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A UNIVERSAL SYSTEM FOR RECORDING VEGETATION.

II. A METHODOLOGICAL CRITIQUE AND AN EXPERIMENT

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INTRODUCTION

Defining structure as "the organization in space of the individuals composing a vegetation type or association" or indeed an isolated stand, Dansereau first presented a scheme for the description and recording of vegetation in 1951 and then a modification of that in 1958. The system has been applied by him to such varied tasks as comparing the structures of bog communities in Eastern North America (Dansereau & Segadas-Vianna 1952), of temperate rainforests in all parts of the world (1957b), of vascular aquatic plant communities in southern Quebec (1959b), of the plant associations of the Saint Lawrence Valley (1959a), and to an illustration of the structure of a coastal podocarp forest stand in New Zealand (1964a). He has also applied it as background to the study of the effects of parasites on vegetation (1958b), and to the distribution of diaspore types (Dansereau & Lems 1957). A preoccupation with the "varieties of evolutionary opportunity" (1952) had led to suggestions of using this scheme as background for the function or behavior of individual populations of plants and animals. This lead was followed, to some extent, by Emlen (1956) in his measuring of avian habitats, and by Bider (1961) in his study of the hare in Quebec and of the vegetation of a vertebrate population in Texas (1962). Dansereau & Arros (1959) applied the 1958 system (1958a), with minor modifications, to the vegetation structure of 86 European associations as described by the SIGMA phytosociologists. Its applicability to mapping was first attempted in 1961 (1961b). In addition, the U. S. Army Corps of Engineers Waterways Experiment Station (WES) has modified the 1951 system to suit their particular needs (Mills et al. 1963), and this modification is continuing (Waterways Experiment Station 1963, Mills & Clagg 1964).

The variation of structure in vegetation is being studied by our group: from such unlike areas as Southeastern Brazil, Baffin Land, the Gaspé Peninsula of Quebec, Puerto Rico, the Azores, New Zealand, metropolitan New York and New Jersey. This multitude of analyses applied to such a range of structures has led us to believe that it would be appropriate to criticize

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and evaluate the 1958 system and to present possible alternatives to what may be shortcomings, since it is intended to have truly universal application.

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PURPOSES OF STRUCTURAL RECORDING

Dansereau, in 1957, referred to his original descriptive scheme as a "shorthand" to the recording of vegetation structure. We will present our present reflections, using the 1958 formulation as a discussion guideline. No major shift from this framework (such as was made between 1951 and 1958) is being proposed herewith. In other words, a "third edition" of the system is not put forth. Figure 1 shows the scheme of six categories used in 1958 and includes the very minor modifications made by Dansereau in 1959: the sequence of the various categories has been changed (from 1958) and the stratification runs upward from 1 to 7 instead of downward; the terminology applied to the categories of "life-form" and "function" has been changed to "habit-form" and "seasonality," respectively; a slight shift has also been made in the E and M alternatives. The term "structural-form," often used hereafter, will refer to the appropriate symbol of "habit-form" in which the "leaf shape and size," "leaf texture," and "seasonality" have been included. The term "life-form," henceforth, will only be used as it has been applied by previous investigators, especially Raunkiaer (1934). The six categories will be discussed below, but Figure 1 will remain throughout this contribution as our standard.

In the design (and/or the modification) of such a shorthand system, the aim is to express all the essential variables for structural comparison with an acceptable degree of repeatability. Structural comparison involves the actual spatial distribution of habit-forms. The general acceptance of a universal system is far in the future and, meanwhile, numerous modifications will be made in any system now being proposed. However, it is our feeling that many investigators will find it useful to apply previously tested methods rather than to design new ones which make comparisons with previous records virtually impossible. It is therefore necessary to develop a system which is applicable by investigators not well versed in taxonomy; to include the variables necessary for making comparisons; to exclude extraneous variables for the sake of clarity. This particular requirement is easier to state than it is to build into the final design of a universal system. If such a system attempts to be unequivocal in its interpretation, and truly universal, it must convey significant differences and similarities between both widely different and closely related vegetation types. It should also be a secondary aim to reduce the burden on the technical skill required: simplicity of symbols is a highly desirable characteristic in any structural diagram. (See Appendix B.)

The need for such structural descriptions is generally recognized (see Küchler 1947 and 1949, Hanson 1958, Phillips 1959, Kendeigh 1961, Spurr 1964). The importance of the matter was re-stated by Dansereau (1957a): "Structure... is one of the outstanding features of vegetation and ranks even before composition in a description of landscape."[3] Fosberg (1961) discussed the method critically but recognized that the scheme does use strictly structural characteristics to describe the vegetation. Wagner (1957) and Hanson & Churchill (1961) acknowledged the advantages of using structure, particularly habit-form, in describing plant communities. Phillips in 1959 and 1964 proposed a student exercise in which vegetation is to be graphed on a structural basis as described by Dansereau (1958a) but did not comment or elaborate on the scheme itself.

It may be well to point out that the system proposed in Figure 1 (not unlike Köppen's which originally inspired it, and Küchler's 1947, 1949) permits an almost indefinite combination of alternatives taken from each of the six categories. It does not automatically result in a classification, although it can be used to build one, as Dansereau has done in setting up ten formation-types (1958a, Table VI and Figures 18, 19).

Robbins (1959), in discussing the use of the profile diagram, stated that in describing an actual strip of forest the symbology as proposed by Dansereau (1951) should be discouraged. Robbins then quotes various features that must be standardized to describe the vegetation of the rainforest and gives some details as regards the actual drawing of the realistic scale-profile.

Let us emphasize once more that our own field procedure consists in making exhaustive relevés, identifying each species (see Figure 7, below), and that sketches of biotopes (as in Dansereau 1957a, Figures A-4 and A-6) are frequently important and that local conditions always dictate yet other detailed observations.

Granted that a drafting of the actual profile in situ has advantages in describing an individual forest structure at a certain time and place, the advantages of utilizing a universal system are, to us at any rate, readily apparent. Beard (1949) presented a list of headings under which data on structure and composition should be collected, and as this paper develops it will become apparent that the system under discussion fulfills the majority of the criteria cited by Beard in a concise and manageable fashion. A comparison of the profile-diagram and the universal system will be shown later in this paper. Druce (1959) commented on the fact that Dansereau's method (by design) avoids a taxonomic inventory. The universal system as proposed only provides the non-taxonomist with a tool for describing vegetation with the same reproducibility as a trained taxonomist; it was never intended to exclude the identification of the species present in the study area.

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[3] This statement has been misinterpreted to mean that structure was more important than composition and could be substituted therefor. Such misreading need hardly be countered here. Of course, a multidimensional description of vegetation is the best! (See Dansereau 1961a.)

It is because of the continuing need to establish guidelines for descriptions of vegetation that the following comments are presented with the anticipation that some of the ideas may eventually become a part of an acceptable universal system for recording structure.

REVIEW OF CRITERIA AND ALTERNATIVES

Three of the six categories of criteria[4] proposed by Dansereau (see Figure 1) will, in this discussion, remain unaltered. To date, the concept and symbology of "coverage," "seasonality," and "leaf texture" have proven satisfactory. On the remaining "habit-form," "stratification," and "leaf shape and size," additional comment will be made, and we will consider auxiliary symbology that may be required to describe the structures more adequately.

Habit-form

The habit-form alternatives have proven to be satisfactory if one accepts the limitations expressed by Dansereau (1951, Table VIII). Primary among these are the facts that the habit-form symbol does not represent the actual crown outline of an individual or groups of individuals, and that it gives no indication of either the type or height of its branching. This problem will be considered later in this paper, in our attempt to adapt the structural diagram to a more accurate representation of the biomass.

In 1951 the term epiphyte (E) was extended to include crust vegetation composed primarily of algae, lichens, fungi, and mosses. But "crusts" are probably more appropriately included in our bryoid alternative (M) as shown in Figure 2. Note also that the epiphytes (E) also include non-rooted aquatic plants. An application of this will be considered later.

In the upper block of Figure 2 we have shown the grid which we have been using these many years and on which we have standardized the stratification and coverage. The habit-form symbols are projected on the lower block as they appear in the appropriate height-class. Note that the percentage value (of coverage) is not the same for all habit-forms in each height-class. Thus, no more than 33 units emerge from the combination of the two categories 1 and 5 of Figure 1. It can be seen further that the use of such symbols restricts the user of the system to a minimum cover value that can be presented in any one height-class. This is discussed below, under requirements of scale. There is an overlap of classification between epiphytes (E) and bryoids (M) in reference to a moss or lichen growing on another plant, but at present the assignment of bryoid will take precedence and epiphytic bryoids will be shown in the appropriate height-class, as indicated on Figure 2, by the use of the bryoid symbol.

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[4] For the sake of clarity in what follows, criteria will refer to those features deemed significant to structural analysis and which are numbered 1 to 6 in Figure 1. Each criterion, when applied, lends itself to many alternatives, and it is the latter which are represented by the symbols that are carried in formulae and diagrams.

Crown outline. In 1958a (Figure 3), Dansereau suggested a series of alternate crown outlines that would fit the symbol proposed to represent all erect woody plants. This is shown here as Figure 3. The use of such alternate crown symbols was recommended when there was a marked deviation from the more-or-less globular crown-shape of such species as Quercus alba or Fagus grandifolia. Work in the field with these eight alternatives so frequently required arbitrary decisions that it seems advisable to reduce their number, as shown in Figure 4. This simpler repertory will result in a greater degree of repeatability since the investigator in the field now has an easier choice to make: if the crown form deviates from the "average" globular (a), then all that remains is to decide whether the greatest width lies above (b), below (c), or at mid-depth (d) of the crown. To simplify the structural diagram, the use of such alternate crown outlines should be limited to woody plants that exceed two meters in height (i.e., omit them in height-classes 1, 2, and 3 of Figures 1 and 2).

Figure 5 shows two examples of the use of alternate crown outlines as we have presented them above. The Colorado spruce forest (Figure 5A) shows the contrast between the standard where only the a crown alternatives of Figures 3 and 4 are used and the substitution of the c alternative of Figure 4. The New Zealand podocarp forest illustrates (Figure 5B1) the contrast between the use of the symbols of Figure 3 (as published by Dansereau 1964a, Fig. 3) with alternatives b and d as well as a, and (Figure 5B2) the symbols of Figure 4, with b and c as well as a. In both instances the second diagram is more satisfactory than the first. This is more obvious for the Colorado forest and it is best justified for the New Zealand forest on the grounds, established above, of a less arbitrary choice.

Range of structural-forms

The structural-form is the combination of the alternatives listed in Figure 1 under the first five categories: 1) habit-form, 2) leaf shape and size), 3) leaf texture, 4) seasonality, 5) stratification. It consists therefore in the insertion of leaf and seasonality alternatives into the basic 33 patterns that appear in Figure 2. Because so many combinations are possible, the variety of structural-forms found on any given site may not find place on the structural diagram since the coverage of any given structural-form may be less than that represented by a single symbol. We have therefore been utilizing, in addition, a "range-diagram" in which appear all the structural-forms present on the site. In our field notes (relevés), a value for coverage and local coverage is always recorded for each species and thus for each structural-form (see Dansereau 1957a, Tables 3-13 and 3-14, Figures 3-39 and 3-40, and Appendix). The use of the range-diagram coupled with the standard structural diagram (of Dansereau 1958a) then gives a rapid indication of the full variety of structural-forms present, their respective stratification, and their relative distribution. In Figure 6 we have shown both the range-diagram and the structural diagram of a stand in Puerto Rico in which a wide variety of structural-forms present in relatively small percentages of cover cannot be plotted on the standard structural diagram. Thus, only 13 structural-forms are retained in the standard diagram (Figure 6.III), whereas 18 appear in the range-diagram (Figure 6.II).

In Figure 7 we have shown the manner in which we prepare a structural diagram from field data, using a laurel scrub stand in the Azores as an example. We start with an inventory (relevé[5]) that accounts for all species present (Figure 7.I). It is then condensed into a "range-diagram" (Figure 7.II) from which the standard structural diagram (Figure 7.III) is then drawn with the aid of additional field notes and diagrams that relate to the biomass as a whole. For convenience in utilizing the range-diagram, the structural-forms have been arranged in descending order of height and then seasonality, leaf shape and size, and then leaf texture, in the same order as they appear in their respective categories in Figure 1. The data displayed in Figure 7 also demonstrate that even though our standard structural diagram is based solely on structural characteristics, our own field methods call for a floristic inventory as a starting point. The non-taxonomist on the same site would start with an inventory of structural-forms (as in Figure 7.II), but the resultant structural diagram (as in Figure 7.III) would (or should) be the same as ours.

Requirements of scale

The loss of information from Figure 7.I to 7.II to 7.III may or may not be significant, depending upon purpose. It has been our custom to plot our standard diagram on squared paper where each square is 10 mm. across. There are eight squares in height, the height-classes 1-7 (Figure 1, category 5) each being one square higher than the next lowest, except 7 which is two squares higher. Twenty-five squares in breadth allow a coverage of 4 per cent for each square. Figure 2 (upper) shows the blank grid which we use.

If it is important for all structural-forms to be shown on the final diagram, a longer strip of two, three, or four of these grids can be constructed. Thus, if there are four, each square becomes equivalent to 1 per cent coverage.

An inverse problem is posed when the total coverage of the vegetation being described is so small that the use of the standard structural diagram is of little value in indicating coverage. Since no symbol can occupy less than one square, if the total vegetation is of the order of one to two per cent, its spatial importance has to be grossly exaggerated! The addition of the range-diagram has furnished us with an inventory of the structural-forms and therefore of the diversity present even if coverage is low, but it does not provide a diagrammatic approach to distribution.

It is possible in both instances to utilize an auxiliary diagram assigning the grid a larger scale (in per cent) convenient for the record concerned and thereby permitting a clearer indication of the distribution of the structural-forms present in small values of coverage. This has been done very effectively by Mills et al. (1963) and by the Waterways Experiment Station (1963).

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[5] This term is now very much in use, and is not readily translated by "inventory." It means a quantitative survey by measurement or estimate of all the species found within a quadrat. Our relevés are all made according to the method outlined in Dansereau 1957a, especially pages 187-200 and Appendix. There are, of course, many other excellent and, for some purposes, better methods (see Phillips 1959, Cain & Castro 1959, Curtis 1959).

In Figure 8 we have shown a spruce-lichen savana in which the use of a supplemental diagram with a grid-unit-value of 0.5 per cent instead of four per cent gives a far more satisfactory picture of the distribution in terms of coverage than if we restrict ourselves to the use of the standard structural diagram.

In our laboratory procedure, therefore, we have come to use the following code: a Roman numeral is placed at the top left-hand corner of the grid to indicate the kind of record which is presented. This is what we have also done in the figures presented in the present contribution.

I: Floristic-structural inventory, species by species (as in Figures 7.I and 8.I);

II: Structural-form range, or range-diagram (as in Figures 6.II, 7.II, 8.II);

III: Standard diagram on 4% coverage per square basis (as in Figures 2, 5, 6.III, 7.III, 8.III);

IV: Auxiliary diagram on 1% per square basis, or on any other appropriate scale (as in Figure 8.IV).

Stratification[6]

Cain & Castro (1959), commenting on the height-classes of Raunkiaer (1934), Küchler (1949), and Dansereau (1951), stated a personal preference for adherence to the original Raunkiaer system for the valid reason of ease of statistical comparison. Figure 9 shows a comparison of these three height-class systems taken from Dansereau (1951) and modified to show the changes indicated by Dansereau (1958a, 1959a) and by Mills *et al.* (1963).

Cain & Castro (1959) suggested that any description of a plant community should include the actual height classes involved, but they did not make any suggestion as how this height indication should or could be made to fit any standard structural diagram. Christian & Perry (1953), working on the systematic description of plant communities by the use of symbols, had also concluded that a fixed universal series of height-classes would not provide the most useful compass for Northern Australian communities. It is, of course, the practice of students of vegetation to record actual stratification and this is what we have always done in the field. The diagrams published in Dansereau's various contributions, therefore, do some violence to the known facts since they force the field data into the nearest previously-set, rigid stratification-class.

The distribution of layers into arbitrary height-classes is not the best means of describing the geometry of vegetation. We have therefore experimented with recording of the actual heights of layers on the structural diagram. Assuming that the proper choice of a vertical scale is made, the

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[6] Stratification was termed "size" in Dansereau's 1951 paper and in others. Height of layers, size, height-classes, and stratification all may be used somewhat interchangeably.

structural diagram will then present the layers in the most realistic fashion possible and will still permit the adaptation to a universal recording system. The requirement for ease of statistical comparison is also met since the actual heights of layers can now be grouped for analysis in any manner the analyst so desires to use. (This procedure may be objected to as a departure from the symbolic scheme of the system, since, on the horizontal scale, no effort is being made to show spacing of individuals at all! A single structural-form symbol, as has been made amply obvious, sometimes represents not only several individuals of one species, but many individuals of several species!)

By "trial and error," a variety of scales was applied to previously prepared structural diagrams. [7] At this time we are utilizing a fourth-root vertical scale constructed in a fashion similar to a logarithmic scale but having several added advantages: 1) it provides, at convenient dimensions, for presenting layering with the desired (and necessary) vertical distortion (i.e., shorter vegetation is depicted in a clearer manner than would be possible using a proportional vertical scale); 2) it provides a satisfactory fit or relationship with Dansereau's previously established arbitrary height-classes (1951, 1958a, 1959a); and 3) it permits the plotting of a zero value which is not possible in the conventional logarithmic scale. A comparison between the height-classes is given in Figure 10: those of Dansereau (1958a, 1959a) as used in Figures 5 to 8 are shown in Figure 10A, and our present fourth-root system of vertical scaling is illustrated in Figure 10B.

As we have previously indicated, the scale shown in Figure 10B not only lends itself to any sort of comparison necessary, including statistical analysis, but there is the added advantage of neither eliminating nor masking field data when the actual height of an observed layer of vegetation is placed into an arbitrary height-class during the preparation of the structural diagram. This is illustrated in Figure 11 where it is shown that if the observed layers of vegetation are placed into height-classes, one observed layer is completely obscured. In addition, this placement is in effect taking a great deal of liberty in assessing biomass. Figure 12 presents three further examples of this method of vertical scaling chosen from highly different structural types. The diagram of the California stand represents nearly the greatest degree of vertical distribution to which the system will be applied; the Caribbean forest shows much complexity of lateral as well as vertical massing; and the Sahuaro thornscrub of Arizona involves unusual habit-forms.

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[7] An interesting question raised by our attempts to establish a suitable vertical scale was "How do you as an observer in the field see vegetation in terms of vertical layering?" It is obvious that we do not view vegetation in a linear sense, but at any particular site just what scale are we using as we establish our vertical layers, assuming we are not actually measuring the heights of individual stems? There is an obvious advantage to presenting a structural diagram for interpretation in as nearly as possible the same perspective in which the original vegetation had been observed (another guarantee against loss of information).

We are bound to waver somewhat in our recommendation to adopt this improved scale, since we cannot really affirm its overall advantage for all purposes.

Leaf shape and size

It should be apparent that in a strictly structural system, the term "leaf" is applied to any leaf-like structures. The system, particularly when being used by the non-taxonomist, does not always recognize leaves as defined by the orthodox morphologist.[8]

The original scheme proposed by Dansereau (1951) combined leaf shape and size into a single category with a single symbolic representation. The terminology applied to the shape was itself suggestive of size. Thus, a was "medium or small" and h was "broad." Although this confusion has now somewhat been cleared in Figure 1, it leaves many arbitrary decisions for the user to make. Maybe a better presentation can be made by separating the original scheme into two sub-categories: leaf shape and leaf size, as has been done by the Waterways Experiment Station group.

We feel that it is more advantageous to modify the widely used leaf-size classification of Raunkiaer (1934) than to propose a completely new one, as has been done by others (see Waterways Experiment Station 1963). Figure 13 shows our proposed scheme and the appropriate symbology. We do believe that the Raunkiaer leaf-size classes are to be retained for many purposes, but we are equally convinced that a further simplification more closely fits the logic of the present scheme and we have therefore lumped the lower four Raunkiaer classes into two (l + n = our r, and m + M = our t).

There are many techniques for determining leaf size. We cannot well consider them in the present context, but we feel that Cooper's (1960) deduction from length-width values provides a fairly safe shortcut and the most rapid means of assessing the pertinent leaf-size class.

If this new procedure is resorted to, the appropriate symbol for leaf shape must now be placed inside the symbol for leaf size. In Figure 14 are shown the leaf shape alternatives. There no longer is any justification for alternatives a and h as they have been used so far (see Figure 1). In fact, one might restrict the range (as we have for crown shape: see Figures 3 and 4) to n, g, and h, where h represents a leaf not many times as long as it is broad; g a leaf very many times longer than broad; and n a short, but essentially linear leaf. The thalloid (q) alternative is primarily different in texture, but it also has an amorphous outline.

The question of whether or not to distinguish the compound leaf remains, in our minds, an open one. It has been discussed previously by Burtt-Davy (1938), Richards, Tansley, & Watt (1940), and by Cain & Castro (1959).

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[8] Some comfort may be derived from the discussions still prevalent among morphologists concerning the nature of the leaf. For instance, the classical example of the non-leaf stem of Ruscus aculeatus is no longer universally accepted.

If one indicates that a leaf is compound and then gives the size of the leaf concerned, he has not necessarily presented an adequate picture of the structural element involved. Similarly, if one indicates that a leaf is compound and gives the size of the leaflet(s), he may be even further removed from presenting an accurate structural picture. Figure 15 shows one method that could be utilized to distinguish the features of leaf and leaflet and still remain within the logic of the standard system. Leaf size would then always refer to the surface area of the whole leaf.

Seasonality

The diagrams published by Dansereau and his collaborators were all based upon knowledge of the taxonomic identity of the plants involved, and the standard diagram (labeled III above) was obtained by going through the procedure of floristic-structural grading (labeled I), and structural-form synthesis (labeled II), as recorded in detail in Figure 7. The seasonality was recorded as a permanent feature of the stand and the coverage shown in the diagrams can be assumed to indicate the peak of vegetative growth. This can only be done if the taxonomic identity of the plant is known.[9]

However, it is of paramount interest to contrast the low-point in leafing with the high-point. A technique has been illustrated by Dansereau (1958a, Figure 9) which consists in replacing the full outlines of the habit-forms by dotted outlines. This figure is reproduced herewith as Figure 16. It will immediately be apparent also that stratification is much affected. The spring and the summer layers may differ in height, coverage, and, of course, in species composition, and therefore in range of structural-forms. In the maple forest many of the geophytes have become as invisible aboveground in the summer as have the ephemeral annuals in the Sahuaro scrub.

Where an instantaneous reading is made, however, and where the identity of the species is not known (or indeed not sought), leaflessness is recorded irrespective of the total phenology of the species. It is largely for this kind of recording that the "leafless" alternative was introduced into the leaf-shape-and-size (and consequently into the leaf-texture) category. The Waterways Experiment Station (1963) investigators made all of their observations on the basis of what could be observed directly in the field at the time and place of sampling. This is, of course, an objective procedure to which we can take no exception. We may point out, however, that where knowledge of species-composition backs the structural recording, a prediction can be made of increase and decrease in coverage as well as shifts in stratification.

Biomass

The primary objective of this recording technique is the comparison between stands of related or unrelated vegetation. Thus, in the various publications mentioned above, similar structures occur in geographically widely

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[9] We have had frequent occasion to complain, when we consulted otherwise finely written and informative floras, that the relative evergreenness of species was not mentioned by the author.

separated environments (see Dansereau 1951, Figs. 16 and 18; and 1957b), whereas the rate of change in structure as a function of time on a single site may be very striking (see Dansereau & Segadas-Vianna 1952, Figs. 3 and 4; and Dansereau 1958a. Fig. 10). The "open" and the "full" diagrams therefore have always contrasted very strongly and it has been felt that somehow this could be taken as an indication of relative biomass (Dansereau 1958c).

A preoccupation with "productivity" is at the very center of ecological thinking at this time (Odum 1964). But the excellent work on primary yield, on energy flow and resource cycling is still very much in the analytic phase, as Duvigneaud (1964) and Duvigneaud & Denaeyer-De Smet (1964) have so graphically demonstrated. Certainly the processes and emergent patterns discernible at the several levels of biological activity are in need of integration (Dansereau 1964b).

Space occupied or relative space occupied combined with the density of the vegetal mass are certainly very important aspects of productivity, and maybe some two-dimensional scheme such as the one we are concerned with can offer a suitable base for comparison. Perhaps our structural diagram should be further modified because of this. If, for example, the field data include crown depths, the structural diagram could be drawn as we have indicated in Figure 17. This is from the same data as Figure 12.1, and it is readily apparent that this type of presentation makes the relationships between vegetation layers far more clear. This is, of course, an approach similar to the coverage-stratification diagram discussed in detail by Cain & Castro (1959). This presentation is also easier to use in making comparisons of vegetative structure than is the profile diagram. Figure 18 is based upon a phytosociological relevé made in October 1964 in a previously well-studied stand, the Hutcheson Memorial Forest, near East Millstone, New Jersey. Actual heights and coverages were recorded utilizing the techniques of Mills et al. We have drawn: (A) a profile diagram; (B) a standard diagram; and (C) a modified structural diagram. More information is conveyed by the modified structural diagram (C) (particularly to the non-taxonomist). This method becomes more useful as the degree of complexity of the stand increases (i.e., a greater number of species and/or structural-forms).

This relevé technique which has generally been used to gather the data used in these studies certainly over-emphasizes cover since it is based on projection, i.e., the amount of vertical shade cast at any particular level (see Figure 9 in Dansereau & Gille 1949). This is obviously an indirect means of estimating total foliage development, for it takes no account of crown depth.

To some users of the system it has also seemed useful to account for stem diameters, height of principal branching, and diameters of principal branches. Mills and his collaborators (Mills & Clagg 1964) have attached a great deal of importance to these features and have proposed classes and appropriate symbols to represent stem diameter, stem habit, type of branching, height of first branching, root habit and height of emergence, as well as root spread (diameter) for above-ground root structures. Dansereau (1958a) limited his recognition of stem modifications above-ground to stilts and buttresses, and that may be sufficient information for most purposes, although estimates of percentage cover in the study area of either stilts or buttresses would provide a more accurate picture of distribution.

In Figure 19 we propose four classes, with the appropriate symbols, for stem diameter. The same criteria would apply to the diameters of principal branches and the symbology would also be the same.

Mills et al. (1963) and Mills & Clagg (1964) limit their recording of the types of branching to either horizontal or divergent, and this is a satisfactory classification. The suitable manner of indicating type of branching is shown in Figure 20. The height of principal (not always first) branching should not be restricted to that of less than three meters above ground, as stated by Mills and collaborators, if we are concerned with the distribution of biomass. In Figure 21 we have shown two methods of indicating the height of principal branching. One of these is useful only if each layer of vegetation is considered separately, but it presents a more accurate picture of biomass. The second method is applicable to any structural diagram but necessitates the division of the height of branching into arbitrary classes.

Many other factors are relevant to biomass distribution, but any method must be governed by a rule of practicability, and repeatability, so that each investigator may decide for himself how far he intends to go and if the end product (i.e., a structural diagram of great complexity) is worth the energy required for its production. Certainly he must question whether the finished structural diagram lends itself to valid comparisons. Each time that another detail is added, the structural diagram moves further from the abstract, and as the diagrams become less abstract they obviously become more difficult to compare. It has been granted from the start that the exhaustive study of a particular stand cannot be carried out with this technique and that nothing will replace an exact profile-tracing which is on scale and realistic, such as Beard (1949), Aubréville (1949), Richards (1952), and Asprey & Robbins (1953) have offered us.

We do not give up the idea, however, that we can adequately describe the structure of vegetation and even evaluate the biomass. But there remain a few points that should be considered.

Dansereau had already indicated (1958a, Figures 6, 7, 8) several means of showing the actual distribution of stems in relation to crown coverage, and that scheme will not be elaborated on in this discussion, except to state that the modification of the width of any of the crown outlines as we have indicated on several of our diagrams (as in Figures 4 and 18) introduces some limitations.

Stem diameter, branching habit, seasonality, leaf shape and leaf size, and leaf texture all contribute to an estimation of the relative density of the crown mass in each layer. The appraisal of the density of a layer is therefore very complex. It can only be clearly resolved by cutting down, one by one, all the plants in a stand and measuring and weighing them. However, a relative index of crown mass density based on field observations may prove to be a useful tool in the analysis of spatial distribution, which in turn is an approximate element of the measure of biomass. To assess the maximum development of biomass of a particular stand, periodicity obviously must be considered.

In Figure 22 we have established an index of relative densities of the crown mass for the mature oak forest described in Figure 18 and have applied it to the same modified structural diagram. Note that such an index gives a rapid indication of the penetration of light and helps to assay the spatial distribution of the biomass of each layer in the understory.

Finally, in Figure 23, all of the above discussion has been applied to the various structural layers of vegetation in the oak forest of Figure 18 in order that they can be compared with the profile diagram and the standard structural diagram. There is no question that each investigator must suit the method to his needs, but the advantages of remaining within the format of a universally acceptable system have been previously enumerated.

Military applications

In 1963, Addor listed four requirements postulated for a system of mapping vegetation for military purposes. It should have:

"a) predictive value (universally applicable) and entirely objective and quantitative;

b) inclusion of all attributes which could conceivably affect any military activity;

c) design such that any combination of effect-producing factors could be extracted and evaluated without reference to any other factor;

d) simplicity, readily learned, and based upon a rapidly executed sampling technique."

As previously indicated, the work done or sponsored by the U. S. Army Corps of Engineers (Waterways Experiment Station 1963, Mills et al. 1963, Mills & Clagg 1964) was based primarily upon that of Dansereau (1951). It is readily apparent that the system of Dansereau (1951, 1958a), even as modified in this present paper, falls far short of the military needs as described further by Addor (1963) when he delimited necessary parameters which included: root habit (type of structure, height of emergence, and spread); armature (including cutting edges, stinging organs, and poisons); distribution; and stem spacing. The Marshall University papers (Mills et al. 1963, Mills & Clagg 1964) have diverged even further from the original Dansereau scheme and, for the most part, have evolved into a far more complex structural description. The classification used by Mills provides a great deal of information that would appear to be far more applicable to their own needs of military survey than would eventually be relevant for general use in a universal system. It is not, however, in what we have called structural-form that the two systems diverge, but in the description of the spatial arrangement of plants.

The Waterways Experiment Station procedure has varied a good deal in the years 1956 to 1965. Appendix A gives the key to the current version used by WES workers. Since the Army method requires the actual plotting on the study site of the exact location of each plant, the actual measurement of heights of individuals, stem diameters, crown depth and outline, height of branching, etc., the method permits a far more quantitative approach to structural descriptions than is possible (or even considered) when utilizing the universal system.

In Figure 24 we have shown the same mature oak stand of Figures 18 and 22 as it would appear in a structural diagram utilizing the methods of Mills *et al.* (1963) and Mills & Clagg (1964). There seems little doubt that the Army system is emphasizing factors that relate primarily to ground mobility, and, of course, this is not true of nor necessarily desirable in the universal system. The contributions of the WES system to our current evaluation of the universal system are quite obvious and there is little doubt that the Army method offers a very representative picture of the biomass of the site concerned.

An even greater contribution of the WES system is the determination of a minimum circular area (or cell) in which an average population of any particular structural type (minimum of 20 individuals) will be found. The diameter of this cell thus characterizes the abundance and distribution of the particular structural type under consideration. For a more comprehensive discussion and the mathematical background of this significant contribution, the papers of Mills *et al.* (1963) and Mills & Clagg (1964) should be consulted.

It is quite apparent that the accuracy of any structural description is dependent upon the degree of accuracy in taking the data in the field. Since the relevés for our group are made as we have indicated in Footnote 5, the WES system cannot be utilized for our data unless, of course, we follow it rigidly as we have done for the oak stand already shown in Figure 18 and redrawn in Figure 22. For our particular needs and for the survey of vegetational structures on a world-wide basis, the possible advantages of utilizing the WES method are far out-weighed by the disadvantage of the time involved in taking the full field-data and in the subsequent analysis and preparation of the structural diagrams. However, there is little doubt that the Army system as described by Mills has a great deal of merit for the analysis of the structure of a particular site with or without regard to the floristic elements involved in the community. The WES system is also readily adaptable to a punch-card or computer-type program of analysis which is always an important factor in the selection of any information-gathering method.

Aquatic plant-communities

It may be that the aquatic environment presents peculiar problems. The system of Dansereau (Figure 1) has been applied to various aquatic communities of southern Quebec (Dansereau 1959b), but a further explanation of the appropriate symbology is now needed in view of modifications proposed in the present paper. The inclusion of non-rooted aquatic plants in alternatives E and M of the habit-forms (see Figures 1 and 2) permits a more adequate description of the strata of aquatic vegetation. In the presentation of the structural diagram (either standard or modified) the water level is indicated by a wavy line as shown in Figure 25. Structural forms are then drawn in the usual manner with the exception that a distinction must be made to separate structures with or without floating leaves. It is apparent that in dealing with aquatic communities there are advantages to utilizing the actual heights of plants rather than height-classes, since the height of the plant at emergence would be more accurately portrayed employing this scheme.

SUMMARY

The universal system for recording vegetation proposed by Dansereau in 1958 has been re-examined in order to question its consistency and logic, to test the flexibility of the method, and to include additional criteria or alternatives (and symbology) for what may prove to be shortcomings.

A simplified version of crown outlines for erect woody plants has been presented, providing a means of greater reliability and repeatability in field observations.

A recommendation has been made that investigators present their data in terms of actual heights of vegetative layers rather than placing them in arbitrary height-classes.

An inventory of structural-forms for each study area has been added as a supplement to the standard structural diagram and is termed a "range-diagram."

The inclusion of floristic elements into the system has been demonstrated to indicate the scheme's versatility.

The category of leaf shape and size has been separated into two distinct criteria—shape and size—and the appropriate symbols are provided for each criterion. The problem of diagramming the structure of a compound leaf has been discussed but not resolved, and the decision would seem to lie with the individual investigator.

Several methods of modifying the standard structural diagram in order to present a more accurate picture of biomass have been experimented with. Along these lines, criteria for recording and describing stem diameters have been established and a possible means of indicating the height of principal branching has been illustrated in a modified structural diagram.

The method itself has been evaluated concerning the requirements for military application. The limits of the method as a means of qualitative description have been further evaluated.

The application of the system to a description of aquatic plant communities has been briefly reviewed and clarified.

The advantages of the universal system for the rapid survey of vegetation have been highlighted and its possible application by the non-botanist clarified and, perhaps, made more generally useful to the worker interested in a rapid inventory of vegetation structure.

With the exception of plotting the actual heights of vegetative layers and the reduction in number of alternate crown symbols, there has been no attempt made to establish a new universal system. However, our current feelings on the problems facing the recording of vegetation on a structural basis have been exposed with the anticipation that the critique and work of others in the field will eventually provide us with a more workable universal system.

LITERATURE CITED

ADDOR, E. 1963. Vegetation description for military purposes. In: Military evaluation of geographic areas. Reports on activities to April 1963. U. S. Army Engineers, Waterways Experiment Station, Vicksburg, Miss., Misc. Paper No. 3-610.

ASPREY, G. F., & R. G. ROBBINS. 1953. The vegetation of Jamaica. Ecol. Monogr., 23:359-412.

AUBRÉVILLE, A. 1949. Climats, forêts et désertification de l'Afrique tropicale. Société d'Editions Géographiques, Maritimes et Coloniales, Paris, 351 pp.

BEARD, J. S. 1949. Ecological studies upon a physiognomic basis. Lilloa, 20:45-53.

BIDER, J. R. 1961. An ecological study of the hare, *Lepus americanus*. Can. Jour. Zool., 39:81-103.

__________. 1962. Dynamics and the temporo-spatial relations of a vertebrate community. Ecology, 43(4):634-646.

BURTT-DAVY, J. 1938. The classification of tropical woody vegetation types. Imperial Forestry Institute, Paper 13:1-85.

CAIN, S. A., & G. M. de Olivera CASTRO. 1959. Manual of vegetation analysis. Harper & Bro., New York, xvii + 325 pp.

CHRISTIAN, C. S., & R. A. PERRY. 1953. The systematic description of plant communities by the use of symbols. Jour. Ecol., 41(1):100-105.

COOPER, A. W. 1960. A further application of length-width values to the determination of leaf-size classes. Ecology, 41(4):810-811.

CURTIS, J. T. 1959. The vegetation of Wisconsin: an ordination of plant communities. Univ. Wis. Press, Madison, xi + 657 pp.

DANSEREAU, Pierre. 1951. Description and recording of vegetatión upon a structural basis. Ecology, 32(2):172-229; also Bull. Serv. Biogéogr., 8:172-229 (1953).

__________. 1952. The varieties of evolutionary opportunity. Rev. Can. Biol., 11(4):305-388.

__________. 1957a. Biogeography: an ecological perspective. Ronald Press, New York, xiii + 394 pp.

__________. 1957b. A preliminary note on the structure variations of temperate rainforest. Proc. 8th Pac. Sci. Congr., Vol. IV (Botany):407-436.

DANSEREAU, Pierre. 1958a. A universal system for recording vegetation. Contrib. Inst. Bot. Univ. Montréal, 72:1-58.

————. 1958b. Effets des parasites sur les structures de végétation. 39e Rapp. Soc. Québec Prot. Plantes (1957), pp. 24-39.

————. 1958c. Vegetation as an indicator of environmental potential. Proc. 9th Pac. Sci. Congr., Bangkok 1957, 20:57-67.

————. 1959a. Phytogeographia laurentiana. II. The principal plant associations of the Saint Lawrence Valley. Contrib. Inst. Bot. Univ. Montréal, 75:1-147.

————. 1959b. Vascular aquatic plant communities of southern Quebec. A preliminary analysis. Trans. Northeast Wildlife Conf., 10th Ann. Meeting, Montreal 1958, Vol. 1:27-54.

————. 1961a. The origin and growth of plant communities. In: Growth in Living Systems, Proc. Symp. on Growth, Purdue Univ. (Indiana), 1960; ed. by M. X. Zarrow; Basic Books, New York, pp. 567-603.

————. 1961b. Essais de représentation cartographique des éléments structuraux de la végétation. In: Méthodes de la Cartographie de la Végétation, Colloques Internationaux du Centre National de la Recherche Scientifique, Paris, 97:233-255.

————. 1964a. Six problems in New Zealand vegetation. Bull. Torrey Bot. Club, 91(2):114-140.

————. 1964b. The future of ecology. BioScience, 14(7):20-23.

————, & J. ARROS. 1959. Essais d'application de la dimension structurale en phytosociologie. I. Quelques exemples européens. Vegetatio, 9(1-2):48-99; also Bull. Serv. Biogéogr., 22:48-99.

————, & A. GILLE. 1949. Ecologie des principaux types de pâturages des environs de Granby. Bull. Serv. Biogéogr., 4:1-56.

————, & K. LEMS. 1957. The grading of dispersal types in plant communities and their ecological significance. Contrib. Inst. Bot. Univ. Montréal, 71:1-52.

————, & F. SEGADAS-VIANNA. 1952. Ecological study of the peat bogs of eastern North America. I. Structure and evolution of vegetation. Can. Jour. Bot., 30(4):490-520.

DRUCE, A. P. 1959. An empirical method of describing stands of vegetation. Tuatara, 8(1):1-12.

DUVIGNEAUD, P. 1964. L'écosystème forêt. Lejeunia, n.s., 20:1-36.

————, & S. DENAEYER-DE SMET. 1964. Le cycle des éléments biogènes dans l'écosystème forêt. Lejeunia, n.s., 28:1-148.

EMLEN, J. T., Jr. 1956. A method for describing and comparing avian habitats. Ibis, 98:565-576.

FOSBERG, F. R. 1961. What should we map? In: Méthodes de la Cartographie de la Végétation, Colloques Internationaux du Centre National de la Recherche Scientifique, Paris, 97:23-35.

HANSON, H. C. 1958. Principles concerned in the formation and classification of communities. Bot. Rev., 24(2):65-125.

————, & E. D. CHURCHILL. 1961. The plant community. Reinhold Publ. Corp., New York, xii + 218 pp.

KENDEIGH, S. C. 1961. Animal ecology. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, x + 468 pp.

KÜCHLER, A. W. 1947. A geographic system of vegetation. Geogr. Rev., 37: 233-240.

————. 1949. A physiognomic classification of vegetation. Ann. Assoc. Amer. Geogr., 39:201-210.

MILLS, H. L., et al. 1963. Quantitative physiognomic analysis of the vegetation of the Florida Everglades. Marshall Univ. Huntington, West Virginia, v + 65 pp. + 62 figs.

————, & S. E. CLAGG. 1964. The physiognomy of vegetation: a quantitative approach to vegetation geometry based upon the structural cell concept as the minimum sample size. Marshall Univ., Huntington, West Virginia, 104 pp. + appendix.

ODUM, E. P. 1964. The new ecology. BioScience, 14(7):14-16.

PHILLIPS, E. A. 1959. Methods of vegetation study. Henry Holt & Co., New York, xvi + 107 pp.

————. 1964. Field biology. A.I.B.S., Biol. Sci. Curr. Study, D. C. Heath & Co., Boston, xii + 100 pp.

RAUNKIAER, C. 1934. The life forms of plants and statistical plant geography. Clarendon Press, Oxford, xvi + 632 pp.

RICHARDS, P. W. 1952. The tropical rain forest: an ecological study. Cambridge Univ. Press, xviii + 450 pp.

————, A. G. TANSLEY, & A. S. WATT. 1940. The recording of structure, life-form and flora of tropical plant communities as a basis for their classification. Jour. Ecol., 28:224-239.

ROBBINS, R. G. 1959. The use of the profile diagram in rain forest ecology. Jour. Biol. Sci., 2(2):53-63.

SPURR, S. H. 1964. Forest ecology. Ronald Press Co., New York, vi + 352 pp.

WAGNER, P. L. 1957. A contribution to structural vegetation mapping. Ann. Assoc. Amer. Geogr., 47(4):363-369.

WATERWAYS EXPERIMENT STATION. 1963. Environmental factors affecting ground mobility in Thailand. Appendix D: Vegetation. U. S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, Miss., Tech. Rep. No. 5-625, 63 pp.

1. HABIT-FORM

Symbols

W erect woody plants
L climbing or decumbent woody plants
E epiphytes and crusts
H herbs
M bryoids

2. LEAF SHAPE & SIZE

o leafless
n needle, spine, scale, subulate
g graminoid
a broad: medium or small
h broad and large
v compound
q thalloid

3. LEAF TEXTURE

o leafless
f filmy
z membranous
x sclerophyll
k succulent or fungoid

4. SEASONALITY

Symbols

d deciduous or ephemeral
s semideciduous
e evergreen
j evergreen-succulent or evergreen-leafless

5. STRATIFICATION

7 more than 25 meters
6 10 - 25 meters
5 8 - 10 meters
4 2 - 8 meters
3 0.5 - 2 meters
2 0.1 - 0.5 meters
1 0.0 - 0.1 meters

6. COVERAGE

b barren or very sparse
i interrupted, discontinuo
p in patches, tufts, clump
c continuous

FIGURE 1. Scheme of six categories of criteria to be applied to a structural description of vegetation types (slightly modified from Dansereau 1958a, 1959a).

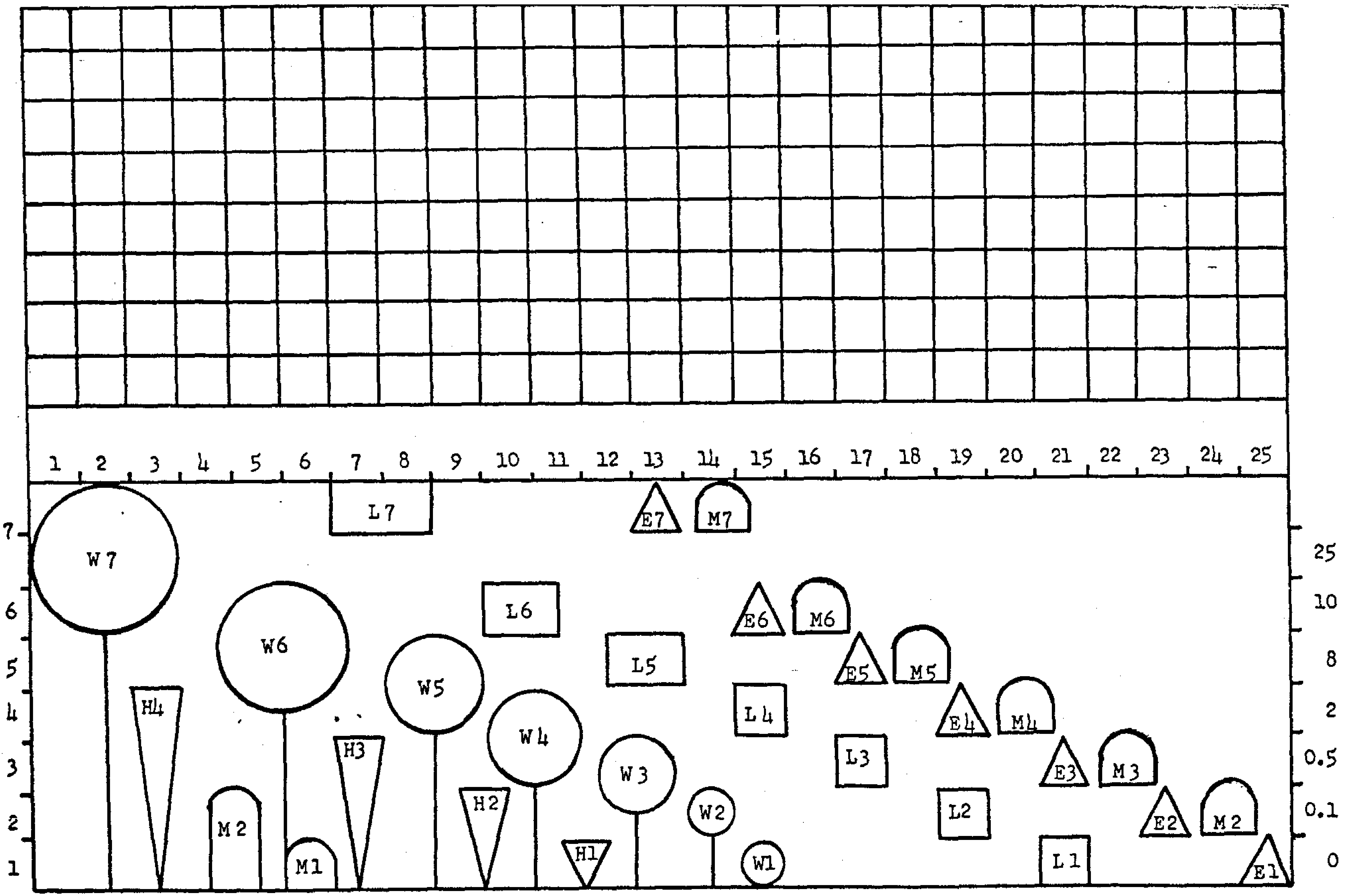


FIGURE 2. The upper block shows the grid serving as a matrix for structural diagrams. It consists of 1 cm. squares, 25 horizontally, each equal to 4% of coverage; 8 vertically, scaled in meters as follows, from the bottom: 0.1, 0.5, 2, 8, 10, 25. The lower block shows all allowable positions of the various habit-forms.

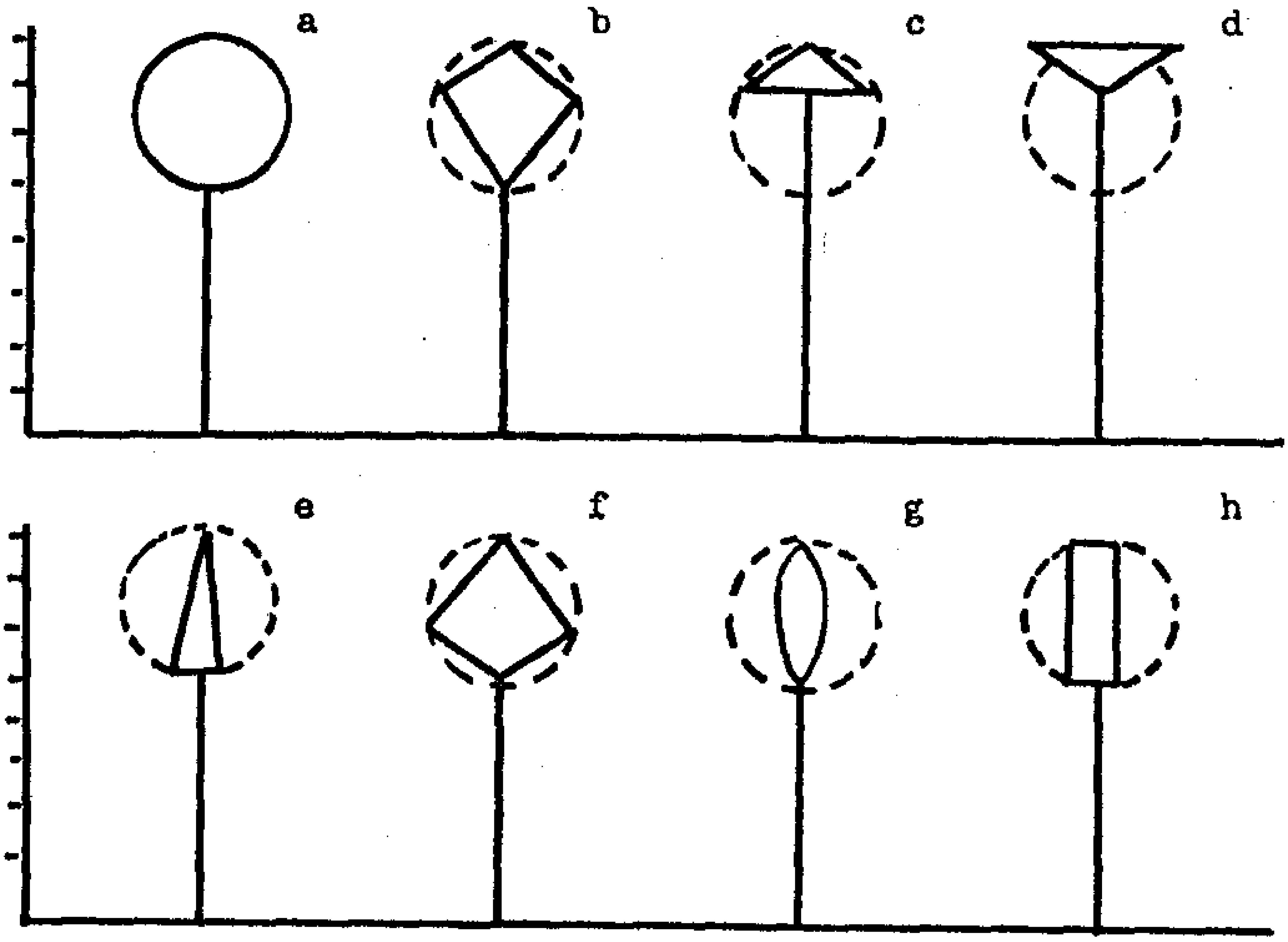


FIGURE 3. A series of alternate crown outlines for tall woody plants (from Dansereau 1958a, Fig. 3).

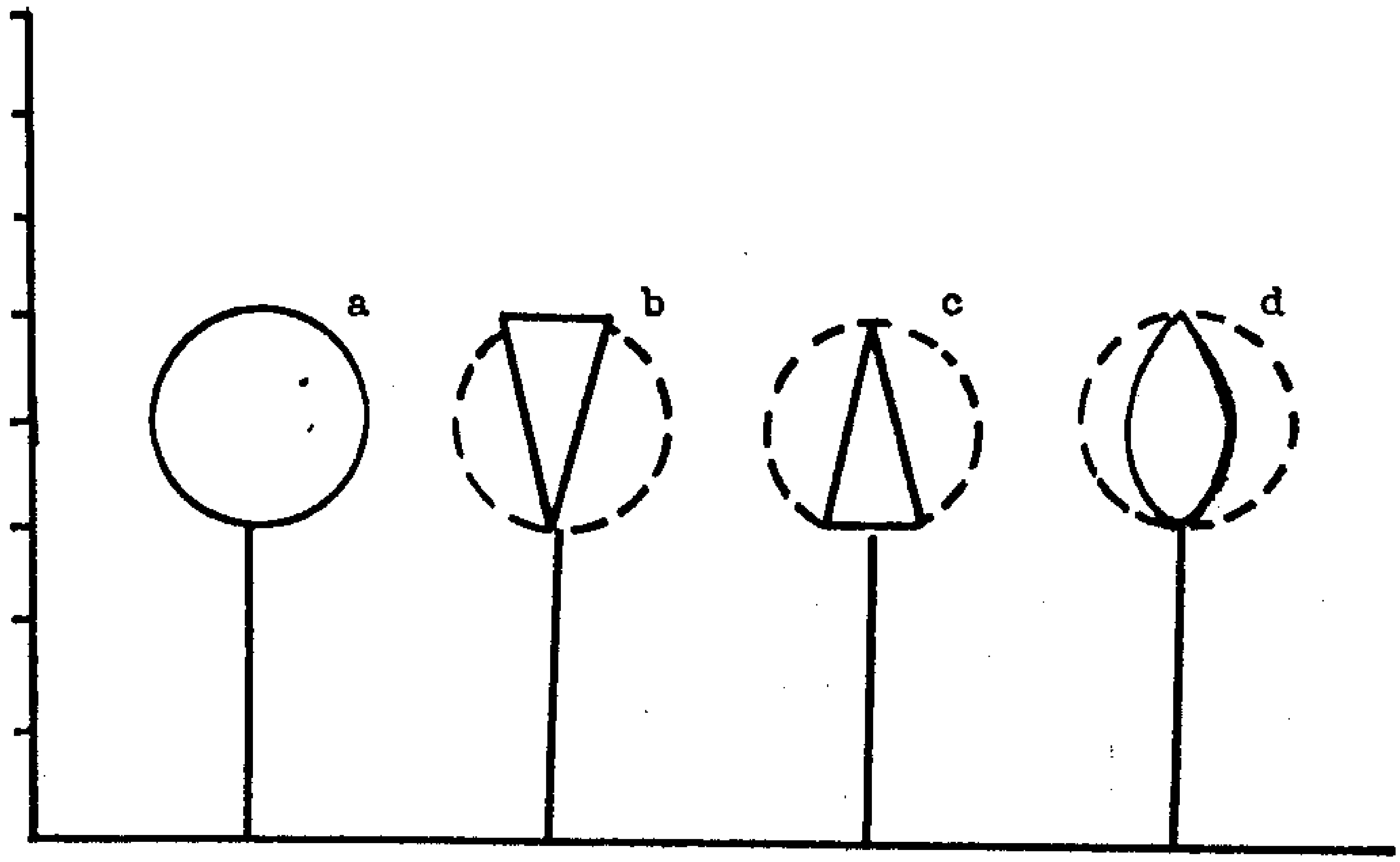


FIGURE 4. A simplified symbology for presenting alternate crown outlines for erect woody plants exceeding 2 meters in height. This is a modification of Figure 3 and is similar to a scheme utilized by Mills & Clagg 1964.

Note that:

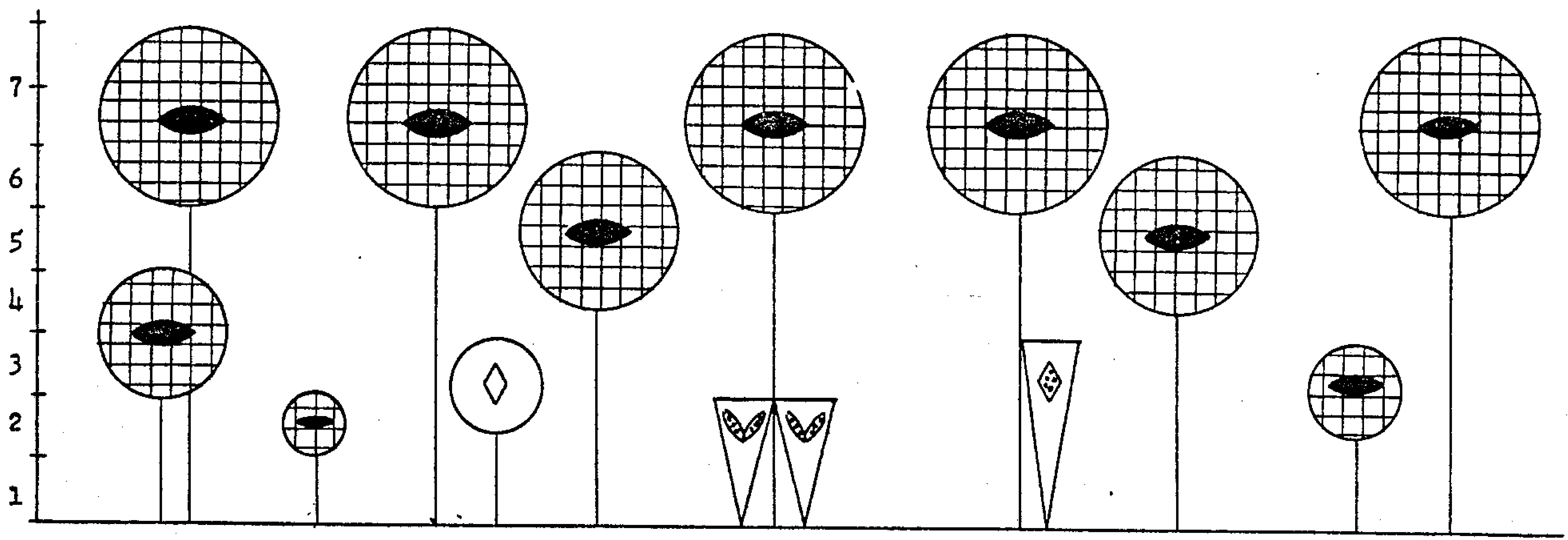
Symbol a of Figure 4 remains the same as symbol a of Figure 3.

Symbol b of Figure 4 now represents symbols b and d of Figure 3.

Symbol c of Figure 4 now represents symbols c, e, and f of Figure 3.

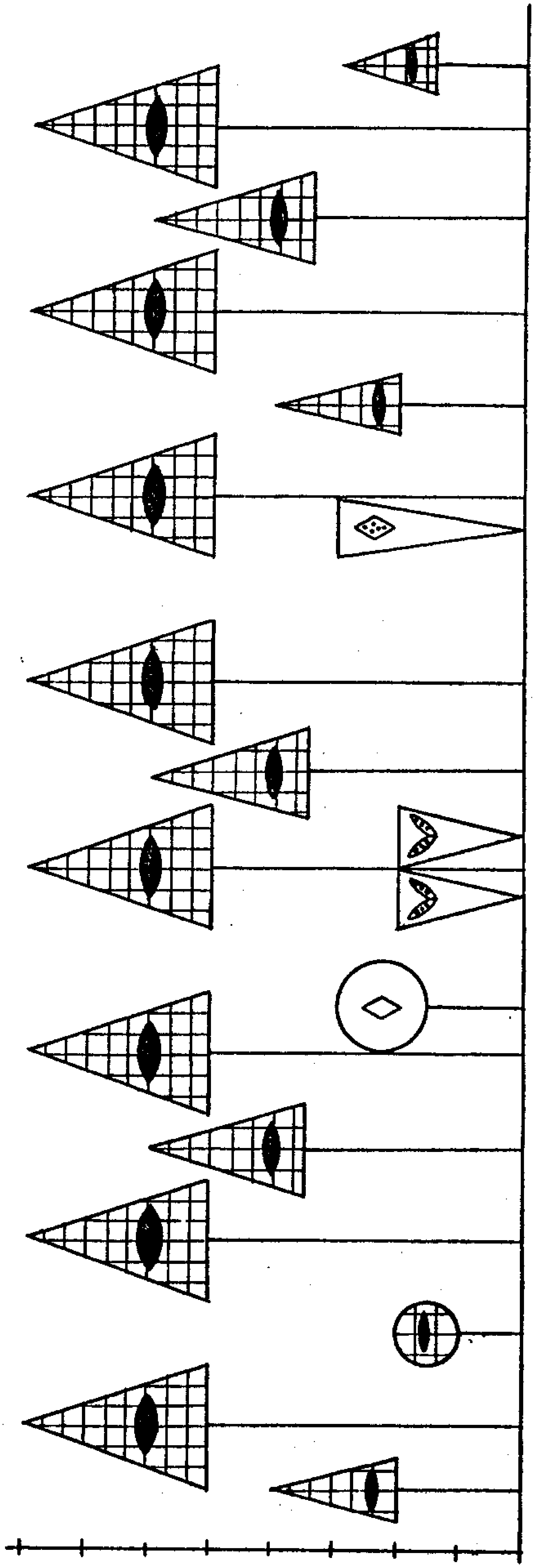
Symbol d of Figure 4 now represents symbols g and h of Figure 3.

FIGURE 5. Two examples of the use of alternate crown symbols. A1 represents a spruce forest in Upper Hidden Valley (Colorado), plotted with the conventional habit-form symbols for all erect woody plants. A2 is plotted with the alternate crown outlines proposed in Figure 4. B1 shows a coastal podocarp forest near Tahakopa, New Zealand, in which the alternate crown outlines described in Figure 3 are used (as published in Dansereau 1964, Figure 3), and B2 illustrates the simplified version of Figure 4.



5.A1

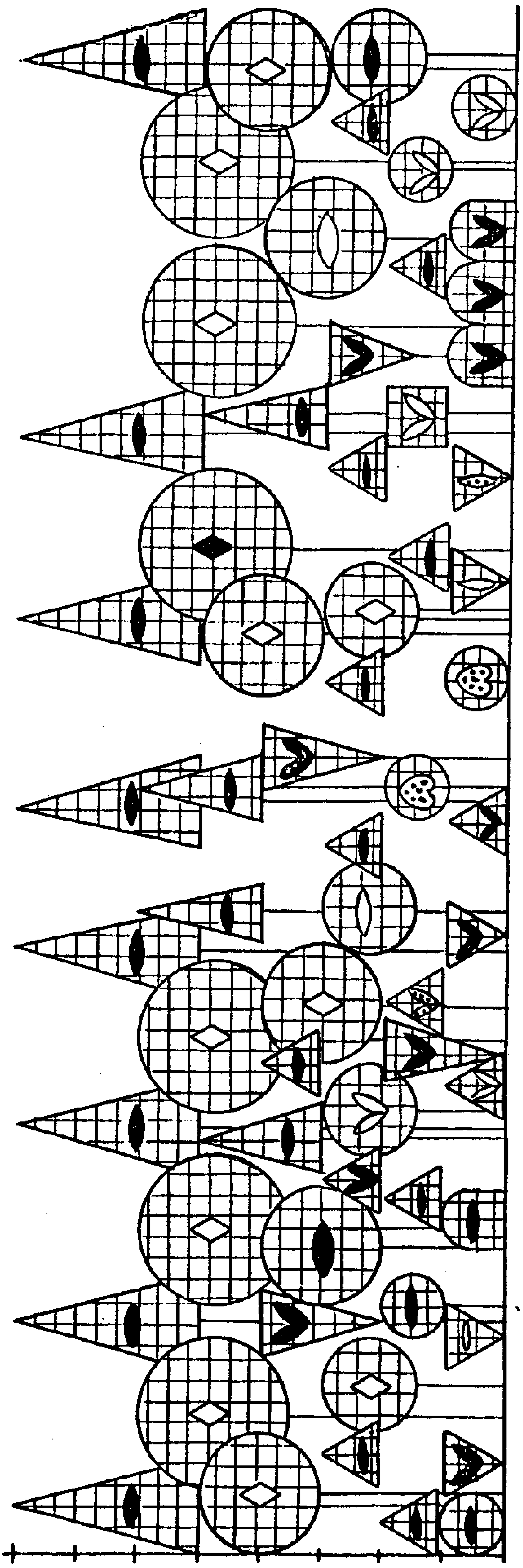
630624-04



5.A2

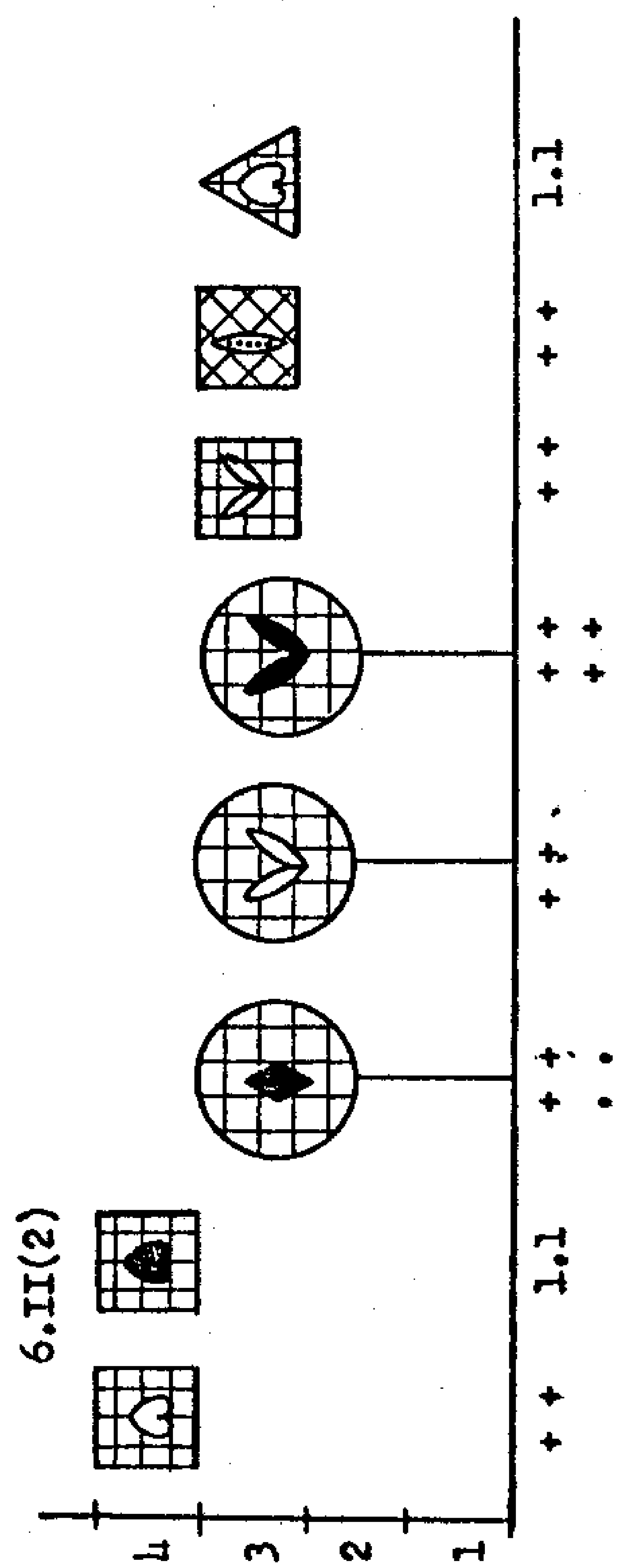
5.B(1)

610617-09



5.B(2)


6.II(1)
1.1
3.3
1.1
1.1
6
5
4
3
2
1


6.II(2)
1.1
1.1
4
3
2
1

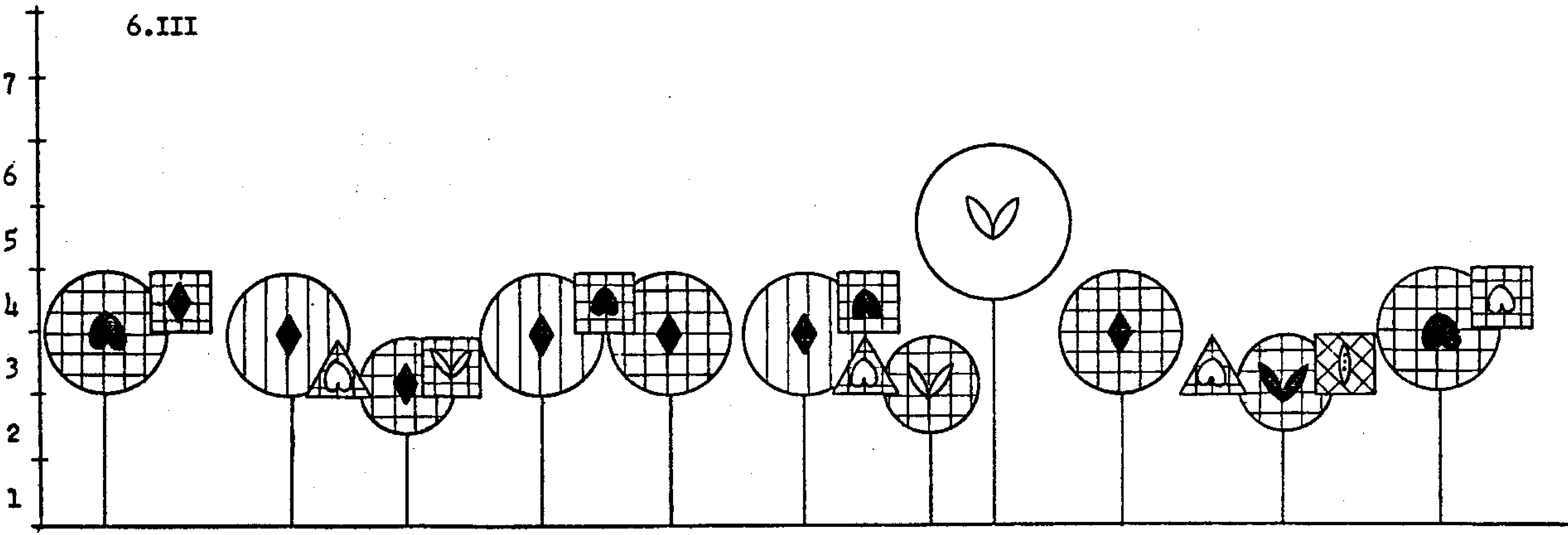


FIGURE 6. A <u>Bursera-Gyminda</u> scrub near Vega Alta, Puerto Rico (630311-11). The "range diagram" (6.II) shows all of the structural forms present; some of them do not appear in the final structural (or standard) diagram (6.III) because their individual coverage is less than the coverage allowed for a single symbol in any particular height-class concerned.

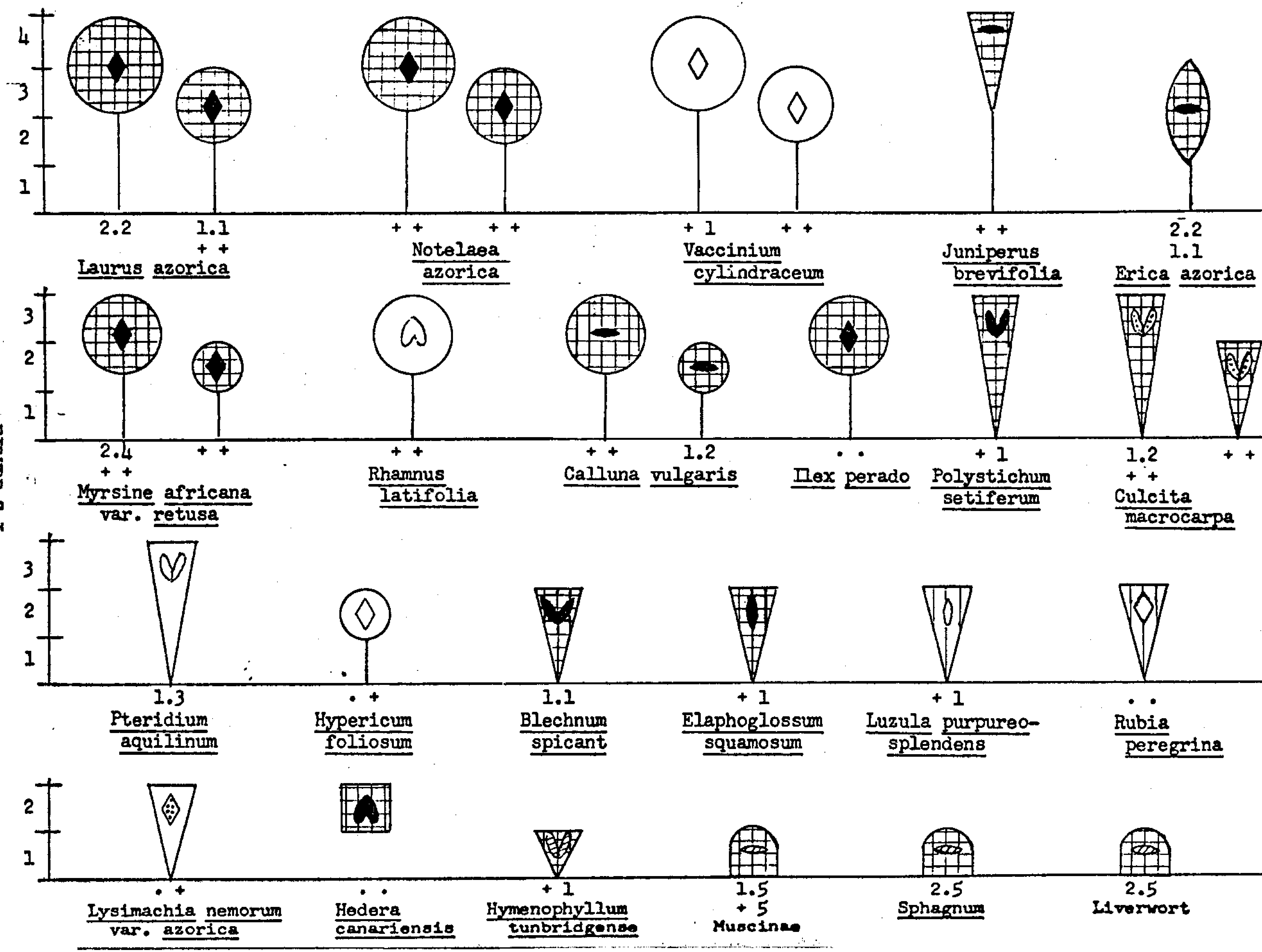

4
3
2
1
2.2
1.1
+ +
Laurus azorica
+ +
+ +
Notelaea azorica
+ 1
+ +
Vaccinium cylindraceum
+ +
Juniperus brevifolia
2.2
1.1
Erica azorica
3
2
1
2.4
+ +
+ +
Myrsine africana var. retusa
+ +
Rhamnus latifolia
+ +
1.2
Calluna vulgaris
• •
Ilex perado
+ 1
Polystichum setiferum
1.2
+ +
+ +
Culcita macrocarpa
3
2
1
1.3
Pteridium aquilinum
• +
Hypericum foliosum
1.1
Blechnum spicant
+ 1
Elaphoglossum squamosum
+ 1
Luzula purpureo-splendens
• •
Rubia peregrina
2
1
• +
Lysimachia nemorum var. azorica
• •
Hedera canariensis
+ 1
Hymenophyllum tunbridgense
1.5
+ 5
Muscinae
2.5
Sphagnum
2.5
Liverwort

FIGURE 7.I

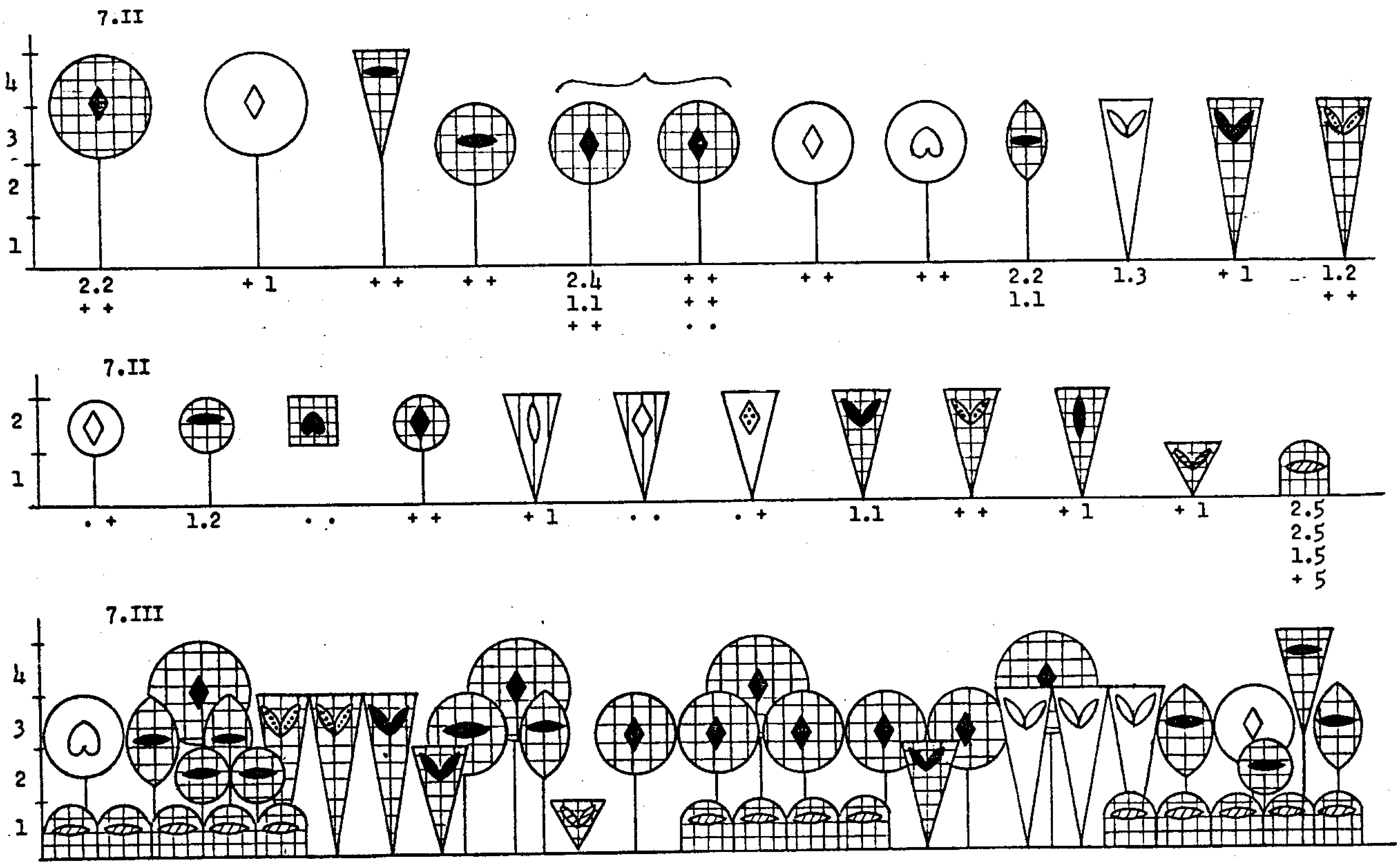
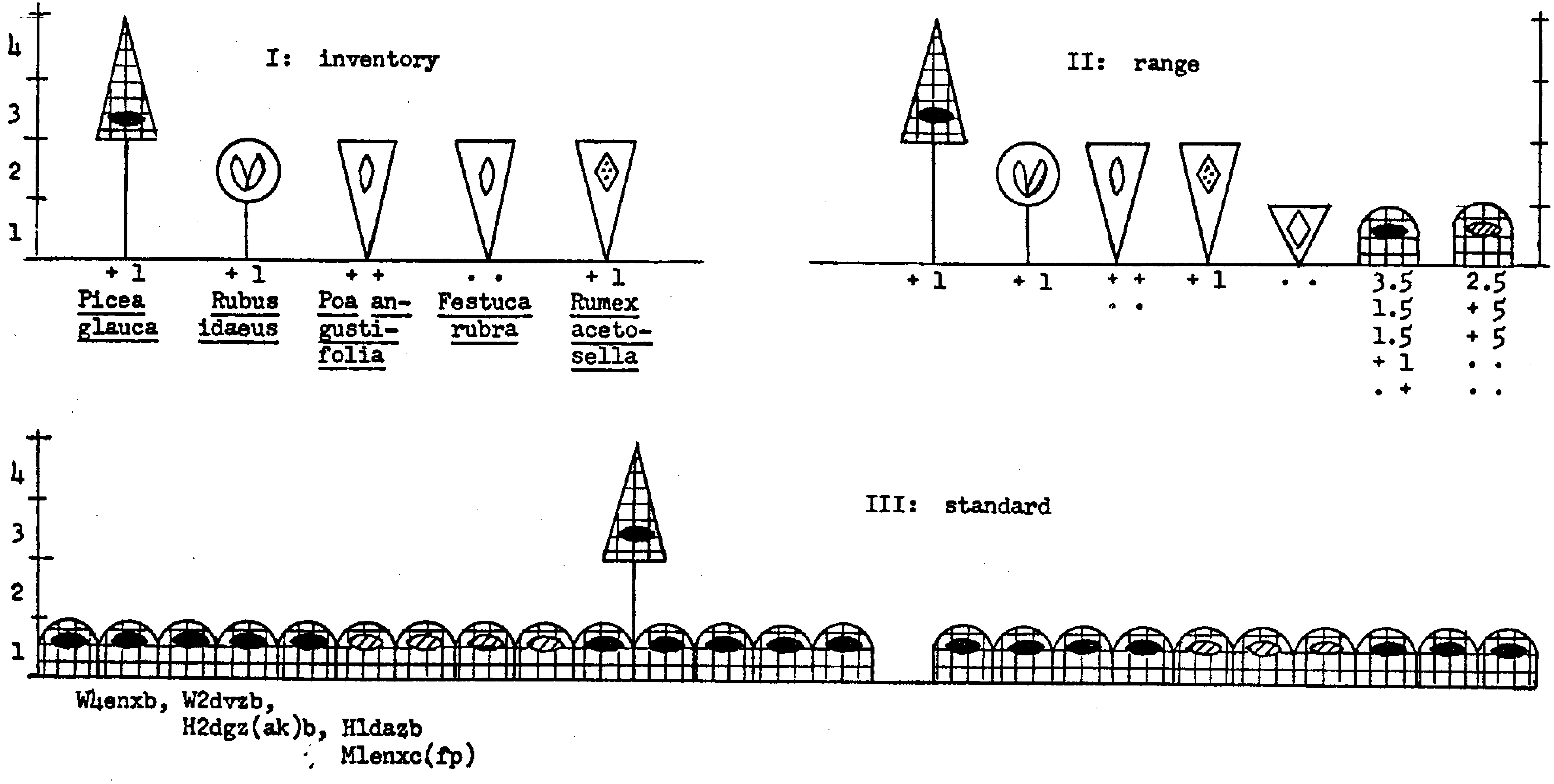


FIGURE 7. A laurel scrub at Terra Brava (Island of Terceira, Azores; 640525-04). 7.I shows the floristic inventory (23 species), with the appropriate structural form and both coverage and local coverage classes. 7.II is the range diagram, with 23 structural forms also. 7.III is the standard structural diagram.



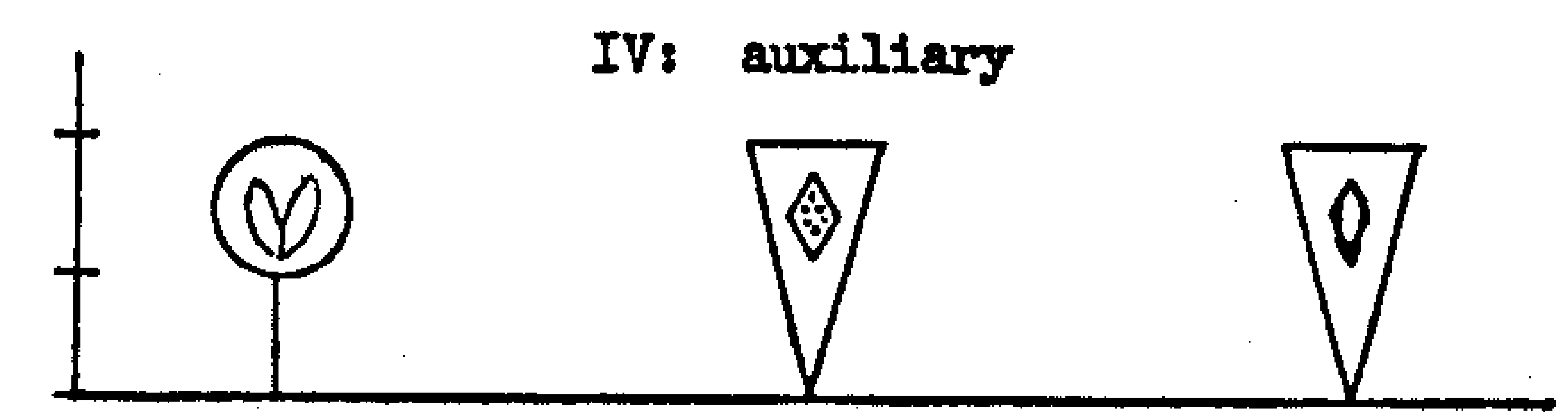


FIGURE 8. A spruce-lichen savana at Coin-du-Banc (Gaspé Peninsula, Quebec), which illustrates the value of the auxiliary diagram. 8.I is the floristic-structural inventory (lacking layer 1). 8.II is the range-diagram. 8.III is the standard structural diagram with its horizontal grid-unit-value of 4%. 8.IV is the auxiliary diagram with a grid-unit-value of 0.5%. (620713-13)

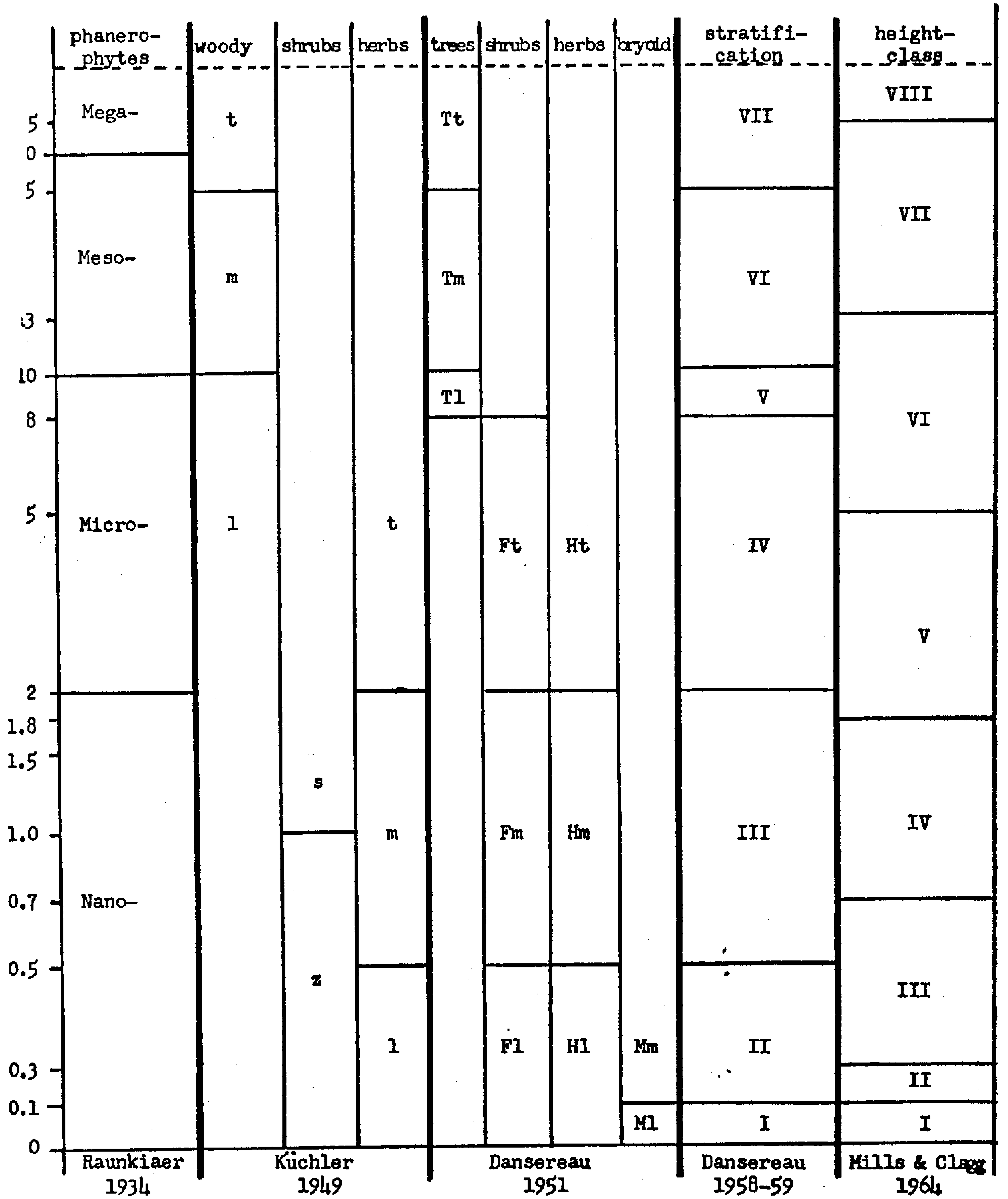


FIGURE 9. A comparison of various height categories (in meters) modified from Dansereau (1951) to include Dansereau (1958a-1959a) and Mills & Clagg (1964).

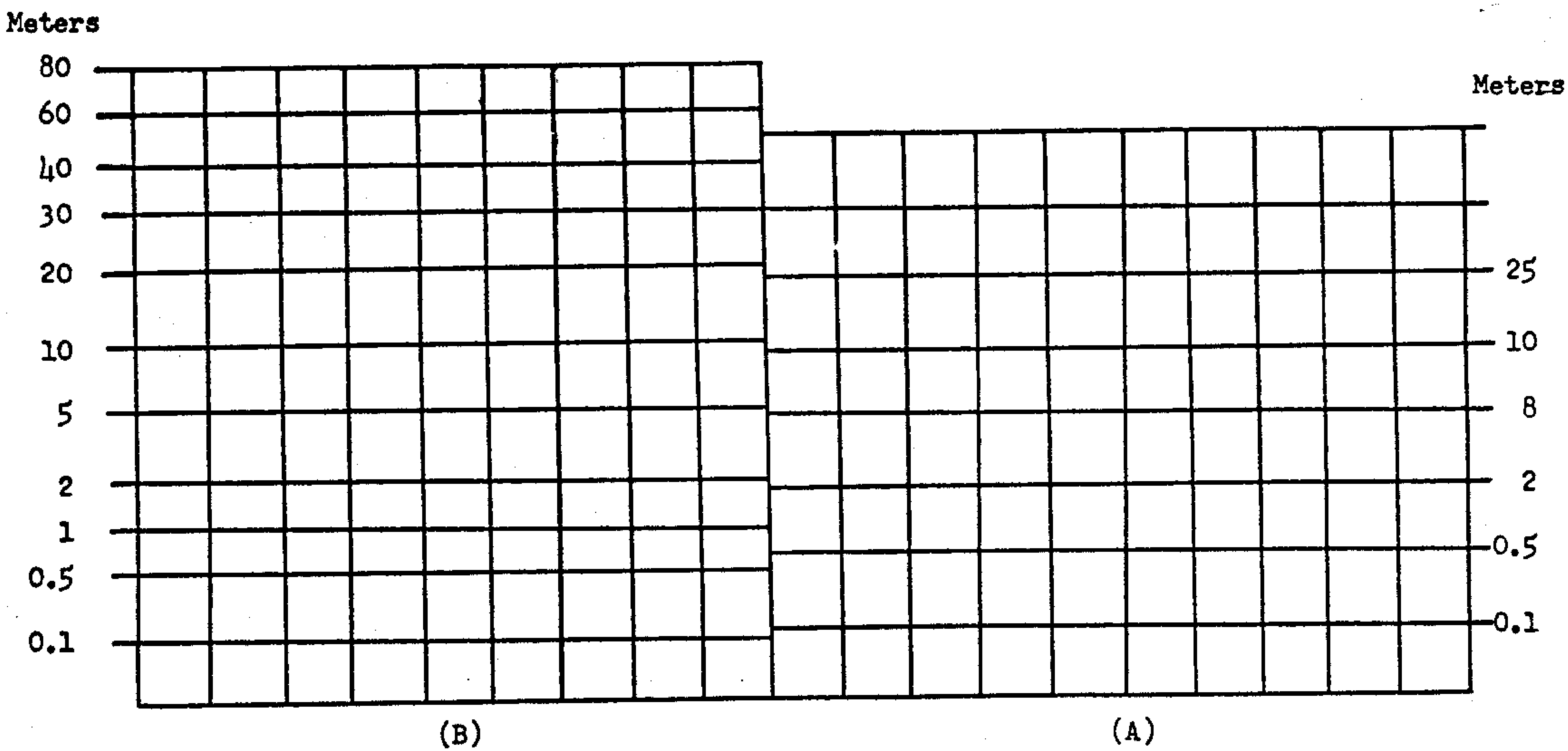


FIGURE 10. A comparison of our present fourth-root system of vertical scaling (B) and the 1958-1959 height-classes of Dansereau (A).

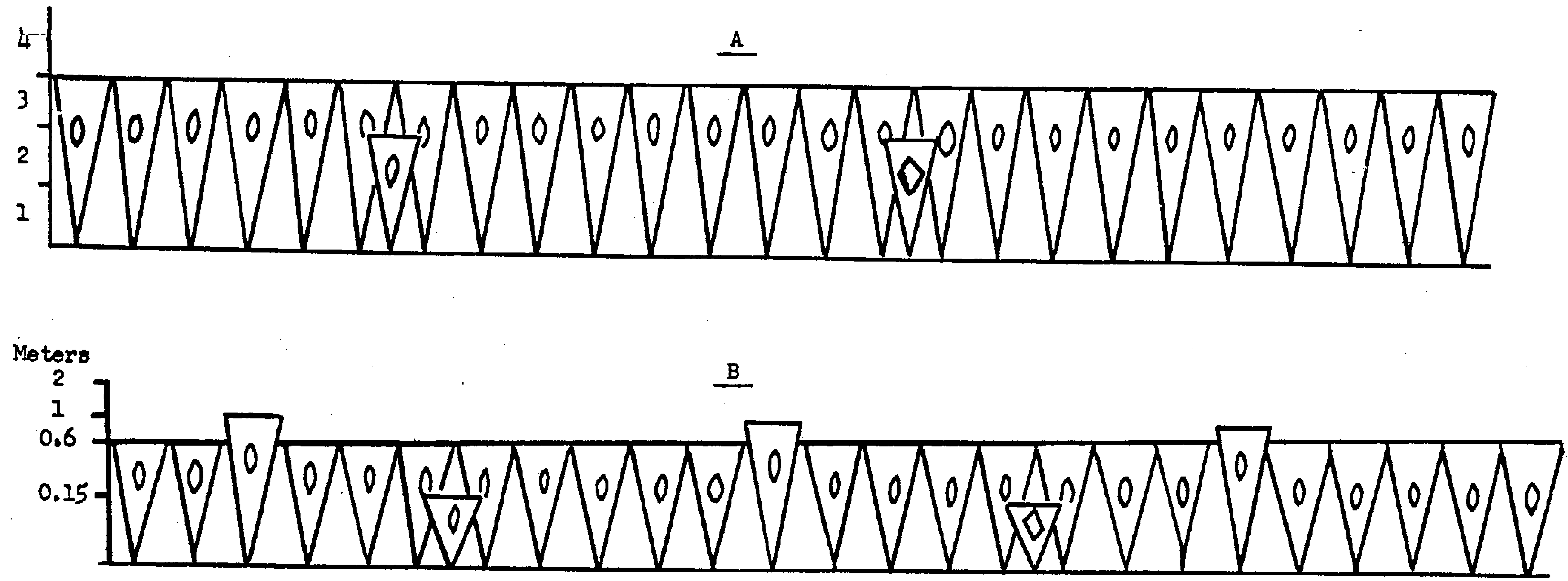
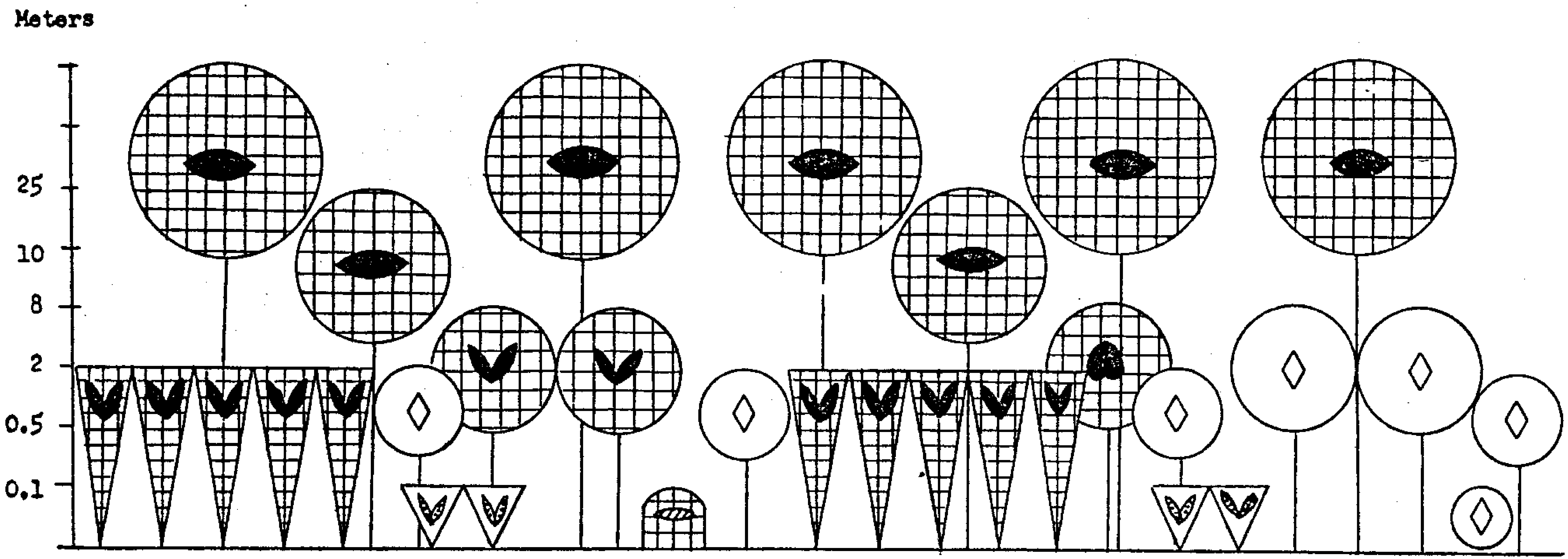


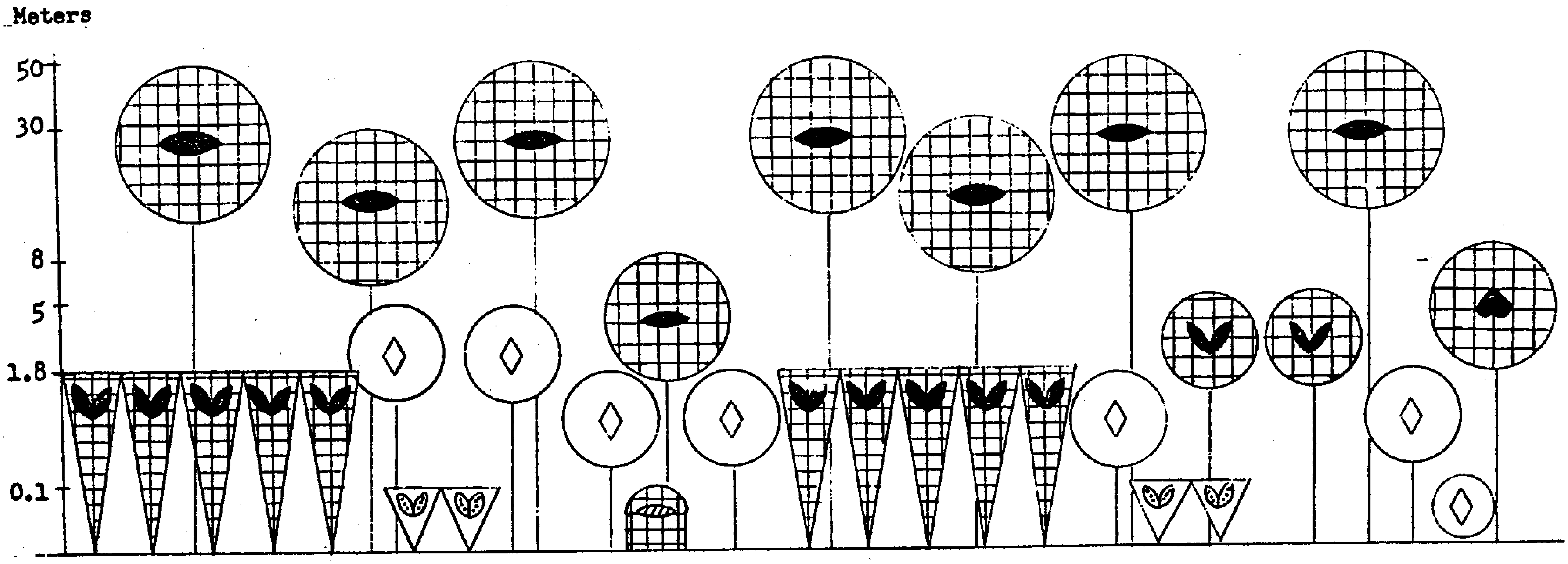
FIGURE 11. A comparison between the two methods of vertical scaling indicated in Figure 10. This stand of Elymus arenarius, as observed in the field at Cap-de-Méchins (Gaspé Peninsula, Québec), was recorded as:

Height in cm.	% Cover
100-60	10
60-15	90
15- 0	less than 10

If this information is used to prepare a standard structural diagram as shown in A, then two observed layers (100-60 and 60-15 cm.) must be placed in height class 3 and diagrammed as a single layer of vegetation. Note that in B where the layers are plotted as they were observed in the field, the above situation is avoided and a more realistic diagram of the actual vegetation emerges.



12.1(A)



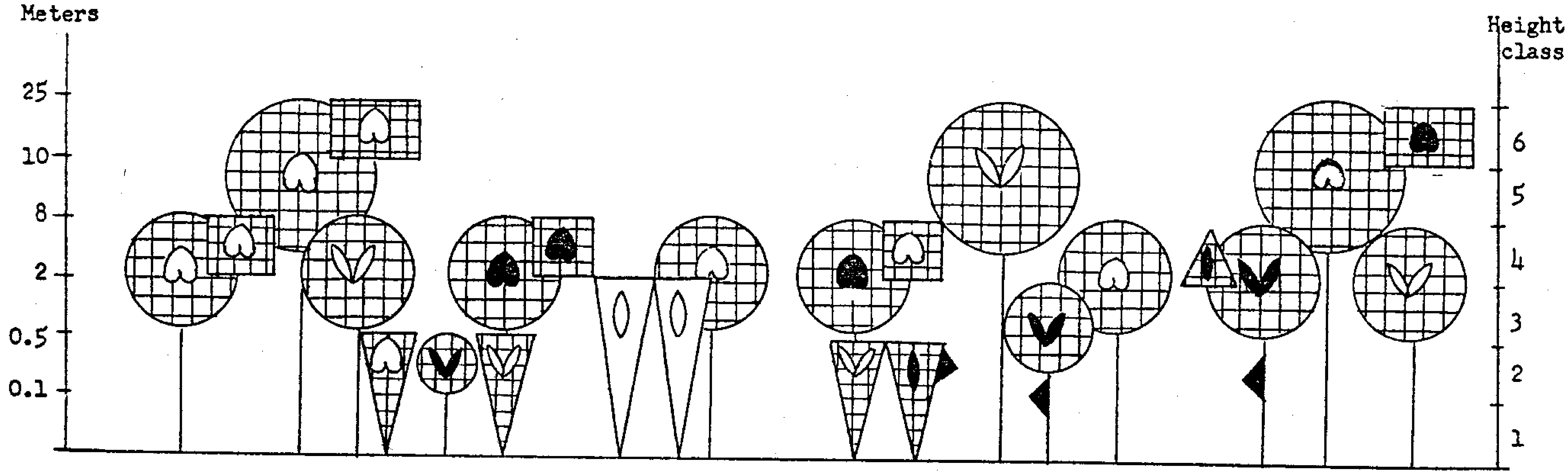
12.1(B)

FIGURE 12. Three examples comparing the standard diagrams (A) as plotted in Figures 5 to 8 and in Figure 10A, and the projection achieved (B) by using the fourth-root scale proposed in Figure 10B.

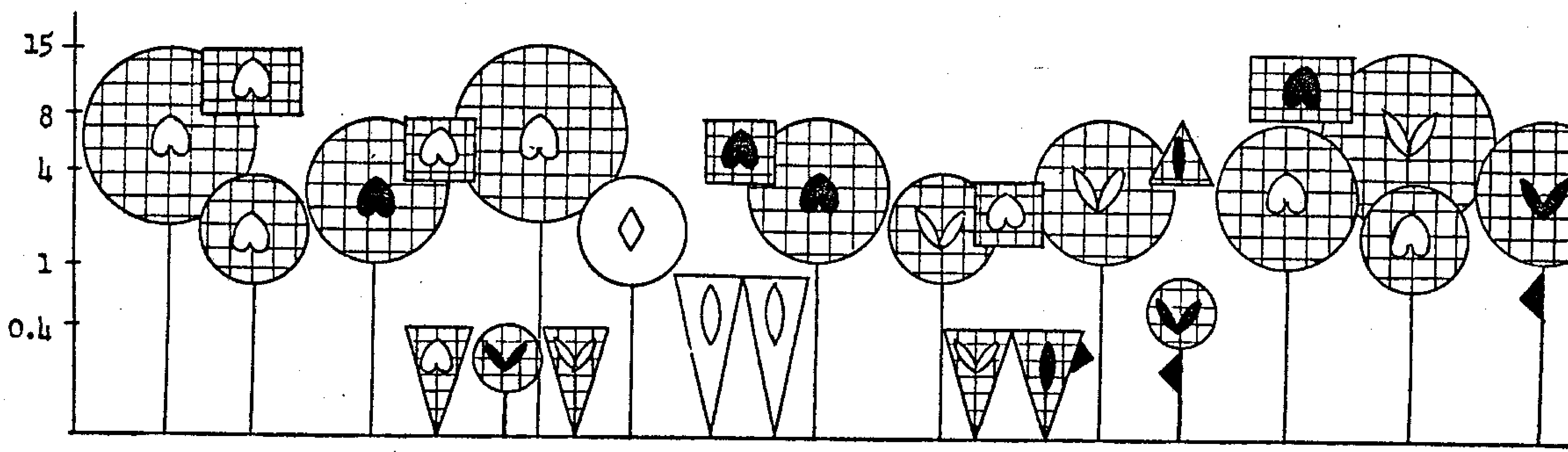
12.1: A redwood forest stand at Prairie Creek State Park, California (620824-09).

12.2: An Andira-Quararibaea forest in the limestone hills of Puerto Rico, near Hato Tejas (630311-04).

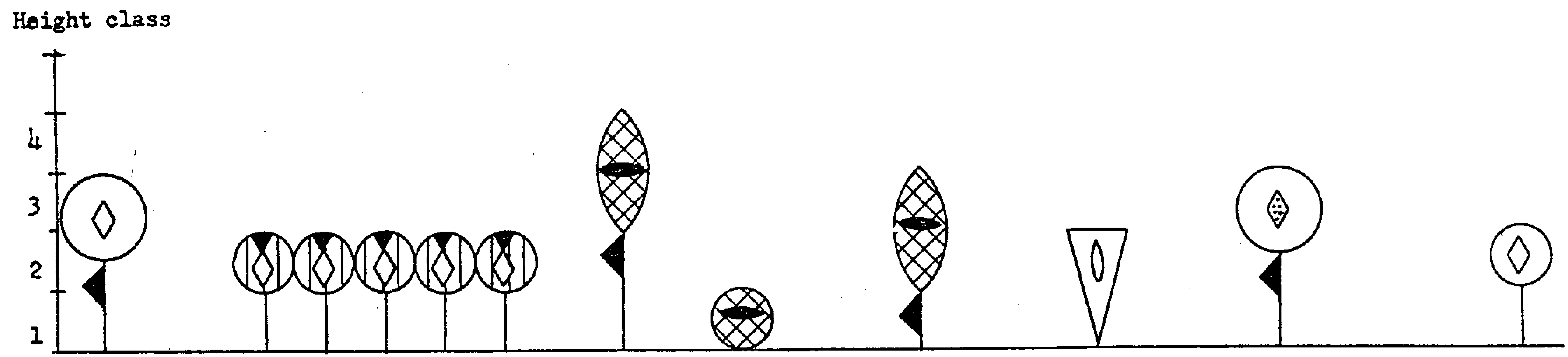
12.3: A sahuaro savana, near Tucson, Arizona (620427-02).



12.2(A)



12.2(B)



12.3(A)

12.3(B)

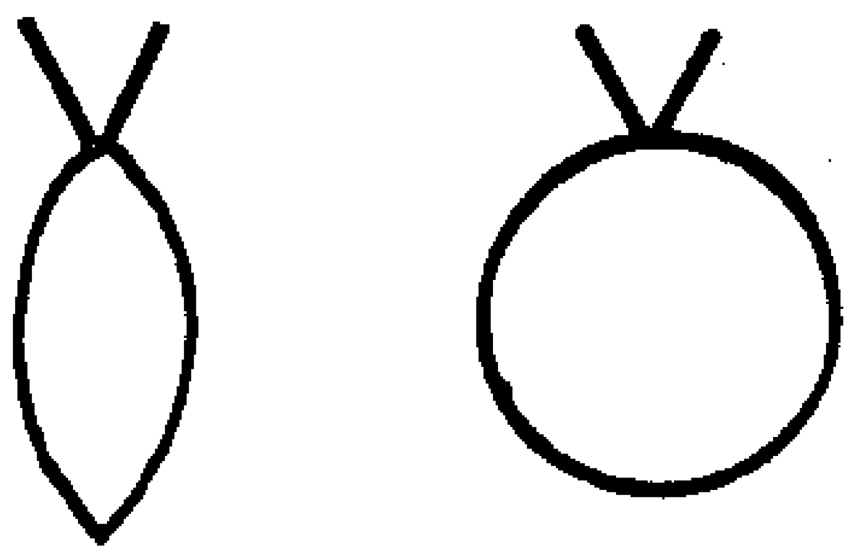
New distribution			Raunkiaer 1934		
r	◇	small (less than 2.25 sq. cm.)	Class 1	l	leptophyll (less than 25 sq. mm.)
			Class 2	n	nanophyll (25-225 sq. mm.)
t	□	medium (2.25-182.25 sq. cm.)	Class 3	m	microphyll (225-2025 sq. mm.)
			Class 4	M	mesophyll (2025-18,225 sq. mm.)
u	▽	large (182.25-1640.25 sq. cm.)	Class 5	MM	macrophyll (18,225-164,025 sq. mm.)
y	⬡	very large (more than 1640.25 sq. cm.)	Class 6	MMM	megaphyll (more than 164,025 sq. mm.)

FIGURE 13. Suggested distribution of leaf-size classes and their equivalence to those of Raunkiaer (1934).

o		leafless
n	⬬	needle, spine, scale, or subulate
g	♦	narrow
h	●	broad
q	♣	thalloid
v	♥	compound

FIGURE 14. The proposed alternatives and appropriate symbols for the category of leaf-shape to be used with Figure 13.

A



B

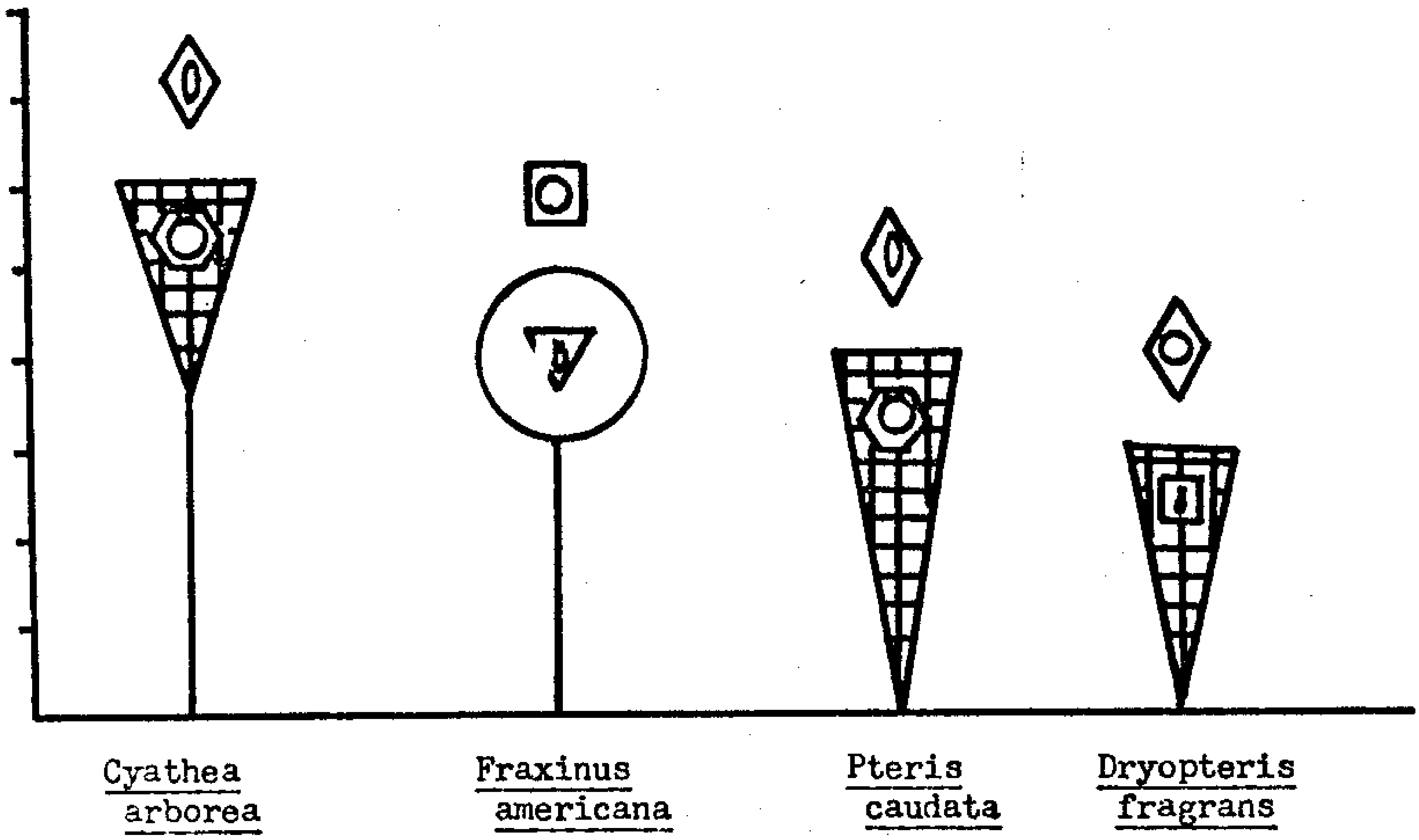


FIGURE 15. A method of indicating a compound leaf structure in greater detail than could be applied under the scheme of Figure 1. A shows the appropriate symbol which could be used to note the compound leaf (this symbol would be placed inside the proper symbol for leaf size as indicated previously). The size and the shape of the leaflets could then be described on the range-diagram using the same criteria as applied to leaf shape and size in a manner illustrated in B above. Plant names are indicated here only as a matter of reference.

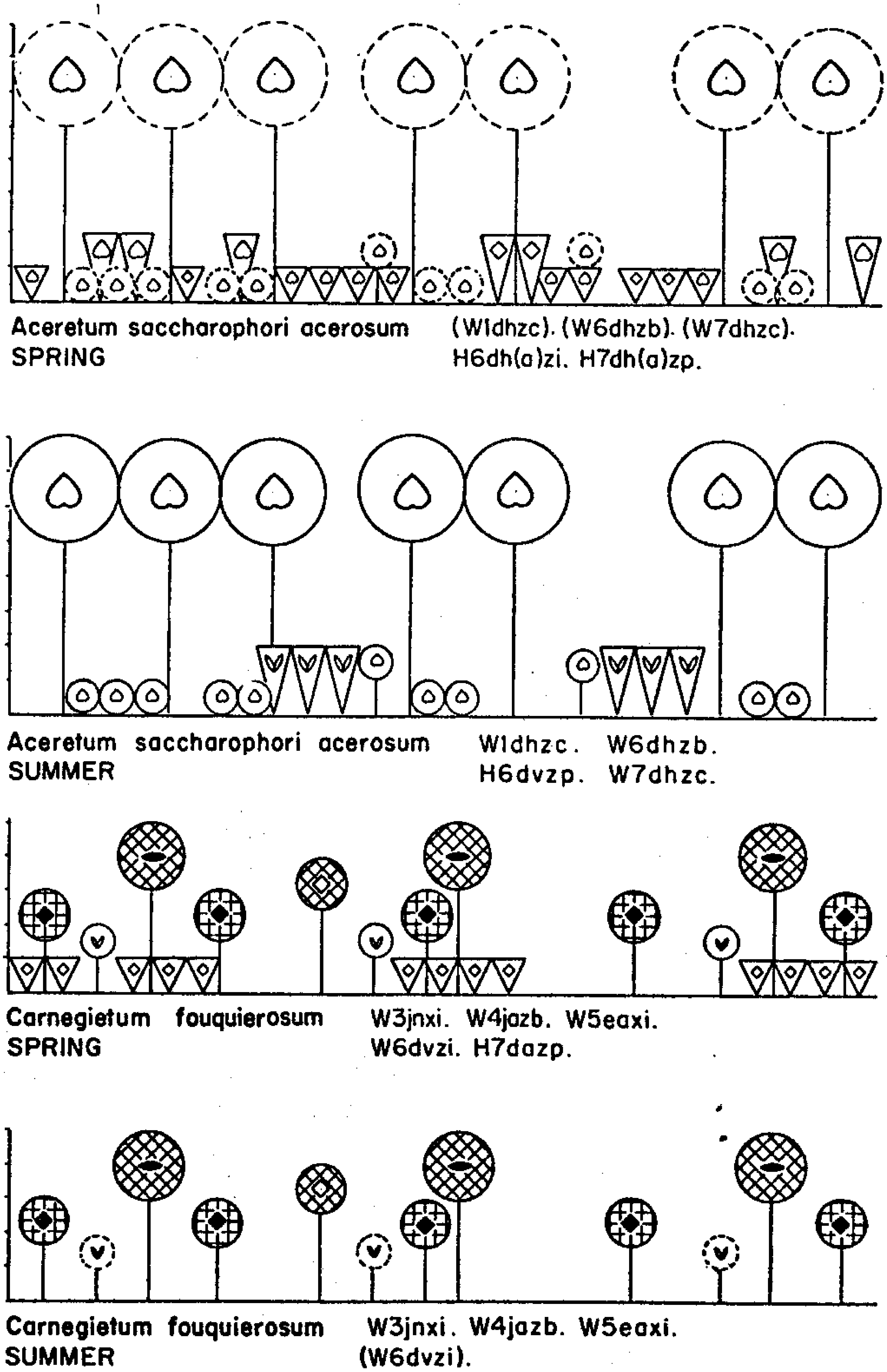


FIGURE 16. Seasonal change in coverage in a maple forest and in a sahuaro desert. The dotted outlines represent the leafless stage. (From Dansereau 1958a.)

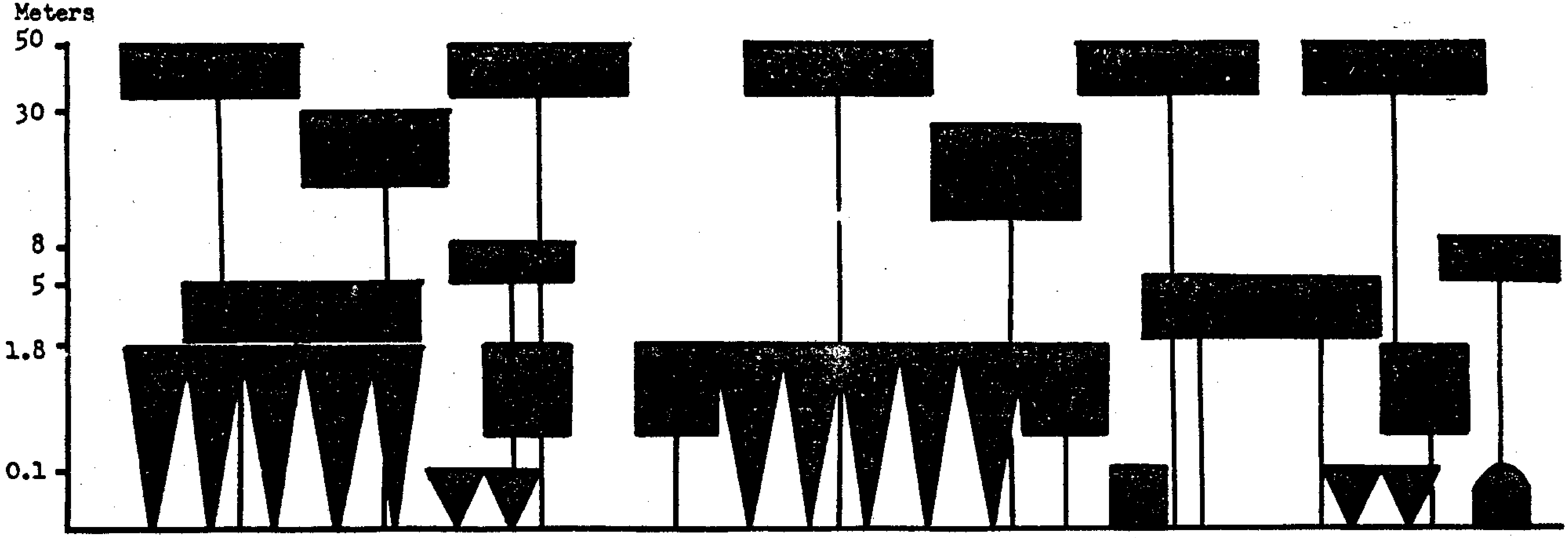


FIGURE 17. A modified structural diagram of a Sequoia stand in California (see Figure 12.1); details other than habit-form have been omitted. Heights are on the fourth-root scale, as in Figure 10B.

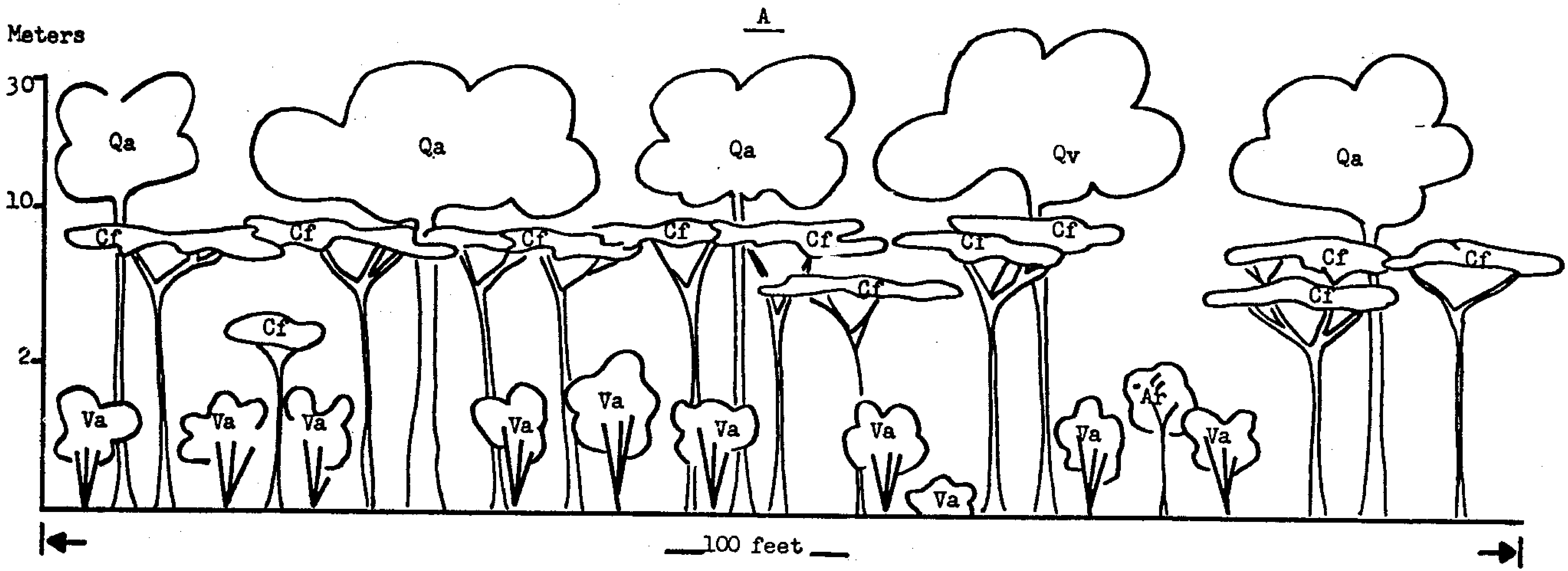


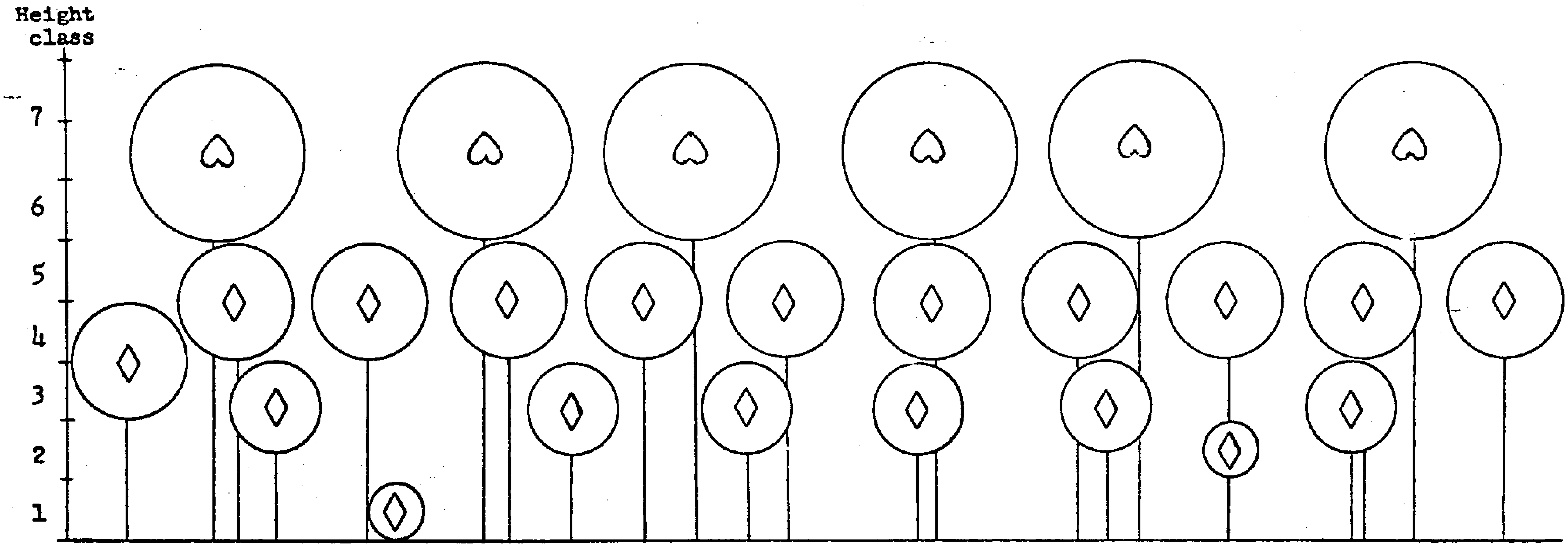
FIGURE 18. Three profiles drawn from a phytosociological relevé taken in Hutcheson Memorial Forest (East Millstone, New Jersey).

(A): A realistic profile, showing outline of individuals belonging to the following species:

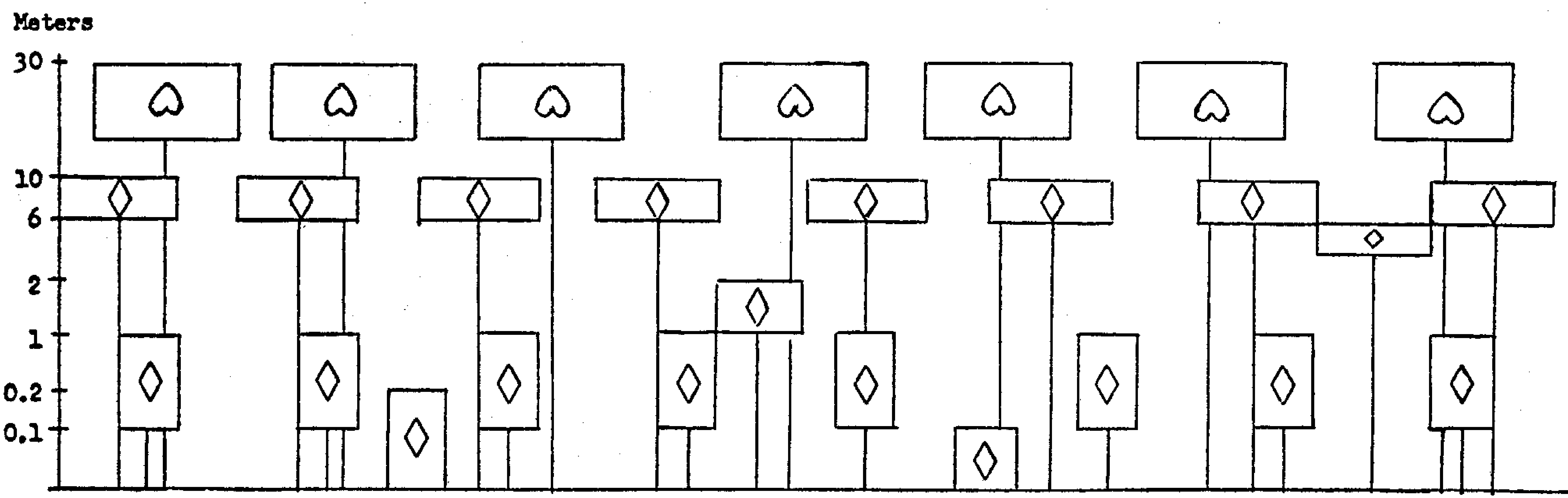
Qa	Quercus alba	Cf	Cornus florida
Qv	Quercus velutina	Ar	Acer rubrum
Va	Viburnum acerifolium		

(B): A standard diagram

(C): A modified structural diagram after the pattern of Figure 17.



B



C

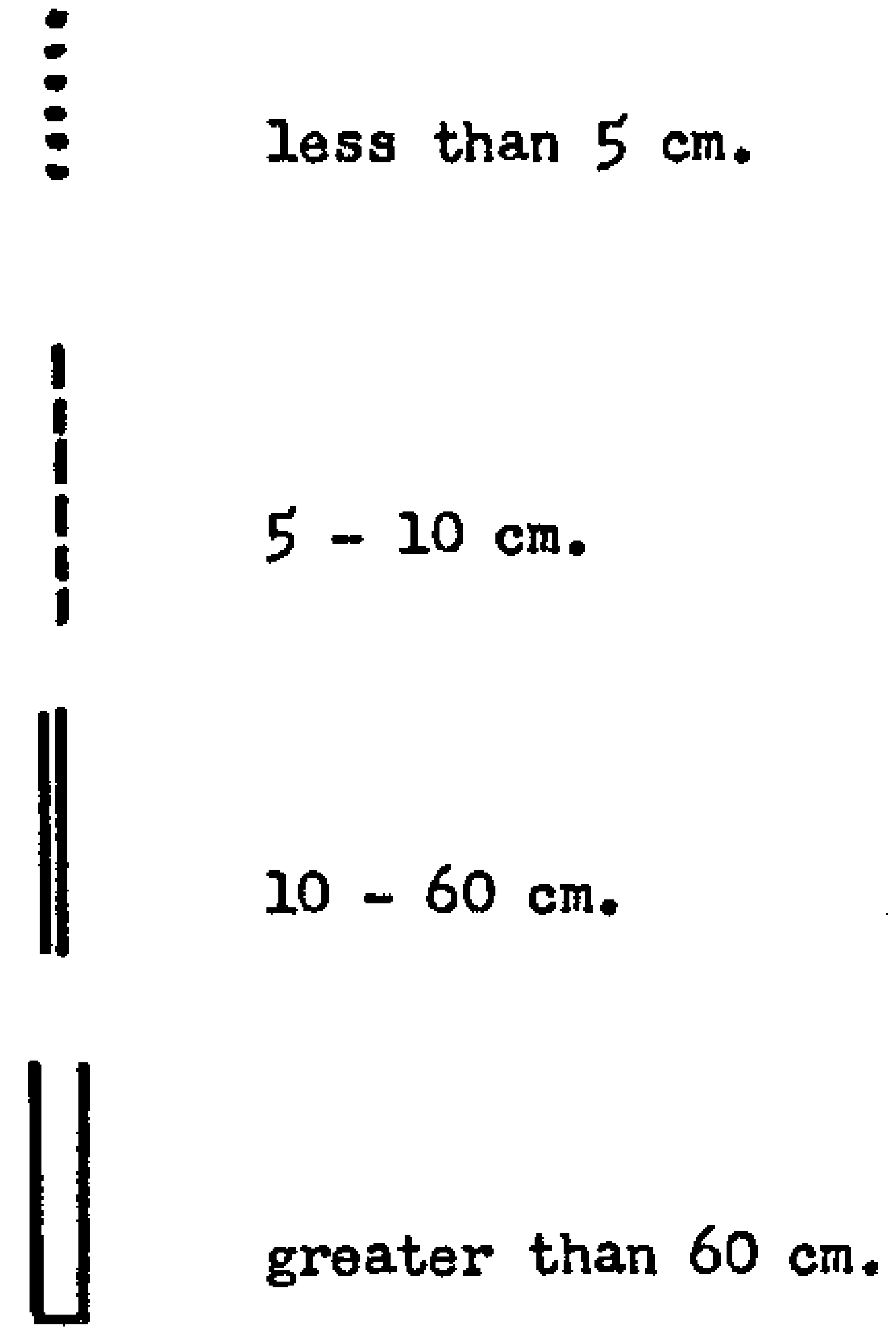


FIGURE 19. Proposed alternatives and appropriate symbology for stem diameters to be used with a modified structural diagram.

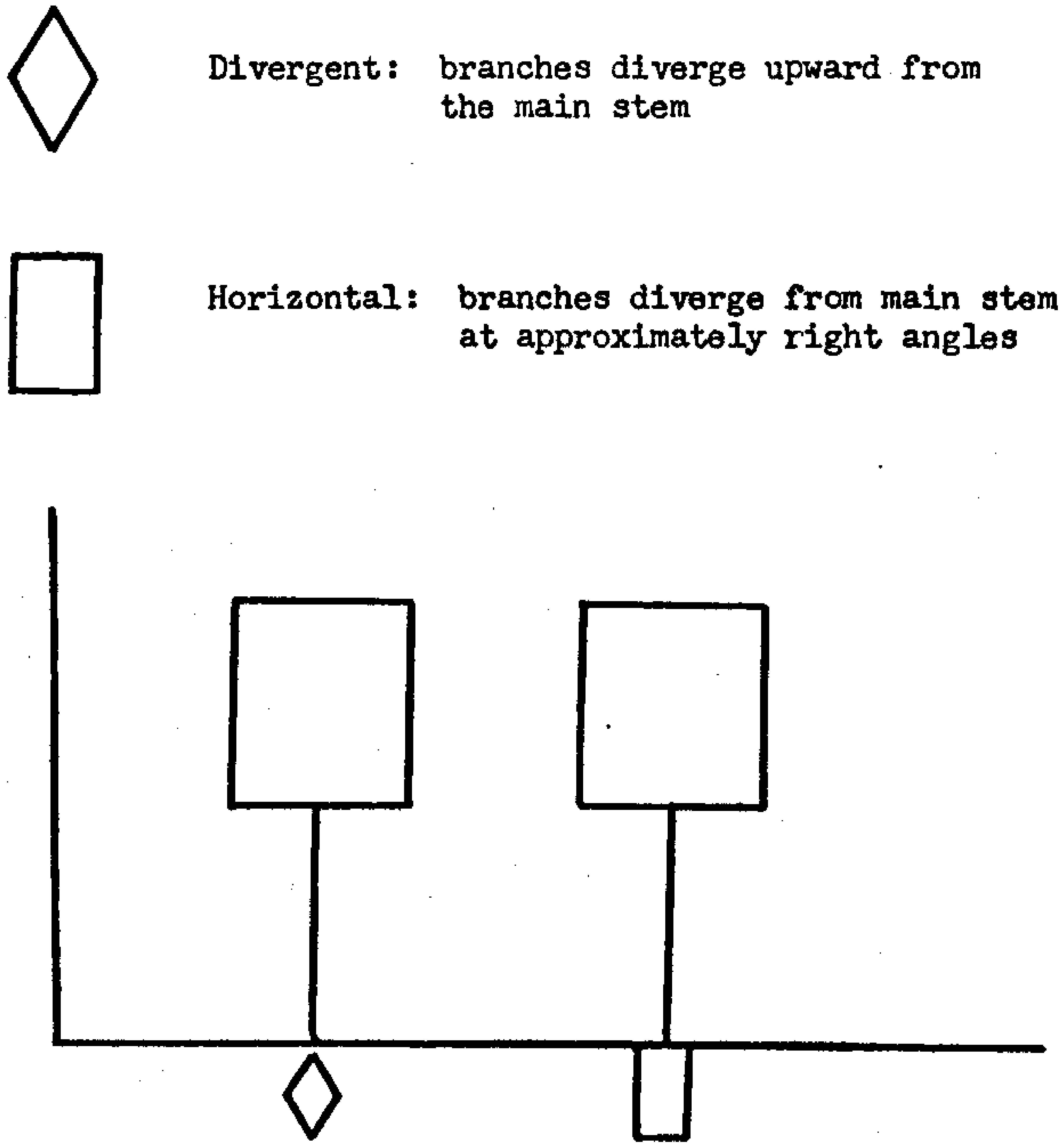
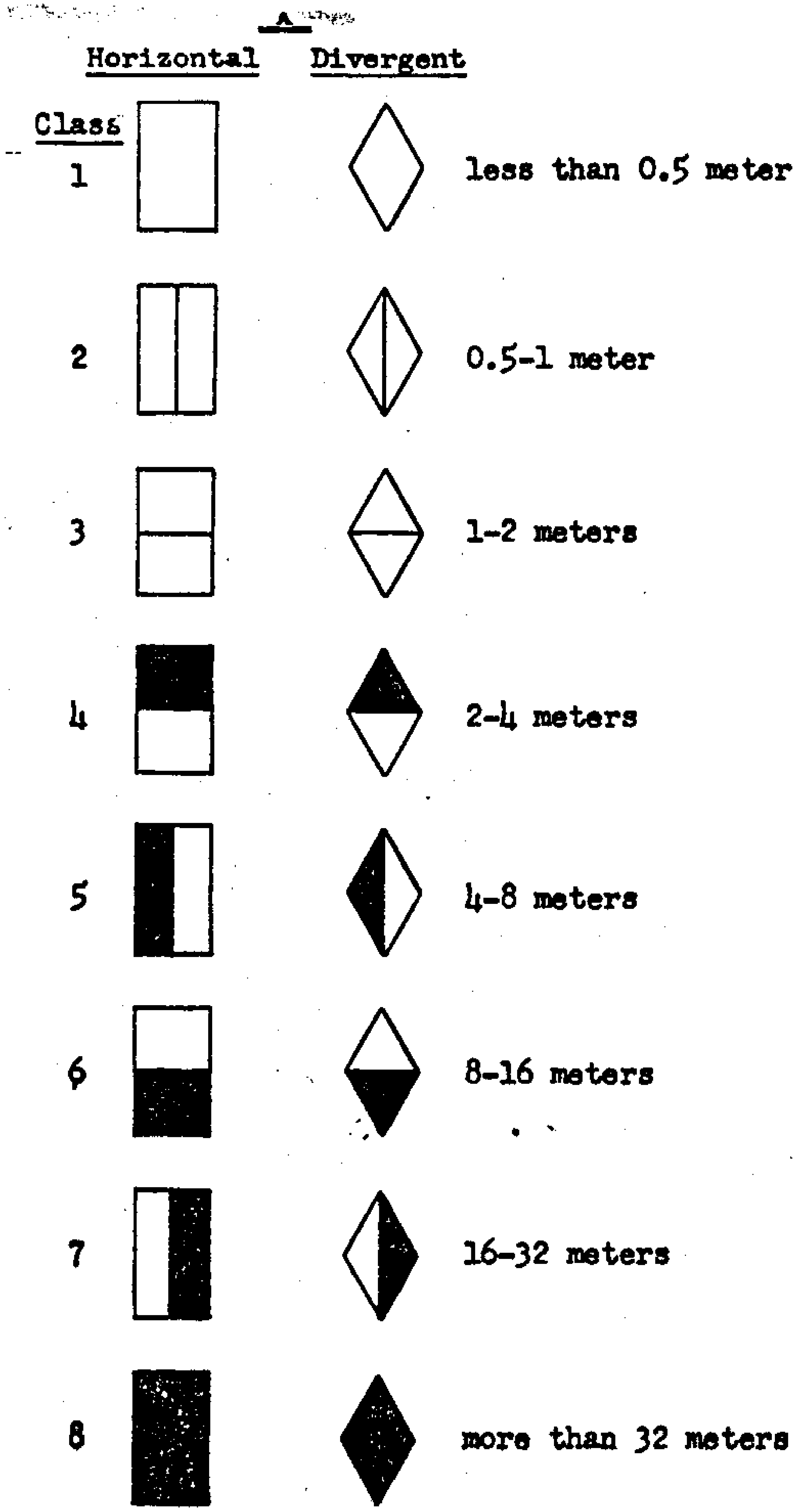


FIGURE 20. Types of principal branching (from Mills & Clagg 1964) to be used with a modified structural diagram.



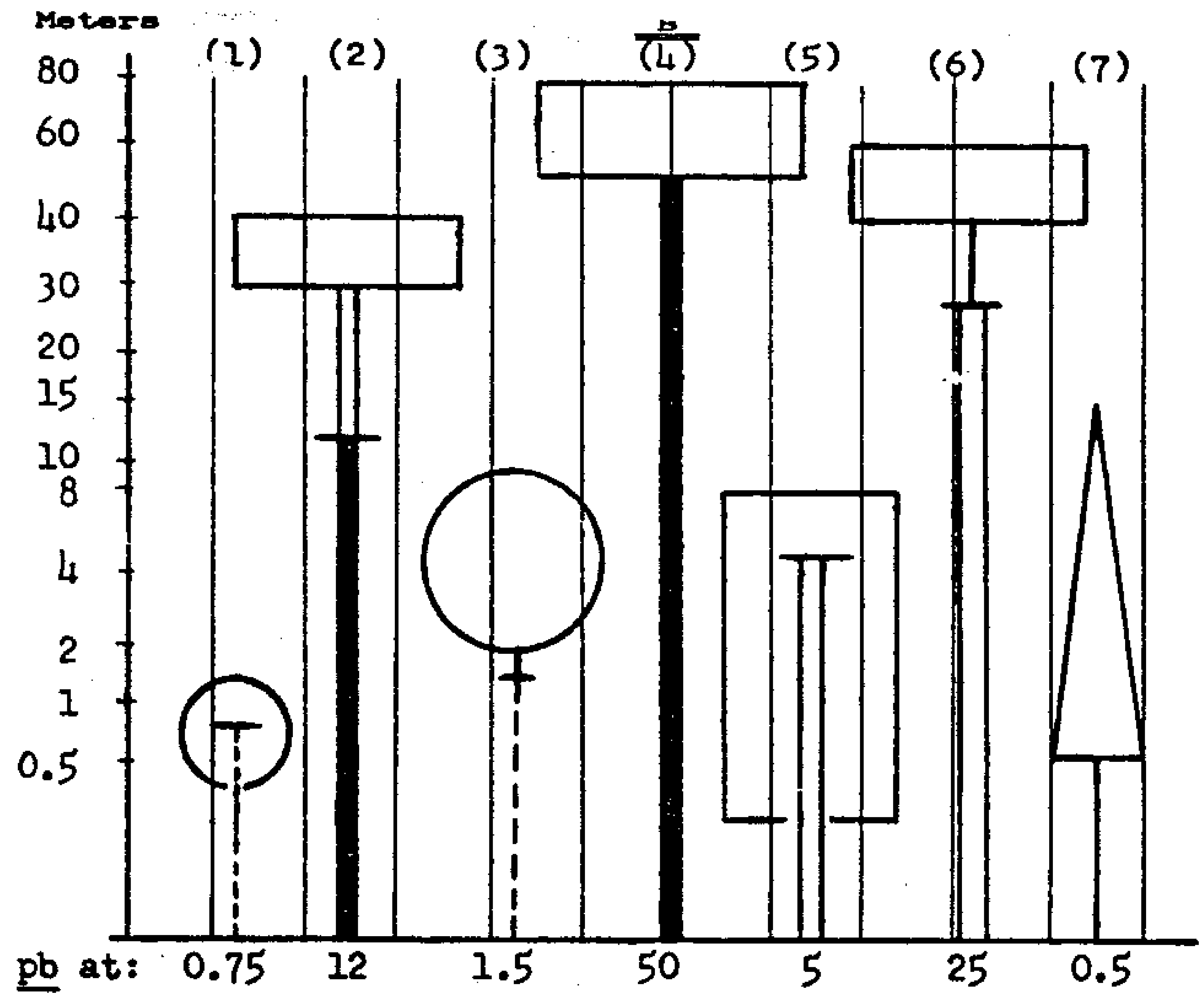


FIGURE 21. Two methods of indicating the height of principal branching (pb) to be applied to a modified structural diagram. Method B presents a more accurate representation than that of A, but if total cover in lower layers is high Method B can be applied only if each layer is treated separately.

B.— (1) and (3) with standard crown symbols (Dansereau 1958a). (7) (stem diameter not indicated) with alternate crown symbol (Fig. 4 and Dansereau 1958a) modified to show crown base coinciding with height of pb. With the alternate crown symbols of page 11 and Fig. 17: (4) indicates pb occurring at crown base; (5) pb above crown base; (2) and (6) pb below crown base. In (2) diameter of principal branches (or of stem above pb) is shown, whereas in (6) and (3) it is not. It can generally be assumed that pb is divergent if below crown base, but is more likely to be horizontal if at crown base. In type (1) branching symbol will interfere with seasonality, leaf shape and size, and texture symbols. This is also true of (5), but the type of branching represented here should not occur frequently.

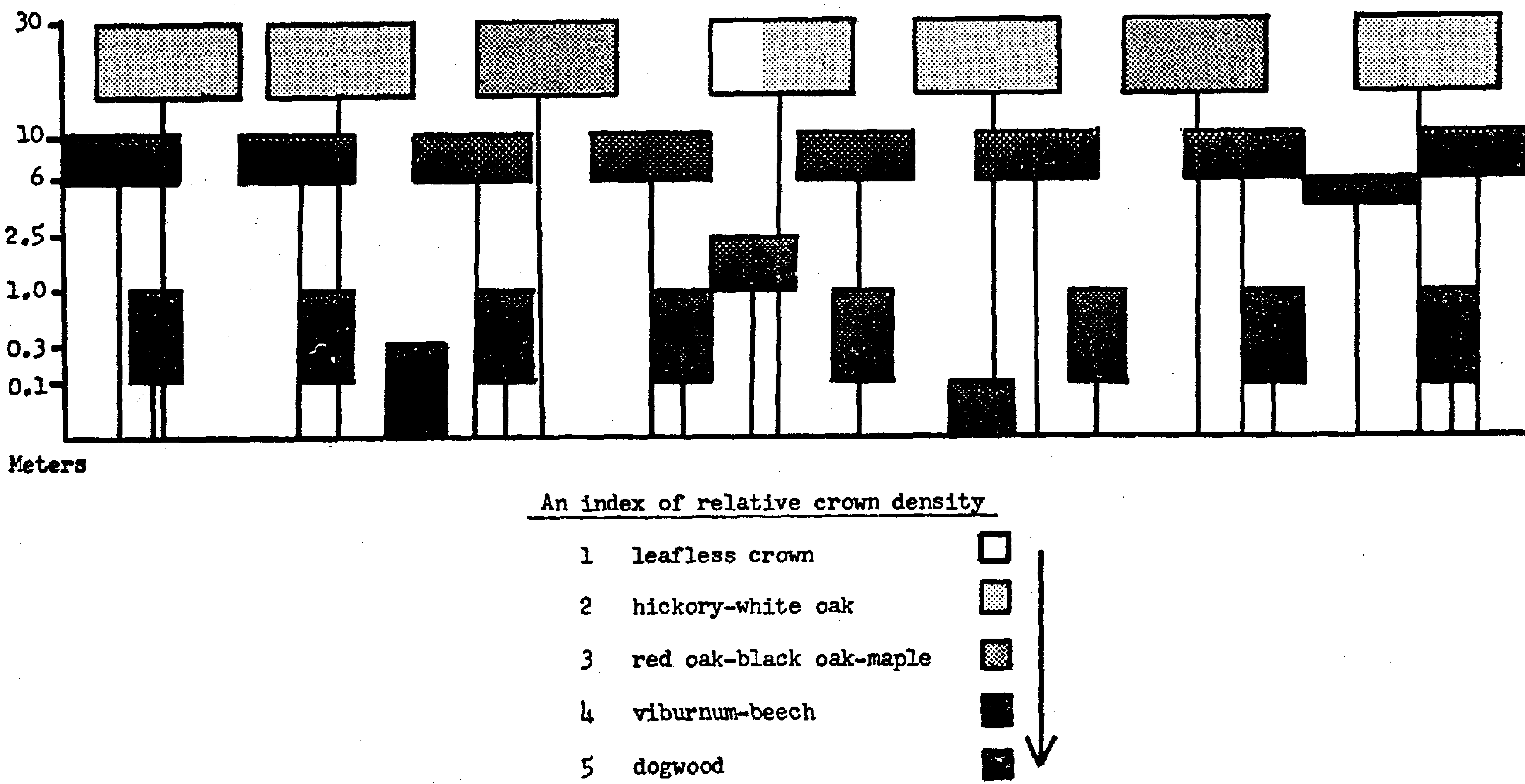


FIGURE 22. An index of the relative densities of the crown mass applied to the structural layers of the mature oak forest shown in Figure 18, in an attempt to further illustrate the distribution of biomass.

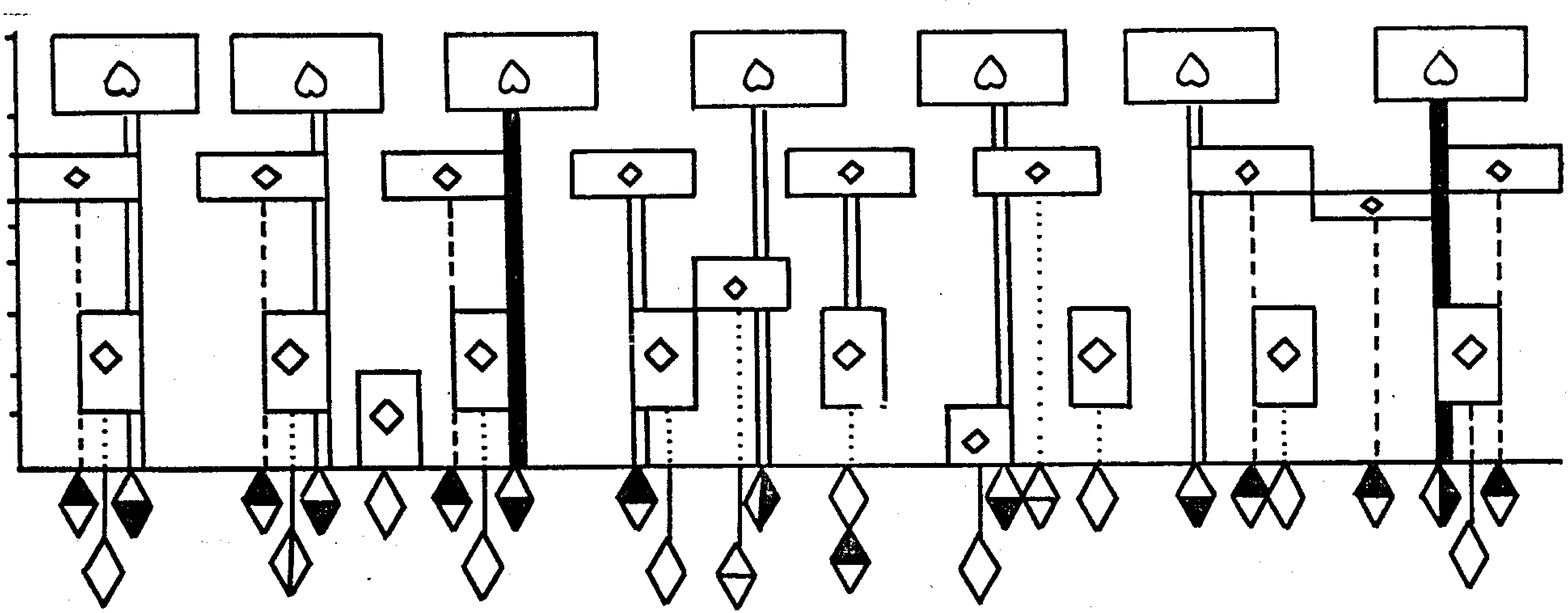


FIGURE 23. A further modified structural diagram of the mature oak stand of Hutcheson Memorial Forest (see Figures 18 and 22) which includes the following information:

1) height of vegetation layers
2) crown depth
3) seasonality
4) height of principal branching
5) stem diameters
6) leaf shape and size
7) leaf texture
8) coverage

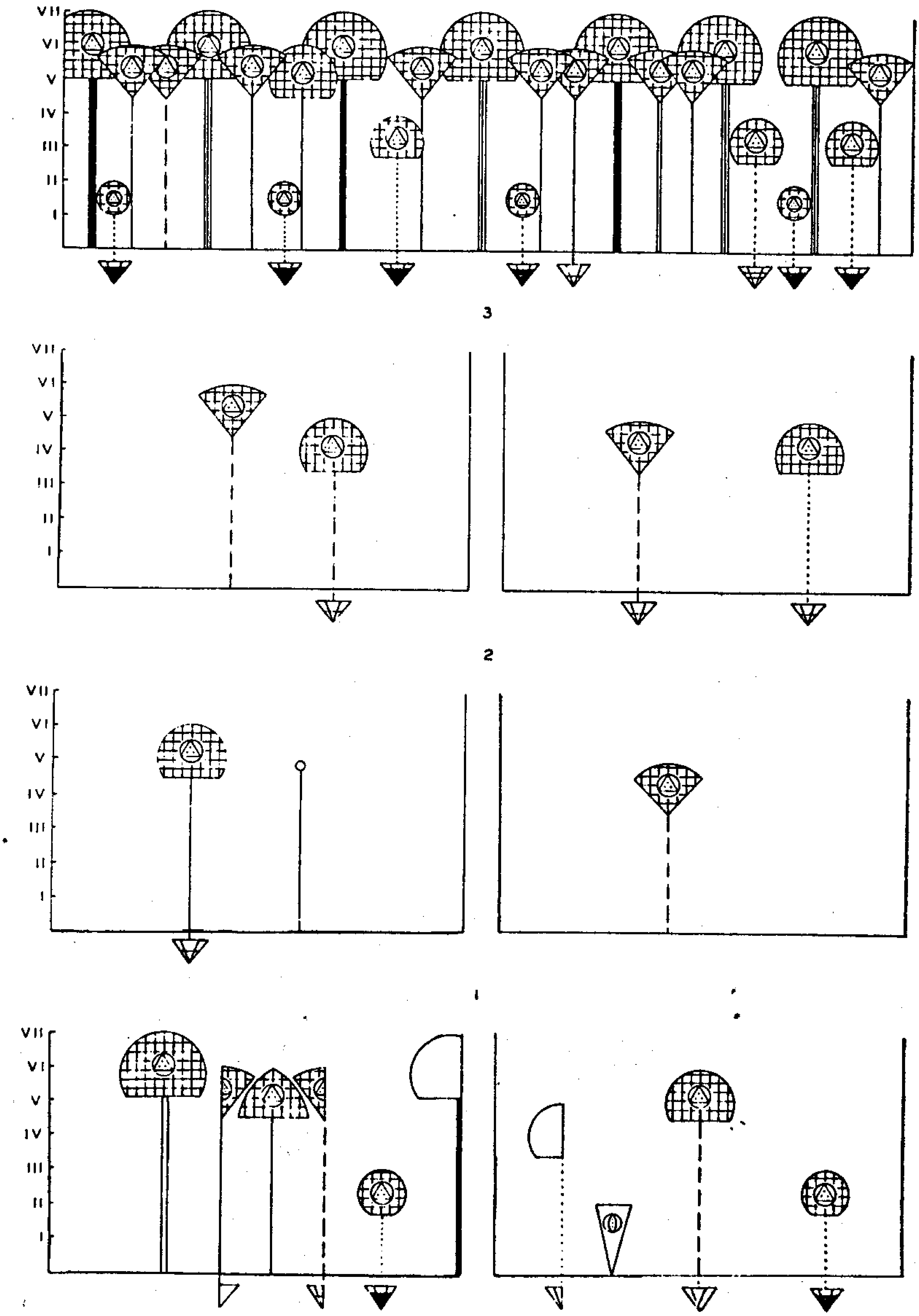


FIGURE 24. An application of the WES method of recording (see Appendix A) to the same mature oak stand of Figure 18.

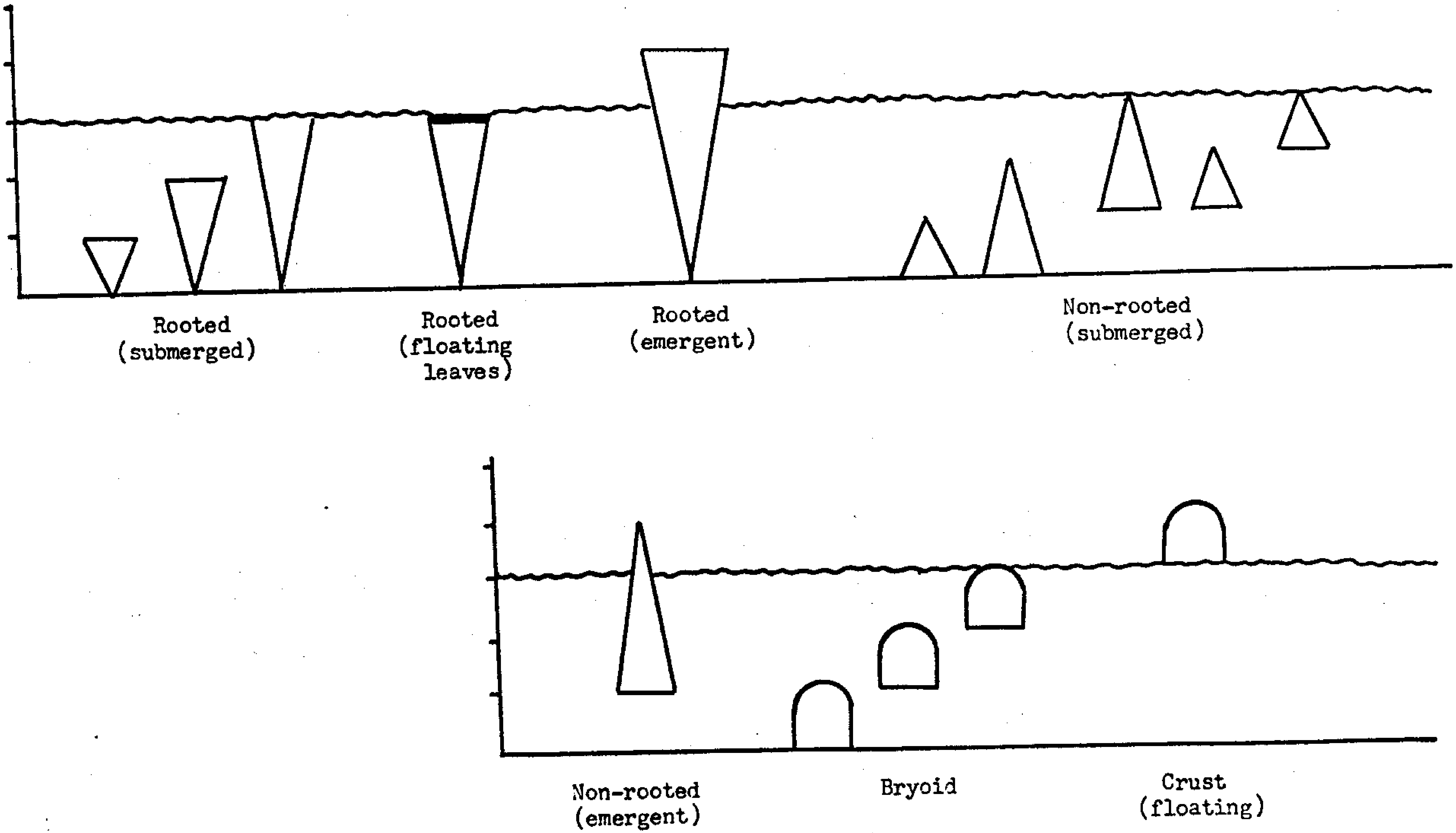


FIGURE 25. Habit-form symbols suggested for use in the structural description of aquatic plant communities.

APPENDIX A

The system used by Mills & Clagg 1964, pp. 59-68.

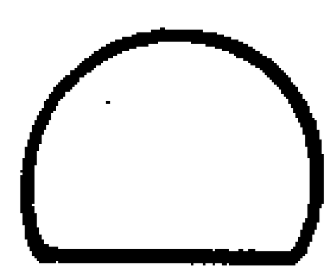
VEGETATION SYMBOLIZATION

SHAPE CHARACTERISTICS

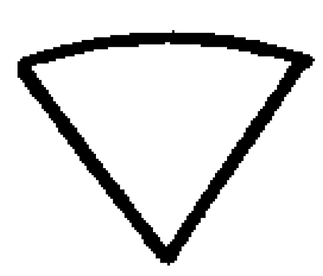
Crown (or plant) shape: leaf and/or branch mass projected upon a vertical plane

Definition

Woody plants:

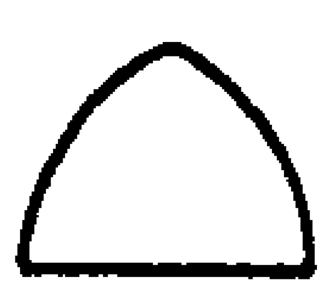


Round: top of crown hemispherical or nearly so, base of crown rounded or broad. Isodiametric.

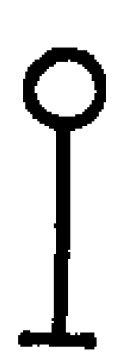


Flat-topped: top of crown flat or nearly so, base of crown rounded or compressed. Horizontal diameter of crown outline is greater near top (broadest above vertical midpoint).

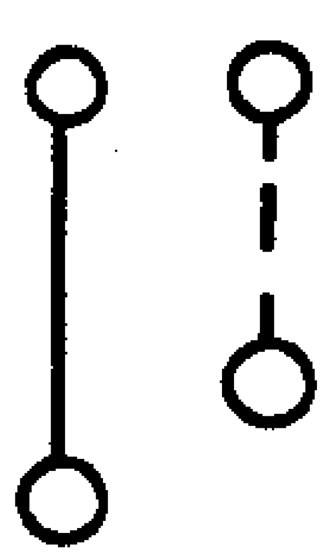
Pointed: top of crown conical or pointed, base of crown rounded or broad. Horizontal diameter of crown outline is greater near bottom (broadest below vertical midpoint).



Spindle: top of crown conical or pointed, base of crown slender or compressed. Crown outline elongated vertically with greatest horizontal diameter occurring near vertical midpoint (broadest at vertical midpoint).



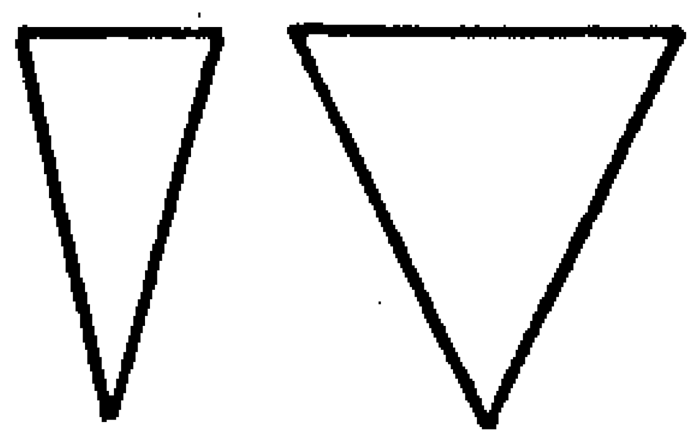
Crownless: branch and leaf mass absent.



Log: detached horizontal and crownless woody vegetation; length of log depicted by height class; "log" symbol that does not come to base line indicates that one end of log is off ground to height class of symbol base; this assumes that one end of log is always in contact with ground.

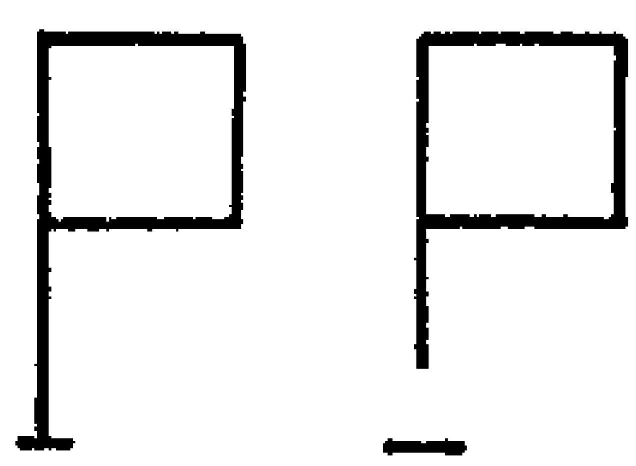
Class I & II: all class I & II woody symbolized with full round crown symbol.

Non-woody plants:



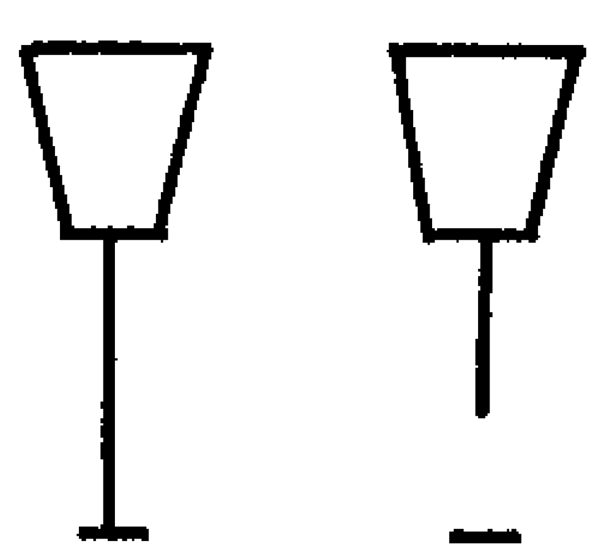
Non-woody: not classified as to shape (symbolized as an inverted isosceles triangle, one or two grids wide with vertical dimensions corresponding to height classifications).

Special plants: Lianas, Vines, Air plants, Decumbent Plants (Lianas, Vines, and Air plants symbolized at height at which most of the leaf mass occurs).



Woody Lianas and Vines: A - stems not twined around, or attached to, other plants

B - stems twined around, or attached to, other plants



Non-woody Lianas and Vines: C - stems not twined around, or attached to, other plants

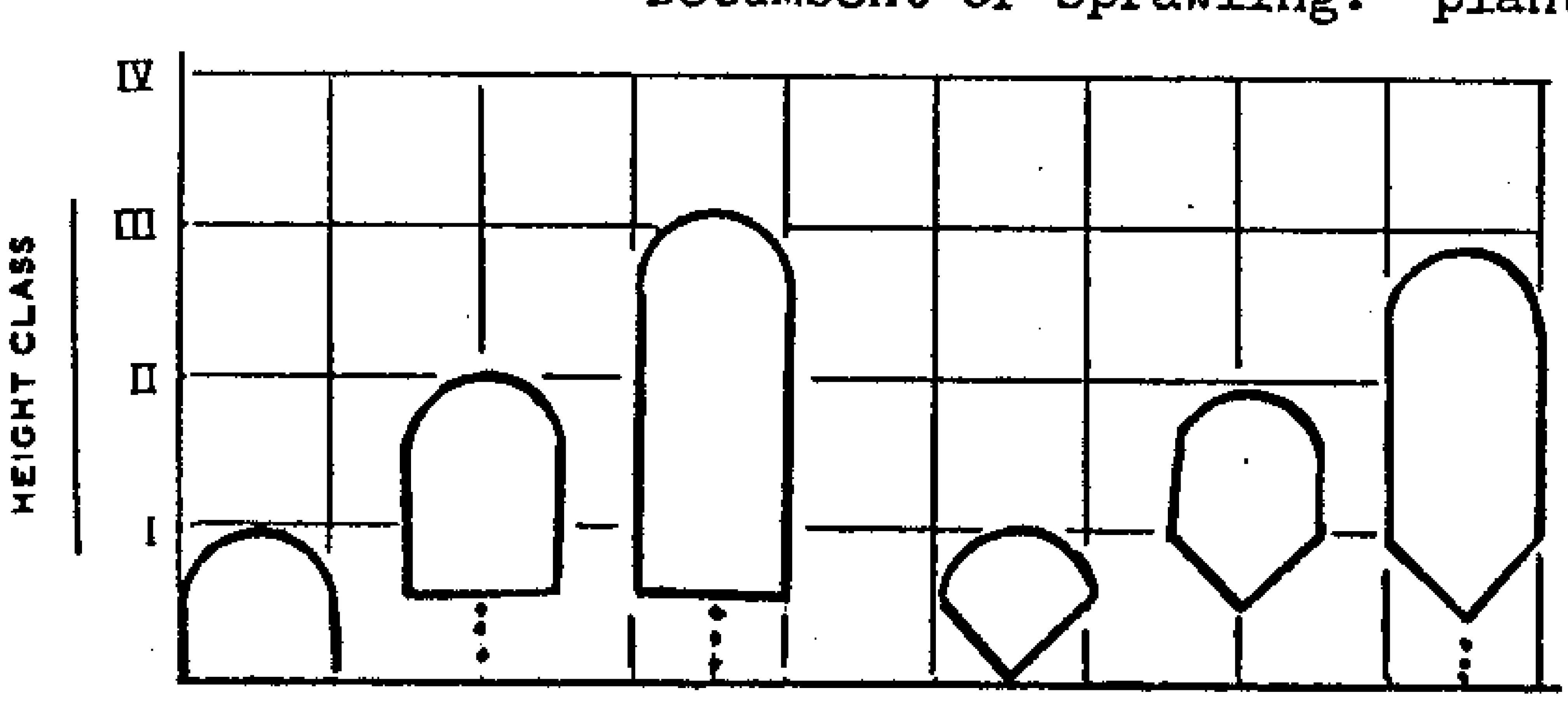
D - stems twined around, or attached to, other plants

Air Plants: touches the symbol of the plant on, or in which it is growing.

E - Woody

F - Non-woody

Decumbent or Sprawling: plants that creep along the ground but do not climb on other plants; symbolized at height to which plant is growing.



G - Woody

H - Non-woody

PLACEMENT AND VALUE OF WOODY CROWN SYMBOLS

Height of plants: all plant crown shape symbols are drawn to touch the line representing their height class.

Size of crown shape symbols: as the height of the erect woody plant being represented decreases, the round, flat-top, pointed, and spindle symbols become smaller, vertically and horizontally, as indicated in the Crown Shape and % Value Table below.

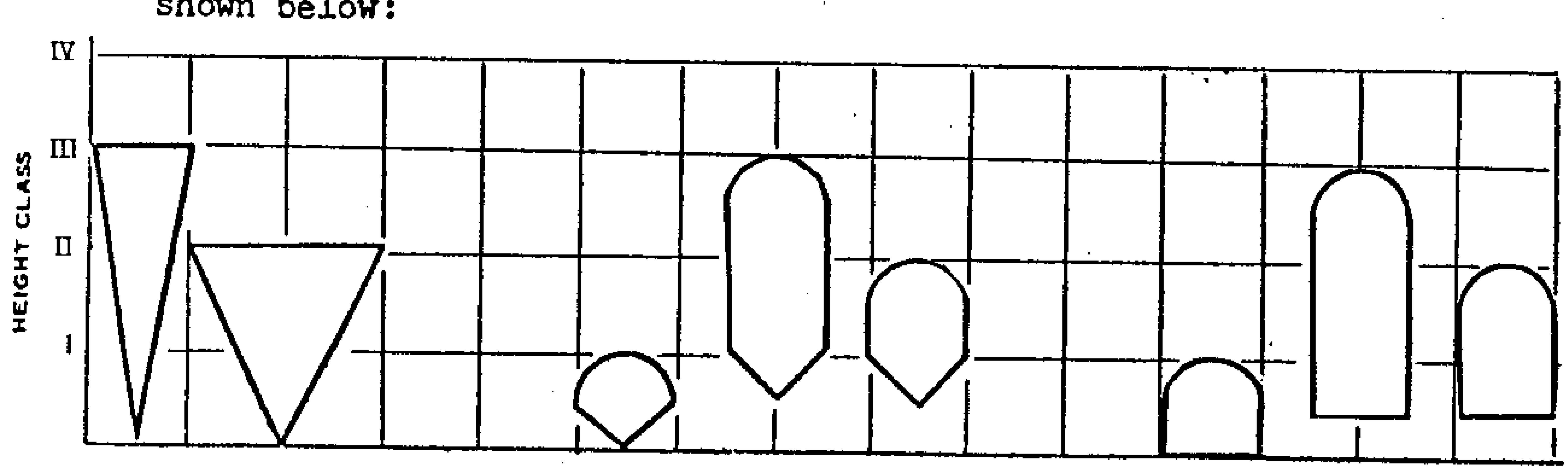
Crown Shape and Per Cent Value (at 4, 3, 2, 1% per grid)

Round
Flat-top
Pointed
Spindle

Height class	Width	Height*	4% grid value	3% grid value	2% grid value	1% grid value
8	3	2	12	9	6	3
7	2.5	1.75	10	7.5	5	2.5
5 & 6	2	1.5	8	6	4	2
3 & 4	1.5	1.25	6	4.5	3	1.5
1 & 2**	1	1	4	3	2	1

* Height and width stated in units of the basic grid
** Always drawn with full round crown symbol

All other crown symbols, woody and non-woody plants, cover one grid square in width, with the exception of the non-woody plant symbol which may be two grids wide if the draftsman so elects, and crownless and logs which have no cover connotations. The height of the Liana, Vine, and Air Plant symbols are one grid, with the exception of the non-woody plant symbol and decumbent symbol: these are drawn to the height of the plant. The possible exceptions are shown below:



Height

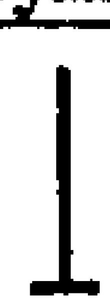
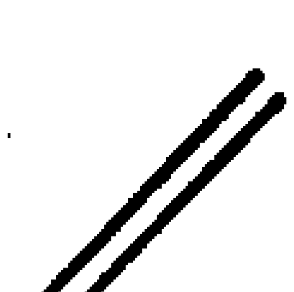
Class	Range of Values	*Measure Stem Diameter at:
VIII	More than 35 m.	1.5 m.
VII	13 - 35 m.	1.5 m.
VI	5 - 13 m.	1.5 m.
V	1.5 - 5 m.	1.0 m.
IV	0.7 - 1.5 m.	0.3 m.
III	0.3 - 0.7 m.	0.1 m.
II	0.1 - 0.3 m.	Ground level
I	Less than 0.1 m.	No stem symbol used

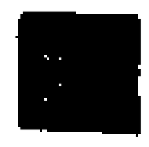
*NOTE: if stem branches or divides below the point specified, measure the diameter just below the point of division

Stem Diameter: see "height class" table for point at which stem diameter is measured

Symbol	Range of Values
	Less than 2.5 cm.
	2.5 - 7.5 cm.
	7.5 - 15 cm.
	15 - 30 cm.
	30 - 60 cm.
	More than 60 cm.

Stem Habit: omit on height class I plants

Symbol	Definition
	Erect: stem supports crown by its own strength
	Slash: detached woody vegetation possessing crown, with or without leaves, which are not vertical (erect) or horizontal (log); used with all woody plant crown shape symbols (except crownless); (place symbol in "crown shape"); depict at height class the slash occurs, but use "crown shape" symbol of size denoting height class into which total length of slash would fit

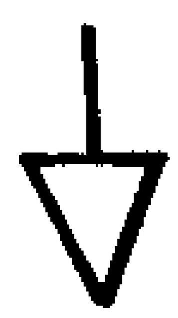
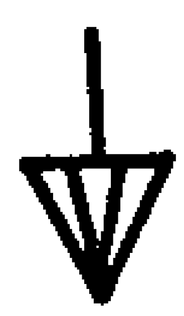


Decayed: placed on woody plant symbol where decay occurs (to be used only where hardness does not exceed non-woody characteristics

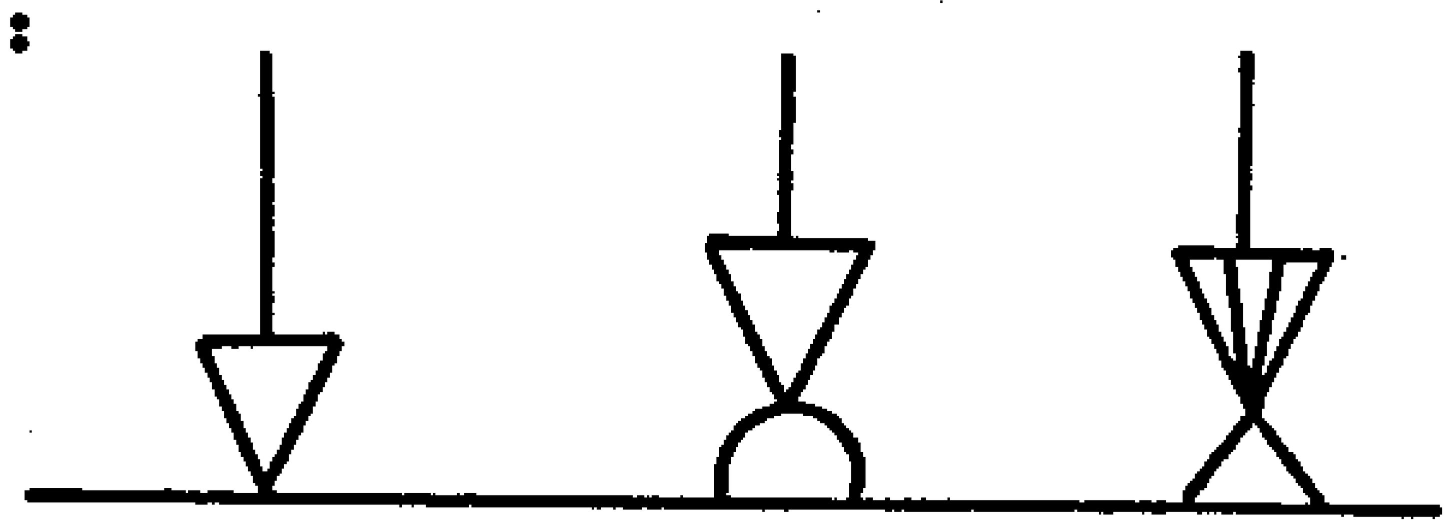
NOTE: see shape characteristics of crowns for stem information on Lianas, Vines, and Decumbent plants

Branching Habit: omit on height class I plants and on plants that branch at heights greater than 3.0 m., but use on all other woody plants except woody decumbents

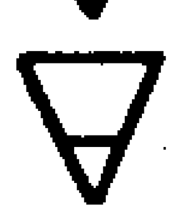
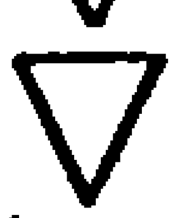
Type of branching: place symbol at base of stem symbol or on top of "root habit" symbol

Symbol	Definition
	Horizontal: branches diverge from main stem at approximately right angles
	Divergent: branches diverge upward from main stem

Examples:

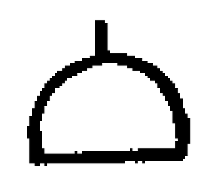
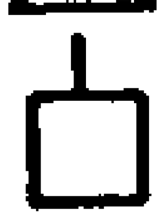


Height of first branching: place symbol inside "type of branching" symbol

Symbol	Definition
	Less than 0.5 m. above ground
	0.5 - 1.0 m.
	1.0 - 2.0 m.
	2.0 - 3.0 m. ("type of branching" symbol blank)
(none)	More than 3.0 m. (no modification of basic stem symbol)

<u>Root Habit:</u> above ground structures only; omit on height class I, II, and III: i.e., less than 0.7 m. tall

<u>Type of structure:</u> place symbol at base of stem symbol

Symbol	Definition
	Stilt or prop roots (e.g., mangrove)
	Enlarged base (e.g., cypress)
	Plank buttresses

<u>Height of emergence:</u> point at which root modification diverges from stem; place symbol inside "type of structure" symbol

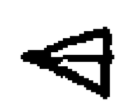
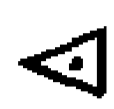
Symbol	Definition
⊥	Less than 0.3 m. (no modification of basic "stem" symbol as "type of structure" not used at this height)
(none)	0.3 - 0.6 m. ("type of structure" symbol left blank)
—	0.6 - 2.0 m.
=	More than 2.0 m.

<u>Spread:</u> diameter of root modification at ground level; place symbol inside "type of structure" symbol

Symbol	Definition
	Less than 2 x stem diameter (no modification of basic "stem" symbol; not recorded)
(none)	2-5 x stem diameter ("type of structure" symbol left blank)
/	5 - 15 x stem diameter
Λ	15 - 45 x stem diameter
▲	More than 45 x stem diameter

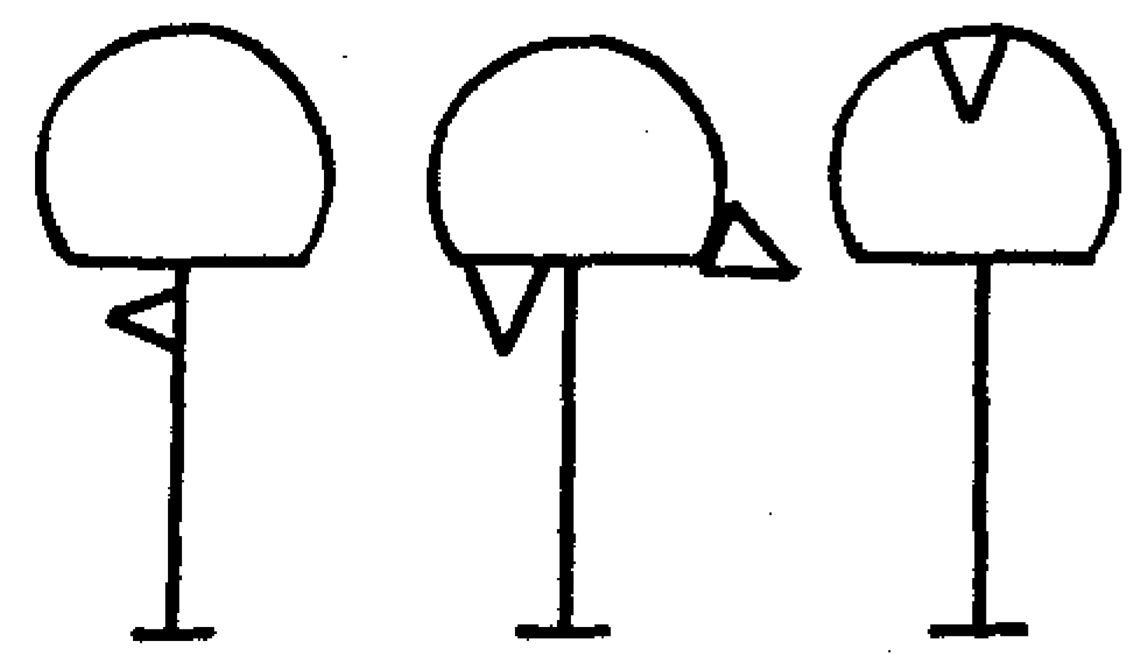
SPECIAL PROPERTIES

Armature:

Symbol	Definition
	Spines less than 5 mm. long
◀	Spines more than 5 mm. long
◁	Cutting edges
	Stinging organs (nettles)
□	Poisons

Position

Stem Leaf Fruit

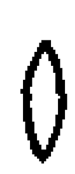


FOLIAGE CHARACTERISTICS

Leaf size: area of leaf; place symbol in the approximate center of the "crown shape" or plant symbol

Symbol	Definition
(none)	Less than 1 sq. cm. in area
○	1 - 150 sq. cm.
□	More than 150 sq. cm.

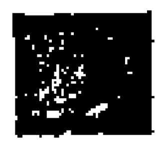
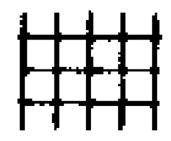
Leaf shape: place symbol in the approximate center of the "crown shape" or plant symbol, or in center of "leaf size"

Symbol	Definition
△	Broad and flat (length/width less than or equal 5)
	Long and flat (length/width more than 5)
	Needle or awl (shaped like needle or awl)

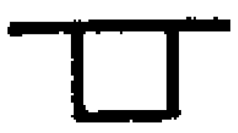
Leaf texture: place symbol inside "leaf shape" symbol

Symbol	Definition
(none)	Filmy, translucent
	Membranous (does not permanently deform when wrapped around a pencil; place ventral, i.e., "upper," surface next to pencil)
	Hard (permanently deforms when wrapped around a pencil; place ventral, i.e., "upper," surface next to pencil)
	Succulent (more than 2 mm. thick)

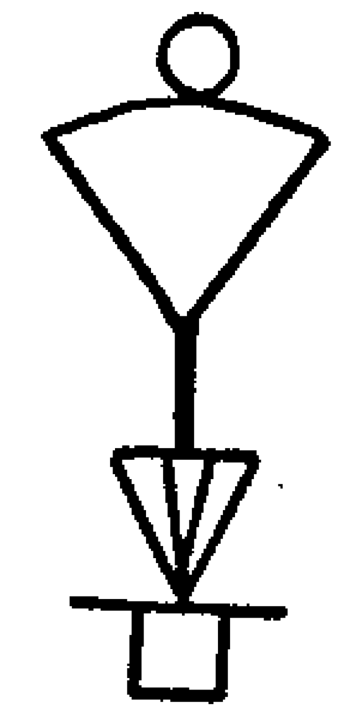
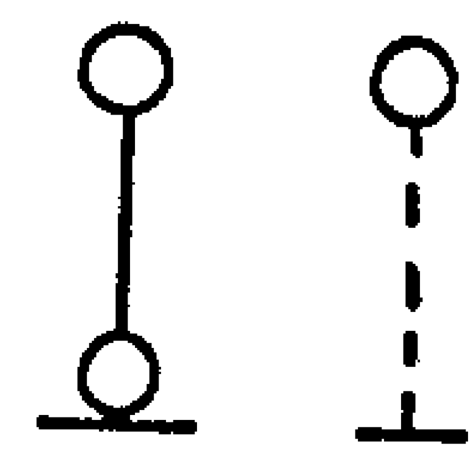
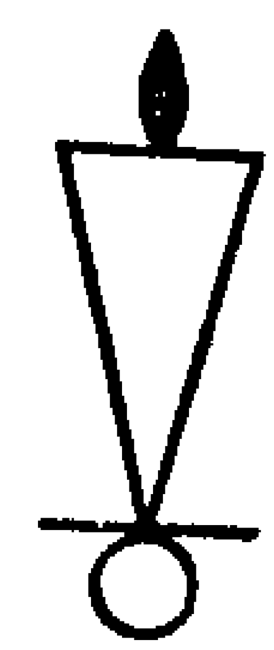
<u>Leaf presence</u>: place symbol between "leaf size" symbols and outline of "crown shape" or plant symbol

Symbol	Definition
(none)	Leaves absent
	Leaves absent, but twigs and/or branches green
	Leaves absent, use for fungi (plants which are never green) and for decayed stem system (slash and crownless)
	Leaves dead, but clinging
	Leaves present and green

<u>DISTRIBUTION CHARACTERISTICS</u> (spatial arrangement of plants)

Symbol	Definition
(none)	Random: symbols arranged in non-regular pattern (if coverage is 100% all symbols touch)
	Clusters: plants in groups, but mechanically independent; plant shape not obviously affected by associates. Individuals are considered to be in clusters if each has nearest neighbor distance less than .565 A/p and greater than .2825 A/p.
	Clumps: plants in close association; stems independent but plant shapes obviously affected by associates. Individuals are considered to be in clumps if each has a nearest neighbor distance less than .2825 A/p.
	Grid: all plants having approximately uniform distances to four, five, or six neighbors
	Row: plants closely spaced in one direction, much more widely spaced in another
	Strip: elongate patches

QUANTITATIVE CHARACTERISTICS - DENSITY DISTRIBUTION

Symbol	Definition	Position
	Yp (plateau diameter): symbol, with diameter figure, is positioned over, under, in, or otherwise associated with the first full crown symbol for the type to which it applies. On other plant symbols within a particular height class with which this Yp is associated, only the identical Yp symbol is shown, but without the Yp value. In instances where only one-half a symbol is all that is necessary to indicate the per cent of cover, the Yp symbol and value are associated with the one-half symbol.	 
	The Yp figure represents the diameter of a circle in the area of which would be found 20 individuals of the plant type symbolized.	
	Distribution characteristics as to clumps and clusters are accompanied with the Ypc value under the appropriate symbol thé first time it appears on the left of the diagram. The Ypc has the same application as the Yp, except that it applies to clumps or clusters rather than individual plants	

APPENDIX B

Drafting Instructions

The system proposed in the present memoir is universal to the extent that it can be applied to data collected by various investigators using different field methods. The system itself is somewhat rigid and the fitting of actual field data into the stratification and coverage categories presents difficulties and demands that consistent decisions be made unless the system itself has been applied directly in the field. Such has not been the custom of the senior author (Dansereau 1957a, especially its Appendix A), who has made it a practice to record the field situation as it was and without reference to pre-established categories of stratification or coverage.

To aid the uninitiated in constructing the diagrams used in the "universal" system, therefore, we will attempt to set down a few suggestions. The following steps will be in order.

1. Determine into which of the 7 height classes the layers recorded in the field fit the best. Use the top of the layer as the criterion. Two or more layers may be combined into one height class. Arbitrary decisions must occasionally be made, sometimes even based on one's recollection of the stand.
2. Indicate the four essential structural characteristics for each species: habit-form, seasonality, leaf shape and size, and leaf texture (Figure 1).
3. Using the standard grid provided (see Fig. 2), draw a "range diagram" showing every structural type present, grouped by height class, with symbol sizes based on the outline in Table I. Under each symbol list the coverage and local coverage values for all species that are depicted by it at that height. A symbol is repeated in each height class, with respective coverage values. (Please refer to Figures 7 and 8.)
4. Calculate the coverage values represented by each structural type within each height class so as to obtain a total cover value approximating the percentage cover already indicated (from field data) for that height class. (The range of percentages used for the cover scale is as follows: 5 = 81-100%; 4 = 61-80%; 3 = 41-60%; 2 = 21-40%; 1 = 5-20%; + = 1-4%; • = 0.5% (rarely considered). Refer to Dansereau 1957a, Table 3-13, Fig. 3-39.) The total is arrived at by adding the minimum percentage cover allowable for each of the cover-scale values which have been recorded for the layer in question and then by further adjusting these values within the limits of the maximum percentage cover that is obtained by totaling the highest percentages for each recorded value. Most commonly the values between the minimum and median prove most usable. (A mental picture of the relevé is of obvious advantage here.) Please refer to example following Item #5.
5. Determine the number of symbols needed to express the coverage of each structural type. This is based on the grid-unit value of 4% and on the size of each symbol (Table I), some of which may have a value up to 12%. There frequently is overlap of epiphytes and lianas in the same layer so that percentages in that layer can be adjusted somewhat.

TABLE I

Diameters in grid units corresponding to habit-form and stratification formulae (see also Figure 2).

Formula			Symbology	
Habit-form	Stratification	meters	Height of top of symbol (on vertical grid)	Diameter of crown symbol in grid units (horizontal)
W	7	> 25	8	3
W	6	25-10	6	2.5
W	5	10- 8	5	2
W	4	8- 2	4	2
W	3	2- 0.5	3	1.5
W	2	0.5-0.1	2	1
W	1	0.1-0.0	1	1
L	7		8	2
L	6		6	1.5
L	5		5	1.5
L	4		4	1
L	3		3	1
L	2		2	1
L	1		1	1
E	7		8	1
E	6		6	1
E	5		5	1
E	4		4	1
E	3		3	1
E	2		2	1
E	1		1	1
H	4		4	1.5
H	3		3	1
H	2		2	1
H	1		1	1
M	3		3	1.5
M	2		2	1
M	1		1	1

Example. In Figure 7, W4eax has cover values of 2.2 and + + which are equivalent to a minimum cover value of 22%. W4daz and W4enx both have minimum cover values of 1%. Maximum cover values for these structural types are 44, 4, and 4%, respectively. Total cover for layer was recorded in the field as 35%. Since the standard woody symbol in this layer occupies 2 grid units (8% cover) it was decided to include 4 W4eax symbols (32%). Since 1 W4daz symbol would have represented twice the maximum allowable cover for this type, 1 W4enx symbol (4%) was included to bring total represented cover to 36%.

6. If local coverage indicates clumping (Fig. 1, symbol p), symbols should be grouped, depending on the number available in that layer. Table II illustrates a possible guide for clumping.

TABLE II

Cover values refer to combinations of phytosociological coefficients, as described in Dansereau 1957a: Table 3-13 and Fig. 3-39 for the first digit (coverage), Table 3-14 and Fig. 3-40 for the second digit (local coverage). The vertical scale on the left lists the number of symbols (see Item #5 herewith) to be represented in a standard structural diagram. This applies to structural types (sometimes including several species) that bear the symbol p of Figure 1. Thus, 4-4-1 means 4 contiguous symbols in one part of the diagram, 4 more farther on, and 1 isolated symbol.

Number of symbols used for a structural type	Cover values				
	• +, + 1, 1.2, 2.3, 3.4, 4.5	+ 2, 1.3, 2.4, 3.5	+ 3, 1.4, 2.5	+ 4, 1.5	+ 5
3	2-1	3	3	3	3
4	2-2	3-1, 2-2	4	4	4
5	2-2-1	3-2	4-1, 3-2	5	5
6	2-2-2	3-3	4-2	5-1	6
7	2-2-2-1, 2-2-3	3-3-1	4-3	5-2	6-1
8	2-2-2-2	3-3-2	4-4	5-3	6-2
9	2-2-2-2-1, 2-2-2-3	3-3-3	4-4-1	5-4	6-3
10	2-2-2-2-2	3-3-3-1	4-4-2	5-5	6-4

7. Make a trial diagram for spacing. In setting up this drawing, remember that W and H symbols in the same layer may not overlap. Lower-layer symbols, however, may overlap those of upper layers. L and E symbols may overlap W and H in the same layers.

8. Figure 2 illustrates the total range of outline symbols used in the universal system, whereas Table III herewith suggests template sizes that fit best, allowing for variation in size of pen point used. These symbols can be drawn

with a compass and straight-edge, but a better consistency of shape and size (as well as ease of drafting) results from using templates with various sizes of circles, triangles, diamonds, squares.

9. For the leaf shape and size symbols, arcs of certain circles are suggested. It is best to mark the ends of the arc used so as to always have the same size. Dimensions must be adjusted, however, depending on the size of the habit-form symbols into which they must fit. A bit of juggling of arcs must be done to obtain the proper shape for the h and v characteristics. It is a help, also, to place a grid sheet (8 or 10 squares to the inch) under the drawing.

10. To indicate the evergreen, semideciduous, and succulent alternatives, we suggest a grid of 8 squares to the inch for symbols in height classes 7 down to 4 (or 3). For lower height classes, and for epiphytes and lianas in all layers, use a grid of 10 squares to the inch (or smaller).

TABLE III

Suggested template sizes (in inches) for representing structural-forms (see Figs. 1 and 2, Table II). Circle arcs for leaf shape and size alternatives are those for use within large symbols; these must be graded down to fit within the symbols for L, E, and M, and for W and H in height classes 1 and 2.