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AN ORDINATION TECHNIQUE BASED ON THE BEST POSSIBLE STAND-DEFINED AXES AND ITS APPLICATION TO VEGETATIONAL ANALYSIS[1]

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Abstract. An ordination technique for the analysis of vegetation data is described. The procedure resembles the Wisconsin method in the use of stands to define axes and Beals' formula to calculate stand axis positions. Differences from the Wisconsin method are: (1) axes are spatially related in a geometrically acceptable manner and (2) the best possible stand-defined axes are objectively selected. The method is simpler to understand than principal components "factor" analysis, and much less computation is required if there are many species in the data. Without modification of the method, a three-dimensional ordination was obtained for each of three sets of data, two from the North American prairies and one from the Canadian boreal forest. Hence, the technique objectively selects axes from "real" data in accordance with its design, but as yet we cannot say how effective it is in the display and interpretation of species interrelationships.

INTRODUCTION

The development of rapid and efficient field sampling methods (Lindsey 1955, Cottam and Curtis 1956, Penfound and Rice 1957, and many others) has permitted phytosociologists to amass large quantities of data. In turn, the analytical problems posed by a mass of data, coupled with a desire to increase objectivity, have fostered mathematical techniques of analysis. One of the most widely used techniques for phytosociological analysis is ordination (Greig-Smith 1964). Apparently, the most objective and mathematically precise means of ordination is factor analysis (Dagnelie 1960, Orloci 1966, Austin and Orloci 1966), but to the ecologist with limited mathematical training this is a complex procedure. However, workers in Wisconsin (Bray and Curtis 1957, Beals 1960) have developed an alternative and conceptually simple ordination technique in which calculated dissimilarities between stands are directly used to define axes. This method has been widely applied in vegetational studies (Curtis 1959, Gittins 1965, Beals 1965, Orloci 1966, and others).

Stand-ordination procedures seek to place stands in relation to one another through their positions on each of a number of axes; the axis-selection procedure is therefore crucial to the successful display of vegetational patterns. With the Wisconsin method, stand pairs that define axes (stand-defined axes) are chosen from those that are phytosociologically very different (distant), and the length of the axis is made equal to the calculated distance between them (e.g., Beals 1960). There appears to be no a priori reason, however, why axes defined by distant stands should have more ecological meaning than axes defined by stands that are separated by short distances. While widely separated stands may indeed represent the extremes of a vegetational gradient, this can only be inferred through prior knowledge of the vegetation; distantly related stands may in fact share few or no compositional relationships with many other stands in the study and therefore have little value as reference stands in ordination. Swan and Dix (1966) and Newsome and Dix (1968) attempted to ensure the ecological value of distant reference stands by selecting mutually different reference members that shared at least an arbitrary minimum of compositional relationships with other stands in the matrix. In each case, the resultant ordination yielded a strong correlation between a sample of ordination distances and corresponding matrix values. However, these techniques embodied an arbitrary criterion for axis selection specifically selected to suit the data at hand, and we consider this to be undesirable.

Orloci (1966) noted a fault in the geometric constructions used to interrelate ordination axes by the Wisconsin method. The two stands used as reference members for a Y axis are required to be mutually quite different and yet fall close together on the X axis. When, as happens frequently, these two stands do not lie at the same point on the X axis, it is, of course, geometrically incorrect to place them at the ends of a Y axis perpendicular to the X axis. Orloci (1966) introduced a geometrically sound alternative that

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overcame this shortcoming, but still used the distant stand criterion for axis selection.

In short, the application of the Wisconsin method to phytosociological data is sometimes difficult and unsatisfying because of its arbitrary axis-selection procedure. We offer an alternative technique that avoids these troublesome characteristics but retains the relative simplicity of the Wisconsin method.

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The Method

Phytosociological ordination has the following conceptual base. Theoretically, stands can be located by their species composition in a euclidean space of dimension equal to the number of species present. Each species could represent an axis and the position of a stand on each axis would then be given by the frequency, normalized frequency, or other measure of the species being used. In intuitive terms, we desire to find a section through this space which emphasizes the main features of the vegetation. We assume that, in a given study area, the distribution of many species is significantly regulated by a limited number of factors. If this assumption is correct, a small number of axes should reflect the main features of the vegetation. The ecologist wishes to find such axes.

In practice, we want to find a small number of axes that produce a spatial disposition of stands having interstand distances closely approximating the corresponding distances in the data matrix. To do this, we replace the distant stand criterion for axis selection by a mathematically objective and more rational criterion. The space defined by n species may be represented by any set of n orthogonal (perpendicular) axes, $X_1, X_2, \ldots X_n$. Now, in a space defined by mutually perpendicular axes, Pythagora's theorem states:

$$d_{ij}^2 = X_{1ij}^2 + X_{2ij}^2 + \ldots X_{nij}^2$$

where d_{ij} is the calculated distance between stands i and j and where X_{1ij}, X_{2ij}, and X_{nij} are the distances between stands i and j along the first, second, and n^{th} axes respectively. Summing over all stand pairs we find:

$$\sum_{ij} d_{ij}^2 = \sum_{ij} X_{1ij}^2 + \sum_{ij} X_{2ij}^2 + \ldots + \sum_{ij} X_{nij}^2$$

Thus, all interstand distances in a matrix (here represented as the sum of squares of interstand distances) can be placed in a euclidean space, partitioned among n orthogonal axes (Orloci 1966). If possible, we wish to represent these interstand distances as closely as possible on one or a few orthogonal axes only. It seems reasonable to choose, as the first axis, that one which accounts for the highest proportion of the sum of squares for all interstand distances (e.g. the axis with the highest $\sum_{ij} X_{1ij}^2$) because the disposition of stands on this axis is the best single approximation we can presently make to the distance relations in the matrix. The second axis is selected to be that one perpendicular to the first which accounts for the highest proportion of the remaining sum of squares of interstand distances (the sum not accounted for by the first axis). Similarly, further axes may be selected as the orthogonal components which best account for a residual sum of squares. We have adopted this criterion for axis selection.

To construct ordination axes we decided to use a geometric procedure based on Pythagora's theorem because of its conceptual simplicity. Beals (1960) first used this theorem to order stands on an axis, and Orloci (1966) has applied it to construct successive axes and interrelate them orthogonally. Our procedure is geometrically equivalent to Orloci's scheme.

In the following outline of our procedure, the construction of the X_1, X_2, and X_3 axes is described in some detail, followed by a brief outline of how the method may be extended to further axes, if desired. The X_1, X_2, and X_3 axes are respectively termed X, Y, and Z to conform with common parlance.

The X *axis*

The geometric constructions used to obtain stand positions on an X axis are illustrated in Fig. 1. In each diagram of the figure, two stands, A and B, define an X axis: the line passing through A and B. The distance between A and B is a value from the matrix of interstand distances. P is a third stand placed in space by matrix distances AP and BP. The position of P on the X axis is obtained by dropping a perpendicular hPx to intersect X at Px. Px is located at a distance α measured from A along the X axis. Applying Pythagora's theorem to the construction it can be shown (Beals 1960) that:

$$\alpha = \frac{AB^2 + AP^2 - BP^2}{2AB} \quad (1)$$

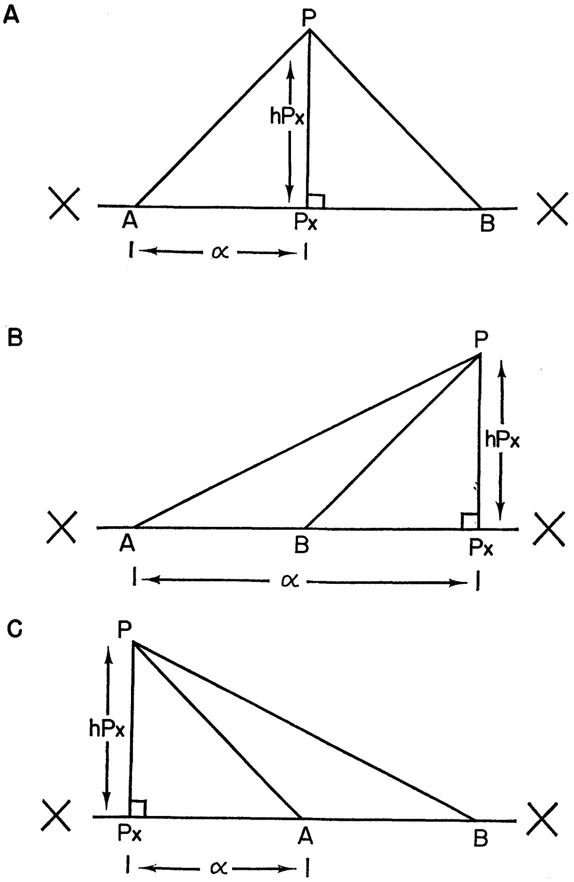

FIG. 1. The geometric constructions used to select and construct an ordination X axis. The triangles represent all possible constructions required to place a stand P on an X axis defined by stands A and B. Terms are described in the text.

which is Beals' formula. Beals' formula also applies when the projection of P onto the X axis does not fall between stand A and B (see Fig. 1B and C). α is positive when Px is to the right of A (Fig. 1A and B) and negative when Px is to the left of A (Fig. 1C). This formula is used to calculate the positions of all stands P on an X axis defined by two stands A and B.

The sum of squares of interstand distances along an X axis is:

$$\sum_{ij} X_{ij}^2$$

where $X_{ij} = \alpha_i - \alpha_j$ is the distance on the X axis between the i^{th} and the j^{th} stands. A simple formula to calculate $\sum_{ij} X_{ij}^2$ is derived as:

$$\sum_{ij} X_{ij}^2 = \sum_{ij} (\alpha_i - \alpha_j)^2 = \sum_{ij} (\alpha_i - \overline{\alpha} + \overline{\alpha} - \alpha_j)^2$$

$$= \sum_{i=1}^{m} \sum_{j=1}^{m} (\alpha_i - \overline{\alpha})^2 + \sum_{i=1}^{m} \sum_{j=1}^{m} (\alpha_j - \overline{\alpha})^2 -$$

$$2 \sum_{i=1}^{m} (\alpha_i - \alpha) \sum_{j=1}^{m} (\alpha_j - \overline{\alpha})$$

$$= m \sum_{i=1}^{m} (\alpha_i - \overline{\alpha})^2 + m \sum_{j=1}^{m} (\alpha_j - \overline{\alpha})^2 - 0$$

$$= 2m \sum_{i=1}^{m} (\alpha_j - \overline{\alpha})^2$$

$$= 2mS.S._x$$

where $S.S._x$ is the sum of squares of stand positions on the X axis and m is the number of stands.

There are as many possible stand-defined X axes as there are different stand-pair comparisons in the matrix. On each of these axes the other stands may be located permitting the calculation of a $2m\ S.S._x$ value as above. It is a simple matter to select, with the aid of a computer, that one of the $m(m-1)/2$ possible stand-defined X axes which accounts for the largest proportion of the sum of squares of interstand distances. In other words we choose the axis which has the highest

$$S.S_x = \sum (\alpha - \overline{\alpha})^2$$

$$= \sum \alpha^2 - \frac{(\sum \alpha)^2}{m} \qquad (2)$$

Formula (2) is used for computation where α is calculated from formula (1).

The proportion of the sum of squares for all interstand distances (e.g. the matrix sum of squares) accounted for by an X axis is:

$$\sum_{ij} X_{ij}^2 / \sum_{ij} d_{ij}^2 \quad \text{or} \quad 2mS.S._x / \sum_{ij} d_{ij}^2 \qquad (3)$$

since $\sum_{ij} X_{ij}^2 = 2mS.S._x$

For convenience, this fraction, as a percentage, is termed the per cent extraction value of the axis.

The Y *axis*

Stand positions relative to the X axis can be expressed by Pythagora's theorem in terms of two orthogonal components (Fig. 1). Thus, for distance AP, α is the portion represented along the axis while hPx, at right angles to the axis, is a residuum which is the basis for further axis extraction and is calculated for each stand as:

$$hPx = \sqrt{AP^2 - \alpha^2}.$$

When calculated for all stands, hPx provides a matrix residuum for which the Y axis must account as much as possible.

The constructions that place a stand on a Y axis are illustrated in Fig. 2; a perspective drawing is used, since the constructions occupy three-dimensional space. As in Fig. 1, stands A and B define the X axis and any third stand (e.g., C) can be placed at a vertical distance from the X

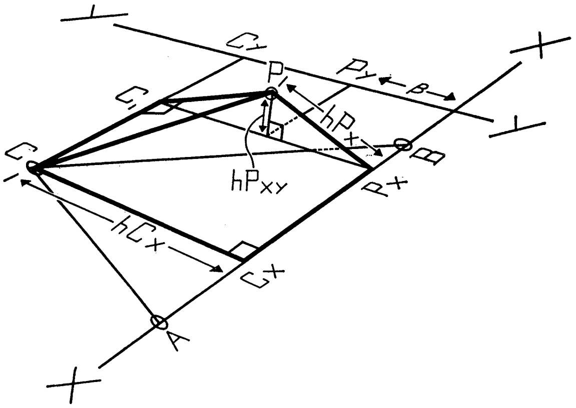

FIG. 2. The geometric constructions used to select and construct an ordination Y axis. One diagram represents all constructions required to place a stand P on a Y axis defined by a plane of three stands: A, B, and C. Terms are described in the text.

axis equal to its residual distance HCx. These three stands now define a plane ABC on which a Y axis is constructed. This axis is made parallel to hCx and perpendicular to the X axis. A fourth stand P is placed in relation to the ABC plane. Stand P is connected by a calculated distance hPx and a matrix distance CP to two points in the plane and therefore lies at the intersection of these distances. P is on the plane if the residual hPx is completely explained by the plane. If not, P lies at some distance above or below the plane. Because hPx is, as a rule, not entirely accounted for by the plane, P is placed above the plane in Fig. 2. A perpendicular hPx locates P on the plane of the two-dimensional model and this point is defined by the axis coordinates Px (already calculated) and Py. Py is obtained by calculating β, the distance of P along the Y axis measured from the point of intersection of the X and Y axes. To calculate β, the constructions in Fig. 2 are completed to produce the triangle C_1PxP, having the characteristics of triangle ABP (Fig. 1A). Since the relative lengths of CP and hPx vary, triangles with shapes corresponding to those in Fig. 1B and C are also generated by the constructional procedures illustrated in Fig. 2. In all cases, β can be calculated from Beals' formula when all sides of triangle C_1PxP are known. Expressed in the terms of Fig. 2

$$\beta = \frac{C_1Px^2 + hPx^2 - C_1P^2}{2C_1Px} \tag{4}$$

where $C_1Px^2 = hCx^2$ and $C_1P^2 = CP^2 - C_1C^2$. Because β is measured from the X axis, it is positive when C and P are on the same side of the X axis and negative when these stands are on opposite sides of the axis.

Using formula (4) β is calculated for all stands P placed relative to a two-dimensional model defined by three stands A, B, and C. Stands A and B have already been selected (X axis). Thus there are $m-2$ remaining (C) stands each of which is combined with A and B to form a plane from which a Y axis is derived in the manner outlined in the figure. That one of the $m-2$ possible Y axes for which $S.S._y$ is greatest is the selected axis because it accounts for more of the matrix residual than any of the others. $S.S._y$ is calculated by substituting β for α in formula (2) and proceeding as before. The proportion of the sum of squares of interstand distances accounted for by the Y axis (per cent extraction value) is obtained from formula (3) when $S.S._y$ is substituted for $S.S._x$.

The Z axis

Before constructing the Z axis, a new matrix residuum must be calculated. For each stand P, this residual is obtained (Fig. 2) from the formula

$$hPxy = \sqrt{hPx^2 - \beta^2}$$

Figure 3 illustrates the constructions for the Z axis. They are founded upon those in Fig. 2; the ABC plane and the X and Y axes of Fig. 3 are perspectively illustrated from the same oblique angle as in Fig. 2. The thickly outlined constructions standing on the plane in Fig. 3 are similar to those resting horizontally on the plane in Fig. 2. The similarities of both are visually apparent. The Z axis is erected perpendicular to the plane passing through the intersection point of the X and Y axes. A stand D has a residual distance to the ABC plane, $hDxy$, which is erected vertically at the location of D on the plane (defined by Dx and Dy). Now $ABCD$ is a three-dimensional model relative to which a fifth stand P, representing all other stands, may be placed. As for D, P has a point on the plane determined by two coordinates, Px and Py (Pxy), and a residual distance to the plane $hPxy$, which is erected from the location of P on the plane. P is positioned in space by the intersection of the matrix distance DP and the residual distance $hPxy$. If $hPxy$ is completely accounted for by the $ABCD$ model, it stands vertically on the plane and parallel with the Z axis. If not, $hPxy$ stands at an angle to the Z axis. Since this is the usual condition, $hPxy$ is drawn obliquely in Fig. 3. The remaining constructions in the figure are now completed to produce triangle D_1PxyP. As for the X and Y axes, the shape of triangle D_1PxyP varies, although the constructional procedure is always the same. This variation here depends on the relative lengths of DP and $hPxy$ that place stand P rela-

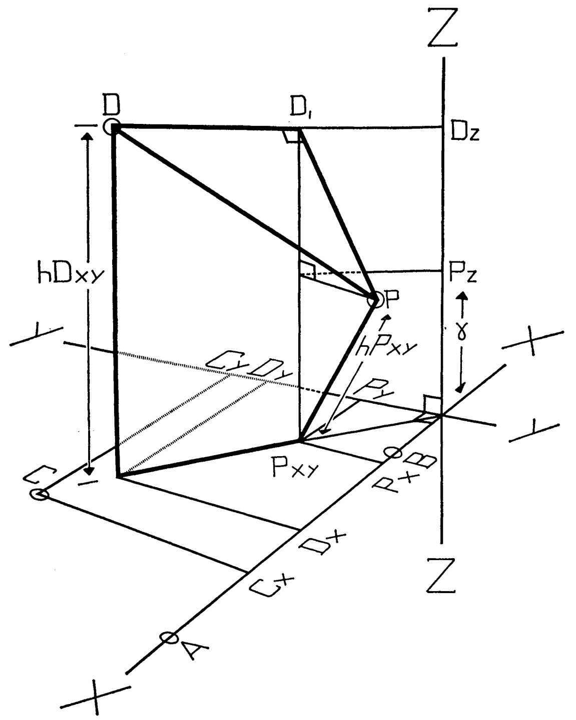

FIG. 3. The geometric constructions used to select and construct an ordination *Z* axis. One diagram represents all constructions required to place a stand *P* on a *Z* axis defined by a three-dimensional model of four stands: *A, B, C,* and *D*. Terms are described in the text.

tive to the *ABCD* three-dimensional model. In all cases γ, the distance of *P* along the *Z* axis measured from the intersection of the axes, can be calculated by Beals' formula when all sides of the triangle are known. Using the terms of Fig. 3, the formula is:

$$\gamma = \frac{D_1Pxy^2 + hPxy^2 - D_1P^2}{2D_1Pxy} \qquad (5)$$

where by construction $D_1Pxy = hDxy$ and $D_1P^2 = DP^2 - (Dx - Px)^2 - (Dy - Py)^2$. γ is positive when *P* is above the *ABC* plane and negative when *P* is below the plane. It is calculated from formula (5) for all stands *P*, relative to a three-dimensional model defined by four stands *ABCD*. Stands *A, B,* and *C* are already selected (*X* and *Y* axes) and there are $m - 3$ *D* stands, each of which is combined with stands *A, B,* and *C* to define a three-dimensional model. Each model generates one *Z* axis; there are $m - 3$ possible *Z* axes from which the best is selected by substituting γ for α in formula (2) and proceeding as before. Formula (3), with $S.S._{\cdot z}$ substituted for $S.S._{\cdot x}$, is then used to find the proportion of the sum of squares of interstand distances (per cent extraction value) accounted for by the *Z* axis.

Subsequent axes

Although further axes were not extracted in the experimental procedure, the construction of a fourth axis is briefly described to indicate how this may be done. The terms are derived from analogy with the foregoing constructions and are, for the most part, not represented in the figures. For stand *P*, there remains a residual distance *hPxyz*, orthogonal to the first three axes. It is one side of a triangle to which Beals' formula can be applied, having known base equal to *hExyz* (the residual for stand *E* after three axes have been removed from the matrix) and calculated side E_1P where:

$$E_1P = \sqrt{EP^2 - (Ex - Px)^2 - (Ey - Py)^2 - (Ez - Pz)^2},$$

EP being the matrix distance between stands *E* and *P*. Now all sides of the basic triangle are known and Beals' formula is derived from it to calculate stand positions on a fourth axis. There are $m - 4$ such axes from which the best is selected and tested as before. Further axes are derived by analogous procedures.

APPLICATION AND DISCUSSION

To demonstrate its use we have applied our method of stand ordination to three sets of data: two from the North American prairie and one from the Canadian boreal forest. To do this, a matrix of interstand distances was first calculated for each data set on an IBM 7040 digital computer, using a euclidean index (Sokal and Sneath 1963, Orloci 1966). The euclidean formula is:

$$d_{ij} = [(X_{1i} - X_{1j})^2 + (X_{2i} - X_{2j})^2 + \dots + (X_{ni} - X_{nj})^2]^{1/2}$$

where *i* and *j* are stands with species scores $(X_{1i}, \dots, X_{ni})$, $(X_{1j}, \dots, X_{nj})$ and d_{ij} is the calculated distance between stands *i* and *j*. For each data matrix the number of stands and species involved in the calculations, as well as the measure of performance representing the species, are listed in Table 1 which also summarizes our findings.

All matrices were successfully ordinated and axes were extracted from each matrix in decreasing order of importance (Table 1); the method functions as planned. Since we have not experimentally compared our procedure with other techniques, we are unable to say how effectively they would have ordinated the same data. However, some comparative observations seem worthwhile.

The ordination here described resembles the Wisconsin method in the use of stands to define axes and Beals' formula to calculate stand-axis positions. It differs from the Wisconsin method

TABLE 1. Per cent extraction of ordination axes

Data	Number of stands	Number of species	Measure of species performances	Per cent matrix extraction			
				Total	X	Y	Z
Upland boreal forest							
Candle Lake, Sask.	89	7	Number of tree species stems per acre (normalized)	36	14	12	10
Upland grasslands							
Red River Valley, N. D. and Manitoba	152	267	% frequency of herb and shrub species	33	16	9	8
Kernen's prairie, Saskatoon, Sask.	50	77	% frequency of herb and shrub species	43	24	10	9

in two respects. First, axes are spatially related in a geometrically acceptable manner. Second, and more important, from all possible stand-defined axes, those which best represent the information in a matrix are selected by a relatively simple yet mathematically sound principle. In theory, this principle is certainly superior to the distant stand criterion of the Wisconsin method. However, it involves some increase in complexity and computational expense and our ordination has yet to be compared with other techniques to determine whether the refinement is a significant one. Because it is based on axes derived from similar geometric constructions, we believe the method is simpler to understand than the analogous but more sophisticated principal components "factor" analysis. Where there are many species in the data our procedure also requires much less computation. Like the Wisconsin method, it should be suited to species as well as stand ordination.

In this study we encountered certain problems that appeared to be associated with the index used for calculating interstand distances. Some observations on this subject seem pertinent.

Austin and Orloci (1966) noted that the $2w/a + b$ index is a noneuclidean distance measure and therefore unsuited to an ordination in euclidean space. At the time of our study we were not aware of this fact and attempted an ordination based on a matrix of $100 - (2w/a + b \times 100)$ dissimilarity values. Our results indicate the practical problems that arise when a non-euclidean index is applied in ordination. Negative residual values were recorded after the construction of the X axis, and the $2w/a + b$ index did not permit all stands to "link up" in space. In fact, this non-intersection seriously affected the calculation of stand positions on the Y and Z axes.

We believe that satisfactory ordination using non-euclidean distance values based on the $2w/a + b$ index should be possible if our procedure is slightly modified. However, this is beyond the scope of the present study. Principal components "factor" analysis can only be applied when the differences between stands are represented as euclidean distances.

For the ordination based on matrices derived with the euclidean distance formula, non-intersecting distances were not, of course, encountered. However, with the euclidean formula, the calculated distance between two stands increases with the number of species for which quantitative measures are available (noted in taxonomic terms by Sokal and Sneath 1963). This has an effect on ordination that was noted through the application of the euclidean index to grassland data from Nelson County, North Dakota (Dix and Smeins 1967). If two stands, one at each end of a hypothetical environmental gradient, each contain few species, while those at intermediate positions contain many, the calculated distance between the two extreme stands, where comparative measures are few, may be less than the calculated distance between one of these stands and a stand near the center of the gradient, where comparative measures are numerous. Thus, vegetational patterns derived with the euclidean index may be distorted and relationships between vegetation and environment obscured. In fact, a form of data commonly found in phytosociology is that in which species (though measurable when they occur) are not found in all stands, so that the data matrix contains many zeros (Williams and Dale 1962). This has an interesting effect on interstand distance calculation. Quantitative differences in species records contribute to interstand distance, yet a species cannot contribute to distance where both values in a comparison are zero. Thus, for data where zero comparisons are abundant, calculated distances may not increase at a rate commensurate with changes in species populations. Our difficulties with the euclidean index seem to reflect this fundamental problem.

A second problem affecting phytosociological ordination also became apparent during this study. Quantitative measures for a species population often change progressively across a gradient; they may rise from zero to a peak and then fall to zero once more (McIntosh 1967, Whittaker 1967, and many others). Two stands having similar quantitative values for a species may be adjacent (on the same side of the peak) or at some distance from each other (on opposite sides of the peak). The species quantities do not reflect the gradient positions of the two stands, yet they are used in the determination of interstand distance.

If phytosociological ordination is to be used for the recognition of species-environment relationships, it seems that attention should be devoted to the effects of zero values and population-gradient patterns on the calculation of interstand distances.

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WEIGHT DYNAMICS OF *EUCALYPTUS* IN THE MALLEE VEGETATION OF SOUTHEAST AUSTRALIA[1]

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Abstract. Methods for the estimation of aerial biomass and its annual increment were devised and with them studies of the weight dynamics of *Eucalyptus* in two stands of mallee vegetation were made. The stands differ in species composition, age, and aerial biomass, yet the eucalypts of both added 6–8% to their aboveground biomass in 1965–66. In the older stand mean stem age is much less than stand age, and active stem replacement processes operate within it. But in the younger stand these processes do not appear, as yet, to have begun, and most stems of *Eucalyptus* in it are of the same age as the stand. Although both stands were fairly productive of plant tissues during the 1965–67 drought, it is likely that

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