VEGETATION - SITE RELATIONSHIPS IN THE HARVARD FOREST*

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Introduction

There is a widespread need in plant ecology for techniques which employ as many kinds of information that can be gained in as short a time as possible and which allow for quantitative analysis of the data. Techniques which require a thorough knowledge of the flora are limited in their usefulness in regions where the number of species is very large and comprehensive keys are not available. In addition, time often precludes the use of objective sampling methods advanced for obtaining the necessary estimates, and precise estimates may not even be appropriate, particularly where chance fluctuations in species composition can amount to a considerable proportion of the variation between sites. Furthermore, it is possible that with regard to particular environmental factors (e.g. fire) the vegetation response may be reflected more in physiognomic appearance than in species composition.

The objectives of this study were twofold. Firstly, to develop a technique for providing estimates of physiognomic characteristics of a stand, and of abundance values for the common species, in as short a time as possible. Secondly, to evaluate the usefulness of these data in describing the vegetation and in defining controlling environmental and other factors.

The study was conducted in the Harvard Forest near Petersham, Massachusetts. The forest has been studied for many years and is therefore well suited to a trial study of this nature as it is possible to compare the results obtained by the method against what amounts to a known situation. The area is described by Stout (1952) and will not be elaborated here beyond mentioning that it lies in the mixed hardwood-conifer region of central New England, and that the sections of the forest used in this study are all on glacial till soils.

Methods

It has been found (cf. Moore et al., 1970) that different surveyors can produce very similar subjective ratings of vegetation characters, provided that the categories are sufficiently broad. Based on this information, preliminary field trials in this study, using such parameters as canopy cover, average height of a species, average basal diameter, ground cover, etc., rated on a basis of 1–5, showed that surveyors seldom differed and then by only one category.

The sampling was accomplished by locating stands in visually homogeneous compartments of the forest selected at random from a map in terms of dominant species and physiognomy. The criterion was simply to continue sampling as long as different, homogeneous areas were encountered. Forty-four stands were eventually sampled.

Within each stand floristic, physiognomic and environmental estimates were made:

Floristic data

Only the woody vegetation was considered, in four layers: over 10 m; 5–10 m; 2.5 m; and less than 2 m. In each layer each species present was given a rating of 1–5, based on a cover/abundance estimate.

In order to subject the data to multivariate analysis a
single importance value is needed for each species in each stand. This was obtained by summing, for each species, the product of the cover-abundance values from each layer and the mean heights of the respective layers (in metres).

**Physiognomic data**

Each of the following characteristics was given a rating of 0–5 in each stand, without regard to species: Large trees over 38 cm dbh (diameter at breast height), medium trees (25–38 cm dbh), small trees (12–25 cm dbh), saplings (2–12 cm dbh), thick bark (over 2 cm), medium bark (0.5–2 cm), thin bark (less than 0.5 cm), canopy cover (open, 0.33, 0.5, 0.66, dense), canopy thickness or live crown length (0.1–0.25 of tree height, 0.25–0.33, 0.3–0.5, 0.5–0.66, over 0.66), cover/abundance of shrubs (woody plants less than 2 m high), cover/abundance of the herbaceous layer, species diversity, proportion of conifers.

In addition to these estimates, the average height of the canopy was measured, using a Haga altimeter, and the mean distance between canopy trees was obtained by locating at random a tree within the stand, measuring the distance to its nearest neighbour and continuing this procedure until 10 distances had been obtained. To ensure consistent estimates a number of basal diameters and bark thicknesses were measured in each stand.

**Site data**

Ratings of 0–5 were given to position in the landscape (1 = crest, 5 = swamp), slope and rock exposure. Aspect was recorded, and a measure of litter depth was made. Forest records were used to obtain 1–5 ratings for soil texture, drainage and soil depth, and also to determine whether or not a soil pan existed.

**Analysis of the data**

Three kinds of information were sought for a satisfactory account of the ecology of the study area. These were (i) the distribution of individual species (23) and physiognomic features (15) in relation to site factors (7); (ii) the number and kinds of vegetation types, and (iii) the overall relationships of the vegetation with respect to environmental gradients.

The first type of information is obtained by a straightforward plot of the importance value of each species and physiognomic character against each of the measured or estimated site factors, with the stands being ordered from minimum to maximum value for the latter. The 304 graphs required in this case were rapidly obtained by means of a simple computer program.

Classification of the stands was carried out on the combined floristic and physiognomic data and on the physiognomic data alone, using a hierarchical, weighed-pair clustering technique based on a matrix of inter-stand correlation coefficients.

The ordination and other information relating environmental and vegetational variation was obtained, in the first instance, using a procedure described by Walker & Wehrhahn (1971). The values for the environmental attributes of the stands are divided by a thousand before being entered into a principal component analysis (PCA) of the total data set, thereby ensuring that the extracted axes are determined only by the vegetation data. However, the loadings on the extracted components can be subsequently adjusted to give the correlations between the environmental attributes and the derived vegetation axes. The environmental data are separately subjected to a PCA on their own, to determine common gradients of variation in the environmental data. The extracted environmental components are often easy to identify and each stand in the study may be given a value for each environmental component by summing the products of the loadings and values (measurements or estimates) of each environmental factor. These ‘environmental gradient’ values are then also entered into the analysis of the total data set, in the same way as the individual environmental variables, to assist in identifying the relationships between vegetation gradients and environmental variation.

Prior to analysis, there are a number of transformations to which the vegetation data can be subjected, and it has been shown (Austin & Greig-Smith, 1968; Walker, 1974) that the type of transformation may markedly affect the results. In this instance analyses were performed on the following forms of the data: (i) the full, raw data matrix; (ii) zero-transformed species data followed by standardization of the species and physiognomic data by equal variance; (iii) analysis of the species and environmental data only following zero-transformation of the species data, with no standardization of variance; (iv) as for the previous one but with a loge transform of the species data; (v) as for the previous one but with a final standardization by equal variance. This last analysis produced a confused configuration of the data and seemed to have resulted in changing the original values to such an extent that they had lost what ecological meaning they may have had. It will not be considered in the results.

Some authors have criticised the use of PCA as an ordination technique. Austin & Noy-Meir (1971) have de-