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SPATIAL ANALYSIS OF POINTS ON TREE STRUCTURES:
THE DISTRIBUTION OF EPIPHYTES ON TROPICAL TREES

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Institute of Statistics Mimeograph Series No. 1971

January, 1990

Spatial analysis of points on tree structures: the distribution of epiphytes on tropical trees

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December 18, 1989

A frequent problem in ecology is determining whether the observed spatial distribution of a plant species can be attributed to a completely random spatial process. Usually the analysis of these data is simplified by the fact that the locations of the plants are the two-dimensional coordinates in a rectangular region. This paper considers a more difficult problem of assessing the spatial pattern of points that lie on a tree structure. The application in this work involves the distribution of a type of epiphyte found in the crowns of a group of tropical trees. These methods, however, are not limited to biological trees and could be useful for the spatial analysis of other treelike structures or networks.

A tree structure imposes complicated constraints on the three-dimensional relationships among different points on the network. For this reason it is not possible to obtain simple analytical expressions for testing statistical hypotheses about the spatial distribution of the observed data. The basic idea behind our approach is to use Monte Carlo simulation of point patterns to test for spatial randomness in the observed data. One advantage of this approach is that it can handle spatial statistics that may be very relevant for a particular problem but may be too complicated to work with analytically.

Our spatial analysis of the bromeliads' distributions in tree crowns yields surprising results. The distribution of plants on different trees appear to depart from a completely random (uniform) pattern both in the direction toward clustering and also toward hyperdispersion (regularity). These results suggest that there may be other factors besides the basic tree architecture that influence the distribution of epiphytes within tree crowns.

The analysis of the spatial distribution of epiphytes in tree crowns requires detailed knowledge of the three-dimensional structure of the tree crown and we believe this is the first instance where the structure of standing trees has been mapped. Because of the novelty of these data some discussion is given on the statistical issues of converting pairs of transit sitings to an xyz coordinate system.

Key Words and Phrases: Spatial statistics, Nearest neighbor distance statistic, Tree maps

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1 Introduction

Often botanical and ecological questions can be formulated in terms of the presence or absence of spatial patterns. These data typically involve the positions or quadrat counts over a two-dimensional rectangular region and many statistical methods have been developed for interpreting such data (Ripley 1981, Diggle 1983). This article considers the extension of these methods to analyze spatial point patterns that are constrained to lie on a tree-structure. Although our application considers structures that are forest trees, there is the potential application to other branching structures such as stream networks, circulatory systems and neural pathways.

The canopy of a tropical rain forest is a rich and largely unexplored ecosystem that plays a vital role in storing and recycling nutrients. Recently the canopy ecosystem has also become an environmental concern. Given the rapid clearing of rain forest for agriculture and grazing, it is important to understand how the destruction of the canopy will effect the amount of nutrients left in the soil. In the past decade, understanding of the organisms and interactions of tropical forest tree canopies has greatly increased due to the use of mountain-climbing techniques for canopy access (Nadkarni 1981, Perry 1984). A sound scientific understanding of the canopy has been hindered, however, by the lack of quantitative data on the distribution and abundance of canopy biota and on the microenvironment of the canopy. In order to study this ecosystem it is necessary to develop means for mapping tree structure and locations of constituent organisms and to identify rigorous statistical methods to interpret these data.

We have developed the capability to efficiently and inexpensively map individual tree crowns, record associated dimensions and biota, and portray the resulting data graphically. In this article we discuss the application of spatial statistics to study the distribution of bromeliads a type of epiphyte that is supported by branches in the tree crown. Epiphytes comprise a significant proportion of the tropical canopy biomass. Their ecological function is to accumulate nutrients derived from atmospheric sources(Nadkarni 1984, 1986, Benzing 1989). For this reason it important to understand the mechanisms that influence their abundance and dispersion.

One way to appreciate the problems in analyzing tree structured data is to examine the data collected for several trees. Figures 1 - 3 are the top and side projections of three of the trees in this study along with the location of bromeliads. Such plots will be referred to as tree maps. The basic question, given these data, is whether the locations of these plants depart

significantly from a completely random pattern. By completely random we mean that the locations of the plants are independent of one another and, with respect to the top view, there is an equal probability of being located anywhere on the tree network (see Section 3 for more discussion of this definition). Because plants are always located on branches, even a random distribution of epiphytes will not appear uniformly distributed in space. This constraint makes it difficult to interpret tree maps such as Figures 1-3 and visually assess the degree of randomness. In fact, these three figures illustrate a range of possibilities for the spatial distribution. For example, consider the median of the nearest neighbor distances (MNND) among these plants. One way to interpret this statistic is to compare the observed value to a reference distribution for this statistic based on the assumption of a completely random distribution of points. For the tree in Figure 1 the MNND lies in the left tail of the reference distribution, suggesting that these plants tend to cluster. The MNND for Figure 2 lies in the right tail of the corresponding reference distribution and thus suggests that the bromeliad locations tend to be hyperdispersed (or regular). The tree in Figure 3 is one where based on the MNND statistic there is no evidence to reject the hypothesis of a completely random distribution. Note that it is difficult visually to distinguish between the distribution of bromeliads on these three trees even though the departures from pure randomness in the first two cases are significant (p-values .05 and .02 respectively). A characterization of the epiphyte distributions from qualitative field observation would be even more difficult.

A statistical analysis of spatial data naturally breaks into two steps: 1) Testing for departures from a purely random point pattern and 2) if departures are found, modeling the point process using appropriate parametric distributions (Diggle 1983). The basic computational tool used in the analysis is to simulate locations on a network of branches given a specified distribution. Such simulated cases can be used to create a reference distribution for a particular test statistic and to quantify how likely it is that the observed statistic came from the specified distribution. This paper concentrates on the first phase of this analysis, because the small sample sizes and heterogeneity of the data limit the amount of modeling. Fitting parametric models in the second step, however, would use the same simulation methods developed for the first part of the analysis. Besides statistical modeling, simulation methods also have an important application in generating sampling designs for the tree crowns.

In this paper we analyze the spatial distribution of tank bromeliads on a set of tropical trees. In Section 2 we describe the determination of xyz coordinates for plant and branch locations from pairs of transit sitings and the specific protocol used to collect the epiphyte data. Due to the novelty of this measurement technique some discussion of the statistical

properties of this method are also included. In Section 3 we review some principles for analyzing spatial data and describe the specific methods used for the bromeliad locations. Section 4 contains the results of testing for random point patterns in the bromeliad distributions while Section 5 has a discussion of these results.

2 Three-dimensional triangulation and the collection of tree crown data

The basic measurement problem is to determine the 3-dimensional coordinates of a set of points from a limited number of remote sites. One method is to locate the points of interest by triangulation using pairs of transit measurements (Figure 4). The two transits are located directly over two fixed reference points, R1 and R2. Without any loss of generality, the cartesian coordinate system may be oriented to have its origin at R1 and for R2 to be located at the point $(L,0,E)$. Here L is the horizontal distance between the reference points and E is the relative difference in elevation. If there was no elevation difference between R1 and R2, the second reference point would lie on the positive X-axis a distance L from the origin. It is also necessary to know the elevation of the transit center above each reference point and these will be denoted by h_1 and h_2 . The horizontal and azimuthal angles measured by the transits are assumed to have the same sense as θ and ϕ in a spherical coordinate system. Sighting at the target from the first reference point yields the pair of angles (θ_1, ϕ_1) and in a similar manner one obtains (θ_2, ϕ_2) from a transit situated over R2.

For each target location *four* angular measurements are made even though the goal is determine only *three* coordinates. This extra angular measurement makes it possible to determine the accuracy of the triangularization. Imagine the line of sights of the two transits as rays that start from the transits and point to target. If there were no error in sighting, then the location of the target is the point where these two rays intersect. In practice the rays will not intersect precisely, and under these circumstances it is reasonable to estimate the position of the target as the location that is "closest" to both rays. Specifically, we find the shortest line segment connecting these two rays and estimate the target's location by the midpoint of this line segment. (The estimated location in Figure 4 is marked by an "X"). A natural estimate of the error is to report the length of this line segment and we will refer to this length as the discrepancy. A formula for the estimated location and the discrepancy is derived in the Appendix.

One might also consider estimating the position using nonlinear least squares or a maximum likelihood estimate. Although these more sophisticated methods could be generalized to handle more than two transit sightings, they are more complicated to compute. Also, their

measure of the discrepancy will not have such a clear geometric interpretation. One advantage of our method is that the calculations can be done on a programmable calculator in the field. Thus sightings that have a large discrepancy can be rechecked immediately while the transit is still in position.

The sample trees in this study consisted of 12 individuals of Sapium oligoneuron (Euphorbiaceae) located in a diary pasture near Monteverde, Costa Rica ($10^{\circ}18'N$, $84^{\circ}48' W$). This study is the first in which the architecture of live tropical trees has been measured in a precise, quantitative manner. Because we were developing a new field technique we chose trees of simple structure and relatively small stature. Also these trees' open crowns and sparse foliage permitted clear visibility from all angles in the surrounding flat grassland. Each tree was mapped from two reference points a distance of 3 meters apart that were located roughly 10 meters from the trunk. A Topcon digital transit, accurate to 30 seconds of a degree, was used to measure direction angles.

Any point on the tree of interest will be referred to as a node. In this study nodes are all intersections, bends of the branches and the centers of the epiphytes. A tree skeleton is constructed by appropriately connecting the nodes by straight line segments. Branches that were smaller than 5 cm in diameter (visually estimated) were not mapped. Due to the proximity of plants and branch forks sometimes a single node was taken as the location of more than one feature. Each epiphyte was classified according to type (bromeliad or mistletoe) and relative size (small, medium or large).

The largest source of error in mapping node locations was not in making the transit measurements themselves, but in pairing sightings from the two reference points. To guard against this problem, before mapping a tree a rough sketch was made of the tree that highlights the connectivity information among the nodes. The 3 meter separation of the reference points was a compromise between allowing for an accurate triangulation and making it easy to identify the same node from two different perspectives. Nodes with a discrepancy of more than .1 meters were omitted from the analysis.

Since it is possible to make gross errors in estimating node positions simply by misidentifying them at one of the reference points it is important to consider a measure of accuracy along with the estimated position. We chose to use the discrepancy although some care needs to be taken in interpreting this value as an error estimate. This section ends by quantifying the relationship between the calculated discrepancy and the actual error in the estimate of a node's coordinates.

Let δ denote the distance between a node's estimated position and its true position and let D denote the discrepancy. A series of simulations were run to study the distribution of δ/D as a function of different distances of the target from the transit base line. Like the field work, the reference points in this simulation were separated by 3 meters but to simplify this analysis we took them to be at the same elevation and also located the transits at these points. In practice, translating the coordinate system from the elevation of the transits to the reference points does not generate any error. Constraining the transits to be at the same elevation may improve the accuracy of this triangulation method but we believe this will be a minor effect relative to the overall variability of the estimate. The nodes were located an equal distance from the two reference points. This optimal placement may reduce the error but we believe that the decrease in accuracy is not substantial provided the angular separation between the reference points with respect to the node is comparable to the equidistant position.

One difficulty of simulating transit measurement errors is that error in the horizontal angles depend on the azimuthal angle. For example an error in the horizontal angle when the azimuthal angle is zero is very different from the same error when the azimuthal angle is close to 90 degrees. This does not reflect the actual measurement process because it is reasonable to assume that the transit may be pointed with equal accuracy in almost any direction. One way of modeling this homogeneity is to locate all the node locations at the same elevation as the transits, that is, the true azimuthal angle is 90 degrees. Equivalently one could assume that the transit's base has been tilted so that the azimuthal angle for the node is at 90 degrees. For such locations one way of approximating the measurement error is to add two independent, $N(0,\gamma)$ random variables to the true horizontal and azimuthal angles.

The distribution of (δ/D) was studied at two levels of γ (.05,.2) and forty different distances ranging from 5 to 20 meters. The two standard deviations levels are rough estimates of the error in using a transit for finding the directions and the error from using a staff compass and inclinometer. (Even though the digital transit has a nominal accuracy of 30 seconds, a more substantial error is incurred by not sighting on exactly the same point from the two different perspectives.) The range of distances of the node to the reference points is similar to those encountered in our tree mapping applications. Figure 5 is a plot of the estimated 50 percentile for the distribution of δ/D as a function of the distance from the node to the reference points. Also plotted are lines fit to these results using least squares. Each percentile used in this plot was calculated from a random sample of 5000 observations. These results show that D tends to be significantly smaller than δ and this bias increases as the

distance increases. Thus one should be cautious about interpreting the discrepancy literally as the measurement error. One explanation for this bias is that δ is result of minimizing the distance between the two line of sights. Since δ is being made as small as possible is not surprising that it underestimates the true error. Two striking features of these results are the linear dependence of the median on distance and the insensitivity to the amount of measurement error. For field measurements that are within the range of the parameters of this simulation one might use this approximate linear dependence to calculate a rough inflation factor for the discrepancy measurement.

Section 3 Spatial statistics for tree structures

This section will discuss methods for interpreting the spatial distribution of points. These statistical problems have been widely studied for regular two dimensional regions (Ripley 1981, Diggle 1983, Greg-Smith 1983) and the basic principles carry over for data restricted to a network. Sterner, et al. (1985) give an example of these methods for 2-dimensional regions applied to the interaction between juvenile and adult tropical trees.

The first step in a spatial analysis is to test for departures of the point patterns from complete spatial randomness (CSR). For a homogeneous two-dimensional region, such as a quadrat of the forest floor, CSR is usually taken to be a Poisson process with constant intensity. Conditioning on the total number of points in the region, this process will yield points whose locations are independent from one another and are uniformly distributed over the region. The corresponding spatial process for a tree structure is one where points are distributed uniformly along the branch segments. Because we are interested in plants being supported by these branches, however, this distribution is not a reasonable one. Each branch presents a certain amount of horizontal or near-horizontal surface area to serve as a platform for the epiphyte. Even a random distribution of the plants should favor branches that present a larger amount of surface area. To account for this constraint on the distribution of epiphytes, we will define CSR to be the result of distributing points uniformly on the XY *projection* of the tree structure. Specifically, the probability that a point will be located on a particular branch will be proportional to the length of the branch when projected onto the XY plane. Conditional on a point lying on a particular branch, the location will be uniformly distributed between the two endpoints. In the context of our analysis, we will refer to this stochastic point process as a completely random spatial process (CRSP). Details for efficiently simulating this point process and more complicated ones are given at the end of this section.

There are a variety of statistics that have been proposed to test for departures from
page 7

CSR. These include the empirical distributions of interpoint distances, nearest neighbor distances and point to nearest event distances. Out of these statistics, the nearest neighbor distance (NND) seemed the most promising because of the sensitivity to clustering and also because of its interpretability. From an biological point of view, it was appropriate to consider the height of the bromeliad above the ground and the horizontal distance of the bromeliad from the center or core of the tree crown. The approach suggested by Diggle (1983) is to compare the empirical distribution of a particular statistic with the expected distribution of the same statistic when point patterns are generated under the assumption of CSR. This analysis was applied to the tree where the largest number of bromeliads (53) were observed. Figure 6 is a plot of the empirical distribution of the nearest neighbor distances for the 53 bromeliad locations (solid broken line) and the expected distribution function when the 53 locations are generated from a CRSP (solid curved line) . In some very simple cases it is possible to derive a closed form expression for the expected distribution function of a spatial statistic under the hypothesis of CSR. In the case of processes restricted to a tree structure this is usually not possible and one must resort to Monte Carlo simulation methods to compute this distribution function. Along with computing the distribution function, one may also find bounds that suggest the amount of variability that one would expect for the empirical distribution function. These bounds are the dashed lines in Figure 6 and are the first and 99th percentiles of the marginal distribution. They should be interpreted in the following manner: For a fixed value the nearest neighbor distance, the probability that the empirical distribution will be beyond either the upper or lower bound is .01.

Although one could consider hypothesis tests based directly on the empirical distribution of a particular statistic, our analysis was restricted to either the mean or the median of the observed distribution. Specifically, we considered the MNND, the average height and the average crown distance as summary statistics for testing departures from CSR. This reduction is appropriate given the small numbers of plants observed for each tree (see Table 1). The median was preferred over the average as a summary of the nearest neighbor distances for two reasons. First, when epiphytes were observed to be close together on a branch these plants were mapped to the same node. Thus some of the nearest neighbor distances are zero. A median statistic is one simple way of making the hypothesis test insensitive to these artificial zeroes in interplant distances. Second, since the distribution of statistics such as the nearest neighbor distances is not known to be symmetric, the median seemed to be a more useful summary of the distribution. Figure 7 is a histogram of 1000 simulated MNND statistics for tree #9 under the hypothesis of CSR. Each value was generated by simulating 53 points on

the tree skeleton following a CSR and then computing the MNND for these random locations. The arrow indicates the observed MNND for the data and is located at the 98th percentile of these values. Thus considering a two sided alternative, the p-value for the test is approximately .04 where the null hypothesis is rejected in the direction of a larger MNND. Note that this result agrees with the more detailed analysis of the distribution described above.

Ripley (1979) discusses several other summary statistics that might be used to test for CSR. Although his discussion is limited to rectangular, two-dimensional regions and it is easy to extend these statistics to processes restricted to tree structures. His simulations indicate that a class of U-statistics based on pairwise distances have much better power than the mean NND for clustered patterns and a statistic of this form was included in our analysis to serve as a benchmark. Let $X_k = (X_{k1}, X_{k2}, X_{k3})^T$ denote the estimated coordinates for the location of the k^{th} bromeliad. Adding a third coordinate to the statistic referred to by Ripley as J let

$$J_3 = \sum_{k < j} \phi(X_k, X_j)$$

where $\phi(X_k, X_j) = \prod_{l=1}^3 (c - |X_{kl} - X_{jl}|)_+$ and $(u)_+ = u$ for $u \geq 0$ and 0 if $u \leq 0$. To compute this statistic we take $c = \text{MNND}$ and evaluate the significance level using the same simulation methods described above.

Besides testing for CSR individually for each tree it is also important to consider how to summarize the individual test results to draw conclusions about the pasture trees as a group. Because tree crown architecture and the number of epiphytes varies among this sample, many of the statistics summarizing the epiphyte distribution can not be compared across trees. The p-values for the individual hypothesis tests were used as a way of standardizing the results. One simple way of testing for an overall departure from CSR is to use the fact that under the null hypothesis the p-values will have a uniform distribution on the interval [0,1]. Thus, we tested for departure from a uniform distribution using a χ^2 goodness-of-fit statistic on the intervals: [0, .9), (.9, .95], (.95, .99], (.99, 1.0]. For the observed data there were not enough counts in the all of these intervals to justify using the usual χ^2 approximation to the test statistic. Instead, the distribution of the goodness-of-fit statistic was found by simulating p-values under the null hypothesis (uniform random variables on [0,1]).

We end this section by outlining the numerical algorithm for simulating a complete random spatial process and some related processes with more structure. The tree structure can be represented as a set of N line segments : $\{S_k\}_{1 \leq k \leq N}$. With this notation, if a_k and b_k are the endpoints of the k^{th} segment, then $S_k = \{\alpha a_k + (1-\alpha)b_k : 0 \leq \alpha \leq 1\}$.

The simulation algorithm requires a set of probabilities for selecting one these segments and then a rule for locating a point on the selected segment. Let p_k be the probability that a point of the spatial process will lie on the k^{th} segment. In the case of uniformity with respect to the X-Y projection we take $p_k = D_k / \sum D_j$ where D_k is the length of S_k when projected onto the x-y plane (the distance between a_k and b_k setting the third coordinate to zero). Using the notation introduced above, a random point X from the spatial processes is generated in two steps:

- 1) Generate a random integer $1 \leq J \leq N$ where $\mathcal{P}(J=k) = p_k$.
- 2) Generate a uniform random number, U and let $X = U a_J + (1-U) b_J$.

Numerical algorithms for generating both J and U efficiently can be found in (ref.). Note that by changing the probabilities associated with the segments one can vary the spatial process. For example if D_k above is replaced by just the three dimensional length of S_k then steps 1) and 2) will simulate a process that is uniformly distributed on the entire tree structure.

Although it is not necessary to simulate a nonhomogenous process to test for a CSR point pattern, simulating such processes are an important part of a numerical technique for estimating parameters. For this reason it is natural to discuss how processes that differ from a CRSP can be simulated on a tree structure. Simulating spatial processes that do not depend on spatial uniformity will follow the two basic steps outlined above but the probabilities for selecting a segment and the rules for locating the point on the segment may be more complicated. As an example, we outline how to generate a simple cluster process.

Suppose cluster centers are distributed according to a CRSP. For each cluster center, N points are distributed uniformly in a ball of radius R about the cluster center. The steps given below could be used to generate the points belonging to a particular cluster.

- 1) Generate a cluster center X_C , using the algorithm for a CRSP described above and let \mathcal{B} denote a ball of radius R centered at X_C .
- 2) Identify all branch segments that are contained in \mathcal{B} . Let $L_k = \mathcal{B} \cap S_k$, $D_k = \text{length of } L_k$ if the intersection is nonempty and $D_k = 0$ otherwise.

Repeat N times:

- 3) Let $p_k = D_k / \sum D_j$ and generate a random integer $1 \leq J \leq N$ where $\mathcal{P}(J=k) = p_k$.

- 4) A point of this cluster is now found by choosing a point uniformly distributed on the line segment L_J .

In order to simulate the entire process one would repeat these steps according to the total number of clusters on the tree. For clarity this example has assumed the number (N) and dispersion (R) of the cluster is fixed. Clearly these quantities can be made random and distinct values could be generated for each cluster.

To simulate a spatial process that is hyperdispersed one could generate a CRSP (or a clustered process) but thin the points according to some rule. For example, one might omit all pairs of points from the CRSP that lie within a critical distance of each other. In this way, one obtains a random point process where points are separated by larger distances than would be expected with respect to a CSR.

4 Results of testing for departures from complete spatial randomness

Tree branches and epiphyte locations were determined for the 12 pasture trees described in Section 2. Table 1 reports some features of the tree structure, the numbers of bromeliads and mistletoes observed, and some summary statistics for the discrepancies. Using more traditional mapping techniques a map was made of the pasture including the locations and elevations of the trees under study (Figure 8). Figure 9 depicts the relationship among the average height of the bromeliads, the average height of points chosen at random with respect to a CRSP and the elevation of the tree. The X-axis in this figure is the same as the X map coordinate from Figure 8 while the Y-axis is the relative elevation.

The hypothesis of CSR for the bromeliad locations was tested using the MNND, mean height, median horizontal distance from the crown center and the U-statistic, J_3 . Table 2 lists the p-values for these tests with respect to a two sided alternative. The plus and minus signs after the p-values indicate the direction in which the null hypothesis is rejected. Thus for tree #3 the p-value for the MNND corresponds to the .874 percentile of the reference distribution. In a similar manner, the p-value of .892- for crown distance is derived from the observed percentile of .054. The χ^2 statistics for testing uniformity of the p-values are reported in the last row of this table along with some approximate significance levels for the goodness-of-fit test for uniformity.

Figure 10 was constructed to investigate possible spatial dependence among the

individual test results. The locations of the trees were coded by the results of the hypothesis tests based on the MNND and the mean height.

5 Discussion and conclusions

The main scientific result of this analysis is the statistical evidence that the spatial patterns of bromeliads depart significantly from CSR. Considering the MNND test statistic this hypothesis is rejected both in the direction of clustering and also in the direction of hyperdispersion. Hypothesis tests based on the average height indicate that the trees host bromeliad distributions that are both significantly above and below the average height that would be expected under the hypothesis of CSR. These varying results suggest that there are other factors besides these simple features of tree architecture that must influence the location of bromeliads in the tree crown. These may be due to biological processes such as bird dispersal of propagules, fungal associations with epiphyte roots, or organic matter associated with branch substrates. Further field observations are needed to explain these results.

In any statistical analysis where numerous hypotheses tests are done it is important to consider the actual significance of the reported results. One reason we have emphasized the results using the MNND statistic is that this was our method of choice before examining the data. Note that even stronger results are obtained by considering the average height. Even if one's attention was restricted to a single test statistic one still needs to be careful about interpreting the set of p-values across trees. We found however that a reasonable test for uniformity of the p-values based on the MNND tests provides strong evidence against the null hypothesis of uniformity.

Applied statistics strikes a balance between formal methods of inference and an informal, exploratory analysis of the data. Perhaps the most important scientific issue is whether there is a simple feature of the tree architecture that explains why trees of the same species exhibit both clustering and hyperdispersion for these bromeliades. We have not been able to find any revealing patterns. This includes examining the spatial distribution of the results for individual tree crowns with respect to the crowns' relative locations and elevations. We also considered the possibility that the bromeliad distribution may be influenced by the presence or absence of mistletoes but found no significant patterns. The pairwise scatterplots of the p-values, do not suggest any strong relationship between the test results. Such a comparison, however must be discounted by the fact that different test statistics for the same tree are probably not independent even for a CRSP. Also, since the tree architecture varies, the joint distribution of the p-values will vary among the trees in this study.

Having found departures from CSR, the next step in a statistical analysis of spatial data is to build a model for spatial process that explains the observed point patterns. Estimating spatial models by maximum likelihood is possible by combining the simulation algorithms described in Section 3 and the methods suggested by Diggle (1985). This second step was not pursued in this study, however, because of the mixed results in testing for CSR. We believe a more appropriate direction is to perform additional experiments to identify the factors that control diversity. For example, the tree maps from this study can be used to direct further measurements of these tree crowns. In particular these results can be used to generate statistically sound sampling designs for investigating the relative availability of nutrients or the microclimate within a crown. Since epiphyte abundance may be related to branch surface area, one important variable missing from our analysis is branch size. This additional measurement was omitted from the current study because it complicated the mapping process. However, inclusion of this variable in future work may aid in interpreting epiphyte distributions. Another factor influencing the distribution of bromeliads is the possible competition with mistletoes. Although there are no obvious patterns among these two types of epiphytes across the sample of trees, a interaction might be present.

Our statistical analysis is conditional on the assumption that the node positions have been measured without error. Because our mapping techniques include a measure of accuracy we have controlled this source of variation and we have assumed that discrepancies accurate to within 10 cm will not bias the subsequent spatial analysis. This assumption might be checked by simulating reference distributions for the test statistics that include the additional variability from measuring the node locations.

One thread connecting all parts of this project is the use of computer intensive methods to handle nonstandard problems. Although the transit angles are easy to measure, the conversion to xyz coordinates is a tedious hand-calculation and is best done using at least a programmable calculator. Because the estimate of node coordinates has a complicated form a Monte Carlo simulation is used to study the reliability of the discrepancy measure. Statistical hypothesis tests for CSR also relied on simulation methods in order to account for the unique branching structure in each tree. Finally, computer graphics are used extensively to visualize the three-dimensional structure of the data.

Our results confirm the value of tree mapping techniques for studying tree crowns. We have described a field technique that is efficient and accurate and have identified statistical methods to interpret the resulting spatial data. The simulation techniques used in this work may also be appropriate for the analysis of point processes on other types of branching

structures or networks.

Acknowledgements The authors are grateful for support from the Whitehall Foundation, the National Geographic Society, the National Science Foundation (BSR86-14935), the American Philosophical Society and the Math Sciences Institute at Cornell University.

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Appendix An estimate of location from a pair of transit sightings

A formula for the estimated target location from two transit sightings can be derived using vector algebra. Let \underline{a} and \underline{b} denote unit vectors pointing in the same directions as the transit sightings. For example,

$$\underline{a} = (\cos(\theta_1)\sin(\phi_1), \sin(\theta_1)\sin(\phi_1), \cos(\phi_1))$$

and \underline{b} is found in a similar manner. The two rays corresponding to the transit line of sights can be parameterized by

$$(0,0,h_1) + \alpha \underline{a}$$

and

$$(L,0,E+h_2) + \beta \underline{b}$$

for $\alpha, \beta > 0$. Let $\underline{d} = (L, 0, E + h_2 - h_1)^T$. The shortest line segment connecting these two rays has end points at $\hat{\alpha}$ and $\hat{\beta}$ where these values minimize the squared distance:

$$(\alpha \underline{a} - (\underline{d} + \beta \underline{b}))^T (\alpha \underline{a} - (\underline{d} + \beta \underline{b}))$$

for all α and β . Setting first partial derivatives equal to zero yields the system of equations

$$\alpha - \beta \gamma = u_1$$

$$-\alpha \gamma + \beta = -u_2$$

where $\gamma = \underline{a}^T \underline{b}$, $u_1 = \underline{a}^T \underline{d}$ and $u_2 = \underline{b}^T \underline{d}$.

Thus,

$$\hat{\alpha} = (u_1 - \gamma u_2) / (1 - \gamma^2), \quad \hat{\beta} = (\gamma u_1 - u_2) / (1 - \gamma^2)$$

and in vector notation the estimated target location (without simplifying) is

$$(0,0,h_1)^T + \hat{\alpha} \underline{a} + (\hat{\alpha} \underline{a} - (\underline{d} + \hat{\beta} \underline{b})) / 2.$$

The discrepancy is the length of the vector $(\hat{\alpha} \underline{a} - (\underline{d} + \hat{\beta} \underline{b}))$.

Table 1
Summary of tree and epiphyte measurements

<u>Tree Id.</u>	<u>#bromeliads</u>	<u>#nodes</u>	<u>bromelaid density¹</u>	<u>median discrepancy²</u>
13	21	48	.75	.02
16	35	109	.35	.02
17	5	59	.12	.02
22	19	89	.31	.01
25	56	156	.42	.02
26	40	116	.45	.02
35	36	87	.59	.03
3	6	49	.95	.01
5	13	91	.18	.03
7	9	62	.18	.02
8	27	71	.52	.01
9	53	109	.58	.03

¹ Bromeliad density (number of plants per meter of horizontal branch length) is calculated by dividing the number of plants by the total length of the branch network when projected on to the X-Y plane.

²Median discrepancy is the median of all the discrepancies for the node positions.

Table 2
 Summary of p-values for testing
 the hypothesis of complete spatial randomness¹

<u>Test Statistics</u>				
<u>Tree Id.</u>	<u>MNND²</u>	<u>Mean Height³</u>	<u>Mean Crown Dist.⁴</u>	<u>J3⁵</u>
13	.480+	.002-	.556-	.168-
16	.406+	.498+	.174+	.400-
17	.520 +	.437+	.922-	.252-
22	.864+	.338+	.014+	.668+
25	.412-	.000+	.980+	.440+
26	.056-	.012+	.004+	.054+
35	.056+	.010-	.182-	.074-
3	.252+	.962+	.892-	.644+
5	.470-	.380-	.036+	.104-
7	.014-	.262-	.216+	.360-
8	.050-	.000+	.892-	.058+
9	.024+	.340+	.118+	.098-
χ^2 statistic for uniformity of p-values ⁶	17.95	75.87	7.675	10.5
Significance level for uniformity test	<.005	<.001	≈.05	≈.1

¹ Complete spatial randomness with respect to the X-Y *projection* of the branch network.

² Median of nearest neighbor distances.

³ Mean vertical height.

⁴ Mean horizontal distance from the trunk.

⁵ U-statistic sensitive to departures from spatial homogeneity (see Section 3).

⁶ χ^2 goodness-of-fit statistic under the null hypothesis of a uniform distribution on [0,1]. The intervals used were [0, .9), (.9, .95], (.95, .99], (.99, 1.0] and the significance of the observed test statistics were determined from simulating 1000 values of the test statistic under the null hypothesis.

Figure Legends

Figures 1-3. Top and side views of reconstructed tree skeletons. The locations of bromeliads on these trees are indicated by symbols representing the relative size of the epiphytes (b=small, c=medium, d=large). Summary statistics on these three trees can be found in Tables 1 and 2 while their relative locations can be inferred from the pasture map in Figure 12.

Figure 4. Geometry of mapping tree positions using a pair of transit sightings.

Figure 5. The relationship between the discrepancy measure and the true error in a mapped position. Plotted are the results of a simulation study to determine the relationship between the discrepancy calculated from pairs of transit sightings (δ) and the actual distance from the estimated position to the target location (D). The plotted points are estimates for the median of the distribution of (D/δ) at 40 different target distances and two levels of error in the transit measurements. The lines were fit by least squares.

Figure 6. Comparison of observed nearest neighbor distance (NND) distribution with the distribution assuming spatial homogeneity. The dotted line is the observed distribution function of the NND for the 53 bromeliads on tree #9. The solid line is the expected distribution function for this statistic under the assumption that the locations follow a completely random spatial process (CRSP). The dashed lines are estimates of the 1% and 99% pointwise percentiles for an empirical distribution of the NND when the positions come from a CRSP.

Figure 7. Histogram of 1000 median nearest neighbor distances (MNND) under the hypothesis of spatial uniformity. These statistics were simulated from 53 points of a completely random spatial process on the tree skeleton of #9. The "X" symbol near the X-axis locates the value of the observed MNND statistic for the bromeliad positions. The observed statistic is at the 98.8 percentile of the simulated values.

Figure 8. Fogden pasture map with tree locations and contour lines of relative elevation.

Figure 9. Average height of bromeliads in relation to elevation and tree height. The tree identification numbers are plotted using the horizontal map coordinate of Figure 9 and the relative elevation. The line segment from these numerals ends at a "+" and marks the mean height for positions in the tree skeleton under the assumption of spatial uniformity. The X symbol locates the observed mean bromeliads height.

Figure 10. Pasture map incorporating test results for individual trees. Contour lines are of relative elevation and each pair of symbols is centered at a tree location. The choice of symbols is based on the test results for the MNND statistic and the mean height reported in Table 2.

"0" = p-value \leq .9

"H" = p-value of MNND $> .9$ in favor of *hyperdispersion*

"C" = p-value of MNND $> .9$ in favor of *clustering*.

"A" = p-value of mean height $> .9$ in favor of being *above* the mean height of branch positions.

"B" = p-value of mean height $> .9$ in favor of being *below* the mean height of branch positions.

Figure 1: Fogden tree #26

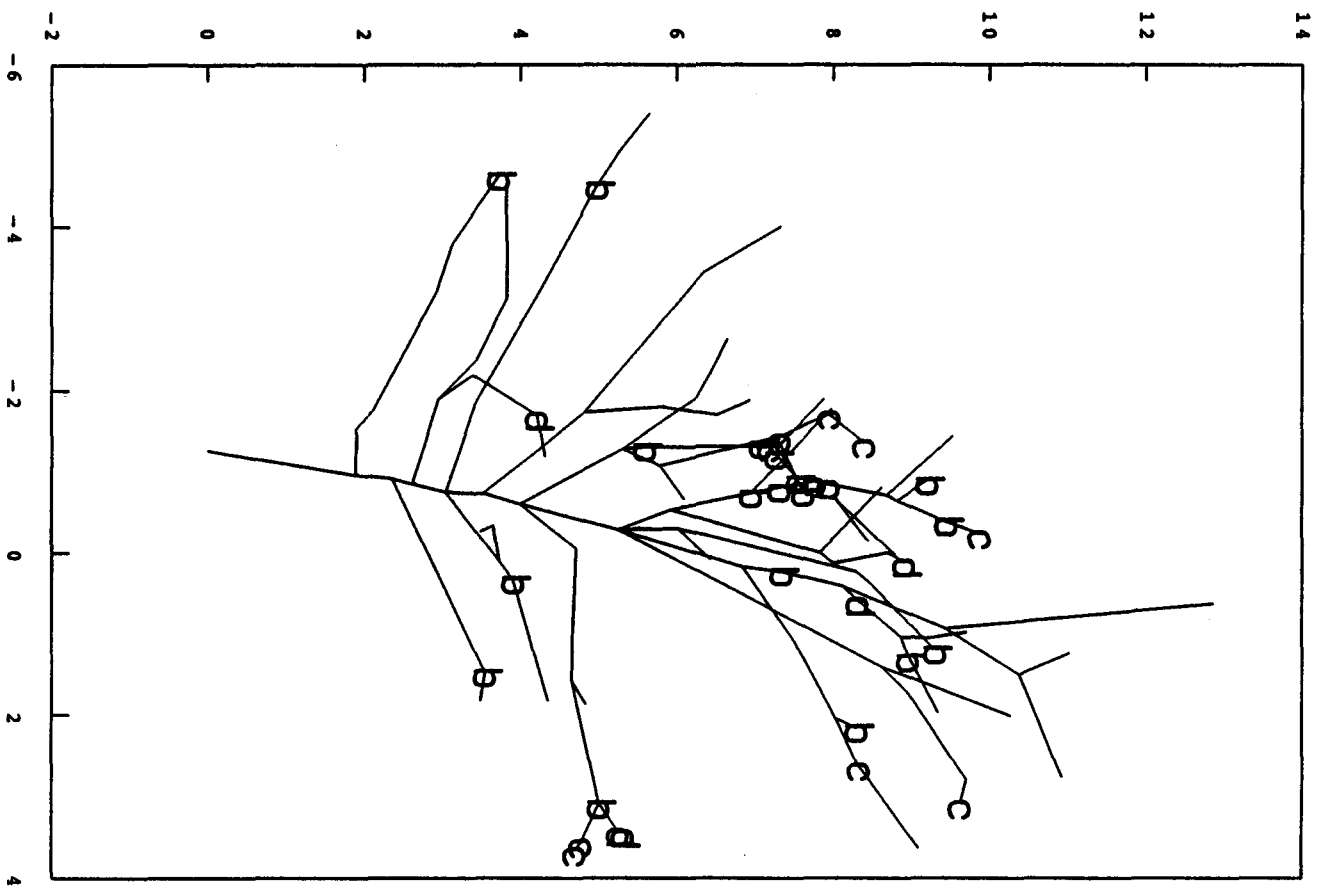
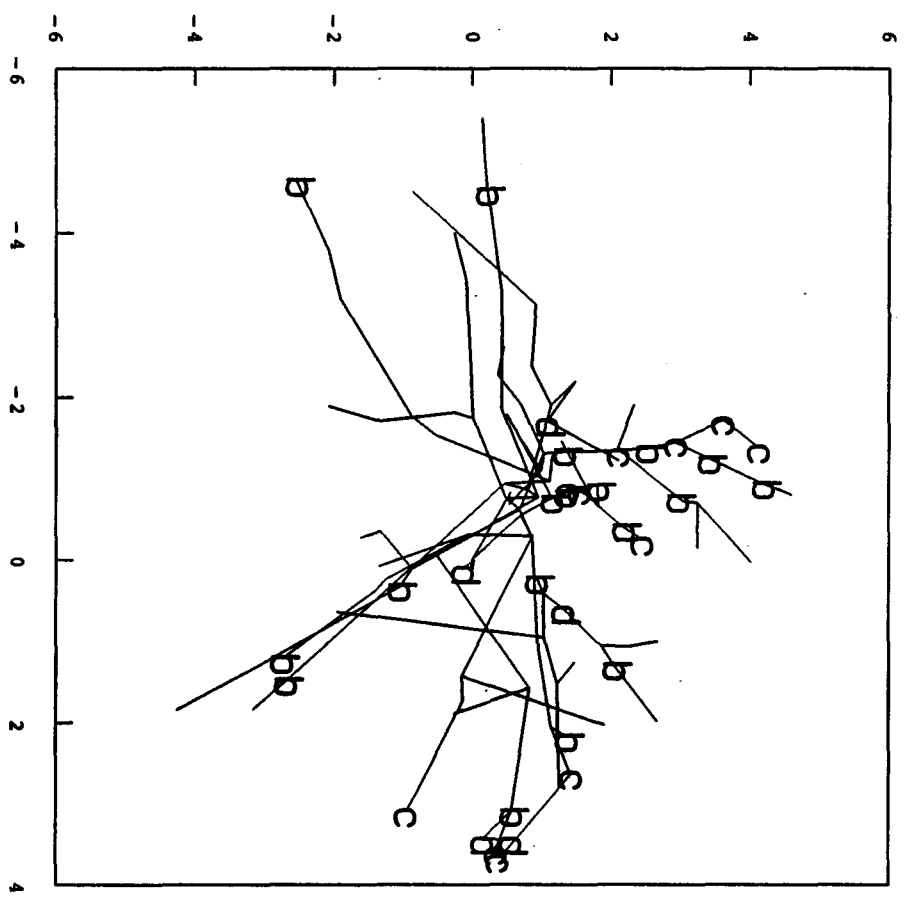


Figure 2: Fogden tree #9

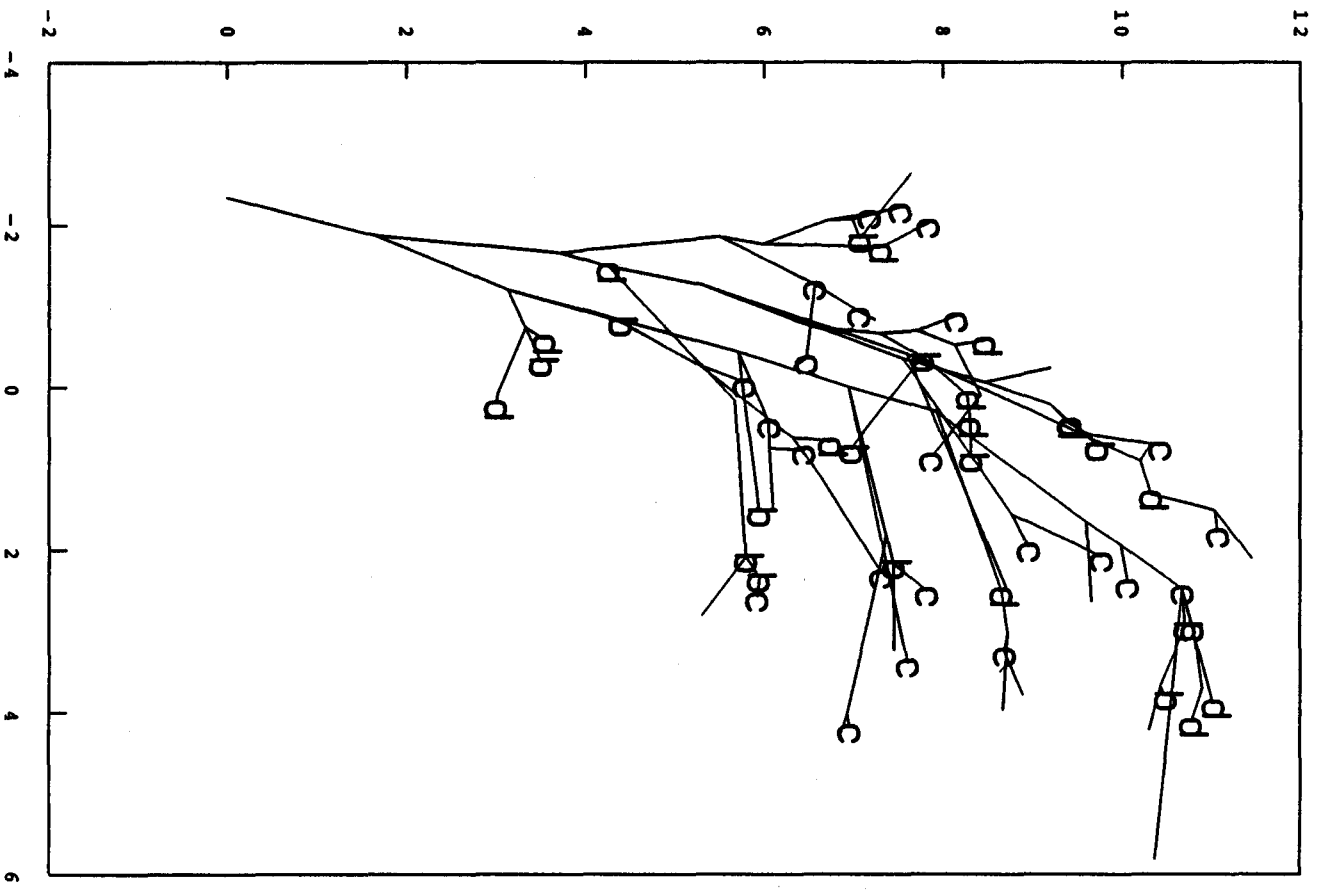
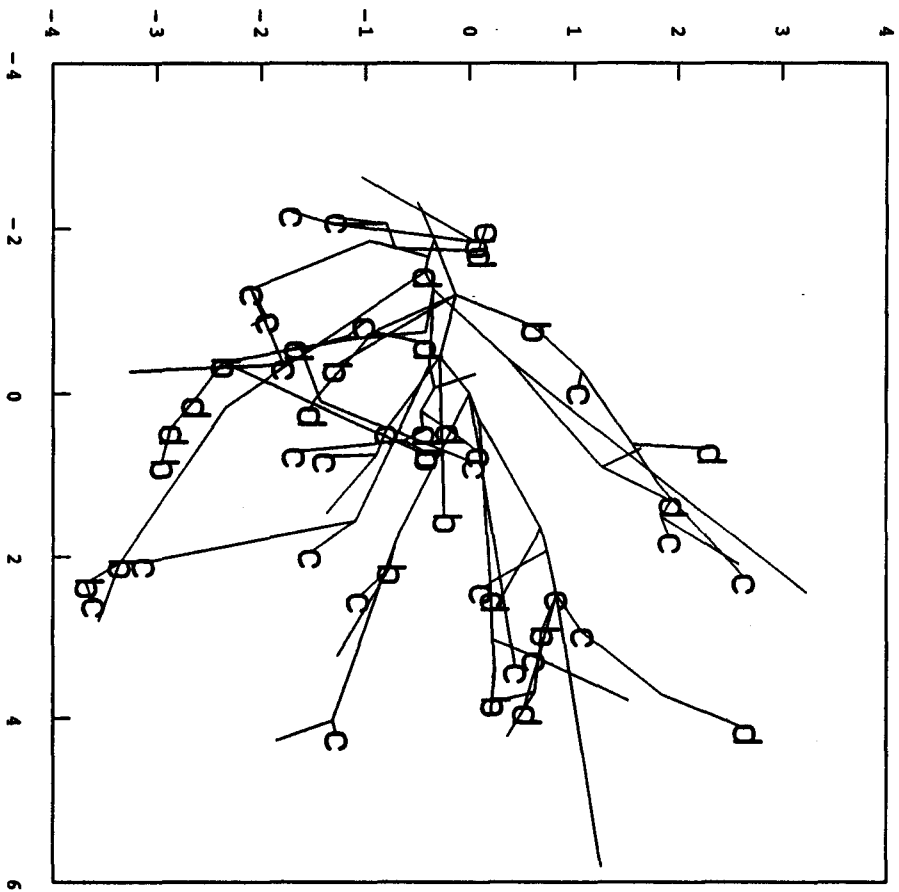


Figure 3: Fogden tree #16

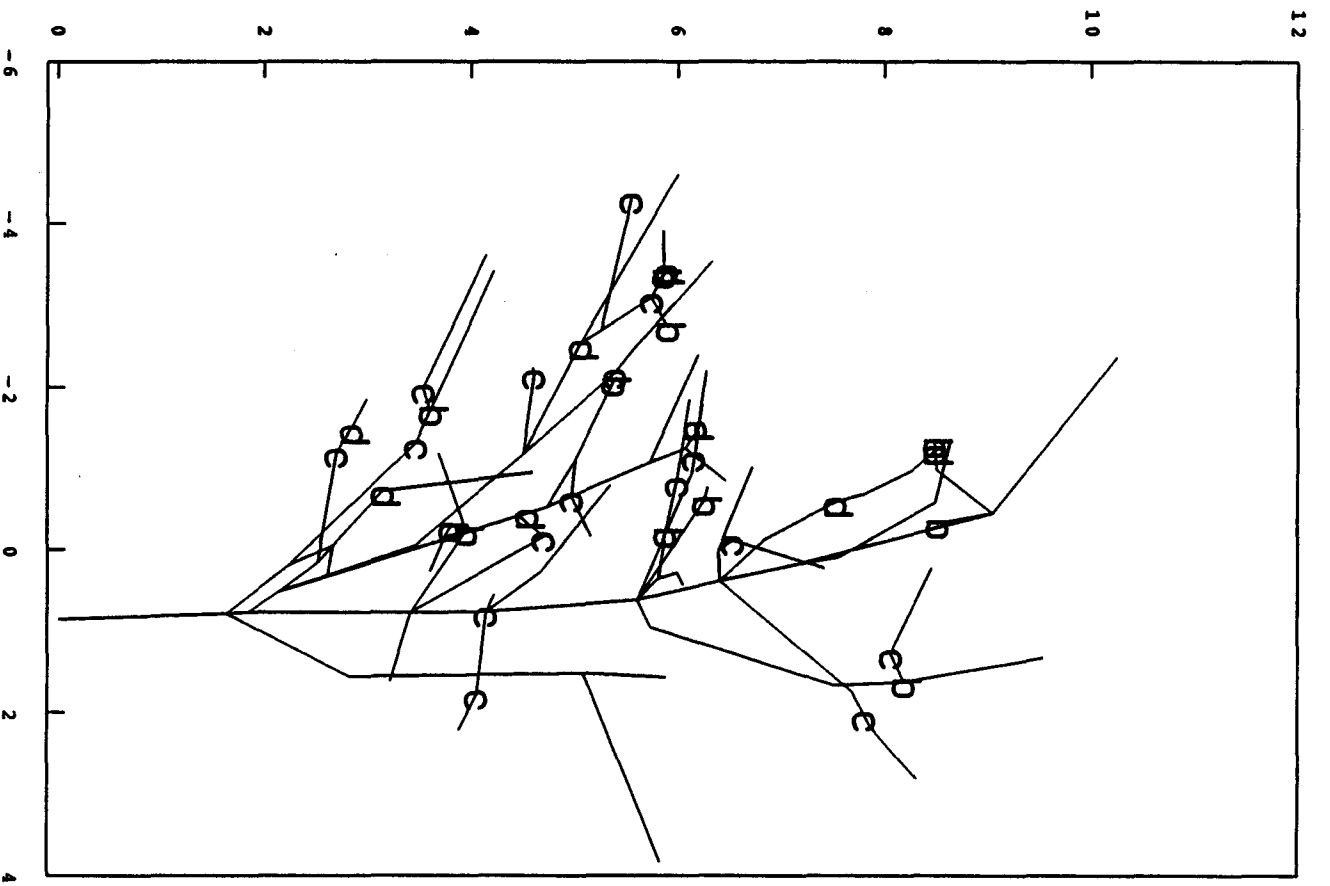
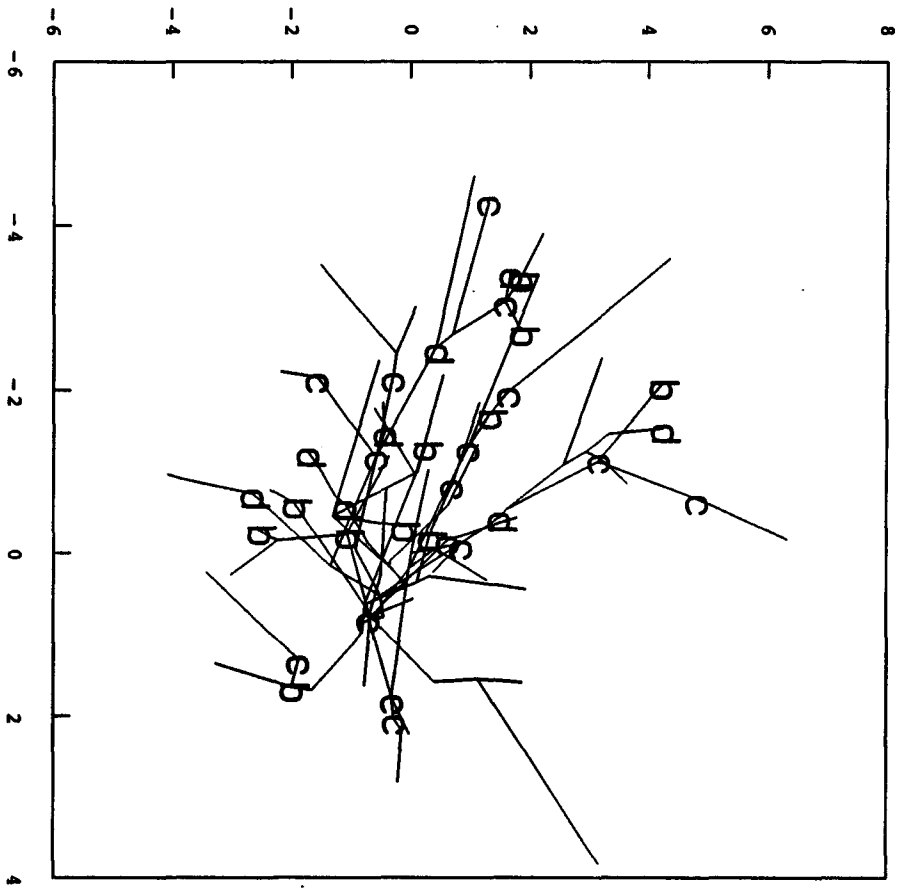


Figure 4: Mapping a remote point using two transit sightings

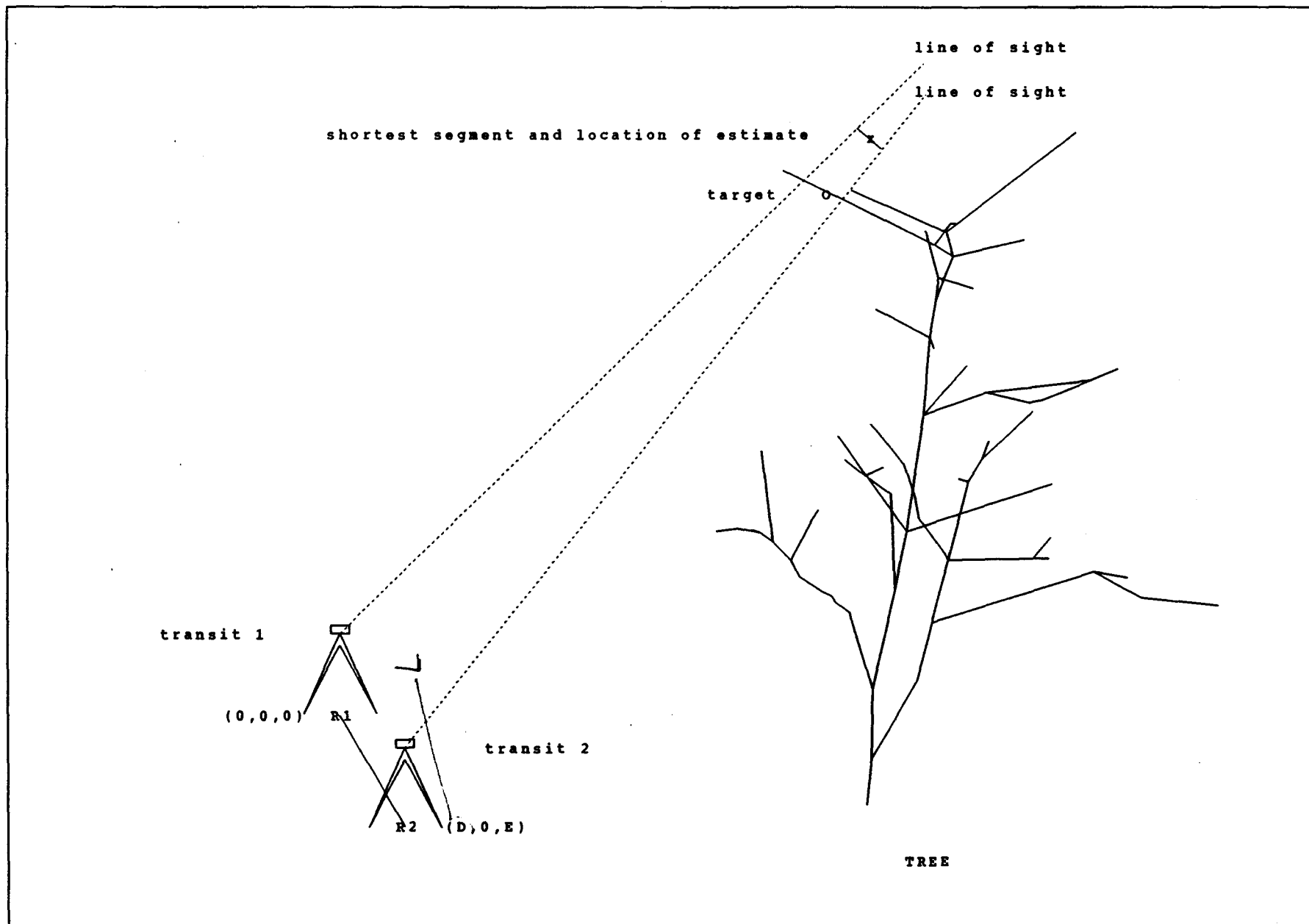


Figure 5 Simulation results for studying the decrepency measure

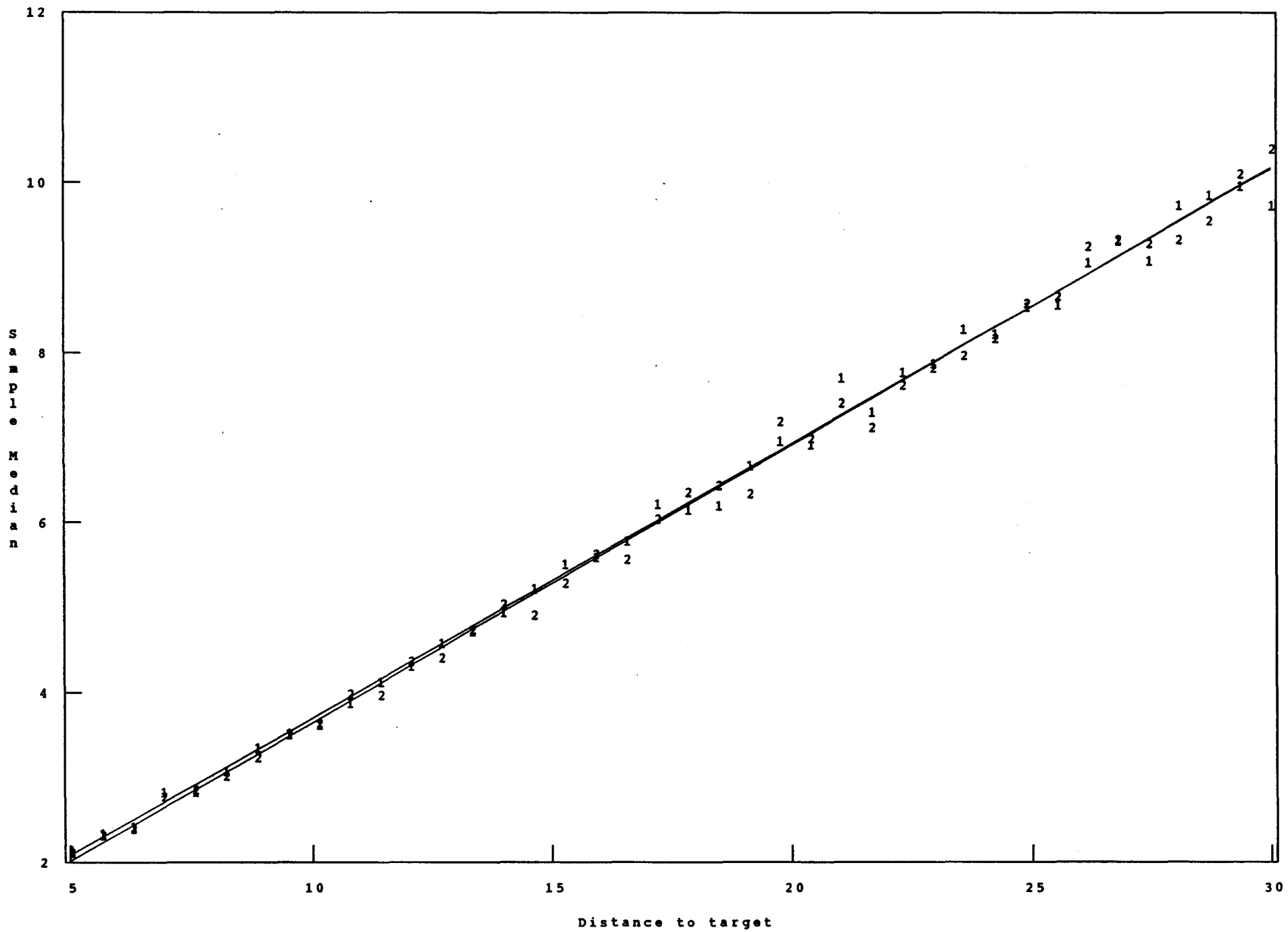


Figure 6: Comparison of observed and expected distributions

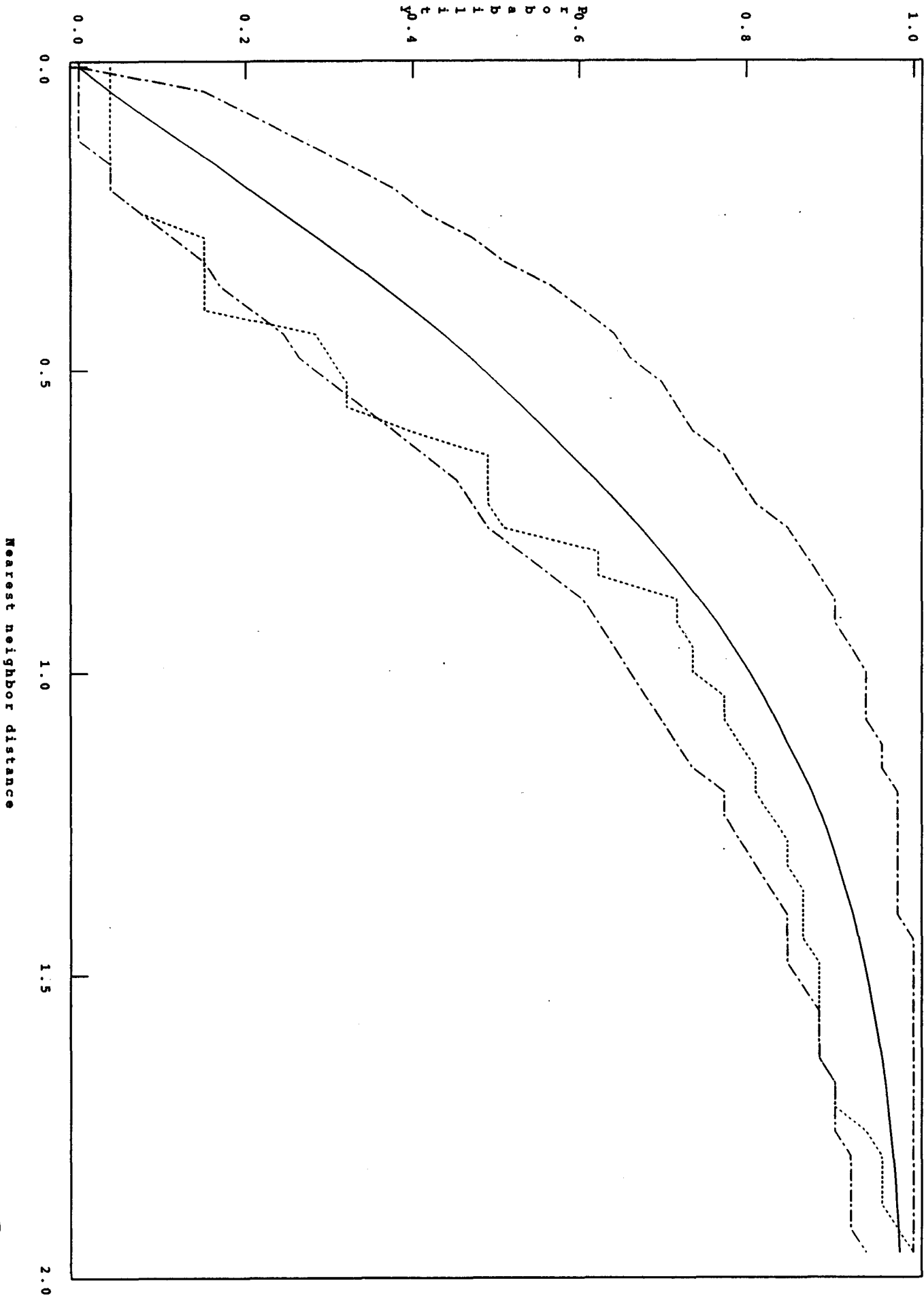


Figure 7: Simulated MNNND statistics

