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Aims and Methods of Vegetation Ecology

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Measuring Species Quantities

6

6.1 QUANTITATIVE VEGETATION PARAMETERS

The more important measurable quantities in community sampling are:

1. Number of individuals or density (= abundance).
2. Frequency, the number of times a species is recorded in a given number of small quadrats or at a given number of sample points.
3. Cover, either of crown and shoot area or of basal area.

In addition, there are several other measurable quantities, such as height, stem diameter, and biomass. The latter is measured in volume (e.g., timber surveys) or obtained through cropping, and is usually expressed in fresh weight, dry weight, or gram calories per unit area.

Many other structural life form criteria are measurable, for example, leaf size, bark thickness, or current year's twig diameters. Also, functional parameters, such as leaf persistence, vegetative reproduction, and shade-tolerance can be subjected to quantitative analyses as has been demonstrated, for example, by KNIGHT and LOUCKS (1969).

Of great importance are the physiological parameters, such as transpiration rate, water potential, net assimilation rates, or other productivity parameters, such as litter production, seed production, annual diameter increment, etc. A widely useful measure related to cover and productivity is the leaf-area index (WALTER 1971). This is the ratio of the total leaf area in square meters (or other area unit) of a plant individual, species, or stand to the ground surface expressed in square meters (or other area unit). Only one side of the leaves is considered in the leaf-area index.

When speaking of quantitative ecology, these parameters definitely belong in the discussion. However, they are measured primarily for experimental rather than descriptive purposes. For the latter, only the first three parameters, listed above, are usually applied.

6.2 DENSITY MEASUREMENTS IN QUADRATS

This parameter relates to the counting of individuals per unit area. Counting is usually done in small quadrats placed several times into the community. Afterwards, the sum of the individuals per species is calculated for the total area sampled by the small quadrats, and the result is expressed in terms of species density per convenient area unit, such as a square meter, an acre (approx. 4000 m^2)* or a hectare (10,000 m^2).

Counting is perhaps the easiest analytical concept to grasp, but it often causes difficulties in application. One difficulty is the recognition of individuals. Trees and single-stemmed annuals present little difficulties, but nearly all other plant life forms do. In spreading shrubs, particularly where standing close together, it is often difficult to decide where one individual begins and another ends. This problem is aggravated in creeping shrubs or krummholz. Bunch-grasses or tufted fern fronds and caespitose or single-stemmed herbs are usually countable, particularly if their individual outlines are well shown. But many other perennial herbs, such as rhizomatous or stoloniferous forms, can

* Exactly 4046.85m^2.

hardly be counted accurately. In grasses it sometimes helps to cut off the shoots near ground level. One may then count individual stems more easily, but still may have difficulties in deciding whether a stem represents an individual plant or just an upright stem or branch coming from a rhizome. It is usually impossible to count individual mosses in a moss carpet.

In those cases, a decision must be made whether one can really count individuals or just parts of individuals. The latter may have little meaning. Although for certain experimental purposes, the number of shoots may be of greater significance than the number of individuals (STEBLER and SCHRÖTER 1887, SPATZ and MUELLER-DOMBOIS 1973). A count of some sort can often be established. It then gives the impression of great accuracy. But unless backed by a proper definition, it may be less accurate than a visual estimate of abundance. Therefore, application of counting as a sampling tool is limited by the plant life forms and their spacing, and accurate counting in all slightly difficult situations requires a good knowledge of plant life forms (see CHAP. 8).

A second difficulty is the marginal effect of the quadrat. The quadrat boundary may go through an individual and a decision has to be made whether to count it or to exclude it. This problem becomes aggravated by denser vegetation and smaller quadrats. The smaller the quadrat the greater the boundary in relation to the area, and the more frequently will a decision be required whether to count a marginal individual or not. Also here, an arbitrary definition helps to ease the problem, if one decides, for example, to include only those individuals that are rooted within the quadrat area; but even this may be difficult to decide.

The boundary problem in counting has been overcome to some extent by the plotless distance measures, such as the random pairs method and the point-centered quarter method (CHAP. 7). However, these are primarily applicable only to woody plants that are randomly distributed.

A third major difficulty is the time it takes to count herbaceous and shrubby individuals. Before investing time in counting, the purpose of the study must be very clear. Counting has particular value in assessing changes in studies of succession or changes caused by treatment in experiments. Also, for comparison of closely similar communities, counting of individuals may reveal important insights. For ordinary descriptive purposes, however, the time factor is often prohibitive, because the result conveys little more meaning than a less time-consuming abundance estimate.

6.21 Size of Density Quadrats. Quadrat size must be related to the size and spacing of the individuals, because counting of numerous individuals per species cannot be done accurately in large plots unless they are subdivided, or the individuals are marked off after each is enumerated. How many individuals (regardless of species) one may count accurately within a given quadrat is almost entirely a matter of judgment. Therefore, the quadrat size is not very important. However, for statistical analysis, a certain limitation is indicated (see discussion under sample size, SECTION 6.4).

In spite of the personal judgment involved in determining suitable sizes for density quadrats, the sizes usually vary within limits for each height stratum. Commonly used sizes are for the tree layer, 10×10 m quadrats; for all woody undergrowth up to 3 m height, 4×4 m quadrats; and for the herb layer 1×1 m quadrats (OOSTING 1956).

This decreasing range shows resemblance to the minimal area sizes stated in SECTION 5.2. But this is only because smaller plants usually occupy less space than larger plants. Otherwise, the two kinds of quadrats are for entirely different purposes: the minimal area quadrats for obtaining a representative combination of species, and the density quadrats for obtaining conveniently an accurate estimate of number of individuals per unit area.

6.22 Shape of Density Quadrats. CLAPHAM (1932) and others (e.g., BORMANN 1953) have demonstrated that the shape of density quadrats also has an effect on the accuracy of the count. Rectangular shapes are more efficient than square or circular shapes, because of the general tendency of clumping in vegetation (GREIG-SMITH 1964).

BORMANN (1953) further qualified this phenomenon. He found that the reduction in variance associated with rectangular as opposed to square sampling units applies only if the long axis of the rectangular plot cuts across any banding in vegetation pattern. Such a perpendicular alignment apparently increases the variation within the sample unit, but it decreases the variation between them. Therefore, the sampling intensity per sample unit is increased and the variance between them is reduced.

This observation does not apply to minimal area plots. Their purpose lies only in sampling a near-complete species composition of the vegetation segment. Therefore, their shape is inconsequential. They may be square, circular, rectangular, or even irregular, if the segment demands such a shape.

shape of minimal area plot inconsequential

6.3 FREQUENCY DETERMINATION

Frequency relates to the number of times a species occurs in a given number of repeatedly placed small sample plots or sample points. It is expressed as a fraction of the total, usually in percent. No counting is involved, just a record of species presence. Frequency is a much more readily established quantitative measure than either the counting of individuals or the measurement of cover.

Small plots or points may either be distributed randomly, for example, by throwing a metal ring, or systematically, by following a regular pattern (FIG. 6.1). In each placement, the species are recorded without regard to their quantity or number of individuals. For comparing different communities, frequency is best expressed as a percentage of the total number of placements, i.e., the so-called "frequency percentage" or "frequency index" (GLEASON 1920) is determined.

In our example, the frequency percentage of the species represented by dots is 84 percent (Fig. 6.1a) and 72 percent (Fig. 6.1b), and the frequency for the species shown by crosses is 24 and 20 percent, respectively. This difference can be decreased only by using a larger number of placements (e.g., 100), which requires much more time.

The determination of frequency was originally developed by RAUNKIAER (1913). It was applied and further developed particularly by Scandinavian and Anglo-American investigators. BRAUN-BLANQUET and his students use frequency determinations only in special cases, as it requires much time in species-rich communities. The method proved to be very useful, however, in the species-poor communities of

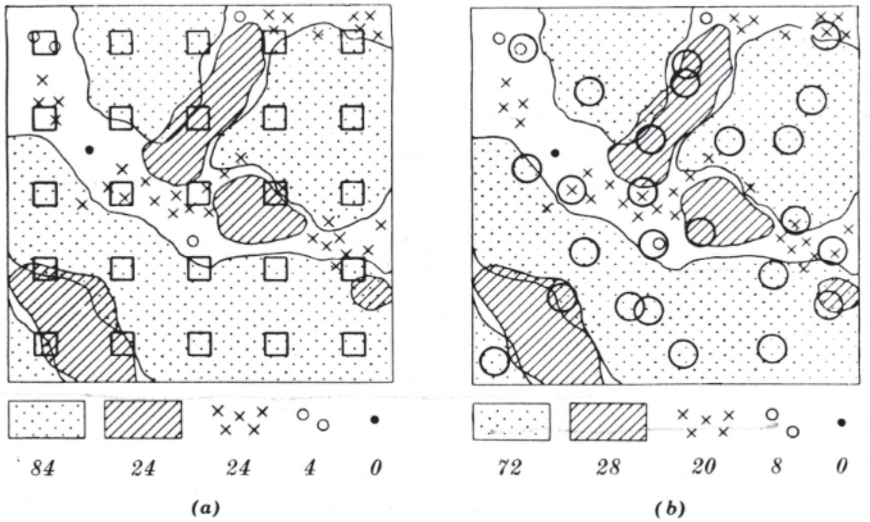

FIGURE 6.1. Frequency determination referring to the sample quadrat or plot shown in FIGURE 5.4: (a) *regular distribution of 25 frequency quadrats;* (b) *random distribution of 25 circular frequency plots.*

the North and in alpine areas, on intensively grazed meadows in the Netherlands (DE VRIES 1949), and in investigations of aquatic and marsh plant communities in Central Europe (TÜXEN and PREISING 1942). Frequency is the most commonly applied quantitative parameter for the analysis of forest undergrowth and herbaceous communities in North American descriptive studies.

6.31 Frequency in Quadrats—a Nonabsolute Measure. Frequency provides for an objective assessment similar to density and cover measurements, but, in contrast, it is a nonabsolute measure. This means that the result is in part a function of the size and shape of the quadrat frame. Depending on the species richness per unit area, a slight increase in frequency-frame size usually results in quite different frequency results for species of intermediate abundance. Since individuals of a species normally show concentrations within an otherwise homogeneous vegetation cover, a rectangular frame is likely to assess a somewhat different frequency than an equally sized square or circular frame. Because the results depend on the frame size and shape, they have meaning only in relation to a particular frame size and shape selected for a determination.

Frequency is often considered a measure of abundance. Therefore it should be related to density. However, GREIG-SMITH (1964) has clarified that frequency rarely gives an indication of number of individuals per species, because, for this to be true, individual plants must be regularly or randomly distributed. Instead, plants are usually contagiously distributed. Therefore, sociability or dispersion, i.e., local or small-area patterns enter into the measure of frequency. A species with a large number of individuals may show low frequency values simply because the individuals are concentrated in patches, whereas a species with the same number of individuals spread out evenly over the sample area may show 100 percent frequency. Therefore, frequency gives a certain indication of uniformity of distribution rather than of density. Of course, a species with few individuals can never show high frequency values, even if they are uniformly distributed, unless the quadrat size is very much enlarged. Therefore, frequency confounds the two parameters of density and dispersion.

Frequency gives little or no indication of cover when determined in frames or quadrats. A species with very small individuals evenly spread out over the sample area will give high frequency values, even though its cover may be insignificant. A species with few individuals but large crown or basal areas that cover a considerable portion of the sample area, will give low frequencies.

However, this depends on the criteria set for what plant part to include or exclude in the frequency count. RAUNKIAER's concept was to count a species, if the perennating bud of an individual of that species was inside the frame. This concept is difficult to apply in the humid tropics, where plants lack seasonal shoot reduction. In North America, the usual criterion is that the plant must be rooted inside the frame (CAIN and CASTRO 1959). In a creeping or matted life form the latter criterion results in lower frequency. Therefore, the perennating bud criterion takes cover somewhat into consideration. A stoloniferous matted grass may be included wherever it is rooted at the nodes. In this case, cover is included in the frequency count, rather than number of individuals. This shows that a number of subjective decisions must be made before one can assess frequency objectively.

Frequency can be made an absolute measure by eliminating the effect of quadrat or frame size. This is accomplished by reducing the quadrat to a point. The point may be a needle, sharpened rod, or a sighting cross made of wires or hairs (such as in rifle telescopes, for example). A needle lowered at predetermined points over a herbaceous cover will either miss or intercept a plant part at each lowering. This technique gives a record of presence or absence for the more abundant species composing the cover. Therefore, in this case frequency is used to measure cover. This method, generally known as the "point-quadrat" method, will be discussed among the methods of measuring cover (see SECTION 6.54).

Another way of determining frequency that does not involve quadrats or boundaries is provided by the Wisconsin distance methods (SECTION 7.6).

6.32 Frame Size for Frequency Determinations. Frame size is primarily a function of plant size and species richness per unit area. If, for example, 20 to 30 species occur in 1 m² of a low (10± cm) herbaceous cover, a subdivision of that frame into one hundred 10×10 cm (0.01 m²) frequency subquadrats appears suitable. A number of 3 to 8 species per frequency frame can be counted conveniently. Any larger number of species slows down the progress considerably.

Such a 100-square quadrat is shown in FIGURE 6.4 (SECTION 6.53). A record of the presence of species in such a grid of quadrats is known as "local frequency" (GREIG-SMITH 1964). Local frequency can also be analyzed in larger frames as long as they are placed into a contiguous matrix.

Since species counting depends on the ease of recognition at any one stage of development, quadrat sizes may vary within limits according to individual preferences of the investigator. In general they can be somewhat larger than quadrats for counting individuals, but the same size may be used for both purposes. Enlarging the frequency quadrat can have the effect of showing a 100 percent frequency for a sparsely represented species, which then would have the same frequency value as the abundantly represented species. DAUBENMIRE (1968) recommends, as an empirical rule, a reduction of the frequency frame size when more than one or two species show a frequency of 100 percent.

CAIN and CASTRO (1959) suggest the following empirical sizes:

Moss layer	**0.01–0.1 m²**	.1 - 4 m²
Herb layer	**1– 2 m²**	10 - 100 m²
Low shrubs and tall herbs	**4 m²**	10 - 25 m²
Tall shrubs	**16 m²**	
Trees	**100 m²**	500 m²

RAUNKIAER used a ring of 0.1 m² size for herbaceous and low undergrowth forest vegetation. Another commonly used unit is 1 m² of either 1×1 m or 0.5×2 m sides. Since the results depend on the frame size, the size must be uniform for comparisons. In the larger quadrats suggested by CAIN and CASTRO for tall shrubs and trees, frequency is usually only a by-product to the counting of individuals or the assessment of basal area or cover. To line out such large quadrats simply for frequency would, for most purposes, be a poor time investment.

6.33 Frequency and Minimal Area. This topic is discussed because a certain confusion exists in the literature, that is, how can one establish the minimal area from frequency data?

If one is interested in sampling a representative species composition in addition to a reasonably accurate quantitative assessment of the more dominant species, the species/area curve should not be ignored. To obtain an adequate species complement of a stand, the area covered by a number of small quadrats for quantitative parameters should approximately equal or exceed the same area in square meters as indicated by the minimal area (RICE and KELTING 1955).

CAIN (1943) experimented with frequency quadrats in an alpine fell-field vegetation and found that the accumulated minimal area obtained from placing several small, even-sized quadrats in a scattered arrangement was very much smaller than the minimal area established from successively enlarged nested plots. He found a minimal area of 32 m² through a successively enlarged, nested plot, while only four randomly placed 0.1 m² plots indicated a minimal area for that community. CAIN considered this small (0.4 m²) minimal area insufficient for a sample of frequency, because a frequency determination from only four quadrats can hardly be expected to yield adequate results. He suggested using twenty 0.1 m² plots, a total sample of 2 m². (The number twenty was an arbitrary choice.) CAIN concluded from his data that many small plots take less time and give a more adequate description of a stand than a single, large plot.

An inspection of CAIN's (1943) species/area curves shows that the 32 m^2 minimal area obtained from the nested plots contained 22 species, while the 0.4 m^2 minimal area obtained from the four 0.1 m^2 frames contained only 15 species. Therefore, CAIN's conclusion of a more "adequate" description can only relate to his satisfaction obtained by an objective and quantitative determination of frequency. But even 20 frame placements are considered too few for almost any community evaluation (GREIG-SMITH 1964).

An adequate description should include nearly all species found in the community. If a sampling scheme ignores one-third of the species composition of the stand, it cannot be used to define the minimal area. Therefore, CAIN's study shows that the minimal area of a community cannot be defined through a species/area curve obtained from random placements of small plots.

By using small quadrats in scattered formation, there is always a chance that species represented by only a few individuals (i.e., the rare ones) are not included in the sample. The inclusion of a rare species influences the shape of the species/area curve just as much as does the inclusion of an abundant species. Therefore, only a system of contiguous or nested plots will define the minimal area adequately. There is no theoretical reason why this cannot be done with small, even-sized quadrats. This would permit the determination of frequency at the same time. But these quadrats must then be placed in a contiguous matrix as is done in the nested plot technique. Thus, the minimal area can be established from frequency data only through what is known as a "local frequency" analysis. In CAIN's example, it would require 320 side-by-side placements of the 0.1 m^2 frame to cover the minimal area of 32 m^2. This would obviously be too time-consuming for the objectives at hand. The same area could be covered with thirty-two 1 m^2 frames. This would permit enumeration of an adequate (i.e., representative or near-complete) species sample of the community combined with a frequency determination of even greater accuracy than suggested by CAIN.

CURTIS and GREENE (1949) referred to CAIN's (1943) findings and restated that frequency samples should be larger than the minimal area. This statement becomes understandable only in view of a minimal area concept that ignores the less frequent (rare) species. However, this interpretation is in disagreement with the original intent of the minimal area concept. It is not surprising, therefore, that some confusion has arisen about the concept and the meaning of the species/area curve.

In trying to find an alternative to the species/area curve, RICE (1967) suggested eliminating altogether the dependency on this curve for finding a suitable sample size. His reason, also held by GOODALL and others, is that the ecologically most important aspect of plant distribution would be the distribution of the quantity of plant material (probably meaning biomass), rather than the distribution of individuals. This is a clear shift in objective, which has little to do with the value of the species/area curve as an indication of the representative species composition of a community. From a different perspective it can just as well be argued that the most important aspect of plant distribution is species diversity. For obtaining the smallest sample area with a maximum number of species of a community, the species/area curve is still the best tool. However, it cannot serve to define the sample size needed to evaluate adequately the number of individuals per species, their cover, or their frequency.

In conclusion it may therefore be well to restate that there are basically two types of sample quadrats: the large minimal area quadrat, which is used for the purpose of sampling a representative species composition in recurring plant assemblages; and the small quadrat adapted in size to height and spacing of species individuals, which is used for the quantitative analysis of individuals per species (or cover or frequency). The density quadrat should be small for the convenience of accurate counting, but not so small as to cause proportionately too high a personal error through the edge effect.

6.4 HOW TO DETERMINE SAMPLE SIZE

The sample size, which relates to the number of times a given density or frequency quadrat should be repeated, is often arbitrarily delimited. In timber volume surveys, it is common practice to set a percentage limit. For example, one may set a standard of 5 or 10 percent sampling intensity. This refers to the area that is covered by the vegetation segment. If the latter covers 6 hectares (15 acres), a 5 percent sample would extend over an area of $0.05 \times 60{,}000\ m^2 = 3000\ m^2$. This area could be sampled, for example, by thirty 10×10 m plots.

GREIG-SMITH (1965) emphasized that the accuracy of the count is not a function of the area sampled, but a function of the number of enumerations. This is related to the factor of spacing. Where the individuals are widely apart, far fewer are counted in the same size of plot than where the individuals are close together. Therefore, in stands with great differences in spacing, it seems advisable to use as many plots as are necessary to count a given number of individuals. As a result, the actual area sampled may vary considerably. Of course, the number of plots to be counted is a function of the variation of individuals between plots. The greater this variation, the more plots are needed.

6.41 A Statistical Approach. In probability-statistics one may use the ratio of the standard error of the mean to the mean as a measure of sample size (GREIG-SMITH 1964). For a POISSON distribution, this can be expressed as

$$\frac{\sqrt{x}}{n} : \frac{x}{n} = \frac{\sqrt{x}}{n} \times \frac{n}{x} = \frac{\sqrt{x}}{x} = \frac{1}{\sqrt{x}}$$

where x is the sum of the enumerations and n the number of quadrats. The ratio of standard error of the mean to the mean reads $1/\sqrt{x}$, and n is cancelled out. Where species individuals are randomly distributed, the accuracy of the density estimate is not affected by the size of the quadrats, only by the number of individuals counted. Such random distributions may be found in tree communities if one considers all tree individuals together as a group regardless of species. However, the ratio applies only where large numbers of sample quadrats or counts of individuals are involved. The larger the total count of individuals, the smaller this error term (FIG. 6.2). However, GREIG-SMITH (1964) points out that such statistical error terms cannot usually be applied to the individuals of single species, because the individuals of a species are rarely randomly distributed. Therefore, the curve is only a guide. The standard error of the mean as $\sqrt{x}/n$ is applicable only to a POISSON distribution, where the mean equals the variance. Where one cannot assume this, calculate the standard error of the mean (SEM) as the variance (s^2) divided by the number of samples (n), *i.e.*, $SEM = s^2/n$, where s = standard deviation. An example is given in the next section.)

6.42 Plotting the Running Mean. A practical guide to estimating adequacy of sample size for small density quadrats is to stop sampling at the point at which additional quadrats do not significantly affect the mean of the more important (or abundant) species. This can be tested by calculating and plotting a cumulative or running mean during the quadrat analysis (KERSHAW 1964).

In practice it is often satisfactory to set an arbitrary standard of sampling size by requiring that a sample be within 5 or 10 percent of a more time-consuming maximum sample.

The two ideas on sample size are closely related, and one may interpret the 5 percent limit as a nonsignificant variation from such a sample size curve (FIG. 6.3). For example, the density count of a small single-stem lichen, *Stereocaulon vulcani,* occurring on recent lava rock in Hawaii was made in eighteen 1 cm^2 quadrats. The cumulative or running mean was calculated for always two quadrats at a time, giving the results shown in TABLE 6.1.

The running mean values are plotted over the number of quadrats in FIGURE 6.3. After an initial greater variation, the curve becomes less variable already after the sixth's quadrat.

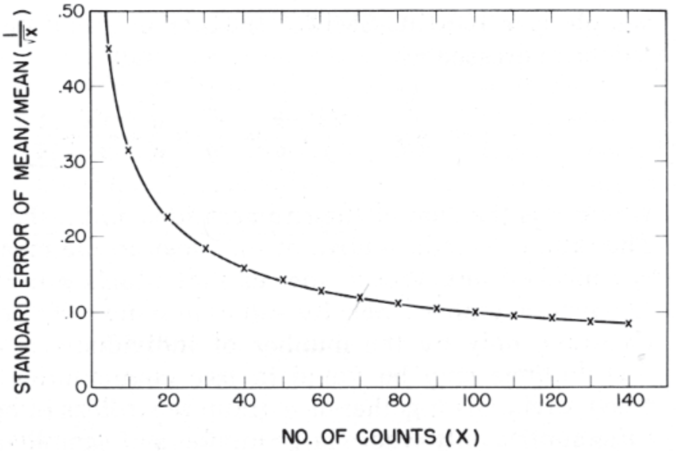

FIGURE 6.2. Relation of standard error of mean/mean ($1/\sqrt{x}$) to number of counts among randomly dispersed individuals. Like the species/area curve this relationship is one of decreasing returns with increasing sample size.

If we intend to stop sampling when the running mean shows insignificant variation, we might choose to stop after 8 quadrats were sampled. Here the mean was identical to that of 18 samples. In other words, a count of 104 individuals gave the same mean as a count of 233 individuals. In applying the criterion to stop sampling, when the running mean comes to within 5 percent of a more time-consuming maximum sample, we might stop counting after 6 quadrats. Five percent of the mean of the arbitrary maximum sample of 18 quadrats is $0.05 \times 13 = 0.65$. Thus, the mean of 6 quadrats of 12.7 lies within 13 ± 0.65. In the latter case, only 76 individuals were counted.

If the *Stereocaulon* individuals were randomly distributed, the error term ($1/\sqrt{x}$) for 72 individuals would be $1/\sqrt{72} = 0.12$ (FIG. 6.2). We may not wish to make this assumption, and instead calculate the error term (SEM/MEAN) by using the formula $\text{SEM} = s^2/n$ (where s = standard deviation). Applied to the first 6 quadrats of the *Stereocaulon* example, the calculation would be as follows:

	Quadrat no. = n	Count x	x^2
	1	13	169
	2	15	225
	3	11	121
	4	9	81
	5	15	225
	6	13	169
Sum	6	76	990

$$\text{MEAN} = \frac{\text{sum x}}{\text{sum } n} = \frac{76}{6} = 12.67$$

$$\text{VARIANCE} = s^2 = \frac{\text{sum x}^2 - \frac{(\text{sum x})^2}{n}}{(n-1)}$$

$$s^2 = \left(990 - \frac{76^2}{(6-1)}\right) = \frac{(990 - 962.67)}{5}$$

$$s^2 = \frac{27.33}{5} = 5.47$$

SEM = standard error of the mean

$$\text{SEM} = \frac{s^2}{n} = \frac{5.47}{6} = 0.91$$

$$\text{Ratio SEM/MEAN} = \frac{0.91}{12.67} = 0.07$$

The result shows that the error term (SEM/MEAN) for the count of 72 *Stereocaulon* individuals is even less than that expected for a random distribution. Therefore, the *Stereocaulon* individuals seem to approach a regular distribution.

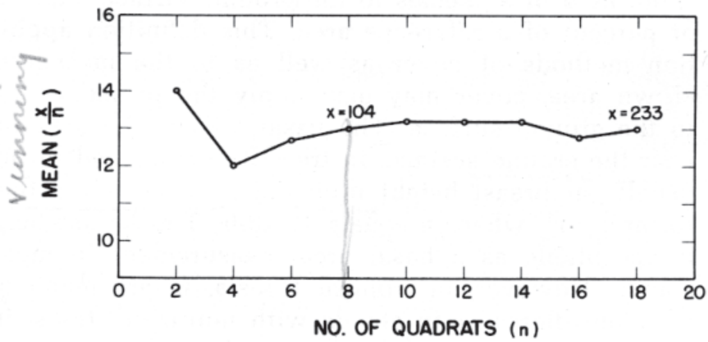

FIGURE 6.3. Plotting of running mean.

TABLE 6.1 Running Mean Number of Stereocaulon *Stems from Each of Two Quadrats for 18 Random Quadrats of 1 cm^2.*

NUMBER OF *STEREOCAULON* STEMS PER CM^2	CUMULATIVE TOTAL NUMBER	RUNNING MEAN
13, 15	28	14.0
11, 9	48	12.0
15, 13	76	12.7
13, 15	104	13.0
13, 15	132	13.2
13, 14	159	13.2
13, 12	184	13.1
11, 11	206	12.9
14, 13	233	13.0

It may be noted that the determination of an adequate sample size for quantitative analysis is handicapped by the same limitation as the determination of the minimal area through the species/area curve. In both cases there is no strictly objective criterion, and a decision has to be made by the investigator. A decision is always subjective, but it should be based on good judgment.

Moreover, the decision of what constitutes an adequate sample size is relatively easy for one-population stands as in the *Stereocaulon* example. A problem is introduced when there are more than one species to be quantitatively assessed. This is the case in almost all plant communities.

It is not always appreciated that in quantitative analyses it is possible only to evaluate the more abundant species with reasonable accuracy.

6.5 COVER MEASUREMENT

Usually cover is defined as the vertical projection of the crown or shoot area of a species to the ground surface expressed as a fraction or percent of a reference area. This definition applies to the estimation methods of cover as well as to the measurement. Instead of crown area, cover may also imply the projection of the basal area to the ground surface. The basal area is the area outline of a plant near the ground surface. In trees it is measured through the diameter, usually at breast height (dbh), i.e., 1.5 m above the ground, by the formula πr^2, where r equals ½ dbh. The breast height measurement is acceptable as a basal area measurement in most temperate tree stands. However, in tropical forests, where many species have distinct butt-flares or in stands with multistem trees, it is necessary to measure the diameters at the tree base, if one claims to have measured the basal area. Even in temperate forests breast height area is smaller than real basal area. The basal area concept is sometimes applied to caespitose life forms such as bunch grasses. Here it relates to the space occupied by the shoot system at ground level.

6.51 Ecological Significance of Cover. Cover as a measure of plant distribution has been emphasized as being of greater ecological significance than density (RICE 1967, DAUBENMIRE 1968). This idea is based on the observation that cover gives a better measure of plant biomass than does the number of individuals.

Plant biomass is the first and second order criterion for the structural classifications developed by FOSBERG (1961) and by UNESCO (ELLENBERG and MUELLER-DOMBOIS 1967a). The first structural divisions are based on spacing and height of the plant biomass. Plant biomass is an indication of the capacity of a vegetation to accumulate organic material if something is known about the developmental status of the community and its use as food supply for animals. Plant biomass has a major influence on the stand climate in terms of light and temperature relations. It influences the water relations through rainfall interception and transpiration rate per unit area, and it is closely related to the volume of circulating nutrients in the ecosystem. Moreover, the amount and characteristics of the plant biomass are of direct importance to the animals associated with the vegetation, because the plant biomass provides their shelter and food.

Plant biomass is evaluated through cover only in conjunction with a measure of depth or height. For descriptive purposes, this is accomplished by the stratification of a community into the various height layers as discussed in CHAPTER 5. Therefore, cover must be evaluated separately for each height layer or vegetation stratum.

Another great advantage of cover as a quantitative measure is that nearly all plant life forms, from trees to mosses, can be evaluated by the same parameter and thereby in comparable terms. This does not apply to density or frequency. However, cover can be measured in several ways, depending on the kind of vegetation and the objectives of the study.

6.52 The Crown-Diameter Method. A method for trees or bushes analogous to the basal area measurement is as follows. A meter tape is laid out on the ground from one side of the crown perimeter of the tree or bush across the center to the other side of the crown perimeter. This results in one diameter reading. Since crowns do not usually form a perfect circle, it is necessary to run at least a second crown-diameter measurement more or less perpendicular to the first one. The crown cover (*cc*) is then obtained from the formula

$$cc = \left(\frac{D_1 + D_2}{4}\right)^2 \pi$$

where D_1 equals the first measured crown diameter and D_2 equals the second measurement. The result can be expressed in square meters of crown cover. To relate the crown-cover measurement to a unit of ground area, it is necessary to measure such a unit of ground area as well. However, this method is not practical where one is interested in the cover by species over a larger area to obtain a more widely representative sample. In that case one can often use the line-intercept method (SECTION 6.55).

6.53 The Quadrat-Charting Method. In low herbaceous vegetation (for example, in pastures) cover can sometimes be charted or mapped from small quadrats. For example, in a square-meter quadrat or frame, the outline of the crown area of certain species or their basal shoot systems can often be drawn to scale on a sheet of paper. This can be

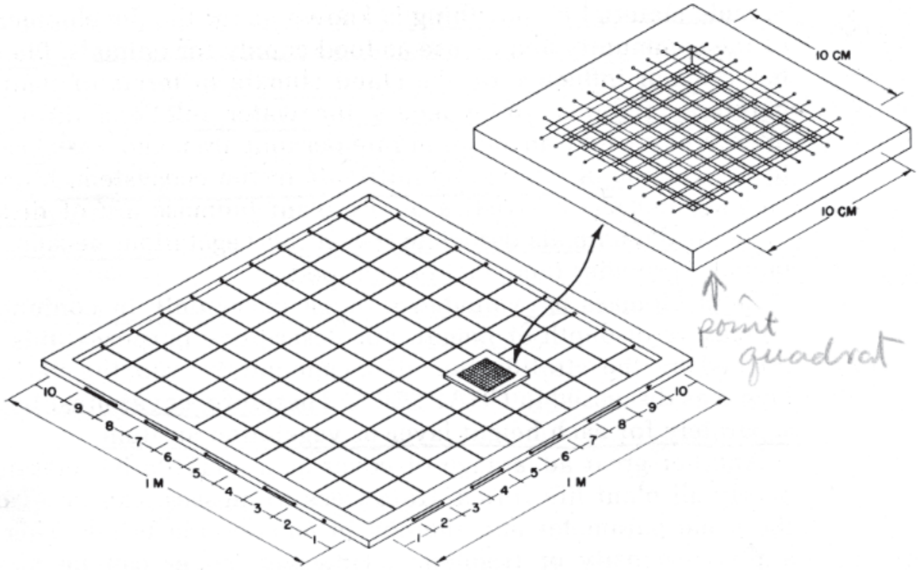

FIGURE 6.4. Square-meter quadrat with 100 dm subsquares for counting local frequency and for charting cover outline of herbaceous plants with solid shoot parts that show almost complete cover within their outlines. A separate decimeter quadrat with 100 subsquares strung from thin nylon thread can be superposed for point frequency measurements of cover. Further explanation in text.

Charting
Pantograph
Photographs

done by subdividing the square meter into 100 square decimeters and by numbering the coordinates of the quadrat frame accordingly, from 1 to 10 (FIG. 6.4). Crown or basal shoot outlines and the area occupied by matted plant forms can thus be transferred quite accurately on a sheet of graph paper.

Where the herbaceous vegetation is taller (for example, in a bunchgrassland) such a 100-square quadrat, when lowered to the ground, may bend down many plants and thus distort or increase their real cover. In that case one can remove a few strings and instead use only twenty-five 2×2 dm squares. Where this still results in the bending and distorting of plants, one can reduce the string-grid to a cross, dividing the frame into four quarters, or one can leave out the string-grid altogether.

Of course, where the plants are so tall that a strong-grid in a square meter frame becomes an obstruction to its positioning on the ground, a 1 m^2 quadrat may be too small a sample area. In that case one can establish a 2×2 m map-quadrat by repositioning the square meter frame four times. Other combinations of sizes are, of course, possible as well.

It must be emphasized that the quadrat-charting method is primarily useful only for permanent quadrats, because mapping a quadrat is time-consuming. Studies of successional or seasonal changes of a herbaceous plant cover on exactly the same place are ideally done in such quadrats. A square-meter frame can easily be positioned by driving two pegs into the ground at diagonal points and recording the compass direction of the frame. It is wise to survey the pegs for easier relocating by measuring their distance and direction to a nearby landmark, such as a boulder, isolated tree, or cross-road.

Another way of charting plant cover in small quadrats is to use a pantograph. The pantograph system is illustrated in FIGURE 6.5.

Similarly, photographic records can be used, which are merely variations of the quadrat-charting method. WIMBUSH, BARROW, and COSTIN (1967) describe a photographic method of determining plant cover of a bunch-grass vegetation. Photographs were taken at 2 m height above the plant cover at prefixed points along a transect. But, photographs often suffer from unclear background, creating difficulty in subsequent interpretation of plant outlines on prints. This is not so where the tree crown canopy is photographed from below. EVANS and COOMBE (1959) made photographs from the ground upwards to interpret the structure of the crown canopy of forests. For this they used an especially adapted hemispherical lens (called the "fish eye" lens), which is excellent for wide-angle canopy photographs. Such photographs can be taken at prefixed points along a transect. The area-distortion on the prints is easily adjusted and the cover can be calculated from the prints by the point-intercept method by using a transparent dot-grid (SECTION 6.54).

The quadrat-charting method can, of course, also be used to map the position of individual plants whose cover is insignificant. Thus, the method is a universal technique for mapping herbaceous or other small plants on small areas.

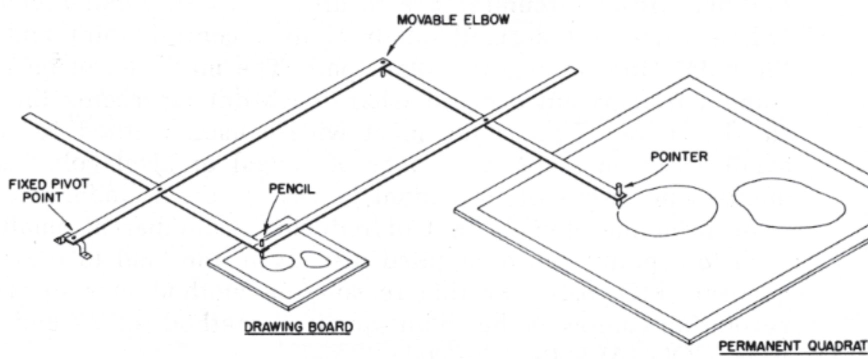

FIGURE 6.5. Pantograph system.

The same method can also be used for trees and other woody plants. But then the quadrat has to be larger, for example, 10×10 m. In that case the quadrat is outlined with string, and a grid of subquadrats can be strung out to convenience. Such larger map-quadrats may have some use in permanent tree plots, but their use is very much more restricted than that of the small chart-quadrats for herbaceous vegetation. The reason is that trees and bushes are long-lived perennial plants on which more detailed periodic measurements are more useful than cover outline and position. The standard detailed measurements on trees include periodic diameter and height measurements.

As a measurement of plant cover, the quadrat-charting method has three major limitations.

1. The cover of plants is merely shown diagrammatically. It still has to be measured.

2. The method is limited to plants whose shoot-outline covers nearly 100 percent. It cannot be used for a mixed plant cover, where the shoot systems are heavily intermingled.

3. The method cannot be used very well to obtain a representative sample of plant species cover over a larger area. It is useful only for a detailed analysis of a small area, i.e., for permanent quadrats.

These three limitations are overcome by the point-intercept method.

6.54 The Point-Intercept Method. When the cover outline of plants has been drawn to scale from the 100-square quadrat in the field to a sheet of graph paper with 100 squares, the plant cover is easily evaluated by counting filled squares and fractions of squares. This evaluation can, of course, be done directly in the field-quadrat without first preparing a map-diagram.

However, when we count fractions of squares, we are, strictly speaking, still estimating cover, instead of measuring it. A common method to measure cover or area outline on maps is to use a planimeter, which consists of a small wheel with a counter that converts the measure of circumference to area. A much simpler method is to reduce each of the small quadrats to a central point and to count the points that intercept a plant part. The method can be applied by using a transparent dot-grid where each dot represents the area of a small quadrat. This is the most widely used method for measuring small areas on maps, the cover of fungal or algal colonies under a microscope, areas of individual leaves, or areas under a curve. The same principle, namely that of reducing a number of small quadrats each to a point, can be applied directly in the field to the 100-square quadrat (FIG. 6.4). For this reason the method was introduced for vegetation studies as the "point-quadrat" method (LEVY and MADDEN 1933, GOODALL 1952, 1953*c*).

6.54.1 Application to Herbaceous Cover. When we lay out the square meter quadrat of FIGURE 6.4 with its 100 dm subsquares on a low herbaceous cover such as a pasture or cut lawn, we could perhaps simply use the cross-points of the string-grid to determine whether or not the vertical projection of a point intercepts with a plant shoot part and to what species each intercepted part belongs.

Apart from the fact that we would then have only 81 cross-points, this method would soon run into difficulties. The main difficulty is that of parallax. By viewing each point formed by the string-grid, two people would probably obtain quite different results. Without a second cross-grid it is possible to aim into various directions under each cross-point. Therefore, it is necessary that a second layer of points is established that matches the first one as shown on the small square-decimeter quadrat on FIGURE 6.4. With such a double grid of cross-points the possibility of aiming at different points under a double-sighting cross is very much reduced.

It would probably be sufficient for most pastures or short-grasslands to reduce each of the 100 dm squares to a single point and to then establish the plant-intercepting points out of 100. As a tool, one could use the small decimeter double-sighting cross by placing it in sequences on each of the 100 subsquares of the square meter frame and by reading off whatever intercepts the central-sighting cross below. To avoid confusion, one can restring the small frame with only one pair of matching crosses in the center or on the side. The position of the double-sighting cross is immaterial. One can also use a knife blade, stick it into the ground and read off the interception, if there is any, at the sharp edge. Such a method, using a bayonet, has been described by POISSONET and POISSONET (1969) for tall-grassland, whereby the bayonet was stuck every 20 cm into the ground along transects. In the decimeter quadrats of the square meter frame this method would not eliminate the possibility of wishful aiming, unless the knife position is prefixed by, for example, the use of a ruler.

The sampling intensity as described by the distance and total number of points is always a question of plant size, variability of species pattern, and objective of the analysis in relation to the time available. The small 100-point frame shown in FIGURE 6.4 was used by one of the authors on species-rich tropical monsoon pastures in Ceylon to measure recovery of the short-grass cover in permanent square meter quadrats following scalping of the grass sod by elephants (MUELLER-DOMBOIS and COORAY 1968).

In the cover analysis, the small 100-point frame was placed on usually six decimeter squares that were each determined randomly from the set of the two coordinates or by stratification from a map diagram. In this way the total cover-sample was 600 points and the percent grass cover in each permanent quadrat was determined for intervals of two months. The small 100-point frame was used only to determine the changing grass cover. Species were not distinguished.

It must be emphasized that the few tools described here have rather limited application, but the point-intercept principle has a very wide application, which extends from microscopic plant life forms (as already mentioned), to trees, and to including the BITTERLICH method for measuring stem cover (SECTION 7.5).

A useful tool for normally sized (20–50 cm tall) herbaceous or dwarf-shrub vegetation, such as meadows or tall-grass, and heath vegetation, including the herbaceous undergrowth layer in many forest stands, is a point-frequency frame such as shown in FIGURE 6.6. The frame shown here, made from wood, is 1 m high and 1 m long. Ten wire pins, or steel rods of the same length as the legs, are slid through holes. These guide holes are bored perpendicular through the two pieces of horizontally fixed lath. The second lath strip eliminates the parallax effect (as does the second cross-grid layer of the small square-decimeter cover frame in FIGURE 6.4). The ten guide holes with their pins are spaced at equal intervals along the linear frame. But the dimensions of the apparatus can be changed to fit the height and spacing of the plants.

The linear frame is mounted with its legs over the strip of herbaceous vegetation to be measured, and the pins are lowered vertically one after the other. Their hits on plant parts are usually recorded by species. Ten placings of the frame result in a record out of 100 sample points. This gives a measure of percent cover for the species that are intercepted by pins. Crown or shoot cover is measured by counting only the first interception or initial touch of each needle with a shoot part; basal area is measured by counting only the hits occurring with stem parts at ground level. The mean height of the plant cover can be determined simultaneously by recording the needle length at each first interception.

For measuring cover, the frame should be held vertically, not obliquely. This requirement becomes even more important if one intends to measure "cover repetition," which was defined by GOODALL (1952) as the number of times a given needle intercepts a plant part when lowered in the same vertical position. If one were to hold the frame obliquely, the number of interceptions would likely be increased, resulting in an overestimate. An estimate of cover repetition may be converted into a measure of yield. Recently, POISSONET (1971) and DAGET and POISSONET (1971) have used the point-frequency method to determine biomass from all interceptions occurring at a point when the wire pin is lowered vertically. Such correlations between number of intercepts per point and biomass must be worked out empirically for each vegetation type, as the relations between volume of standing crop and weight vary from species to species, from place to place, and from time to time.

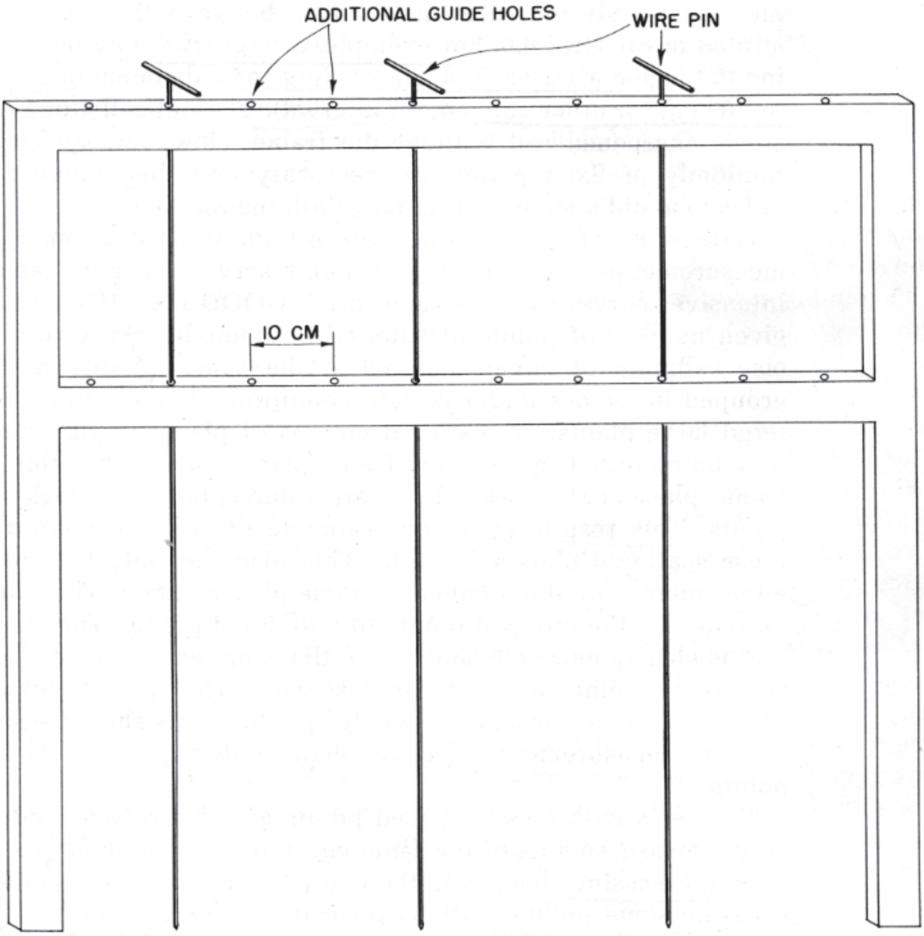

FIGURE 6.6. *Point-frequency frame. Dimensions of frame and number of guide holes or wire pin intervals are adjusted to size and spacing of herbaceous plants. Further explanation in text.*

The frame can be held obliquely (at a 45° angle) for easier overviewing, if one is interested merely in the determination of "relative cover," i.e., the percent cover contribution of each species to the total plant cover. In this case, the slight overestimate of absolute cover per species resulting from the probability of increased hits when needles intercept sideways, is of little consequence (GOODALL 1952).

Instead of ten pins, one can also use the same pin for ten readings, but movement of the pin or rod among guide holes slows down the progress.

Where a larger continuous area sample of a herb cover is desirable, one can simply increase the distance between the points as demonstrated in FIGURE 6.6. For example, a single rod may be used by moving the frame after each single reading for a distance of 30 cm, 50 cm, or 100 cm (or other convenient interval). Theoretically, one could use a single sharpened rod without the frame. However, systematically or randomly prefixed points are necessary and this requires the guide holes to avoid unconscious aiming with the rod end.

Narrow spacing of points is useful for intensive, small-area cover measurements. Wide spacing of points serves for more rapid, but less intensive, surveys of the same area. GOODALL (1952) found that a given number of points distributed individually can give a more precise estimate of cover than when the same number of points are grouped in frames under certain conditions. For example, a few scattered large plants, or scattered clumps of plants of the same species, may be recorded in only few frame placements. But within these few frame placements these plants are intercepted by a high number of points. This results in an overestimate of the cover contribution of these scattered clumped plants. This bias can only be eliminated by either increasing the number of frame placements on the same area, or by reducing the grouped points to individual points. The latter alternative is clearly more efficient, since the same accuracy can be obtained with fewer points and therefore less work. This leads to the conclusion that continuous transects of evenly spaced points should result in more accurate measurements of cover than random placements of grouped points.

Transects with evenly spaced points are also recommended, if periodic remeasurements of the same vegetation is the objective. The accuracy in assessing changes in the plant cover is greatly increased, if one uses the same point locations instead of a new random allocation of points at each subsequent remeasurement (GOODALL 1952).

The number of sample points to be recorded should be related to the variability of the cover. The adequacy of cover sampling is governed by the same principles as discussed for density counts in SECTION 5.55. An arbitrary number of 200 points may give satisfactory results in a relatively homogeneous plant cover. Depending on the familiarity with the species, such a record usually takes only about half an hour.

GOODALL (1952) produced data showing the great effect that the diameter of the pin has on the accuracy of the result. For example, with respect to the grass species *Ammophila arenaria*, a pin diameter of 4.75 mm resulted in 71 percent cover, a pin diameter of 1.84 mm in 66.5 percent cover, and a pin diameter reduced to a point with practically no diameter gave only 39 percent cover.

Therefore, the results are only relative and depend on the diameter at the tip of the pin. This is analogous to the frequency determinations in quadrats, where the result depends on the quadrat size. The closest approximation to an absolute measure of cover is achieved with a rod or pin sharpened to a point. Cover measurement with a sharpened rod does not take more time than measurement with a blunt-tipped one. Theoretically, the double-sighting cross method should give the most accurate results. WINKWORTH and GOODALL (1962) described a crosswire sighting tube made of brass, which has been used successfully in Australian tussock grass covers. The tube of 20 cm length and about 5 cm diameter is equipped with rings that hold a fine crosswire at each end. The tube can be held by hand or mounted on a tripod. The crosswires provide for a practically dimensionless point-sample. Of course, such a tool cannot be used to measure "cover repetition" or biomass.

6.54.2 *Application to Tree Cover.* The point-intercept method is not restricted to application in herbaceous vegetation. A tree canopy cover can be evaluated by the same principle of counting intercepting points. A simple device that has often been used in forest ecological work is the so-called "moosehorn" crown closure estimator (GARRISON 1949, FIG. 6.7). This is a simple boxlike periscope, which in its bottom part contains a mirror that is fixed at a 45° angle. The top of the periscope is equipped with a glass plate having a grid of 25 dots. The observer views the mirror through a peephole by holding the periscope upright and fixed on a Jacob's staff in front of one eye. The instrument has to be completely levelled, which is done by a 2-way level inside the periscope. The number of dots that are intercepted by a portion of the canopy can then be counted. This is repeated at a certain number of predetermined stations in the stand. Crown canopy photographs taken with the "fish-eye" lens are evaluated by the same principle. But the photographs include a wider area per station and can be evaluated more accurately. Such point-intercept analyses are particularly useful if one is interested in seasonal variations of the crown cover. Periodic remeasurements should then be made from the same sampling stations.

There are various modifications of this method. Recently, MORRISON and YARRANTON (1970) converted a rifle telescope into a point sampler by attaching a right-angle prism that permits reading straight downwards and upwards. The rifle telescope is mounted on a supporting stand consisting of a 3 m long aluminum beam that is held up horizontally by a pair of adjustable legs. The telescope is set up in convenient viewing height at about 1.6 m above the ground. It can be moved horizontally along the beam to any position. Therefore, ten or any other number of positions may be chosen at random or systematically along the beam at each setting of the apparatus. The cross hair in the telescope permits sampling one point at a time. The right-angle prism can be turned around by 180° to read the canopy cover per cent (by species)

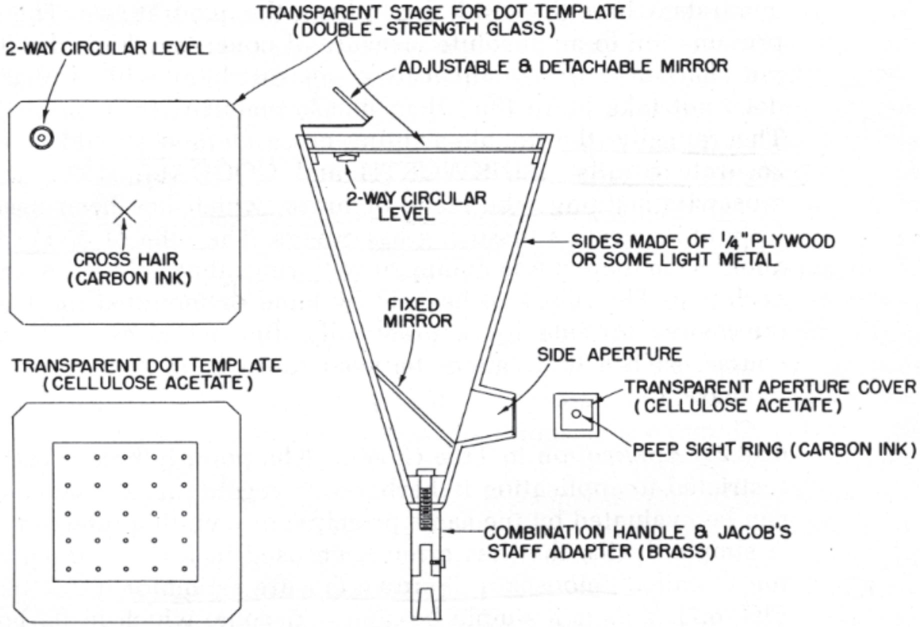

FIGURE 6.7. Sectional view and parts of the "moosehorn" crown closure estimator. (Reproduced with permission from the Journal of Forestry.)

on the same location as the undergrowth vegetation. This appears to be a promising method.

A major disadvantage of the point-intercept method in application to the tree cover is that the height or depth of the crown cover cannot be assessed. Yet, cover layering among trees is ecologically very important. The depth of cover can indirectly be evaluated by measuring light (BUELL and CANTLON 1950, ELLENBERG 1939, EBER 1972). However, light measurements are usually done for different objectives. They are time-consuming and do not offer a proper alternative, because they cannot be expressed in percent cover by species.

This disadvantage does not apply to the line-intercept method, by which the cover of woody plants can be assessed separately for more than one height stratum.

6.55 The Line-Intercept Method. This method for measuring cover was described by CANFIELD (1941). The line-intercept method is based on the principle of reducing the belt-transect, which has two dimensions of length and width, to a line with only one dimension, namely length. A meter tape is laid out on the ground and the crowns that overlap or intercept the line are recorded by species to the nearest 10 cm or whatever accuracy can be recorded conscientiously.

The line-intercept method can only be applied to plants with rather solid, almost 100 percent crown cover or relatively large basal areas. Among herbaceous or low plants these are the same that can be charted from quadrats. But in contrast to the quadrat-charting method, the line-intercept technique is more useful where a cover assessment of a larger area is required. Moreover, the method has a particular advantage for measuring the crown cover of woody plants, shrubs and trees.

Where crowns overlap in layered vegetation, the cover should be measured for each height layer separately. The layers or strata can be defined arbitrarily. In a low-stature forest, convenient strata may be from 0.5 to 2 m, from 2 to 5 m, and from 5 m up. Crown outlines of trees much taller than about 15 m are difficult to assess accurately without a special sighting tool. The upper size limit depends on visibility and the ease of making a vertical projection from the crown outline down to the underlying tape. The accuracy of the method depends largely on the accuracy of the vertical projection. An essential tool in such woody vegetation is a long, thin rod, about 3 m in length. This rod is used to obtain a projection of the crown edge to the tape by holding the rod vertically from the tape to the crown edge.

BORMANN and BUELL (1964) measured trees up to 32 m tall by the line-intercept method. For the vertical projection they used a "cover-sight," described by BUELL and CANTLON (1950). This is the same instrument as the "moosehorn" crown closure estimator described earlier. Except, a single cross-hair was used instead of a grid of dots, and a second cross-hair was mounted in the periscope to eliminate parallax. Furthermore, to facilitate obtaining a true vertical projection of crown perimeters, a plumb bob was hung inside the periscope. LINDSEY (1955) used what he described as a "sighting-level" for locating the vertical projection of the crown outline to the tape. The sighting level is a 5-ft. long stick with a screw mounted into the top end and a carpenter's level mounted at one foot from the lower end of the stick. The carpenter's level is attached in such a way that it can be used to control the stick position in one vertical direction. The stick is held by the observer so that the carpenter's level comes to eye-level position. The top end with the screw is then tilted at a 45° angle towards the observer and the screw is brought in line with the crown perimeter, while the bubble must remain centered. The observer then makes a 90° turn and again brings the three points, crown perimeter, screw and bubble in line by moving to the point along the tape directly beneath the crown outline. The two aiming positions eliminate the need of viewing straight up and down the stick, which would become complicated as a second bubble is required and must be read simultaneously with the first to insure an absolutely vertical position of the stick.

The accumulated length occupied by any one species out of the total meter tape length used for the sample is expressed as the percent cover for that species. The length of tape to be measured depends on the variation in the vegetation segment. However, usually the sample size is limited arbitrarily.

A second, even more important source of error than the relative accuracy of vertical projection is the crown outline itself. As stated before, the method is strictly applicable only to plants with almost 100 percent crown density that at the same time also have a solid or continuous crown outline. If a tree has bushy branches that reach across the line with gaps in between, the gaps should be excluded from measurement for greater precision. But there are many situations where this is difficult to do. Moreover, small within-plant gaps may be ecologically insignificant, and it may be more meaningful to ignore small gaps. DAUBENMIRE (1968) has come out in favor of "rounding out" canopy edges and "filling in" internal gaps on the argument that these gaps may be part of the ecological territory of an individual. Such a decision requires some prior knowledge of the ecological behavior of the species on the part of the investigator. As long as his judgment is consistent and the reasons for his judgment are explained, the method can still be considered objective and reproducible.

The same problem applies to the density of foliage. Where leaves are shed from certain branches, it may be equally valid to ignore such branches as to include them. Here, the judgment of what to include or exclude requires some knowledge of seasonal behavior of the tree species in question. If these two points about crown density and outline are well understood and taken into consideration, the method can be applied to woody vegetations that do not conform to the ideal of solidly covering crown outlines.

The line-intercept method has also been applied to counting individual plants, in conjunction with their measurement of cover (BUELL and CANTLON 1950). However, tree density is more conveniently assessed by other methods (see CHAP. 7).