are relatively long-lived and which will form part of the mature associations.

In practically every case, the character of the new stand was apparent within only two growing seasons of the hurricane. The absence of later successful invasion of seedlings is attributable in part to competition from growth already established, and in part to unfavorable environment in the blowdown areas.

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THE USE OF DISTANCE MEASURES IN PHYTOSOCIOLOGICAL SAMPLING[1]

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Introduction

A number of methods have been described in recent years which utilize spacing distances instead of fixed-area plots for the sampling of plant communities in compositional studies. All of these methods possess certain obvious advantages when compared to the standard plot techniques, since they all are more efficient in terms of results obtained per man-hour expended. They are faster, require less equipment and fewer workers, and are much more flexible, in that there is no need to adjust the sample size for the particular density of the vegetation type under study. The advantage in speed is particularly great, with savings of 90% or more commonly obtained. Currently, the main disadvantage of these distance methods lies in their unfamiliarity, which raises doubts as to their precision and limitations. The purpose of the present paper is to compare some of the methods, as used on three natural forests and an artificial random population, with respect to their relative accuracy and other characteristics.

In a stand of any plant community, the component individuls exist in a certain number, distributed over a certain area. This characteristic, called density, may be determined for each species separately, or for each life form (*e.g.*, trees) independently of species. In fixed-area plot sampling, a relatively small portion of the total area is examined, usually by means of a number of separate subsamples. In each of these subsamples, the density is determined directly by counting and the result expanded to total density per stand (or per acre) by use of the ratio between sample size and stand size. Instead of this idea of the number of plants per unit area, a more useful concept is the amount of area per plant, the *mean area* (M), which is the reciprocal of the density. When plant abundance is given as mean area, the way is immediately opened for the use of distance between plants as a measure of that

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abundance, since the $\sqrt{M}$ is a direct indication of the spacing of the plants. It follows that a measurement of the actual spacing in the field can lead to an accurate estimate of the mean area and the density. All of the distance methods so far proposed are based on this simple relation. They differ primarily in their choice of the distances to be measured so as to arrive at a correct determination of the actual spacing.

The actual number of individuals per unit area is only one of the characteristics of a plant community that may be measured and is frequently of lesser importance than certain other characteristics, especially when different stands of the same formation or type are being studied, all of which are relatively similar in absolute density. The same is true for measures of total dominance, such as the basal area of all trees per acre. This information may be of value in a timber cruise, or in other economic estimates, but is frequently of limited utility in basic phytosociological investigations. The use of extensive studies of many stands of related community types in a given region is coming to be recognized as the best approach to an understanding of regional vegetation, as opposed to the older procedure where an intensive study was made of one or a few "characteristic" stands. In such extensive studies, the use of a number of analytical characters on a relative basis, such as relative frequency, relative density and relative dominance, provides more useful information than that derived from the same characters on an absolute basis. Any sampling method, therefore, should be able to accurately provide such relative information in addition to the absolute values.

The distance measuring methods of community study have all appeared since 1947, when Cottam described the random pairs method for sampling forest trees. Subsequent investigations have been concerned with the use of distance either for the determination of density or for the study of the randomness of dispersion of the population. Skellam, in 1952, suggested that the distance between each individual in the population and its nearest neighbor might be used to study randomness, through a comparison of the observed distribution of such distances with those expected from theory. Cottam, Curtis, and Hale (1953) used the point-centered quarter method for measurement of density and a number of relative characteristics. They also reported certain properties of the distances between random points and closest individuals (point to plant) and of the distances between nearest neighbors (plant to plant). Hopkins (1954) compared the average distance between nearest neighbors with the average distance between random points and closest individuals as a means of measuring aggregation. This had been suggested independently by Moore (1954) who also used these measurements to determine densities. Clark and Evans (1954) also used the nearest neighbor distances in a study of aggregation. All of the methods have thus been used for density determination and some of them in addition have been used for the study of randomness. In view of the wide interest, it has seemed desirable to compare the characteristics of the methods under comparable conditions.

Methods

Three forest communities and an artificial random population were each sampled by five methods—the closest individual, the nearest neighbor, the random pairs, the point centered quarter, and the quadrat. The three natural communities were first mapped by plane table and transit procedures so that each tree was accurately located and its species and basal area indicated on a map drawn to $\frac{1}{192}$ scale ($\frac{1}{16}$ inch equals one foot). The three forest communities were chosen to represent a wide range in species complexity, tree size, and tree density. Peavey Falls Woods is located on the Menominee Indian Reservation in Shawano County, eastern Wisconsin. Jack Pine Woods is in Bayfield County, northern Wisconsin. Wingra Woods is located on the University of Wisconsin Arboretum in Dane County, southern Wisconsin. Details about species composition, density, and dominance of these stands are given in the tables. The Peavey Falls Woods map covered an area of 1.63 acres which contained 600 individuals. The Jack Pine Woods map covered an area of 0.48 acres containing 330 individuals. The Wingra Woods map covered an area of 5.37 acres which contained 543 individuals. A rectangular area was drawn in the center of the map large enough to include most of the mapped individuals, but with a border at least two trees wide between the edge of the rectangle and the edge of the map. This rectangular area was then divided by a 10 x 10 place grid into 100 equal sub-units. Within each sub-unit, 100 permanent sampling points were located by means of a random numbers table. The same sampling points were used for each method, and all data are based on a total of 100 sampling points for each method for each stand. No method of mutual exclusion was used in the location of the sampling points so that any tree could be, and in many cases was, sampled more than once with the same method. The populations on the maps were considered to be infinite.

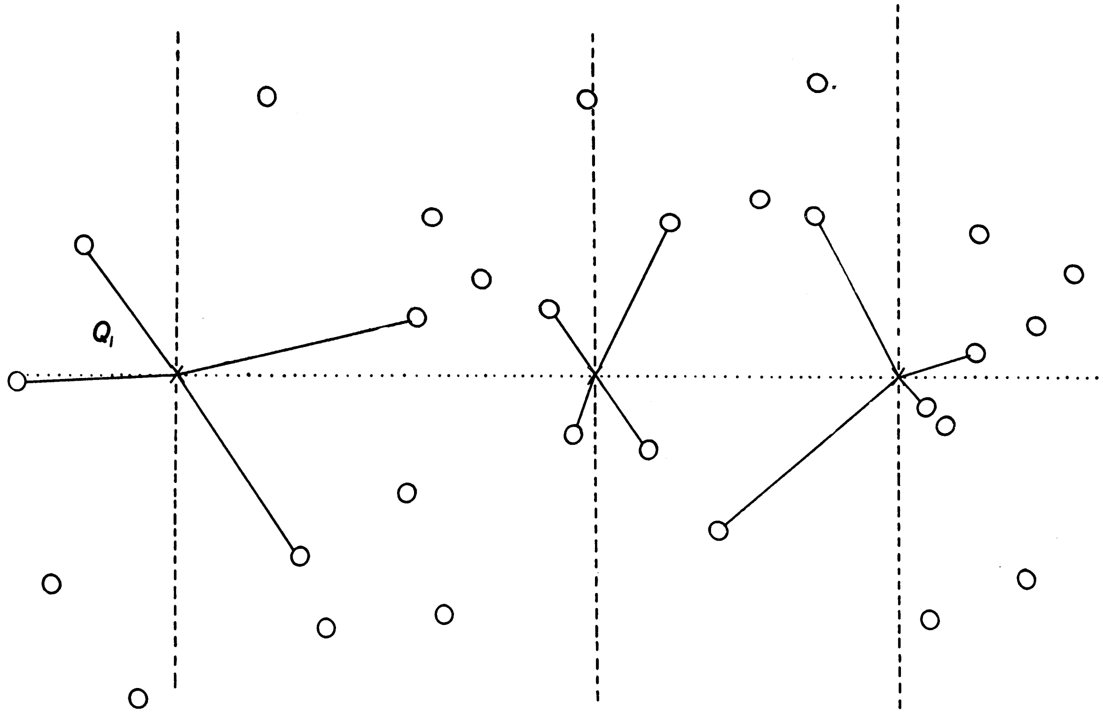

FIG. 1. Point to Plant Methods. X's are sampling points. Dotted lines are paced compass lines between points. For the closest individual method, distance is measured from the sampling point to the plant closest to it, regardless of direction (Q_1). For the quarter method, the area around the point is divided into four 90° quarters (dashed lines) and distance is measured from the point to the closest tree in each quarter. Solid lines on the figure represent measured distances.

The artificial random population of 1,000 individuals was the same as that used by Cottam, *et al.* (1953). No basal areas were available, since each individual was considered as a point in space. Sampling followed a stratified random system like that used on the natural communities.

Closest individual method. (Figure 1).—This is the simplest of the point to plant methods. The distance from the sampling point to the closest tree is measured, and the species and basal area of the tree are recorded. The mean of the distances from the sampling point to the closest individual has been found to equal 50 per cent of the square root of the mean area. This was demonstrated empirically by Cottam, *et al.* (1953) and theoretically by Morisita (1954). The average point to closest individual distance is therefore multiplied by a correction factor of 2.00 to convert it to square root of the mean area.

Nearest neighbor method. (Figure 2).—As used by Cottam, *et al.* (1953), the nearest neighbor distance is the average distance from each individual in the population to its closest neighbor. Many of the values are duplicates, since paired neighbors (which have each other as nearest neighbors) make up a significant portion of the total population. Hamming and Gilbert (1954) showed that 62% of the total number of individuals in a random population are in these isolated pairs. Clark and Evans (1955) confirmed this relationship for both artificial and natural populations. Morisita (1954) demonstrated that, in a randomly distributed population, the distance between nearest neighbors is equal to one-half the square root of the mean area. Using other symbols and terms, Clark and Evans (1954) independently arrived at the same conclusion. The latter investigators state that a random sample of the individuals in the population will also yield a mean distance equal to one-half the square root of the mean area. This is undoubtedly correct, but requires an additional explanation in connection with the present problem. Clark and Evans point out that in order to obtain a truly random selection of the individuals in the population, it is necessary to number all the individuals in the population and select the individuals to be sampled by lot. As an approximation, they recommend establishment of quadrats at random and measurement of the nearest neighbors of the individuals within the quadrats. Neither of these methods is satisfactory for the present purpose, since both of them are so time consuming that their use would destroy any advantage this method may have.

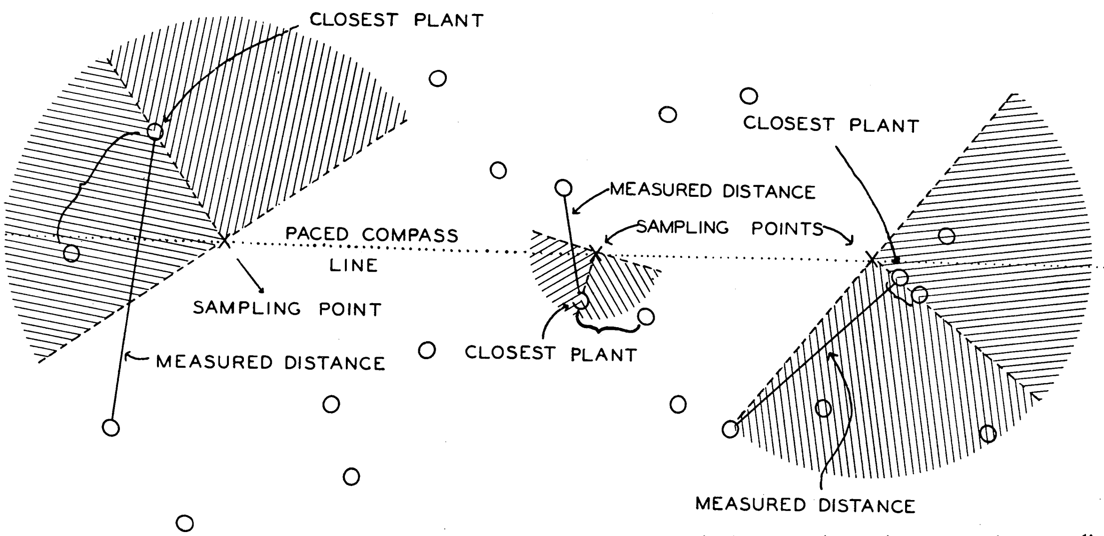

FIG. 2. Plant to Plant Methods. With both of the plant methods, the plant closest to the sampling point is located. Nearest neighbor distance is measured between the bracketed plants at each point. For the random pairs method, an angle of exclusion of 180° (shaded area) is erected with its vertex at the sampling point and its bisector extending through the closest plant. Distance is measured from the closest plant to the plant closest to it that is outside the angle of exclusion (solid line).

The method for tree selection used in the present study was to choose the individual closest to each sampling point (the same tree to which distance was measured in the closest individual method) and to use this tree as the tree from which distance to its nearest neighbor was measured. This does not provide the truly random sample called for by Clark and Evans, and does not yield the same results. In a series of artificial random populations, which were examined by a 100 per cent sample, it was found that the average distance between paired individuals was 37 per cent of the square root of the mean area while the average distance between non-paired neighbors was 66 per cent. A stratified sample, by the method outlined above, of one of these artificial populations showed that only 50 per cent of the distances measured were between paired neighbors, as opposed to the 62 per cent expected from a truly random sample of the individuals. Also, the distances between these paired individuals which were sampled was 47 per cent of $\sqrt{M}$ as opposed to the 37 per cent figure for all the paired neighbors on the population. The nearest neighbor method, as described, not only samples fewer of the paired neighbors than occur proportionately in the population, but tends to sample those paired neighbors that are far apart more often than those that are very close together. As a result, the average distance between individuals with the nearest neighbor method, as here used, is approximately 60 per cent of $\sqrt{M}$ instead of 50 per cent as in a 100 per cent sample. The use of a set of individuals chosen in this manner and their nearest neighbor distances involves multiplication of observed distances by a correction factor of 1.67 instead of the theoretical 2.0, to obtain the correct $\sqrt{M}$. The nearest neighbor method gave a sample of 100 distances and 200 trees for 100 sampling points.

Random pairs method. (Figure 2).—Considerable confusion appears to exist about the random pairs method and its uses and limitations. Some investigators have used it with success (Dimit and Russell 1954) but other workers have reported difficulties (Shanks 1954, Rice and Penfound 1955). The method is based on the use of an angle of exclusion to denote a series of pairs of plant individuals for further sampling of species, size and spacing distance. As originally described (Cottam and Curtis 1949) an exclusion angle of 160° was recommended but it was later shown (Cottam, *et al.* 1953) that the average distance between pairs was a linear function of the angle of exclusion for 0° to 260°. Since a 180° angle is most convenient in the field, its use is recommended. The actual distances obtained with the 180° angle should be multiplied by a factor of 0.80 to obtain the correct distance (Cottam and Curtis 1955).

As used here, the random pairs method involves the choice of the closest tree to each of the stratified sampling points, the erection of a 90° exclusion angle on either side of the line between the sampling point and the closest tree, and the selection of a second tree, outside of this total

180° angle, which is closest to the first individual. Basal areas and intertree distances are recorded, thus giving a sample of 100 distances and 200 trees for 100 sampling points.

Point-centered quarter method. (Figure 1).—This method is a very old one, having been used by the Federal surveyors making the original survey of government lands in the middle of the last century (Stearns 1949). As adapted for ecological use (Curtis 1950), each sampling point is considered the center of the four quarters (quadrants), with orientation given by the compass line of traverse. At each point, the closest tree to the point in each of the four quarters around the point is chosen as the sample. Distances are measured from the point to each of the four trees, and their species and basal areas recorded. The average of the four distances is equal to $\sqrt{M}$, as demonstrated empirically by Cottam, *et al.* (1953) and theoretically by Morisita (1954). Additional information of interest can be obtained by arranging the distances about each point in order, from the shortest (Q_1) to the longest (Q_4). It has been shown (Morisita 1954) that the Q_1 distance, which is the distance from any point to the individual nearest to that point, is equal to 0.5 $\sqrt{M}$ and is thus the same, on the average, as the distance between any individual and its closest neighbor. The Q_1 distance is identical to the closest individual distance as given above. The Q_2 distance is equal to 0.80 $\sqrt{M}$, the Q_3 to 1.12 $\sqrt{M}$, and the Q_4 to 1.57 $\sqrt{M}$, while Q_m, which is the average of Q_1 Q_2, Q_3, and Q_4, exactly equals $\sqrt{M}$. As used here, the point-centered quarter method gives 100 Q_m distances and 400 trees for every 100 sampling points.

Quadrat method.—The standard quadrat method involved the placement of a quadrat centered directly over each sampling point. The quadrats were equal to 4 times the population mean area in size, so they could be expected to contain 4 individuals on the average in a random population (Curtis and McIntosh 1950). For each quadrat, the species and basal area of each tree were recorded as well as the total number of trees. A sample of 100 points thus gave a variable number (approximately 400) of individuals.

For the natural populations, the importance value (Curtis and McIntosh 1951) was calculated for each species, considering each point as analogous to a quadrat for frequency determination. Relative densities and relative dominances were calculated in the usual way. It is important to realize that these importance values (the sum of relative values of frequency, density, and dominance) are independent of distances or absolute densities per unit area. For certain comparative studies where they may be of considerable interest, it is unnecessary to measure the distances at all, but such a practice is not recommended for most investigations.

Results

Computation of density and dominance with the distance methods requires the determination of the following:

1. Mean distance. This is determined by adding all the distances in the sample and dividing this figure by the total number of distances.

2. Relative density and relative dominance. These are determined from the following equations:

$$\text{Relative density} = \frac{\text{Number of individuals of the species}}{\text{Number of individuals of all species}} \text{ x } 100$$

$$\text{Relative dominance} = \frac{\text{Total basal area of the species}}{\text{Total basal area of all species}} \text{ x } 100$$

3. Basal area per tree. This is determined by dividing the total basal area by the number of trees.

The mean distances are used to determine mean area and density per unit area. All other absolute measures are computed from the density per unit area figure. As has been stated in the section on methods, the mean distances obtained with each method, except the quarter method, must be multiplied by a correction factor, which is constant for the method, in order to arrive at the correct square root of the mean area. The quarter method gives the correct square root of the mean area directly. After correction, the distances are squared to give mean area, and the mean areas are divided into the unit area to give number of trees per unit area.

A comparison of the results obtained with the four distance methods and the quadrat method on the mapped stands and the artificial population is presented in Table I. After correction, the distances are all within 5 per cent of the actual square root of the mean area, and trees per acre are within 10 per cent of the actual values.

Total basal area per acre is obtained by multiplying number of trees per acre by the mean basal area per tree. Absolute values for number of

TABLE I. Comparison of results from the various methods with each other and with the population parameters

Method	Closest individual	Nearest neighbor	Random pairs	Quarter	Quadrat	Actual
			ARTIFICIAL POPULATION			
Distance	16.19 mm.	18.85 mm.	40.18 mm.	32.05 mm.	32.26 mm.	31.65 mm.
Corrected distance	32.38	31.48	32.14	32.05	32.26	31.65
Mean area	1048.46	990.99	1032.98	1027.20	1040.71	1001.72
			WINGRA WOODS			
Distance*	10.75	13.05	26.91	21.02	20.17	20.75
Corrected distance	21.50	21.79	21.53	21.02	20.17	20.75
Mean area	467.25	474.80	463.54	441.84	406.83	430.56
Trees/acre	93	92	94	99	107	101
Basal area per tree†	179.2	180.5	189.4	200.1	179.0	188.6
Basal area per acre‡	115.7	115.3	123.7	137.6	133.0	132.3
			PEAVEY FALLS WOODS			
Distance	5.21	6.80	13.68	10.58	11.07	10.89
Corrected distance	10.42	11.46	10.94	10.58	11.07	10.89
Mean area	108.58	129.05	119.68	111.94	122.54	118.69
Trees/acre	401	338	364	389	373	367
Basal area per tree	119.7	118.4	105.9	107.0	103.5	102.2
Basal area per acre	333.3	277.9	276.8	289.0	268.1	260.5
			JACK PINE WOODS			
Distance	3.93	4.80	10.52	7.77	8.22	8.00
Corrected distance	7.86	8.02	8.42	7.77	8.22	8.00
Mean area	61.78	64.32	70.90	60.37	67.57	64.00
Trees/acre	705	677	614	722	645	681
Basal area per tree	23.1	22.0	22.7	22.8	21.4	21.6
Basal area per acre	113.1	103.6	97.0	114.5	96.1	102.2

*Distances for the natural populations have been converted to feet.
†Basal areas per tree are in square inches.
‡Basal areas per acre are in square feet.

trees per unit area of any species, and basal area per unit area of any species are determined by multiplying the relative figures for density and dominance by total trees per acre to determine density, and by total basal area per acre to determine dominance. An alternative computation for basal area per acre for a species is to multiply number of trees per acre of the species by the basal area of the average tree of the species. Basal area of the average tree of the species is determined by:

$$\frac{\text{Total basal area of the species}}{\text{Total number of trees of the species}}$$

Either computation will produce the same result.

Since basal area per acre is determined by multiplying basal area per tree by number of trees per acre, and all absolute density values are determined from the figure for trees per acre, it is apparent that the accuracy of all absolute values is dependent in part upon an accurate figure for number of trees per acre. It follows that care should be taken to insure that the sample of distances is adequate, and that the measurements are made with accuracy.

The number of distances required to produce an adequate sample varies with the method employed. Table II shows coefficients of variation for the four methods on each of the populations. In all cases, except the nearest neighbor method for the Jack Pine stand, the coefficients of variation are similar for each method for all populations. Coefficients of variation are highest with the closest individual method and lowest with the quarter method. The fact that the quarter method gives the lowest coffiecient of variation is not surprising in view of the fact that each recorded distance is actually the mean of the four distances Q_1, Q_2, Q_3, and Q_4 for each point, and any large deviation of one of these distances at any point is likely to be compensated by an opposite deviation of the others.

A standard error of less than 10 per cent of the mean is considered satisfactory for most biological work. A more stringent requirement was placed on the distance measurements because these distances must be squared before density may be determined. It was desired that the standard error of the distance measurements be such that,

TABLE II. Variability of distances. Figures in boldfaced type are coefficients of variation. Figures in italics are number of distances required to yield a standard error of less than 4.65 per cent of the mean

	Closest individual	Nearest neighbor	Random pairs	Quarter
Artificial population	49.5%	46.9%	32.9%	23.7%
	114	*102*	*50*	*26*
Peavey Falls Woods	56.1	45.0	39.1	23.6
	146	*94*	*71*	*26*
Wingra Woods	54.3	46.3	36.2	28.8
	136	*99*	*61*	*38*
Jack Pine Woods	51.2	35.6	36.4	25.6
	121	*59*	*61*	*30*

when they were converted to densities, the plus or minus figures be within 10 per cent of the mean density. This condition is met with standard errors of the distances of 4.65 per cent or less. The figures in italics on Table II show the number of distances required to bring the standard error of the distances to 4.65 per cent of the mean distance. Less than 40 quarter distances are required, but more than 100 closest individual distances.

The adequacy of sampling of basal areas is determined by two factors: the number of trees encountered in the sample and the range and distribution of the sizes of the trees. Neither of these factors is greatly influenced by the method of sampling, except that the methods encounter a different number of trees per point, and those methods which measure the basal areas of only one or two trees per point will require four or two times as many points for the same adequacy of sample as is obtained with the quarter method, which measures four trees at each point.

The differences that may be encountered in sampling forests of this region are shown by a comparison of the two stands which differ most widely in basal area characteristics: Peavey Falls Woods and Jack Pine Woods. Peavey Falls Woods has many small hemlocks (*Tsuga canadensis*) which average 40 square inches in basal area. The next most common species is white pine (*Pinus strobus*), ranging in size from 50 to 1169 square inches basal area, with an average of about 200 square inches. Jack Pine Woods, on the other hand, is an even-aged stand of small jack pines (*Pinus banksiana*) in which the basal areas range from 12 (the lower limit mapped) to 45 square inches. Coefficients of variation for the basal areas per tree of these two stands were computed. The data were transformed by a square root transformation. Coefficients of variation range between 58 per cent and 66 per cent for the different methods in Peavey Falls Woods and between 17 and 18 per cent in Jack Pine Woods. The number of trees required to produce a standard error of the transformed data of less than 10 per cent of the mean is very uniform for the different methods in either stand, but approximately 10 times as many trees must be sampled in Peavey Falls Woods as in Jack Pine Woods. The number of points required in either case is less than that required for an adequate sample of distances. In almost all cases, a sample of sufficient size to give an adequate sample of distances will produce an adequate sample of basal areas as well.

It has been stated in the section on methods that, in some cases, relative values for frequency, density, and dominance as used in the calculation of importance values are adequate, and in such cases, distances need not be measured. Importance values for the three mapped stands are shown in Table III as computed for the four distance methods and the quadrat method. It can be seen that the five methods result in very similar importance values for all species. The only trend is a slight lowering of the importance value for the most common species in the methods having the largest number of trees per sample (quarter and quadrat methods). This is due to the fact that relative frequency for the common species drops as number of trees per sample is increased, with a corresponding rise in relative frequency for the species of medium occurrence.

TABLE III. Importance values (sum of relative frequency, density, and dominance) obtained for the natural populations

Species	Closest individual	Nearest neighbor	Random pairs	Quarter	Quadrat
	PEAVEY FALLS WOODS				
Tsuga canadensis	128	120	126	116	116
Pinus strobus	99	96	96	84	94
Acer rubrum	34	43	39	57	50
Acer saccharum	28	21	26	31	26
Betula lutea	4	9	5	6	9
Betula papyrifera	—	2	2	1	2
Quercus borealis	5	2	2	2	1
Ostyra virginiana	2	2	2	2	2
Abies balsamea	—	—	1	—	1
	WINGRA WOODS				
Quercus borealis	218	213	212	207	209
Quercus alba	55	61	64	63	61
Quercus velutina	14	15	16	19	19
Carya ovata	13	11	8	10	12
	JACK PINE WOODS				
Pinus banksiana	300	299	300	294	297
Betula papyrifera	—	2	—	6	3

The rare species are unaffected, but fluctuate due to the inadequacy of the sample of these species.

Discussion

Since all the distance methods here discussed are based on the same general principle, it is to be expected that they would all yield similar results if an adequate sample is used. The data presented indicate that this is the case, and the problems concerned with selection of method are not concerned with relative accuracy. All are equally accurate if an adequate sample is used. As regards personnel and equipment, the methods are also about equal. The basic requirements are a tape for measuring distances and basal areas, and a compass. All of the methods can be used by a single individual without undue loss of efficiency, but a team of two in which one man acts as recorder is probably more efficient as well as more accurate, since a single individual finds that the chief limitation to his speed is the necessity for stopping and recording the data. An additional instrument that greatly increases speed is a good optical range-finder. Such an instrument is available which has a 6 inch base and is accurate to within half a foot at 40 feet. The accuracy of the instrument probably exceeds the accuracy of a tape in many forest stands, where the presence of underbrush makes the measurement of distances between trees with a tape difficult at times.

Evaluation of the merits of the methods must be based on other criteria than accuracy or personnel. Probably the most important factor is the time required to obtain an adequate sample. It is obvious that the method requiring the measurement of a single tree and a single distance at a point requires less time per point than the quarter method, which requires the measurement of four distances and four basal areas at a point. The greater amount of time required per point with the quarter method is, however, more than balanced by the smaller variability of the results with this method, which results in the necessity for fewer points. No single answer can be given to the question of how many points are required to give an adequate sample with the different methods. This depends on the data to be taken and the nature of the stand. The number of points required to yield adequate figures may be different for each phytosociological character to be determined. The characteristics of the methods will therefore be considered in relation to their ability to measure density and basal areas.

Absolute density is based on the distance measurements, and the results indicate that the quarter method requires the fewest points. The variability in the case of distance measurements is a characteristic of the method, when populations with an approximately random dispersion are used. Of the two methods measuring two trees at a point but only one distance, the random pairs method with a 180° angle requires fewer points and is preferable for that reason. The closest individual method is the most variable of all and is not recommended for distance determinations, although it has uses, in conjunction with some of the other distance methods, is measuring randomness or aggregation.

The above discussion is based on theoretical considerations and presupposes a random, or at least an objective, location of the sampling points and a population of individuals that has a spatial distribution approaching randomness. There are also some subjective considerations that become important in the field. The usual method of locating the points at which samples are taken is to pace a compass line. Subjective bias enters in the process of walking the compass line. Repeated sampling of the same stands with different investigators indicates that some individuals have a tendency to subconsciously place the sampling points so that large or unusual trees occur in the sample more commonly than they occur in the stand. This may be the case in spite of the fact that a pre-determined compass line and a predetermined number of paces between points were used. This bias is relatively unimportant with most workers and is probably never deliberate, but it does exist. It is mentioned here because it has a bearing on the choice of method. Bias of this sort will influence the data obtained by the closest individual method more than the others, since only one tree at a point is measured, and subconscious deviation form the compass line toward a single tree is relatively easy. It is much more difficult to place a point, consciously or otherwise, so that two trees or four trees at a point can be predetermined. Distances are even more subject to the influence of this bias than are tree species when the closest individual method is used, but the mean distance from the point to trees in four quarters is affected very little if at all.

Basal Areas

The adequacy of the sample of basal areas appears to be dependent almost entirely on the number of trees sampled, and the number of trees required to give an adequate sample is a character of the population, not of the method. Number of trees required will depend on the nature of the stand, with those stands having trees of fairly uniform size requiring fewer points than stands in which trees of all sizes occur. Here the choice of method is primarily a matter of deciding whether it is more economical of time and effort to measure many points with one or two trees, or fewer points with four trees per point. The subjective bias mentioned above is an argument in favor of the quarter method, and the possibility that the presence of a species may influence the species or size, or both, of the tree nearest it is an argument opposed to the use of the nearest neighbor method.

This discussion has so far concerned itself with a comparison of the four distance methods and the quadrat method. There remain several important considerations that are common with all distance methods, and many of them apply to the quadrat method as well. Perhaps most important is the necessity for using the mean distance and mean basal area of the data from all the points to determine absolute density and dominance. The distance methods should be considered as consisting of two samples, a sample of distances and a sample of tree species and basal areas. This point has led to some confusion in the literature. When density per acre and basal area per acre are computed independently for each point, the results, as Shanks (1954) has pointed out, may be greatly in error.

Two different errors are introduced by this procedure. The first is due to the fact that distances must be squared before density may be computed. The methods used in this paper are based on squaring the mean distance, and the correction factors given apply only when this procedure is followed. Squaring the individual distances and then computing the mean of these squared distances will always result in a higher figure than the square of the mean of the same distances, unless all the original distances are equal.

The second source of possible error is the extreme variability introduced by multiplying the number of trees per acre by basal area per tree at each point. An attempt to correlate basal area per point with mean distance per point for the quarter method showed that distance and basal area at each point are independent of each other in the range of forest types studied, as would be expected from biological considerations. The chance combination of a short distance and large basal area at a single point will result in a wide range of basal areas per acre, if the points are considered one by one. For example, treatment of the Peavey Falls quarter data as separate samples results in a range of basal areas per acre from 29 square feet to 4384 square feet.

It must be pointed out, however, that the values for basal area per tree and density per acre are independent and are multiplied by one another to obtain basal area per acre for the stands. This means that basal areas per acre are less reliable than either of the two components when considered separately. In some cases, errors in the two compensate for one another, as in the case with the 180° random pairs data for Jack Pine Woods (Table I). Here the number of trees per acre is low, and the basal area per tree is high, with the result that the two combined produce an answer for basal area per acre that has a smaller percentage error than either of the original figures. On the other hand, the quarter data for the same stand show too many trees per acre and too large a basal area per tree with the result that, although the two components are within 10 per cent of the actual values, the basal area per acre value is in error by approximately 12 per cent.

A second consideration that is important with all methods, including the quadrat method, is the necessity for objectivity in the selection of the sampling points. This is best accomplished by the introduction of some randomization technique. The method of point selection recommended for use with the distance methods is one of paced compass lines, and an element of randomness may be introduced by varying either the number of paces or the direction of the compass line according to a pre-determined system involving the use of random numbers. Other more rigorous techniques for randomization are available, but they are so time consuming that their use would nullify one of the principal advantages of the distance methods—speed. It is important that whatever technique for the selection of sampling points is used, it must be followed with extreme care. Any relaxation of the controls on point selection allows the possibility of subjective bias.

A final consideration in connection with the distance methods is their behavior when populations with a considerable degree of aggregation are sampled. Aggregation of total trees in forest stands is usually so slight that it does not present a serious problem, although individual species are frequently non-random. A complete treatment of the problem of aggregation is beyond the scope of this paper, but it should be mentioned that when trees are noticeably clumped, with open spaces between the clumps, none of the distance methods as here described will give an accurate density.

Aggregation tends to increase distances obtained with the closest individual, random pairs, and quarter methods, and tends to decrease the distances obtained with the nearest neighbor method. Several methods for measuring aggregation have been published, but no methods that give accurate densities for such populations are available. Quadrat data in aggregated stands are so variable that the number of quadrats required is almost impossible to attain. At the moment it must be said that we know of no good method for measuring the density of aggregated populations.

Summary and Conclusions

Four distance methods, including two point-to-plant and two plant-to-plant methods, were used on three mapped stands and artificial population. The data were compared with results obtained with the quadrat method, and with the known population parameters. It was found that all the distance methods were capable of yielding accurate results when an adequate sample was used, but that the size of an adequate sample varied with the method.

The closest individual method has the advantage of simplicity. Only one tree and one distance are measured at each point. An additional advantage is that the mathematical characteristics of the method have been worked out, and the observed distance need only be multiplied by a factor of 2.0 to give square root of mean area. The disadvantages of the method are the extreme variability of the results, which necessitates the sampling of many points before an adequate sample is obtained, and the susceptibility of the method to subjective bias.

The nearest neighbor method gives less variable results than the closest individual method, but still requires a larger number of sampling points than either of the other methods. It, too, is simple, requiring only the location of the tree nearest the sampling point, and the measurement of the distance from that tree to its nearest neighbor. The results obtained with this method do not agree with the results based on mathematical theory, largely due to the fact that the method of sampling does not provide a random sample of the trees, but rather tends to under-sample trees that are close to one another. This results in a correction factor of 1.67 rather than the theoretical 2.00. The method does, however, yield consistent results in all stands in which it has been used.

The random pairs method with an 180° angle of exclusion is less variable than the two previously discussed. It has been more widely used than the other methods. One disadvantage is that the mathematical theory behind the method has not been worked out.

The quarter method gives the least variable results for distance determinations, provides more data on tree species per sampling point, and is least susceptible to subjective bias. The mathematical characteristics are known. It requires no correction factor, the mean of the distances equalling the square root of the mean area. The apparent disadvantage of requiring more time per point is compensated for by the necessity for sampling fewer points.

It is the opinion of the authors that the quarter method is, in most respects, superior to the other distance methods studied, and its use is recommended.

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