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.

* Nomenclature follows 'Gleason, H. A. and A. Cronquist. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. D. Van Nostrand Co. Inc., Princeton, N.J. 810 p.'

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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. No attempt was made to define types. 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 $\log_e$ 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 demonstrated the distortions which result from bell-shaped species distribution curves. Whittaker & Gauch (1973) in particular have condemned the use of PCA in all but a few circumstances and have suggested that the Bray-Curtis (B-C) ordination based on Sørensen's coefficient of community is the best of the ordination techniques. In view of this, two B-C ordinations were carried out, one based on the coefficient of community and the other on the percentage similarity coefficient (as defined in Gauch & Whittaker, 1972). They were performed using only the floristic data as the first of these coefficients cannot be applied to variables which have non-zero values for all stands.

Results

Graphs

Of the 304 graphs relating individual species and physiognomic estimates to each environmental gradient, only 30 showed a sufficiently strong trend to warrant further examination. The information they contain is summarized in the other analyses and they are therefore not presented here. Their value lay in helping to interpret the cluster analyses and ordinations. The low proportion of species/environment graphs that showed a definite trend may indicate that chance is an important factor in the distribution of individual species within the study area. With respect to the physiognomic characters, the only clear trend was an increase in total canopy cover with decreasing position on the slope. With the exception of spruce bogs, the highest canopy cover occurred on the lower slopes.

Cluster analyses

Results from analysis of the combined data set were biased in favour of the floristic data, owing to the greater number of species (23) than estimates of physiognomy (15). In addition to the combined data, the physiognomic data were therefore analysed separately to determine vegetation

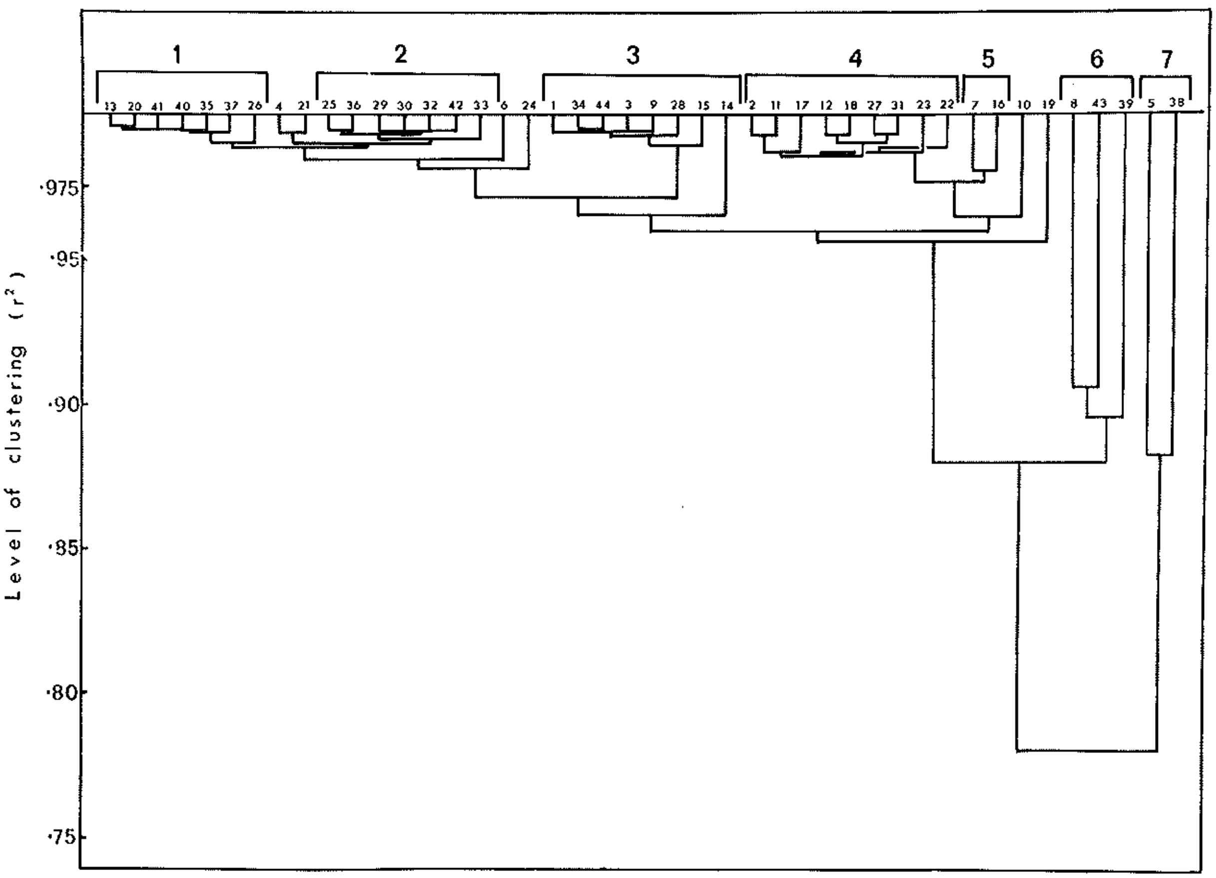

Fig. 1. Cluster analysis of 44 stands of vegetation based on 15 physiognomic attributes.

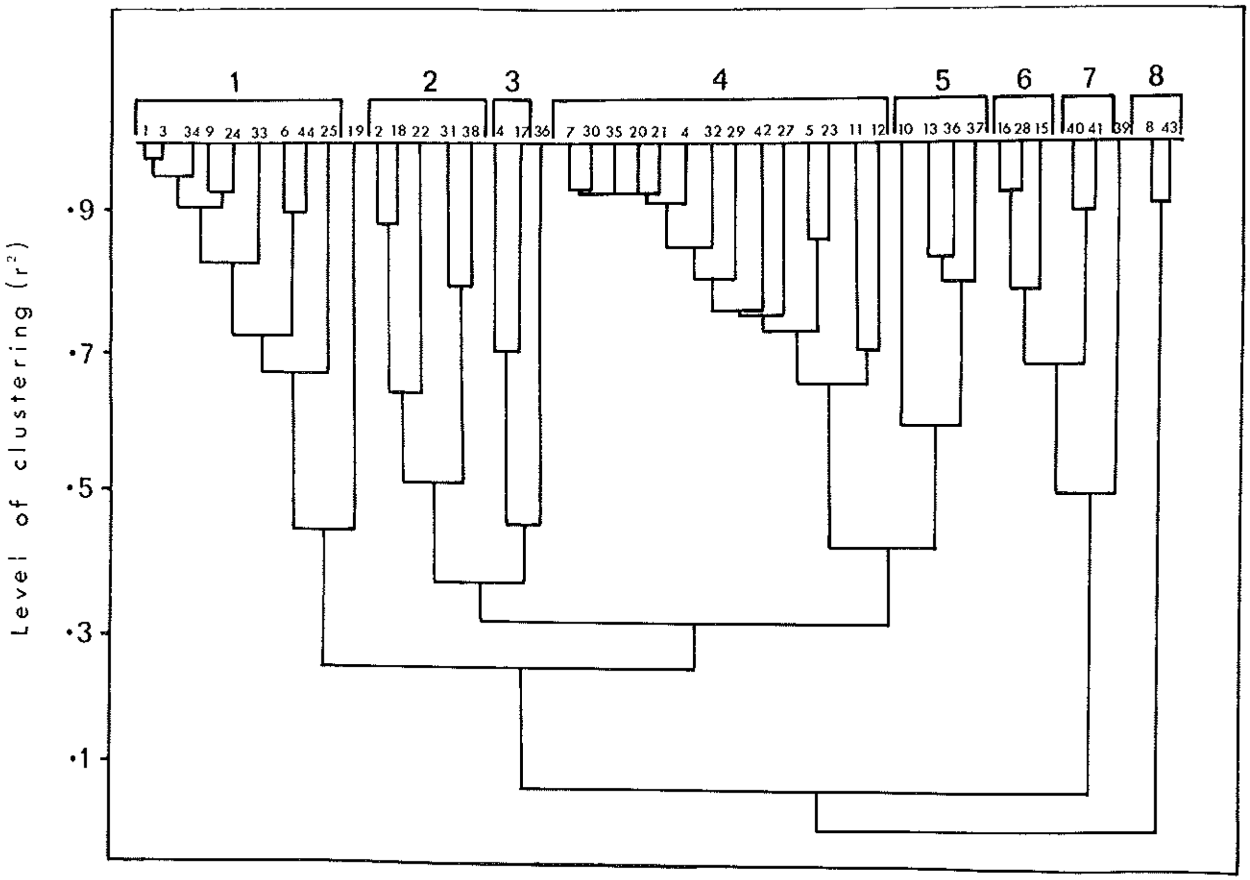

Fig. 2. Cluster analysis of 44 stands of vegetation based on cover/abundance estimates of 23 species and 15 physiognomic attributes.

types based on stand morphology only. The results of the two analyses are presented in Figures 1 and 2.

The groups resulting from analysis of the physiognomic data (Fig. 1) can be distinguished primarily on the basis of disturbance. Group 1 comprises high stands of mature trees with large basal diameters and a low density. The mean canopy height is 30.9 m and the mean distance between nearest neighbours is 4.7. m. None of the seven stands in the group showed any evidence of disturbance. Group 2 consists of somewhat younger stands. The mean canopy height is 23.1 m and the mean distance is 3.2 m. Three of the seven stands have evidence of old logging and signs of logging in some of the others was debatable. Group 3 is characterized by the lack of disturbance and the dominance of conifers. The stands consist mostly of tall, large diameter trees. The stands in Group 4 are just recovering from recent logging, hurricanes or fire. They are stands of rather dense, coppicing trees. Mean canopy height is 17.6 m and mean distance is 2.7 m. Five of the nine stands show clear evidence of past logging. Group 5 consists of two stands of fairly tall, dense trees (mean distance of 2.0 m) with thin bark. Canopy heights are 20 and 22 m. There was no evidence of disturbance. Group 6 is an odd group. Two of the stands are in a black spruce (*Picea mariana*) bog and one is on a skeletal upland soil. All stands are open, consisting of trees with a mean height of 12 m and a mean distance of 7.6 m. Disturbance could not be assessed. Group 7 consists of two heavily disturbed stands. Both show clear evidence of recent logging and in one there is evidence of a recent fire. Canopy height is 10.0 m in both and the mean distances are 1.5 and 1.3 m.

With respect to the analysis of the species data (Fig. 2) eight groups have been distinguished. They are characterized as follows: The stands in Group 1 are dominated by hemlock (*Tsuga canadensis*), having large trees with a low density. The site factors vary considerably and there are no common features for all stands. The stands in Group 2 are either dominated by red maple (*Acer rubrum*), or have this species as a co-dominant. Yellow birch (*Betula lenta*), ash (*Fraxinus americana*), and white pine (*Pinus strobus*) are the common co-dominants. The environment is very variable but includes, particularly, stands that are very wet. Two recently disturbed stands with a mixture of many species form Group 3. Group 4 is dominated by red oak (*Quercus rubra* = *Q. borealis*) sometimes with fairly high proportions of *Acer rubrum*, black birch (*Betula nigra*) and other species. This group of stands is distinguished by the lack of any extreme site factors. It occurs on average, well drained soils, on all slopes, with moderate amounts of rock exposure. Group 5 consists of stands fairly similar to the previous one, but with dominance shared by *Betula lenta*, sugar maple (*Acer saccharum*) and/or *Fraxinus americana* as a significant component. Stands in Group 6 are dominated by *Pinus strobus* and occur on flat, sandy-

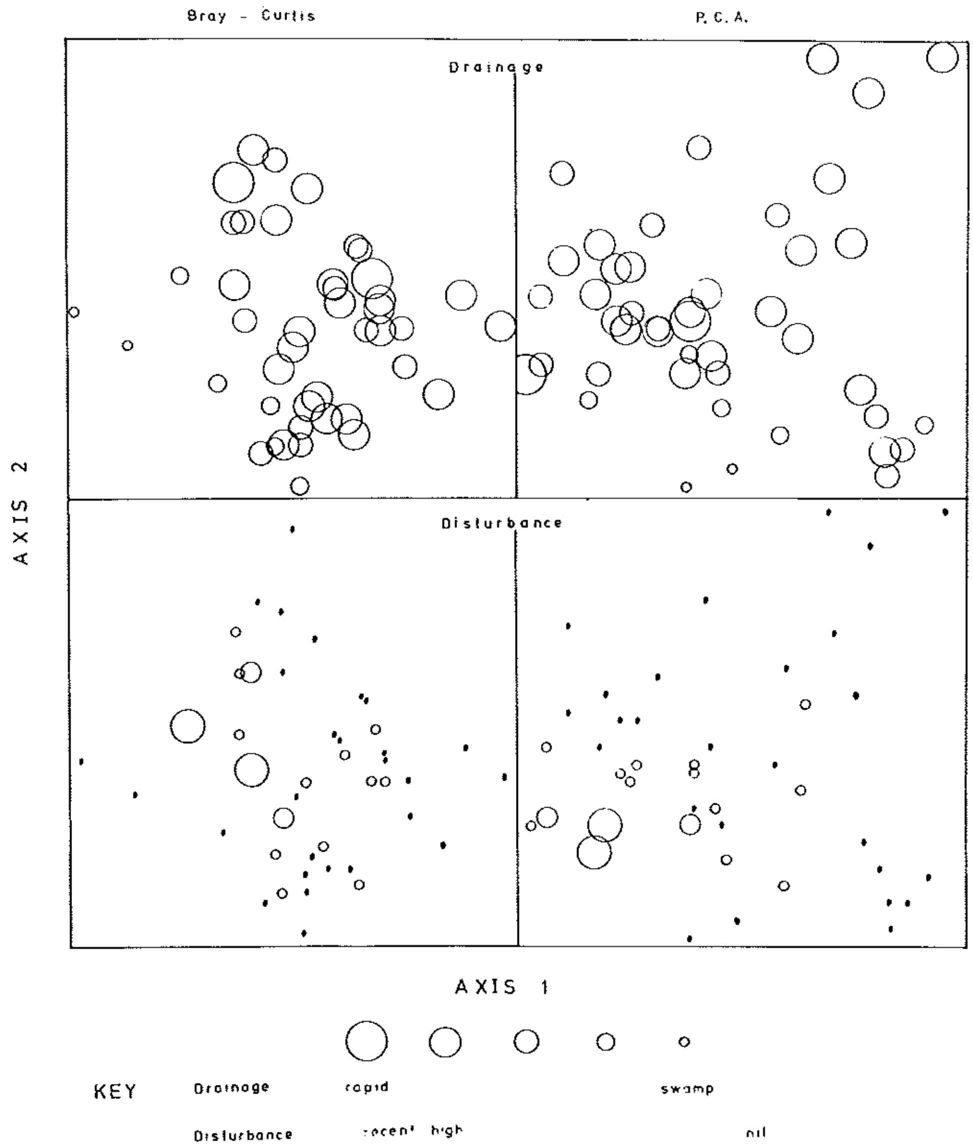

Fig. 3. A comparison of ordinatons by principal component analysis (PCA) and the Bray-Curtis (B-C) technique based on cover/abundance estimates of 23 species in 44 stands.

loam sites with rapid drainage. Two stands dominated by *Pinus strobus*, hickory (*Carya ovata*) and white oak (*Quercus alba*) constitute Group 7. Group 8 is a spruce bog (*Picea mariana*).

Superimposing the environmental estimates on to the cluster analysis based on the species data has separated out the sites with extreme environmental factors, i.e. bad drainage, swamp or disturbance. But it has been of little help in explaining the variation in vegetation on some of the sites which remained unclassified (see Fig. 2).

Ordination

Analysis of floristic and physiognomic data

In order to evaluate the results of the two methods of

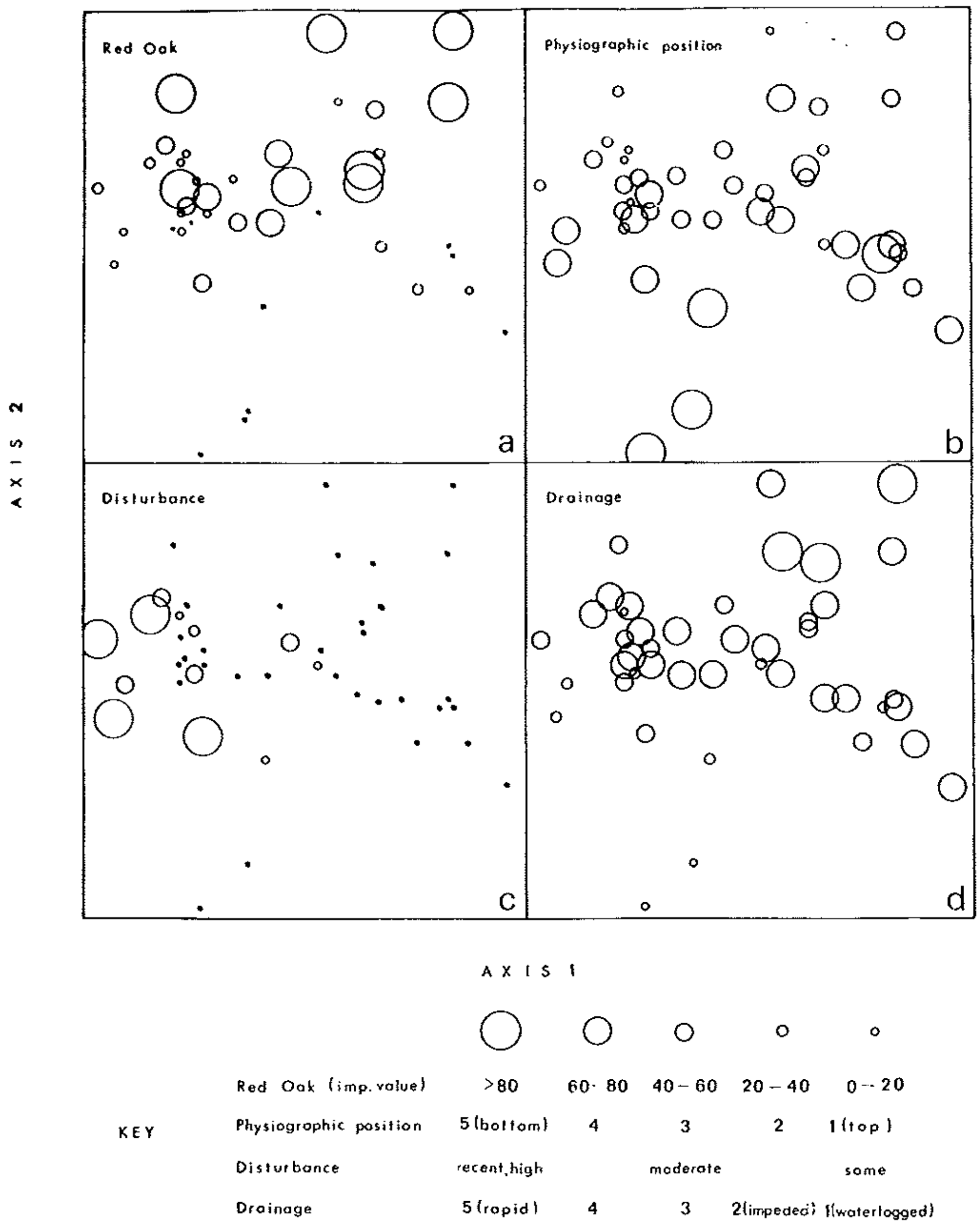

Fig. 4. The first two axes of an ordination of 44 stands based on a principal component analysis of combined floristic and physiognomic data.

ordination, environmental data were superimposed on the ordinations performed after transformations of the vegetation data, and for each an ecological interpretation was attempted. In general, the interpretations obtained from the PCA were more clear-cut than those from the B-C ordination. To illustrate this, the relationships between two-dimensional stand ordinations and the two most important environmental factors (as described later) are presented in Fig. 3. These comparative ordinations were based on floristic data only and were in all cases less informative than the ordinations based on combined floristic and physiognomic data (Fig. 4). Nevertheless, PCA demonstrates a primary disturbance gradient and a secondary drainage gradient. The B-C ordination indicates a rather ill-defined drainage gradient, and practically no indication of a disturbance gradient. The comparisons suggest that the interpretation derived from PCA is the more reliable of the two and, consequently, only the results of the PCA are described.

Analysis of the untransformed data produced a three-pronged configuration of the first two axes that appears typical of distorted gradients which result from a large number of zero values (Swan, 1970). There was no satisfactory interpretation of the axes. In contrast to the untransformed data the other analyses were more informative, leading to similar conclusions, though with varying degrees of clarity. The inclusion of the physiognomic data was of considerable help in identifying the nature of the first component. The use of a logarithmic transformation following zero-transformation resulted, in this instance, in an over-emphasis of the least sampled species so that they contributed more to the total variance than did the most abundant species. This was due to the cover-abundance estimates being already in a logarithmic form. The most useful results were those from the zero-transformed data which had been either standardized by equal variance (full data set) or left unstandardized (species and environmental data only), and which were not subjected to a logarithmic transformation.

Analysis of environmental data

Analysis of the environmental data alone showed almost one half of the total variation to be associated with a common moisture gradient, with good drainage and the presence of a soil pan being at opposite ends (E_1). A further one fifth of the variation is reflected in what is best described as a soil depth gradient, with percentage rock exposure and soil depth being at opposite ends (E_2). The third gradient with one tenth of the total variation is apparently topographic with percentage rock exposure and position in the landscape being of greatest influence (E_3). The major trends in the environmental data may therefore be described as a moisture gradient, a rock exposure and soil depth gradient, and a topopographic gradient. The remaining gradients (E_4, E_5) reflect residual variation related to these factors plus other variation which, at this stage, takes no pattern at all. From the environmental analysis five values, one for each of the above gradients, were derived for each stand (as described earlier) and entered into the analysis described below.

Analysis of combined floristic, physiognomic and environmental data

The variables with the highest percentage variance accounted for by the first six principal components (h^2 column in Table 1) are predominantly physiognomic. This first component accounts for 21 % of the variance in the total data set (Table 1). It represents a disturbance gradient, from recently logged or burned stands – small in stature with thin trees and a high density, with characteristic species (high negative loadings) being grey birch (*Betula populifolia*), trembling aspen (*Populus tremuloides*), black cherry (*Prunus serotina*), white birch (*Betula papyrifera*) and *Quercus alba*, through various intermediate stands with varying species combinations, to tall stands (30 m or more) of large diameter trees, low density and usually a fairly low species diversity, with characteristic species (high positive loadings) being beech (*Fagus grandifolia*), *Tsuga canadensis*, *Betula lenta*, *Acer saccharum* and some basswood (*Tilia americana*) and *Ostrya virginiana*. The ordination of stands (Fig. 4a) shows that the dominant species differ from the characteristic ones. *Quercus rubra* is the dominant species in the mature stands at the undisturbed end of the gradient (Fig. 4c), but since it also occurs in all other segments of the disturbance gradient it has a low loading on this axis. The only environmental variable with a significant loading is percentage rock exposure, being correlated with mature, undisturbed stands.

The second component (10 %) is indicative largely of the species data and an overall soil moisture gradient. There is a gradation from well drained sites, usually on the upper slopes, to poorly drained sites in swales or bog. Neither position in the landscape or drainage shows a perfect trend, but their combined effect is such that stands at the 'dry' end of the gradient occur on upper slopes or

TABLE 1. Principal component analysis of standardized data for species cover/abundance values, physiognomic estimates and environmental variables. See text for an explanation of initial data manipulation prior to analysis. The communality values (h^2) indicate the proportion of an attribute's variance which is associated with the first six components. Attributes E_1 - E_5 are derived from an initial analysis of only the environmental variables, and represent the first five principal environmental components.

ATTRIBUTE		PRINCIPAL COMPONENTS						
		F_1	F_2	F_3	F_4	F_5	F_6	h^2
Acer pensylvanicum	1	.20	-.39	.39	.04	-.27	.05	.42
A. rubrum	2	-.24	.11	.12	.21	.24	-.61	.55
A. saccharum	3	.37	.54	-.03	.19	.29	.14	.57
Betula lenta	4	.21	.17	-.22	.41	-.33	-.16	.42
B. nigra	5	.14	.32	.31	.39	-.34	.22	.54
B. papyrifera	6	-.34	.12	-.12	.17	-.40	.12	.34
B. populifolia	7	-.71	.06	-.25	-.31	.17	.17	.70
Carpinus caroliniana	8	.07	.33	-.30	-.16	.64	.24	.69
Carya ovata	9	.10	.09	.56	-.20	.09	.36	.50
Castanea dentata	10	.12	.22	.68	.22	-.30	.11	.67
Fagus grandifolia	11	.68	.04	-.28	.01	-.09	.19	.59
Fraxinus americana	12	.20	.47	.00	.26	.42	-.31	.61
Hamemalis virginiana	13	.18	.31	-.02	.15	-.23	-.02	.20
Ostrya virginiana	14	.43	.36	-.00	-.23	.36	.51	.75
Picea mariana	15	-.04	-.51	.12	.45	.32	.11	.60
Pinus strobus	16	-.04	-.12	.69	-.43	.07	-.20	.73
Populus grandidentata	17	-.04	-.03	.18	-.34	.06	-.44	.35
P. tremuloides	18	-.32	.29	-.15	-.15	.24	-.21	.33
Prunus serotina	19	-.46	-.02	.48	-.48	-.13	.05	.69
Quercus alba	20	-.31	.20	.33	-.49	.26	.11	.57
Q. rubra	21	.02	.69	.18	.24	-.06	-.09	.58
Tilia americana	22	.29	.52	-.16	.20	.23	.15	.49
Tsuga canadensis	23	.56	-.13	-.59	-.09	-.15	.03	.70
canopy height	24	.79	.32	.26	.01	-.06	-.04	.81
canopy cover	25	.24	.62	-.08	-.33	-.40	-.20	.76
canopy density	26	-.47	-.33	-.07	-.06	-.03	.10	.34
trees > 38 cm DBH	27	.81	-.08	.26	-.22	-.13	-.06	.81
25 - 38 cm "	28	.86	-.18	.16	.10	-.03	.00	.80
12.5 - 25 cm "	29	-.03	-.05	.05	.32	-.00	-.28	.19
< 12.5 cm "	30	-.80	.00	-.11	-.01	-.26	.25	.78
mean distance apart	31	.37	-.39	.29	.28	.19	.49	.72
diversity rating	32	-.60	.41	.15	-.03	-.13	.19	.60
% conifers	33	.51	-.59	-.15	-.38	.05	-.03	.78
bark > 2.0 cm	34	.74	-.15	.08	-.30	-.16	-.14	.71
.5-2.0 cm	35	.81	.13	.14	-.13	.10	.07	.73
< .5 cm	36	-.72	.22	-.00	.07	-.23	.33	.73
shrub cover	37	-.10	-.38	.36	.45	.30	-.01	.58
herbaceous cover	38	-.39	-.10	.49	.30	.30	-.14	.60
topographic position	39	.03	-.34	.09	.22	.22	-.06	.23
% slope	40	.03	.28	.00	-.05	-.38	.23	.28
% rock exposure	41	.32	.30	.08	.28	-.30	.19	.40
soil texture	42	.09	-.39	.25	.42	.25	.21	.50
drainage	43	-.05	.39	-.08	-.38	-.20	.21	.38
soil depth	44	.19	.03	-.25	-.06	.31	-.04	.20
litter depth	45	.18	-.35	-.05	.20	.23	-.17	.28
soil hard-pan	46	.08	-.09	.13	.46	.18	-.07	.28
E_1	47	.10	-.40	.07	.37	.35	-.13	.45
E_2	48	.12	.07	.24	.38	-.29	.20	.34
E_3	49	.27	.19	-.12	.03	.08	.01	.13
E_4	50	-.12	-.11	.07	-.01	.06	.17	.06
E_5	51	.29	.31	-.18	.01	.00	.22	.25
percentage variance extracted		21	10	8	7	6	5	

Erratum Table I : 7th line from above, B. populifolia, column F_6, read .11 instead of .17.

have rapid drainage whereas those at the opposite end have the reciprocal (Figs. 4b and 4d).

Apart from the two *Pinus mariana* stands at the one extreme of the ordination, the wet end of the gradient is typified by red maple stands which are practically monodominant and which occur in swales. However, because *Acer rubrum* also occurs in abundance over the remainder of the gradient in mixed stands, it does not have a high loading on this component and cannot be considered as a characteristic species. Species with high positive loadings (dry end of the gradient) are *Quercus rubra*, *Acer saccharum*, *Tilia americana* and *Fraxinus americana*. *Pinus mariana* is the only species which characterizes the wet end. The environmental factors with significant (though not very high) negative loadings are heavy texture, low position in the landscape and the bad drainage gradient (E_1) from environmental ordination. Good drainage has an equivalent positive loading.

The third gradient, which accounts for only 8% of the total variance, seems to be at least partly due to soil depth. *Pinus strobus*, chestnut (*Castanea americana*) and *Carya ovata* have strong, positive loadings and soil depth has a negative loading. Soil texture has the next highest loading and heavy texture is negatively correlated with depth. The soil depth gradient (E_2) has an equivalent loading. *Tsuga canadensis* is the only species with a strong negative loading, and therefore associated with deeper soils. It must be emphasised, however, that the environmental loadings are all low and it is reasonable to suspect that some other factor may well be the dominant influence.

The fourth gradient (7%) is apparently accounting for residual variance in the species data and, as with the remaining two extracted components, has little ecological meaning.

Discussion

The aim of this study was to evaluate the usefulness of rapidly and subjectively obtained data relating to physiognomic and floristic composition of forest stands, subjected to subsequent numerical analysis. The study was undertaken without prior knowledge of the species or type of forest, and after it was completed the results were discussed with local workers who conduct research in, and have a long term intimate knowledge of, the Harvard Forest. The conclusions reached in this study were compared with those derived from the accumulated experience of these experts.

The classification of the study area into the eight vegetation types, described in the Results, conforms fairly closely to the forest types recognised by the local experts. However, some of the types, and in particular *Acer rubrum* swale, should have been more clearly defined. The analysis failed to bring out a *Fraxinus americana* dominated community which occurs on upland swales (areas with a hard pan layer just beneath the surface of the soil). One group in the analysis, however, consisted of stands which were characterised by *Betula lenta* and *Quercus rubra* with fair amounts of *Fraxinus americana*.

The suggested relationships between major gradients of vegetational variation and the environment agreed with the experts' concepts of the ecology of the forest, with disturbance playing the dominant role (21%), drainage accounting for much of the residual variation (10%) and soil depth/texture accounting for the remainder (8%). With respect to particular species, however, some erroneous conclusions were reached. *Ostrya virginiana*, *Tilia americana* and striped maple (*Acer pensylvanicum*) achieved greater importance than their degree of sampling warranted. This was most probably due to the increase in the contribution of these species to the total variance following zero-transformation.

A conclusion reached in the analyses was that the end points of environmental gradients, or clearly defined types, were adequately described and explained, but there were insufficient samples of the rather diverse stands of vegetation which occur on relatively undisturbed, average upland. The next stage in a long-term study of this forest would be a more detailed examination of these ill-defined intermediate sites.

As a general conclusion regarding the ecology of the area, the fact that only 46% of the variation in the vegetation data could be accounted for by common trends suggests that random variation is a major feature in the composition of the tree vegetation. Had all plant species been included in the study, it is likely that there would have been a higher percentage of common variance, since species in the field layer are more sensitive to small changes in the environment. Nevertheless, it appears that chance is an important factor governing the distribution of tree species in this area, and the results obtained here support Raup's (1964) contention, regarding these forests, that '. . . the proportional species content and basic structure of the vegetation of an area at any one point in time has been more likely the product of the last major disturbance than of necessary relationships within a community'.

The techniques used for analysing the data were satisfactory. The better performance of PCA, as opposed to B-C ordination, is at variance with other recent findings and there are two possible explanations for this. Firstly, an ordination based on two reference stands in a situation where several interacting environmental gradients are operating simultaneously, has limited potential. Swan et al. (1969) and van der Maarel (1969) have demonstrated how the choice of reference stands can be accomplished so as to approximate most closely the axis of maximum variation. However, if the relationships between stands are considered as distances in an n-dimensional hyperspace, where n is the number of species and distance is equivalent to overall dissimilarity in these species, it is conceivable that the axis which represents the maximum amount of common variance need not touch any particular stands. The fewer the number of stands the less likely it will be that a line between any two reference stands will closely coincide with the direction of maximum variation. As the number of stands increases, though, so distortion due to this factor will decrease. Secondly, the common practice of applying PCA to a correlation-coefficient matrix, rather than a variance/co-variance matrix, is generally unsound in situations where differences in species abundance and variance are ecologically significant (Walker & Wehrhahn, 1971). Furthermore, it would seem that zero-transformation of species data is an important first step in PCA.

With respect to the original objectives of the study, it appears that rapidly obtained estimates of vegetation characteristics can be successfully analyzed using a variety of multivariate techniques. In this instance, the main limitations to increased reliability of the results lie not in the type of estimates obtained for the sites, nor in the techniques of analysis, but rather in how well the samples of stands represents the study area. In a study where time in the field is a limiting factor, the chances of successfully interpreting vegetation/environment relationships will be greater if all vegetation/site combinations are assessed at a reasonable level of precision than if an incomplete sample is measured very accurately. This in no way denies that, where time permits, the use of more detailed, objective measurements will enable more subtle relationships to be defined. In particular, the inclusion of understory species would allow for a clearer definition of forest types.

Summary

Forty-four sites in the Harvard Forest were assessed with respect to overall physiognomy of the vegetation, cover-

abundance estimates of the woody species and several environmental variables. The data were subjected to cluster analysis and ordination. In the latter, principal component analysis produced more acceptable and clear-cut results than a Bray-Curtis ordination. The major gradient of vegetational variation is due to disturbance, followed by a moisture gradient and what appears to be a soil texture and soil depth gradient. The high proportion of variance which is not associated with common trends in the vegetation suggests that random variation is an important factor in the composition of the forest. The data obtained from the rapid estimates of physiognomy and species composition, and the methods used for analysing them, are considered to be satisfactory. The success of the approach lies in how well the number of sites used represents the study area as a whole.

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