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# Aims and Methods of Vegetation Ecology

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## The Count-Plot Method and Plotless Sampling Techniques

#### 7.1 DIFFERENCE BETWEEN COUNT-PLOT AND RELEVÉ METHODS

We describe a plot as any two-dimensional sample area of any size. This includes quadrats, rectangular plots, circular plots and belt-transects (which are merely very long rectangular plots). Belt-transects are often simply called strips or transects.

The count-plot method consists in its simplest form of outlining a sample area in a tree stand and then counting all trees by species in size classes. Thus, a plot is essentially a density-quadrat. Among North American ecologists the count-plot method is well known as the "quadrat method." To the continental European ecologist, however, the term

quadrat method would rather imply the releve method, which is based on a minimal area quadrat as described before. The two concepts are very different, although both can be combined in the analysis of forest communities. Their difference is related to a basic difference in the major vegetation analysis problems that evolved on the two continents.

In continental Europe, the number of indigenous tree species is relatively small and in most European forests the few tree species present are planted. In such plantation stands, the attention was channelled to the undergrowth vegetation, and the undergrowth vegetation was intensively studied as to its response to spatial environmental variations. Therefore, in continental Europe, the undergrowth vegetation in forests presented the greater analytical challenge, and analysis problems of

the tree layer were left primarily to the forester.

In contrast, in North America, particularly in Eastern North America, where several of the ecological tree analysis techniques arose, the number of tree species is much greater than in Europe. Here, the quantitative tree analysis techniques were developed from standard timber survey methods, because the natural distribution and diversity challenge. We use "stand structure" here to mean the numerical distrigiven stand. Since size in woody plants is related to age, it is possible in many cases to make predictions of stand development from such structural analyses. This form of analysis has always been a preoccupation of North American vegetation ecologists, because of their greater interest in the time changes or dynamics of vegetation over large areas. In contrast, the continental European vegetation ecologist's main interest was always in the small area spatial environmental variations as indicated primarily by herbaceous plants.

#### TIMBER SURVEY METHODS

In forest inventory work, systematic sampling is often done by strips or transects which permit continuous sampling within a specified stripwidth. The strip-width depends on the size of the trees and their spacing. It must be possible to count the trees conveniently. Therefore, the strip-width will usually vary within limits of 1-5 m to either side of the center line.

The standard records taken are an enumeration by species within diameter classes above a predetermined minimum diameter, starting usually at 1 or 4 inches (2.5 or 10 cm) at breast height (i.e., 1.5 m above the ground). The minimum diameter is arbitrarily determined Trees

diameter diameter

with diameters less than the arbitrary lower limit (saplings and seed-lings) are usually enumerated in 1 ft (30 cm) height classes. Where these smaller trees are densely stocked, they are counted in smaller subplots. The enumeration by species in relation to strip-width and strip-length allows calculation of the density (number) of each species per unit area. The diameter class record provides for subdividing the density estimate per species by size classes. This information can be utilized for a structural analysis, which may indicate the trend of development of the tree populations in the community. At the same time the diameter record permits the conversion to another important measure, basal area (ba), which is the actual space covered by the tree stem. This is obtained through the well-known formula,  $ba = (\frac{1}{2}a)^2 \times \pi$ , where d stands for diameter.

In North American ecological studies it has become customary to use tree basal area (stem cover) as an estimate of dominance (CURTIS, 1959). In forestry, however, height is used as an estimate of dominance and basal area as the basic value for timber volume calculations.

A modification of the strip-width method is the circular plot method, in which small sample plots are placed at predetermined intervals along the transect. The intention is to spread the sampling grid across the segment, wherever the segment is too large for sampling in continuous strips. The sampling intensity will thus be reduced, but the distribution across the entire stratum is maintained. The size of the circular plots should be a function of the size and spacing of the trees to permit accurate enumeration. But the diameter of the circular plot can be roughly twice the strip-width in the same vegetation, because the circular plot is usually quartered for easier counting. Such subdividing facilitates keeping track of the tree tally.

In sloping terrain, plot sizes are usually slightly enlarged to allow for relating the quantitative information to areas on maps, which are horizontal projections. Slope corrections are applied by obtaining the slope in degrees with an Abney level or other suitable instrument and then by multiplying the downslope distance of the plot with the secant of the slope. For example, on a 15° slope, a 10 m long plot length would be enlarged to  $10 \times 1.035 = 10.35$  m. However, where mapping of quantitative data is not the objective, slope corrections should also not be applied, because such corrections result in an overestimate of the quantitative parameters on slopes as compared to those on level ground.

The plot boundaries must be accurately located wherever counting is involved. In contrast, where species quantities are estimated as in the releve method, boundary accuracy is not so critical. To obtain an accurate right angle in quadratic or rectangular plots, it is useful to use the Pythagorean principle. For example, from the plot corner, a 4 m

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long line may be established in the first direction. Then a 3 m long line is established perpendicular to the first line. The right angle formed by these two lines is then checked by measuring a distance of 5 m between the 4 m and 3 m points of the two plot sides.

Transects or strips, circular plots, rectangular or quadratic plots, all have one important criterion in common. They are two-dimensional area sampling units with specified boundaries that must be laid out in the stand.

#### 7.3 EXAMPLE OF A COUNT-PLOT ANALYSIS

The following example of a tree density, structural and basal area analysis illustrates records typical of the plot or quadrat method.

The quantitative plot analysis relates to a small-area-sample (120 m²)

in a tropical rain forest on the Hawaiian Islands.

TABLE 7.1 shows the raw field data, which was recorded by three students in about one hour. All individual trees were measured at their base with a caliper and called out by species in 5 cm diameter classes, using the class-limits or ranges as shown. Basal diameter rather than diameter at breast height was used because many trees were multistemmed, branching near the base below breast height. Moreover, basal diameter is the best measure of the true basal area. The problem of where to measure the diameter is, of course, different if one wants to establish the volume of the trees. This was not the objective in this analysis. The record was made in a 6 m wide belt-transect of 20 m length. The requirement for counting individual trees was arbitrarily determined to be a minimum of between 45 to 50 individuals in two general size classes, trees under 2 m tall and trees over 2 m tall. The enumeration was done in 3×5 m=15 m² subplots, one subplot at a time. When the eighth subplot was done, the total enumeration resulted in 48 trees under 2 m tall and 45 over 2 m in stem-height. With this the current sampling objective was accomplished.

The small trees up to 2 m tall, which all had basal diameters of less than 3 cm, were additionally enumerated in five height classes (TABLE 7.2) to analyze the tree-reproduction in more detail.

7.31 Interpretation of Stand Structure. One objective of the quantitative plot method is to analyze and interpret the trend of numbers of individuals in size classes of the tree species in the stand. However, a trend can only be established when a sufficiently large number of individuals has been recorded; arbitrarily we may say a minimum of 30

TABLE 7.1. Example of a Stand-Structure Analysis by the Plot Method. Tropical Rain Forest on Tantalus Mt., Honolulu, Hawaii, at 420 m Elevation. Enumeration in  $6\times20$  m Belt-Transect (120 m<sup>2</sup>). Raw Data.

			NUMBEI	R OF TREE	S IN SPECIES	
DIAMETE AT BASE CLASS (CM)	R RANGE (CM)	ACACIA KOA	METROSI- DEROS COLLINA	PSIDIUM	CITHAR- EXYLUM CAUDATUM	APPROX- IMATE HEIGHTS
1	( 0- 2)	0	0	25	23	< 2 m
5	(3-7)	0	0	19	3)	
10	(8-12)	0	1	10	0}	2-5 m
15	(13–17)	1	0	4	0)	
20	(18-22)	0	0	0	0\	
25	(23-27)	1	2	0	0	
30	(28-32)	0	0	1	0 (	
35	(33-37)	0	0	0	0	5–10 m
40	(38-42)	1	1	0	0	
75	(73-77)	1	0	0	0/	
Total		4	4	59	26	93
Totala	>3 cm	4	4	34	3	45

<sup>&</sup>lt;sup>a</sup> Number of trees with over 3 cm basal diameter on  $100 \text{ m}^2 = 45/1.2 = 37.5$ . (To obtain an estimate of number of trees per acre, multiply by 40; to obtain an estimate of number of trees per hectare, multiply by 100.)

TABLE 7.2. Tree Reproduction <2 m Stem Height in 50 cm Height Classes on Same Area (120 m<sup>2</sup>) as Stand on TABLE 7.1.

		NUMBER OF STEMS IN SPECIES			
HEIGHT CLASS	RANGE (CM)	PSIDIUM GUAJAVA <sup>a</sup>	CITHAREXYLUM CAUDATUM		
1	< 10	0	0		
2	11- 50	7	11		
3	51-100	6	4		
4	101–150	9	5		
5	151-200	3	3		
Total		25	23		

a Psidium guajava here had only vegetative reproduction; all from root sprouts.

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individuals per species (using FIG. 6.2 as a guide). Therefore, only the numerical distribution among the size classes of *Psidium guajava* can be considered as giving a reliable trend for this example (TABLE 7.1). For an adequate numerical trend in *Acacia koa* and *Metrosideros collina*, the sample area would need to be about 8 to 10 times as large. Or, 8 to 10 such plots would need to be established and analyzed from this stand to present a reasonably reliable developmental trend for these two species.

A brief interpretation of TABLE 7.1 is as follows.

The native Acacia koa (Leguminosae) occurs with only four individuals on the 120 m² plot. These four show a wide range of diameters (from 15 to 75 cm) and therefore can be assumed to be of different ages. (The tropical rain forest trees do not show annual rings, thus there is no easy way to determine their ages.) The size-distribution of Acacia koa indicates that the species has maintained itself over a period of time. Its occurrence is not related merely to one event in time, when conditions were favorable for reproduction. If that were so, one would expect the four individuals to be concentrated in one or two size classes. However, the continued maintenance of Acacia koa is questionable from this analysis, because there was no reproduction in the stand (trees under 2 m).

The same interpretation can be made for the second native tree

species, Metrosideros collina (Myrtaceae).

The exotic *Psidium guajava* (Myrtaceae) is present with one tall, mature individual (in the 5 to 10 m layer), 14 subcanopy trees (up to 5 m tall), 19 saplings (just over 2 m tall) and 25 suckers (here defined as reproduction, under 2 m tall, TABLE 7.2). The number-trend indicates that this exotic tree species is well established in this rain forest, and that it is maintaining its position by abundant reproduction. It is possible that the quantitative importance of *Psidium guajava* may even increase in the future and that its vigorous reproduction may be a factor that contributes to the absence of reproduction among the two native tree species. However, this is merely an indication obtained from this analysis. Several more plot analyses and, perhaps, experimental research is needed to verify this indication of competitive replacement.

Citharexylum caudatum (Verbenaceae) is represented only by small trees. Most are under 2 m tall. This species is a recent invader as shown by its concentration of numbers in the reproduction class, the largest number of individuals are from 11 to 50 cm tall (TABLE 7.2). Currently, there were no recently germinated seedlings under 10 cm size. Nevertheless the species seems to establish itself as the second quantitatively important exotic tree component in this stand.

7.32 Density and Dominance Relations. A second objective of the plot method is to establish quantitatively the density and dominance

relations among the tree species of the stand.

The density relations were already shown on TABLE 7.1. From this it is clear that the two exotic tree species (Psidium guajava and Citharexylum caudatum) are far more abundant than the two native tree species (Acacia koa and Metrosideros collina). In TABLE 7.1 it is easy to determine the number of trees by species for any convenient unit of reference area. However, when converting a tree count of a sample area to an acre or hectare, one should be aware that this is merely an estimate. The estimate can be strengthened by increasing the sample size, i.e., the number of plots. How many plots one should use to obtain a reliable estimate per acre or hectare can be determined through the "running mean" (see SECTION 6.42).

According to convention among North American vegetation ecologists, dominance for trees is usually defined as stem cover, and stem cover is the same as basal area. TABLE 7.3 shows the basal-area cal-

culation for the plot-example of TABLE 7.1.

TABLE 7.3 shows that Acacia koa is by far the most dominant tree in this rain forest stand. Psidium guajava and Metrosideros collina are of about equal secondary dominance, and Citharexylum caudatum shows only a minor quantitative importance with respect to this parameter. Thus, the density and dominance relations are very different in this stand.

The quantitative plot method can, of course, also include measurements of the undergrowth vegetation. How this is done in standard

quantitative field analyses is discussed in SECTION 7.7.

The same stand served for the example of a releve analysis (TABLE 5.2). A comparison of the two kinds of analyses shows that their information contents are very different.

#### 7.4 PLOTLESS SAMPLING TECHNIQUES

In both the releve and quantitative plot methods, the basic sampling unit is a two-dimensional reference area. Plotless sampling means sampling without such a prescribed area unit. Plotless methods are available for all three commonly used quantitative parameters:

1. Frequency. As we have discussed already, when a frequency frame or sampling quadrat is reduced to a dimensionless point, frequency becomes an absolute measure. The result of such point-sampling is expressed in percent of hits or interceptions. When the number of

TABLE 7.3 Total and Mean Basal Area (cm²) for Each Tree Species on 120 m² (calculated from TABLE 7.1). Reproduction Ignored.

DIAMETER	BASAL		NUMBER OF TRE	ES ^ BASAL	AREA
CLASS	AREA	ACACIA	METROSIDEROS	PSIDIUM	CITHAREXYLUM
(CM)	$(CM^2)$	KOA	COLLINA	GUAJAVA	CAUDATUM
5	19.6	0	0	312.4	58.8
10	78.5	0	78.5	785.0	0
15	176.7	176.7	0	706.8	0
20	314.2	0	0	0	0
25	490.9	490.9	981.8	0	0
30	706.9	0	0	706.9	0
35	962.1	0	0	0	0
40	1256.7	1256.7	1256.7	0	0
75	4417.9	4417.9	0	0	0
Total		6342.2	2317.0	2571.1	58.8
Number o	f trees	4	4	34	3
Mean basa	al	1585.6	579.3	75.6	19.6
area/tre	e	0.53%	0.19%	0.21%	0.005%

Tree basal area in square meters on 100 m<sup>2</sup> = 
$$\frac{\text{overall total}}{1.2}$$
: 10,000 =  $\frac{11,289.1}{12,000}$  = 0.94 m<sup>2</sup> or 0.94 percent total stem cover.

points is high (say at least 100 to 200 points) and the distance between points is closer than the shoot outline of most plants, the point-frequency result becomes a measure of cover. No plot or quadrat is necessary.

A second form of assessing frequency without use of quadrats is to record the presence or absence of plants near points. Frequency near sampling points is often recorded in the distance methods that will be discussed in SECTION 7.6.

- 2. Cover. As mentioned above, one form of assessing cover without quadrats is through a dense network of frequency points. A second plotless method is the line-intercept method, which—as discussed before—is based on the reduction of a belt-transect to a single line of only one dimension, namely length.
- 3. Density. The number of individuals of an area or in a stand can be determined by measuring the distance between individuals or between sampling points and individuals. The sampled distances can be converted to two-dimensional units or areas by squaring.

We already discussed two of the important plotless methods, the point-intercept (SECTION 6.54) and the line-intercept methods (SECTION 6.55). The point-intercept method, in its usual form, is mostly applied to herbaceous vegetation. The line-intercept method is perhaps most generally useful for open-grown woody vegetation. In both cases, the result is, of course, applied to a specified area in terms of either absolute or percent cover. Thus, in a wider sense, a plot or releve is used also in plotless sampling, because the results of the plotless sample must be extrapolated to an area for proper interpretation. This area may also be a map unit.

It remains to discuss two important plotless techniques that evolved from the timber survey methods. One is the determination of stem cover or tree basal area through a modification of the point-sampling technique, the other relates to the determination of stem density through the measurement of distances.

#### 7.5 BITTERLICH'S VARIABLE RADIUS METHOD

BITTERLICH (1948) discovered a remarkably efficient way to measure stem cover in tree stands by applying the point-frequency principle. Since stem cover is the same as tree basal area, and since basal area is one of the basic units for tree volume determination, the method is of great value to forest inventory work (GROSENBAUGH 1952). But also, since stem cover by species is defined as their dominance, and since cover or dominance is one of the most important quantitative parameters in vegetation ecology, the BITTERLICH method has become an important quantitative method, particularly in North American vegetation ecology.

**7.51 The Technique.** Trees are counted in a circle from a central sampling point with an angle-gauge. Only trees that are larger in diameter than a specified angle are included in the count. The others are ignored. Therefore, the circular plot around the central sampling point has no fixed radius; instead, the radius varies with the diameter of each tree counted. This also renders the method plotless, because no fixed area-sample is involved.

When trees are counted in this manner with an angle-gauge, their number is proportional to their stem or basal area per unit ground area.

The standard North American angle-gauge is usually made of a 33-inch long stick. Mounted at one end is a 1-inch wide cardboard, plastic, or metal cross-piece and at the other end a similar piece with a notch or peephole. The angle-gauge is held with the peephole or notch at the

eye like an Abney level and pointed with the 1-inch wide cross-piece horizontally at each tree surrounding the sampling point. The point aimed at on each tree must be at a fixed height, usually breast height. The same ratio or angle of  $1^{\circ}45'$  can be obtained with a 33 cm long gauge and a 1 cm wide cross-piece. When using a round stick, a peephole or notch is not even necessary (FIG. 7.1). Only those trees are counted whose diameter exceeds the cross-piece. Therefore, small diameter trees are included in the count only if they are close to the observer, while large-diameter trees are included at greater distances away from the observer. With the 1:33 gauge, trees counted will not be further away from the sampling point or observer than 33 times their diameter. Thus, a tree with a 4-inch (10 cm) diameter must be within  $4\times33=132$  inches (3.35 m) of the sampling point, while a 20-inch tree will be included if it is within  $20\times33=660$  inches (16.8 m).

The selection of the 1:33 ratio for construction of the gauge, or the equivalent sighting angle of 1°45′, was recommended by GROSEN-BAUGH (1952), because the tree count at this angle permits immediate calculation of the basal area in square feet per acre. This is done by multiplying the count by 10. Thus, if 12 trees are counted, the basal area per acre is 120 ft². If, for example, 10 of these are pines and 2 are spruces, then pine occupies a basal area per acre of 100 square feet and spruce 20. Of course, these should be mean values of a number of sampling points to result in a reliable estimate per acre.

BITTERLICH (1948) recommended a gauge ratio of 1.41 cm to 100 cm giving a much narrower sighting angle (50') and more than twice the tree count per sampling point. At this ratio, the tree count divided by 2 results in the basal area in square meters per hectare. A still simpler ratio for calculation is 2 cm to 100 cm or 1:50, which is equivalent to a sighting angle of 1°10'. The resulting count is directly equal to the basal area in square meters per hectare. The latter angle permits a still

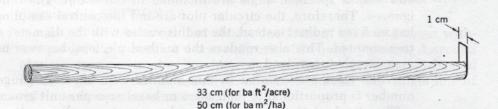


FIGURE 7.1. BITTERLICH angle-gauge for measuring basal area by counting of trees. The gauge is held with the plain end at the eye and pointed horizontally with the cross-piece end to each tree surrounding a sampling point. Any tree that appears larger in diameter than the cross-piece is counted, any tree smaller is excluded.

greater sampling intensity per point than the sighting angle recommended by GROSENBAUGH and used in several North American ecological studies (e.g., SHANKS 1954, RICE and PENFOUND 1955, 1959).

A more sophisticated angle-gauge, developed subsequently by BIT-TERLICH, is the so-called "Spiegelrelascope." This is a small, compact optical instrument that provides for specified angles by a set of bands that serve as comparison bars. The instrument is equipped with an automatic slope correction that can be switched off, if one is not interested in obtaining basal area data for projecting on maps. The Spiegelrelascope is not so useful under low light intensity, because the visibility through the instrument is then much impaired.

Recently foresters and ecologists have adopted clear-glass prisms as the most popular angle-gauge. When viewing through a prism, tree stems appear displaced to one side. Where the displacement is within the trunkline, the tree is counted; where the displacement is outside, the tree is ignored. A borderline tree is counted as half-tree (DIL-WORTH and BELL 1972:32). Prisms with angles ground to specifications can be obtained through engineering supply stores.

7.52 The Principle. To understand how the BITTERLICH method works, we may assume a 10×10 m sample plot stocked with trees. An estimate of stem cover or basal area can be obtained by mapping the stand to scale with the stem areas forming circles. Then, a large number of random points may be superimposed on the map. According to the point-frequency principle, the number of random points that intercept stem areas out of the total number of random points will be proportional to the ratio of stem area to total area.

For example, if 10,000 random points are used and 50 fall into circles, the proportion will be 50 out of 10,000 or 0.005 (0.5 percent). For the 100 m<sup>2</sup> plot this would result in a stem cover or basal area of  $0.005 \times 100 = 0.5$  m<sup>2</sup>. The value of 0.005 also represents the mean number of trees intercepted per sampling point.

Measuring stem cover in this form would be most inefficient, because of the mapping process. For direct field application an impractically large number of sample points would be required to yield an accurate result.

BITTERLICH improved the efficiency of the method by mathematically enlarging the stem area of each tree.

On our map, we may assume a 100 times enlargement of each small circle radius. This would be equivalent to a stem-area or circle-area increase of  $100^{\circ}$ . Note that the ratio of circumference to diameter  $(\tau=3.14)$  is maintained in this proportionate enlargement. Probably, then the total map would be covered with these enlarged circles. More-

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over, many of the enlarged circles would overlap. Almost each of the 10,000 random points would now intercept a circle or enlarged stem area, and many points would intercept several overlapping circles. The result of this geometric exercise would be that the efficiency of each sampling point in terms of interceptions or hits is increased in proportion to the stem-area enlargement factor, namely by 100°. The mean number of trees intercepted per sampling point would now be 0.005 × 10.000=50.

However, the result of interceptions at each point would be fictitious in terms of the real stem area. The overestimate would be the same as the area-enlargement factor, i.e., 10,000 times. Therefore, to reduce the number of interceptions of the sampling points from the fictitious to the real, the number of interceptions needs to be divided by 10,000. This can be expressed as follows:

Applied to our example,

stem area = 
$$\frac{50 \times 10,000}{10,000 \times 10,000} = 0.005$$

This shows that the method has been modified from the standard point-intercept method, but the final answer is the same.

In the field application of BITTERLICH's method, the stem diameters and areas are increased by the angle-gauge. If we put, for example, a 1:50 angle-gauge with its 1 cm wide cross-piece on top of a stick that has a diameter of 1 cm, we have the enlarged radius (R) for that stick. With that radius, formed by the 50 cm piece of the angle-gauge, we can describe a circle area whose diameter is now 100 cm and whose area has been increased by  $100^2$ . The area-enlargement factor is the ratio of the enlarged area  $(R^2\pi)$  to the actual stem area  $(r^2\pi)$ ; i.e.,  $R^2/r^2$ . In this case it is  $50^2/0.5^2 = 100^2$ . If the stick was a thin sapling in a field situation, it would just be included in the count, because the sampling point (the observer's position, or exactly the viewing-end of the anglegauge) just intercepts the fictitiously enlarged stem area. Similarly, if we look over the 1:50 angle-gauge to a tree at some distance, the stem area of that tree is automatically enlarged by  $100^2$ , if the tree is wider than the cross-piece or just covered by it.

The area-enlargement factor of 100<sup>2</sup> obtained with the 1:50 anglegauge was recommended by BITTERLICH, because the average tree count per sampling point is then equivalent to the stem area or basal area in square meters per hectare. This is so, because the area enlargement factor is the same as the number of square meters contained in a hectare. This is shown by substituting these values in the following basic equation.

basal area = 
$$\frac{\text{mean count per sampling point}}{\text{area-enlargement factor}} \times \text{unit reference area}$$

Results per hectare for the 1:50 gauge can be reduced to:

basal area in 
$$m^2 = \frac{\text{mean count per sampling point}}{100^2} \times 10,000$$

basal area in m2=mean count per sampling point

GROSENBAUGH (1952) recommended the 1:33 angle-gauge for American foresters, because of their general preference to express basal area results in square feet per acre. For this purpose, the 1:33 ratio is convenient, since the area-enlargement factor  $(66^2=4356)$  is exactly one-tenth the number of square feet in an acre. Therefore, with a 1:33 angle-gauge the basic equation becomes:

basal area in ft<sup>2</sup> = 
$$\frac{\text{mean count per sampling point}}{66^2} \times 43,560$$

basal area in ft2=mean count per sampling point×10

Even though trees are counted in the BITTERLICH method, the basal area estimate does not provide for a density estimate. Neither can one obtain a frequency count from this method, because here the species presence per sampling point is merely a function of diameter size, not of surface area sampled.

Therefore, the method is useful only where a stem cover value alone is satisfactory. This quantity, however, is very rapidly obtained. The method seems particularly useful for tree evaluation in the releve analysis, when estimate scale values are used for undergrowth plants. Both are rapid survey methods that complement each other (BENNINGHOFF and CRAMER 1963)

7.53 Calibration of BITTERLICH Gauge. The simple BITTERLICH gauge as illustrated in FIGURE 7.1 can be used for accurate measurements of basal area per unit ground area, if one knows how to calibrate the instrument. For calibration one selects a nearby tree and views at it over the gauge. The cross-piece or comparison bar must exactly cover or contain the width of the tree. This usually requires change of the observer's position. When the correct distance is obtained, the position

is marked on the ground. Then the distance from the position-point to the center of the tree is measured. Secondly, the diameter of the tree is measured. The two values, distance and diameter are then substituted in the calibration equation shown in FIGURE 7.2.

The calibration principle can be used also to measure the diameter of a tree from a distance. This can be useful on steep slopes. In that case, the distance may be obtained by a range finder. How to calculate the tree diameter from a measurement with a BITTERLICH gauge is explained in FIGURE 7.2.

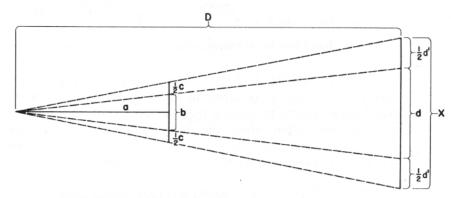


FIGURE 7.2 Calibration principle of BITTERLICH gauge. Legend: a=length of BITTERLICH gauge; b=width of sighting bar; d=diameter of tree; D=distance from observer to tree. Further explanation in equations below.

$$a:D = b:d (1)$$

For calibration (1) is rewritten to read

$$D = -\frac{\mathbf{a}}{\mathbf{b}} \times \mathbf{d} \tag{2}$$

For measuring tree diameter from a distance (2) is rewritten to read

$$d = \frac{D}{a} \times b \tag{3}$$

However, a tree may be larger or smaller than b. Let d+d' be X= the diameter of a bigger tree:

$$X:d = (c+b):b \tag{4}$$

$$X = \frac{(c+b)}{b} \times d \tag{5}$$

or

$$X = \frac{(c+b)}{d} \times \frac{D}{a} \times b \tag{6}$$

#### 7.6 THE WISCONSIN DISTANCE METHODS

**7.61 Concept of Mean Distance as a Measure of Density.** Related to the timber survey methods are the distance methods for estimating den-

sity which were developed by the Wisconsin Plant Ecology Laboratory (WPEL). These were perfected primarily for the tree layer of the plant community (CURTIS 1959).

Plotless techniques were developed which are based on the idea that the number of trees per unit area can be calculated from the average distance between the trees.

If we consider a plantation stand in which the trees are situated at regular intervals of 3 m each, we can quickly determine the number of trees per unit area from these intervals. The spacing of such plantation trees results in a number of 3×3 m quadrats that always form the intervening areas between four corner trees. The quadrats are connected into a contiguous grid of quadrats. We can now imagine a shifting of these quadrats so that a tree becomes the central point in each quadrat. No size-change of the quadrat is involved, and it is clear that each tree occupies an area of 3×3 m=9 m<sup>2</sup>. In this plantation stand, the 9 m<sup>2</sup> quadrat is also the mean area per tree. If we now want to establish the number of trees per hectare (ha) of such a plantation stand, we simply divide the mean area into the reference area:

number of trees = 
$$\frac{\text{unit reference area}}{\text{mean area}}$$
  
number of trees per ha =  $\frac{10,000 \text{ m}^2}{9 \text{ m}^2}$  = 1111

Therefore, the problem of determining the number of individuals on an area reduces to finding the mean area of an individual. This mean area can be visualized in a natural (nonregular) stand, not as an even-sided quadrat, but as a quadrangle that is described by four individuals at its end-points.

The important problem in the distance methods is to locate the distance that gives the best estimate of the square root of the mean area per tree. This is done by averaging a number of specifically selected distance-measures in the stand.

In the quantitative plot method this distance is easily established after the number of individuals is known. The mean area per tree is equal to the plot area divided by the number of trees. Applied to the example in TABLE 7.1, the mean area (MA) and mean distance (D) are:

MA = 
$$\frac{\text{plot area}}{\text{number of trees}} = \frac{120 \text{ m}^2}{45} = 2.67 \text{ m}^2$$
  
D= $\sqrt{\text{MA}} = \sqrt{2.67} \text{ m}^2 = 1.64 \text{ m}$ 

The major advantage of estimating number of individuals through their mean distance rather than through the standard way of counting them in quadrats, plots, or strips is that no plot boundaries are required. This, in many situations, saves considerable time (CURTIS 1959), because tree distances are usually shorter and more easily measured than boundaries.

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**7.62 Miscellaneous Distance Methods.** Different distance methods are proposed in the literature and are currently applied in vegetation and population studies. It seems therefore necessary to introduce at least those methods that have been tried and tested and that are still used in various combinations for methods research.

The choice of pairs of individuals to be measured for their distance is theoretically more complicated in a natural stand than in a regular stand. PIELOU (1959) emphasized that this choice must be truly random. To obtain a truly random choice, all trees in a stand would have to be labelled with a number. Thereafter, one can select individual trees with the aid of a random numbers table. These randomly selected trees may then serve as the trees from which a sample distance is measured to their nearest neighbor. However, the need for prior labelling of all trees would defeat the practicability of the distance method. Therefore, various shortcut methods have been proposed. All of them operate from sampling points, which may be established either randomly or systematically.

One method is to select pairs of individuals nearby randomly selected points. The individuals that are closest together near the point are chosen for sampling the distance between them. This method became known as the "nearest neighbor method" (COTTAM, CURTIS and HALE 1953, COTTAM and CURTIS 1956).

Another method was even simpler. It involved merely to measure the distance from a randomly selected point to the nearest tree. This became known as the "closest individual method" (COTTAM, CURTIS and HALE 1953, COTTAM and CURTIS 1956)

A third method that gained considerable popularity for a while among North American vegetation ecologists, was the so-called "random pairs method" (COTTAM and CURTIS 1949, COTTAM, CURTIS and HALE 1953, COTTAM and CURTIS 1956). Like the nearest neighbor method, the random pairs method involved a distance measure between two individuals instead of a distance measure between a point and an individual. After establishing the sampling point either at random or systematically (at intervals along a transect), one looks for the nearest tree from the sampling point. This tree serves for measuring a distance to a second tree. Facing this first tree, the investigator

spreads out his arms to both sides. In this way, two imaginary lines are established; the first line through facing the nearest tree from the sampling point, the second line through the outstretched arms of the observer. The purpose of this is to establish a 180° exclusion angle to exclude any neighboring tree in that sector where the first tree stands for the distance measure. The second tree to which the sample distance is measured is the nearest tree behind the outstretched arms of the observer. The procedure is diagrammed in FIGURE 7.3.

Through empirical testing it was established that these three methods give acceptable mean area and therefore density estimates for random populations, but with certain correction factors. These corrections are for the nearest neighbor method 1.67×the mean distance (D), for the closest individual method 2×D, and for the random pairs method 0.8×D (COTTAM 1955).

In their important research methods paper, COTTAM and CURTIS (1956) tested these three distance methods for their sampling efficiency against a fourth method, the so-called point-centered quarter method. The latter method does not require a correction factor and is as simple in its application as the closest individual method, but four times as sampling-intensive. This also means that it requires less time in the field. The point-centered quarter method was therefore considered the most efficient of the available distance methods. It has since gained wide acceptance.

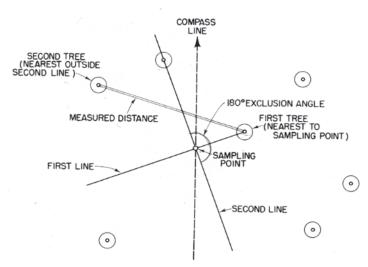


FIGURE 7.3. Random pairs method.

7.63 The Point-Centered Quarter Method. In the point-centered quarter method four distances instead of one are measured at each sampling point. Four quarters are established at the sampling point through a cross formed by two lines. One line is the compass direction and the second a line running perpendicular to the compass direction through the sampling point. The line-cross can also be randomly established by spinning a cross over each sampling point. The distance to the midpoint of the nearest tree from the sampling point is measured in each quarter (FIG. 7.4).

The four distances of a number of sampling points are averaged and when squared are found to be equal to the mean area occupied by each tree. COTTAM and CURTIS (1956) tested the reliability of this method on several random populations by checking the result with the plot method. They ranked the four quarter (Q) distances of each sampling point by computing the mean of the shortest (Q1), the second shortest (Q2), the third (Q3) and the longest (Q4) distances. The following estimates of the correct mean area per tree (MA) were found to apply to each of the different sets of mean distance.

Q1 shortest =  $0.5 \sqrt{MA}$ Q2 =  $0.8 \sqrt{MA}$ Q3 =  $1.12\sqrt{MA}$ Q4 longest =  $1.57\sqrt{MA}$ Q mean of 4 =  $1.0 \sqrt{MA}$ 

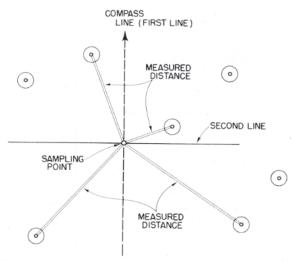


FIGURE 7.4. Point-centered quarter method.

Therefore, no correction factor is needed when the four quarter distances are averaged; and  $MA = D^2$ , where D = the mean distance of four point-to-nearest-tree distances taken in each of four quarters. Mathematical proof of the workability of this method has been given by MORISITA (1954).

Of course, the accuracy increases with the number of sampling points, and a minimum of 20 points is recommended (COTTAM and CURTIS 1956).

The method has two limitations (NEWSOME and DIX 1968) for field applications. An individual must be located within each quarter, and an individual must not be measured twice. Therefore, stands with wide spacing of individuals present a problem in using this method. The second limitation applies also to the random pairs method.

The parameters obtained in the distance methods are:

- Species.
- 2. Density (from mean distance).
- 3. Diameter (and therefore basal area and dominance).
- 4. Frequency (as the occurrence of a species at a sampling point).

The same parameters are also obtained from plots. However, the distance methods have an advantage in that they do not require laying out of plot boundaries. This saves considerable time. It also eliminates to a certain extent the personal error from judging whether boundary individuals are inside or outside the quadrat.

7.64 Example of a Point-Centered Quarter Analysis. The following example relates to the same tropical rain forest stand that served for the releve example (SECTION 5.3) and for the quantitative plot example (SECTION 7.3). The point-centered quarter example is shown only for five sampling points to save space (TABLE 7.4). It is recommended to sample at least 20 points per stand. The adequacy of sampling points can, of course, also be determined by plotting the running mean as described in SECTION 6.42.

In the example analysis in TABLE 7.4, trees with basal diameters less than 3 cm were omitted. These included all woody plants under 2 m height. The small trees could, however, be sampled as a second size category from the same sampling points with each four distances. The objective was to determine (from individuals taller than 2 m):

- 1. the density for each tree species,
- the dominance of each tree species, and 2.
- the frequency of each tree species. 3.

A second objective was to convert these absolute values into relative values as an example for deriving the importance value, which will be discussed in SECTION 7.67.

TABLE 7.4 shows the raw data for five sampling points that were arranged in a transect, one point every 5 m. TABLE 7.5 shows the derivation of the mean basal area by species. This value is needed to determine the dominance of the species, which is a combination of number and basal area.

**Limitations of the Distance Methods.** The point-centered quarter method has become well accepted as shown by many vegetation studies (CAPLENOR 1968, HABEK 1968, RISSER and ZEDLER 1968, NEW-SOME and DIX 1968, among others). Apart from its less complicated field application and greater information value per sampling point, the method seems more reliable than the random pairs method. This is based on the observation that the distances of trees to sampling points are more truly random than the distances among trees located through sampling points (COTTAM, CURTIS and HALE 1953, PIELOU 1959).

However, the point-centered quarter method is similarly applicable only to random distributions. Plot studies are more reliable where plant individuals are not randomly distributed (SCHMELZ 1969). Yet plots or quadrats are not fully reliable either. The reason is that a plot may also include either aggregations or underdispersed groupings of individuals in contagiously distributed species combinations. Clumping of individuals or contagious distribution applies to nearly all plant life forms, except trees and annuals. But even among the latter life forms nonrandom distributions are the norm for the individuals of single species in mixed-species stands. Therefore, the method should not be applied to single species in mixed stands. Instead, it should be applied only to broad size classes as shown in the preceding example, where the method was applied to tree individuals of all species taller than 2 m. The density of each species is subsequently established by partitioning the total density estimate.

GREIG-SMITH (1964) has cautioned against applying the pointcentered quarter method to herbaceous life forms, such as bunch grass vegetation, because the resulting density values are inaccurate where the distribution of individuals occurs in aggregations. This has been supported by RISSER and ZEDLER (1968) who found in Wisconsin grassland that the point-centered quarter method consistently underestimated the number of individuals in contagiously distributed species. This can be explained by the greater probability of a sampling point to fall between the clumps of individuals than within the clumps in contagious distributions in which the clump diameter is small. By falling

TABLE 7.4. Quantitative Analysis by Point-Centered Quarter Method. Five Sampling Points, One at Every 5 m Along 110°, Starting at End of Convex, Gently Sloping Ridge Below Pauoa Flats Trail Going Upslope Toward the Trail. Raw Data, March 4, 1972.

SAMPLING POINT	QUARTER NUMBER	DISTANCE (M)	SPECIES	DIAMETER AT BASE (CM)
1	1	0.7	Psidium guajava	5.5
	2	1.6	Acacia koa	42.5
	3	3.5	Metrosideros collina	17.0
	4	2.0	Metrosideros tremuloides	25.0
2	1	1.1	Psidium guajava	4.0
	2	0.8	Psidium guajava	5.0
	3	1.9	Psidium guajava	5.0
	4	1.8	Psidium guajava	4.0
3	1	1.3	Acacia koa	75.0
	2	0.7	Psidium guajava	3.0
	3	1.5	Metrosideros collina	9.0
	4	2.0	Metrosideros collina	23.0
4	1	3.1	Acacia koa	14.0
	2	4.7	Psidium guajava	6.0
	3	1.1	Psidium guajava	5.0
	4	1.9	Acacia koa	12.0
5	1	2.5	Acacia koa	23.0
	2	2.2	Acacia koa	18.0
	3	1.4	Psidium guajava	5.0
	4	2.8	Metrosideros collina	25.0
		Total 35.6		

Results:

Mean distance (D) = 35.6/20 = 1.78 m

Absolute density =  $Area/D^2$ 

Where D = mean distance

Number of trees per 100 m<sup>2</sup> =  $100/(1.78)^2 = 100/3.17 = 31.5$ 

Absolute dominance = mean ba per tree × number of trees in species

Where ba = basal area Number of trees in species

SPECIES NUM	BER IN QUARTERS	NUMBER OF TREES IN 100 M <sup>2</sup>
Acacia koa	6/20=0.3	$0.3 \times 31.5 = 9.4$
Metrosideros collina	4/20 = 0.2	$0.2 \times 31.5 = 6.3$
Metrosideros tremuloides	1/20 = 0.05	$0.05 \times 31.5 = 1.6$
Psidium guajava	9/20 = 0.45	$0.45 \times 31.5 = 14.2$
		Total 31.5

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TABLE 7.5. Mean Basal Area by Species for the 20 Trees Shown in TABLE 7.4.

ACAC KOA		METROSID COLLIN		METROSID TREMULO		PSIDIU GUAJA	
DIAMETER (CM)	BA (CM²)	DIAMETER (CM)	BA (CM <sup>2</sup> )	DIAMETER (CM)	BA (CM <sup>2</sup> )	DIAMETER (CM)	BA (CM²
42.5	1418	17.0	227	25.0	491	5.5	24
75.0	4418	9.0	64			4.0	13
14.0	154	23.0	415			5.0	20
12.0	113	25.0	491			5.0	20
23.0	415					4.0	13
18.0	254					3.0	7
						6.0	28
						5.0	20
						5.0	20
Total ba	6772		1197		491		165
Mean ba	1129		299		491		18
Therefore,	dominan	ce of				Dominance	rank
Acacia k			1129×	9.4=10613 cm	2/100 40	1	
Metrosid	eros colli	na	299×	6.3 = 1884  cm	2	2	
Metrosid	eros trem	nuloides	491×	1.6= 786 cm	$1^2$	3	
Psidium :	guajava		$18 \times 14.2 = 256 \text{ cm}^2$			4	
				13539 cm	$\frac{1}{n^2/100}$ m <sup>2</sup>		
Absolute fr	requency	= number of po	oints wit	h species ×100			
Acacia k	oa .		~	= 80 percent			
Metrosideros collina				e 60 percent			
Metrosid	eros tren			= 20 percent			
Psidium	guajava		$=\frac{5}{5} \times 100$	=100 percent			
				260 percent			

between clumps, the point to plant distances will be longer than average. The longer distances result in an overestimate of the mean area per individual and thus in an underestimate of density.

The opposite, namely overestimation of the number of individuals, is true for regularly distributed individuals. This is shown in FIGURE 7.5. In a regular, quadrangular distribution, such as often found in a planted tree stand, the correct mean area is obtained by squaring the shortest distance between any two trees. This result would be obtained only by sampling point 1 in FIGURE 7.5. Such locating may occur once in a very large number of random point placements or not at all. The most

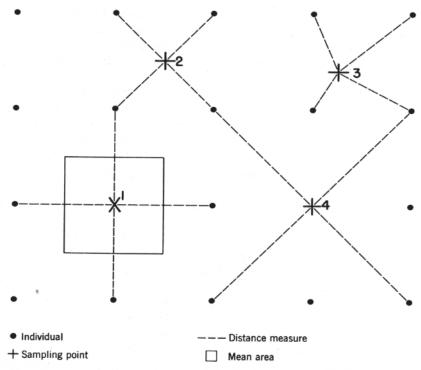


FIGURE 7.5. Application of point-centered quarter method to a regular distribution of individuals. Here only sampling point 1 gives the correct estimate of mean area. Further explanation in text.

common placement would be between trees, such as indicated by points 2 and 3. At these positions the mean distance of four quarters and therefore the mean area will always be underestimated. This will result in a considerable overestimate of tree density. Only position 4 would result in an overestimate of mean distance and thus an underestimate of density, as is found for contagiously distributed individuals. However, for a sampling point to give this result, not only must the point fall directly on a tree, but also the quarter dividing lines must pass through the center of the nearest trees, which would render them invalid for inclusion in the sample. This also shows that the boundary problem, found to be a disadvantage in any plot method, is not entirely eliminated in the plotless methods. However, it is highly improbable that position 4 will occur randomly. Instead, tree density can always be expected to be overestimated by this method when applied to regularly distributed individuals. This is true also for rectangular and rhombic regular distributions.

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**7.66** Modifications to Overcome These Limitations. Several modifications were suggested to overcome the pattern problem in the distance methods to extend their use to single species population studies. These modifications employ combinations of point-to-plant and plant-to-plant distance measures.

CATANA'S (1963) "wandering quarter method" begins with a sampling point and a quarter. This is similar to the point-centered quarter method. Except, only one quarter is established at the point. This quarter is laid out in a predetermined compass direction. The compass direction divides the quarter into two 45° pie-sections, and the nearest tree to the point is measured in this quarter. Thereafter, this nearest tree becomes the vector of a second quarter that is laid out in the same compass direction as the first one. A second distance is measured from the first tree to its nearest neighbor tree in that quarter. This procedure is continued for 25 distances in one compass direction.

Since the nearest tree may rarely stand in the middle of a quarter on the compass line, but usually is found anywhere within the 90° exclusion angle of the quarter, the distance directions are likely to shift in an irregular zigzag line during the progress. This shifting along the transect

is responsible for the name "wandering" quarter method.

If contagious distributions occur in the 25 distances measured along a transect, there should then be a series of short, within-clump distances and one or more long, between-clump distances. CATANA (1963) describes how to detect the two kinds of distances and suggests a correction to obtain a realistic mean distance. However, one problem is the commonly low number of gap- or between-clump distances obtained, which may not give a statistically valid sample for contrasting them to the usually high number of within-clump distances. CATANA therefore suggests sampling four transects arranged to one another in form of a quadrat. The resulting 100 distance-measures should contain a sufficient number of gap-distances for correction if the pattern is contagious.

CATANA tested his method on four artificial populations of 1000 individuals each. In the first truly random population, the wandering quarter method estimated 1025 individuals. In two slightly contagious populations the estimates were 815 and 836 respectively. In a fourth population that tended to be regular, the estimate was 1285 individuals. Thus, the method still underestimates density in contagiously distributed populations and gives strong overestimates, where the distribution tends to be uniform.

Recently, BATCHELER (1971) suggested a further modification. This consists of measuring the distance to the nearest individual from the sampling point. From this individual, the distance is measured to its

nearest neighbor, and then a third distance is measured to the next nearest neighbor. Therefore, three distances are measured at a sampling point—one point-to-plant distance and two plant-to-plant distances. No quarter or exclusion angle is used apparently.

BATCHELER points out that the point-to-nearest-plant distance (several times repeated) gives the true mean distance for a random population and that the two additional plant-to-plant distances supply the data for correction of departure in pattern. As correction he suggests dividing the sum of the point distances by either the sum of the nearest neighbor distances or by the sum of the second-nearest neighbor distances and to use this fraction as an exponential function.

According to the point-centered quarter test by COTTAM and CURTIS (1956), the shortest point-to-plant distance gives only 0.5 of the true mean distance in a random population. The true mean distance is obtained only by measuring the point-to-plant distance in a 90° exclusion angle.

BATCHELER's method requires intensive testing, before it can be recommended for general use.

It is apparent that distance methods for the estimation of density of single species are still in the research stage. The methods are not yet reliable for nonrandom populations. They were included in the discussion because further methods-research may soon extend their scope to nonrandom populations.

However, this restriction does not apply to the same extent when all species in a stand are sampled together. Taken together, trees in a stand approach random distribution and then the point-centered quarter method is useful (COTTAM and CURTIS 1956).

Moreover, it is important to realize that two independent sets of data are obtained by the distance methods. The unreliability does not apply to the diameter and frequency measurements, which are independent of the correct mean distance. Therefore, mean basal area per tree can be accurately derived from the diameter measurements (computation as in TABLE 7.3, SECTION 7.32, or TABLE 7.5. SECTION 7.64), but mean basal area per acre or hectare, which is derived through multiplication with density, is dependent on pattern. The point-centered quarter method is widely used in spite of this possible bias in density estimate, because the data is commonly expressed in relative values. This will be further explained in the next section.

LINDSEY, BARTON and MILES (1958) have shown that 0.1 acre (400 m²) circular plots delimited with a range finder are still more efficient for density evaluation than the point-centered quarter method in stands without view-obscuring undergrowth. The circular plot method

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also has the advantage that the accuracy of the density count is less affected by departures in pattern from randomness. LINDSEY et al suggest a combination of BITTERLICH's technique for basal area and the circular plot method for density and frequency as the most efficient quantitative method in forest stands. But this suggestion holds only for forest stands in which the stem of each tree is visible near breast-height from a central sampling point.\*

For a structural analysis, tree diameters are desirable. These may be measured from the center of the circular plot by using a BITTERLICH gauge as explained before (FIG. 7.2). However, visibility may be limited in stands with dense shrubby undergrowth. In such situations either belt-transects or the point-centered quarter method may be more efficient.

**7.67 The Importance Value.** The distance methods yield three quantitative parameters—density, basal area, and frequency. These are, of course, also obtained in the quantitative plot methods.

Any one of the three parameters may be interpreted as an "importance value" (WHITTAKER 1970). This depends on which of the values the investigator considers most important for a particular species, group of species or community. For example, tree seedlings may occur with a high frequency in an undergrowth layer, while in terms of cover, they may be insignificant. However, their high frequency may be of great importance as indicating a new stage of uniformly distributed reproduction. In this case their high frequency may be interpreted as of high "importance."

Yet, it has become common practice, in quantitative descriptive studies that employ the distance measuring techniques, to use the so-called importance value of CURTIS (1959) for the presentation of results. This importance value (I.V.) is defined as the sum of relative density, relative frequency, and relative dominance.

The absolute values for density, dominance, and frequency were defined already in the point-centered quarter example (SECTION 7.64).

The corresponding relative values for the example shown in TABLE 7.4 are shown on the following page.

The importance value may be converted into the so-called "importance percentage" by dividing the importance value by three (RISSER and RICE 1971).

The importance value of a species reaches a maximum of 300 in stands consisting of only one tree species. Two monodominant (single tree species) stands with different numbers of trees per acre and different basal areas will have the same importance value for each species.

<sup>°</sup>To lay out a circular plot, calculate the radius (R) from the area (A) as  $R = \sqrt{(A/\pi)}$ . Example for 0.1 acre plot  $R = \sqrt{(400 \text{ m}^2/3.14)} = 11.3 \text{ m}$ .

1. Relative density = 
$$\begin{array}{c} \text{number of individuals of species} \\ \text{total number of individuals} \end{array} \times 100$$

Acacia koa
$$\frac{9.5}{31.5} \times 100 = 30 \text{ percent}^{\circ}$$
Metrosideros collina $\frac{6.3}{31.5} \times 100 = 20 \text{ percent}$ Metrosideros tremuloides $\frac{1.6}{31.5} \times 100 = 5 \text{ percent}$ Psidium guajava $\frac{14.3}{31.5} \times 100 = 45 \text{ percent}$ 

100 percent

2. Relative dominance = 
$$\frac{\text{dominance of a species}}{\text{dominance of all species}} \times 100$$

Acacia koa
$$\frac{10,613}{13,539} \times 100 = 78.4$$
 percentMetrosideros collina $\frac{1884}{13,539} \times 100 = 13.9$  percentMetrosideros tremuloides $\frac{786}{13,539} \times 100 = 5.8$  percentPsidium guajava $\frac{256}{13,539} \times 100 = 1.9$  percent

3. Relative frequency = 
$$\frac{\text{frequency of a species}}{\text{sum frequency of all species}} \times 100$$

Acacia koa 
$$\frac{80}{260} \times 100 = 30.8 \text{ percent}$$
Metrosideros collina 
$$\frac{60}{260} \times 100 = 23.1 \text{ percent}$$
Metrosideros tremuloides 
$$\frac{20}{260} \times 100 = 7.7 \text{ percent}$$
Psidium guajava 
$$\frac{100}{260} \times 100 = 38.5 \text{ percent}$$

100.1 percent

4. Importance value (I.V.) = Relative density + relative dominance + relative frequency

	RELATIVE DENSITY	RELATIVE DOMINANCE	RELATIVE FREQUENCY	I.V.	I.V. Rank
Acacia koa	30.0	78.4	30.8	139.2	1
Metrosideros collina	20.0	13.9	23.1	57.0	3
Metrosideros tremuloides		5.8	7.7	18.5	4
Psidium guajava	45.0	1.9	38.5	85.4	2

o Note, same as number of species occurrences in quarters.

In this case, the importance value does not convey any quantitative difference. Yet, it incorporates quantitative differences as soon as a second tree species appears in the stand. Two stands, each stocked with the same two species, will hardly ever show the same importance values per species. For example, one of the two species may be present with exactly the same number of individuals, the same basal area, and the same frequency, but the second species may show differences in its basal area between the two stands. This renders the importance values of the first species also different for each stand. The disparity between stands increases greatly with each additional species. The summing of the three parameters into one has the effect of increasing the difference between the same species among stands of similar species composition. The importance value therefore underscores the individualistic viewpoint (SECTION 3.13).

The use of relative rather than actual parameters is of limited information value. Densely vegetated and sparsely vegetated habitats can have the same relative densities, relative basal areas, and relative frequencies. Therefore, the importance value gives no idea of species biomass or cover, which are considered of even greater ecological significance in plant distribution than absolute density (FOSBERG 1961, RICE 1967, DAUBENMIRE 1968).

## 7.7 LITERATURE EXAMPLES OF QUANTITATIVE FIELD ANALYSES IN NORTH AMERICA

In contrast to the example of a semiquantitative relevé analysis of a forest stand given in CHAPTER 5, quantitative field analyses cannot be adequately described by citing only one example. The main reason is that the kind of analysis varies with the objectives—whether the vegetation is to be described for classification, ordination, succession and population-structure, or other purposes.

Measurements of any or all of the three quantitative parameters can certainly be applied to small plots of European releve size in the same way as they are often applied to the larger sample stands for continuum analysis. But these more accurate measures require more time. It is therefore always necessary to balance the time it takes to establish a quantitative measure against the objectives of the study. If the primary purpose is to describe vegetation through recurring plant assemblages or to portray the spatial variation of a vegetation type, it seems more appropriate to use the time for more releves with semi-quantitative estimates than to present only few releves with accurate quantitative evaluations. This is based on the observation that vegeta-

of an

tion varies from place to place, even if one samples for similarity or constancy in patterns. Moreover, an objective quantitative analysis does not eliminate the fact that selection of a sample area is subjective.

If the objectives are to determine the developmental or successional trends of the woody plant populations of a forest community, it is necessary to enumerate the different woody plant species in size classes for a structural analysis. In contrast, developmental trends of herbaceous plant species can only be properly evaluated by periodic reassessments in permanent plots. For this, measurements are more appropriate than estimates in most cases. Measurements are also more useful for a close comparison of similar communities.

Five uncomplicated examples of quantitative analyses in forest stands and three in nonforest communities are cited from the literature to bring out the major trends. There are many more variations. In fact, almost any specific problem requires its own modifications of methods. For this reason we suggest that the previously described techniques be used as creative options for specific questions rather than as rigid tools for any situation. The quantitative descriptive methods will be compared to the releve method in the conclusions (SECTION 7.73).

7.71 Forest Communities. Here are the five examples of quantitative analyses in forest stands.

7.71.1 Forest Vegetation in Western North America (DAUBENMIRE). In addition to a cover class rating very similar to the BRAUN-BLANQUET scale in value and application (SECTION 5.42), DAUBEN-MIRE (1968) uses quantitative measures when the objectives of the analysis aim at more than classifying associations. For this he uses plots of 15×25 m in forest vegetation of Washington and Idaho. These 375 m<sup>2</sup> plots are divided into three strips each of 5×25 m (FIG. 7.6). In these, trees from 1 m height (i.e., from sapling size) upwards are counted by diameter-at-breast-height (dbh) classes. For shrubs and herbs, frequency is determined in 20×50 cm (0.1 m²) subplots placed at 1 m intervals along the two sides of the central 5×25 m strip. This results in 50 systematic 0.1 m<sup>2</sup> frame placings per plot, or in a total sample of 5 m<sup>2</sup>.

The more abundant and uniformly distributed undergrowth plants are objectively evaluated in this way. All plants noted outside the frequency frames are added to the specie's list. Cover is estimated in each frame placement.

DAUBENMIRE uses a similarly rigorous vegetation segmentation as that applied by KRAJINA (1965, 1969) in western Canada, by GRANDTNER (1966) in Quebec and in European vegetation studies. DAUBENMIRE then places his plots centrally into the tentative vege-

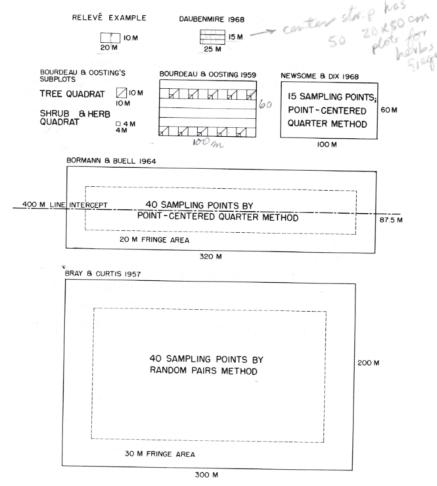


FIGURE 7.6. Comparative sizes of sample stands.

tation segments. Thus, his community studies are in essence releve analyses in recurring plant communities.

7.71.2. Eastern Hemlock-Hardwood Forest (BORMANN and BUELL). In most quantitative analyses the emphasis lies on accurate description of the variation throughout broadly defined dominance-communities (i.e., communities defined by dominant species only). Unlike the releve analysis, in which the limit of homogeneity is defined by the uniformity of the undergrowth vegetation, the sample is spread out over a much larger area.

For example, BORMANN and BUELL (1964) sampled a seven acre (28,000 m²) stand of an old-age hemlock-hardwood forest (Tsuga cana-

densis—Fagus, Fraxinus, Betula, Ulmus, Tilia) in Vermont as follows: Trees of 10 cm dbh or greater were sampled by the point-centered quarter method (SECTION 7.63) at 40 sampling points. The sampling points were located along 12 base lines, each 23 m apart. The sampling points were spaced 20 m apart and none was less than 20 m from a boundary. FIGURE 7.6 shows the probable dimensions of this 28,000 m² sample unit.

Smaller trees (between 2.5 and 10 cm dbh) and saplings (between 30 cm height and 2.5 cm dbh) were counted at each sampling point in 1×10 m quadrats. Tree seedlings less than 30 cm tall were counted in fifty 0.5×2 m quadrats located 15 m apart along the base lines. Cover was measured by the line-intercept method for two tree layers and one shrub layer. The two tree layers were defined as 3.6 to 12 m and 12 to 32 m tall. These two layers were measured along a 400 m line running across the long dimension of the stand. The shrub cover, probably including all woody plants below 3.6 m height, was measured along 10 m lines at each of the 40 sampling points. Herbaceous plants were assessed in the same 0.5×2 m quadrats as the tree seedlings. But herbs were not counted; instead their cover was estimated in the 50 quadrats. In addition, herb species were listed from the entire stand.

Thus, the sampling layout was systematic to insure a uniform assessment of the  $28,000~\text{m}^2$  community. In addition to the 160~distance measures, a count sample of smaller trees was made in  $400~\text{m}^2$ , and of seedlings in  $50~\text{m}^2$ . Cover of herbs was estimated for  $50~\text{m}^2$  and that of woody plants over a length of 400~m.

The objectives of the survey were primarily to describe the stand with modern methods of vegetation measurement, and to determine the successional trend of the stand. The second objective is well accomplished for woody plants by such a structural (i.e., number per size class) analysis.

7.71.3 Live Oak Forest, North Carolina (BOURDEAU and OOSTING). BOURDEAU and OOSTING (1959) studied the live oak (Quercus virginiana) forest in North Carolina. This is likewise a broadly defined dominance-community occurring as stabilized vegetation on coastal dunes. Seventeen stands or locations were described by species lists, and five of these subjected to quantitative analysis. These five stands were selected because they were considered large enough. In each stand, an area of 60×100 m (1.5 acres) was outlined and divided into six 10×100 m strips (FIG. 7.6). Of these, two were randomly selected and partitioned into 10 m sections. Along each strip five alternate 10×10 quadrats were then sampled, resulting in a total sample-area of 1000 m². In these, all woody plants above 2.5 cm dbh were counted by diameter. Woody plants with less than 2.5 cm dbh were not counted,

but their crown cover was estimated together with that of the herbs in  $4\times4$  m plots nested in a predetermined corner of each of the ten  $100~\text{m}^2$  quadrats. Thus, the total area-sample for undergrowth plants was  $160~\text{m}^2$ . Species occurring outside the quadrats were recorded also.

The objectives were to obtain a detailed analysis of the structure of this community as a representative record. No effort was made to distinguish finer patterns in the undergrowth.

7.71.4 Upland Forest of Southern Wisconsin (BRAY and CURTIS). BRAY and CURTIS (1957) sampled the upland forest of southern Wisconsin for a continuum analysis and ordination. This is a mixed hardwood forest containing about 16 prevalent broad-leaved tree species. The whole southwest half of Wisconsin, occupied by this hardwood forest, was considered one community for this purpose. The forest area was mechanically stratified into geographic subsections to provide for a balanced sampling. Within these, 59 stands were selected that were at least 15 acres (6 hectare) in size. (FIG. 7.6). The stands were homogeneous in the tree layer, reasonably undisturbed, and occurred on well-drained soils.

Within each stand the trees, probably meaning all woody plants above 10 cm dbh, were measured by the random pairs method at 40 sampling points. Therefore, 40 distances were measured and the 80 trees were recorded by species and diameter. The lines, along which the 40 sampling points were located at predetermined intervals, started always at least 30 m from the edge of a forest. Shrubs and herbs were sampled in twenty 1×1 m quadrats at alternate sampling points for frequency.

7.71.5 Cypress Hills Forest, Alberta and Saskatchewan (NEWSOME and DIX). A description of this forest in Canada was presented by NEWSOME and DIX (1968). In contrast to Eastern North American mixed forests, this Canadian forest is dominated by only three tree species, Picea glauca, Pinus contorta, and Populus tremuloides. These species often form monodominant stands, but mixtures of Pine-Populus and Picea-Populus are common also.

The primary objective was to study the species composition on forestcovered habitats for elucidating patterns of floristic variation by ordination techniques and to explain these in relation to environment.

Six requirements were set for a forest stand to be acceptable for sampling:

- The tree canopy needed to cover at least 60 percent of the ground.
  - · Immature stands were excluded.

- A stand had to extend over at least 0.6 hectare (1.5 acres) (FIG. 7.6).
- Its species composition had to show a certain minimum of homogeneity (subjectively determined).
- Likewise its habitat had to be uniform, for example, stands with microtopographic variations exceeding 5° were excluded.
- Stands obviously disturbed by windfall, fire, or cutting were excluded; less obviously disturbed stands were accepted.

Sample stands were located throughout the Cypress Hills forest so as to include as much variation in species composition and habitat as could be discerned.

Seventy-nine stands were selected in this way. The trees from 9.4 cm (3.7 inches)\* diameter at breast height on upwards were sampled by the point-centered quarter method for density (number/area), basal area (dominance), and frequency. The number of point samples was 15. Therefore, 60 trees were measured per stand (The outline and intervals between sampling points are not reported). Fifteen sampling points yielded results that were within 5 percent of 30 sampling points.

Saplings, classified as trees with diameters at breast height from 2.5 to 9.3 cm (1 to 3.6 inches) were sampled at each point in 50.2 m<sup>2</sup> arms-length quadrats. The quadrat method was used whenever the following two requirements of the point-centered quarter method could not be met:

- That an individual be located within each quarter.
- That an individual must not be measured twice.

Since saplings were sparse in many stands the quadrat method was used in most cases.

Seedlings, shrubs, and herbs were recorded by frequency in  $0.5 \times 0.5$  m frames. These were placed 30 times in each stand; 30 such quadrats gave results, whose mean was within 10 percent of 50 quadrats. Seedlings, in addition, were counted in each quadrat.

- 7.72 Herbaceous and Low-Shrub Communities. Here are three examples of quantitative analyses in nonforest communities.
- 7.72.1 Alpine Communities in New Hampshire (BLISS). During his reconnaissance of the vegetation above timberline BLISS (1963) noted continua and discontinua in these alpine communities. On this basis he

<sup>°</sup> This is the lower class-limit of a 4 inch or 10 cm tree, which is a commonly used cutoff point for a broad size class of trees.

delimited the general spatial relations among them. He then located areas of  $6\times10$  m within these segments, which were representative of a specific community type. Therefore, his plots were chosen subjectively. Excluded were rock outcrops and ecotones (transition zones). Within the  $6\times10$  m areas he established  $4\times8$  m plots. In view of the small size of the alpine plants, these 32 m² plots probably satisfied the minimal area requirement. However, for a quantitative analysis, the 8 m side of each plot was subdivided into strips of 1 m width running perpendicular to the slope. Of these, four were selected at random for the sample. In this way, the sample-area was further reduced to 16 m². In each  $1\times4$  strip he counted individuals per species in five  $20\times50$  cm  $(0.1 \text{ m}^2)$  frames. These were placed systematically, every 0.5 m, along each of the four  $4\times1$  m strips. Twenty such frame placements were sampled in each plot, resulting in a total area of 2 m²

It is doubtful that this area satisfied the minimal-area requirement. Grasses and shoots of sedges were counted by bunches as individuals. The individuality of heath shrubs could not be ascertained, thus, they were counted by stems. This may have resulted in a mixture of counts of branches and individuals. Cover was estimated by perpendicularly projecting the shoot outline of the plants in each quadrat. Since this was repeated 20 times over a 2 m² area, the average cover percent was probably assessed quite accurately. But it was estimated and not measured. Density and frequency were measured out of 20 quadrats, with frequency a by-product of the density analysis.

We think the sampling applied by BLISS combined some features of the releve method with that of the more typical North American quantitative methods. The similarities to the releve method are the fine degree of stratification for recurring plant assemblages, the initial cohesive sample-area, and the small plot size of 32 m² area. These, of course, were necessitated through the time-consuming density analysis.

The purpose of the analysis was the description of plant communities of this alpine region as part of a larger project on plant productivity. The detailed density analysis was definitely justified for the second purpose, the productivity study. But for a mere description of the alpine communities, it probably would have been more efficient to list the plants of the total 32 m² plot area instead of only a 2 m² area within each plot, and to apply a semiquantitative estimate rating. Thereby much time could have been saved, more plots could have been analyzed in the same time, and a more complete and thorough community classification could have been established. This is not meant as a criticism, only as a clarification of methods in relation to the objectives. A quantitative analysis per se is not always better, although it often is favored because it is quantitative.

7.72.2 Herbaceous Wetland Communities, Saskatchewan (WALKER and WEHRHAN). The herbaceous wetlands as defined by WALKER and WEHRHAN (1971) are mixed sedge-grass-forb communities occurring in seasonally wet depressions surrounded by large wheat fields in the Canadian prairies. The depressions range in size from a few square meters to several hectares.

The objective of studying these communities was to analyze their place-to-place floristic variation in relation to edaphic variables.

The sample stands were selected according to the following criteria; (a) absence of any discernable past cultivation, (b) absence of severe grazing or mowing, (c) restricted to nonextreme wetland communities (called marsh-meadow and shallow marsh), (d) low salinity. Thirty-four stands in the vicinity of Saskatoon were selected. In each stand the species were analyzed for frequency in twenty placements of a 0.25 m² frame. The rather small number of frame placements was considered sufficient in view of the great variation between (rather than within) stands. The vegetation data was processed by an ordination technique.

The total sample covered only 5 m² per stand, which is probably smaller than the minimal area of these communities. However, plants found outside the frequency frames were also listed. No sample stand size is reported, except that the communities varied from a few square meters to several hectares in size. It is thus possible that communities with fragmentary species composition (of too small an area) were included as sample stands. The stand outline was probably the total community. No information is given on how the frame placements were arranged. It is possible that they were placed in scattered formation systematically across the stand, concentrated in the center, or randomly assigned throughout the variously sized stands.

7.72.3 Shrub and Grass Communities in Montana (BRANSON, MILLER and McQUEEN). The study by BRANSON, MILLER and McQUEEN (1970) relates to the investigation of dryland community patterns in the semiarid, cool-temperate zone of the mid-western United States. These patterns consist of a mosaic of grass and low-shrub communities of sagebrush and saltbush. In contrast to the interrupted distribution of the wetland communities in Saskatchewan, the dryland communities investigated in Montana occurred in a contiguous pattern.

As in the previously described study, the objective of BRANSON et al. was to investigate the variation of the floristic pattern in relation to edaphic variables in order to find environmental explanations for the local plant distributions.

The authors recognized 14 dominance communities from the start, which were divided into an upland and a lowland group. All communi-

ties were sampled by the point-intercept method. The seven upland communities were sampled by a continuous 329 m transect. The low-land communities were more widespread and thus were sampled by systematically spaced 15 m transect sections.

The point-intercept sampling was done with a frame of 10 vertically oriented pins. The pins were spaced 5 cm apart. Therefore, 20 points were used per meter transect distance. This is a very high sampling intensity. The same results could probably have been obtained with 10 or even only 5 points per meter.

The result of the upland community analysis is shown in FIGURE 7.7. Twelve plant species are listed. Their exact distribution along the 329 m (1080 ft) transect is shown, and the species quantities are diagrammed in black by percent cover. The community boundaries were drawn subjectively as the last step in the preparation of FIGURE 7.7. Therefore, the scheme is not an objective classification, but it clearly shows several discontinuities or vegetation boundaries. The reader can also recognize readily the authors' community classification concept, which is based on the spatial dominance (shoot cover)-changes among the species. The first and last Nuttall saltbush communities differ primarily by the high rock component in the first community. Therefore, these are dominance communities rather than communities identified and classified by differential species (see CHAP. 9).

In this study, as in the previous one, no sample stand size is given. Instead, as reference area one may consider any whole dominance-community that was evaluated by a single transect of points.

**7.73 Conclusions.** Many other variations of quantitative field analyses could be cited, but the main trends and principle differences from the relevé analysis should be quite clear by now.

7.73.1 Forest Communities. Major emphasis in quantitative analyses has so far been put on the tree stratum in forest communities. The tree layer is sampled across a large-sized stand, usually along transects, but it is also often sampled by random points or quadrats. Earlier, 10 × 10 m quadrats were used for counting the trees by species in diameter classes. More recently, the 10 × 10 m quadrats have been replaced by the distance-methods, which require less time, although this advantage is not always apparent (LINDSEY, BARTON and MILES 1958). In forests with sparse shrubby undergrowth, belt-transects or circular plots (with range-finder) may be a faster sampling unit for density estimates than points and distances. It should also be remembered that two-dimensional sampling units (plots) may have a greater chance to integrate variations in pattern (departures from randomness) than points and distances. Therefore, plots are more likely to give more accurate density estimates. The smaller woody plants and herbs in



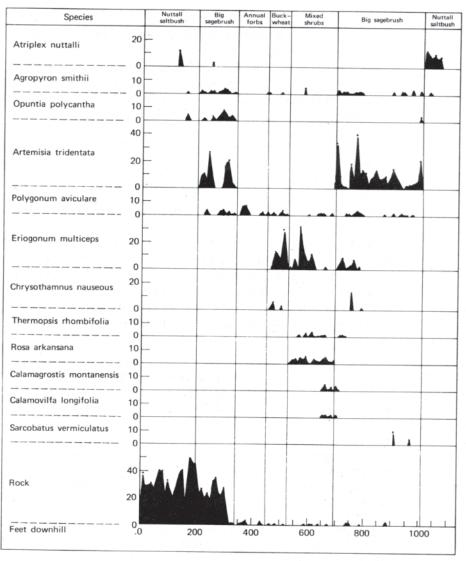


FIGURE 7.7. Abundance of species and contacts with rocks for upland species. (From BRANSON, MILLER and McQUEEN 1970:393. Reproduced with permission from Ecology.)

forest communities are usually recorded in quadrats. The quadrats are more or less adapted in size to the respective height strata. Shrubs and small trees are often recorded in 16, 10, or 4 m² quadrats and herbs in 1 and/or 0.1 m² quadrats. For the undergrowth plants, cover is more commonly assessed than density, but, more often, frequency is considered sufficient for descriptive purposes.

In addition to certain differences in technique and objectives, the five cited forest examples differ primarily in sampling intensity and size of sample stand.

Of the three studies employing distance measures for trees, BRAY and CURTIS' study is the least intensive. Forty distance measures involving 80 trees for dbh were considered sufficient for a forest cover extending over 60,000 m². In BORMANN and BUELL's study 160 distances were measured in a 28,000 m² forest, and in NEWSOME and DIX's study 60 distances in 6000 m². On the basis of one distance measure, this represents an area of 1500 m² in the first study, 175 m² in the second, and 100 m² in the third.

The lesser intensity in BRAY and CURTIS' study may have been balanced by a greater homogeneity requirement for the tree layer in their survey.

A major departure from the semiquantitative relevé analysis is apparent in the sampling of the lesser vegetation. The herb vegetation was sampled in all studies across the same area outline as the tree stratum, but a much smaller area was actually sampled.

This is shown in the following tabulation, which compares the examples in order of decreasing attention given to herbaceous undergrowth.

REFERENCE	SAMPLE PLOT AREA FOR TREES (m²)	SAMPLE PLOT AREA FOR HERBS (m²)	RATIO: TREE TO HERB PLOT
Releve'			-
(SECTION 5.3)	200	200	1:1
BOURDEAU and			
OOSTING (1959)	6,000	160	37.5:1
DAUBENMIRE			
(1968)	375	5	75:1
BORMANN and			
BUELL (1964)	28,000	50	560:1
NEWSOME and			
DIX (1968)	6,000	7.5	800:1
BRAY and			
CURTIS (1957)	60,000	20	3,000:1

The comparison reemphasizes that quantitative analyses of undergrowth or herbaceous layers give information only on a fraction of the sample stand. The less abundant species are never adequately evaluated. In sample stands stratified for undergrowth homogeneity, the

minimal area sample should be between approximately 50 to 200 m<sup>2</sup> in temperate forests (SECTION 5.2). The studies of BOURDEAU and OOSTING (1959) and of BORMANN and BUELL (1964) could be considered adequate from this point of view, but, since the large-sized sample stands were not selected for undergrowth homogeneity (only for tree layer homogeneity), it can be said that not one of the five quantitative forest studies we cited satisfied the minimal area requirement. If plant species outside the quantitative sample quadrats are not also evaluated (or at least listed as present) important information will be lost.

The two continuum studies (NEWSOME and DIX 1968, BRAY and CURTIS 1957) show the least intensive undergrowth evaluation. In BRAY and CURTIS' study this seems to be related to a difference in concept and objectives. While undergrowth species are not ignored. they are regarded as relatively unimportant. CURTIS (1959) considers them merely dependents of the dominants. Although this is true in some situations, many studies have given evidence of their relative independence. For example, NEWSOME and DIX found that many undergrowth species occur outside the forest and most are relatively independent of the species composition of the dominants.

Such a scattered sample of 1 m2 in every 3000 m2 over sample stands of 60,000 m<sup>2</sup>, as used in the BRAY and CURTIS study, can hardly be expected to yield sufficient data to document the existence of associations among undergrowth plants, or among plants belonging to a vertical cross-section of forest strata.

A rough time-comparison of the quantitative forest analyses with the forest relevé analyses can be made as follows. It took about 45 minutes to complete the 200 m2 relevé analysis discussed in SECTION 5.3. The count-plot analysis example (given in SECTION 7.3) took about 1 hour. This covered an area (120 m²) about half the size of the releve and included a count of about 100 trees-still an insufficient sample. The point-centered quarter analysis example of 5 points with 20 distances (given in SECTION 7.63) took about 30 minutes. In the latter analysis we ignored the small trees under 2 m height, which were included in the count-plot analysis. Thus, the two quantitative methods took about the same time. It is possible that a larger sample would have come out in favor of the distance method.

However, this comparison gives a general indication of the time required for the various analyses described. While a standard relevé analysis may take 1 hour, any quantitative analysis will take more time. Of course, if such details as a rough species list and a determination of tree size classes are made in advance, a quantitative analysis can be done more quickly.

The 15 sampling points (60 trees) in NEWSOME and DIX's study by

point-centered quarter method may have taken 1 to 2 hours. The 15 count-quadrats of 50 m² each for the saplings may have added another hour or two. The 30 small (0.25 m²) frequency frame placements also must have added about 2 hours to the analysis. Thus, we estimate that the quantitative field analysis of NEWSOME and DIX took from about 4 to 8 hours per sample plot.

The 40 distance measures of 80 trees at 40 points in BRAY and CURTIS' study must have taken at least 2 hours per stand, because of the wide spacing of each point. Their 20 frequency frame placements must have added another 2 hours field analysis time. Thus, the two studies for continuum analysis must have taken from half-a-day to a day per stand. It is probably not possible to complete more than one such large sample stand per day. In contrast, it is relatively easy to complete four forest releve analyses per day as described in SECTION 5.3.

7.73.2 Herbaceous and Low-Shrub Communities. In the three quantitative examples of nonforest communities, the same spectrum of parameters (density, cover, and frequency) was assessed as in the forest communities. However, in contrast to the tree stratum, density is the most complicated parameter to assess in communities whose dominant strata are herbaceous. This complication became apparent through the BLISS study of alpine communities, in which only selected species were counted, while the parameters evaluated for all species were cover and frequency. BLISS emphasized that the counting of low-shrubs, bunchgrasses and sedges in his study was for subsequent productivity research. Such a counting effort would not be warranted for a classification or ordination of these alpine communities. For the latter purposes, his cover and frequency evaluation in 20 small quadrats per stand was sufficient.

Species cover in this study was estimated in 20 small (0.1 m²) frames. This poses another question regarding the reliability of a cover estimate: Is it more adequate to (a) evaluate cover accurately in a small part of the plot (2 m² out of 60 m²) or (b) estimate cover with the general BRAUN-BLANQUET scale over the entire plot? Only a comparison of methods would give an answer. For the purposes of a classification or ordination, the second method appears more expedient, because it takes much less time and relates to the whole sample plot.

An evaluation restricted to 20 frequency frame placements per stand was also considered sufficient by WALKER and WEHRHAN for describing the wetland communities in Saskatchewan. If all species present in a "minimal area" were first carefully recorded, and then species quantities were evaluated by such a rapid quantitative method as ap-

plied by 20 frequency frame-placements, the difference between the relevé method and this kind of quantitative method would only lie in the accuracy of assessing the more abundant species. It is then still debatable whether 20 frequency placements give a better estimate of species quantity than a cover estimate per species. Many investigators would say that the 20 frame placements give a more objective measure of species quantities, but this judgment should depend on the reproducibility of the results with the given quantitative method.

Depending on the number of species present, the determination of frequency by 20 frame placements would extend the time required for a standard releve analysis by about 30 to 60 minutes. The question the investigator then faces is, whether he should invest this extra time in evaluating the more abundant species by such a quantitative method, or whether he considers the time more usefully spent in starting another releve with the BRAUN-BLANQUET scale.

Another problem, discussed in SECTION 6.31, is that frequency in quadrats is not an absolute measure. Without any doubt, a far better quantitative value is cover. The measurement of cover by the pointintercept method as done in the study of grass and shrub communities in Montana by BRANSON et al. is by far the most meaningful quantitative analysis of such nonforest communities for descriptive purposes. In such species-poor communities, as found in this area of Montana, it may even be possible to include in the measure of cover nearly all species that are found in the minimal areas of such communities. But even in species-rich communities, in which again only the more abundant species could be measured adequately by this method, the pointintercept method holds the greatest promise. This is so, because (a) the method gives an absolute measure, (b) the parameter measured is considered ecologically the most significant of the three (SECTION 6.51), (c) cover can be assessed for all plant life forms including the trees (SECTION 6.54.2) and (d) the point-intercept method gives the same measure as is aimed at by the estimate scales (SECTION 5.42).

The sampling intensity of the BRANSON et al. study was very high and consequently the time investment must have been high as well. Depending on species richness of a herbaceous or low-shrub community and the familiarity of the investigator with the species, a sample of 200 points taken with a point-frequency frame (FIG. 6.6, SECTION 6.54) may take between 30 and 60 minutes. In most situations a 200 point sample resulting in a measure of percent cover of the more abundant species seems a better time investment than the placement of 20 frequency frames for the quantitative description of herbaceous and low-shrub communities.

However, both parameters, cover and quadrat-frequency, may com-

method (

plement each other in studies where one aims at more than the description of spatial variation of a plant cover. For example, if one is interested also in the time-variation of a herbaceous cover, one may find species frequency in quadrats to be a less fluctuating parameter than cover in the seasonal behavior of a perennial grassland. The degree of variation of these parameters can in itself be of important information, for example, for the grazing value.

7.73.3 Size of Sample Stands. Further differences in concept between the releve' method and the quantitative methods are shown by the different sizes of sampling units. It is interesting to note that in FIGURE 7.6 each of the six sample units is subjectively selected, each of them with great care. The sampling within all but the first, however, was done by quantitative methods.

Also, these six sample stands were all chosen for their homogeneity in vegetation cover. They undoubtedly include the minimal area of each community for which they were selected as samples. For this reason they could all be referred to as relevés. However, the four large sample stands are not relevés in the strict sense, because they include a much larger area than the minimal area.

The difference in sample stand size rests on a difference in the homogeneity concept of the authors. Only two degrees of homogeneity have to be recognized to explain this difference. The small-sized sample stands were delimited by the uniformity of the small-sized vegetation—the herbs and small shrubs. The large-sized stands were delimited by the tree vegetation.

A second difference is that the relevé method aims with each sample stand (relevé) at a sample of a near-total species composition of a concrete community. In contrast, the standard quantitative methods aim at sampling the more abundant species. For the reason also, the forest sample stands are large. However, if the minimal area is not used as a guide to size, the guide to size is limited by the author's decision as to how many species he intends to sample adequately. In the count-plot example given in SECTION 7.3 only one tree species (Psidium guajava) may be considered adequately sampled with over 30 individuals on 120 m². If the other two important native tree species (Acacia koa and Metrosideros collina) were to be sampled adequately (with at least 30 individuals per species), the sample stand would have to be enlarged to at least 800 m² (0.2 acre).

However, for a complete stand analysis, both aspects, the near-total species record and an adequate sample of the more abundant species, can and should be combined. In forest stands this can be done as follows: A forest stand sample should always be delimited by the

homogeneity or uniformity of the lesser vegetation and the habitat. In mountainous terrain and in level terrain with small-area water table variations, this will result in relatively small sample stands such as shown in FIGURE 7.6 by the relevé example (200 m²) and by DAUBEN-MIRE's sample stand size (375 m²). To obtain an adequate enumeration of the more important tree species, it will then be necessary to add more relevés of the same vegetation type. In level terrain without distinct habitat variations, the relevé should be enlarged for enumeration of the tree layer by watching that the undergrowth-homogeneity is maintained for the larger sized sample area. In the latter case, the original near-total species relevé, which only needs to be a little larger than the minimal area of the community, may form a nested plot within the larger sample stand.

In contrast, quantitative concepts requiring contiguous, large uniform dominance-communities tend to exclude a number of extreme variations in any regional vegetation cover. Many cover variations may be too small for the arbitrarily decided minimum sample area. Therefore, only part of the regional vegetation cover can be described by such an approach. For purposes of classification this would impose a severe disadvantage. For example, BRAY and CURTIS' 15 acre sample stand requirement would be impossible to apply in most mountainous regions.

Yet, continuum analysis is not limited by sample unit size, degree of entitation, or regional characteristics of the vegetation. It can be carried out in narrowly defined communities that are sampled by small plots, if these are distributed over the total geographic range of recurrence of these communities. In this case, the difference between the classification and continuum approach dissolves, because the question is no longer which of the two approaches is more objective or whether continuity or discontinuity is the truer abstraction of the nature of the community. It is merely a question of whether the investigator is interested in the portrayal of the complete vegetation cover of specific regions or whether he is interested in limiting his description to an accurate enumeration of the abundant species only.