ISSN 0308 3675

MERLEWOOD RESEARCH AND DEVELOPMENT PAPER

No 105

NUMERICAL ANALYSIS OF SOIL PHYSIOLOGICAL DATA

by

P J A HOWARD and D M HOWARD

Institute of Terrestrial Ecology
Merlewood Research Station
Grange-over-Sands
Cumbria
England
LA11 6JU

September 1985

SUMMARY

1. Soil samples (0-10 cm) were collected at 4-week intervals for 56 weeks from 48 woods in and around the English Lake District, and pH, loss-on-ignition, moisture content, oxygen uptake, and cellulase and phosphatase activities were measured.

2. Expressing results on a loss-on-ignition basis was more informative than on an oven-dry basis, because of differences in loss-on-ignition between soil samples.

3. In a principal component analysis of each property over the 14 samplings, the first component values represent "smoothed" between-plot differences, other components pick out plots which behave differently from the majority at certain times. There was little within-plot variation in pH and loss-on-ignition.

4. On a loss-on-ignition basis, the only significant correlations between first component values, and between plot means, were phosphatase with oxygen uptake and cellulase with pH. Moisture content was not significantly correlated with any of the other properties.

5. None of the principal component analyses showed any evidence of the existence of distinct clusters of plots; the plots formed a continuous series, with some outliers, with respect to all the properties studied.

6. A priori groups, based on (i) pH <3.8, (ii) pH 3.8-5.0, (iii) pH >5.0, showed no significant difference in moisture content on a loss-on-ignition basis. However, oxygen uptake was significantly lower in (i) than in (ii). Cellulase activity was significantly greater in (iii) than in (i) and (ii). Phosphatase activitiy was significantly lower in (i) than in (ii), and there appeared to be a peak at pH 3.8 to 5.0.

Suggested citation

HOWARD, P.J.A. & HOWARD, D.M. 1985.

Multivariate analysis of soil physiological data. (Merlewood research and development paper no. 105) Grange-over-Sands: Institute of Terrestrial Ecology.

C O N T E N T S

1. INTRODUCTION

Soil biologists often wish to make comparisons both within and between different soil-vegetation types. Such comparisons may be made for a variety of purposes, but the soils are usually regarded as systems which differ biologically, physiologically, and chemically. One problem in such studies has been the comparison of soils with respect to processes or variables which show marked fluctuations in amplitude with time. This paper describes work on a range of woodland soils in north-west England, and shows how such data may be handled.

2. METHODS

2.1 Description of the area and sampling methods

The English Lake District proper is composed of rocks of the Ordovician (Borrowdale Volcanics, Skiddaw Slates, Coniston Limestone) and Silurian (flags, slates, grits, shales) systems of the Lower Palaeozoic group. Around them is a roughly circular girdle of newer strata, partly of Carboniferous age (Basement Conglomerate and Carboniferous Limestone) and partly belonging to still newer deposits of the Permian and Triassic systems. The area is covered by a variable thickness of drift of local origin, which on the plots sampled (Figure 1) rarely exceeded 1 m depth, and was mostly much less. Apart from those on the limestones, the soils are mostly acidic, but less so if they are locally influenced by the presence of calcite (Borrowdale Volcanics) or calcareous bands (Silurian).

In the central Lake District, the annual rainfall exceeds 3810 mm (150 in), falling to about 1143 mm (45 in) at the periphery (Pearsall and Pennington 1973).

Forty-eight woods in and around the Lake District were selected, one from each of forty-seven groups resulting from an association analysis of two hundred woods in the area (Bunce 1969) plus Meathop Wood IBP site. These woods thus represent the range of diversity of semi-natural (in the sense of Westhoff 1970) woodland vegetation in the area. Six of the woods were on limestone. Each of the woods was visited once every four weeks, ie twelve woods were sampled each week. Samples were collected for fourteen of these four-weekly periods (see Appendix 1 to 3).

Within each wood, a plot was selected at random and a permanent marker was placed to locate a 1.6 m x 1.6 m sampling grid. At each sampling, a numbered sampling square (20 cm x 20 cm) was selected randomly, the same number being used for each wood. Samples were collected from the L, L/F, and H layers, and from the 0 to 5 cm depth in the A horizon; the organic layers did not occur in all profiles. Tubes of buffered sucrose solution for estimation of mean soil temperature (Bocock et al, 1974, 1977) were placed on and below the L or L/F layer and at 5 cm depth in the A horizon in a permanent square. These tubes were changed at each sampling.

2.2 Laboratory methods

In the laboratory, litter and L/F material was shredded and the soil was passed, in the fresh moist state, through a 4 mm sieve. Subsamples were used for the following measurements:

pH was measured with a glass electrode, adding the minimum quantity of distilled water to the material. With soil, this meant adding sufficient water to make a thick paste.

Loss-on-ignition (LOI) of the oven dry material was determined at 550°C and expressed as percent OD.

Moisture content was determined by oven drying for 40 hours at 105°C (OD)

Oxygen uptake was measured in a Gilson respirometer (Umbreit et al 1964) using specially-designed flasks (Howard 1968) with a bath temperature of 15°C. This temperature was chosen because it is approximately the summer mean soil surface temperature, and because we found it to be the lowest practicable temperature for cellulase measurements.

Cellulase was determined by the method of Benefield (1971). The soil was buffered at its own pH, and the buffer solution contained a small quantity of penicillin to inhibit microbial growth during the 48 hours incubation at 15°C. Three samples of each soil were incubated, two tests and one blank, and the mean of the adjusted test values was taken.

Phosphatase: A slightly modified version of the method of Hoffman (1967) was used. The soil was incubated for three hours at 13°C with disodium phenylorthophosphate reagent, buffer (at the soil pH), and toluene. The phenol released from the reagent by phosphatase was determined colorimetrically by complexing with dibromoquinonechlorimide.

Dehydrogenase was determined by a method similar to that of Lenhard (1956), but examination of the results, and further detailed studies, threw doubt on the validity of the method (Benefield et al 1977). These results will not be considered further.

2.3 Statistical methods

PCA is a method of displaying relationships among multivariate data (Rao 1964; Hope 1968; Seal 1968). Initially, the objects are referred to a set of axes which represent the original variables. By a linear transformation each object is referred to a new set of axes, or components, which are orthogonal (uncorrelated). The first component is the axis of maximum variability and successive components are axes of diminishing variability. In effecting this transformation, the eigenvalues (latent roots) and eigenvectors (latent vectors) of the correlation matrix are calculated. It can be shown that the sum of the variances of the original variates is retained in the sum of the eigenvalues, and each eigenvalue gives the proportion of the total variance accounted for by the corresponding component. Since the sum of the eigenvalues also equals the trace of the matrix, which for a correlation matrix equals the number of variables, the percentage of the total variability accounted for by each component is given by expressing its eigenvalue as a percentage of the number of variables.

Associated with each eigenvalue is an eigenvector. These vectors may be represented in various forms (Hope 1968). In our case they are normalized so that the sum of squares of the elements of each eigenvector is unity. Each eigenvector element corresponds to one of the original variables. By squaring the appropriate element, we can obtain the proportion of a component's variance which is accounted for by a particular variable. The component value for each individual is calculated by multiplying the appropriate column eigenvector by the row vector of the standardized data, obtained by subtracting the variable mean from each value and dividing by its standard deviation.

It is necessary to decide on the number of components which have any practical importance. Jeffers (1967) found that, in practice, only those components with eigenvalues of unity or greater are likely to have any

practical importance, but it should be noted that this is only an approximate guide and the next one or two components should also be examined. A detailed consideration of the information conveyed by a component is needed to establish its practical value. We have used Jeffers' rule of thumb in the present study. Interpretation of the eigenvector weightings may then be attempted fairly simply by considering those variables whose absolute weightings are greater than 0.75 times that of the largest (absolute) eigenvector element, although this arbitrary value should not be overstressed (Jeffers 1967). If both positive and negative weightings are 'significant' in an eigenvector, this indicates a contrast between the corresponding variables. In the interpretation of a PCA, it can be useful to have a printout of the standardized data.

Principal component analysis of a covariance or correlation matrix requires the original data to be on interval or ratio scales. Disordered multistate data, such as are obtained by allocating arbitrary codes to observations such as absent, rare, common, abundant (eg. Howard et al 1980) are not suitable. If all the data are binary, the sums of squares and cross-products matrix should be analyzed. Here the data are all measured on ratio scales.

Single-linkage cluster analysis (Gower & Ross 1969) was used to explore the relationships among the points in the space of the first few principal components. This clustering method was chosen because, unlike most other methods, it does not tend to impose a structure on the data and is therefore a useful method for exploratory work. It will also reveal distinct groups of points if they exist.

The correlation coefficients between component values and between plot means of the different data groups were calculated.

A two-way analysis of variance was carried out on the data for each variable, the two factors being plots (48 levels) and sampling times (14 levels). Bartlett's test for homogeneity of variances was applied, but it is known to be sensitive to non-normality, so Scheffe's test, which is relatively insensitive to departure from normality, was also carried out. Where necessary, variance-stabilizing transformations were sought. However, two-way Anova is fairly robust to heterogeneity of variances provided that there are no missing values.

One-way analysis of variance and Tukey's Honestly Significant Difference (of pairs of means) were also used to test a priori divisions of the observations (Section 3.8).

3. RESULTS

L, L/F, and H layers were not present in all samplings, so the data were analysed separately. This paper presents the results for the 0 to 5 cm depth mineral soil samples.

A preliminary examination was made of the nature of the variation expressed in the data. The purposes of this were:

(a) to determine the dimensionality of the data;

(b) to explore the interrelationships between the dimensions;

(c) to eliminate the variables which contribute little or nothing to the study (cf Fourt et al 1971).

The first step was a principal component analysis (PCA) of the data for pH, LOI, moisture content, oxygen uptake, and cellulase and phosphatase activities, separately, with the 14 sampling periods treated as variables.

If the elements of the first eigenvector are all equal and of the same sign, then each element will have the value 0.2673. This is so because the sum of the squared eigenvector elements is unity and there are 14 of them. Each element will be the square root of 1/14. The component values are obtained by multiplying each standardized data value by the corresponding eigenvector element and summing over all 14 sampling periods. If all the first eigenvector elements are equal and of the same sign, all samplings contribute equally to the first component values, and the latter will be proportional to the means of the 14 samplings. In other words, the first component values will represent the order of the woods with respect to the property concerned taken over the 14 samplings.

If the first eigenvector elements are of the same sign, but some are smaller than 0.2673 and some are larger, the relative contributions of the samplings will be different, and the first component value will no longer be directly proportional to the simple mean value, but to a weighted mean. The components are orthogonal partitions of the total variance. The square of an element of an orthonormal eigenvector gives the proportion of the variance in a component accounted for by the corresponding variable, in this case the sampling. If some eigenvector

elements are smaller than 0.2673, the corresponding samplings will have less of their variance expressed in the first component and more in others. Conversely, if some elements are larger than 0.2673, more of their variance will be expressed in the first component and less in others.

3.1 Individual PCA's of pH, loss-on-ignition, moisture content, oxygen uptake, cellulase and phosphatase data.

pH: There is little variation either within or between samplings, the coefficients of variation within samplings ranging from 16 percent to 20 percent and the mean pH ranging from 4.19 to 4.33. The correlation coefficients between samplings are all greater than 0.75, and many are greater than 0.9 ($p < 0.001$).

Only the first component is of practical importance, accounting for 92 percent of the total variance. The eigenvector elements are all of the same sign and have very similar values, showing that the fourteen samplings contribute almost equally to the variance expressed in the first component. The first component values (Figure 2) represent the relative positions of the plots with respect to pH, the greatest positive component value representing the plot with the greatest pH, and vice-versa. The other possible source of variation is time of sampling, which includes a small amount of spatial variation within the sampling quadrat. The absence of other components of practical importance suggests that either –

(a) there is no variation of the property with time, or

(b) there is variation with time, but all the plots vary in the same way, so that the plots do not show variation with time relative to each other.

We expected (a) to be true, as Frankland et al (1963) found that possible monthly differences in pH, loss-on-ignition, and certain chemical elements could not be detected against the spatial variability. Inspection of our data showed very little variation of pH values within plots, and two-way analysis of variance showed that 91 per cent of the variance was between plots and less than one per cent was between samplings.

Loss-on-ignition: The coefficients of variation within samplings range from 40 percent to 59 percent and the mean loss-on-ignition between samplings from 26 percent to 32 percent. Correlation coefficients between samplings range from 0.57 to 0.89 ($p < 0.001$). Only the first component is of practical importance, accounting for 77 percent of the total variance. The eigenvector elements all have very similar positive values, showing that the 14 samplings contribute almost equally to the variance expressed in the first component. Here, too, we expected that we would not detect any significant variation in loss-on-ignition between samplings.

Moisture content: The coefficients of variation within samplings for moisture content (OD basis) range from 47 percent (sampling 6) to 70 percent (sampling 2) and the mean moisture contents between samplings from 106 percent to 139 percent. Correlation coefficients between samplings range from 0.54 to 0.89 ($p < 0.001$).

On an OD basis, the first two components, accounting for 82 percent of the total variance, are of practical importance. The eigenvector elements for the first component (which accounts for 75 percent of the total variance) all have similar values with the same sign, and the first component values (Figure 3) represent the relative moisture contents of the plots. The eigenvector for the second component contrasts samplings 2 and 3 with sampling 11, showing that this component has discriminating power based on those samplings. Examination of the component plot (Figure 3) shows that plots 28 and 24 had the greatest positive and negative second component values respectively. The original and standardized data show that the moisture contents of these plots exhibited linear trends, plot 28 decreasing, and plot 24 increasing, with time. In samplings 2 and 3, the difference between the plots was maximum, whereas at sampling 11 there was little difference.

The two wettest plots (24 and 27), which were usually so wet that the soils could be poured from the polythene bags, did not have the greatest moisture contents on OD basis. This was attributed to their low organic matter contents. The moisture contents were therefore divided by the loss-on-ignition values to give what Crump (1913) called the coefficient of humidity. The coefficients of variation within samplings for the coefficient of humidity range from 27 percent to 37 percent (sampling 3) and the mean coefficient of humidity between samplings from 3.5 to 5.0.

Correlation coefficients between samplings range from 0.46 to 0.96 ($p < 0.001$), the weakest correlations occurring between the first five samplings.

For the coefficient of humidity, two eigenvalues are of practical importance, accounting for 85 percent of the variance. In the first eigenvector (accounting for 78 percent of the variance), all the elements have the same sign, but those corresponding to the first two samplings are less than 0.75 times the largest element. This suggests that, although the first component values represent the relative wetness of the plots, the first two samplings contribute less to the between-plot variation than do the remaining 12 samplings. The first component values (Figure 4) show that the two very wet plots (24 and 27) have the greatest positive component values, while plot 28, which had the greatest positive first component value on OD basis, had a relatively lower value when corrected for loss-on-ignition. Apart from the two outliers, the plots form a more compact group when moisture content is corrected for loss-on-ignition than when it is expressed on an OD basis (Figure 3).

The eigenvector for the second component (on LOI basis) shows three large positive elements (samplings 2, 3, and 5). Only plot 24 has an unusually large (negative) second component value, and this plot had its lowest value for both original and standardized data on those samplings. The data for this plot follow the linear trend noted in the moisture content on OD basis, but the data for plot 28 do not show such an obvious trend on LOI basis as on OD basis.

Oxygen uptake: The coefficients of variation within samplings for oxygen uptake (OD basis) range from 45 percent to 67 percent (sampling 2) and the mean oxygen uptakes between samplings range from 5.6 to 7.8 μl/g OD/hour. Correlation coefficients between samplings range from 0.19 (NS) to 0.78 ($p < 0.001$) and it is noticeable that data for samplings 12 and 14 are least intercorrelated with those of other samplings.

On an OD basis, three eigenvalues are of practical importance, accounting for a total of 72 percent of the variance. In the eigenvector for the first component (which accounts for 56 percent of the variance), only samplings 12 and 14 have elements which are less than 0.75 times the largest (absolute) element. For the remaining samplings, the first component values represent the relative oxygen uptakes of the plots.

However, samplings 12 and 14 have large (negative) weightings in the eigenvector for the second component which accounts for a further 9 percent of the variance. The three greatest (absolute) second component values were for plots 25 (-3.48), 13 (3.27), and 4 (-2.96). Plots 25 and 4 had their greatest oxygen uptakes at samplings 12 and 14, and these uptakes were the greatest for all plots on those samplings, on the basis of both original and standardized data. These large oxygen uptakes coincided with the greatest moisture contents of the two plots, but these were not the greatest moisture contents of all plots on those samplings. Plot 13 had low rates of oxygen uptake on samplings 12 and 14, that on sampling 14 being the lowest for this plot (original and standardized data), although these values did not coincide with notably small moisture contents. Thus, the second component has identified certain plots, which, for various reasons, behaved differently from the rest on samplings 12 and 14. The first component values represent the relative oxygen uptakes of the plots, with low weightings for samplings 12 and 14.

The eigenvector of the third component has large negative elements for samplings 9 and 2. The two largest (absolute) third component values are for plots 28 (-3.24) and 35 (2.88). Plot 28 had its greatest oxygen uptake on sampling 2, which coincided with the greatest moisture content for this plot. Plot 28 had its greatest standardized oxygen uptake at sampling 9, and this was the greatest value for all plots on that sampling. It coincides with the second largest moisture content on this plot, which was also the greatest value for all plots at that sampling. On both samplings 2 and 9, the oxygen uptake of plot 35 was small.

The coefficients of variation within samplings for oxygen uptake (LOI basis) range from 27 percent to 37 percent, and the mean oxygen uptake between samplings from 19 to 25 µl/g LOI/hour. Correlation coefficients between samplings range from 0.08 (NS) to 0.71 ($p < 0.001$), data for samplings 10 and 12 having noticeably low intercorrelations with those for the other samplings.

Four eigenvalues, accounting for a total of 72 percent of the variance, are of practical importance. In the first component, accounting for 44 percent of the variance, only the eigenvector elements corresponding to samplings 10 and 12 are less than 0.75 times the greatest (absolute) value. Those samplings are also the only ones which have elements greater than 0.75 times the greatest (absolute) value in the second eigenvector.

This is rather similar to the results obtained on OD basis, but with the emphasis on different samplings. The first component values represent the relative oxygen uptakes on a LOI basis, with low weightings for samplings 10 and 12. The plot of the first and second component values (Figure 5) is different from that for the data on OD basis, because of differences in loss-on-ignition between sampling squares on certain plots.

The second component accounts for a further 12 percent of the variance and the greatest (absolute) second component values are for plots 24 (4.64), 17(-3.27) and 27(2.87). On sampling 10, plot 24 had its smallest oxygen uptake (the second smallest value for all plots on that sampling), and greatest coefficient of humidity (greatest for all plots on that sampling). Plot 24 had its next smallest oxygen uptake (for both original and standardized data) on sampling 12, and this also corresponded with a large coefficient of humidity (the second largest on that sampling).

Plot 27 had small (but not its smallest) oxygen uptakes on these samplings, and these correspond to large values of coefficient of humidity (the largest on sampling 12, the second largest on sampling 10). It seems fairly clear that at these large values for coefficient of humidity (9.59 to 11.40) the soils are waterlogged and oxygen uptake is depressed.

Plot 17 had its greatest oxygen uptake (original and standardized data) on sampling 10, and this was the greatest oxygen uptake for all plots on that sampling. That plot had its second greatest oxygen uptake (using original data, or third greatest for standardized data) on sampling 12. On both samplings, this plot had small (but not the smallest) values for relative humidity (3.99 and 5.08).

In the third eigenvector, the largest elements correspond to samplings 4 and 14. Plot 47 has the largest (absolute) third component value (-3.19), and this plot had fairly large oxygen uptakes on samplings 4 and 14. This component accounts for a further 8 percent of the total variance.

In the fourth eigenvector, there is a contrast between samplings 12 and 14 (positive) and sampling 7 (negative). The greatest (absolute) fourth component values are for plots 25 (2.85) and 7 (-2.54). Plot 25 had its maximum oxygen uptake on samplings 12 and 14, whereas plot 7 had its maximum on sampling 7 and its smallest values on samplings 12 and 14.

Cellulase: On an OD basis some samplings, notably 1 and 4, show considerable variability, with coefficients of variation of 102 percent and 99 percent respectively. Sampling 10 has the smallest coefficient of variation, 60 percent. Mean cellulase activity ranges from 0.02 to 0.05 mg glucose/g OD/48 hours. Correlation coefficients between samplings range from -0.002 (NS) to 0.91 ($p < 0.001$), samplings 1 to 3 showing low correlations with other samplings. Data for many of the samplings are highly correlated with only a few preceding or succeeding samplings.

On an OD basis, three eigenvalues are of practical importance, accounting for a total of 73 percent of the variability. The first component accounts for 38 percent of the total variance. In the first eigenvector, all the elements are positive, but only those for samplings 4 to 12 are greater than 0.75 times the largest element. Together those elements account for 86 percent of the variability in the first component, as against 64 percent if all the vector elements were equal. The first component values represent the relative cellulase activities of the woods with low weightings for samplings 1 to 3, 13 and 14.

The second component accounts for a further 24 percent of the total variance. In the eigenvector for the second component, there is a contrast between samplings 1, 4, and 5 on the one hand, and 11 to 14 on the other. The greatest positive second component value is for plot 37, and the greatest negative value is for plot 43. The data show that plot 37 had high cellulase activities on samplings 1, 4, and 5 and low activities on samplings 11 to 14, while the reverse was true for plot 43.

In the third component, which accounts for 10 percent of the variation, there is a contrast between samplings 2 and 3. Plot 6 has the greatest negative third component value, and plot 13 the greatest positive value. Plot 6 had low cellulase activity at sampling 2, and plot 13 had a high activity. At sampling 3 the positions were reversed.

On a LOI basis, samplings 13 and 14 show the greatest variability with coefficients of variation of 105 percent and 100 percent respectively. Sampling 6 has the smallest coefficient of variation, 62 percent. Mean cellulase activity ranges from 0.09 to 0.19 mg glucose/g LOI/48 hours. Correlation coefficients between samplings range from -0.01 (NS) to 0.93

($p < 0.001$). As for the data on an OD basis, samplings 1 to 3 show low correlations with other samplings and there are groups of samplings with large correlations.

Three, possibly four, eigenvalues are of practical importance, the first three together accounting for 76 percent of the total variance. The pattern of large eigenvector elements is different from that obtained from the data on OD basis. In the first component, which accounts for 51 percent of the total variance, samplings 5 to 14 have eigenvector elements greater than 0.75 times the largest element. These samplings account for 92 percent of the variance in the first component, as against 71 percent if the eigenvector elements were all equal. On both OD and LOI basis, the smallest elements of the first eigenvector are those corresponding to the first three samplings. As with moisture content, the relative positions of the plots with respect to cellulase activity, as given by their first component values, is different on OD basis and on LOI basis.

The second component accounts for a further 17 percent of the total variance. In the eigenvector for the second component, the largest elements correspond to samplings 4, 5, and 7. Plot 43 has the greatest negative (and absolute) second component value (Figure 6), and that plot had low values for cellulase activity (LOI basis) on those samplings (Figure 6). Conversely, plot 26, with the next greatest (absolute) second component value (and greatest positive value) had large cellulase activities on those samplings.

In the third component, accounting for 8 percent of the variance, large positive eigenvector elements corresponding to samplings 1 and 2 are associated with high levels of cellulase activity on certain plots, notably 24 and 9 in sampling 2, and 17 and 42 in sampling 1. In the fourth component, accounting for nearly 7 percent of the variance, a large negative eigenvector element for sampling 3 corresponds to a high level of cellulase activity at plots 48 and 27 on that sampling.

Phosphatase: The coefficients of variation within samplings for phosphatase (OD basis) range from 44 percent (sampling 6) to 82 percent (sampling 1) and the mean phosphatase activity is between 701 and 1222 μg phenol/3 hours/g OD. Correlation coefficients between samplings range from 0.14 (NS) to 0.84 ($p < 0.001$).

The first three eigenvalues are of practical importance, together they account for 77 percent of the total variance. In the first component, which accounts for 59 percent of the variance, the eigenvector elements are all of the same sign, and only those corresponding to the first and last samplings are less than 0.75 times the greatest value. That is, the first component values represent the relative phosphatase activities of the plots, with low weightings for samplings 1 and 14. The greatest (both absolute and positive) first component values are for plots 13 and 28. The largest negative values are for plots 19 and 22. Plot 28 also has one of the two greatest (positive) first component values for loss-on-ignition, moisture content, respiration (OD basis), and cellulase activity (OD basis), while for each of those properties, plot 22 has one of the two lowest (i.e. most negative) first component values.

The second component, which accounts for a further 10 percent of the total variance, has large eigenvector elements for samplings 1 and 4. The scatterplot of the component values shows that plot 46 has an unusually large second component value, and this plot had large phosphatase activities (and also large loss-on-ignition and moisture content), on samplings 1 and 4.

Component three, accounting for 8 percent of the variation, shows a contrast between samplings 1, 10,12, and 14 on the one hand, and 6, 7, 8, and 9 on the other. Plots 11 and 37 have fairly high phosphatase activities on samplings 10, 12, and 14, while plot 30 has low phosphatase activity on those samplings and high activity on samplings 6 to 9.

On a LOI basis, the coefficients of variation within samplings range from 28 percent to 35 percent (sampling 3) and the mean phosphatase activity ranges from 2134 to 4862 μg phenol/3 hours/ g LOI. Correlation coefficients between samplings range from 0.23 (NS) to 0.82 ($p < 0.001$).

As with the data on an OD basis, three components are of practical importance, and together they account for 75 percent of the variance. In the first component, which accounts for 58 percent of the total variance, low weighting is again given to the first sampling, but in this case the other low weighting is for sampling 4. The first component values (Figure 7) represent the relative phosphatase activities of the plots, with low weightings for samplings 1 and 4 (Figure 7). In the second component, which accounts for a further 9 percent of the total variance, there is a

contrast between samplings 4 and 12. As on an OD basis, plot 46 has the largest second component value, and had high phosphatase activity on sampling 4 and low activity on sampling 12. Plot 49 showed similar behaviour, while plot 17 showed the reverse. In the third component, the only eigenvector element greater than 0.75 times the largest (absolute) element was that corresponding to the first sampling. On that sampling some plots (e.g. 46) had high phosphatase activities, whilst others (e.g. 42 and 47) had low activities.

3.2 Correlations between the component values of the pH, loss-on-ignition, moisture content, oxygen uptake, cellulase and phosphatase data.

The signs of component values are arbitrary, and so the signs of coefficients of correlation between them are also arbitrary. In the case of our first component values, the signs are meaningful because the first component values are in a similar order to the mean values for the plots. Coefficients of correlation between the first component values will therefore be of the same sign as those between the mean values.

The significant linear correlations between the component values of the data on an OD basis (Table 12), are shown diagrammatically in Figure 8 with the signs omitted.

The first components of loss-on-ignition, moisture content, oxygen uptake, cellulase, and phosphatase are significantly intercorrelated. It is interesting that of these, only the first component of cellulase is not significantly correlated with the first component of pH ($r = -0.07$). Cellulase component 2 is positively correlated with the first components of loss-on-ignition ($r = 0.44$), phosphatase ($r = 0.56$), oxygen uptake ($r = 0.49$), and moisture content ($r = 0.35$). The first component of pH is negatively correlated with the first components of loss-on-ignition ($r = -0.61$), phosphatase ($r = -0.42$), oxygen uptake ($r = -0.50$), and moisture content ($r = -0.46$), and with cellulase components 2 ($r = -0.40$) and 4 ($r = -0.29$).

A subsidiary group of component correlations (Figure 8) contains phosphatase components 2, 3 and 4, oxygen uptake components 2 and 3, cellulase component 3, and moisture content component 2. There are some significant intercorrelations in this group, and it is linked to the main group by a negative correlation between cellulase component 1 and oxygen uptake component 3 ($r = -0.43$).

On a LOI basis, the correlations are rather different (Table 14 & Figure 9), and the components fall into two distinct groups. The first phosphatase component is significantly correlated only with the first oxygen uptake component ($r = 0.61$). The second component of the coefficient of humidity is negatively correlated with the first components of respiration ($r = -0.32$) and pH ($r = -0.45$), and the third component of cellulase activity ($r = -0.48$). The first pH component is positively correlated with the first ($r = 0.44$), and negatively with the second ($r = -0.32$) and fourth ($r = -0.29$) components of cellulase activity.

It is interesting that the first component of the coefficient of humidity is not significantly correlated with any of the other first components. It is positively correlated with the second ($r = 0.64$) and fourth ($r = 0.31$) components of oxygen uptake and negatively correlated with the fifth ($r = -0.31$). Oxygen uptake component 2 is positively correlated with phosphatase commponent 2 ($r = 0.45$) and negatively correlated with phosphatase component 4 ($r = -0.30$). Oxygen uptake component 3 is negatively correlated with phosphatase components 2 ($r = -0.30$) and 4 ($r = -0.43$).

3.3 Correlations between mean values (over 14 samplings) and first component values, and correlations among mean values, for pH, loss-on-ignition, moisture content, oxygen uptake, cellulase and phosphatase data.

Correlations between means and first component values.

The mean values on both OD basis and LOI basis are given in Tables 1 to 10. It is interesting to compare the means with the first component values in order to compare the ordering of the plots with respect to the properties measured (Table 11). All of the correlation coefficients are large ($r > 0.950$), and apart from cellulase on both OD and LOI basis, all the correlation coefficients are equal to, or greater than, 0.995. For pH and loss-on-ignition, $r = 1.000$.

Comparison of the tables of mean values and first component values shows that for pH the orders of the plots are the same. For loss-on-ignition, 9 plots are in different positions. In the case of moisture content (OD basis) and coefficient of humidity, there are also a few plots which do not occupy the same positions in the tables of first component values and

means of 14 samplings, but these involve only plots being interchanged within small blocks, no plot differs by more than a few places in the comparison of the tables. With oxygen uptake (OD and LOI basis) we find several plots in different positions, but also not displaced by many positions in the tables. These comparisons show that, except for pH and loss-on-ignition, large correlation coefficients do not guarantee that the orders of the plots will be the same on the basis of first component values and means of 14 samplings. The differences in the orders are greater for cellulase, and are related to the percentage of the total variance accounted for by the first component (Table 11), which is only 38 percent for cellulase (OD basis), 44 percent for oxygen uptake (LOI basis), and 51 percent for cellulase (LOI basis).

Correlations among the means

The correlations among the means (OD basis) are shown in Figure 10, and are very similar to the correlations among the first component values (Figure 8). On a loss-on-ignition basis, only two correlations are significant, oxygen uptake and phosphatase ($r = 0.626$, $p < 0.001$) and cellulase and pH ($r = 0.457$, $p < 0.01$). This agrees with the correlations among the component values (Figure 9).

Tests for non-linearity were also carried out. In some cases a quadratic equation gave a better fit but with little increase in r^2.

3.4 Principal component analysis of the pooled pH, loss-on-ignition, moisture content, oxygen uptake, cellulase and phosphatase first component values.

If the first component values for the individual properties represent the order of the soils with respect to the overall levels of those properties, and exclude the effects of those samplings on which some soils show large deviations from the overall mean for the sampling, then a principal component analysis of these component values should provide information on the relative positions of the plots with respect to all the properties taken together, and they should do this more effectively than the mean values which are affected by sampling variation.

OD basis: As was reported in Section 3.2, the first components of loss-on-ignition, moisture content, oxygen uptake, cellulase, and phosphatase are significantly positively intercorrelated, and all except

the first component of cellulase are significantly negatively correlated with the first component of pH (Table 12 & Figure 8).

Only the first two eigenvalues are of practical importance, together they account for 83 percent of the total variance (Table 13). The first component, accounting for 68 percent of the total varaiance, is due chiefly to loss-on-ignition, oxygen uptake, phosphatase, and moisture content. The second component, which accounts for a further 16 percent of the total variance, is dominated by cellulase and pH, which together account for 99 percent of the variance in that component. The first and second components are plotted in Figure 11.

The single linkage dendrogram showed that a single large group rapidly formed at low levels of distance, and grew to absorb all the points. This seems to be an example of "expanding balloon" type of clustering. There are no clear discontinuities.

LOI basis: As was reported in section 3.2, the only significant correlations between the first component values are between pH and cellulase ($r = 0.439$, $p < 0.01$) and between oxygen uptake and phosphatase ($r = 0.616$, $p < 0.001$). (Table 14).

The first three eigenvalues are of practical importance, together they account for 81 percent of the total variance (Table 15). The first component, accounting for 41 percent of the total variance, is essentially a combination of all the variables except coefficient of humidity. The second component, accounting for 22 percent of the total variance, contrasts oxygen uptake and phosphatase with coefficient of humidity, pH and cellulase. The third component, which accounts for a further 18 percent of the total variance, is due chiefly to coefficient of humidity, which accounts for 70 percent of the variance in that component. The first and second components are plotted in Figure 12, the first and third in Figure 13.

In the single linkage dendrogram, a large group soon formed and joined with a separate group of 5 plots (26, 43, 45, 44, 47) and then with the remaining points. This seems to be simply an example of the "expanding balloon" type of clustering, and there appear to be no important discontinuities.

3.5 Principal component analysis of pH, loss-on-ignition, moisture content, oxygen uptake, cellulase and phosphatase mean values of 14 samplings for each plot.

If the mean values over 14 samplings approximately represent the relative positions of the plots, then a principal component analysis of these mean values should provide information on the relative positions of the plots with respect to all the properties considered together.

OD basis: pH shows least variation, with a coefficient of variation of 17 percent. The remaining variables all have very similar coefficients of variation (41 percent to 48 percent). The lower half-matrix of correlation coefficients shows very highly significant ($p < 0.001$) positive intercorrelations between all variables except pH, which is negatively correlated with oxygen uptake, loss-on-ignition, and moisture content ($p < 0.001$), and phosphatase ($p < 0.01$). pH shows a low negative correlation coefficient with cellulase, which is not significant at $p < 0.05$ (cf Figure 10).

Only the first two components, accounting for 85 percent of the total variance, are of practical importance. The first component, which accounts for 70 percent of the total variance, is dominated by loss-on-ignition, oxygen uptake, phosphatase, and moisture content. The second component, accounting for 15 percent of the total variance, is dominated by pH and cellulase, which together account for 97 percent of the variance in that component. A plot of the first and second component values was very similar to that obtained in Section 3.4 (Figure 11), and is not given.

LOI basis: The lower half-matrix of correlation coefficients shows that the only significant correlations are between oxygen uptake and phosphatase ($r = 0.626$, $p < 0.001$), and between pH and cellulase ($r = 0.457$, $p < 0.01$).

The first three components, accounting for 82 percent of the total variance, may be considered to be of practical importance. The first component, which accounts for 42 percent of the total variance, is essentially a combination of all the variables except coefficient of

humidity, which has a low weighting. The second component, accounting for 22 percent of the total variance, is mainly a contrast between coefficient of humidity and oxygen uptake, these two variables account for 56 percent of the variance in that component. The third component, accounting for 18 percent of the total variance, is dominated by coefficient of humidity, which accounts for 64 percent of the variance in that component. Again plots of the component values were very similar to those obtained in section 3.4 (Figures 12 & 13), are not given.

3.6 Principal component analysis of the pooled moisture content, oxygen uptake, cellulase and phosphatase first component values.

OD basis: In section 3.4 the results are given for the physiological properties plus pH and loss-on-ignition. Here, we leave out pH and loss-on-ignition as they are soil factors which may influence the other properties and obscure relationships. The first component values of moisture content, oxygen uptake, cellulase, and phosphatase are all highly significantly positively intercorrelated. Only the first component has an eigenvalue greater than unity. It accounts for 72 percent of the total variance and is due chiefly to oxygen uptake, phosphatase, and moisture content. The second component accounts for 17 percent of the total variance (the first and second account for nearly 90 percent of the total variance), and is dominated by cellulase which accounts for 85 percent of the variance in that component.

The single linkage dendrogram showed that at a low level of distance, three groups were formed consisting of 13, 14, and 14 plots, with 7 single outlying plots. These groups did not appear when the data were expressed on a LOI basis. Comparison of the PCA output with the first components from which the correlation matrix was calculated suggested a strong relationship to moisture content.

An analysis of variance and Tukey's Honestly Significant Difference test were carried out on these three groups for the first component values from this analysis (output), the individual first component values used to calculate the correlation half-matrix (inputs), and for comparison the first component values for pH and loss-on-ignition. The results were as follows:

	Groups		
	1-2	1-3	2-3
First component values (output)	***	***	***
Moisture content first component values	**	***	NS
Oxygen uptake " " "	***	***	***
Cellulase " " "	NS	NS	NS
Phosphatase " " "	*	***	***
pH " " "	NS	NS	NS
LOI " " "	**	***	*

Significant difference at $p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***.

Within the groups, the ranges of values were:

	Group		
	1	2	3
First component values (output)	2.06	0.69	-0.14
	0.98	0.16	-1.40
Moisture content 1st component values	-0.40	4.84	5.01
	-3.93	-2.98	-2.55
Oxygen uptake 1st component values	-0.90	0.86	3.99
	-3.87	-4.03	-0.51
Cellulase 1st component values	3.32	4.81	2.26
	-2.98	-2.56	-2.08
Phosphatase 1st component values	-1.38	0.63	3.64
	-4.02	-3.10	-1.44
pH 1st component values	7.17	10.75	7.21
	-1.82	-4.06	-4.30
LOI 1st component values	-1.27	1.76	6.27
	-4.51	-2.57	-2.76

Although the ranges of the output component values do not overlap, the ranges of the input values, and the first component values of pH and loss-on-ignition, overlap to varying extents. Notably, the values for pH and cellulase show considerable overlaps, suggesting that they did not contribute much to the groupings of the output component values. The correlations between the output first component values and the inputs, and those of pH and loss-on-ignition, confirm this:

Correlation between		r
Output first component value and	pH	0.450**
" " " " "	LOI	-0.901***
" " " " "	Moisture input	-0.872***
" " " " "	O_2 uptake input	-0.927***
" " " " "	Cellulase input	-0.639***
" " " " "	Phosphatase input	-0.927***

The main contributors to the grouping of the first component values are phosphatase, oxygen uptake, and moisture content, which we have shown are themselves highly intercorrelated.

LOI basis: Only oxygen uptake and phosphatase are significantly correlated ($r = 0.616$, $p < 0.001$). The first three eigenvalues are of practical importance, together they account for 91 percent of the total variance. The first component, accounting for 44 percent of the total variance, is due mainly to phosphatase and oxygen uptake, which together account for 81 percent of the variance in that component. The second component, accounting for 25 percent of the total variance, is due chiefly to the coefficient of humidity, which accounts for 81 percent of the variance in that component. The third component, accounting for a further 21 percent of the total variance, is dominated by cellulase, which accounts for 76 percent of the variance in that component.

The single linkage dendrogram showed that at an early stage a large group formed which gradually absorbed the remaining points at increasing levels of distance. This is another example of the "expanding balloon" type of clustering, and shows that there are no discontinuities.

3.7 Analysis of variance of the pH, loss-on-ignition, moisture content, oxygen uptake, cellulase and phosphatase data.

The first component values of the variables (Section 3.1) give rankings of the plots for the variables. Subsequent components illustrate different aspects of the between-sampling differences. Because the components are orthogonal, the first component gives an overall ranking of plots with sampling differences removed, i.e. they represent "smoothed" between-plot differences. However, the PCA does not tell us if the between-plot differences illustrated by the first component values are significant or not.

A two-way analysis of variance was carried out on each set of data, the two factors being plots (48 levels) and sampling times (14 levels). Bartlett's test was highly significant between plots for all data except phosphatase. It was thought that this might be due, at least partly, to non-normality. However, Scheffé's test for homogeneity of variances, which is relatively insensitive to departure from normality, also showed highly significant differences between plots. For most sets of data it was not possible to find a transformation which would fully stabilize the variances. However, two-way Anova is fairly robust to heterogeneity of variances provided that there are no missing values.

For each variable there were very highly significant differences between plots, and the differences between samplings were very highly significant for all variables except pH, for which the differences were significant only at the 5 percent level.

The between-plots differences will be discussed in Section 3.8, the between-sampling differences in Section 3.9.

3.8 Differences between plots.

The most obvious a priori difference is whether the plots are on limestone or acidic rocks. As the first component values represent the relative order of the plots with respect to the different variables with sampling differences removed, Table 16 gives the results of a one-way Anova of the first component values of limestone and non-limestone plots. There are significant differences for loss-on-ignition and moisture content on OD basis, but the difference for moisture content disappears when the results

are expressed on a LOI basis. However, on a LOI basis there is a significant difference for cellulase.

The meaning of these differences is difficult to interpret on the first component values, but it is easier if the analysis is performed on the means of the 14 samplings for each plot, which can be used as a first approximation to the first component values. This analysis (Table 17) shows that on an OD basis soils from plots on limestone have significantly lower loss-on-ignition and moisture content than those from the non-limestone plots. On a LOI basis the only difference is that cellulase activity is greater on the limestone plots.

However, the division into limestone and non-limestone plots is not very satisfactory, firstly because there are only 6 limestone plots and 42 non-limestone plots and secondly (and ecologically more importantly) because these soils are developed on drift. Where the drift overlies limestone the surface soil properties depend on the depth to limestone, or whether or not the plot receives drainage from limestone. Five of the six limestone soils sampled have mean pH in the range 5.3 to 6.4, and two non-limestone soils have mean pH values in this range. One soil on limestone had a mean pH of only 4.4. A division on the basis of pH would appear to be more meaningful than one on the basis of underlying rock.

Mainly on the basis of studies in northern England, Pearsall (1938, 1952) recognized the occurrence of ground flora communities which corresponded, in a general way, with soil biology and humus type:

(1) Mull, on the more nearly base-saturated, often calcareous, soils with pH greater than 4.8 to 5.0.

(2) Mor, on base-deficient ('hydrogen') soils with pH less than about 3.8 to 4.0.

(3) Transitional soils within those limits.

This suggests a basis for an initial division into acidic (pH < 3.8), intermediate (pH 3.8 to 5.0), and base-rich (pH > 5.0) soils. The means of the data grouped in this way are plotted in Figures 14 to 22. Table 18 gives the results of a one-way Anova followed by Tukey's HSD

of the first component values divided into groups on the basis of those pH values. On OD basis, loss-on-ignition, moisture content, and oxygen uptake are similar in that the acidic soils are different from those in either of the other groups, and those of the intermediate group are not different from those of the base-rich group. This appears to be due to the relationship between oxygen uptake, moisture content, and loss-on-ignition, because on a LOI basis there are no significant differences between the groups. Also, on a LOI basis, for cellulase the acidic group is different from the base-rich group and so is the intermediate group, but the acidic and intermediate groups are not significantly different. This result is nearly the same as the division into limestone and non-limestone soils. For phosphatase, the acidic group is significantly different from the intermediate group. However, the mean value of the basic group lies between those of the other two groups and is not significantly different from either. Thus, there is a peak of phosphatase activity in the range pH 3.8 to 5.0.

A similar analysis on the means of the 14 samplings for each plot (Table 19) shows similar results except that on a LOI basis for oxygen uptake the lowest mean is for the acidic group and the other two groups are similar (Figure 18). For cellulase the greatest mean is for the base-rich group and the other two groups are similar (Figure 20), and for phosphatase the largest mean is for the intermediate group (Figure 22), again there is a peak of phosphatase activity in the range pH 3.8 to 5.0.

3.9 Differences between samplings.

Differences between samplings were very highly significant for all variables except pH, for which the differences were significant only at the 5 percent level. Although there is a significant difference between samplings for pH, the range of variation is generally small (Table 1). The coefficients of variation for the plots between samplings range from 2 to 13 percent.

There were very highly significant differences between samplings for loss-on-ignition, the greatest mean values occurring in the acidic group in the first 5 samplings, i.e. May to September (Figure 14). The coefficients of variation were greater than for pH, ranging from 7 to 42

percent (Table 2). There is little suggestion of any increase in loss-on-ignition after litterfall (samplings 6, 7, and 8), and at sampling 14 (May-June) the mean loss-on-ignition was lower than a year previously. The implication of the initial decrease in the acidic group is that different site conditions favoured decomposition of previously-accumulated organic matter.

Moisture content (OD basis): Soils of the acidic group had their greatest moisture contents during the first two samplings. Soils of the other two groups showed a slight tendency for moisture content to increase with time (Figure 15). Coefficients of variation for the plots ranged from 8 percent to 52 percent (Table 3).

The coefficient of humidity (moisture content on a LOI basis) of the acidic and intermediate groups showed similar variation in time, whereas that of the base-rich group showed a marked increase after sampling 5 (Figure 16). Coefficients of variation of the plots ranged from 5 percent to 39 percent (Table 4).

Oxygen uptake (OD basis): Although there is some suggetion of a relationship with moisture content in samplings 1 to 6 (May to October) for the acidic group, there is little evidence of any relationship thereafter, except for the peak at sampling 12 (March to April, Figure 17). Coefficients of variation for the plots ranged from 17 percent to 71 percent (Table 5).

Oxygen uptake (LOI basis) varied markedly with time (Figure 18) and did not seem to be strongly related to coefficient of humidity. The coefficients of variation for the plots ranged from 13 percent to 68 percent (Table 6).

Cellulase (OD basis) showed considerable variation with time (Figure 19) that did not appear to be much related to moisture content. Coefficients of variation for the plots ranged from 28 percent to 98 percent (Table 7).

Cellulase (LOI basis) showed marked variation with time (Figure 20) which did not seem to be strongly related to coefficient of humidity. The coefficients of variation for the plots ranged from 28 percent to 92 percent (Table 8).

Phosphatase (OD basis) also showed considerable variation with time (Figure 21). Harrison and Pearce (1979) found that when the mean phosphatase activities of the 48 plots at the 14 sampling times were plotted, there were peaks at samplings 2, 4 and 5, 8 and 9. Figure 21 shows that the peak at sampling 2 was due to the acidic group. The peak at sampling 4 was strongly influenced by the acidic group, and that at sampling 5 by the intermediate group. All groups contributed to the peaks at samplings 8 and 9, soils of the acidic group showing the strongest peak. Coefficients of variation of the plots ranged from 20 percent to 76 percent (Table 9).

Phosphatase (LOI basis) showed less variation with time (Figure 22) than on OD basis. The peaks at samplings 2, 4, 8 and 9 in the acidic group (Figure 21) are much reduced, as is the peak at sampling 5 in the intermediate group. The coefficients of variation of the plots ranged from 16 percent to 45 percent (Table 10).

4. DISCUSSION

This study has shown that the problem of comparing soils with respect to variables which show marked fluctuations in amplitude with time can be overcome using principal component analysis. The first component represents "smoothed" between-plot differences, the remaining components pick out plots which behave differently from the majority at certain times. This use of the lower components is interesting, as it poses questions concerning the reasons for this differential behaviour.

If there is relatively little seasonal variation in the properties, the order of the mean values of the plots over the 14 samplings will not be substantially different from the first component values. The coefficients of correlation between the means and first component values (Table 11) are all large, the smallest being cellulase activity ($r = 0.955$). Perhaps the main advantage of principal component analysis is the additional information it provides about variation in time.

Principal component analysis and analysis of variance showed that there was little within-plot variation in pH and loss-on-ignition over the 14 samplings. Our coefficients of variation are slightly larger than those of Ball and Williams (1968), who found that seasonal variation in pH and loss-on-ignition in two Welsh Brown Earths was small within the main growing season.

An interesting result is the lack of clear clusters in any of the component scatterplots. The soil plots sampled formed a continuous series with respect to all the properties studied, and combinations of them, except for the two outling plots with respect to coefficient of humidity (Figure 4). This agrees with the results of Bauzon et al (1974), who applied correspondence analysis to CO_2 evolution, chemical properties, and enzyme activities of surface horizon samples from 5 French forest soils. Their ordination chart showed that only calcic mull samples formed a distinct group, eutrophic mull, mull-moder, and mor formed a continuous series.

On an oven dry basis, the first components of loss-on-ignition, moisture content, oxygen uptake, cellulase and phosphatase are significantly intercorrelated. The pattern of correlations among the means is essentially the same as that among the first component values (Figures 8 and 10). As the soil water-holding capacity is due chiefly to organic matter, and as soil organic matter is a substrate for soil organisms, it seems reasonable to suppose that these intercorrelations are strongly influenced by relationships of the individual properties to loss-on-ignition, and that these properties are better expressed on a LOI basis when soils of different loss-on-ignition are being compared. When this is done, the first phosphatase component is significantly correlated only with the first component of oxygen uptake. The first cellulase component is significantly correlated only with the first component of pH, and the first component of moisture content (coefficient of humidity) is not significantly correlated with any of the other first components (Figure 9). The correlations between the means of the 14 samplings agree with this.

Coefficient of humidity appears to be a better measure of the relative wetness of soils than is moisture content on OD basis. The coefficient used here differs from that of Crump (1913) in that he used air dry soil rather than oven dry, but the principle is the same. The lack of

significant correlation between phosphatase activity (LOI basis) and pH is due to the non-linear nature of the relationships between these two variables, phosphatase having its greatest activity in the range pH 3.8-5.0 (Table 19). Oxygen uptake shows some increase above pH 3.8 but the spread of values probably accounts for the lack of a significant correlation. It is interesting that coefficient of humidity does not vary significantly linearly with pH. There are significant differences with pH on OD basis (Table 19), but this turns out to be due to the different organic matter contents. The lack of significant correlations between coefficient of humidity and phosphatase activity, and between coefficient of humidity and oxygen uptake, is also interesting and is brought out in the PCA of the means of the 14 samplings for the plots. Only coefficient of humidity had a low weighting on the first component (Table 15). For oxygen uptake, the explanation seems to be that as long as the coefficient of humidity is above some minimum threshold value and below a level which would cause anaerobiosis, oxygen uptake is largely independent of relative wetnesss. Not much seems to be known about the factors affecting phosphatase activity.

As the coefficient of humidity was not widely adopted as a method for expressing soil moisture content, nothing is known about its relationships with other properties. Pyatetskiy (1976) gave a table of wilting moisture contents and ash contents of a range of peat soils. Coefficients of humidity calculated from those data are: eutrophic peats 1.2-1.5, mesotrophic peats 1.1-1.5, oligotrophic peats 1.3-2.5. Our lowest mean coefficient of humidity is 2.9 (Table 4), and this plot (17) did not have the lowest oxygen uptake (LOI basis). It seems unlikely that oxygen uptake in these soils was generally inhibited by too little moisture, although seasonally it may have been inhibited by too much.

The PCA of the mean valules of the plots over the 14 samplings for all the properties (section 3.5) was not much different from that of the corresponding first component values (section 3.4), except that in the second component the signs of the second and third eigenvector elements were reversed. On a LOI basis the PCA's were similar. For some purposes PCA is more useful because of the first component values represent "smoothed" between-plot differences which are independent of large variations at particular sampling times. The latter appear as separate components and are themselves of interest. However, for some purposes, such as the partitioning of the sites into the three pH groups, the mean values are more appropriate.

Interest in the role of micro-organisms in soil processes has led some workers to search for a method which will provide an "index" of "biological activity". Given the wide range of biochemical processes carried out by micro-organisms, differences in the capacities of micro-organisms to carry out those processes, and the number of factors influencing both, the idea that one single measurement would adequately represent the diversity of biochemical processes in soils would appear to be extraordinarily naive.

On a LOI basis, both first components and means of 14 smaplings for each plot show no significant correlations between phosphatase activity and cellulase activity. Phosphatase is significanatly correlated with oxygen uptake but cellulase is not. This means that any one of these activities cannot be taken as representative of the others. This conclusion is supported by the work of other authors. Studying enzymes extracted from coniferous leaf litter, Spalding (1977, 1980) found that cellulase activity was strongly correlated with mannase activity ($r = 0.93$), but less so with invertase ($r = 0.33$), β-glucosidase ($r = 0.37$) and polyphenoloxidase ($r = 0.29$).

Frankenberger and Dick (1983) found that none of 11 enzyme activities studied in A_1 horizon samples was significantly correlated with CO_2 evolution, but 10 of the enzyme activities were significantly correlated with oxygen uptake. None of the enzyme activities, or CO_2 evolution or oxygen uptake, was significantly correlated with soil pH, although several were significantly correlated with soil C, and 4 were significantly correlated with total N. Only one enzyme (urease) was significantly correlated with CEC and none was significantly correlated with clay content. In soils collected under mixed broadleaves, Voets et al (1975) found that phosphatase activity was not significantly correlated with saccharase, β - glucosidase, or urease activities. Some pairwise correlations of the other enzymes were significant, others were not.

However, statistical significance of a correlation coefficient means only that it is not zero. A statistically significant correlation coefficient may be associated with only a weak relationship. Thus, in the work of Spalding cited above, $r = 0.29$ was significant, but $r^2 = 0.084$ means that the bivariate relationship accounted for only a little over 8 percent of the variance, nothing to get excited about.

Other papers with similar results are Hankin et al (1974) and Ladd and Butler (1972).

In controlled experiments on the growth of bacteria and fungi on a soil with added glucose-sodium nitrate, Nannipieri et al (1979) concluded that no single measurement (CO_2 production, urease, phosphatase, or protease activities, amounts of amino acids and amino sugars) could be said to represent "bioactivity". Peak CO_2 evolution preceded those of the other criteria. Urease and phosphatase activities were significantly correlated with bacterial but not with fungal biomass. The other criteria were not correlated with biomass. The authors concluded that for a better understanding of the soil system, the use of only one or two criteria is too simplistic (see also Nannipieri et al 1978).

Furthermore, correlations between activities observed in one year may not be found in another (Hersman & Temple 1979).

None of the properties individually showed any tendency for the plots to fall into distinct groups. PCA's of the plot mean values, or the first component values, of all the properties taken together also failed to produce clear groups. However, using a priori groups based on (1) pH < 3.8, (2) pH 3.8-5.0, (3) pH >5.0, significant differences among means could be demonstrated. On a LOI basis oxygen uptake, cellulase and phosphatase activities were all distributed differently among the groups (Table 19), emphasizing the futility of trying to use any one measure as an "index of biological activity".

Variaton of the properties with sampling time can be looked at in two ways. The graphs of the mean values of the soils divided into acidic, intermediate, and base-rich groups (Figures 14-22) show various interesting features. Soils of the acidic group were wetter (coefficient of humidity) than those of the other two groups after sampling 5, i.e. from September to the following May. Oxygen uptake, cellulase and phosphatase activities were not obviously related to relative wetness. Cellulase (LOI basis) showed a peak at samplings 2 (June) and 6 to 9 (October to January). It is reasonable to suppose that the later peak follows litter-fall and also, possibly, death of roots as the mainly deciduous trees become dormant. Samplings 5 to 14 have large elements on the first eigenvector, and account for 92 percent of the variance in the first component, as against 71 percent if the eigenvector elements were all equal. Figure 20 shows a low cellulase activity at sampling 12, then an increase. The peak in June is difficult to explain.

The marked seasonal variation shown by phosphatase activity on OD basis becomes, on a LOI basis, a slow increase to a maximum in January (Figure 22). For soils with pH less than 3.8 there is also a peak at sampling 4 (August).

ACKNOWLEDGEMENTS

We thank Mr. C.B. Benefield for doing most of the sampling and for doing the colorimetric measurements of cellulase activity, Mr. J.K. Adamson for assisting with the sampling, and Dr. A.F. Harrison for the colorimetric determination of phosphatase activity. We are also grateful to Allan Nelson and Sarah Beattie of NERC Computing Service for help with producing the figures.

5. REFERENCES

BALL, D.F. & WILLIAMS, W.M. 1968. Variability of soil chemical properties in two uncultivated Brown Earths. J. Soil Sci., 19, 379-391.

BAUZON, D., PONGE, J.F. & DOMMERGUES, Y. 1974. Variations saisonnières des caractéristiques chimiques et biologiques des sols forestiers interprétées par l'analyse facorielle des correspondances. Rev. Ecol. & Biol. Sol, 11, 283-301.

BENEFIELD, C.B. 1971. A rapid method for measuring cellulase activity in soils. Soil Biol. & Biochem., 3, 325-329.

BENEFIELD, C.B., HOWARD, P.J.A. & HOWARD, D.M. 1977. The estimation of dehydrogenase activity in soil. Soil Biol. & Biochem., 9, 67-70.

BOCOCK, K.L., LINDLEY, D.K., GILL, C.A., ADAMSON, J.K. & WEBSTER, J.A. 1974. Harmonic analysis and synthesis: Basic principles of the technique and some applications to temperature data. Merlewood Research & Development Paper, No 54, 29 pp.

BOCOCK, K.L., BAILEY, A.D. & ADAMSON, J.K. 1977. The sucrose inversion method of measuring temperature and its application. Merlewood Research & Development Paper, No. 69, 26 pp.

BUNCE, R.G.H. 1969. Projects 100 and 102: Site classification and classification of Lake District woodlands. Merlewood Research & Development Paper, No 9, 16 pp.

CRUMP, W.B. 1913. The coefficient of humidity: a new method of expressing the soil moisture. New Phytol., 12, 125-147.

FOURT, D.F., DONALD, D.G.M., JEFFERS, J.N.R. & BINNS, W.O. 1971. Corsican pine (Pinus nigra var. maritima (Ait.) Melville) in southern Britain. Forestry, 44, 189-207.

FRANKENBERGER, W.T. & DICK, W.A. 1983. Relationships between enzyme activities and microbial growth and activity indices in soil. J. Soil Sci. Soc. Am., 47, 945-951.

FRANKLAND, J.C., OVINGTON, J.D. & MACRAE, C. 1963. Spatial and seasonal variations in soil, litter and ground vegetation in some Lake District woodlands. J. Ecol., 51, 97-112.

GOWER, J.C. & ROSS, G.J.S. 1969. Minimum spanning trees and single linkage cluster analysis. Appl. Statist. 18, 54-64.

HANKIN, L., SANDS, D.C. & HILL, D.E. 1974. Relation of land use to some degradative enzymatic activities of soil bacteria. Soil Sci., 118, 38-44.

HARRISON, A.F. & PEARCE, H.T. 1979. Seasonal variation of phosphatase activity in woodland soils. Soil Biol. & Biochem., 11, 405-410.

HERSMAN, L.E. & TEMPLE, K.L. 1979. Comparison of ATP, phosphatase, pectinolase and respiration as indicators of microbial activity in reclaimed coal strip mine spoils. Soil Sci., 127, 70-73.

HOFFMAN, G. 1967. Eine photometrische Methode zur Bestimmung der Phosphatase-Aktivität in Böden. Z. PflErnähr. Düng. Bodenk., 118, 161-172.

HOPE, K. 1968. Methods of multivariate analysis. Univ. London Press, 288 pp.

HOWARD, P.J.A. 1968. The use of Dixon and Gilson respirometers in soil and litter respiration studies. Merlewood Research & Development Paper, No. 5, 13 pp.

HOWARD, P.J.A., HORNUNG, M. & HOWARD, D.M. 1980. Recording soil profile descriptions for computer retrieval. Merlewood Research & Development Paper, No. 78, 47 pp.

JEFFERS, J.N.R. 1967. Two case-studies in the application of principal component analysis. Appl. Statist., 16, 225-236.

LADD, J.N. & BUTLER, J.H.A. 1972. Short-term assays of soil proteolytic enzyme activities using proteins and dipeptide derivatives as substrates. Soil Biol. & Biochem., 4, 19-30.

LENHARD, G. 1956. Die Dehydrogenaseaktivität des Bodens als Mass fur die Mikroorganismentätigkeit im Boden. Z. PflErnähr. Düng., 73, 1-11.

NANNIPIERI, P., JOHNSON, R.L. & PAUL, E.A. 1978. Criteria for measurement of microbial growth and activity in soil. Soil Biol. & Biochem., 10, 223-229.

NANNIPIERI, P., PEDRAZZINI, F., ARCARA, P.G. & PIOVANELLI, C. 1979. Changes in amino acids, enzyme activities, and biomasses during soil microbial growth. Soil Sci., 127, 26-34.

PEARSALL, W.H. 1938. The soil complex in relation to plant communities. II. Characteristic woodland soils. J. Ecol., 26, 194-209.

PEARSALL, W.H. 1952. The pH of natural soils and its ecological significance. J. Soil Sci., 3, 41-51.

PEARSALL, W.H. & PENNINGTON, W. 1973. The Lake District. London: Collins, 320 pp.

PYATETSKIY, G.Y. 1976. Wilting moisture produced by the properties of peat soils. Sov. Soil Sci., 8, 213-218.

RAO, C.R. 1964. The use and interpretation of principal component analysis in applied research. Sanhkya Ser. A, 26, 329-358.

SEAL, H.L. 1968. Multivariate statistical analysis for biologists. London: Methuen, 209 pp.

SPALDING, B.P. 1977. Enzymatic activities related to the decomposition of coniferous leaf litter. J. Soil Sci. Soc. Am., 41 622-627.

SPALDING, B.P. 1980. Enzymatic activities in coniferous leaf litter. J. Soil Sci. Soc. Am., 44, 760-764.

UMBREIT, W.W., BURRIS, R.H. & STAUFFER, J.F. 1964. Manometric techniques. USA: Burgess Publ. Co., 4th edition, 305 pp.

VOETS, J.P., AGRIANTO, G. & VERSTRAETE, W. 1975. Etude ecologique des activites microbiologiques et enzymatiques de sols dans une foret de feuillus. Rev. Ecol. & Biol. Sol, 12, 543-555.

WESTHOFF, V. 1970. New criteria for nature reserves. New Scientist, 46 (697), 108-113.

Table 1. pH, mean and coefficient of variation of 14 samplings for each plot.

Plot No.	Wood name		Mean pH	CV %
48	Meathop Wood	(L)	6.4	9
44	Eaves Wood	(L)	5.7	5
24	Routing Gill		5.7	3
27	Low Wood, Elterwater		5.6	8
42	Arnside Knott	(L)	5.6	6
45	Nichols Wood	(L)	5.4	7
19	Honeybee Wood	(L)	5.3	8
43	Roudsea Wood		4.9	10
23	Low Wood, Hartsop		4.8	3
25	Wetsleddale		4.5	3
22	Martindale		4.5	3
38	Castle Head		4.5	2
7	Low Eskholme		4.4	7
18	Durham Bridge	(L)	4.4	4
13	Tower Wood,		4.4	3
49	Hall Wood, Kentmere		4.4	4
36	Overside		4.3	4
21	Barton Park		4.3	4
26	Bowers Wood		4.3	4
9	Church Stile		4.2	4
16	Lamb Howe		4.2	2
31	Great Knott		4.1	3
34	Thwaite Head		4.1	7
17	Low Fell		4.1	3
47	Roeburndale Forest		4.1	4
39	Crag Houses		4.0	5
8	Side End		4.0	4
20	Addyfield		4.0	3
1	Duddon Bridge		4.0	3
3	Nibthwaite		4.0	4
4	Throughton Hall		4.0	4
32	Intake, Skelwith		3.9	3
29	High Bowkerstead		3.9	4
35	Stonethwaite Fell		3.8	7
33	Town End		3.8	5
12	Elleray		3.8	6
11	High Wood		3.7	5
30	Elder Coppice		3.6	3
37	Low Hows		3.6	3
15	Birks Brow		3.6	6
2	Wall End		3.6	5
46	Low Wood, Haverthwaite		3.6	13
5	Undercrag		3.5	3
10	Stang Ends		3.4	5
14	N of Seatle		3.4	3
40	Scales Wood		3.4	3
28	Tarn Hows		3.3	5
6	Torver Common		3.3	5

(L) on Carboniferous Limestone

Table 2. Loss-on-ignition (% OD), mean and coefficient of variation of 14 samplings for each plot.

Plot No.	Wood name		Mean LOI % OD	CV %
28	Tarn Hows		63.6	26
11	High Wood		52.0	24
14	N of Seatle		50.9	29
13	Tower Wood		49.2	23
6	Torver Common		48.0	12
37	Low Hows		46.3	9
30	Elder Coppice		42.3	28
46	Low Wood, Haverthwaite		41.2	42
35	Stonethwaite Fell		40.0	37
15	Birks Brow		37.1	25
39	Crag Houses		35.9	36
40	Scales Wood		34.3	24
2	Wall End		34.2	12
34	Thwaite Head		33.7	19
5	Undercrag		33.3	28
10	Stang Ends		31.8	29
4	Throughton Hall		30.6	21
25	Wetsleddale		29.1	15
12	Elleray		28.9	20
3	Nibthwaite		28.6	29
8	Side End		27.6	21
33	Town End		26.8	22
29	High Bowkerstead		26.7	27
20	Addyfield		26.1	14
7	Low Eskholme		24.5	28
45	Nichols Wood	(L)	23.9	18
16	Lamb Howe		23.8	10
17	Low Fell		23.4	16
31	Great Knott		22.9	11
27	Low Wood, Elterwater		21.0	20
36	Overside		20.0	14
43	Roudsea Wood		20.0	24
32	Intake, Skelwith		19.9	25
21	Barton Park		19.7	14
1	Duddon Bridge		19.7	7
9	Church Stile		19.3	26
24	Routing Gill		18.9	24
48	Meathop Wood	(L)	18.7	14
42	Arnside Knott	(L)	18.5	8
18	Durham Bridge	(L)	18.1	9
23	Low Wood, Hartsop		16.9	11
38	Castle Head		16.7	11
49	Hall Wood, Kentmere		16.4	17
19	Honeybee Wood	(L)	13.6	7
44	Eaves Wood	(L)	13.5	7
26	Bowers Wood		13.0	16
22	Martindale		12.8	7
47	Roeburndale Forest		11.6	12

(L) on Carboniferous Limestone

Table 3. Moisture content (% OD), mean and coefficient of variation of 14 samplings for each plot.

Plot No.	Wood name		Mean moisture content % OD	CV %
28	Tarn Hows		329.2	28
11	High Wood		240.2	29
37	Low Hows		216.3	8
13	Tower Wood		215.2	24
14	N of Seatle		212.7	29
27	Low Wood, Elterwater		208.5	29
6	Torver Common		201.5	14
40	Scales Wood		191.6	24
30	Elder Coppice		170.6	30
46	Low Wood, Haverthwaite		165.5	45
24	Routing Gill		163.3	52
10	Stang Ends		150.4	28
5	Undercrag		144.6	24
15	Birks Brow		142.9	27
4	Throughton Hall		138.9	25
35	Stonethwaite Fell		134.0	28
3	Nibthwaite		126.7	30
39	Crag Houses		120.8	48
34	Thwaite Head		120.8	31
7	Low Eskholme		119.7	29
33	Town End		118.6	20
2	Wall End		117.4	17
12	Elleray		117.0	38
8	Side End		116.2	28
31	Great Knott		114.7	10
29	High Bowkerstead		113.4	32
20	Addyfield		113.1	14
25	Wetsleddale		100.5	30
43	Roudsea Wood		98.9	24
1	Duddon Bridge		98.3	22
16	Lamb Howe		97.9	17
32	Intake, Skelwith		96.4	20
21	Barton Park		88.1	23
9	Church Stile		83.4	26
36	Overside		76.6	21
49	Hall Wood, Kentmere		76.1	12
18	Durham Bridge	(L)	75.8	18
23	Low Wood, Hartsop		71.5	17
45	Nichols Wood	(L)	71.3	26
48	Meathop Wood	(L)	68.5	18
17	Low Fell		65.3	34
47	Roeburndale Forest		64.1	13
26	Bowers Wood		58.2	22
19	Honeybee Wood	(L)	57.8	18
38	Castle Head		54.9	21
42	Arnside Knott	(L)	54.2	13
44	Eaves Wood	(L)	51.0	18
22	Martindale		41.6	21

(L) on Carboniferous Limestone

Table 4. Coefficient of humidity, mean and coefficient of variation of 14 samplings for each site.

Plot No	Wood name		Mean coefficient of humidity	CV %
27	Low Wood, Elterwater		9.9	15
24	Routing Gill		8.2	34
40	Scales Wood		5.6	8
47	Roeburndale Forest		5.5	6
28	Tarn Hows		5.2	10
31	Great Knott		5.0	9
1	Duddon Bridge		5.0	24
7	Low Eskholme		5.0	28
43	Roudsea Wood		5.0	11
32	Intake, Skelwith		4.9	8
10	Stang Ends		4.8	9
49	Hall Wood, Kentmere		4.7	14
37	Low Hows		4.7	5
11	High Wood		4.6	8
4	Throughton Hall		4.5	17
26	Bowers Wood		4.5	19
33	Town End		4.5	9
21	Barton Park		4.5	16
3	Nibthwaite		4.5	10
13	Tower Wood		4.4	10
5	Undercrag		4.4	8
9	Church Stile		4.4	14
20	Addyfield		4.4	12
19	Honeybee Wood	(L)	4.3	18
29	High Bowkerstead		4.2	15
14	N of Seatle		4.2	14
23	Low Wood, Hartsop		4.2	12
6	Torver Common		4.2	14
18	Durham Bridge	(L)	4.2	16
8	Side End		4.2	16
16	Lamb Howe		4.1	17
12	Elleray		4.1	29
30	Elder Coppice		4.0	8
46	Low Wood, Haverthwaite		4.0	11
15	Birks Brow		3.9	17
36	Overside		3.8	15
44	Eaves Wood	(L)	3.8	18
48	Meathop Wood	(L)	3.7	15
34	Thwaite Head		3.6	25
35	Stonethwaite Fell		3.5	16
25	Wetsleddale		3.4	20
2	Wall End		3.4	10
39	Crag Houses		3.3	19
38	Castle Head		3.3	20
22	Martindale		3.3	25
45	Nichols Wood	(L)	3.0	25
42	Arnside Knott	(L)	2.9	13
17	Low Fell		2.9	39

(L) on Carboniferous Limestone

Table 5. Oxygen uptake (μ l/g OD/h), mean and coefficient of variation of 14 samplings for each plot.

Plot No.	Wood name		Mean oxygen uptake	CV %
13	Tower Wood		12.4	38
28	Tarn Hows		11.6	36
37	Low Hows		11.1	18
30	Elder Coppice		10.7	40
35	Stonethwaite Fell		10.0	45
6	Torver Common		9.6	24
39	Crag Houses		9.2	54
11	High Wood		9.1	28
3	Nibthwaite		8.6	54
8	Side End		8.1	40
4	Throughton Hall		7.8	42
14	N of Seatle		7.8	43
34	Thwaite Head		7.8	27
5	Undercrag		7.7	29
46	Low Wood, Haverthwaite		7.4	59
15	Birks Brow		7.4	31
25	Wetsleddale		7.1	58
33	Town End		7.1	35
29	High Bowkerstead		7.1	38
40	Scales Wood		6.8	33
12	Elleray		6.6	26
20	Addyfield		6.6	32
24	Routing Gill		6.6	31
45	Nichols Wood	(L)	6.1	34
9	Church Stile		6.0	44
18	Durham Bridge	(L)	5.9	28
16	Lamb Howe		5.9	27
7	Low Eskholme		5.7	44
36	Overside		5.4	37
21	Barton Park		5.4	43
48	Meathop Wood	(L)	5.1	23
31	Great Knott		5.1	21
10	Stang Ends		5.1	32
2	Wall End		4.9	32
17	Low Fell		4.4	47
43	Roudsea Wood		4.4	28
32	Intake, Skelwith		4.1	39
1	Duddon Bridge		4.0	34
49	Hall Wood, Kentmere		3.7	29
44	Eaves Wood	(L)	3.6	28
47	Roeburndale Forest		3.1	39
42	Arnside Knott	(L)	3.0	18
23	Low Wood, Hartsop		3.0	43
26	Bowers Wood		2.9	41
38	Castle Head		2.7	34
19	Honeybee Wood	(L)	2.7	17
27	Low Wood, Elterwater		2.6	71
22	Martindale		2.4	27

(L) on Carboniferous Limestone

Table 6. Oxygen uptake (µl/g LOI/h), mean and coefficient of variation of 14 samplings for each plot.

Plot No.	Wood name		Mean oxygen uptake	CV %
24	Routing Gill		35.3	35
18	Durham Bridge	(L)	32.3	28
9	Church Stile		30.0	28
3	Nibthwaite		28.9	24
8	Side End		28.7	18
48	Meathop Wood	(L)	27.6	19
44	Eaves Wood	(L)	27.1	21
21	Barton Park		26.3	29
33	Town End		26.3	18
36	Overside		26.1	26
45	Nichols Wood	(L)	25.6	27
47	Roeburndale Forest		25.6	27
39	Crag Houses		25.2	29
29	High Bowkerstead		25.2	22
4	Throughton Hall		25.1	27
20	Addyfield		25.0	27
13	Tower Wood		24.9	26
30	Elder Coppice		24.8	14
35	Stonethwaite Fell		24.6	23
16	Lamb Howe		24.6	20
37	Low Hows		24.1	13
34	Thwaite Head		23.5	19
25	Wetsleddale		23.4	43
5	Undercrag		23.1	16
12	Elleray		23.1	21
7	Low Eskholme		22.9	33
26	Bowers Wood		22.6	28
31	Great Knott		22.5	13
43	Roudsea Wood		22.4	14
49	Hall Wood, Kentmere		21.9	17
19	Honeybee Wood	(L)	20.4	14
6	Torver Common		20.3	24
1	Duddon Bridge		20.2	31
15	Birks Brow		19.9	13
32	Intake, Skelwith		19.7	25
22	Martindale		19.5	22
17	Low Fell		19.2	47
40	Scales Wood		19.1	15
28	Tarn Hows		18.6	24
46	Low Wood, Haverthwaite		17.6	23
11	High Wood		17.5	17
23	Low Wood, Hartsop		17.4	30
38	Castle Head		16.4	22
42	Arnside Knott	(L)	16.0	18
10	Stang Ends		15.9	20
14	N of Seatle		14.9	29
2	Wall End		13.8	26
27	Low Wood, Elterwater		13.1	68

(L) on Carboniferous Limestone

Table 7. Cellulase activity (mg glucose/g OD/48h), mean and coefficient of variation of 14 samplings for each plot.

Plot No.	Wood name		Mean glucose mg	CV %
28	Tarn Hows		0.0768	60
37	Low Hows		0.0661	75
13	Tower Wood		0.0637	64
6	Torver Common		0.0604	86
30	Elder Coppice		0.0549	49
48	Meathop Wood	(L)	0.0546	57
2	Wall End		0.0544	54
19	Honeybee Wood	(L)	0.0528	44
46	Low Wood, Haverthwaite		0.0500	66
26	Bowers Wood		0.0458	44
39	Crag Houses		0.0455	54
18	Durham Bridge	(L)	0.0432	44
34	Thwaite Head		0.0429	67
43	Roudsea Wood		0.0411	88
24	Routing Gill		0.0407	72
4	Throughton Hall		0.0391	37
40	Scales Wood		0.0387	35
35	Stonethwaite Fell		0.0385	98
5	Undercrag		0.0370	55
3	Nibthwaite		0.0363	77
29	High Bowkerstead		0.0362	73
14	N of Seatle		0.0341	40
45	Nichols Wood	(L)	0.0340	47
47	Roeburndale Forest		0.0328	38
9	Church Stile		0.0307	60
15	Birks Brow		0.0302	91
27	Low Wood, Elterwater		0.0299	90
38	Castle Head		0.0296	66
7	Low Eskholme		0.0268	79
33	Town End		0.0249	70
25	Wetsleddale		0.0243	42
23	Low Wood, Hartsop		0.0242	63
42	Arnside Knott	(L)	0.0240	63
11	High Wood		0.0239	64
12	Elleray		0.0234	91
16	Lamb Howe		0.0232	58
10	Stang Ends		0.0221	73
8	Side End		0.0215	61
1	Duddon Bridge		0.0208	55
31	Great Knott		0.0202	42
17	Low Fell		0.0200	84
32	Intake, Skelwith		0.0197	49
21	Barton Park		0.0192	56
36	Overside		0.0186	35
20	Addyfield		0.0168	86
44	Eaves Wood	(L)	0.0163	28
49	Hall Wood, Kentmere		0.0140	82
22	Martindale		0.0103	36

(L) on Carboniferous Limestone

Table 8. Cellulase activity (mg glucose/g LOI/48h), mean and coefficient of variation of 14 samplings for each plot.

Plot No.	Wood name		Mean glucose mg	CV %
19	Honeybee Wood	(L)	0.3857	42
26	Bowers Wood		0.3671	49
48	Meathop Wood	(L)	0.2994	57
47	Roeburndale Forest		0.2803	36
18	Durham Bridge	(L)	0.2402	43
24	Routing Gill		0.2270	87
43	Roudsea Wood		0.2067	92
38	Castle Head		0.1786	64
9	Church Stile		0.1759	85
2	Wall End		0.1589	50
45	Nichols Wood	(L)	0.1502	48
23	Low Wood, Hartsop		0.1468	67
29	High Bowkerstead		0.1409	74
37	Low Hows		0.1389	73
3	Nibthwaite		0.1368	79
27	Low Wood, Elterwater		0.1352	73
39	Crag Houses		0.1318	52
34	Thwaite Head		0.1313	67
6	Torver Common		0.1305	87
30	Elder Coppice		0.1301	38
42	Arnside Knott	(L)	0.1295	59
4	Throughton Hall		0.1293	36
46	Low Wood, Haverthwaite		0.1278	65
13	Tower Wood		0.1263	57
28	Tarn Hows		0.1216	53
44	Eaves Wood	(L)	0.1210	28
5	Undercrag		0.1175	63
7	Low Eskholme		0.1160	85
40	Scales Wood		0.1154	34
1	Duddon Bridge		0.1052	52
21	Barton Park		0.1019	67
35	Stonethwaite Fell		0.0991	70
32	Intake, Skelwith		0.0974	41
16	Lamb Howe		0.0963	53
36	Overside		0.0959	44
31	Great Knott		0.0898	43
17	Low Fell		0.0874	83
33	Town End		0.0872	60
49	Hall Wood, Kentmere		0.0858	75
25	Wetsleddale		0.0857	44
22	Martindale		0.0819	39
8	Side End		0.0802	62
12	Elleray		0.0793	80
10	Stang Ends		0.0775	80
15	Birks Brow		0.0759	61
14	N of Seatle		0.0693	35
20	Addyfield		0.0641	76
11	High Wood		0.0471	56

(L) on Carboniferous Limestone

Table 9. Phosphatase activity (µg phenol liberated/g OD/3h), mean and coefficient of variation of 14 samplings for each plot.

Plot No.	Wood name		Mean phenol µg	CV %
13	Tower Wood		2331	28
28	Tarn Hows		2180	39
37	Low Hows		1835	30
6	Torver Common		1667	36
46	Low Wood, Haverthwaite		1621	76
3	Nibthwaite		1535	36
35	Stonethwaite Fell		1468	33
11	High Wood		1436	32
30	Elder Coppice		1384	54
18	Durham Bridge	(L)	1303	24
8	Side End		1236	33
34	Thwaite Head		1236	29
15	Birks Brow		1233	35
40	Scales Wood		1182	29
4	Throughton Hall		1176	40
39	Crag Houses		1111	42
25	Wetsleddale		1088	33
29	High Bowkerstead		1048	33
33	Town End		1008	58
9	Church Stile		1006	30
7	Low Eskholme		997	33
5	Undercrag		949	20
16	Lamb Howe		918	24
45	Nichols Wood	(L)	916	24
20	Addyfield		860	30
12	Elleray		834	39
10	Stang Ends		814	26
49	Hall Wood, Kentmere		811	41
24	Routing Gill		811	37
14	N of Seatle		804	50
21	Barton Park		794	32
43	Roudsea Wood		782	27
27	Low Wood, Elterwater		781	35
17	Low Fell		765	42
31	Great Knott		759	29
32	Intake, Skelwith		751	47
42	Arnside Knott	(L)	680	31
23	Low Wood, Hartsop		649	31
36	Overside		637	28
38	Castle Head		616	24
48	Meathop Wood	(L)	615	31
44	Eaves Wood	(L)	590	29
1	Duddon Bridge		582	28
2	Wall End		559	41
26	Bowers Wood		556	31
47	Roeburndale Forest		542	56
22	Martindale		424	22
19	Honeybee Wood	(L)	402	33

(L) on Carboniferous Limestone

Table 10. Phosphatase activity (µg phenol liberated/g LOI/3h), mean and coefficient of variation of 14 samplings for each plot.

Plot No.	Wood name		Mean phenol µg	CV %
18	Durham Bridge	(L)	7239	24
3	Nibthwaite		5405	22
9	Church Stile		5257	20
49	Hall Wood, Kentmere		4813	27
13	Tower Wood		4761	16
47	Roeburndale Forest		4523	42
8	Side End		4507	29
44	Eaves Wood	(L)	4390	29
26	Bowers Wood		4337	32
24	Routing Gill		4271	27
7	Low Eskholme		4154	27
21	Barton Park		3976	22
37	Low Hows		3967	29
29	High Bowkerstead		3967	21
43	Roudsea Wood		3936	19
45	Nichols Wood	(L)	3876	24
16	Lamb Howe		3847	19
4	Throughton Hall		3814	32
23	Low Wood, Hartsop		3806	24
42	Arnside Knott	(L)	3749	35
35	Stonethwaite Fell		3736	16
32	Intake, Skelwith		3722	36
38	Castle Head		3712	23
25	Wetsleddale		3694	26
27	Low Wood, Elterwater		3634	18
34	Thwaite Head		3624	19
33	Town End		3605	38
46	Low Wood, Haverthwaite		3585	43
6	Torver Common		3531	37
28	Tarn Hows		3506	31
40	Scales Wood		3483	23
48	Meathop Wood	(L)	3404	38
15	Birks Brow		3394	35
22	Martindale		3334	25
17	Low Fell		3327	45
31	Great Knott		3294	25
20	Addyfield		3267	23
36	Overside		3150	20
30	Elder Coppice		3137	30
39	Crag Houses		3122	25
19	Honeybee Wood	(L)	2975	35
5	Undercrag		2949	22
1	Duddon Bridge		2947	26
12	Elleray		2844	29
11	High Wood		2770	20
10	Stang Ends		2723	39
2	Wall End		1614	36
14	N of Seatle		1566	33

(L) on Carboniferous Limestone

Table 11. Correlations between mean values of 14 samplings and first component values for the 48 plots.

Variable	Correlation coefficient	Percentage of variance in first component
pH	1.000	91.6
LOI	1.000	77.4
OD basis		
Moisture content	0.999	75.3
Oxygen uptake	0.999	55.8
Cellulase	0.955	38.4
Phosphatase	0.995	59.3
LOI basis		
Coeff. of humidity	1.000	77.7
Oxygen uptake	0.997	44.3
Cellulase	0.986	50.6
Phosphatase	0.999	57.8

Table 12. Correlation half-matrix for the first component values of pH, loss-on-ignition, moisture content, oxygen uptake, cellulase and phosphatase, OD basis.

	pH	LOI	Moisture	O_2 Uptake	Cellulase
pH	1				
LOI	-.612***	1			
Moisture content	-.463***	.878***	1		
Oxygen uptake	-.497***	.866***	.733***	1	
Cellulase	-.070	.466***	.452**	.436**	1
Phosphatase	-.421**	.794***	.729***	.898***	.440**

Table 13. Eigenvalues and eigenvectors for the first two components of the correlation matrix in Table 12.

	Component 1	2
Eigenvalues	4.05	0.94
Percentage of variance	67.6	15.6
Cumulative percentage	67.6	83.2
Eigenvectors		
pH	0.30	-0.67*
Loss-on-ignition	-0.48*	0.08
Moisture content	-0.44*	-0.03
Oxygen uptake	-0.46*	0.01
Cellulase	-0.27	-0.74*
Phosphatase	-0.45*	-0.06

*Eigenvector element greater than 0.75 times the largest (absolute) element.

Table 14. Correlation half-matrix for the first component values of pH, moisture content (coefficient of humidity), oxygen uptake, cellulase and phosphatase, LOI basis.

	pH	Humidity	O_2 Uptake	Cellulase
pH	1			
Humidity	0.168	1		
Oxygen uptake	.230	.042	1	
Cellulase	.439**	.107	.201	1
Phosphatase	.259	.115	.616***	.249

Table 15. Eigenvalues and eigenvectors for the first three components of the correlation matrix in Table 14.

	Component 1	2	3
Eigenvalues	2.05	1.10	0.92
Percentage of variance	41.0	21.9	18.4
Cumulative percentage	41.0	62.9	81.3
Eigenvectors			
pH	-0.46*	0.43	0.27
Humidity	-0.20	0.49*	-0.84*
Oxygen uptake	-0.51*	-0.50*	-0.11
Cellulase	-0.44*	0.41	0.43
Phosphatase	-0.54*	-0.40	-0.17

*Eigenvector element greater than 0.75 times the largest (absolute) element.

Table 16. Analysis of variance of the first component values of pH, LOI, moisture content, oxygen uptake, cellulase and phosphatase (OD and LOI basis) for limestone and non-limestone plots.

pH	Limestone ≠ Non-Limestone	$p < 0.001$
<u>OD basis</u>		
LOI	Limestone ≠ Non-limestone	$p < 0.05$
Moisture content	Limestone ≠ Non-limestone	$p < 0.001$
Oxygen uptake	Not significant	
Cellulase	Not significant	
Phosphatase	Not significant	
<u>LOI basis</u>		
Coeff. of humidity	Not significant	
Oxygen uptake	Not significant	
Cellulase	Limestone ≠ Non-limestone	$p < 0.001$
Phosphatase	Not significant	

First component values have arbitrary signs, so whether limestone sites have values greater or less than those of non-limestone sites has no meaning.

Table 17. Analysis of variance of the plot mean values for pH, LOI, moisture content, oxygen uptake, cellulase, and phosphatase (OD and LOI basis) for limestone and non-limestone plots.

	Mean for Limestone	Mean for Non-limestone	Difference ± SE	
pH	5.5	4.1	1.4 ± 0.24	L > N***
OD basis				
LOI	18	29	11 ± 5	L < N*
Moisture content	63	131	68 ± 24	L < N**
Oxygen uptake	4.4	6.6	2.2 ± 1.1	NS
Cellulase	0.037	0.034	0.003 ± 0.007	NS
Phosphatase	751	1042	291 ± 185	NS
LOI basis				
Coeff. of humidity	3.6	4.5	0.9 ± 0.5	NS
Oxygen uptake	25	22	3 ± 2	NS
Cellulase	0.221	0.126	0.09 ± 0.029	L > N**
Phosphatase	4272	3633	639 ± 387	NS

NS Not significant
* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

L = Limestone plots
N = Non-limestone plots

Table 18. Analysis of variance of the first component values of LOI, moisture content, oxygen uptake, cellulase, and phosphatase (OD and LOI basis). Plots divided into 3 groups on the basis of mean pH over 14 samplings.

1st component values of	Mean values in range pH < 3.8 (A)	3.8-5.0 (I)	pH > 5 (B)	Significant difference (Tukey's HSD)
Output	-1.34	0.45	0.96	A≠I**; A≠B**
Input (OD basis)				
LOI	3.46	-1.11	-2.66	A≠I***; A≠B***
Moisture content	3.11	-1.26	-1.35	A≠I***; A≠B**
Oxygen uptake	1.93	-0.44	-2.17	A≠I* ; A≠B**
Cellulase	1.15	-0.73	0.51	A≠I*
Phosphatase	1.50	-0.23	-2.12	A≠B*
Input (LOI basis)				
Coeff. of humidity	-0.06	-0.49	2.00	NS
Oxygen uptake	-1.32	0.53	0.61	NS
Cellulase	-1.00	-0.13	2.49	A≠B*; I≠B*
Phosphatase	-2.12	1.06	0.14	A≠I**

Signs are arbitrary for component values, so < or > is not appropriate.

No of sites in A = 14
I = 27
B = 7

NS Not significant
* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

Table 19. Analysis of variance of the plot mean values for LOI, moisture content, oxygen uptake, cellulase, and phosphatase (OD and LOI basis). Plots divided into 3 groups on the basis of mean pH over 14 samplings.

Variables	Mean values in range pH < 3.8 (A)	3.8 - 5.0 (I)	pH > 5.0 (B)	Significant difference (Tukey's HSD)
OD basis				
Loss-on-ignition	40.8	23.9	18.3	A > I***; A > B***
Moisture content	180	99.3	96.4	A > I***; A > B**
Oxygen uptake	8.1	5.9	4.3	A > I* ; A > B**
Cellulase	0.043	0.030	0.036	A > I*
Phosphatase	1250	962	685	A > B*
LOI basis				
Coeff. of humidity	4.4	4.2	5.1	NS
Oxygen uptake	19.9	23.8	23.6	A < I*
Cellulase	0.106	0.136	0.207	A < B**; I < B*
Phosphatase	3048	4047	3757	A < I**

No. of sites in A = 14
I = 27
B = 7

NS Not significant
* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

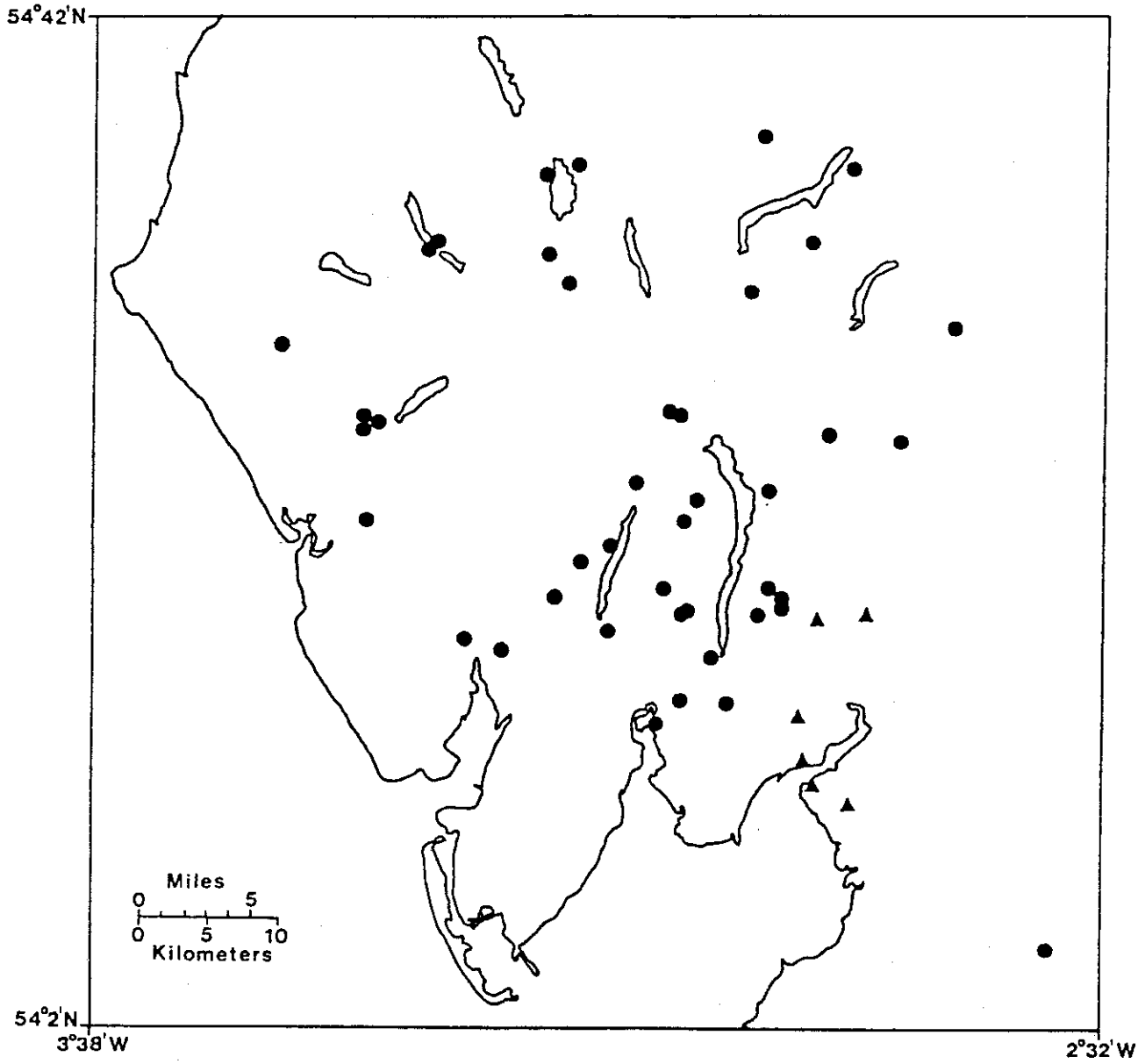

Figure 1. Map showing the locations of the 48 sampling sites.

●Sites on acidic rocks ▲Sites on Carboniferous Limestone.

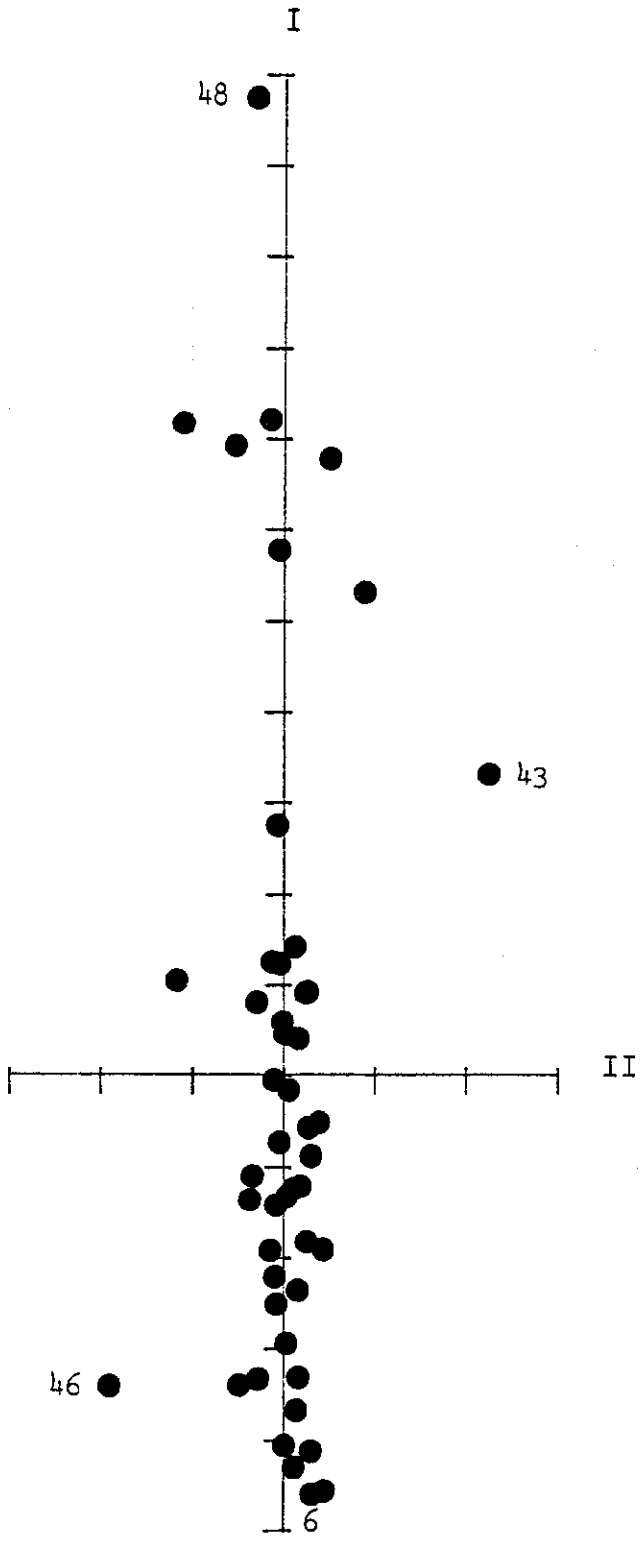

Figure 2. First and second component values of pH.

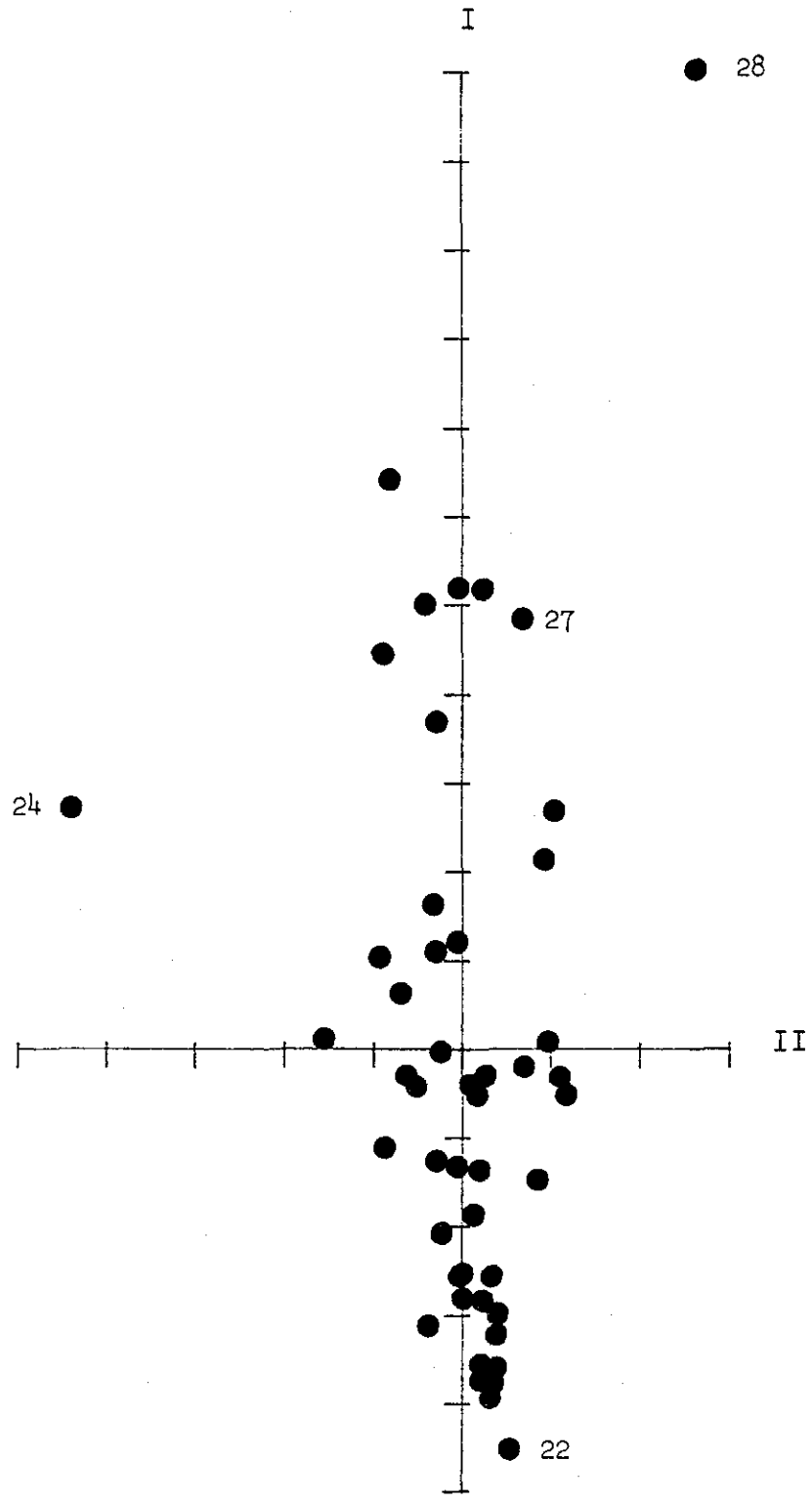

Figure 3. First and second component values of moisture content (OD basis).

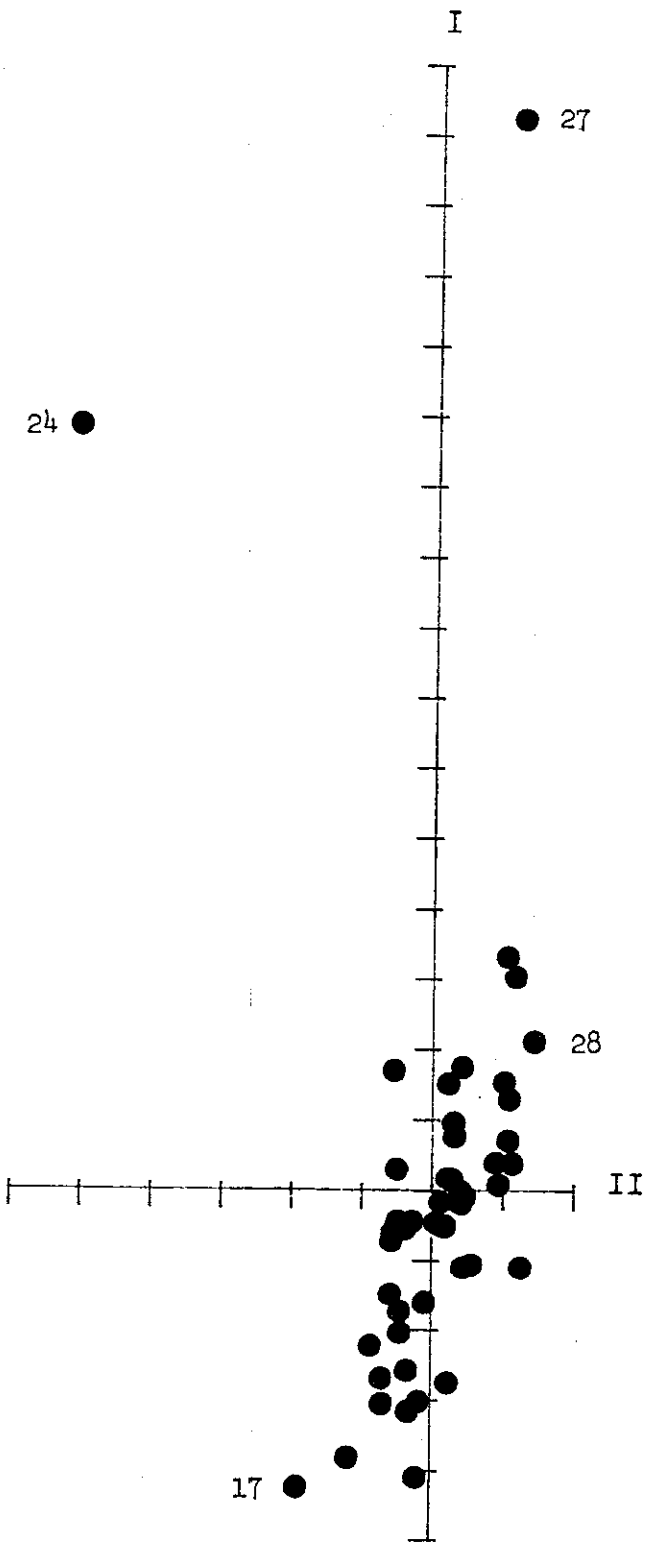

Figure 4. First and second component values of coefficient of humidity (moisture content/g LOI).

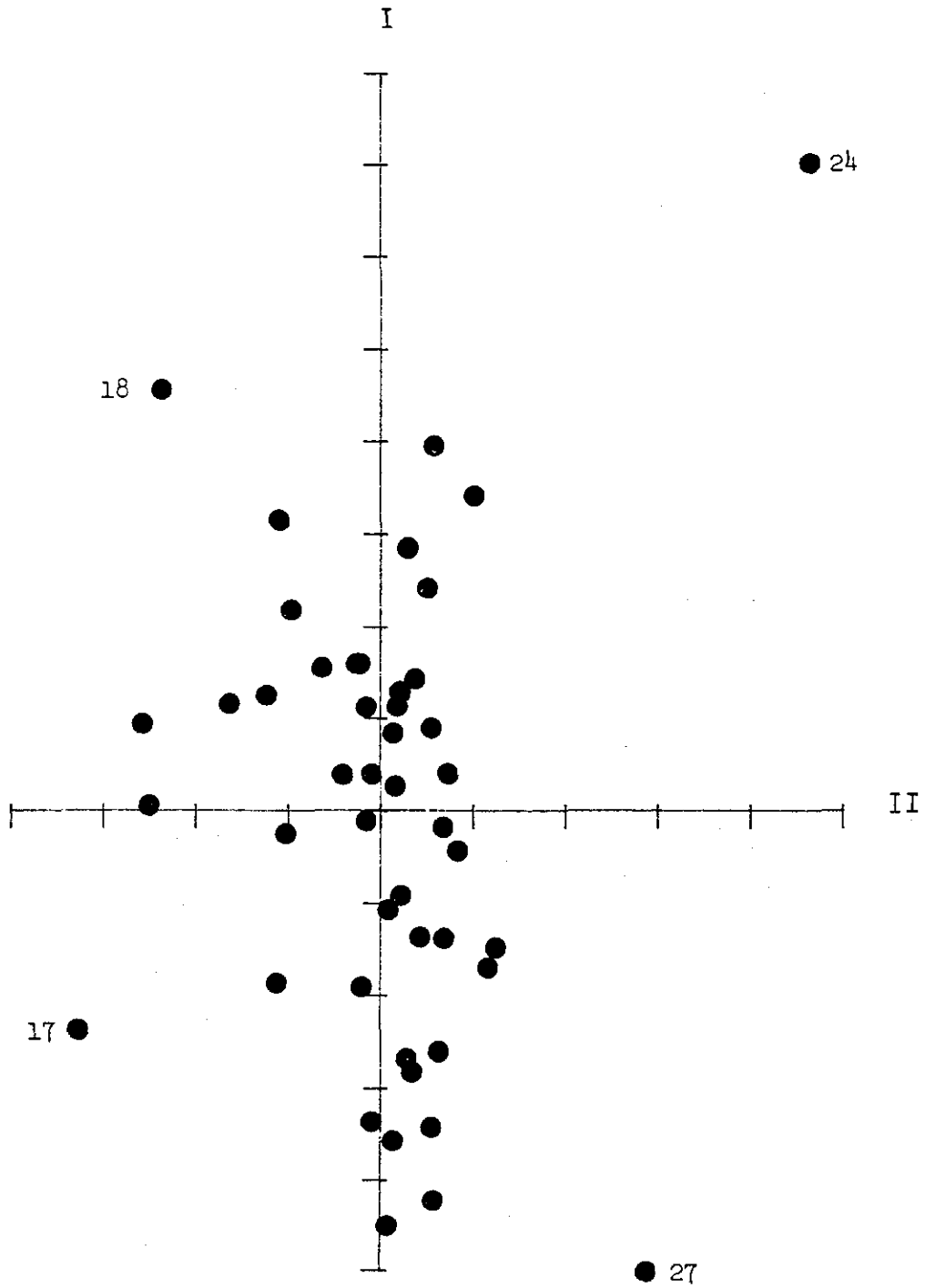

Figure 5. First and second component values of oxygen uptake (LOI basis).

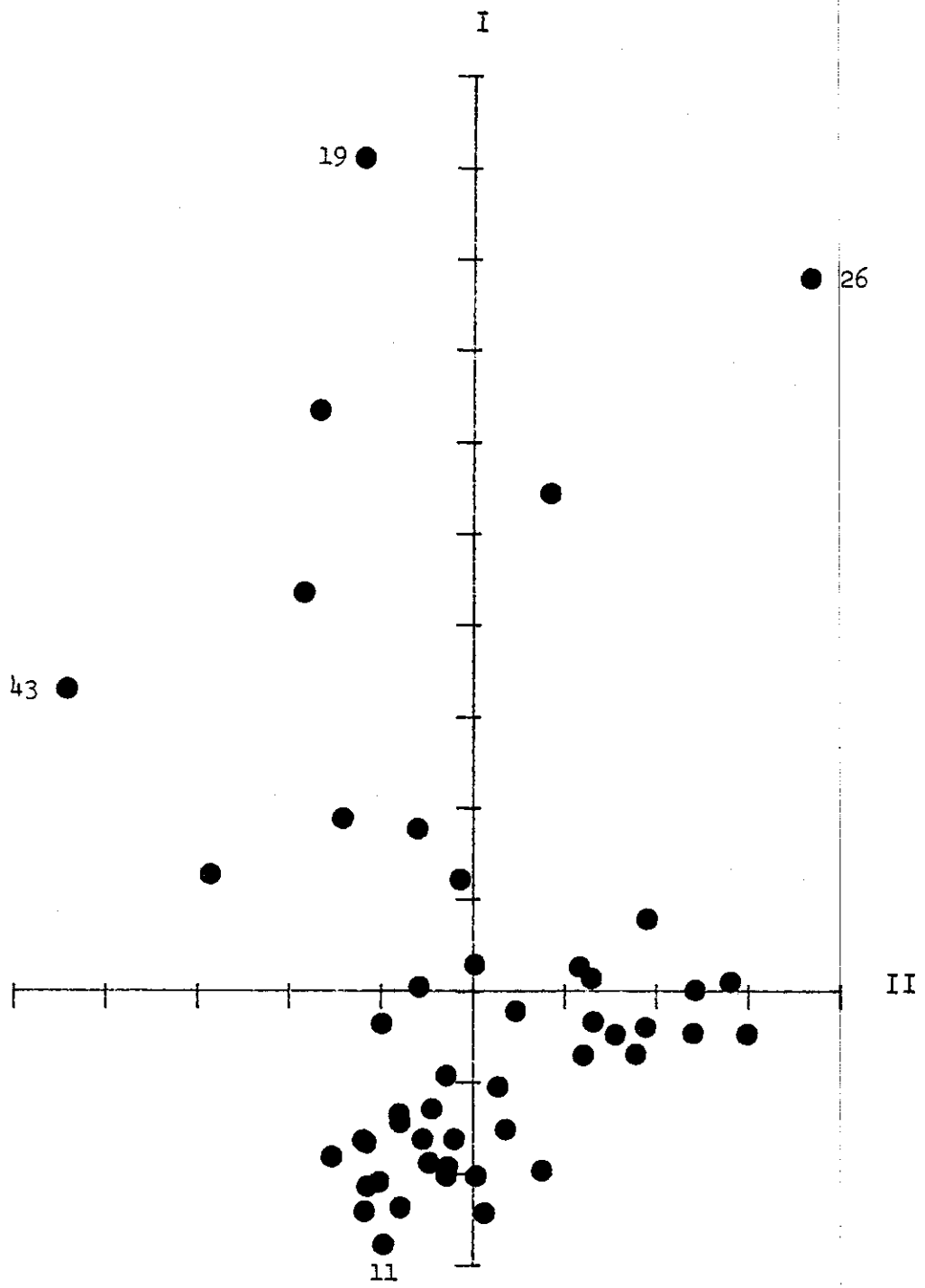

Figure 6. First and second component values for cellulase activity (LOI basis).

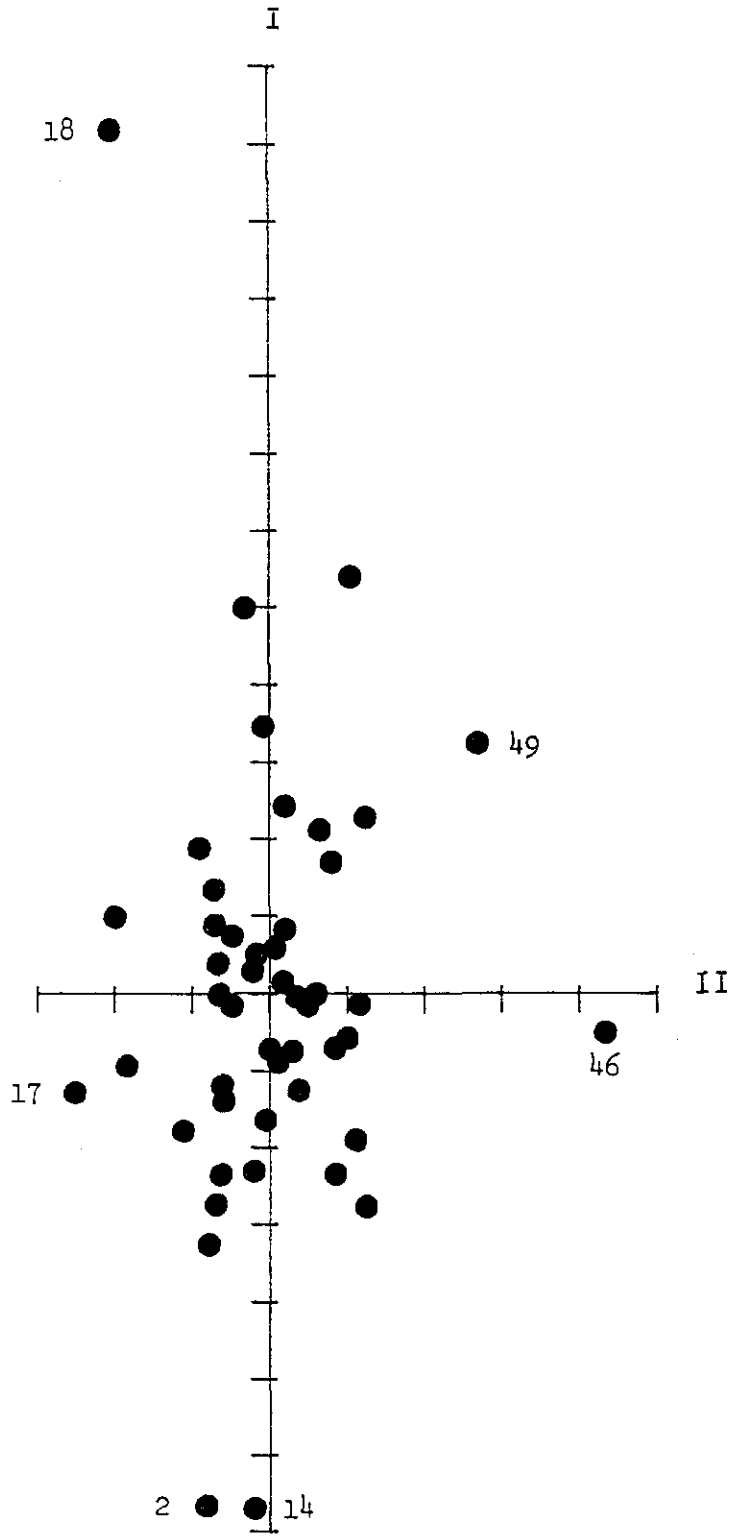

Figure 7. First and second component values for phosphatase (LOI basis).

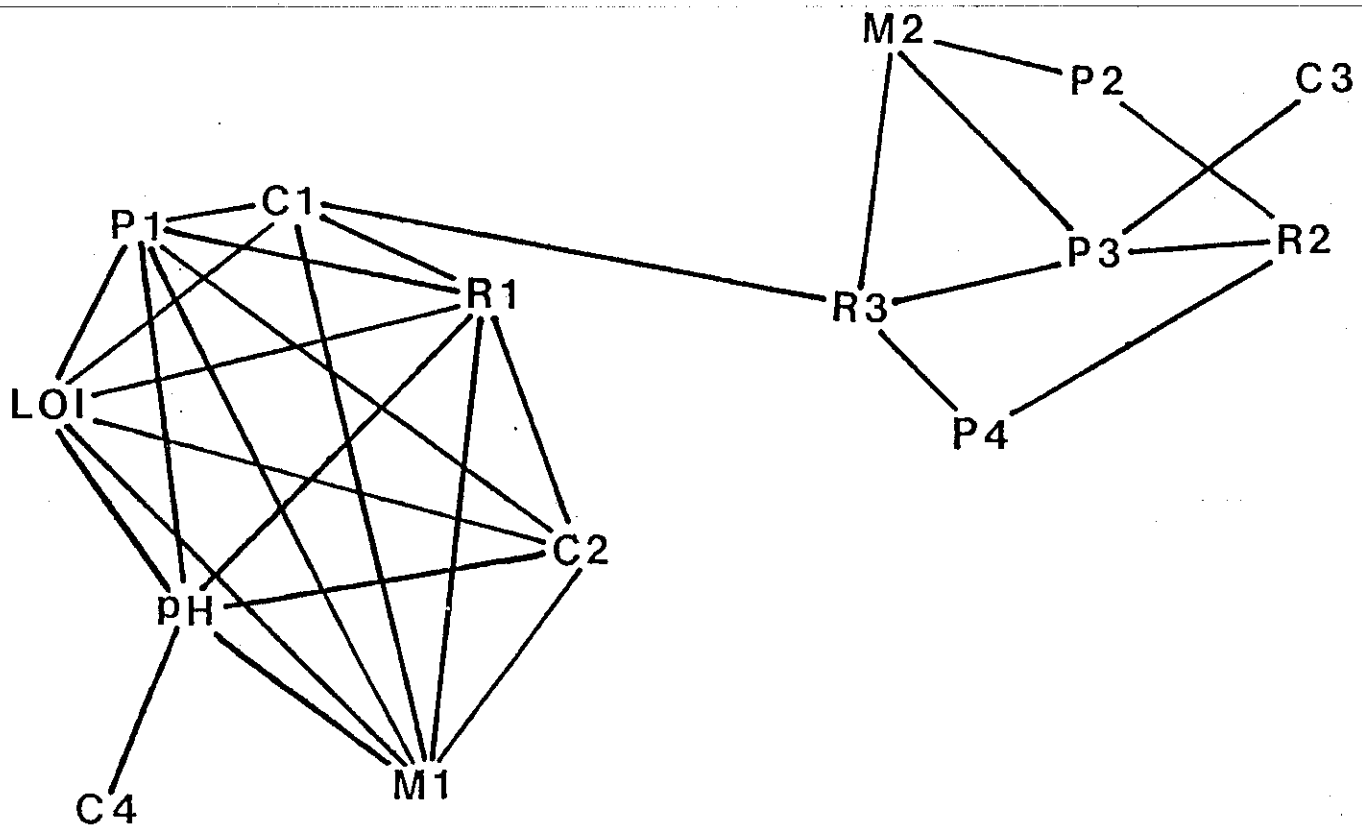

Figure 8. Significant ($p < 0.05$) correlations between components (OD basis). M moisture content, R oxygen uptake, C cellulase, P phosphatase. The number is that of the component.

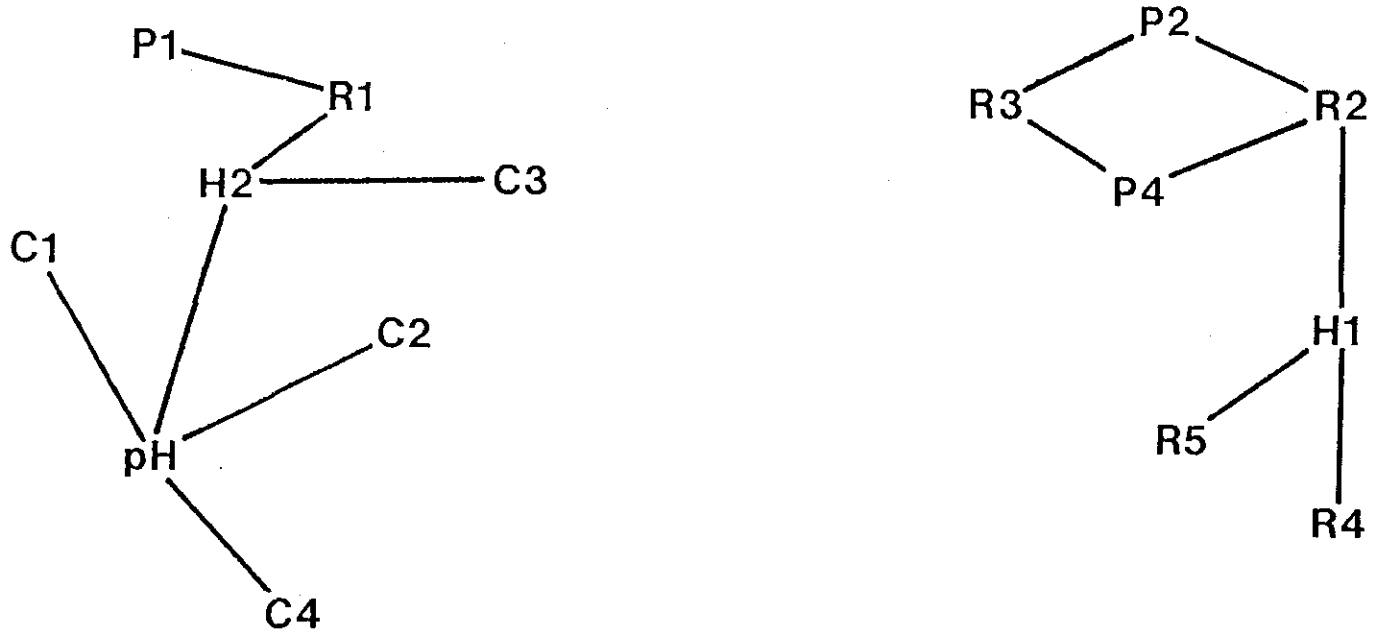

Figure 9. Significant ($p < 0.05$) correlations between components (LOI basis). M moisture content, R oxygen uptake, C cellulase, P phosphatase. The number is that of the component.

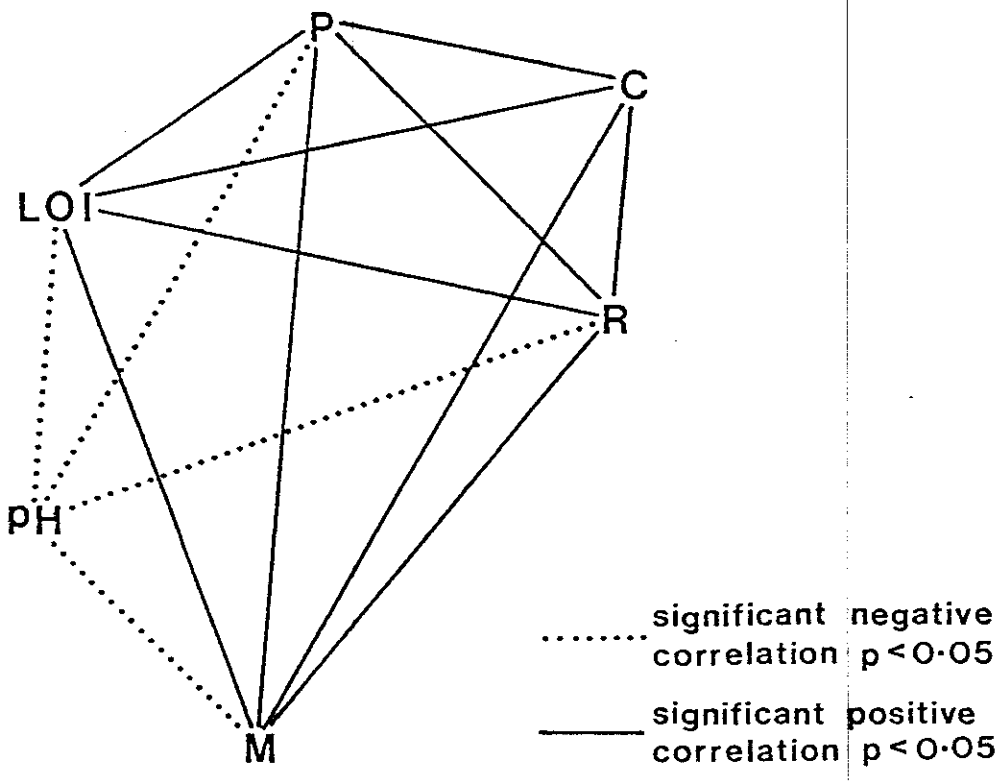

Figure 10. Correlations among the means of the 14 samplings (OD basis). M moisture content, R oxygen uptake, C cellulase, P phosphatase.

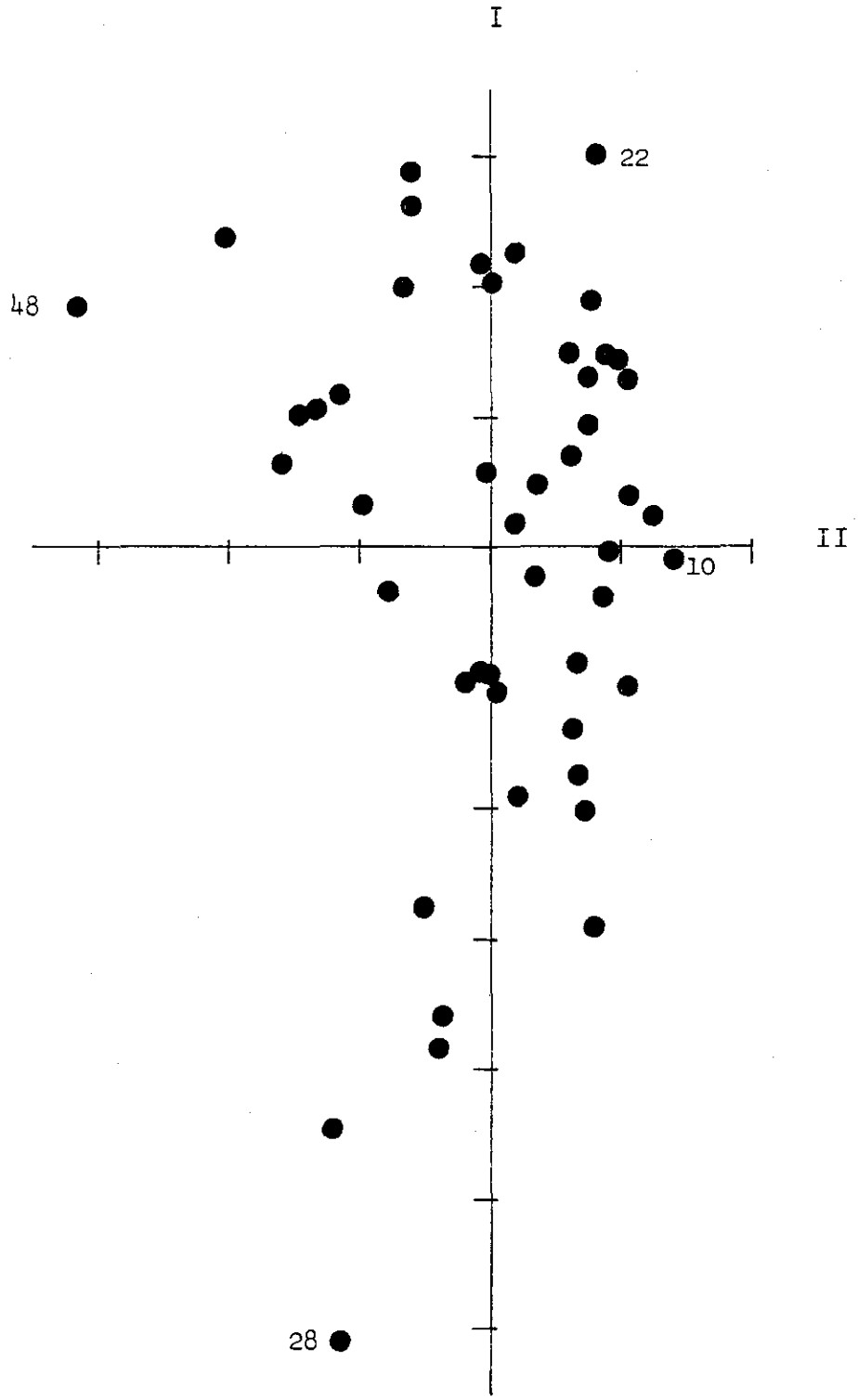

Figure 11. First and second component values of the combined pH, loss-on-ignition, moisture content, oxygen uptake, cellulase and phosphatase first component values (OD basis).

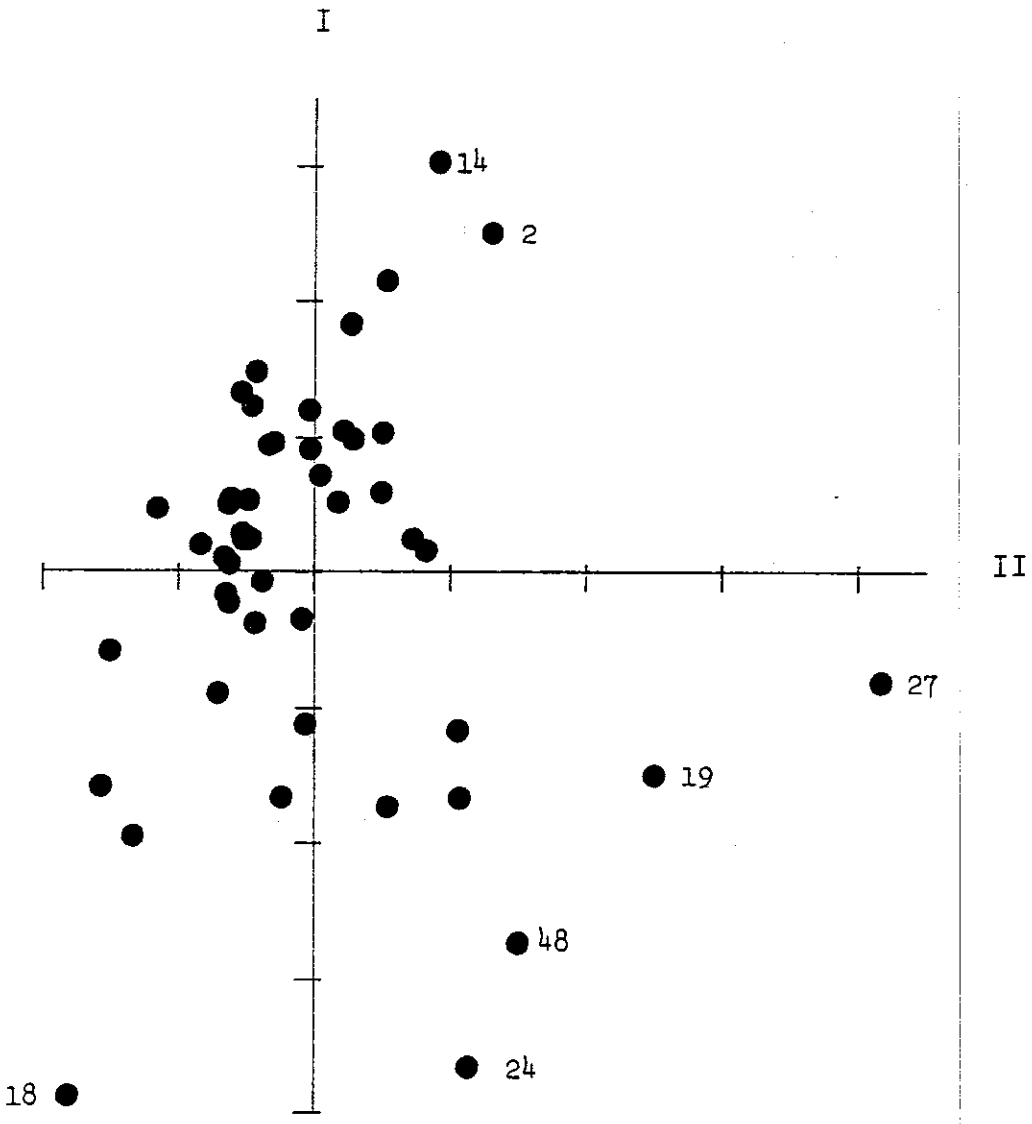

Figure 12. First and second component values of the combined pH, moisture content (coefficient of humidity), oxygen uptake, cellulase and phosphatase first component values (LOI basis).

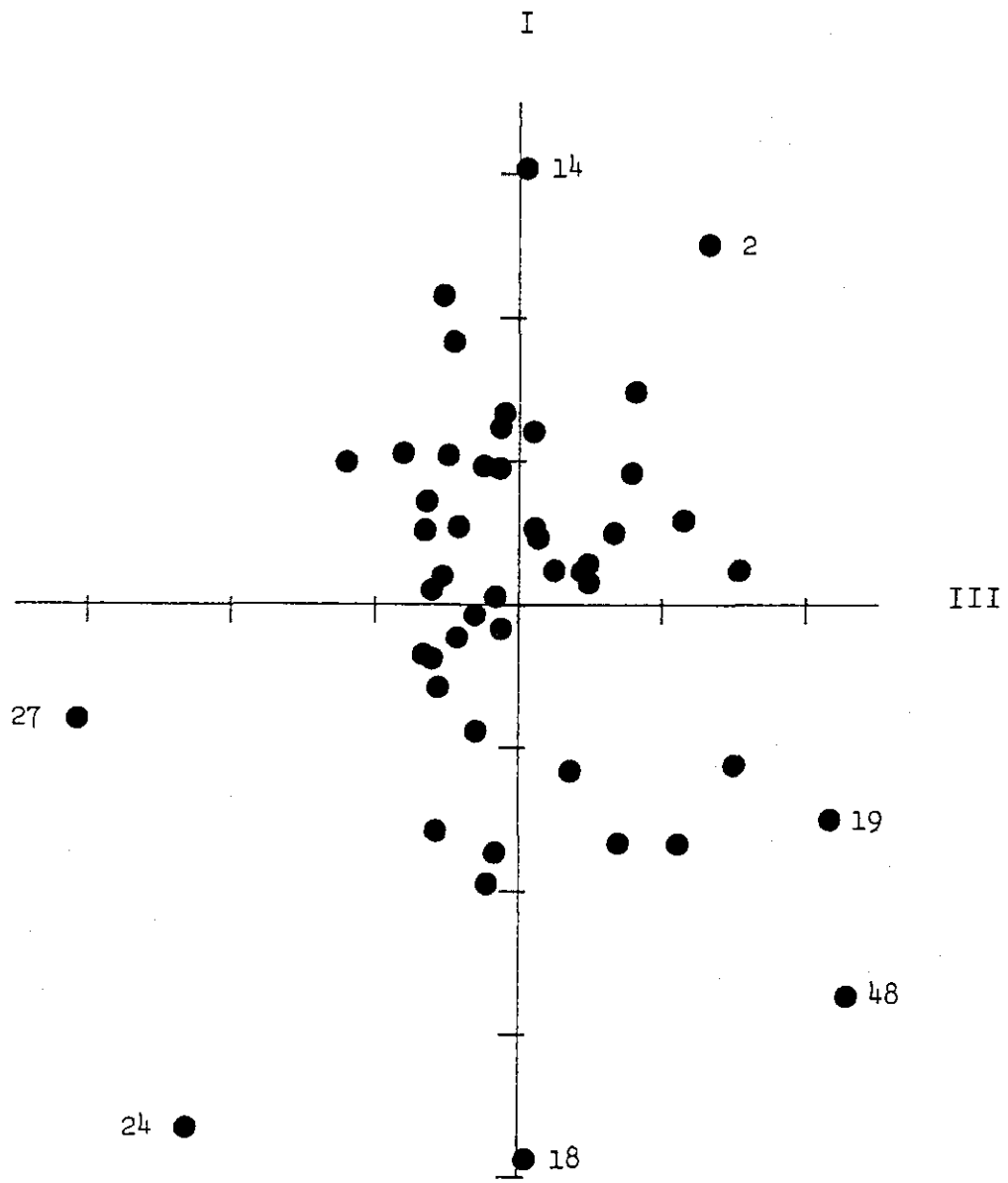

Figure 13. First and third component values of the combined pH, moisture content (coefficient of humidity), oxygen uptake, cellulase and phosphatase first component values (LOI basis).

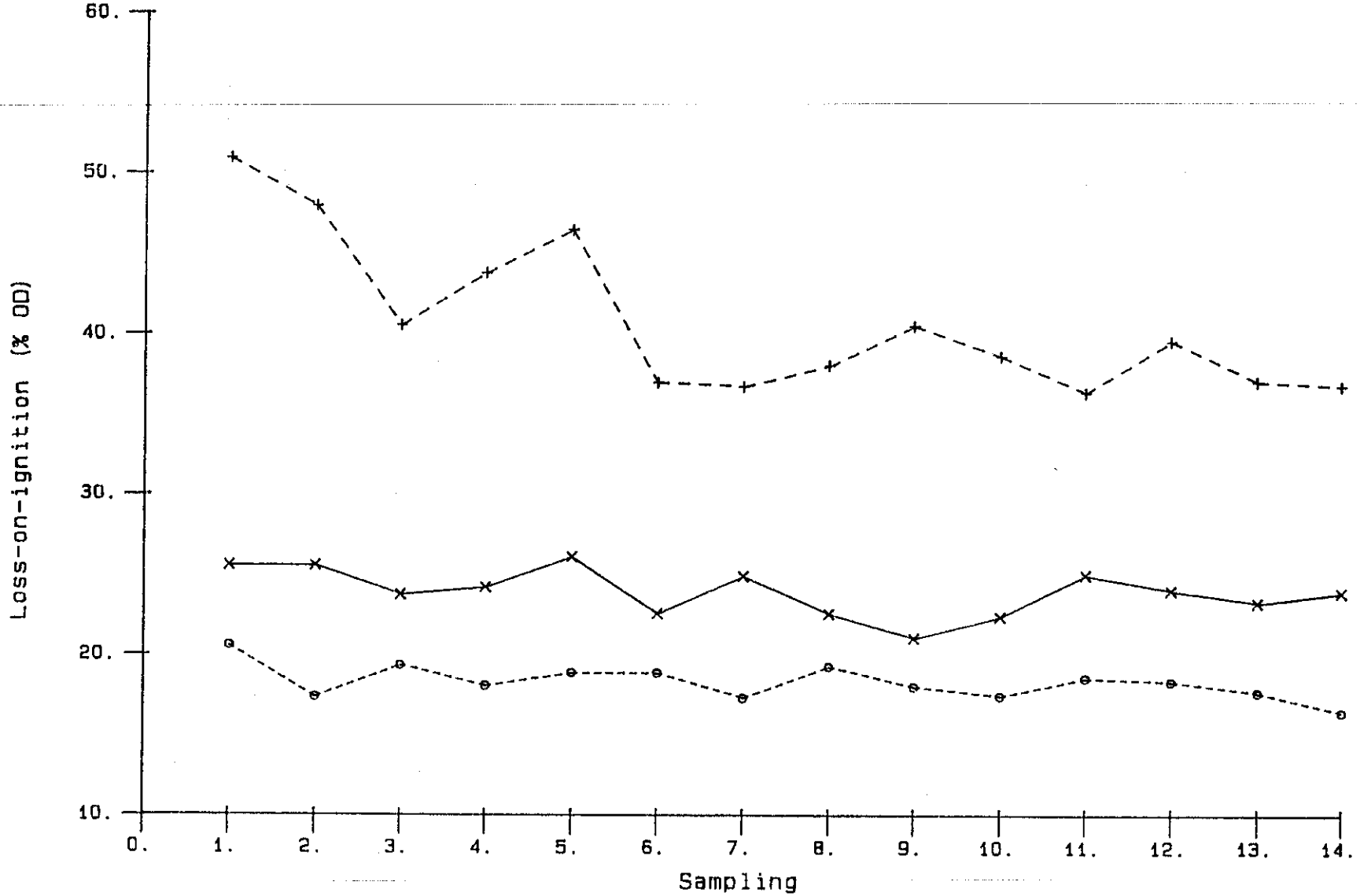

Figure 14. Mean loss-on-ignition of groups of plots formed by pH<3.8 pH 3.8-5.0 pH>5.0

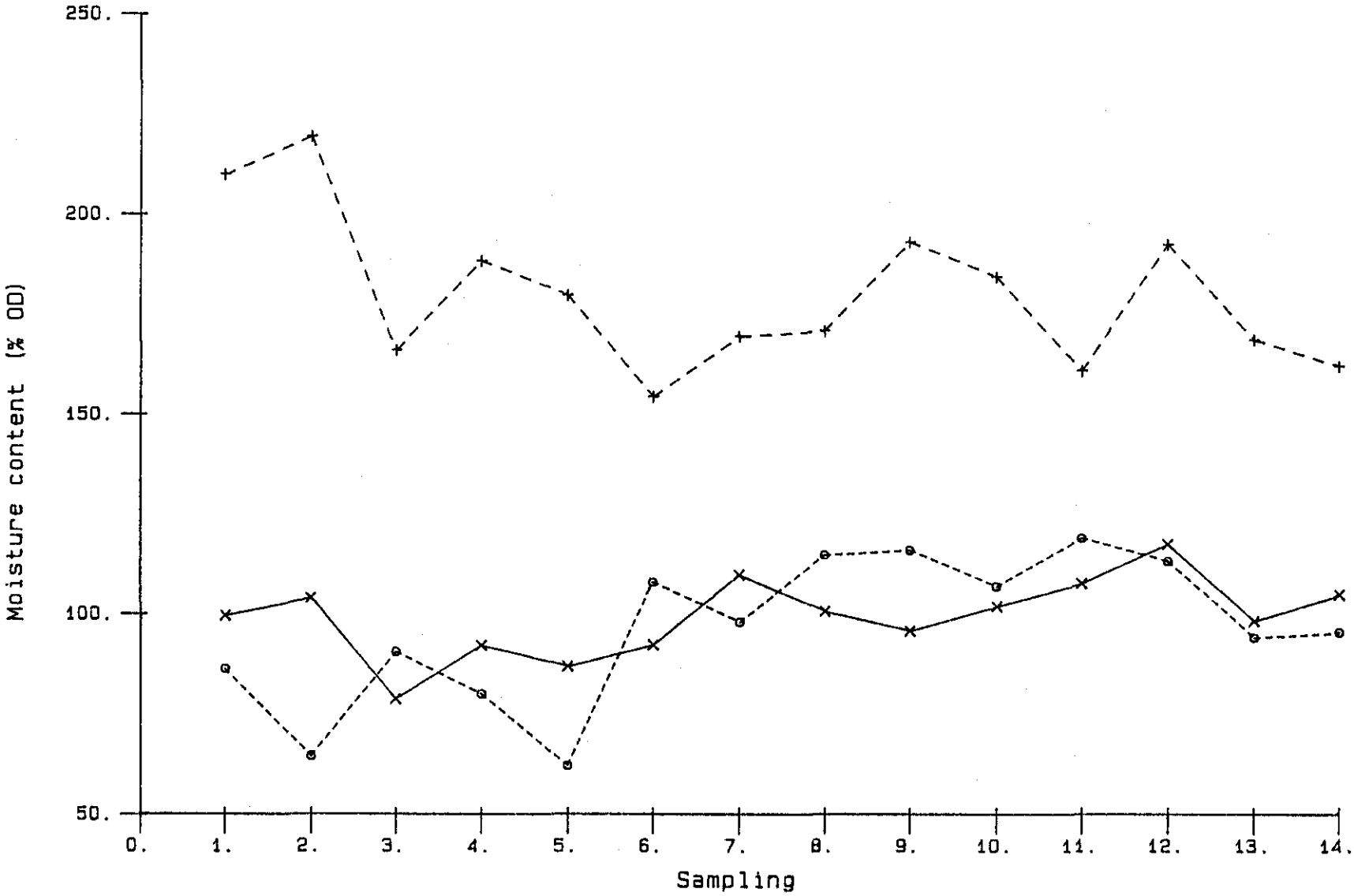

Figure 15. Mean moisture content (% OD) of groups of plots formed by

pH<3.8 pH 3.8-5.0 pH>5.0

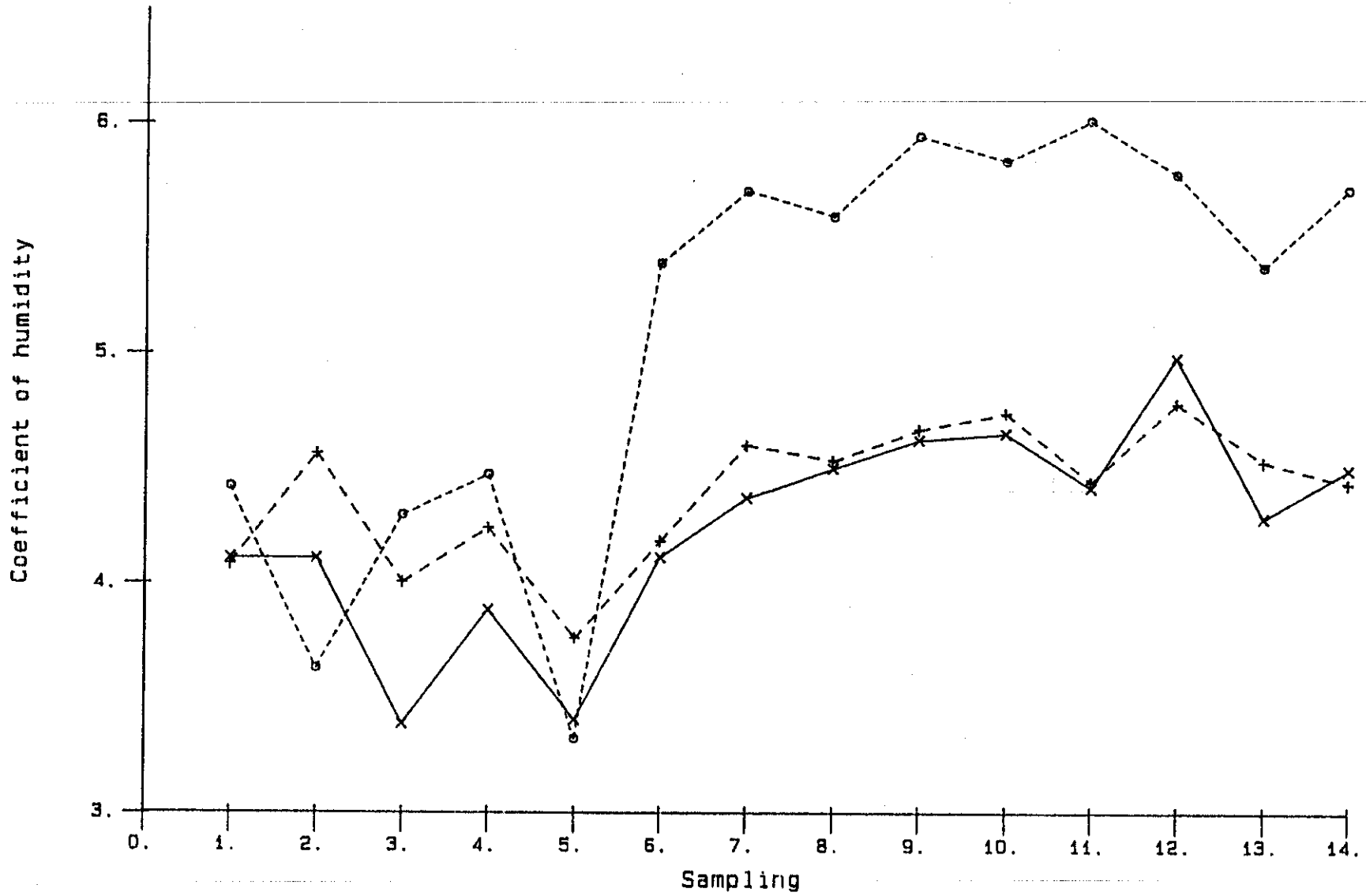

Figure 16. Mean coefficient of humidity (moisture content/g LOI) of groups of plots formed by pH<3.8 ---+--- pH 3.8-5.0 ——×—— pH>5.0 -----●-----

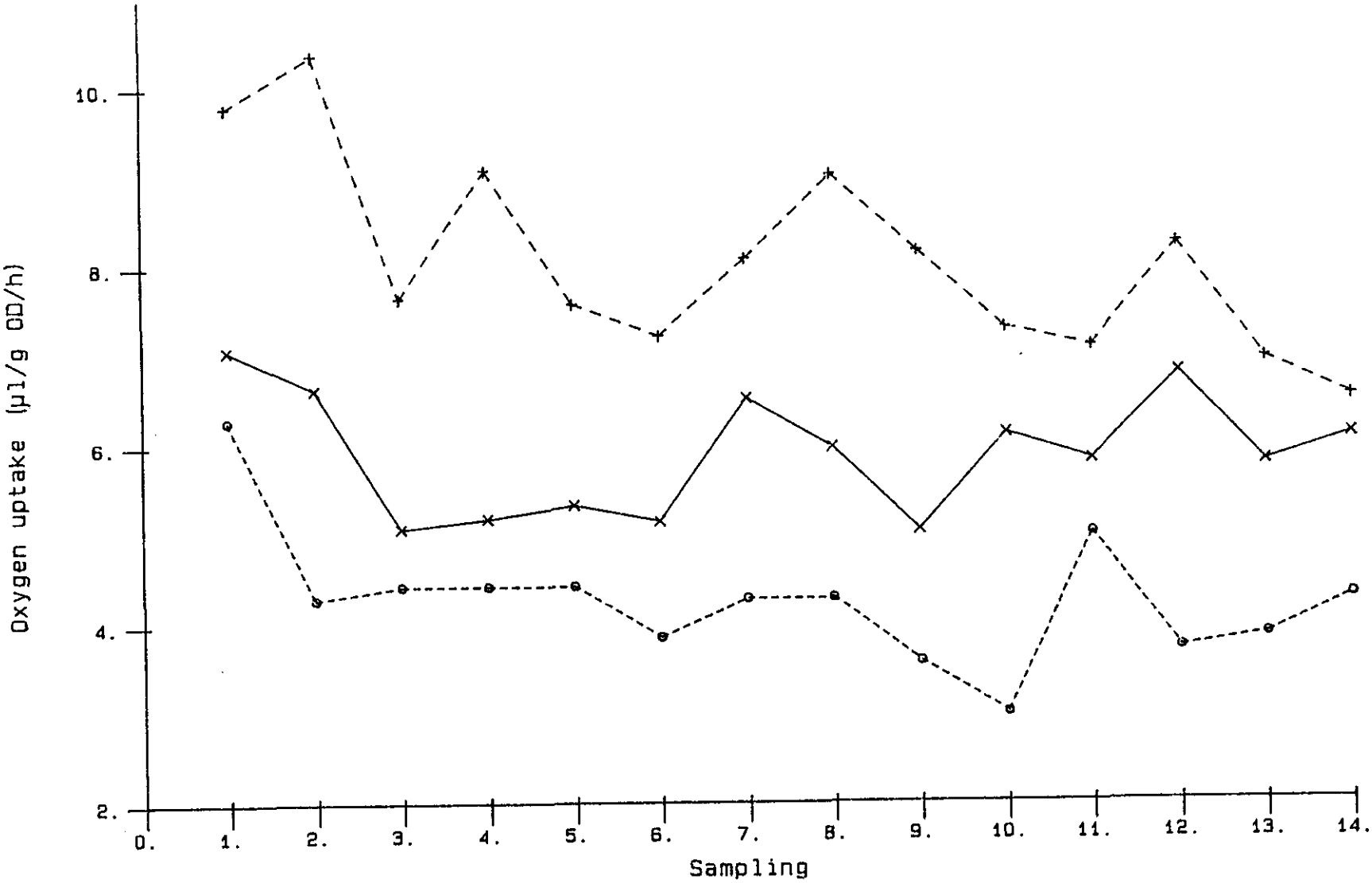

Figure 17. Mean oxygen uptake (OD basis) of groups of plots formed by

pH<3.8 pH 3.8-5.0 pH>5.0

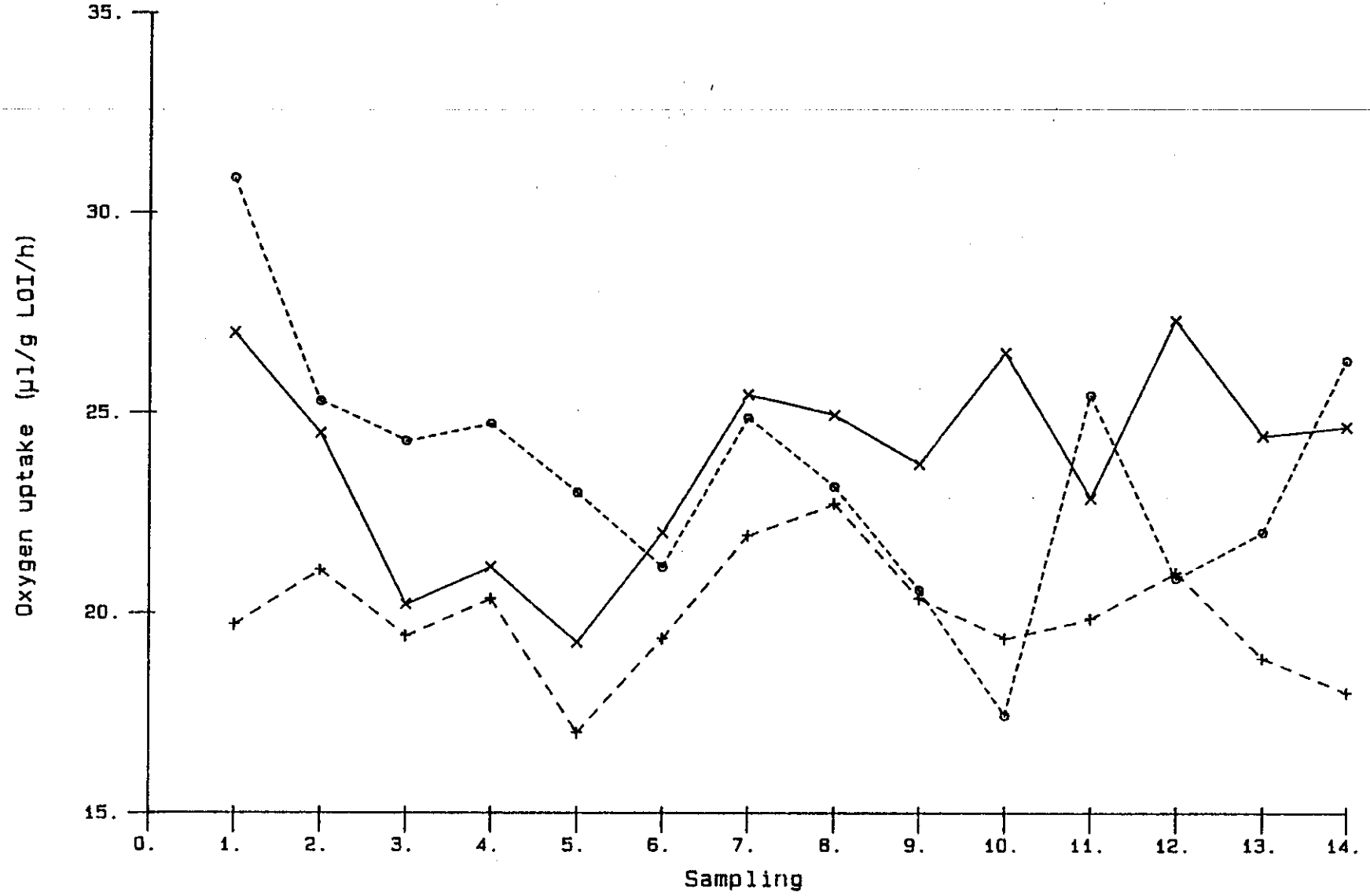

Figure 18. Mean oxygen uptake (LOI basis) of groups of plots formed by pH<3.8 pH 3.8-5.0 pH>5.0

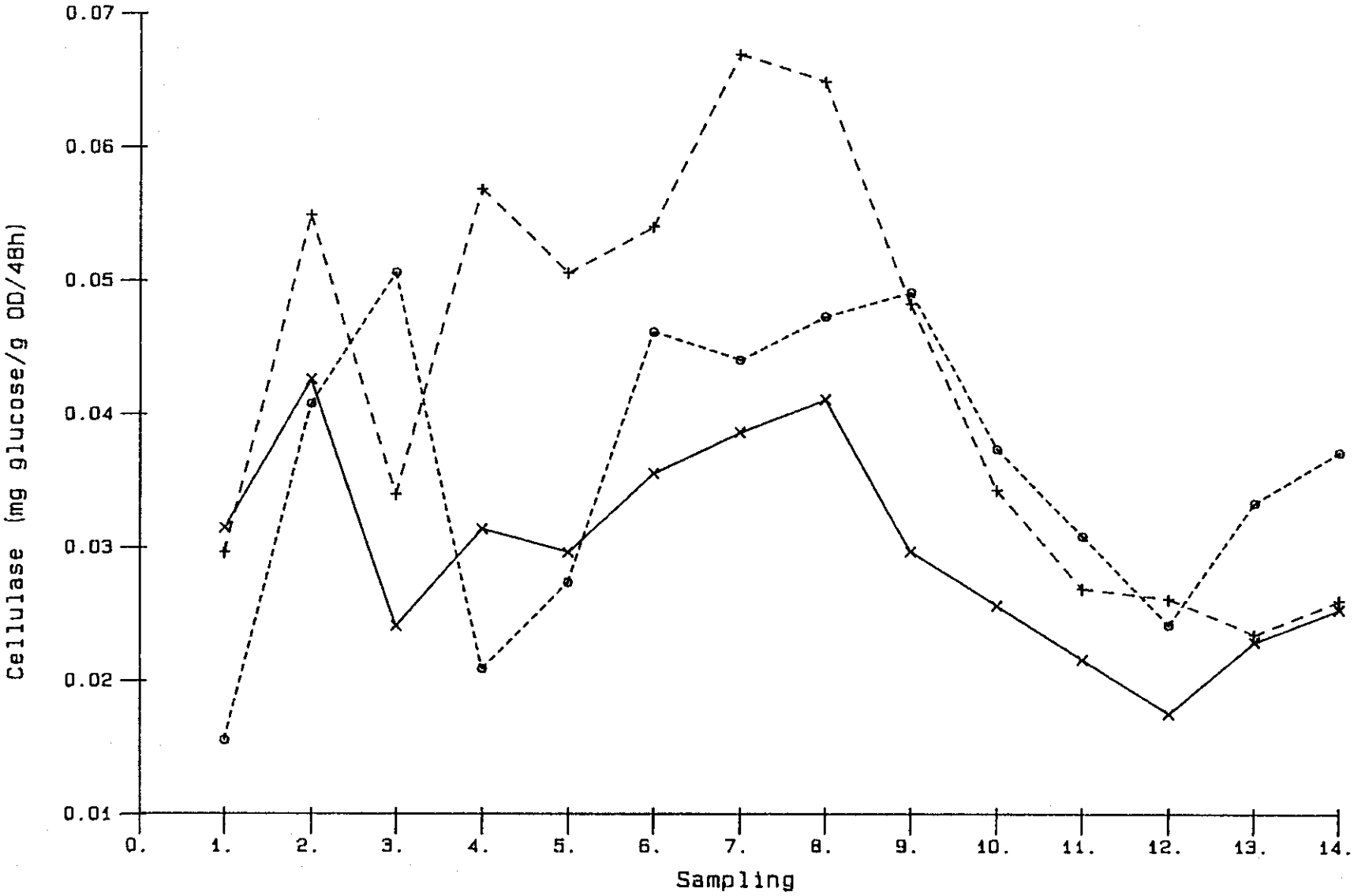

Figure 19. Mean cellulase activity (OD basis) of groups of plots formed by

pH<3.8 pH 3.8-5.0 pH>5.0

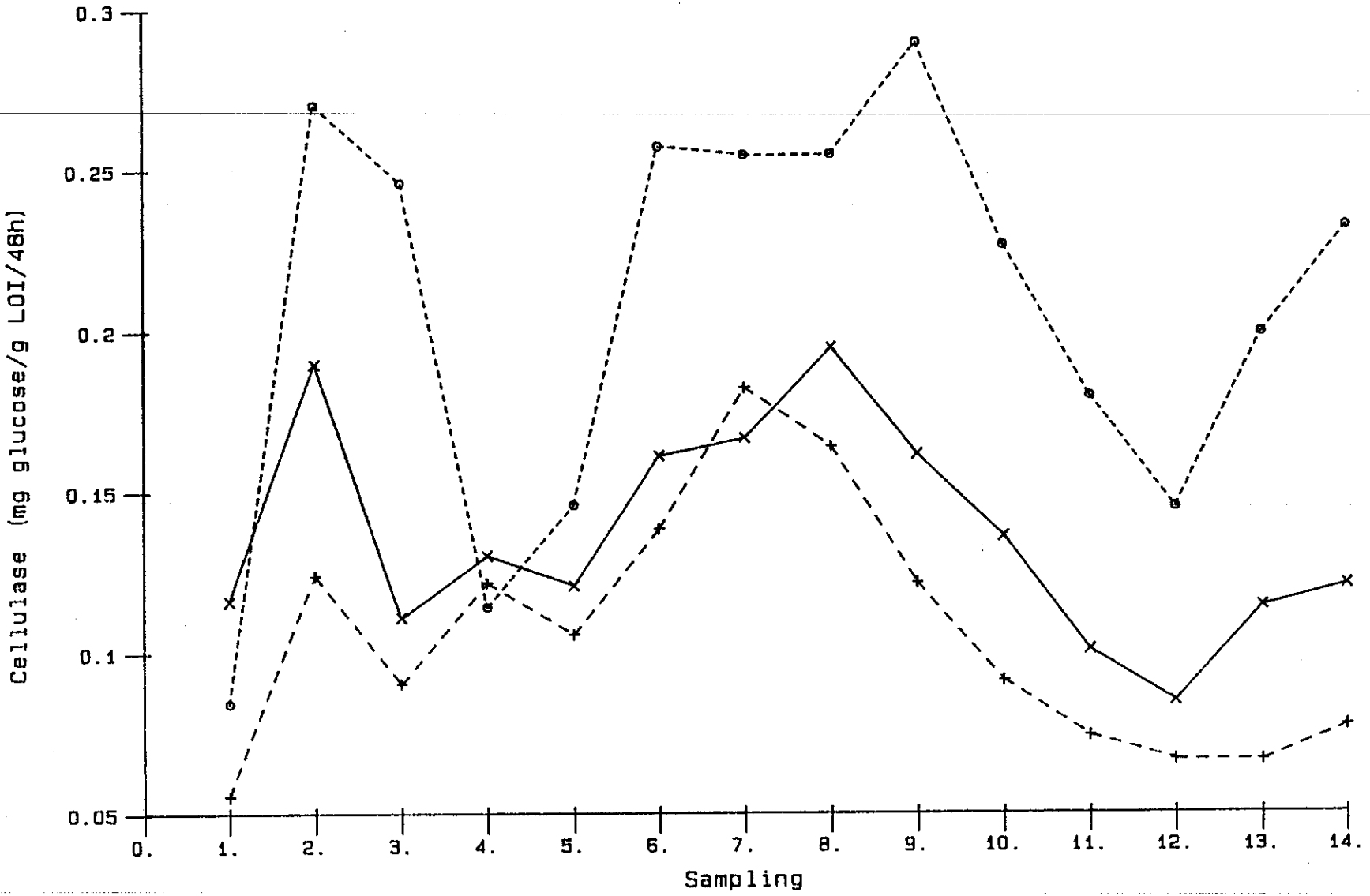

Figure 20. Mean cellulase activity (LOI basis) of groups of plots formed by pH<3.8 pH 3.8-5.0 pH>5.0

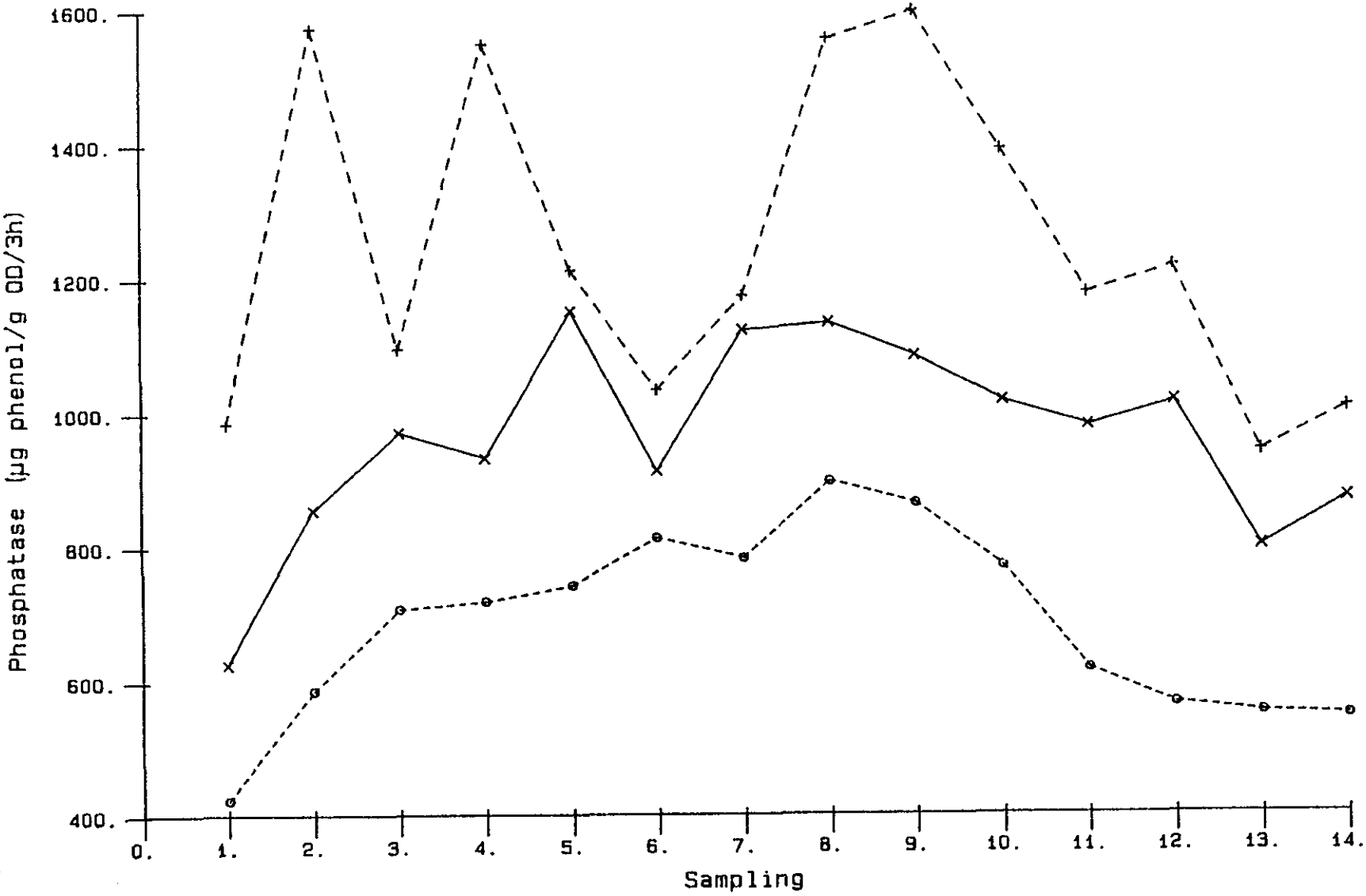

Figure 21. Mean phosphatase activity (OD basis) of groups of plots formed by

pH<3.8 pH 3.8-5.0 pH>5.0

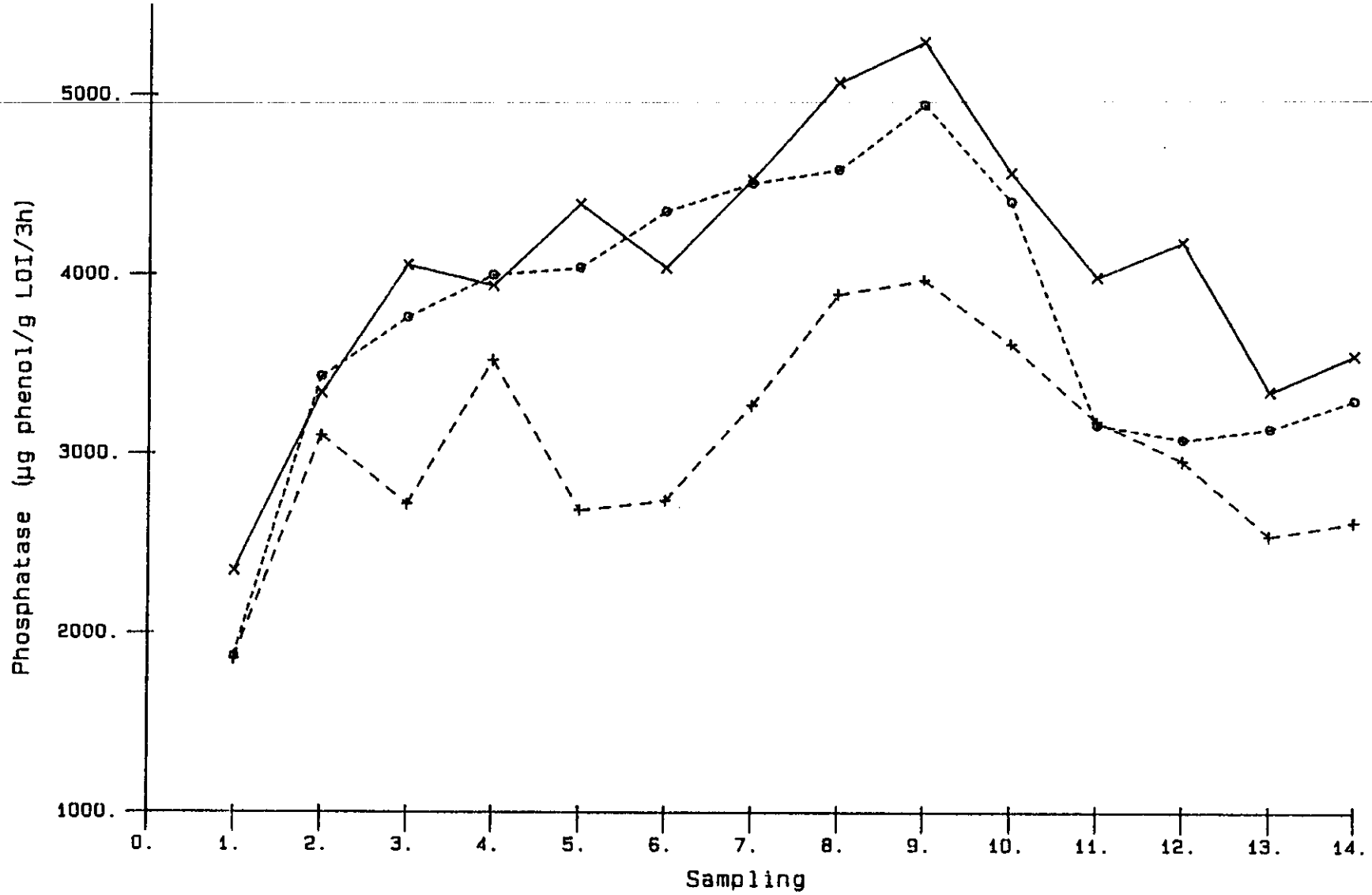

Figure 22. Mean phosphatase activity (LOI basis) of groups of plots formed by pH<3.8 pH 3.8-5.0 pH>5.0

Appendix 1. List of woods

Plot No.	Wood name		Sampling Group	Nat. Grid Ref.
1	Duddon Bridge		2	NY 194884
2	Wall End		3	SD 220875
3	Nibthwaite		3	SD 297880
4	Throughton Hall		3	SD 254916
5	Undercrag		3	SD 275940
6	Torver Common		3	SD 298946
7	Low Eskholme		2	SD 123968
8	Side End		2	NY 065095
9	Church Stile		2	NY 128042
10	Stang Ends		2	NY 120035
11	High Wood		2	NY 122046
12	Elleray		5	SD 412992
13	Tower Wood		7	SD 370870
14	North of Seatle		7	SD 382838
15	Birks Brow		8	SD 410919
16	Lamb Howe		8	SD 419913
17	Low Fell		8	SD 420908
18	Durham Bridge	(L)	8	SD 446898
19	Honeybee Wood	(L)	8	SD 482906
20	Addyfield		8	SD 403900
21	Barton Park		4	NY 470228
22	Martindale		4	NY 440170
23	Low Wood, Hartsop		4	NY 401132
24	Routing Gill		4	NY 405250
25	Wetsleddale		4	NY 540112
26	Bowers Wood		4	NY 505028
27	Low Wood, Elterwater		5	NY 338051
28	Tarn Hows		3	SD 315995
29	High Bowkerstead		7	SD 353906
30	Elder Coppice		5	SD 350968
31	Great Knott		7	SD 335918
32	Intake, Skelwith		5	NY 345047
33	Town End		5	SD 360983
34	Thwaite Head		7	SD 352904
35	Stonethwaite Fell		1	NY 266138
36	Overside		1	NY 250220
37	Low Hows		1	NY 250160
38	Castle Head		1	NY 270229
39	Crag Houses		1	NY 171172
40	Scales Wood		1	NY 165165
42	Arnside Knott	(L)	6	SD 445775
43	Roudsea Wood		7	SD 330822
44	Eaves Wood	(L)	6	SD 470760
45	Nichols Wood	(L)	6	SD 435825
46	Low Wood, Haverthwaite		7	SD 349838
47	Roeburndale Forest		6	SD 615655
48	Meathop Wood	(L)	6	SD 435795
49	Hall Wood, Kentmere		5	NY 452034

(L) on Carboniferous Limestone

There were originally 49 woods, but wood 41 had to be omitted from the sampling.

Appendix 2. Sampling periods.

No.	Dates					
1	1971	24	May	–	15	June
2		21	June	–	13	July
3		19	July	–	10	August
4		16	August	–	7	September
5		13	September	–	5	October
6		11	October	–	2	November
7		8	November	–	30	November
8		6	December	–	28	December
9	1972	3	January	–	25	January
10		31	January	–	22	February
11		28	February	–	21	March
12		27	March	–	18	April
13		24	April	–	16	May
14		22	May	–	13	June

Appendix 3. Sequence for sampling the plots.

Date	Sampling Group	Plot No.
Monday May 24th 1971	4	21, 22, 23, 24, 25, 26
Tuesday May 25th	7	13, 14, 29, 31, 34, 42, 45
Monday May 31st	2	1, 7, 8, 9, 10, 11
Tuesday June 1st	8	15, 16, 17, 18, 19, 20
Monday June 7th	1	35, 36, 37, 38, 39, 40
Tuesday June 8th	3	2, 3, 4, 5, 6, 28
Monday June 14th	6	41, 43, 44, 46, 47
Tuesday June 15th	5	12, 27, 30, 32, 33, 48

This sampling pattern was repeated for each of the 14 sampling periods.