NUMERICAL METHODS FOR THE ESTABLISHMENT OF ASSOCIATIONS*

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Dedicated to Prof. J. Braun-Blanquet at the occasion of his 90th birthday

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The concept of the Association as a fundamental unit of vegetation has provided the basis for phytosociological studies throughout Europe. In particular the methodology of tabular sorting developed by Braun-Blanquet (1964) has provided a method whereby variation in vegetation can be delimited, defined and described through Associations. (See Westhoff & van der Maarel 1973 for a survey of the Braun-Blanquet approach and its spread throughout the world). Within complex tropical and subtropical rain forest vegetation, there has been some debate concerning the existence of Associations (Richards 1952). Even where the concept has been accepted there remain formidable problems in identifying Associations in practice. The perplexing heterogeneity and patchy distribution of plant species in rain forests has confused the application of phytosociological methods developed for use in temperate vegetation (Schulz 1960). That patterns do exist in rain forest, even at the smallest scales, is clear from the work of Ashton (1964) and Williams, Lance, Webb, Tracey & Connell (1969b). The problems arise from the difficulties of choosing sample sizes appropriate to the definition of Associations, apparent in the results of Poore (1968), and the admixture of determinate, environmentally determined, variation, with probabilistic and determinate variation due to biotic and chance factors (Aubreville 1938, Webb, Tracey & Williams 1972, Williams, Lance, Webb, Tracey & Dale 1969a). These two factors combined with the laboriousness of tabular sorting with large numbers of species and the lack of autecological information, all serve to make syneological studies particularly difficult in this vegetation type. If the Association concept is to retain its present pre-eminent position in phytosociology, then some new means of establishing Associations would seem to be necessary.

Dale & Quadraccia (1973) have described a technique, using a computer interactively, which reduces the labour of tabular sorting. They concluded however that such an approach, while reducing the clerical labour and the possibility of copying errors, still required a considerable commitment of skilled phytosociologists’ time. This latter could only be reduced by introducing more effective methods of sorting the observed data. Such methods have, of course, been described under the aegis of numerical taxonomy, and the work of Webb, Tracey, Williams & Lance (1967) and Austin & Greig-Smith (1968) has shown that these methods can be useful. Yet these applications have not been wholly successful, and serve to raise again the speculations of Williams, Lambert & Lance (1966) concerning the degree to which numerical methods do serve as a simulation of traditional phytosociological methods. Within the Braun-Blanquet approach itself a trend towards numerical techniques for the establishment of Associations can be traced (see, e.g. Westhoff & van der Maarel 1973, van der Maarel 1974), the results of which have to be awaited.

In this paper we propose to examine a new method of numerical analysis of vegetation data. The method seems, to us at least, to more closely simulate traditional practice.

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than any previously used method of numerical classification. Further it leads to a natural definition and interpretation of the Association, and also provides interesting links between classification and ordination methodologies. The example we shall discuss is not intended to be a definitive study of the rain forests of North Queensland; the data are insufficiently extensive to serve such an aim. Neither shall we claim that the method we describe is the best possible means of defining Associations, for alternative methods do exist even if they have been little examined. Until such examination has been made, the comparative effectiveness of the alternatives must be in doubt. Instead this paper will serve its purpose if it encourages phytosociologists to reexamine their own methods for it is only from an explicit account of these that a good numerical simulation method can be developed.

### Data

The floristic data used in the study were derived from three tropical rain forest plots located in North Queensland. Bailey’s Creek, north of Daintree River, and Gregory Falls, west of Innisfail, are situated on the lowlands (below 200 m altitude) with a mean annual rainfall of 3200 mm and 3600 mm respectively. The Bailey’s Creek forest is on a red earth derived from basic volcanic rocks interbedded with schists, while the Gregory Falls plot is on a typical basaltic krasnozem. The third plot, Windin, south-east of Atherton, is at an altitude of 760 m, with a mean annual rainfall of 3200 mm, and also on a basaltic krasnozem. All plots were 0.1 ha in area and located in apparently uniform terrain in mature forest not subjected to logging. Further details of the plots are given in Webb, Tracey, Williams & Lance (1967a). The Bailey’s Creek and Gregory Falls plots were subdivided into 12 stands while the Windin plot was subdivided into 5 stands. This difference in subdivision could be regarded as reflecting changes in minimal area, although such considerations were not in fact the original cause of the differences. In view of the work of Webb et al. (loc.c.) only tree species were used in the analysis, including seedlings greater than 0.5 m in height together with understory and canopy trees. The restriction is not due to program limitations.

Original records were made of tree densities within the stands, but to conform to the method of analysis, and to simulate the use of cover/abundance scales, the data were recorded into nine classes:

- Class No.: 0, 1, 2, 3, 4, 5, 6, 7 and 8
- Density range
  - of stems present: 0, 1, 2, 3, 4–6, 7–12, 13–26, 27–54, > 54

The scale is roughly logarithmic, and any other scale could be substituted. These scales serve a useful purpose since they indicate the degree of precision of recording of the data. Our method can in fact tolerate variations in scales between stands, so that both Braun-Blanquet and Domin data could be included within a single analysis. However standardisation to a single scale simplifies comparisons between analyses. In all 156 species were recorded, 70 each for Windin and Gregory Falls, and 76 for Bailey’s Creek. Thus the whole data consists of coded records for 156 species in 29 stands, and resembles in its formal properties the data used in traditional table sorting.

### Models and methods

We shall be concerned throughout this paper with a single method – the two-parameter method of Macnaughton-Smith (1965) first used in vegetation studies by Dale & Anderson (1973). With one minor exception the details of the method and program are as given in Dale & Anderson (loc.c.) and we shall not repeat them here. In particular, as in the previous paper only initial estimates are used for parameter values.

Williams’ et al. (1966) speculations on the relationships between traditional tabular sorting and numerical classification have been revised recently by Češka & Roemer (1971) and Moore, Fitzsimmons, Lambe & White (1970). Češka and Roemer emphasized the symmetry of treatment of stands and species in the traditional methods which contrasts with the distinction commonly made in numerical studies between normal (stand grouping) analyses and inverse (species grouping) analyses. The need for symmetry had nevertheless been appreciated earlier, in the work of Lambert & Williams (1962) on nodal analysis and Tharu & Williams (1966) on concentration analysis. The two-parameter method is symmetric in its treatment of species and stands, and this point has an important bearing on the significance of the Association.

There is a further difference between traditional and numerical methods which has received much less attention. Most numerical methods in normal analysis seek groups of the stands within which each species has a constant abundance value, the so-called minimal variance property (Wishart, 1969). This is true of the Češka–Roemer