be kept in mind that these are bioclimatic zones. They do not identify vegetation types. They are simply zones of a certain climatic character, and they always contain a variety of real vegetation types.

2.4.1.2 Landscape Classifications

In contrast to the bioclimatic methods, the landscape classification methods usually give greater emphasis to actual vegetation characteristics. They do this by integrating vegetation and certain aspects of the environment into ecosystem or landscape types. The 10 physiognomic–environmental world vegetation types mapped on the Brockmann-Jerosch map (in Woodwell, 1978) or the 104 soil-vegetation formations used by Rodin *et al.* (1975), which were used for presenting world primary production and phytomass values, are such landscape types.

Five landscape classification methods have proven their usefulness in different situations. Examples of these are the schemes of Krajina (1965, 1969), Hueck (1966), Hueck and Seibert (1972), UNESCO (1973), Ellenberg and Mueller-Dombois (1967a), Ellenberg (1973), Gaussen (1954, 1957, 1964) and Gaussen *et al.* (1964, 1965, 1967). These methods are particularly suitable for small and intermediate map-scales. I exclude discussion of landscape classifications particularly adapted to large-scale mapping.

Krajina's biogeoclimatic zonation scheme has been applied to a 1:1.9 million map of British Columbia (Krajina, 1969, 1974). In this classification system, plant community and soil types are integrated through detailed regional studies at the large map-scale range. Krajina calls these integrated units 'biogeocoenoses' in the tradition of Russian authors (Sukachev and Dylis, 1964). For outlining biogeoclimatic zones in the small map-scale range, he uses Köppen's bioclimatic scheme as a guide. However, the zonal boundaries are adjusted with the aid of information from soil and topographic maps. Each of Krajina's zonal units is characterized by a zonal soil type, zonal climate type and zonal vegetation type. The latter he defines as climatic climax vegetation, which is restricted to normally well drained soils on level to moderately varied (but not steep) topography. Mature vegetation on excessively or poorly drained soils is called an edaphic climax. Other variations include mature vegetation on alluvial flats or bogs, or vegetation on steep slopes. The latter are called topographic climax types. Krajina considers edaphic and topographic climax types to be significant parts of his zonal units. He therefore gives equal weight to these and to climatic climax vegetation in describing biogeoclimatic zones. Krajina's scheme therefore clearly recognizes the mosaic nature of vegetation types in the zonal map units.

Hueck's scheme for mapping the vegetation of South America at a scale of 1:8 million (Hueck and Seibert, 1972) is rather informal. Like Krajina's, it has been worked out by classifying vegetation from detailed observations in the field. Hueck's method is based on extrapolating the prevailing, existing natural and semi-natural vegetation across segments of the landscape which may now be under agriculture, urbanization or may be variously disturbed through fire and grazing. The extrapolation is based on an assessment of the total environment—i.e., climate, geology, soil, topography and history. The major tools used were existing maps.

It is interesting to compare, for example, Hueck and Seibert's map of Venezuela with the Holdridge map of Venezuela published at a scale of 1:2 million (Ewel *et al.*, 1968). The Hueck and Seibert map, although four times smaller in scale, contains more information about the vegetation. For example, it shows the ecologically important gallery forests along the Orinoco River; these are missing from the Holdridge map because it uses only mean annual rainfall and temperature relationships as a predictor. In short, important edaphic plant formations will not appear on bioclimatic maps but do appear on carefully done landscape maps.

The UNESCO system (1973) was developed for mapping the world's vegetation at a scale of 1:1 million (Ellenberg and Mueller-Dombois, 1967a). This project (Fontaine, 1978) involves mapping the world on map sheets, each of approximately state or province size. UNESCO set up an International Committee for Vegetation Mapping to develop an appropriate classification system, since none of the existing schemes was found to be suitable. A scheme based largely on work by Schmithüsen and Ellenberg was then developed. This scheme makes use of physiognomic units, which are further defined by environmental criteria. In principle, these units are similar to the Schimper (1898) units or the Brockmann-Jerosch and Rübel (1912) units shown by Woodwell (1978).

The system is hierarchical, with a top level consisting of five formation classes, as follows:

(1) Closed forests.
(2) Woodlands or open forests.
(3) Scrub or shrubland.
(4) Dwarf-scrub and related communities.
(5) Herbaceous vegetation.

Satellite imagery at the intermediate range may allow a mapper to outline such broad classes of existing vegetation.

At the second level, called the formation subclass, closed forests are subdivided into mainly evergreen, mainly deciduous and extremely xeromorphic forests.

The third level is called the formation group, which under 'closed forests mainly evergreen', for example, recognizes the tropical rain (or ombrophilous) forest. The tropical rain forest is then subdivided into eight actual formations:

(1) Tropical lowland rain forests.
(2) Tropical submontane rain forests.
(3) Tropical montane rain forests.
(4) Tropical subalpine rain forests.
(5) Tropical ombrophilous cloud forests.
(6) Tropical ombrophilous alluvial forests.
(7) Tropical ombrophilous swamp forests.
(8) Tropical evergreen bog forests.

These formations are further subdivided into subformations where useful. For example, the tropical montane rain forest is subdivided into a broad-leaved subformation (the most common), a needle leaved subformation, a microphyllous subformation, and a subformation rich in bamboo.

The UNESCO system is primarily a physiognomic system, but it also uses environmental terms for recognition. For example, lowland and submontane rain forests are separated by a topographic (climatic) boundary which has to be determined in each particular situation. In some tropical forest areas this boundary may correspond to a physiognomic or floristic segregation, but in others it may not. One can therefore also use this system in a landscape sense. For example, one may extrapolate a lowland rain forest as the typical physiognomic formation across a totally disturbed rain forest terrain.

Ellenberg's (1973) classification of world ecosystems brings a functional viewpoint to the UNESCO scheme. It begins with the biosphere as the largest ecosystem. This is subdivided into five mega-ecosystems:

M—Marine ecosystems (saline water as life medium).
L—Limnic ecosystems (fresh water as life medium).
S—Semi-terrestrial ecosystems (wet soil and air as life medium).
T—Terrestrial ecosystems (aerated soil and air as life medium).
U—Urban-industrial ecosystems (structures and creations of man as primary life medium).

The first four are considered natural or predominantly natural mega-ecosystems for which the sun provides the main energy source; the fifth is considered artificial and its energy sources are primarily fossil fuel or atomic power. In addition to life medium and energy source at the first level, Ellenberg incorporates five other functional criteria at the lower levels. These are:

(1) Biomass and productivity.
(2) Factors limiting the activity of primary producers, consumers and decomposers (e.g., seasonality).
(3) Regulating mechanisms of nutrient loss or gain (e.g., fire).
(4) Relative role of secondary producers (i.e., herbivores, carnivores, parasites and other mineralizers).
(5) The role of man (i.e., his role in the origin, development, energy flow and mineral cycling of the ecosystem, particularly in supplementing energy sources).

Four human roles are recognized in Ellenberg's scheme. These are:

(1) The harvesting of organic materials and minerals, which are significant for the metabolism of an ecosystem.

(2) The adding of minerals, organic materials or organisms.
(3) The adding of abnormal substances which are detrimental to important organisms or organism groups (toxification).
(4) The changing of species composition by suppressing existing species or by the introduction of alien species.

A rating scale of from one to nine is suggested for expressing the degree of each kind of human interferences, i.e., one (no toxification) to nine (excessive toxification).

The units below the mega-ecosystems are called macro-ecosystems. These are subdivided into meso-ecosystems, which in turn are divided into micro-ecosystems.

The macro-ecosystems are distinguished on the basis of biomass and productivity at a very general level: forest, grassland, desert, etc. Meso-ecosystems form the basic unit in Ellenberg's scheme and refer to such types as tropical evergeen rain forests with their animal life and cold-deciduous broad-leaf forests with their animal communities. Micro-ecosystems are such divisions as lowland, submontane, montane, etc.

The Ellenberg scheme also includes a biogeographic separation into nine regions, such as tropo-American, tropo-African, tropo-Asian, Australian, etc. Each of these biogeographic regions can be subdivided into biogeographic subregions or provinces. The system of biotic regions devised by Dasmann (1973) may be usefully applied here. Ellenberg's classification system has not been tested by actual mapping, but it should be similar to the UNESCO system, the only difference being that it adds significant functional information to a scheme which is primarily structural.

Gaussen's regional landscape system is perhaps the most complete of those discussed thus far. It has been applied successfully to south India (Gaussen *et al.*, 1961; Blasco, 1971) and Sri Lanka (Gaussen *et al.*, 1964, 1965). Gaussen's system involves the mapping of vegetation–landscape units at a scale of 1:1 million. Several of these maps have been produced at the French Institute in Pondichery, India.

These 1:1 million international vegetation maps cover a region the size of an individual state, province or large island (such as Sri Lanka) on a single fold-out sheet. The maps show the major vegetation zones, which correspond in level of detail to the biogeoclimatic zones of Krajina in British Colombia. For Sri Lanka, which is approximately 420 km long and 220 km wide in its widest part, Gaussen *et al.* (1964) recognize six vegetation zones plus a seventh narrow coastal zone of mangroves. The vegetation zones are named after two to four characteristic tree genera and are called vegetation series—for example, the *Manilkara–Chloroxylon* series, which is a xerophytic vegetation zone found in two places in Sri Lanka.

The zones are outlined on the basis of a bioclimatic analysis using the annual sequence of temperature and precipitation plotted at a ratio of 1/2. This bioclimatic analysis is combined with an analysis of prevailing physiognomic vegetation types and characteristic key species or genera. Major soil types at the soil order level are also included, but mapped independently on a smaller scale (1:5 million) inset map. Thus, the main criteria are synthesized from the vegetation and the climate (Mueller-Dombois, 1968). Gaussen's zones are therefore landscape units rather than physiognomic vegetation types.

Within each zone are shown a few generalized vegetation types which give some idea of the structural 'noise'. For the xerophytic *Manilkara–Chloroxylon* zones in Sri Lanka, for example, Gaussen *et al.* recognize two generalized or prevailing vegetation types, namely, semi-deciduous forest and scrub-woodland. These generalized physiognomic units can be outlined by satellite imagery. In this case they were outlined from standard aerial photographs or mosaics at a scale of 1:32 000 and from already existing forest type maps (Gaussen *et al.*, 1965).

Gaussen's maps also show where natural vegetation has been removed and the prevailing use on converted lands. The land use is indicated by overprint symbols on a white background. White indicates total conversion.

In brief, Gaussen's maps provide a storehouse of ecological information on the natural resources of any region mapped by this landscape system. The maps show existing vegetation, vegetation potential, current uses of the land, climate, soils, topography, geology and administrative divisions. The only problem is that they are rather hard to read because they contain so much information. Map overlays would reduce the problem. Nonetheless, a user willing to spend some time looking over a Gaussen map can find as much information on it as in a thoroughly descriptive text. Indeed, so much integrated information is usually not found in a single book.

2.4.2 Methods for Mapping Existing Plant Communities

Methods concerned with characterizing and outlining existing plant communities differ from those concerned with potential vegetation in that the former extract mapping criteria solely from the structure of the vegetation. Environmental, historical or biotic factors, which may strongly determine the structure of a particular vegetation, are analysed independently. Thus, the focus is strictly on the pattern of the vegetation. Community patterns are established first, and the search for the causes of the patterns comes second. This approach (criterion 6 in Table 2.1) has certain advantages. For example, the procedure for mapping vegetation is relatively straightforward and thus much less time-consuming than the mapping of vegetation potential by landscape procedures. Direct vegetation mapping also avoids the pitfalls of circular reasoning.

For classification and mapping purposes it is useful to recognize both vegetation architecture and vegetation floristics. Vegetation architecture includes all recognizable forms of vegetation structure but usually excludes the floristic aspects. (The term 'vegetation structure' refers to all of the morphological characteristics of a vegetation, i.e., to its physiognomy and its species composition.) Vegetation floristics is primarily concerned with the distribution of plant species and species-population structure. A number of methods have been developed for classifying and mapping existing vegetation by using either architecture or floristics, or both.

2.4.2.1 Architecture of Vegetation

Classification schemes based on vegetation architecture use four structural criteria. These are (1) plant cover or spacing, (2) plant height or stature, (3) canopy and foliage characteristics and (4) plant growth form or life form. The difference between certain formalized schemes is simply that they use these four basic structural attributes in different sequences or combinations and with different subdivisions.

Four well-known examples of formalized architectural vegetation schemes are briefly characterized in the following discussion. Some related informal approaches are then mentioned. The four examples relate to the different schemes of Dansereau, Küchler, Fosberg and Specht. (The rather new and original approach to classifying tropical rain forest architecture pioneered by Webb (1968) and Webb *et al.* (1970) is discussed later under Problems and Measures in Mapping Tropical Vegetation.)

Dansereau's (1951, 1957) profile-diagram method offers a highly schematic and detailed approach to the mapping of vegetation architecture. Dansereau uses six categories for abstracting architectural characteristics from a given segment of vegetation in the field, namely, (1) plant life form, (2) plant size, (3) coverage, (4) foliage seasonality, (5) leaf shape and size and (6) leaf texture. Each of these six categories is further subdivided. For example, he recognizes six life-form types: trees, shrubs, herbs, bryoids, epiphytes and lianas. Each life-form type is represented by a symbol to show the plant type on a profile diagram. For example, a tree is symbolized by a circle above a vertical line ($\overset{\circ}{|}$), a shrub by a circle above an inverted triangle ($\overset{\circ}{\nabla}$), a herbaceous life form by an inverted triangle alone (∇). The profile diagram is prepared in the field on graph or cross-section paper using eight spaces on the *y*-axis or height scale and 25 spaces on the *x*-axis or length scale for any vegetation segment. The *y*-axis shows the height of the life-form types in metres, while the *x*-axis shows the life forms in estimated quantities with appropriate spacing so as to convey the vertical crown or shoot projection as accurately as possible. Height and coverage are usually estimated, but they can be measured if necessary. Other structural characteristics are superimposed on the stylized symbols. For example, a deciduous tree-life form is represented by an open circle which symbolizes the crown. An evergreen tree-life form is indicated by cross-hatching of the circular crown symbol. A semi-deciduous tree-life form is indicated by vertical hatching. The same is done for shrub and herbaceous life forms, where applicable.

Leaf shapes are indicated similarly. For example, an inverted heart inside a circular crown symbol indicates a broad-leaved tree-life form. The use of such symbols makes Dansereau's profile diagrams somewhat difficult to understand. The method is straightforward, however, and when applied properly can convey considerable detail about the particular architecture of any given plant community sample.

Classification is done by sorting the profile diagram samples according to their similarity. Dansereau classifies vegetation from below, but he does not prescribe vegetation units or classes. Mapping is done by spatial extrapolation from a number of samples.

Küchler's (1947, 1949, 1967) formula method classifies vegetation architecture by using a hierarchical approach. It starts by dividing vegetation at the first level into two broad categories: 'basically woody' and 'basically herbaceous'. Küchler recognizes seven basically woody vegetation types, each with a letter symbol:

B = Broadleaved evergreen.
D = Broadleaved deciduous.
E = Needleleaved evergreen.
N = Needleleaved deciduous.
A = Aphyllous vegetation.
S = Semi-deciduous (B + D).
M = Mixed (D + E).

Three dominantly herbaceous vegetation types are also recognized:

G = Graminoid vegetation (all grassland and sedge communities).
F = Forb vegetation.
L = Lichen and moss cover.

These broad categories are then further distinguished by the dominance of specialized life forms within them, such as C = Climbers, K = Stem-succulents, T = Tuft plants (such as palms, cycads or tree ferns), V = Bamboos and X = Epiphytes.

A further subdivision is prevailing leaf characteristics: sclerophyllous = h (i.e., hard-leaved), soft-leaved = w, succulent-leaved = k, large = 1 ($> 400 \text{ cm}^2$), small = s ($< 4 \text{ cm}^2$) and other leaf sizes in between. A fifth subdivision is by height of the vegetation cover, for which Küchler uses eight classes, from 1 = <0.1 m to 8 = >35 m. A sixth and final characterization is spacing or coverage, divided into six classes. These are c = continuous (> 75 per cent) cover, i = interrupted (50–75 per cent) cover, p = parklike or in patches (25–50 per cent) cover, r = rare (6–25 per cent) cover, b = barely present or sporadic (1–6 per cent) cover and a = absent or very scarce (< 1 per cent) cover.

Küchler says that any vegetation sample can be classified by a short formula using his various criteria and subcriteria. For example, the formula B8CX refers to a very tall (> 35 m) broadleaved everygreen forest with climbers and epiphytes. Other symbols can be added for further architectural specification, for example, c for continuous cover. Küchler claims that his method works for mapping vegetation at all geographic scales. Of course, it should be kept in mind that one can outline or map vegetation realistically only in the large and intermediate map-scale ranges.

Fosberg's (1961, 1967) general purpose classification is also hierarchical, classifying vegetation cover first into three categories: closed, open and sparse. This approach is appealing from the perspective of remote sensing. A closed vegetation cover is defined as one in which the crowns of trees are mostly interlocked or the shoots of grasses are closely intermingled. An open vegetation cover is defined as one in which tree or shrub crowns are only partly interlocked and are often free-standing, so that one can see their individual outlines. The same applies to open grassland, where one can recognize individual bunches, for example. Sparse vegetation cover occurs where the spacing between individual plants is more than twice their crown or shoot outlines, or where there are groups of plants spaced widely apart. This category includes desert vegetation.

Fosberg's subdivision into closed, open and sparse vegetation cover is called primary structural grouping. Each of the three primary groups is then further subdivided into so-called formation classes. Seventeen formation classes are recognized in the closed vegetation category. These include such types as forest, scrub and dwarf scrub, which are closed woody vegetation types distinguished by stature or height. Other types of closed vegetation are closed scrub with scattered trees, open scrub with closed ground covers, tall savannah (closed tall-grass cover with scattered trees) and short-grass covers such as those found in many pastures, either natural or man-made. Also recognized among the closed formation classes are two aquatic vegetation types, floating meadows and submerged meadows. Such vegetation types are included here only if they form a dense mat.

Ten formation classes of open vegetation are recognized, such as steppe-forest, steppe-scrub and steppe (open grassland), but only four formation classes of sparse vegetation are recognized, namely, desert forest, desert scrub, desert herb vegetation and sparse submerged meadows.

Thus, Fosberg's system divides the world's vegetation cover into 31 formation classes: 17 closed, 10 open and 4 sparse.

Fosberg's next criterion (at the third level) is based on foliage persistence. The formation class of closed forests, for example, is divided into evergreen and deciduous forests, called formation groups. These are further subdivided into formation types. For example, Fosberg recognizes nine formation types within the closed evergreen formation group:

(1) Multistratal evergreen rain forest.
(2) Evergreen swamp forest.

(3) Gnarled evergreen forest.
(4) Evergreen hard-wood orthophyll forest (orthophyll = normally sized leaves).
(5) Evergreen soft-wood orthophyll forest.
(6) Evergreen broad sclerophyll forest.
(7) Evergreen narrow sclerophyll forest (narrow = needleleaved).
(8) Evergreen bamboo forest.
(9) Microphyllous evergreen forest.

The formation types are further subdivided where possible into subformation types, for which Fosberg gives particular examples. For the multistratal evergreen rain forest, for example, he cites the dipterocarp forests of Malaya and Borneo. Note that Fosberg does not mention whether the formation types are tropical, subtropical or temperate. The same applies to the schemes of Dansereau and Küchler. The architecture of forest formations is not always distinct at the borders of geographically or thermally defined belts of vegetation.

Specht's (1970, Specht *et al.*, 1974) Australian modification can be regarded as an adaptation of Fosberg's scheme to the peculiarities of Australian vegetation. Fosberg's (1967) system was accepted for classifying research sites for the International Biological Program (IBP) and similar natural, semi-natural or cultivated vegetation types. The primary IBP purpose in this context (Mueller-Dombois and Ellenberg, 1980) was to provide an inventory of important vegetation types for conservation purposes.

Australian researchers were not satisfied with Fosberg's system, since it did not take account of the special character of Australian vegetation (Specht *et al.*, 1974). On the basis of plant coverage, they recognized four instead of three structural groups, namely, dense (70–100 per cent cover), mid-dense (30–70 per cent cover), sparse (10–30 per cent cover) and very sparse (< 10 per cent cover). On the basis of stature or height they recognized five classes of predominantly woody vegetation and two classes of predominantly herbaceous vegetation. The five height classes are defined as: (1) trees > 30 m tall, (2) trees from 10 to 30 m tall, (3) trees from 5 to 10 m tall, (4) shrubs from 2 to 8 m tall and (5) shrubs from 0 to 2 m tall. In contrast, Fosberg (1967) outlines only three stature classes for woody plants, namely, forests (major crown biomass above 5 m), scrub (major crown biomass between 0.5 and 5 m) and dwarf scrub (crown biomass mostly below 0.5 m).

Specht's two classes of Australian herbaceous vegetation are defined as hummock grasses (from 0 to 2 m tall) and herbs (including mosses, ferns, hemicryptophytes, geophytes, therophytes, hydrophytes and halophytes). Fosberg recognizes tall grass, short grass, broadleaved herb vegetation, closed bryoid vegetation, submerged meadows and floating meadows.

The differences between Fosberg's and Specht's schemes are not fundamental. However, the Australian scheme of four coverage classes, more classes of height to distinguish between types of forest (which in Australia are mostly comprised of different species of *Eucalpytus*), and the emphasis on hummock grasses are apparently more appropriate for Australian vegetation. The Australian scheme, moreover, has a certain appeal because of its simplicity. The two major classifying criteria, cover and height (including life form), are arranged in a table in which the four cover classes are the column heads and the stature classes constitute the row heads. The table body gives the formation type names that result from the combination of stature and cover. Twenty woody formation types are given, such as tall closed forest, closed forest, low closed forest, etc. Among the herbaceous formations are two hummock grass formations (sparse and very sparse) and 19 other herbaceous formations. Oddly enough, however, savannah formations (i.e., grassland with scattered trees or shrubs) are not emphasized in Specht's scheme.

Informal synusial approaches have also been found useful for classifying and mapping vegetation architecture (Mueller-Dombois and Ellenberg, 1974). The term 'synusia' (Gams, 1918; Lippman, 1939) pertains to another structural vegetation-unit concept, namely, the species of the same life-form type growing together in the same community. In its simplest form a synusia can be described as a structural subunit within a plant community. (Daubenmire (1968) has used the term 'union' for the same concept.) That is, the tree stratum, shrub stratum, herb stratum and moss carpet on a forest floor, which may all occur together as overlapping layers in a single forest stand, can each be referred to as a generalized synusia. However, different life-form types may occur within the same layer, and these are considered to form the synusiae. For example, the tall-tree stratum of a forest may contain two tree-life forms, evergreen and deciduous trees. Each is said to form a separate synusia. Synusial approaches to classification have been reviewed by Barkman (1978). They can be used in mapping and as a means of connecting vegetation architecture and floristics with vegetation structure and function. The basis of the synusial approach is a life-form classification that includes both structure and function.

The simplest approach is the layer-diagram method. A sample stand or *relevé* can usually be described by its horizontal stratification, or layering. The limits of the horizontal strata are indicated by the various height levels of the major crown or shoot biomass. These can be arbitrarily determined, but they should follow the height stratification if it is indicated in the community. The horizontal extent of each layer can be estimated or measured.

Once the height limits (in metres) and coverage (usually in per cent) of each layer are recorded for sample plots or belt-transects, the information can be presented in a simple layer diagram. The diagram shows the height limits on the y-axis and the percentage of cover of each layer on the x-axis. Examples are given in Figure 2.2.

Such layer diagrams would appear to be useful tools for mapping plant biomass from sample plots. The quantitative distribution of forest layers indicates the vertical and horizontal distribution of the plant biomass of a stand. Accuracy could be increased by allometry, and the percentages of wood and foliage could be shown by subdivision of each layer.

Another widely known method is the profile-diagram method of Davis and Richards (1933–34) and Beard (1946, 1978). The method consists of outlining a sample belt-transect. Belt width depends on stocking density, and length may be adjusted to represent the size dimensions and within-variations of a vegetation. In forests, a length of 50 to 70 m is usually adequate for one sample. But several profile diagrams are needed for adequate sampling of the same forest type. The positions of trees above a certain size are first mapped to scale in a vertical map projection, using a string grid and metre tape. Next, the horizontal or profile view is obtained by outlining or drawing tree sizes, crown forms, crown length, branching and stem characteristics in silhouette view from a certain distance alongside the belt-transect. Photographs may help, but they are not sufficient in themselves, primarily because their backgrounds are not clear.

Two such profile diagrams are shown as Figures 2.3 and 2.4. These were prepared for the same montane rain forest as the layer diagrams shown in Figure 2.2. Profile diagrams give us certain details about major species composition, but they also portray vegetation architecture by providing considerable detail about vertical and horizontal spacing and the distribution of wood and foliar material. One can also identify on them certain life-form functions, such as the deciduous or evergreen composition of tree species. The preparation of profile diagrams requires considerably more time than that of layer diagrams, and they usually cannot be used to show undergrowth vegetation.

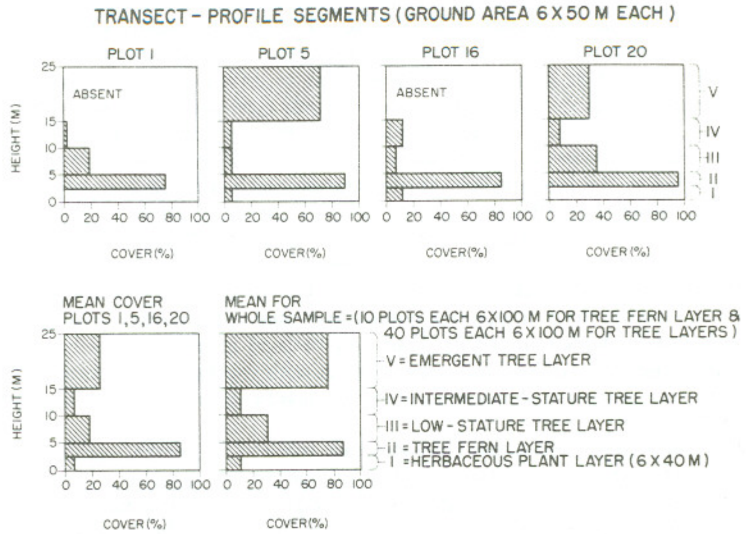


Figure 2.2 Layer diagrams of a tropical montane rain forest in Hawaii. The sample plots were taken systematically in a homogeneous *Acacia koa–Metrosideros polymorpha–Cibotium* spp. (tree fern) forest of 80 ha size. They show considerable variation in structure, particularly with regard to the presence and absence of the emergent tree layer (from Cooray, 1974). The samples relate to the Kilauea rain forest located at the N-end of Transect 2 on Figure 2.8, p. 70. The following figures (2.3, 2.4, 2.5 and 2.6) all relate to the same forest

These limitations are overcome in a third display method, the plant life-form spectrum. Such diagrams allow portrayal of the entire synusial structure of plant communities. For classifying the individuals or species of a sample stand into synusiae, one can profitably use the plant life-form classification of Raunkiaer (1937).

Raunkiaer's system is a structural-functional classification of plant types. It includes important functional aspects in the sense that plants are classified according to their seasonal behaviour. The five basic Raunkiaerian plant types are: (1) phanerophytes, i.e., perennial plants exceeding 0.5 m in potential height, (2) chamaephytes, i.e., perennial plants that do not usually rise above 0.5 m in height or that periodically throw off their shoots or branches when they extend beyond that height limit during the favourable season, (3) hemicryptophytes, i.e., perennial plants that dry up periodically to a small remnant shoot system close to the ground, although their dry shoot system may remain standing, (4) geophytes, i.e., perennial plants that reduce their entire shoot system during the unfavourable season and survive by

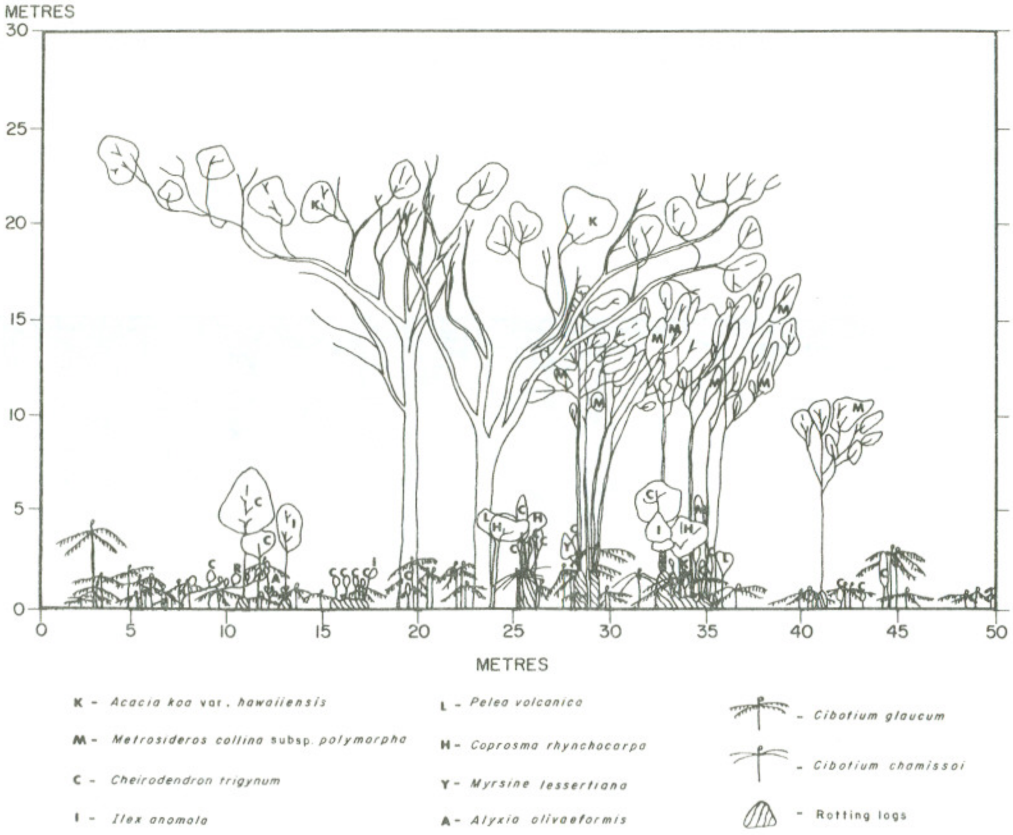


Figure 2.3 Profile diagram with dominant canopy tree species (*Acacia koa*). The diagram is a sample taken in the same forest as the layer diagrams on Figure 2.2 (from Cooray, 1974)

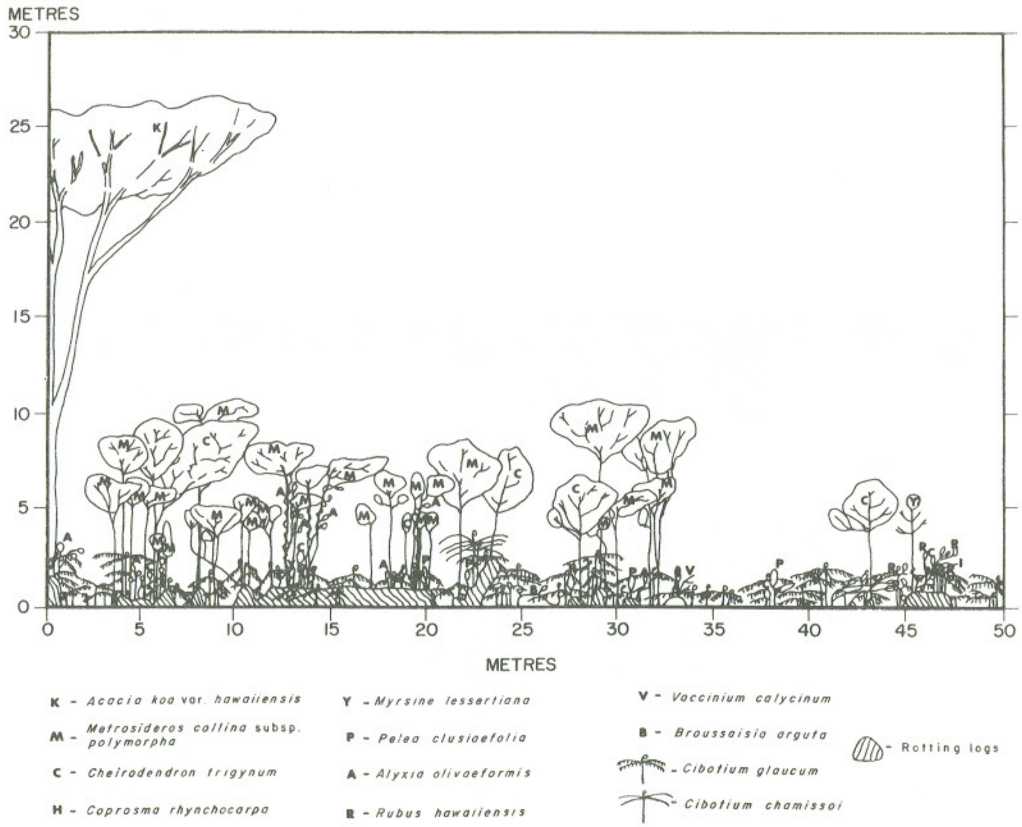
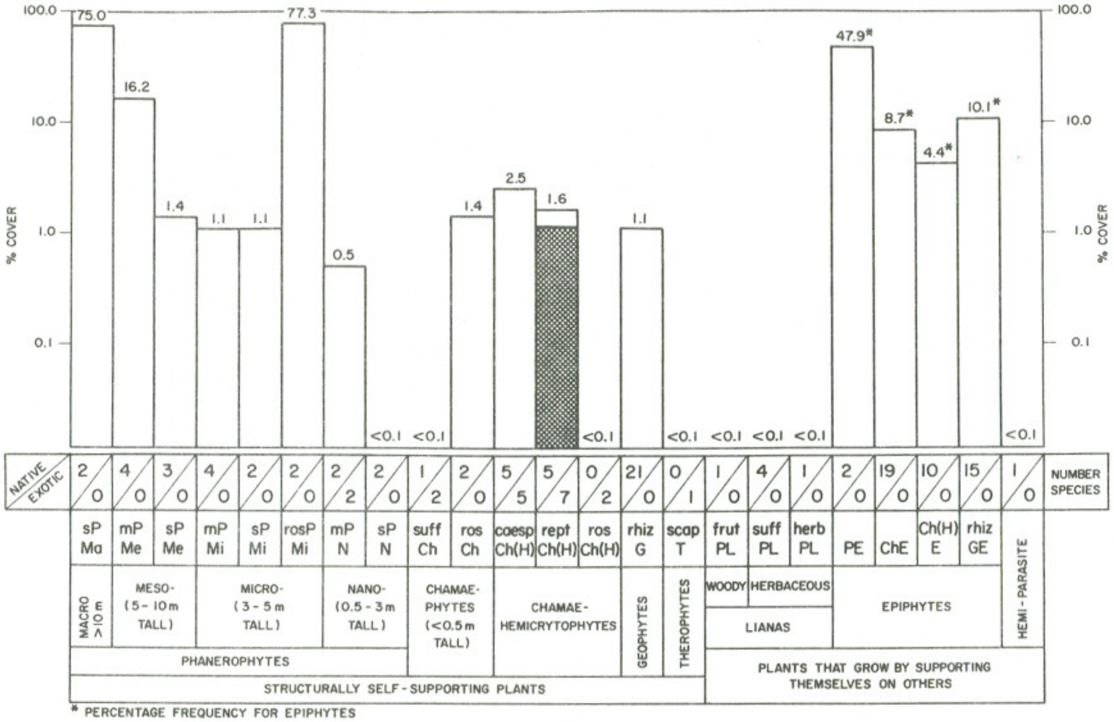


Figure 2.4 Profile diagram with 'gap phase' occupied by advanced growth of *Metrosideros collina*. Diagram represents another sample taken in the same forest as the layer diagrams on Figure 2.2 (from Cooray, 1974)



* PERCENTAGE FREQUENCY FOR EPIPHYTES

Figure 2.5 Quantitative life-form spectrum of vascular plants in a tropical montane rain forest in Hawaii. Refers to same forest as Figure 2.2. ▩ = cover of exotic species >0.1 per cent. Symbols: s = sclerophyllous; m = malacophyllous (soft-leaved); ros = leaves or fronds in rosettes; suff = suffrutescent (semi-woody); caesp = caespitose (branched from base or bunch-habit); rept = reptate (creeping or matted); rhiz = rhizomatous (modified stem imbedded in soil or organic matter); scap = scapose (single stemmed); frut = frutescent (woody); herb = herbaceous (from Mueller-Dombois *et al.*, 1981) underground storage organs and (5) therophytes, i.e., annuals which survive only in seed form during the unfavourable season.

These five plant life-forms are the structurally self-supporting types. There are also plant life-forms that grow by supporting themselves on others, such as epiphytes and lianas. Raunkiaer's system was developed in the temperate zone, and his system was originally seen as an adaptation to a summer–winter seasonality. It was found, however, that the same basic plant adaptations have also evolved in response to seasonal rainfall in the tropics and subtropics. The plant life-form system has been further modified by Ellenberg and Mueller-Dombois (1967b) to emphasize structural-functional plant behaviour during the favourable season and to make the system also applicable to the humid tropics. Further refinement is still possible and perhaps desirable with regard to such different functional traits as shade tolerance and shade intolerance, and growth rates when these become better known. The architectural studies of tropical trees by Tomlinson and Gill (1973), for example, may be usefully combined with the existing life-form system.

It has also been found that the functional aspects of life-form types are related not only to seasonality but also (in different proportions and detail) to such characteristics as resistance to fire and other mechanical damages, such as herbivory. Moreover, the member species of a narrowly defined synusia are usually strong competitors for similar resources in a community ranking in competitive relationship next to the individuals of the same species (Mueller-Dombois and Ellenberg, 1974).

The diagrammatic representation of such life-form spectra or synusial structures is done in the form of simple histograms, where the *x*-axis serves to present each life-form type or synusia side by side and the *y*-axis and histogram blocks serve to indicate the quantity of each synusia. Figure 2.5 is such a quantitative life-form spectrum or synusial diagram and was prepared for the same Hawaiian rain forest as the layer and profile diagrams shown in Figures 2.2, 2.3 and 2.4. Of these, the life-form spectrum gives the most complete information. With this diagram comes a complete species list on which each species is identified by its life-form type. For the purpose of mapping plant biomass, however, the simpler profile diagrams—particularly the layer diagram—may be the most appropriate.

It may be noted that all of the architectural classification schemes discussed earlier make use of synusial structure in varying degrees of detail and generalization. Fosberg's system, for example, could easily be portrayed in the form of layer diagrams, with one layer diagram accompanying each formation type. Dansereau's stylized profile-diagram method is closely related to Beard's more informal method, but Dansereau's method gives more detail on the lesser synusiae. In information content, Dansereau's method stands somewhere between Beard's profile-diagram method and the quantitative synusial diagram.

These diagrammatic data display methods can be used as mapping tools in the sense that they help to define the structural patterns of a vegetation cover. They can therefore be used to define map units. As an example, Figure 2.6 shows a very large-scale vegetation map of the Hawaiian rain forest plot from which the previous diagrams were prepared. Four patterns were recognized by using these methods, and the patterns were then mapped from a very large-scale colour aerial photograph (1:1500; i.e., 1 cm = 15 m). The map shows structural-dynamic patterns, i.e., patterns that are not related to any underlying pattern of site or habitat variation.

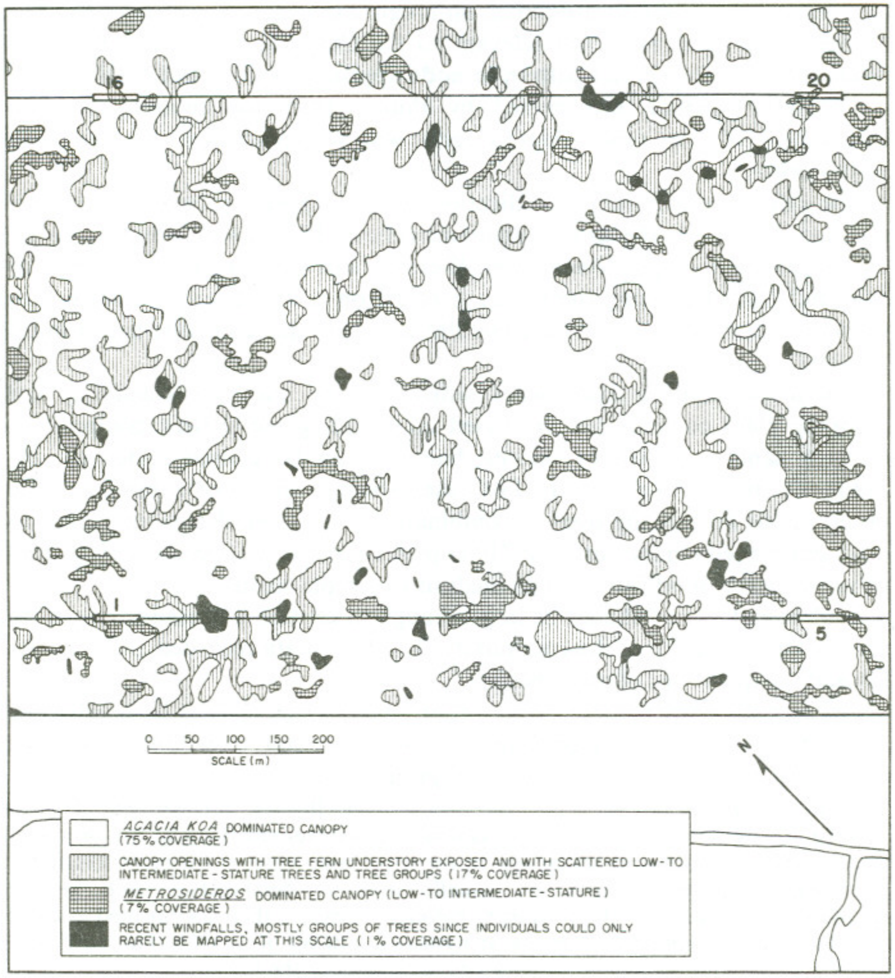


Figure 2.6 Vegetation map of montane rain forest showing four structural-dynamic patterns at a very large scale (1:8333). An 80 ha research site inside a larger homogeneous montane rain forest (the Kilauea rain forest) on the east flank of Mauna Loa. Site is located at the N-end of Transect 2 on Figure 2.8 (p. 70) (from Mueller-Dombois *et al.*, 1981)

2.4.2.2 Vegetation Floristics

Classifications based on floristics use existing patterns of plant species distribution as the primary means of mapping. There are two approaches. The first uses species distributions to define floristic provinces, while the other uses species distributions to define intrinsic species patterns (i.e., the noda or phytocoenoses). The first approach, although important to an understanding of vegetation patterns, is not relevant to the CO_2 question and will not be discussed here. The species pattern or noda approach is discussed briefly.

The term 'nodum' was coined by Poore (1955) for denoting a plant community of any rank. Poore's term was a replacement for the term phytocoenosis.

The only contemporary classification and mapping system based on the nodum approach is the Braun–Blanquet system (1928, 1965), which is widely used in central Europe (Tüxen, 1970; Westhoff and van der Maarel, 1978). The field and data-processing methods are based on a wealth of experience with vegetation and have proven their usefulness in both the temperate and tropical regions.

The major floristic approaches which can be used for classfying and mapping plant communities are based on sampling the floristic composition through sample stands, or relevés. Samples can be chosen systematically, randomly or selectively. In the last case, which is the most common, aerial photographs are usually used in combination with ground reconnaissance to distinguish preliminary patterns. These patterns are then documented in deail or subsequently modified through analysis of sample stands.

Each sample stand should be large enough to contain a cross-section of the species representative of the community. The basic data recorded are a species list and the quantities of each species.

Once an adequate number of vegetation samples (relevés) has been collected, the data are analysed according to one of several techniques: two-way tabulation, polar ordination and dendrogram cluster.

These approaches are all based on sampling the floristic composition of given vegetation covers through a number of sample stands or relevés. Samples can be placed systematically, randomly or selectively. In the latter case, which is the most commonly practiced, aerial photographs are usually used in combination with ground reconnaissance to distinguish preliminary patterns. These are then documented in detail or subsequently modified through the analysis of a number of samples. The number of samples varies with the size of the area and variability of the vegetation cover.

Each sample stand should be of a certain minimum size to contain a species composition nearly representative of the community or vegetation segment sampled. The basic data recorded in each sample is a species list (as complete as possible) and the species quantities.

Once an adequate number of vegetation samples (relevés) has been collected, the data are analyzed and synthesized according to either one of the above-mentioned three techniques or their derivatives.

The two-way tabulation technique. This is the original data-processing or synthesis tabulation technique of Braun-Blanquet, which has in recent years been variously simulated through computer application (Cêska and Roemer, 1971; Lieth and Moore, 1971; Spatz and Siegmund, 1973; Mueller-Dombois and Ellenberg, 1974; Westhoff and van der Maarel, 1978). It consists of entering the sample stand or relevé information together into one initial table, the so-called 'raw table.' Relevé numbers are entered in any order in the table head, one column for each relevé. Species names are entered on the left side of the table also in any order, one species in each successive row. Species quantities are entered into the table body for each species and the relevé in which the species was recorded.

After all species and relevés are entered, the raw table is then reordered into a 'constancy table'. This process involves counting in the raw table the number of times each species is present in the stands and recording this value (called constancy or frequency) on the right side of each species row. When this is done, species with high constancy values are temporarily eliminated from further consideration. The same is done with species of low constancy values.

The reason for taking these two steps is that species present in all or nearly all of the relevés cannot be used very well for subdividing the relevé set, since they are characteristic of the whole set. Similarly, species present in only one or two or a small proportion of the relevés cannot be used for subdividing the set because their presence is too sporadic to indicate trends.

The next step in the process involves only species with intermediate constancy values. Certain arbitrary threshold values are usually used to define the intermediate range of constancy, such as from 3 per cent to 65 per cent. These ranges are adjustable to the data set, however. The constancy table is then prepared by noting all species of intermediate constancy from high to low.

The third step involves scanning the table for species that occur together in a number of relevés. In other words, the analyst looks for species which have a high degree of association in their distribution. If he does not find such associated species, he may find single species which show a distribution trend which differs more or less strongly from that of others.

There may be a second set of species which shows a tendency to have a distribution trend which is more or less exclusive to the first set or single species. This second set is then also identified. It is usually possible to isolate at least two sets of mutually more or less exclusive groups of species which show a greater within-group similarity of distribution, i.e., some degree of within-association. For this purpose it is useful to set threshold values. For example, one might look for two species which occur together in at least 50 per cent of their relevés but occur alone in no more than 10 per cent of the other relevés. Other threshold values sometimes used are 66/10, 66/20 or 50/20. Cêska and Roemer (1971) offer five options.

Once two more or less mutually exclusive distribution trends are determined, the species involved are transferred to a third table, called an 'ordinated partial table'. The associated species of the first group are listed one under the other, and the second mutually exclusive group (or individual species, as the case may be) is listed beneath the first group. An order will usually become self-evident at this point. Further improvement may be obtained by consolidating the distribution trends through rearranging the relevé order, so that one associated group appears on the left side of the table and the other on the right. Of course, there may be more than one or two associated species groups, particularly in larger sets of relevés. The next table is obtained by rearranging the species and relevé order until the distribution trends of the associated and differentiating species groups or individuals are most evident.

When this is done, all of the hitherto excluded species are reentered in sequence, usually following the species used to differentiate the set of relevés. This final table is called a 'differentiated table'. It shows no differences in data from the raw table, but the species and relevé order has been rearranged so that the clearest species distribution and association trends are now evident.

The ecological trends associated with the species and relevé patterns are then searched for. The underlying ecological gradient may be related to soil moisture, topographically related factors, successional or dynamic relationships, or a combination of influences. Correlations with certain factors or combinations of factors may be established and may serve to suggest causal relationships or hypotheses. The next step may involve experimental analysis of the distribution hypotheses or the mapping of the patterns through the use of the differential or key species which have been worked out in the differentiated table. Some of these species may be dominants (in terms of height or cover). Mapping is usually done through a combination of ground observation and remote sensing.

Thus, the two-way tabulation technique provides, among other things, for determining key species for the mapping of floristically defined vegetation types.

The polar ordination technique was introduced by Bray and Curtis (1957) as an alternative data display technique. They felt that a geometric display of individual relevés in relation to one another according to their own floristic content would show more adequately the varying nature or continuum trends of the vegetation.

This method consists of first calculating the similarity relationships between each and every pair of sample stands or relevés in the set under comparison. The formulae used for calculating floristic similarities between stands are generally based on the proportion of common species in two relevés or on the quantitative proportion of common species in each comparison. Most commonly used is the quantitative modification of Sørensen's (1948) index of similarity proposed by Motyka *et al.* (1950). However, there are many other indexes which are equally useful. Many papers discuss the various merits of the indexes, but the usefulness of any index depends primarily on the vegetation itself (Mueller-Dombois and Ellenberg, 1974). Once the similarity indexes for the relevé set are determined, they are listed in a similarity matrix.

Polar ordination is the next step. This involves a geometric display of the similarity matrix in as accurate a constellation as possible. Because of the multivariate relationships of the similarity values, this is by no means easy. In the original Bray and Curtis version, the two stands or relevés with the greatest dissimilarity were selected to form the end points of the x-axis. These stands are then plotted, using their dissimilarity as the measure of geometric distance on the axis. All of the other relevés are then plotted on the same axis by using for each relevé the two geometric distance measures (or dissimilarity values) that each shares with the relevé at each end of the axis. The plotting procedure was originally done by graphical procedures. Later, the Pythagorean theorem introduced for this step by Beals (1960) was used.

When all of the relevés are plotted, one will usually find that their geometric distances do not display the dissimilarity values of the matrix very well. In other words, the geometric distances show a great deal of distortion along the first axis. For this reason, a second axis (the y-axis) is established by using a relevé near the centre of the x-axis which displays a high dissimilarity to the two reference relevés at the end points of the x-axis. This 'poorly fitted' relevé then becomes the first end point on the y-axis. The relevé most dissimilar to the first becomes the second end point. All of the remaining relevés are once again plotted with regard to the dissimilarities they share with this second pair of relevés. Thus, each relevé is positioned on each axis.

At this point, usually, the ordination is tested by comparing the geometric distances of the two-axis plot with the dissimilarity values shown in the matrix. If there is a significant correlation between the two, the ordination is considered an acceptable display of the values of the similarity matrix. If no significant correlation appears, one can either try different relevés as end points of the axes or establish a third axis, a z-axis. The z-axis can then be used to develop a three-dimensional display.

Much research has gone into finding a better way of selecting the end-point relevés for the x- and y-axes. This work has been reviewed by Whittaker and Gauch (1978), McIntosh (1978) and Cottam *et al.* (1978). The major problem is to find end-point relevés which are strongly dissimilar but which at the same time share some resemblance to the rest of the relevés to be ordinated. Extreme end-point relevés may simply be sample stands that have little in common with the rest of the set.

A large number of other ordination methods have been proposed—e.g., factor analysis (Dagnelie, 1960, 1978) and principal component analysis and position vectors technique (Orloci, 1966, 1967, 1978), but the modified polar ordination technique developed by the Wisconsin School remains one of the most powerful and robust for this approach (Whittaker and Gauch, 1978).

One value of ordination is in finding underlying environmental factor gradients or successional gradients that can be used to explain the floristic vegetation patterns displayed on the diagrams. Its second value is to test intuitive classifications of plant communities by mathematical procedures. Polar ordination, therefore, is useful for plant community classification, but it was not really designed to be a classification technique.

The dendrogram technique, sometimes called the cluster analysis technique, is a mathematical tool explicitly designed for classification purposes, including plant community classification (Sokal and Sneath, 1963). Basically, the dendrogram technique also involves a diagrammatic display of the content of a similarity matrix and in this respect is similar to polar ordination. But instead of displaying relevé similarities or dissimilarities by geometric distance, dendrograms display them in the form of 'clusters'. These clusters are mathematically computed levels of similarity, indicated on the *y*-axis of each dendrogram, at which two or more relevés are joined. The joining of certain relevés at certain levels of similarity indicates a cluster, or community type.

The centroid, polythetic and agglomerative dendrogram technique begins with a search for the two relevés with the greatest similarity. These two are then compared with the relevé that shares the next highest similarity to one of the first two relevés; or the first two relevés are averaged into a single synthetic relevé. In that case a new set of similarity indexes is computed between the synthetic relevé and the others. Although the details of the various procedures differ, the underlying goal is to sequentially compare all relevés to one another. The relevés are clustered in sequential algorithms at continuously decreasing levels of similarity until they all are clustered.

It is quite rare for relevés to display complete similarity. But at a very low level of similarity, say five per cent, all of the relevés may be united in a single cluster. The reason is that they are likely to have at least one species in common.

The ecologically most important information in any dendrogram is found not in the very high-similarity or very low-similarity clusters but in those occupying the intermediate range. In this intermediate range one usually finds the clusters that provide usefully generalized information.

The problem in the dendrogram technique is to identify the set of intermediate-range clusters which are useful for community classification. (The same problem exists in the synthesis tabulation technique when the investigator looks for associated species groups in the constancy table.) Arbitrary guidelines have been devised (Orloci, 1978) for objective cluster recognition, but the problem has not yet been totally resolved. It is difficult to make plant community classification an automatic matter. The reason for this difficulty is that similarity levels within or between ecologically meaningful clusters or plant community types cannot be reduced to one level alone. If it was attempted, the natural variation in vegetation would be violated, and the result would be an arbitrary or meaningless classification.

One further point should be mentioned. The two-way tabulation technique is superior in two ways to the polar ordination and dendrogram techniques. The differentiated table displays the species by name and with their quantitative variation among the whole set of relevés. The other two techniques are more abstract, in that the investigator must make a special determination of the species which are responsible for the displayed variation.

Of course, one can usually also use these two techniques for arranging and displaying species relationships. One can, for example, ordinate by species rather than by relevés, or one can build a dendrogram on species distribution similarities rather than relevé similarities. But this is not the same as building species–relevé blocks and seeing the species distributions at the same time on the display tool as in a differentiated synthesis table. An ordination tool called 'reciprocal averaging' introduced by Hill (1973) is said to display species and relevé groupings in coordination (Whittaker and Gauch, 1978), and this may become a tool as powerful as the two-way tabulation technique.

Another powerful technique in classifying vegetation from the standpoint of floristics is the structural analysis of species populations. The tree species-population analysis technique is essentially a forest mensurational technique (Meyer, 1952) which has proved to be of equivalent ecological value to the other techniques discussed.

This technique involves enumerating species individuals by size in sample quadrats (belt-transects, circular plots or one of the more popular distance measures). Usually used as a measure of size are diameter at breast height (dbh) for trees over two metres tall and height for seedlings and saplings under two metres tall. Both measures can also be applied at the same time, or others can be used, such as basal area and volume. The number of trees enumerated in a sample should be at least 30 to 50 in each class (i.e., trees over or under two metres) so that definite trends can be tabulated or plotted into curves (Mueller-Dombois and Ellenberg, 1974). The curves can then be interpreted. For example, an inverse J-shaped distribution would indicate a large number of small juvenile trees and perhaps normal mortality trends in successively larger groups, indicating a stable population. Such a trend may be indicative of a climax tree species. A large number of large-sized trees with few or no small trees would indicate a poorly reproducing population, possibly a pioneer tree species. Considerable work has gone into interpreting curve trends mathematically and ecologically (Leak, 1965; Hett and Loucks, 1971; Goff and West, 1975), but they are only trends and do not convey definite answers. Additional information has to come from autecological and synecological studies of the communities and environment of the study area. In this respect the number/size distribution curves used for the analysis of the population structures of tree species are like the display techniques discussed earlier. They provide trend indications rather than conclusive answers, but they are still extremely valuable.

It should be noted here that one problem in the study of tropical rain forest ecology is the practical impossibility of determining tree ages. But age estimates are useful additional information in conjunction with number/size distribution curves.

The techniques that have been discussed here are useful for classifying forest communities into successional groups, provided that spatial variations in habitat are understood and taken into consideration. The extrapolation of successional trends from data on trees and stands occurring in different locations is scientifically suspect unless it can be shown that the habitats are similar or identical. When this is demonstrable, data on population trends add a powerful tool for determining and classifying dynamic relationships among plant communities. Hence, a thorough classification of forest communities should make use of both spatial and structural-temporal analysis techniques.

2.4.3 Problems and Measures in Mapping Tropical Vegetation

Tropical vegetation has been studied much less than temperate zone vegetation, although the taxonomic diversity of tropical rain forests is a well-established fact. The high diversity makes the definition of tropical plant communities and their mapping particularly difficult. However, there are several simplifying approaches.

2.4.3.1 Bioclimatic Methods

Except perhaps for Thornthwaite's method, the bioclimatic classification methods were formulated with tropical vegetation in mind. This is apparent in Köppen's classification, clearly, in the Holdridge system and also in Walter's climate-diagram method. Whitmore (1975) found the simple seasonality scheme of Mohr (1933) to be most appropriate for matching climate with the major zonal forest types in southeast Asia. Mohr considered monthly rainfall in Indonesia to be 'wet' when it exceeds 100 mm and to be 'dry' when it measures less than 60 mm. On this basis he developed a formula, the number of dry months divided by the number of wet months. Whitmore used the climate diagrams of Walter and Lieth (1960) to extract seasonality data for a nomogram which shows the mean number of dry months plotted over the mean number of wet months. A diagonal axis drawn from the value of 12 dry months on the y-axis to the value of 12 wet months on the x-axis shows the range of Mohr's quotient (Q), from infinity to zero. On this nomogram Whitmore defines four bioclimatic zones for southeast Asia:

Type A = Wet or perhumid tropical zone, that is, up to 1.5 dry months ($Q = 0.143$)
Type B = Moist or humid tropical zone, that is, 1.5 to 3 dry months ($Q = 0.143$ to 0.333)
Type C/D = Moderately dry tropical zone, that is, 3 to 6 dry months ($Q = 0.333$ to 1.0)
Type E/F = Dry tropical zone, that is, climates with more than 6 dry months ($Q = 1.0$ upwards)

On Whitmore's small-scale bioclimatic map, much of the Malay Peninsula, Borneo, Sumatra and New Guinea are shown as Type A. The Type B climate is shown for southeast Java, southern and eastern Borneo and the central Philippines. On western Java, southern New Guinea, Thailand and the northern and southern Philippines one finds a moderately dry (Type C/D) climate. On the islands east of Java and in much of northern Australia one finds a dry tropical (Type E/F) climate. The tropical rain forest of northern Queensland is shown as occurring in a moderately dry (Type C/D) climate.

This dry month/wet month ratio can, of course, only be used for tropical bioclimatic mapping. Rainfall seasonality is apparently the most important environmental characteristic related to spatial differentiation in tropical vegetation types. Only Walter's climate-diagram method can readily be used for detailed, region-specific, bioclimatic mapping. It should also be pointed out that Mohr's system can only be used to characterize tropical lowland climates. Tropical mountain climates require special consideration of temperature relationships. These can be obtained from Walter's climate diagrams.

Kartawinata (1977) used Mohr's bioclimatic system in combination with Walter's diagram method in somewhat modified form to characterize 24 ecological zones in

Indonesia. He also applied Krajina's (1973) biogeoclimatic zonation scheme as a systematic tabulation device.

2.4.3.2 Landscape Classifications

The landscape classifications discussed earlier are all applicable to small- and intermediate-scale mapping in the tropics. Krajina's bioclimatic zonation scheme, developed primarily for British Columbia, has been applied to the Hawaiian Islands (Krajina, 1963) and to Indonesia (Kartawinata, 1977). Gaussen's system is widely applied, particularly in the tropics of southeast Asia. Moreover, his system is closely related to the UNESCO system, and Ellenberg's world ecosystem classification builds on the UNESCO system.

Beard (1978) reviewed the physiognomic approach to classifidation with particular attention to tropical vegetation. He emphasizes the confusion among Anglo-American ecologists (also reviewed in detail by Shimwell, 1971) which was caused by the successional classification scheme of Clements. Clements (1916, 1928) considered a bioclimatic unit or a vegetation zone to represent a formation in spite of the various physiognomic units, such as grassland, scrub and forest, which are usually encountered in a vegetation zone. Clements regarded these variations as successional types which would all converge in time toward the climatic climax. Moreover, Clements did not define these vegetation variations in a zone physiognomically but merely floristically by dominant species.

Tansley and Chipp (1926) argued against Clements' idea that all vegetation variations in a climatic zone would converge to a climatic climax and recognized other stable types as edaphic or topographic climaxes. Because of this argument, physiognomic or more detailed structural and floristic studies were neglected in the English-speaking countries but not in central Europe or Russia.

British ecologists who worked in the tropical countries of the commonwealth then re-emphasized the need for physiognomic classification and mapping. This began with Burtt-Davy (1938) and Champion (1936) and continued through Richards (1952) in particular, who together with Davis devised the profile-diagram method (Davis and Richards, 1933–34) as a realistic tool for describing vegetation.

A convergence of the purely physiognomic approach with the landscape approach is apparent in Beard's (1955, 1978) formation-series approach. Beard uses profile diagrams in a more generalized context by showing typical formations (based on vegetation architecture) in relation to climatic gradients. This is a very effective approach which should be used wherever possible as a tool for map interpretation. It has been applied by many authors, including Whittaker (1975) in his discussion of major ecoclines. But it should be understood that both Beard's formation series and Whittaker's major ecoclines are landscape units rather than real vegetation units. They demonstrate potential physiognomic vegetation, not existing vegetation.

A more detailed approach is Whitmore's (1975) treatment and classification of the tropical rain forests of southeast Asia. Whitmore recognizes 16 types of tropical forest formations:

(1) Tropical lowland evergreen rain forest.
(2) Tropical lower montane rain forest.
(3) Tropical upper montane rain forest.
(4) Tropical subalpine forest.
(5) Heath forest.
(6) Forest over limestone.
(7) Forest over ultrabasic rock.
(8) Beach vegetation.
(9) Mangrove forest.
(10) Brackish-water forest.
(11) Peat swamp forest.
(12) Fresh-water swamp forest.
(13) Seasonal swamp forest.
(14) Tropical semi-evergreen rain forest.
(15) Tropical moist deciduous forest.
(16) Other formations of increasingly dry seasonal climates.

The last two formation types are described as monsoon forests, while the first 13 are tropical rain forest types. Poore (1978) considered Whitmore's 16 formations more useful for the classification and conservation purposes of the International Union for the Conservation of Nature (IUCN) than the 14 types suggested in the UNESCO scheme. Poore believes that Whitmore's types can also be extrapolated quite satisfactorily to the American and African tropics.

The difference between Whitmore's types and Whittaker's major ecoclines is that Whitmore recognizes not only the relationships of vegetation to bioclimates but also to major variations in soil and topography. Variations in relation to topography are also recognized in the UNESCO system, but Whitmore gives more detail on edaphic differentiation. Rodin *et al.* (1975) used a similar landscape formation concept for their productivity and phytomass estimates. They called their units soil-vegetation formations and recognized 10 such units for the humid tropical belt.

Whitmore's 16 formation types can be grouped by environmental factors as follows:

(a) Formations dominantly controlled by lowland climates = 4 (1, 14, 15, 16).
(b) Formations dominantly controlled by topographic factors, mostly mountain climates and associated factors = 3 (2, 3, 4).
(c) Formations dominantly controlled by edaphic factors = 9 (5, 6, 7, 8, 9, 10, 11, 12, 13).

Whitmore's formations are not physiognomic formation types; they are landscape units or landscape formation types. Very little emphasis is given to vegetation architecture in Whitmore's types. In fact, one may expect to find several physiognomically or architecturally different vegetation types in each of Whitmore's units. This becomes further apparent from Whitmore's observation that most of the tropical rain forest in southeast Asia has been disturbed by shifting cultivation and thus is not original but secondary forest. Such secondary forests may differ from place to place even on the same soil substrate, and one may expect to find a mosaic of successional vegetation types within each of Whitmore's formation types. These secondary forests and successional types will have different physiognomies or architectural characteristics and thus different biomass relationships.

2.4.3.3 Methods for Mapping Existing Vegetation Structure

The profile-diagram method developed by Davis and Richards (1933–34), the more formalized profile-diagram procedure of Dansereau (1951), the schemes of Küchler (1967) and of Fosberg (1967), and the layer-diagram and life-form spectrum methods all are useful for mapping tropical as well as temperate forest architecture.

Küchler and Sawyer (1967), for example, mapped an area covered with tropical moonsoon forest vegetation in northwest Thailand at a scale of 1:30 000 using Küchler's system. The authors defined phytocoenoses by both architectural criteria and characteristic species composition. Fosberg's system has been used to map two national parks in Sri Lanka, one covered dominantly by evergreen sclerophyll monsoon forest, the other dominantly by deciduous scrub vegetation (Mueller-Dombois, 1969, 1970). The maps were prepared from air-photo mosaics at a scale of 1:32 000. Mapping by dominant species was not possible in this vegetation because of the great species diversity in both woody and herbaceous vegetation types. Approximately 20 to 30 purely structurally defined types were mapped for each national park (each was approximately 80 000 to 100 000 ha in size). Where necessary, the Fosberg system was expanded to recognize finer subdivisions. An aerial photo key for objective mapping procedures was developed (Mueller-Dombois and Ellenberg, 1974: 489) which provided for quantitative definitions of map units, so that a trained interpreter could carry out independent mapping at the same level of detail and unit integration.

In the tropical rain forest territory of Hawaii forest types have been mapped at a scale of 1:48 000 by using both dominant species and non-floristic structural criteria (Mueller-Dombois *et al.*, 1977). The map units were systematically worked out, again following Fosberg's mapping principles, to obtain internationally comparative information values. In fact, it would be insufficient to map vegetation in the Hawaiian rain forest by dominant species because of the broad ecological amplitude of *Metrosideros polymorpha* and the tree fern species of *Cibotium*. The problem is similar to that in central Europe, where undergrowth vegetation and a combination of characteristic species provide better large-scale mapping criteria than dominant species do.

The usefulness of the structural (non-floristic) classification approach has already been tested in one case. Becker (1976) applied morphological data collected from tree ferns (*Cibotium* spp.) to test an existing map classification (Mueller-Dombois and Fosberg, 1974) of the montane rain forest in and near Hawaii Volcanoes National Park. By applying tree fern data, such as stem density, height, top-trunk diameter and number of fronds to a multivariate analysis using the dendrogram technique, Becker found that these tree fern data alone were sufficient to arrange his sample stands into an ecological series. This meant that tree fern architecture could be used as an indicator of habitat in that area.

Webb (1968, 1978) has pioneered physiognomic–architectural approaches for the classification of Australian rain forests. He and his collaborators (Webb *et al.*, 1970, 1976) have dealt with such data by numerical methods, particularly by using the two-way tabulation and dendrogram techniques. Webb found a good correlation between purely structural (non-floristic) characteristics and environmental factors. His dendrogram classification of the northeastern Australian tropical rain forest resulted in the nine types given in Table 2.4 (synthesized from Webb, 1968, 1978).

It is interesting that all rain forests in Australia (11° to 20 °S latitude) are called vine forests by Webb (Table 2.4). This designation also applies to Webb's subtropical forests (20°–32 °S latitude). The first physiognomic criterion used by Webb is evergreenness versus deciduousness (as in Küchler's system). The term 'raingreen' in Table 2.4 is applied to Australian tropical forests with at least a minor proportion of deciduousness.

Table 2.4 Tropical rain forest types of NE Australia according to Webb (1968, 1978) 1978)

Structural types of tropical rain forest in Australia	Mean rainfall (mm)	Soil fertility (rating)
A. *Strictly evergreen*		
1. Mesophyll vine forest	3644 (seasonal)	Medium
2. Mesophyll fan-palm vine forest	3644 (seasonal)	Medium (seasonal swamp)
3. Notophyll vine forest	1594 (monsoonal)	Calcareous or siliceous sands
B. *Raingreen*		
4. Complex mesophyll vine forest	3644 (seasonal)	High
5. Mesophyll feather-palm vine forest	3644 (seasonal)	High–medium (seasonal swamp)
6. Mixed mesophyll-notophyll vine forest	3644 (seasonal)	Medium
7. Semi-deciduous mesophyll vine forest	3049 (strongly seasonal)	High–medium (alluvial)
8. Semi-deciduous notophyll vine forest	1600 (monsoonal)	Medium
9. Deciduous vine thicket	1222	High–medium–low

Below this first level, prevailing leaf size is used—i.e., mesophyll >12.5 cm, notophyll 12.5 to 7.5 cm and microphyll <7.5 cm. Prevailing microphyllous trees, such as those associated with the southeast Asian heath forests of Whitmore (1975), are not apparent in the Australian tropical rain forests. The term 'complex' in Table 2.4 refers to forests highly variable in leaf size, while 'mixed' refers to a prevailing mixture of two leaf sizes. In addition to leaf size, specialized tree forms (tree ferns, palms, etc.) are also used for subdividing. Spacing, or coverage, is not used in Webb's system, although it is the first-level criterion in Specht's (1970) Australian scheme and is also used in Fosberg's system and others.

Webb defines his structural types in such a way that they are useful as site indicators in a broad sense. This is apparent in that each type is characterized by either a particular rainfall regime, by type of soil, or by a combination of climate and soil. In his 1968 paper Webb provides a field key for the identification of general habitat types through the use of vegetation architecture. In this respect Webb's structural vegetation classification is primarily a landscape scheme.

Habitat identification is not implied in Dansereau's, Küchler's, Fosberg's or Specht's schemes. Those schemes are based strictly on vegetation architecture alone. An ecological meaning can be applied to such strictly architectural units, however, through the analysis of environmental, historical or dynamic-successional factors (see, e.g., Brünig, 1970).

It may be noted that schemes using only vegetation architecture are more useful for the mapping of plant biomass than those using vegetation indicators for habitat identification. That Webb's scheme belongs to the latter can be seen from the absence of coverage and stature among his criteria. These two structural characteristics are the most important ones for phytomass mapping.

However, primary production cannot be mapped by any purely vegetation–architectural scheme, since environmental factors and vegetation potential are the critical factors. Webb's scheme thus might be adaptable to the mapping of primary production in the tropical rain forests of Australia. This approach could also be extended to other tropical regions.

2.4.3.4 Environmental Gradient Analysis

Whittaker (1967) distinguished two approaches to environmental gradient analysis, direct and indirect. Direct analysis means analysing vegetation response to a known environmental gradient. Indirect analysis means analysing the environment in relation to a known vegetation gradient. These two approaches are clearly analogous to the bioclimatic and landscape methods. Bioclimatic mapping is a direct form of environmental gradient analysis that is applied in small- and intermediate-scale maps, while direct environmental gradient analysis is usually associated with local or regional field work and large-scale maps. Whittaker's (1956, 1960, Whittaker and Niering, 1965) mountain-slope analyses are typical examples, and so are Ellenberg's (1950, 1952) gradient analyses of agricultural weed communities in Europe. Landscape mapping, such as shown on Hueck and Seibert's (1:8 million) map of South America, is a typical case of indirect gradient analysis, but in the small map-scale range. An example of indirect gradient analysis in the intermediate to large-scale map range is Webb's (1968, 1978) approach to the subhumid and seasonal tropics of Australia.

There are problems in mapping tropical vegetation with respect to both approaches. The reason is high species diversity, which presents two different kinds of difficulties.

One problem is in identifying such a large number of species particularly in areas where taxonomic information is insufficient. It prompted Webb (1959, 1968) to look for vegetation–architecture alternatives for classifying tropical rain forests, and it is the same problem that traditionally has led to a general preference for physiognomic over floristic approaches to classifying and mapping tropical forest vegetation.

A more fundamental problem, however, is the character of the distribution of tropical forest species. Even in rather large sample plots, most of these species are represented by only one or two specimens (Ashton, 1964, 1965; Poore, 1964, 1968; Letouzey, 1978). Another, but much smaller, group of species are so widespread, however, that they show no response to seemingly wide variations in soil. A third group of species—those with intermediate ranges of distribution and abundance that might be expected to reflect spatial changes in soil substrate—often seem to be rare or absent in tropical forests. Knight (1975), for example, did not find any tropical forest species that responded significantly to soil variations in Panama. On the other hand, Ashton (1964) found forest stands to cluster in relation to soil and local topography in the dipterocarp forests of Brunei. By using ordination techniques he obtained a fair clustering of stands with similar floristics in similar habitats. The environmental gradient trends indirectly established by Ashton were supported further by Austin *et al.* (1972) using different multivariate techniques.

It is perhaps too early to generalize about the spatial relationships of tropical forest species and habitats on large-scale maps because there have been so few studies of this sort. Whitmore (1975) emphasizes that practically nothing is known about small-area variations in the distribution of tropical species in relation to variations in habitat. Small-area patterns in tropical rain forests have primarily been identified so far in a dynamic sense as gap phases, building phases and mature phases. A few people also refer to a breakdown phase (Leibundgut, cited in Mueller-Dombois and Ellenberg, 1974: 398; Zukrigl, Eckhardt and Nather, cited in Walter, 1976: 15). The breakdown phase in the montane rain forest of Hawaii, however, is so conspicuous (Mueller-Dombois *et al.*, 1977; Mueller-Dombois, 1980a) that the phenomenon has been called dieback, or forest decline. It is still popularly thought to be caused by a disease (Thompson, 1978).

These phases are the most obvious architectural variations and need urgent attention in different rain forest areas, since dynamic phasing patterns are a key to understanding ecosystem maintanence under natural conditions. But studies of pattern and process in tropical rain forests cannot advance until the responses of vegetation to habitat variations are also clarified. One can be too easily tempted to deduce dynamic relationships from structural variations which in reality are the result of spatially different environmental situations.

Direct gradient analysis and the use of vegetation–architecture characteristics as the response phenomena may be the way to proceed. The direct approach has not been used much in tropical forests. It will permit more precise determination of the vegetation potential of different habitats in a local forest management unit, i.e., on large-scale maps. Such studies are urgently needed for mapping primary production and other site capability and fragility information that is needed for tropical forest management.

2.5 A COMBINATION METHOD FOR APPLYING SATELLITE IMAGERY TO VEGETATION MAPPING AND FOREST LAND CLASSIFICATION

Satellite imagery has added a significant dimension to the array of remote sensing capabilities. In the context of this paper, two aspects of satellite imagery are particularly important. One is LANDSAT imagery. The other is the possibility of extending the mapping of actually existing vegetation from the large-scale to almost the small-scale map range. Satellite imagery—available in standard black-and-white format at an approximate scale of 1:500 000—allows one to recognize the outlines of actual vegetation even when reduced to the lower limit of the intermediate-scale range, a mapping scale of 1:1 million.

This is the map scale for which the physiognomic–ecological classification scheme of UNESCO was prepared. Thus, it should be possible to use 1:1 million satellite imagery to outline the 225 physiognomic–ecological units recognized in the UNESCO scheme if one has additional information, which can be combined with this approach. The scheme provides for the mapping of real vegetation–natural, semi-natural and cultivated. The internationally integrated terminology of the UNESCO classification goes a long way toward removing the ambiguousness inherent in many vegetation terms. This ambiguity, a long-standing handicap in global understanding of vegetation-type similarities (Burtt-Davy, 1938; Richards *et al.*, 1940; Vareschi, 1968; Latouzey, 1978), has thus been resolved, to some extent at least.

Except for a few successful tests in the Central American tropics (Küchler and Montoya-Maquin, 1971), however, the UNESCO system has not been applied over any significant area of the globe. Fontaine (1978) states that UNESCO and FAO are collaborating in applying the UNESCO classification to the production of vegetation maps at a scale of 1:1 million, but an important question remains: To what extent is satellite imagery intended for use in the 1:1 million mapping process? Without the use of satellite imagery, the 1:1 million maps will tend to become maps of potential natural vegetation—i.e., site or landscape maps—rather than maps of existing vegetation. Maps of potential vegetation are valuable for different purposes, of course, but satellite imagery has provided the capability to extend the mapping of real vegetation to broad overview scales. This has never been possible before and should allow for more exact inventories of phytomass.

2.5.1 Imagery in Mapping

The following specific proposals are made for applying satellite imagery to vegetation mapping and forest land classification.

2.5.1.1 Structural Elements

Remotely sensed images provide certain basic elements of what is sensed. Nine are generally recognized (Estes and Simonett, 1975):

(1) Size (i.e., scale).
(2) Shape.
(3) Shadow.
(4) Tone or colour.
(5) Texture (rough or smooth).
(6) Repetition of pattern.
(7) Site (i.e., the indirect indication of what is there, e.g., a black spruce swamp).
(8) Association (objects commonly associated with one another).
(9) Resolution (which puts a limit on what can be recognized on the image).

There are some striking analogies between these elements and the basic structural criteria used in mapping vegetation in the field. *Size* relates to map-scale, which determines to a large extent what kinds of vegetation structure or community type can be recognized. *Shape* relates to the outlining of vegetation units, which in some cases may be self-evident but in others very difficult to identify. *Tone* or colour variations are usually used to aid in determining the boundaries of plant communities, which may be recognizable by differences in albedo. Aside from topographic considerations, *texture* may be translatable into open, closed or sparse vegetation, the primary structural groups in Fosberg's (1967) scheme. At larger aerial photographic scales, texture may be translatable into grassland with scattered woody plants, closed grassland, scrub or forest, depending largely on albedo. *Shadow* can sometimes be translated into height of a forest on large-scale photographs. Shadow as a structural element is used for timber volume surveys from aerial photographs (Thorley, 1975). However, at this level of detail the use of stereopairs rather than shadow is the more common means for evaluating tree height and topographic variation. *Repetition of pattern* on remotely sensed images aids in the classification of plant communities according to structural similarities, while *site* in remote-sensing terminology refers to the recognition of landscape units, i.e., vegetation plus habitat. Such landscape units, which are rather generalized entities from the viewpoint of vegetation architecture, are commonly recognizable on satellite images. *Association*, which in remote-sensing terminology refers to repeating patterns of plant communities in spatial contact, provides an explanatory dimension which is often omitted from plant community classifications which have not been put to the test through mapping.

An important advantage of satellite imagery is the broad overview that these images provide. A person with some geographic knowledge may be able to recognize a particular area from small-scale satellite images without resorting to an atlas. On the other hand, small-scale images suffer from low resolution, which means that it is possible to recognize only limited amounts of detail.

2.5.1.2 Non-Technical Classifications

In the *Manual of Remote Sensing*, Thorley (1975) reviews the classification of forest land in the temperate United States and Canada, in temperate Europe, in the temperate southern hemisphere (particularly Australia, New Zealand and Chile), and in the tropical zone. He points out that forest areas in North America are mapped by dominance types, such as the Douglas-fir and the lodgepole pine forests. The same sort of forest classification is practised in New Zealand. In Australia, forests are classified for commercial purposes into three broad classes—productive, semi-productive and low-grade. Physiognomic formation concepts are apparently applied in the tropical zone, but there is no uniformity within the tropics nor within any of the temperate areas. Moreover, the manual gives almost no guidelines for mapping forest land from satellite imagery. The focus of attention is on conventional aerial photography, which is in the large-scale range, most commonly from 1:10 000 to 1:50 000.

According to Thorley, however, satellite imagery at the scales of 1:100 000 to 1:500 000 is used for a number of forestry purposes, including damage assessment (such as pollution damage, fireloss and insect and disease damage) and land classification. Indeed, there are many recent forestry papers which are concerned with the application of multispectral satellite imagery to forest land classification. Es (1976) applied such imagery to the classification of the tropical dry-deciduous forest of central India and reports that such imagery could be used to distinguish forested from agricultural areas. Within the forested area Es could distinguish two groups in terms of size, woody vegetation taller than 15 m and woody vegetation less than 15 m high. Tiwari (1976) was able to distinguish such units as forest, scrub and grass cover. Sicco Smit (1974) applied SLAR images to the mapping of tropical rain forest in

Colombia and was able to distinguish broad vegetation types on the basis of physiographic features. Wacharakitti (1975) reports that he could distinguish five landscape types in northern Thailand: evergreen forest, mixed deciduous forest with teakwood (*Tectonia grandis*), dry dipterocarp forest, rice fields and areas of shifting cultivation. Driscoll and Spencer (1972), using satellite imagery, concluded that only generalized vegetation types could be identified in Colorado, such as Ponderosa pine forest, herbaceous upland vegetation and hydrophyte vegetation. Jobin and Beaubien (1974) were able to recognize such types as *Picea mariana* and *Abies balsamea* forests on Anticosti Island from both black and white and colour imagery provided by ERTS-1, while Lawrence and Herzog (1975), using the same source of imagery for two areas in central Oregon, concluded that forest cover type could not be adequately described by species name alone. These examples may suffice to indicate that satellite imagery in the normally available intermediate-scale range can only be used to outline broad vegetation types.

2.5.1.3 Accessory Information at Satellite Image Scales: the Broad Structure

As an example of how to use accessory information at satellite image scales, Figure 2.7 gives a 1:1.3 million satellite image of the island of Hawaii. On this image one can recognize three clear patterns. These are ocean, land and clouds. But there are also certain obvious patterns on the land itself. For example, there are some significant topographic configurations indicating mountains. On the mountain in the southern half of the image one may recognize a large crater-like depression. However, it is not easy to determine the height of these mountains from the image. Two large patches of dark colour occur on the east side of the island. One might suspect that these were forest-covered areas, but even if we found out with the help of improved spectral bands and some enlargement or colour-change techniques that these dark patches are indeed forest-covered areas, how can we find out what kind of forest this is? Our approach is to use existing information mapped at approximately the same geographic scale. Such information may be used in any sequence or form, but the more important elements for vegetation mapping are climate, topography, soil and the vegetation itself.

2.5.1.4 Climate and Topography

Figure 2.8 is a topographic map of the island of Hawaii with 21 climate-diagrams. This map is reduced to approximately the same scale as Figure 2.7, i.e., 1:1.5 million. The additional information in Figure 2.7 indicates at once that the northern mountain on the satellite image is Mauna Kea and the southern mountain Mauna Loa.

Figure 2.8 also indicates that both mountains are of approximately the same height. The uppermost contour line for both mountains is 13 000 ft (3965 m).

Figure 2.7 Satellite image of the Island of Hawaii at 1:1.3 million. 1973 LANDSAT image from Dec. 1978–Jan. 1979 issue of the *Plain Brown Wrapper*, an Ames Research Center publication

The exact altitude of each mountain could easily be obtained from a more detailed topographic map. The east flank of Mauna Kea slopes seaward along transect 6 from above 4000 m to sea level over a distance of only 40 km (27 mm on map).

The climate diagrams were prepared according to the method of Walter (1957). The abscissa on each diagram represents the 12 months of the year from January to January, with July in the middle (since Hawaii is in the

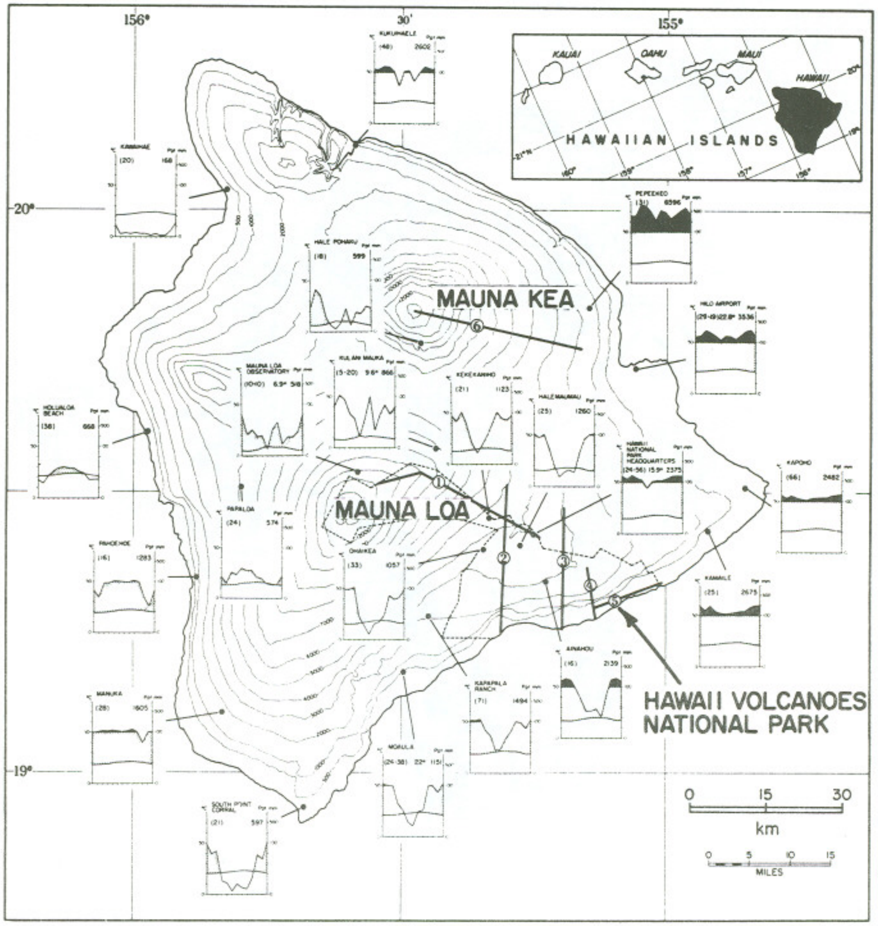


Figure 2.8 Climate-diagram map of the Island of Hawaii at 1:1.5 million (from Mueller-Dombois, 1966a). It shows 21 climate diagrams prepared after Walter (1957). The abscissa on each diagram portrays the months from January to January with July in the centre. The left-side ordinate gives the air-temperature scale, from 0 upwards in 10 °C intervals. The near-horizontal curve is the mean month-to-month temperature curve. The right-side ordinate gives the precipitation scale, from 0 to 100 mm upwards in 20 mm intervals and from 100 mm (the black areas on some diagrams) in 200 mm intervals. The mean month-to-month precipitation curve is the uneven line on each diagram. Pronounced dry seasons are indicated in black. Station name, years of record and mean annual precipitation are shown at the top of each diagram. Transects 1 to 6 relate to ecosystem profile diagrams; one of these (Transect 6) is shown on p. 76.

northern hemisphere).* The left-side ordinate on each diagram gives the temperature scale in 10 °C intervals, starting from 0 °C. The right-side ordinate on each diagram gives the precipitation scale in 20 mm intervals, from 0 to 100 mm. Above 100 mm the scale is reduced by 10% so that the next interval above 100 mm represents 200 mm. The black area on the diagrams indicates monthly precipitation in excess of 100 mm. Diagrams with black areas across the top are typical for rain forest areas in the tropics. The mean monthly rainfall or precipitation curve, which is plotted with reference to the right-side ordinate, is the uneven curve. The mean monthly temperature curve, plotted with reference to the left-side ordinate, is always a smooth curve that follows almost a straight line trend on each diagram. This temperature curve shows that we are in the tropics, since the difference between summer and winter mean air temperatures is very small. This curve does not change in shape because of rising altitude; it is merely displaced downward, so that at the Mauna Loa Observatory, for example, the mean monthly temperature never exceeds 10 °C, and the annual mean temperature as shown on that diagram is only 6.9 °C. This temperature curve and mean value are typical for tropical alpine environments. At the south end of the island are tropical seasonal climates, which are indicated wherever the rainfall curve falls below the temperature curve. The west coast has a reversal of seasonality into humid summer and dry winter. On the northwest side of the island is a typical climatic desert (at Kawaihae). Here the rainfall curve remains below the temperature curve throughout the year. This Hawaiian climate compares in dryness with the western Sahara Desert (Walter *et al.*, 1975).

In Figure 2.7 the dark pattern around the top cannot be forest, since this is an alpine environment. The large dark patch of the east flank of Mauna Kea, however, is a forest-covered area. The climate diagrams of Pepeekeo and Hilo Airport in Figure 2.8 inform us that this must be tropical rain forest because both diagrams show rainfall in excess of 100 mm for each month of the year. Since the forested area is topographically delimited near 2000 ft (610 mm), it cannot be lowland tropical rain forest. Its upper extent, according to the satellite image, goes to about 9000 ft (2745 m), and we may wonder whether this is all included in the montane rain forest. The climate-diagram density is not quite sufficient to give us this answer; the answer may be obtainable from other sources.

2.5.1.5 Vegetation and Soil

The vegetation zone map of Ripperton and Hosaka (1942) shown in Figure 2.1 gives us an answer to the question of where to draw the upper boundary of the montane rain forest. According to this map, the montane rain forest (zone 6)

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* Similar diagrams for areas in the southern hemisphere show January in the centre of the x-axis (Walter *et al.*, 1975).

gives way to the upper montane rain forest (zone 7) at approximately 5500 ft (1800 m). This is followed by a distinctly different vegetation zone which represents subalpine open forest and scrub up to about 12 000 ft (3935 m). Here the satellite image offers corrective information, since there is a distinct colour change from dark to light at about 9000 ft (2745 m). This is the upper limit of the mamane (*Sophora chrysophylla*) tree line on the east flank of Mauna Kea.

Note that the northward extension of the montane tropical rain forest on Mauna Kea, as shown on the Ripperton and Hosaka map, does not appear on the satellite image in Figure 2.6. This area has been converted to pasture. It could be that Ripperton and Hosaka ignored this grassland variation and mapped this area as potential montane rain forest, or that the forest conversion took place after 1942. The former seems more probable in light of the next comparison, soil evaluation.

Figure 2.9 shows the soil-order map of the island prepared by Uehara (1973), with minor modifications. Recent lava flows were transferred from the geology map of Abbott (1973) on to the soil map. It becomes evident from comparison of the maps that the soil substrates under Ripperton and Hosaka's vegetation zones are quite variable. In the montane rain forest zone, for example, one finds large areas of histosol (organic soils composed of woody peat on lava bedrock), minor areas of lithosol (prehistoric lava flows), and recent (historic, i.e., <200 years old) lava flows, particularly in the saddle between the two mountains. Further north, much of the east-flank rain forest zone below Mauna Kea is underlain by entisol, i.e., a weakly developed latosol or tropical reddish-brown clay not yet strongly leached of soil nutrients.

The northward extension of Ripperton and Hosaka's montane rain forest zone, which on the satellite image shows an absence of forest, is covered by the same entisol as the forested portion. This supports the contention of Ripperton and Hosaka that the pasture site probably has the potential to support a closed montane rain forest or may revert to rain forest if pasture use is discontinued. On the other hand, the comparison also shows that Ripperton and Hosaka ignored significant substrate variations, such as recent (historic) lava flows. Such substrates are not yet covered by mature rain forest. Instead, they are covered with open woody vegetation, often only scrub. Therefore, Ripperton and Hosaka's vegetation zones are not quite equivalent to Krajina's (1963) biogeoclimatic zones of Hawaii, which are somewhat more narrowly defined landscape units.

With respect to the interpretation of the satellite image, we can now be certain that the dark-coloured patch on the east flank of Mauna Kea is a tropical montane rain forest. This forest is not uniform in plant biomass, nor is it uniform in terms of primary production. Its primary production rate varies with the major substrate types and is clearly lowest on the recent lava flows and next lowest on the lithosols. For a more precise analysis of plant biomass and primary production, one must go from an intermediate to a large-scale map.

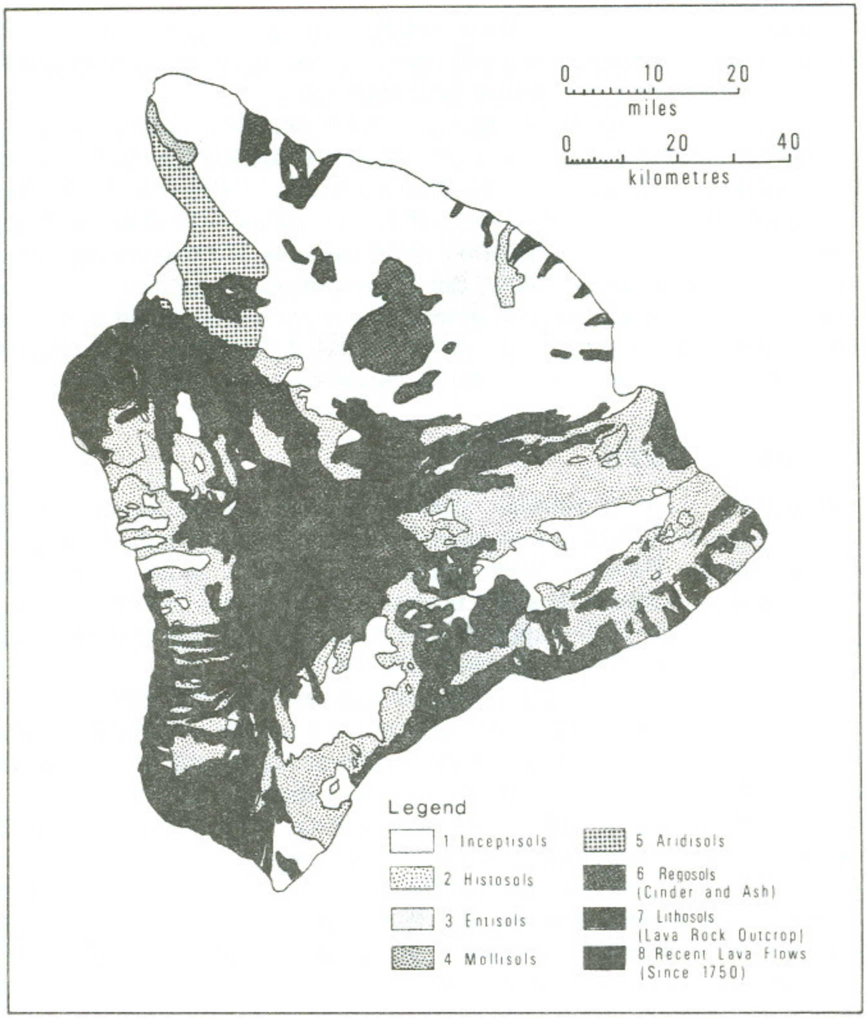


Figure 2.9 Soil order map of the Island of Hawaii at 1:1.3 million after Uehara (1973), modified. Compare with vegetation map, Figure 2.1, p. 33

2.5.2 Accessory Information at the Large-scale Level: the Fine Structure

Large-scale information is an aid to mapping from satellite images for two reasons. One is that the broader landscape types identified on satellite images may often show tonal and textural within-variations, the meaning of which are very difficult to interpret. But it should not always be necessary to do so by acquisition of ground truth. In fact, doing so may not be very helpful. The enlargement from satellite image to field environment may prove too great to be practical. Instead, one may use standard aerial photographs. But unless these are already interpreted, one still has to do the field work. It is therefore most efficient to make use of existing large-scale maps.

A second reason is that basic vegetation and habitat information is usually derived from field samples whose results can be extrapolated with confidence only in the large-scale range (i.e., from approximately 1:10 000 to 1:100 000). For example, Whittaker's (1956, 1960) well-known mountain gradient analyses show details of habitat and vegetation which can only be projected on large-scale maps. Such details, of course, can be generalized for application in the intermediate-scale range, but such generalizing is not accomplished well by a simple averaging procedure. It requires evaluation of the spatial and temporal fine structure peculiar to each broader landscape unit or vegetation zone.

2.5.2.1 Map Availability

Unfortunately, most ecological vegetation and habitat classifications (including vegetation ordinations and environmental gradient analyses) are not shown on maps. However, there are numerous areas which have been mapped on large scales, particularly in Europe. Küchler has compiled a four-volume international bibliography of existing vegetation maps (Küchler and McCormick, 1965; Küchler, 1966, 1968, 1970, 1980).

There are not many large-scale ecological maps available for tropical forests areas, but many of these areas have been assessed for exploitation purposes. De Rosayro (1974) reviewed the progress of forest inventories in 14 tropical Asian countries for the period 1958 to 1969. His tabulation gives the country, agency, scale of photography, year, methodology, forest types and areal coverages of these inventories. It is not known, however, how many of these inventories have resulted in maps. Large-scale vegetation and forest-type maps are usually not published because of their high cost and primarily local purpose. They are often on file, however, in the various forestry or land survey departments and can usually be obtained.

2.5.2.2 Map Interpretation

Generally speaking, large-scale vegetation maps are not easy to interpret. Among other things, they sometimes lack ready information on the location of the mapped area itself. This deficiency can easily be overcome by adding a small insert map that shows the large-scale map area within a continent, subcontinent or island.

A second and more important problem is that most maps are two-dimensional. They do not portray the third dimension easily unless they are specially prepared topographic maps, such as the map in Figure 2.10. Such maps, however, are single-purpose maps, and one cannot show much other information on them.

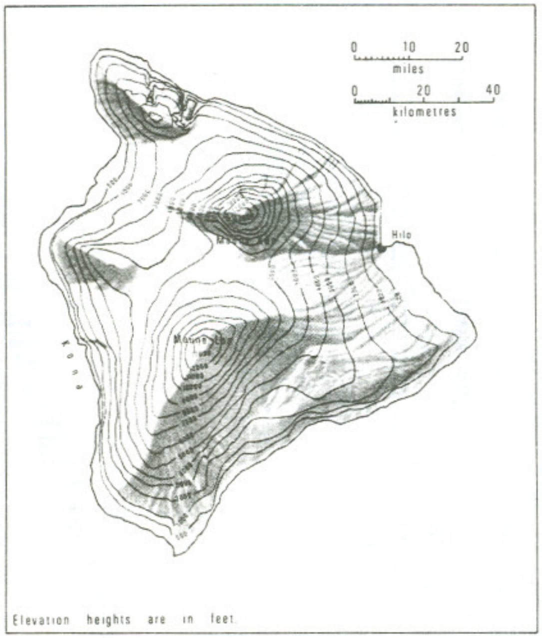
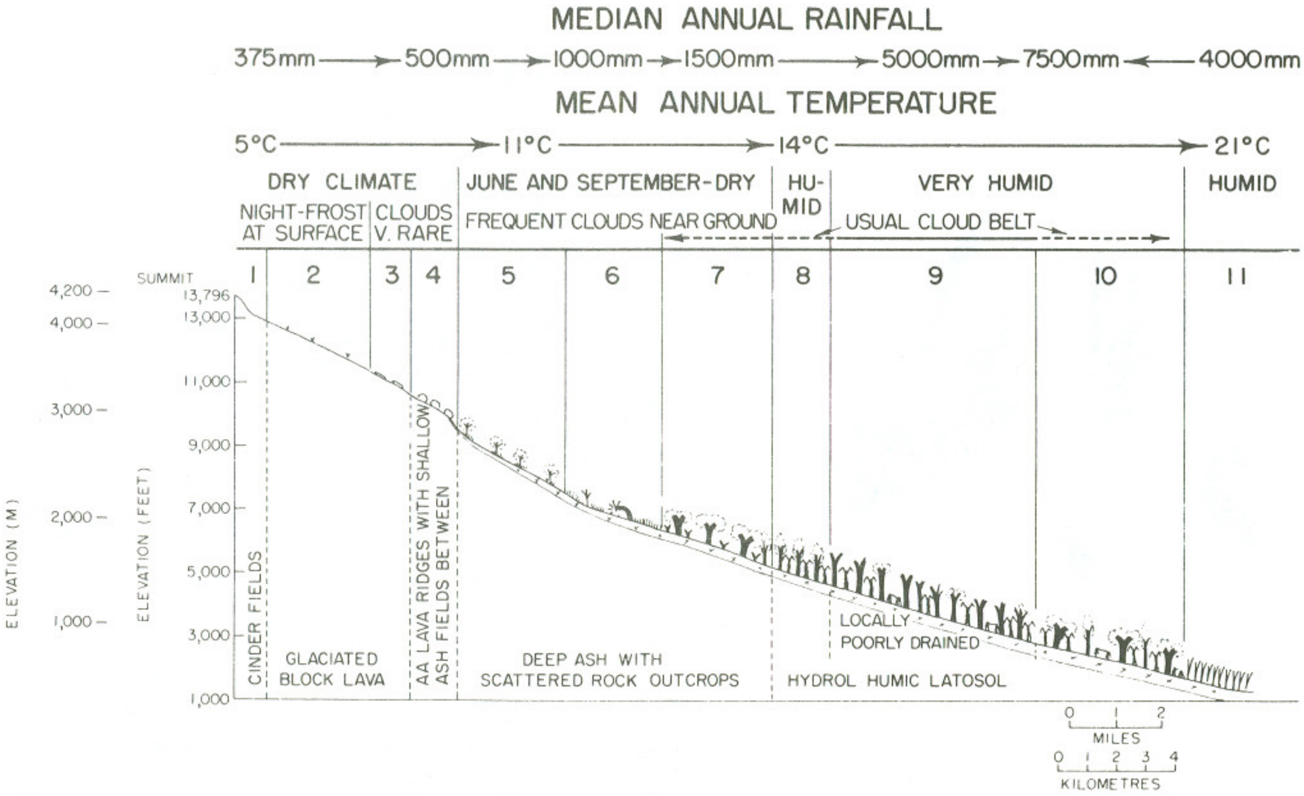


Figure 2.10 Topographic map of the Island of Hawaii at 1:1.2 million. Compare with satellite image shown on Figure 2.7, p. 68

A useful key to map interpretation for ecological purposes is a topographic ecosystem profile, shown in Figure 2.11. This profile diagram was prepared from vegetation map information (obtained through ground truthing) projected initially on 1:12 000 aerial photographs. The completed map was then reduced to 1:48 000. The profile diagram was extracted from this map and from other large-scale topographic, soil and climatic maps. The diagram here is further reduced to a scale of 1:217 000, which is in the intermediate-scale range. The diagram information, however, was based on extrapolation of actual field samples, and the diagram therefore closely reflects the actual field situation. (The profile diagram represents transect 6 on the climate-diagram map in Figure 2.8.)

Profile diagrams of this sort allow one to portray the major ecosystem components—climate, topography, vegetation and soil—in relation to one another. There is not always a clear correspondence of climatic type and vegetation type, or of vegetation with substrate, as can be seen in Figure 2.11.

With the help of Ripperton and Hosaka's (1942) vegetation map of Hawaii it was possible to delineate the montane tropical rain forest on the satellite image. The profile diagram indicates a further breakdown into three types, numbers 8, 9 and 10 on Figure 2.11. Type 9 is an open-structured rain forest which exhibits a high proportion of crown loss due to canopy dieback. The


MEDIAN ANNUAL RAINFALL
375mm → 500mm → 1000mm → 1500mm → 5000mm → 7500mm ← 4000mm
MEAN ANNUAL TEMPERATURE
5°C → 11°C → 14°C → 21°C
DRY CLIMATE
JUNE AND SEPTEMBER-DRY
HU-MID
VERY HUMID
HUMID
NIGHT-FROST AT SURFACE
CLOUDS V. RARE
FREQUENT CLOUDS NEAR GROUND
USUAL CLOUD BELT
1
2
3
4
5
6
7
8
9
10
11
SUMMIT
13,796
13,000
11,000
9,000
7,000
5,000
3,000
1,000
4,200
4,000
3,000
2,000
1,000
ELEVATION (M)
ELEVATION (FEET)
CINDER FIELDS
GLACIATED BLOCK LAVA
AA LAVA RIDGES WITH SHALLOW ASH FIELDS BETWEEN
DEEP ASH WITH SCATTERED ROCK OUTCROPS
LOCALLY POORLY DRAINED
HYDROL HUMIC LATOSOL
0 1 2
MILES
0 1 2 3 4
KILOMETRES

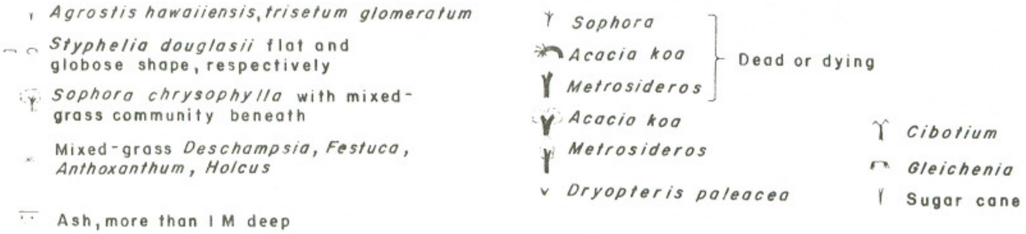


Figure 2.11 Topographic ecosystem profile relating to east-slope of Mauna Kea, Transect 6 on Figure 2.8, p. 70. Ecosystem type names are as follows: 1. Alpine stone desert with crustose lichens, 2 *Agrostis–Trisetum* grass desert, 3 *Styphelia* low-scrub desert, 4 Scattered, globose *Styphelia* scrub, 5 Scattered *Sophora* trees with herbaceous fog-drip communities (treeline vegetation), 6 Grassland with scattered, dying *Sophora* and *Acacia koa* trees, 7 *Acacia koa–Metrosideros–Dryopteris paleacea* forest, 8 Closed *Metrosideros–Cibotium* forest, 9 *Metrosideros–Cibotium–Dicranopteris* forest with dead and dying *Metrosideros* patches, 10 *Acacia koa–Metrosideros–Cibotium–Dicranopteris* forest, 11 Cultivated sugar cane (from Mueller-Dombois and Krajina, 1968)

satellite image shows a lighter shade in the dark-coloured part on the east flank of Mauna Kea which appears to correspond to this dieback forest, which can be interpreted as a natural breakdown phase (Mueller-Dombois *et al.*, 1977; Mueller-Dombois, 1980a). The satellite image shows this lighter shade pattern in the montane tropical rain forest to extend south into Hawaii Volcanoes National Park. It would not, however, be safe to interpret all of this as dieback forest or breakdown phase from the satellite image. A forest can be open-structured for many reasons. A safer interpretation of the lighter shade pattern is simply 'open forest' (versus 'closed forest' for the darker shade pattern). Yet one must also be cautious in extrapolating lateral patterns from profile diagrams. The profile diagram represents only one transect. For a more accurate interpretation, one either needs several profile diagrams or a large-scale map. A third problem of interpretation, however, is that large-scale vegetation maps do not always give the same information even if they are prepared at exactly the same scale for exactly the same area.

At the 1954 World Forestry Congress, Sukachev suggested that his method of mapping should become the standard one for forestry purposes (Ellenberg, 1967). De Phillippis made a counter-proposal that several methods should be compared. Later, a contest to map 420 ha in Switzerland was held using the mapping schemes of Braun-Blanquet, Aichinger, Schmid, and the Eberswalder soil-vegetation method (Mueller-Dombois and Ellenberg, 1974).

The resulting maps, all prepared at a scale of 1:10 000 and showing some general resemblances, were all different in detail. The Braun-Blanquet map was based primarily on the mosaic of natural and semi-natural species groupings indentifiable at this large scale. The Aichinger map was based on the successional behaviour of certain key species in relation to types of habitat and silvicultural influences. Schmid's map was based on plant synusiae and the floristic province concept, while the map using the Eberswalder approach was based primarily on soil and habitat characteristics, treating plant species only as indicators of habitat where they had obvious indicator value.

This shows that the user of a vegetation map must be aware of the purposes for which a particular map was prepared. It is particularly important to distinguish between vegetation maps which aim at portraying the intrinsic patterns of vegetation and those which use vegetation to indicate site capability. Both types of maps are useful, but they cannot be used for the same purposes. (See also Daubenmire, 1973.)

2.6 SUMMARY AND CONCLUSIONS

This paper has reviewed methods of classifying and mapping terrestrial vegetation with three main objectives in mind: (1) improved accuracy in estimating world phytomass, (2) improved accuracy in extrapolating primary production from field samples and (3) the monitoring of tropical forest loss.

While a great deal of data on phytomass and primary production has been accumulated by the various IBP projects, very little attention has been given to the question of how to extrapolate these organic production estimates at various spatial levels. In other words, ecosystem functioning has received most of the attention in research funding, while ecosystem structure has been neglected. But questions about the global carbon cycle have underlined the need to focus more attention on ecosystem structure, particularly in tropical forest regions.

Our knowledge of ecosystem structure is now at about the same stage as our knowledge of ecosystem functioning prior to IBP. That is, the methodology for evaluating ecosystem structure from detailed to general and vice versa is quite well worked out except in the tropics at the large-scale level. In contrast, there is a considerable amount of knowledge available on other regions, particularly the northern temperate areas. This information needs to be synthesized, region by region, to deal with the global carbon question. Moreover, research on ecosystem structure in tropical forest areas needs to advance rapidly to match the functional research now under way in the Man-and-The-Biosphere projects concerned with tropical forests. Practically nothing has been done as yet at the large-scale map level (see also Whitmore, 1975; Ashton, 1978; Letouzey, 1978).

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