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**A PHYTOSOCIOLOGICAL STUDY OF SOLIGENOUS MIRES
AND SPRINGS IN THE NORTH PENNINES**

by

Jennifer C. Duckworth

**A Dissertation submitted in partial fulfilment of the requirements for the degree
of Master of Science in Ecology by Advanced Course**

University of Durham 1993

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SUMMARY

Soligenous mires and springs have a moving water component and are typically developed on sloping ground. Although many studies have described this vegetation, few have focused on it.

A stratified method was employed to sample this vegetation in the North Pennines. The vegetation was surveyed using the methods of the National Vegetation Classification (Rodwell 1991). Environmental variables were measured with a view to identifying those of major importance in influencing the vegetation composition.

200 samples were collected and classified using TWINSpan (Hill 1979). The floristically similar end-groups generated by TWINSpan were assigned to 13 community types, which were described and related to those discussed in previous studies.

Ordination of the species and samples was carried out using DECORANA (Hill 1979) and showed a floristic gradient that appeared to be related to the pH and conductivity of the samples. A second gradient appeared to be related to the moisture status of the substrate.

Both the classification and ordination highlighted how the vegetation is essentially a continuum and that the classification of vegetation is a somewhat arbitrary process.

The relationship between the vegetation composition and environmental factors was investigated by means of CANOCO (Ter Braak 1988). The most important factor was found to be pH, along with soil moisture status, altitude and to a lesser extent, soil type and bedrock. There is a close correlation between pH and the calcium status of a substrate and it has been suggested that calcium is the most important soil factor influencing vegetation composition. The ability of certain species to act as indicators of the calcium and base status of a substrate was discussed.

Soligenous mires and springs are of major conservation importance in the region. These habitats play host to several rare plant species, are important for wading birds and can be thought of as 'hotspots' of biodiversity. Because of their small size and fragmentary nature, soligenous mires and springs are particularly vulnerable to the various threats facing the uplands. The need for further study to determine the extent of this habitat in Britain was emphasised.

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1: INTRODUCTION

1.1: Mires - some definitions and terms

In its broadest sense, the term 'mire' has been used to denote the entire range of deposits of waterlogged peat, together with their drainage systems and vegetation. These can then be classified according to their topographic and hydrological features, into bogs and fens - a division favoured by continental ecologists. Bogs are influenced solely by water that falls directly onto them as rain or snow, and can be termed 'ombrogenous', whilst fens are influenced by water derived from outside their own immediate limits (Gore 1983). Fens can further be classified into those that are topogenous and those that are soligenous. Topogenous fens occur where local relief results in the water table being permanently high, such as in depressions or on extensive flat areas. In contrast, fens are soligenous when wetness of the ground is maintained by gravitational seepage of water, either as surface run-off or as percolating ground water. Thus soligenous fens have a moving water component, whilst that of topogenous fens is static. In Britain however, the term 'fen' is used almost exclusively to describe lowland topogenous fens, and those that are soligenous are usually referred to as 'mires'. Indeed, McVean & Ratcliffe (1962) and Ratcliffe (1964) used the term 'mire' in a much narrower sense, as a synonym for soligenous mires.

Upland soligenous mires are usually developed on slopes of varying steepness, amongst a wide range of other vegetation, from dry grasslands and heaths to blanket bog. Contact with the mineral soil serves to enrich them with dissolved ions carried by the moving water (Ingram 1967). The mineral ion content of the seepage water affecting mires varies greatly, but mainly according to the chemical composition of parent material both in the superficial deposits and underlying bedrock. The pH of mire soils depends largely on the content of exchangeable Calcium, which is closely related to that of the irrigation water (Ratcliffe 1964).

Soligenous mires are often sub-divided into three categories, oligotrophic, mesotrophic and eutrophic. Ratcliffe (1964) has defined these categories on the basis of exchangeable calcium content, which, subject to occasional discrepancies is closely correlated with pH. The *Handbook of European Sphagna* (Institute of Terrestrial Ecology 1990) uses these terms on a more comparative basis, to describe the range between nutrient-rich waters with a near neutral reaction ('eutrophic') and nutrient-poor waters with a distinctly acid reaction ('oligotrophic'), with 'mesotrophic' waters intermediate between these extremes. The latter terminology will be used in this study.

Depending on the permanence of waterlogging, the soils of soligenous mires are more or less anaerobic and reducing, with the basal mineral horizons usually strongly gleyed. Because the rate of decomposition of humus depends on base-status as well as on aeration, mesotrophic and eutrophic mires tend to have less peaty soils than oligotrophic types of comparative wetness (McVean & Ratcliffe 1962).

Springs and flushes are closely related to soligenous mires, both edaphically and floristically and frequently grade into them. They are soligenous sites, but where the flow of water is more localised and rapid. Ratcliffe (1964) separates springs from flushes using the following, somewhat arbitrary criteria: springs mark the emergence at the ground surface of a concentrated flow of free drainage water, whereas the flow is more diffuse and often less rapid in a flush; and springs usually have little or no bare ground, whilst in flushes, a good deal of the mineral substratum is usually exposed giving a stony or gravely appearance.

1.2: Background to Phytosociology

Phytosociology is the discipline which concerns itself with the study of vegetation; its floristic composition, structure, development and description (Poore 1955a). The development of phytosociology and discussion of the various schools of thought is reviewed in detail by Whittaker (1962), McIntosh (1967) and Shimwell (1981); what follows here is a summary.

Traditionally, the British approach to phytosociology has been different from that followed on the continent, with the two chief continental schools, Zurich-Montpellier (e.g., Braun-Blanquet 1932) and Uppsala (e.g., Nordhagen 1936 in Shimwell 1981), concerning themselves with the rather rigorous taxonomic classification of vegetation types.

There are two conflicting viewpoints as to the nature of the plant 'community'. McIntosh (1967) suggests that, in its extreme form, one treats vegetation as being composed of well-defined, discrete integrated units which can be combined to form abstract classes or types reflective of natural entities in the real world, whilst the other holds that vegetation changes continuously and is not differentiated except arbitrarily, into sociological entities.

Goodall (1954) emphasised the importance of treating variation in vegetation as a continuous variable and advocated the use of ordination methods in vegetation

description. In ordination methods stands of similar floristic composition and abundance are initially arranged together on a relatively small number of axes of variation within a multidimensional system, with the distances between stands related to their floristic similarity. In classification approaches, floristically similar groups of stands are assembled together in an attempt to simplify a large and complex mass of raw data (Birks 1973). There followed a debate lasting many years as to whether to classify or to ordinate. It eventually came to be realised that the two methods are not mutually exclusive, and could even complement each other, in that they serve different needs and may reveal different aspects of the data pattern.

Towards the beginning of the 1970's, many phytosociological treatments of different kinds of British vegetation were appearing, but they used different methods or approaches and did not appear to follow a 'common thread' and so a need was identified for a systematic phytosociological treatment of British vegetation, using standard methods in the field and in analysis and classification of the data (Rodwell 1991). This was developed as the National Vegetation Classification (hence known as the NVC), which is now widely used in vegetation surveys in Britain.

1.3: Previous studies

Several previous studies have mentioned the vegetation of soligenous mires and springs, although none in Britain have focused exclusively on it. In contrast, there have been many such studies in Scandinavia, e.g., Sjörs (1950) and Persson (1962), possibly because this type of vegetation is extensively developed there.

Many phytosociological studies have described the vegetation of a particular area, and so the kind of vegetation with which this study is concerned has been treated in many of those describing upland areas, such as Huntley (1979) on Caenlochan NNR in Scotland, Birks (1973) on the Isle of Skye and Edgell (1969) on Cader Idris in Wales. Studies focusing on the North Pennines include: Eddy *et al.* (1969) on Moor House NNR, Pigott (1956) on Upper Teesdale and Jones (1973) on Widdybank Fell in Upper Teesdale.

Certain studies concern the vegetation of a large area of which the most noteworthy are those on the plant communities of the Scottish Highlands (McVean & Ratcliffe 1962) and the vegetation of Scotland (Ratcliffe 1964). Rodwell (1991) has published a comprehensive account of the Plant Communities of Britain, in which soligenous mires, springs and flushes are all treated.

Despite the fact that many authors describe and discuss such vegetation, often in some detail, the information on the distribution and variation in these communities remains rather sparse. In the North Pennines, at least, previous work has concentrated on the vegetation of the two National Nature Reserves, Moor House and Upper Teesdale, largely ignoring the rest of the area.

1.4: Study aims

This study aims to sample the vegetation of soligenous mires and springs in the North Pennines and assign it to communities using multivariate classification techniques. The communities defined can then be compared to those described in previous studies on this kind of vegetation. Ordination methods will be used in order to identify the major directions of floristic variation in the vegetation sampled. This variation can then be related to environmental factors using direct gradient analysis techniques, with a view to identifying those environmental factors that have a major influence on the vegetation composition.

2: THE STUDY AREA

The study area consisted of land over 350m within the North Pennines Area of Outstanding Natural Beauty (AONB), with the exception of the south of this area around Brough and Stainmore, which was not surveyed.

The North Pennines AONB takes in parts of the counties of Cumbria, Durham and Northumberland and can be considered to lie between the A69 Newcastle to Carlisle road marking the so-called 'Tyne gap' to the north and the A66 Bowes to Penrith road to the south. A steep scarp marks the western edge of the Pennines, to the west of which lies the Eden valley, whilst the dip slope to the east has more of a gentle gradient. Three rivers arise in the North Pennines, the Tees, Tyne and Wear, their valleys serving to dissect the upland relief. The peaks of Cross Fell (893m), Great Dun Fell (847m) and Little Dun Fell (842m) are located in the western region of the North Pennines in NY 63 and NY 73 and mark the highest points in the whole of the Pennine chain.

A broad uplift affects the North Pennines known as the 'Alston Block', which imparts a gentle easterly dip to the strata, so that the oldest rocks outcrop in the west, and as one goes progressively eastwards, younger rocks are exposed. The North Pennines consist of rocks of Carboniferous age of the Yoredale series, which are laid down in alternating layers of limestone, sandstone and shales. An important feature of the Upper Teesdale

area of the North Pennines, is the Great Whin Sill quartz-dolerite intrusion. This igneous rock was emplaced as hot magma into the Carboniferous sediments and baked those sediments above and below the Sill causing contact metamorphism. According to Johnson (1978), limestones are particularly reactive to this, with the pure forms undergoing recrystallisation. Where exposed today, this is known as 'sugar limestone' and is associated with some of the unique plant communities found on Cronkley and Widdybank fells in Upper Teesdale.

There is a widespread tendency throughout the whole of the Pennines for drainage to be impeded, resulting in the formation of soils that are described as hydromorphic, characterised by wetness, poor aeration and in most cases, acidity. Waterlogging may be caused either by the impervious nature of the substrate, or by the topographic position of the site in relation to the true water table (Pigott 1978). A sharp contrast exists between the relatively young, shallow mineral soils and the considerable depths of peat that have accumulated, with the two soil types often occurring adjacent to each other.

The climate of the region is characteristic of that experienced in other upland areas in Britain. It has been described in Chandler & Gregory (1976), in its ultimate form, as having a combination of: low temperatures; severe wind exposure; excessive precipitation; cloud and humidity; persistent winter frost and snow cover; deficiency of sunshine; poor visibility; continual ground wetness and low rates of evaporation. Indeed, the North Pennines have been described by Manley (1936) as "the coldest part of England." In Upper Teesdale, there will usually be over 50 days in the year with snow present on the ground in the morning, though the period May - September is largely free of this (Pigott 1978). Some climatic statistics for the region, taken from *Climatological maps of Great Britain* (Institute of Terrestrial Ecology 1982), are summarised in Table 1.

		Highest peaks e.g., Great Dun Fell	Rest of North Pennines Region
Mean air Temp (°C)	January - March	-2 - 0	0 - 2
	July - September	4 - 6	6 - 8
Mean rainfall (mm/day)	January - March	>4	3 - 4
	July - September	4 - 5	3 - 4

Table 1: Climatic statistics for the North Pennines

The North Pennines has a history of mining, especially for lead, but most of the region is agricultural. Much of the lower-lying land has been enclosed and improved, but the

higher level land remains as rough grazing, for the most part by sheep but with some cattle grazing in places. Some areas are managed as grouse moor. Two National Nature Reserves, Upper Teesdale and Moor House are situated within the North Pennines AONB.

3: METHODS

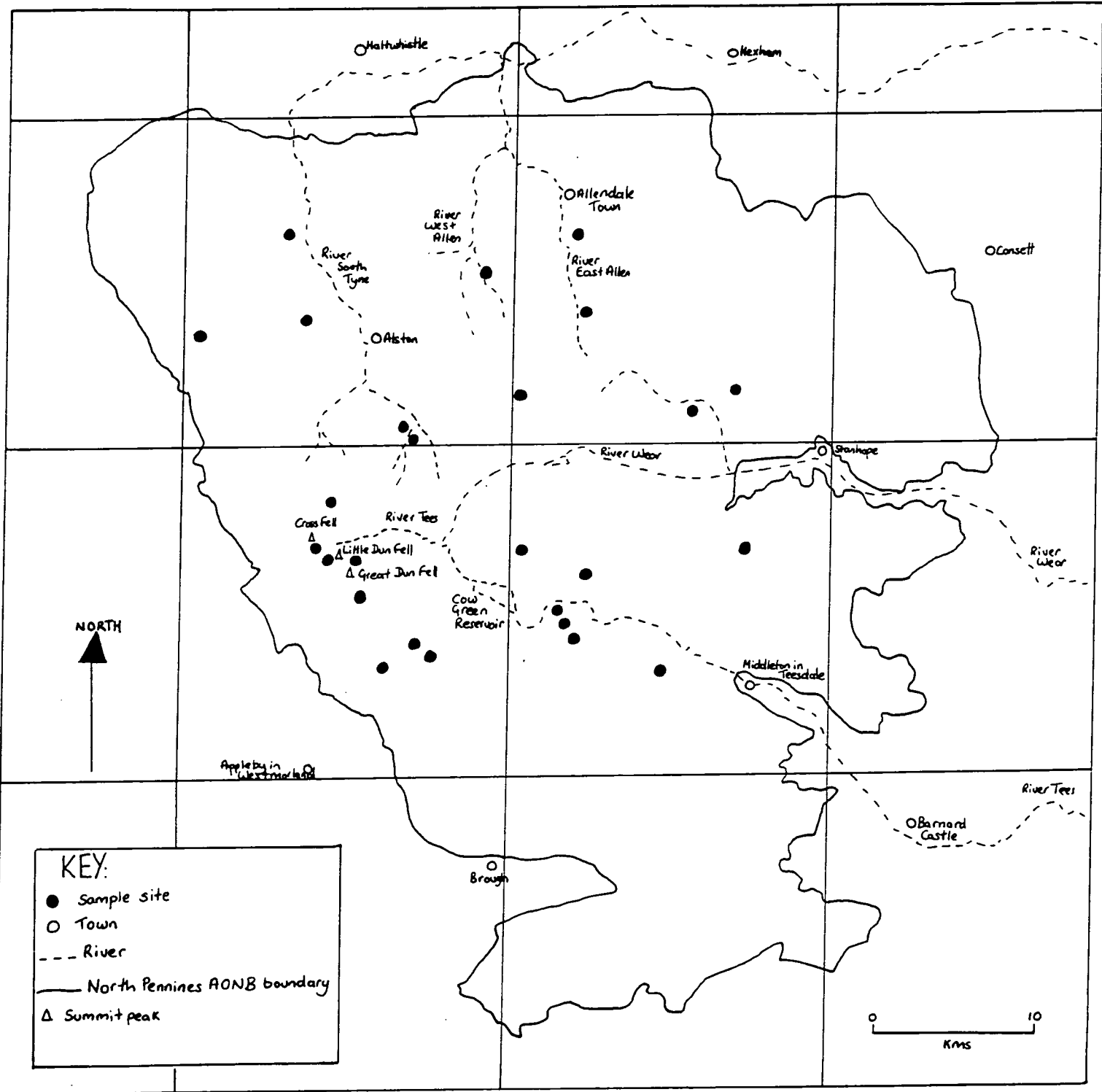
3.1: Sampling method

It was beyond the scope of this survey to describe all the soligenous mire and spring vegetation in such a large geographical area, so some kind of sampling method was necessary. A random sampling method is not suitable in that it is highly unlikely that sample points would 'land' on suitable vegetation. A systematic method would be unsuitable for this same reason. Some element of subjectivity is thus inevitable both in the location of sample sites, and the selection of stands once there.

To ensure that the whole of the study area was represented, the area was divided into 10 x 10 km OS grid squares, with samples located in each square, i.e., a stratified sampling method was employed. An attempt was made to locate at least 10 samples in each square. In most cases, this was possible except in a few areas to the north of the study area, where less than 10 samples were taken because of a lack of suitable vegetation or because access permission was refused. Figure 1 shows the location of sample sites within the study area.

The location of mire and spring vegetation to sample within each square was aided by looking at the relevant 1:25 000 OS map and looking for springs marked on the map, or the presence of shake holes beneath which springs often emerge, even if not marked on the map. From this starting point, sample sites were selected more or less randomly except when the square was in one of the National Nature Reserves in which case the wardens suggested particular localities.

Figure 1: Map of study area showing location of sample sites



3.2: Vegetation sampling

The field method employed essentially follows that used in the National Vegetation Classification (Rodwell 1991). Samples were taken by placing quadrats in a stand that appeared to be homogenous, with care taken to avoid obvious vegetation boundaries. In this type of vegetation, for example a spring head in an area of otherwise dry *Calluna* moorland, the vegetation boundaries are often clear. However, soligenous mire vegetation covering a larger area, may tend to grade rather imperceptibly into other vegetation types. In cases such as this, where boundaries are more difficult to define, a subjective decision had to be made as to where one stand ended and another began.

Much of the vegetation encountered in this study exists as very small stands - along the edges of rills for example - with several stands only 1 x 1m in size. Despite the fact that Rodwell (1991) rejects quadrats of 1 x 1m as being "generally inadequate for representative sampling," it was felt that 1 x 1m was a suitable size to sample vegetation that is often developed in such small stands. Most of the quadrats were square in shape, but where stands were of a unusual shape, irregularly shaped samples of the same area were used.

All vascular plants and bryophytes occurring in the sample were recorded in the field, with those of doubtful identity collected and subsequently identified in the laboratory. The authorities consulted were: Clapham, Tutin & Moore (1987) for vascular plants; Smith (1978) for mosses and Smith (1990) for liverworts. Some taxa such as *Euphrasia* and *Taraxacum* were recorded to the aggregate. It was not possible to identify certain vegetative sedges and non-fruiting acrocarpous bryophytes beyond the genus level.

A quantitative measure of the abundance of every taxon was recorded using the DOMIN scale, cover being assessed by eye as a vertical projection onto the ground of all the live above-ground parts of the plants in the quadrat. Each sample was numbered and its location noted with a full grid reference.

3.3: Environmental measurements

Altitude was estimated in metres from the OS 1:25 000 series maps, slope measured with a clinometer and aspect with a compass. The % of the quadrat covered by vegetation was estimated by eye as was the mean vegetation height. This information was supplemented by notes and sketches where appropriate on aspects of the vegetation and habitat thought likely to aid interpretation of the data, such as surrounding vegetation type and grazing pressure. Details of bedrock and superficial geology were obtained from 1: 50 000 Geological Survey maps.

Where surface water was present, a 50ml sample was taken for subsequent determination of pH and conductivity. For terrestrial samples, a superficial soil sample (approx 20ml) was taken for pH determination. Soil depth was recorded from the centre of each quadrat using an auger and a crude estimation of the moisture status obtained. Soils were classified in simple terms using texture as a basis into the following categories: no soil present; shallow gravel; clay; silt; coarse grained; peaty gley and peat.

Water and soil pH were determined in the laboratory using a Bibby pH meter (model SMP1), with an equal volume of distilled water added to the soil sample, to form a paste. Water conductivity was determined using a WTW conductivity meter (model LC910).

3.4: Data analysis

Quadrat data were entered using RECORD, which is part of the integrated VESPAN package (Malloch 1988) used to enter and analyse data in the National Vegetation Classification. The data were then put through PREPARE, also part of VESPAN in order to be in the correct format for multivariate classification and ordination.

3.4.1: Classification of vegetation

This was carried out using Two-way Indicator Species Analysis, which has been formulated into the FORTRAN computer program TWINSPAN (Hill 1979). This is a divisive polythetic technique, designed to construct ordered two-way tables by means of identifying differential species. The samples are classified first, followed by the species, using the sample classification as a basis for the species classification. Firstly, the data are ordinated by means of reciprocal averaging and the samples divided into two clusters by breaking the ordination near the middle. This dichotomy is achieved using indicator species the best of which will occur in one group of the dichotomy but not the other. The division process is then repeated on the two sample-subsets to give further clusters and this process usually continues for a total of five divisions, leading to the clustering of floristically similar end-groups.

It should be remembered, however, that TWINSPAN, like any multivariate data analysis method, is merely a tool to facilitate the detection of patterns in data and the end groups given need not rigidly be adhered to. In some cases, a division may have been made on a group which is already floristically similar, giving two sub-sets with very little to differentiate them. Here, it may be preferable to retain the original, larger group. In other cases, certain samples may not appear to 'belong' to a particular end group and may be removed to another where they 'fit' much better.

3.4.2: Ordination

Detrended Correspondence Analysis, implemented by the FORTRAN program DECORANA (Hill 1979), is an ordination method commonly used in community studies and provides species ordinations in addition to a sample ordination. It is an eigenvector method, based on reciprocal averaging, but correcting for the two main faults of this method. It avoids the 'arch effect' encountered in reciprocal averaging, by ensuring that the axes are uncorrelated and independent of each other. The second fault of reciprocal averaging is the compression of the axis ends relative to their middle, which is overcome by rescaling the axes by equalising the product mean within-sample dispersion of the species scores at all points along the gradient.

The species are firstly assigned scores, which are standardised to have a mean of zero and unit length. The samples are then ordinated by weighted averages so that the sample score is the mean score of the species that occur in it. The species are then re-ordinated so that the score of each species is the weighted mean score of the samples that it occurs in. Using these new species scores, the procedure repeats itself and this continues until the scores stabilise, giving the value of the first axis. The other axes are calculated in a similar fashion with an additional detrending step occurring between the first sample ordination and re-ordination of the species (Hill & Gauch 1980). The results can then be plotted on an ordination diagram in which similar species (or samples) are close together and those that are dissimilar, far apart.

3.4.3: Canonical correspondence analysis

Canonical Correspondence Analysis (CCA), implemented by the FORTRAN program CANOCO (Ter Braak 1988), is a direct gradient method whereby ordination axes are produced which have a direct relationship with the environmental variables supplied, in that they reflect the principal correlated patterns of variation between the vegetation and environmental variables. CCA, which is an extension of reciprocal averaging, is an efficient ordination technique when species have bell-shaped response curves with respect to environmental gradients, and is therefore appropriate for analysing data on community composition and environmental variables (Ter Braak 1986).

The results can be plotted as biplots, with species or sample scores represented by points and environmental variable scores by arrows (Ter Braak 1986). Both the relative lengths and direction of the arrows are important, with the environmental variables represented by the longest arrows being the most important. Such diagrams also give an approximate

indication of the 'centres' of the species distribution along each of the environmental variables (Ter Braak 1986).

4: RESULTS

Field work was carried out between early April and mid July 1993, during which a total of 200 samples were taken.

4.1: Classification of vegetation

The end-groups of floristically similar samples generated by TWINSpan were examined and interpreted. Some groups were combined and some samples were moved from one group to another, to give groups of samples which could be thought of as distinct community types.

The presentation of results gives priority to the definition of the vegetation types, rather than to the construction of a hierarchical classification. The basic classificatory unit has been termed 'community', with 'sub-community' denoting sub-groups which could be distinguished within these. This is in keeping with the terminology used in the NVC (Rodwell 1991). In some cases, sub-groups could be recognised which are distinct within the community, but which were not considered 'different' enough to merit sub-community status. These have been called 'variants'. In most cases communities have been named using the Latin names of one or two of the most frequent species.

The species are arranged in tables for each community (Appendix I), with the constancy and abundance values arranged in columns. 'Constancy' refers to how often a plant is found on moving from one sample of vegetation to the next, irrespective of how much of that species is present in each sample. In the tables this is denoted by the roman numerals I-V: 1-20% constancy = I (i.e., the species is found in 1 sample in 5); 21-40% = II; 41-60% = III; 61-80% = IV; 81-100% = V. Species in constancy class V are referred to as 'constants', with those in class IV termed 'near constants'. The term 'abundance' is used to describe how much of a plant is present in the sample, irrespective of how frequent it is among the samples and is given as DOMIN values on the tables.

The first block of species on the tables consists of those constant and near-constant for the community in question. The second block, if present, represents those species preferential to a particular sub-community, whilst the last block of species lists the

general associates of the community, sometimes referred to as 'companions' (Rodwell 1991).

4.1.1: Community descriptions

Sphagnum recurvum - *Juncus effusus* mire (Table 2)

The *Sphagnum recurvum* - *Juncus effusus* community is typically developed on gentle slopes, with a more or less complete vegetation cover dominated by a carpet of *Sphagnum recurvum*. *Polytrichum commune* and *Anthoxanthum odoratum* are also common, and may reach high cover. *Juncus effusus* is the dominant rush, although a variant can be recognised in which it is replaced by *Juncus articulatus*. Surface water is sometimes present, but the water table usually lies just beneath the soil surface. Soil pH values range from 3.8-5.2 (mean = 4.4). Conductivity values are relatively low and range from 37-82 $\mu\text{s/cm}$ (mean = 59 $\mu\text{s/cm}$). The community ranges in altitude from 340-580m; at higher altitudes it tends to be replaced by one of the other oligotrophic *Sphagnum* dominated communities.

Several previous authors have discussed a similar vegetation type, indeed Ratcliffe (1964) describes his *Juncus effusus* - *Sphagnum* mire as being "one of the most widespread upland types of vegetation in the British Isles." Eddy *et al.* (1969) recognise an equivalent community, the *Sphagneto* - *Juncetum effusi* from Moor House NNR, whilst McVean & Ratcliffe (1962) describe a *Sphagneto* - *Juncetum effusi* nodum from the Scottish highlands, also mentioned by Birks (1973) from the Isle of Skye. Birse & Robertson (1976) outline a *Juncus effusus* - *Sphagnum recurvum* community in their study of the lowland and Southern Upland regions of Scotland. In the Carneddau, north Wales, Ratcliffe (1958) discusses a *Juncus effusus* bog community with *Juncus effusus* and *Sphagnum* sp. co-dominant, whilst Edgell (1969) recognises a similar community, the *Juncus effusus* - *Sphagnum recurvum* sociation from Cader Idris. Rodwell (1991) classes this vegetation type as the *Juncus effusus* sub-community of the *Carex echinata* - *Sphagnum recurvum/auriculatum* mire (M6c). This bears considerable affinity to the community described here, despite the fact that the M6 community constant, *Carex echinata*, only reaches constancy II, since it is possible that the sedge may have been overlooked early on in the study, before it came into fruit. No authors mention stands with *Juncus articulatus* replacing *Juncus effusus*. Rodwell (1991) describes a *Juncus acutiflorus* sub-community, but there was no possibility of confusion between the rushes since *Juncus articulatus* was in fruit when both samples were taken.

***Sphagnum auriculatum* - *Agrostis stolonifera* mire (Table 3)**

Two sub-communities can be recognised within this rather species-poor vegetation dominated by *Sphagnum auriculatum*, with surface water present in all stands sampled. The Typical sub-community (relevés 5, 38 & 73) is found on gentle slopes at altitudes ranging from 360-500m. Water pH values lie in the range 4.6-5.3 (mean = 4.9) and conductivity ranges from 43-67 μ s/cm (mean = 51 μ s/cm). The *Saxifraga stellaris* sub-community (relevés 84 & 85) is confined to high altitude areas with both relevés taken from spring heads near the summit of Cross Fell at 830m. The vegetation is slightly more species-rich and is characterised by *Saxifraga stellaris*, *Deschampsia cespitosa* & *Scapania undulata*, the latter described in Watson (1968) as "common in and about mountain springs."

No mention is made of any equivalent to the Typical sub-community in previous studies. The *Saxifraga stellaris* sub-community bears some affinity to the *Philonoto* - *Saxifragetum stellaris* spring, *Sphagnum auriculatum* sub-community (M32a) described by Rodwell (1991) although *Philonotis fontana* was absent from both stands sampled. The lack of *Philonotis* could possibly be explained by geology, with Ratcliffe (1964) suggesting that *Sphagnum auriculatum* is usually the predominant species on more acidic mountains, whereas *Philonotis fontana* dominates where the drainage water is slightly richer. The summit of Cross Fell is composed of sandstone, an acidic bedrock, but the pH values from these relevés are not lower than from where the moss is found in other areas so this explanation is unlikely here.

***Sphagnum* - *Polytrichum commune* mire (Table 4)**

The *Sphagnum* - *Polytrichum commune* community is developed on level or very gently sloping ground with the vegetation cover usually complete. *Polytrichum commune* is constant, often reaching high cover, but dominance is typically reached by either *Sphagnum recurvum* or *Sphagnum cuspidatum*. The community has an altitudinal range of 520-840m, with species characteristic of montane areas such as *Saxifraga stellaris* (Clapham *et al* 1987) confined to relevés taken from the highest elevations. Surface water is usually present with pH values ranging from 3.8-5.3 (mean=4.4) and conductivity values ranging from 49-68 μ s/cm (mean=55 μ s/cm). The variant with *Sphagnum cuspidatum* dominant tends to be more waterlogged and developed on deep peats. The *Sphagnum recurvum* variant grades into the *Sphagnum recurvum* - *Juncus effusus* community with the presence of *Juncus effusus* serving to differentiate the two.

This community shows a weak affinity to the M6 *Carex echinata* - *Sphagnum recurvum/auriculatum* mire of Rodwell (1991), but not to any sub-community therein.

Birks (1973) describes a *Carex - Sphagnum recurvum* nodum from the Isle of Skye, similar to the *Sphagnum - Polytrichum commune* community in some respects, but the former community makes no mention of *Sphagnum cuspidatum* and gives *Carex echinata* as a constant. Ratcliffe (1964) outlines a sub-alpine *Carex - Sphagnum* mire from Scotland, but again, carices are given as dominant. Probably the "nearest" vegetation type is the *Sphagneto - Caricetum* community detailed by Eddy *et al.* (1969) from Moor House NNR. Here both *Sphagnum recurvum* & *Sphagnum cuspidatum* are cited as being "locally important" and several other of the species given are found in the *Sphagnum - Polytrichum commune* community, such as *Eriophorum angustifolium*, *Polytrichum commune* and *Carex nigra*, although the latter, given as a constant by Eddy *et al.* (1969) is only rare.

***Montia fontana - Juncus effusus* spring (Table 5)**

The *Montia fontana - Juncus effusus* community occurs at spring heads with the vegetation typically developed over water above bedrock or shallow gravel, often with incomplete cover. *Montia fontana* and *Juncus effusus* are both constant, although only the former ever attains dominance. A variant can be recognised, shown on the right of the table (relevés 63-140), in which *Stellaria alsine* & *Chrysosplenium oppositifolium* are prominent which alters the physiognomy of the stand. The pH of the surface water shows a wide range of values, from 4.7-7.4 with a mean of 6.0, whilst the conductivity ranges from 44-129µs/cm with a mean of 86µs/cm.

The only previously described community which resembles the *Montia fontana - Juncus effusus* community is the *Poa annua - Montia fontana* nodum described by Eddy *et al.* (1969) from Moor House NNR. A weak affinity can be seen with the M32b *Philonoto - Saxifragetum stellaris* spring, *Montia fontana - Chrysosplenium oppositifolium* sub-community of the NVC (Rodwell 1991), but both the community constants are lacking here.

***Montia fontana - Cardamine pratensis - Stellaria alsine* springs (Table 6)**

This rather incoherent assemblage is less clear-cut in floristic terms than the *Montia fontana - Juncus effusus* community. At least one of *Montia fontana*, *Cardamine pratensis*, *Stellaria alsine* or *Chrysosplenium oppositifolium* are present, but only *Montia fontana* & *Chrysosplenium oppositifolium* are ever dominant. A variant dominated by bryophytes can be recognised, shown to the right of the table, with one of, *Brachythecium rivulare*,

Plate 1: Spring head dominated by *Chrysosplenium oppositifolium* grading into vegetation dominated by *Brachytheceium rivulare* (in foreground)



Plate 2: *Cratoneuron commutatum* dominated spring with *Carex nigra* and *Philonotis calcarea*



Dicranella palustris, *Philonotis fontana*, *Plagiomnium affine*, *Scapania undulata* or *Jungermannia atrovirens* at particularly high cover. These springs show a wide altitudinal range (400-820m) and the surface waters have a pH ranging from 5.6-7.6 (mean=6.6) with conductivity values ranging from 47-398 μ s/cm (mean=177 μ s/cm). In this respect, they are more mesotrophic than the preceding community.

The *Montia fontana* - *Cardamine pratensis* - *Stellaria alsine* springs can be considered intermediate between the *Montia fontana* - *Juncus effusus* community and *Philonotis fontana* - *Saxifraga stellaris* or *Cardamine pratensis* - *Philonotis fontana* communities. No obvious affinities can be found with previously described vegetation types, possibly because this vegetation is an intermediate type. However, elements of the *Poa annua* - *Montia fontana* vegetation of Eddy *et al.* and Rodwell's (1991) M32b *Philonoto* - *Saxifragetum stellaris* spring, *Montia fontana* - *Chrysosplenium oppositifolium* sub-community can be detected and it is feasible that this intermediate vegetation type may have previously been included in either of these communities.

***Philonotis fontana* - *Saxifraga stellaris* spring (Table 7)**

Philonotis fontana is the usual dominant in this rather more species rich community, although in some cases the dominant species may be *Carex nigra*, *Montia fontana* or the mosses *Rhizomnium punctatum*, *Dicranella palustris* or *Calliergon cuspidatum*. With the exception of one relevé (139), this community is confined to altitudes of 680m and above, largely reflecting the distribution of the community constant *Saxifraga stellaris*, an arctic-alpine species. Other montane species such as *Epilobium anagallidifolium* and *Sedum villosum* are represented here. In contrast to the *Montia* dominated communities, the *Philonotis fontana* - *Saxifraga stellaris* spring is typically developed on deeper soils and the community is 'drier' in appearance, with the water table often situated just beneath the soil surface. Soil and water pH values range from 6.0-6.9 (mean = 6.5) & 6.1-6.4 (mean = 6.2) respectively with conductivity ranging from 108-181 μ s/cm (mean = 128 μ s/cm).

Accounts of this type of vegetation have been given by several authors. Rodwell (1991) describes the M32b *Philonoto* - *Saxifragetum*, *Montia fontana* - *Chrysosplenium oppositifolium* sub-community as "one of the most common and widespread types of spring vegetation in the uplands of north west Britain." *Cratoneuron commutatum* and *Cratoneuron filicinum*, both characteristic of basic habitats (Smith 1978), are noted by Rodwell (1991) as scarce or absent from M32b but are present in the *Philonotis fontana* - *Saxifraga stellaris* community at constancy IV & II respectively. This could be explained by the fact that the pH of the soil and surface waters is higher than the value of

4.5-6.0 given by Rodwell (1991), possibly because several samples were taken in limestone areas.

The community also closely resembles the *Philonoto - Saxifragetum stellaris* of Eddy *et al.* (1969), which is not surprising considering virtually all the relevés of this community were taken from Moor House NNR. McVean & Ratcliffe (1962) outline *Philonoto - Saxifragetum stellaris* vegetation from the Scottish Highlands whilst Ratcliffe (1964) describes a similar community, the *Philonotis fontana - Saxifraga stellaris* spring as "the most common type of spring vegetation" in Scotland. Edgell (1969) recognises a *Philonotis fontana - Saxifraga nodum* in the vegetation of Cader Idris. Huntley (1979) mentions a related community, the *Scapania undulata - Philonotis fontana nodum* from Caenlochan NNR, Scotland whilst Pearsall (1950) describes a type of wet montane flush vegetation dominated by *Philonotis fontana* with *Saxifraga stellaris* and *Montia fontana*.

***Philonotis fontana - Cardamine pratensis* mire (Table 8)**

In many respects, the *Philonotis fontana - Cardamine pratensis* mire is the lower altitude equivalent of the *Philonotis fontana - Saxifraga stellaris* community. Although the altitudinal range of the community is wide, from 380-790m, most relevés are under 600m. The montane species characterising the preceding community are replaced here by species such as *Juncus articulatus*, *Trifolium repens* and *Cirsium palustre*. *Montia fontana* and *Chrysosplenium oppositifolium* are much less common in this community. *Philonotis fontana* usually dominates although a variant can be recognised, shown to the right of the table (relevés 12-121) where it is replaced by *Cratneuron filicinum*, *Bryum pseudotriquetrum*, *Bryum pallens* or *Fissidens osmundoides*. This is essentially a mesotrophic community, with soil pH values ranging from 6.0-6.8 (mean = 6.4) and water pH ranging from 5.7-7.6 with a mean of 6.7. Conductivity values vary considerably between 37 and 459 μ s/cm (mean = 203 μ s/cm). The exceptionally low value of 37 μ s/cm may be due to the very heavy rainfall when that sample was taken causing water to literally sheet over the vegetation. Rainwater is generally a poor source of inorganic nutrients (Ingram 1967) and so the direct input of rainwater into the system may account for the low conductivity of the surface water at the time of sampling.

Few previous studies describe equivalent vegetation types. The community can be considered a lowland variant of the *Philonoto - Saxifragetum* of Rodwell (1991). However, it lacks the preferential species from either sub-community described in M32.

Plate 3: *Chrysosplenium oppositifolium*



Plate 4: *Carex nigra* - *Eriophorum angustifolium* mire with *Carex panicea* at high cover



***Juncus effusus* - *Cardamine pratensis* mire (Table 9)**

This common vegetation type is distinctive in appearance and generally species rich. No less than five species are constant, with four at constancy IV. The physiognomic dominant is *Juncus effusus*, with *Carex nigra* also often at high cover. Bryophytes, particularly *Calliergon cuspidatum* and *Climacium dendroides* are prominent, with *Rhytidiadelphus squarrosus* and *Brachythecium rivulare* frequent at lower cover. Vegetation cover is usually complete and the water table is situated just below the surface in the majority of samples. Soil pH values range from 5.1-6.8 with a mean of 6.1. In contrast to much of the vegetation sampled in this study, the *Juncus effusus* - *Cardamine pratensis* mire is frequently developed as large stands, typically in a zone of soligenous influence along the sides of spring lines or at their base.

The *Juncus effusus* - *Cardamine pratensis* mire is related to the Species-rich *Juncetum effusi* of Eddy *et al.* (1969), with many of the species given by them as constant, constant or certainly common. Considerable affinity is also shown with the M23b *Juncus effusus* - *Galium palustre* rush pasture, *Juncus effusus* sub-community of Rodwell (1991). The distribution map of M23b shows no points in the North Pennines. However, this does not necessarily mean the community does not exist in the area - it is possible that M23b was simply not sampled here.

***Calliergon cuspidatum* - *Carex* mire (Table 10)**

This community is similar to the *Juncus effusus* - *Cardamine pratensis* mire in several ways. *Cerastium fontanum*, *Trifolium repens*, *Cardamine pratensis* and *Calliergon cuspidatum*, at high constancy in the preceding community, are also at high constancy here. *Juncus effusus* is only occasional in this community, and never dominant, whilst sedges are more prominent. *Carex panicea*, rare in the *Juncus effusus* - *Cardamine pratensis* mire, is at constancy IV here, often reaching high cover. *Carex nigra* is also frequent and *Carex pulicaris* occasional, but *Carex dioica*, *Carex flacca* and *Carex lepidocarpa*, characteristic of more eutrophic conditions, are rare here. Bryophytes are common, especially *Calliergon cuspidatum*, with *Climacium dendroides* and *Hylocomium splendens* dominant in certain stands. This community can be found in lower altitude areas (370-530m) developed on gentle to moderate slopes. Surface water is rarely present, with the water table usually present just beneath the soil surface. Soil pH values are lower than the preceding community and range from 4.3-7.0 with a mean of 5.6. Relevés 11 & 173 form a distinct sub-community, dominated by *Sphagnum subnitens*, with *Aulacomnium palustre*, *Potentilla erecta* and *Juncus squarrosus* also typical.

The *Sphagnum subnitens* sub-community has no direct equivalent in the literature and few previously described communities are related to the community as a whole. Huntley (1979) outlines the *Carex nigra* - *Equisetum palustre* nodum in which several of the species listed at high frequency are also at high frequency in the *Calliergon cuspidatum* - *Carex* mire. Hilliam (1977) describes a bryophyte-rich community from the southern Isles of Shetland, with several of the species characteristic of this community, such as *Trifolium repens*, *Anthoxanthum odoratum*, *Cerastium fontanum* and *Cardamine pratensis*. However, the sedges given as preferential by Hilliam (1977) include those more indicative of eutrophic conditions, which are rare here.

***Carex nigra* - *Eriophorum angustifolium* mire (Table 11)**

This community is distinctive in appearance, being dominated by one or several sedges. *Carex nigra* is constant, with *Eriophorum angustifolium* & *Carex panicea* frequent and often at high cover. The community is species-poor, with few, if any herbs and bryophytes present. Relevé 111, which is base-poor (pH 4.8) and dominated by *Sphagnum tenellum*, is something of a 'misfit' in the community. This relevé proved difficult to classify and has been placed here owing to the presence of *Eriophorum* and *Carex nigra*. The remainder of the community is more mesotrophic, the soil pH ranging from 6.3-6.7 with a mean of 6.5. This vegetation type is usually developed as small stands on level ground by spring lines. The *Carex nigra* - *Eriophorum angustifolium* mire has no obvious affinities to any vegetation described in the literature.

Open gravel flushes (Table 12)

These very species-poor flushes are developed over base-rich shallow gravels or a slightly deeper coarse substrate. *Carex flacca*, *Carex demissa* and *Juncus articulatus* are frequent, with all species scattered sparsely amongst the exposed substrate. Surface water values range from 6.7-7.4 (mean = 7.2) whilst conductivity ranges from 160-375 μ s/cm with a mean of 238 μ s/cm.

It is not clear whether the vegetation is open and species-poor due to strong irrigation and erosion from the flushing waters, or because the stands represent an early stage of succession and will eventually become more 'developed'. Piggot (1956) & Rodwell (1991) give the former explanation although no communities described in the literature are this species-poor. For example Ratcliffe (1964) describes an open stony community, the *Carex* - *Saxifraga aizoides* flush, as being sparsely vegetated, but species-rich.

***Carex flacca* - *Leontodon autumnalis* mire (Table 13)**

The *Carex flacca* - *Leontodon autumnalis* community is species-rich and typically developed in zones of soligenous influence on moderate slopes, or on more level ground by springs. *Carex flacca* and *Leontodon autumnalis* are constant, with several other species characteristic although no one species is dominant. Herbs are frequent in this community, as are sedges. Bryophytes are less prominent here but *Bryum pseudotriquetrum* and *Ctenidium molluscum* are both common. Two variants can be recognised. The species-poor variant, the block of samples on the right of the table, is only 'species-poor' in relative terms. The species-rich variant has a higher total number of species per sample and a higher frequency of herbs particularly *Primula farinosa*, *Bellis perennis*, *Succisa pratensis* and *Pinguicula vulgaris*. The community ranges in altitude from 380-690m and is developed over limestone or on the Whin Sill of Upper Teesdale. This is a eutrophic vegetation type with the soil pH ranging from 5.7-7.5 (mean = 6.7). Surface water, where present has a pH range of 6.7-7.4 (mean = 7.1) and conductivity ranges from 177-290 μ s/cm (mean = 246 μ s/cm).

Considerable affinity can be seen with the M10b *Carex dioica* - *Pinguicula vulgaris* mire, *Briza media* - *Primula farinosa* sub-community of Rodwell (1991) and to the Species-rich *Carex panicea* - *Ctenidium molluscum* nodum of Eddy *et al.* (There is some possibility that *Carex flacca* & *Carex panicea* may have been confused early on in the study). McVean & Ratcliffe (1962) and Ratcliffe (1964) both describe the *Carex panicea* - *Campylium stellatum* nodum from Scotland, which is similar in many respects. Shimwell (1968) outlines the association *Caricetum lepidocarpae* - *hostianae*, whilst Wheeler (1980) & Jones (1973) describe the *Pinguiculo* - *Caricetum dioicae* community; both of these are related to the *Carex flacca* - *Leontodon autumnalis* mire. Some resemblance can be seen to the *Carex dioica* - *Eleocharis quinqueflora* community of Birse & Robertson (1976), despite the fact that these species are only at constancy I in the *Carex flacca* - *Leontodon autumnalis* mire. They recognise a more base-poor relevé, containing *Drosera rotundifolia* and *Narthecium ossifragum*, as a variant. Relevé 182 is similar to this, containing both species and could perhaps be considered a variant.

***Cratoneuron commutatum* springs (Table 14)**

These springs are dominated by *Cratoneuron commutatum*, which is always present at high cover. *Juncus articulatus* and *Cardamine pratensis* are also frequent. *Bryum pseudotriquetrum* is a prominent bryophyte as are *Philonotis calcarea* and *Philonotis fontana* but none are as dominant as *Cratoneuron commutatum*. The community can be found at a range of altitudes, from 380-790m, usually at spring heads, or along the sides

of rills. Two sub-communities can be recognised, the *Carex nigra* sub-community, represented by the left hand block of samples, and the *Festuca ovina* sub-community. *Carex nigra* is constant and *Festuca ovina* and *Carex flacca* rare or absent in the *Carex nigra* sub-community, with the situation reversed in the *Festuca ovina* sub-community. Although surface water is usually present, in some cases the water table lies just beneath the surface. The community is eutrophic in nature, with little difference in pH and conductivity between the sub-communities. Soil pH ranges from 6.0-6.9 with a mean of 6.5, whilst that of water ranges from 6.2-7.9 with a mean of 7.1. Conductivity values range from 110-532 μ s/cm with a mean of 259 μ s/cm.

The *Carex nigra* sub-community closely resembles the M38 *Cratoneuron commutatum* - *Carex nigra* spring of Rodwell (1991). The *Festuca ovina* sub-community has elements of both M38 and the M37 *Cratoneuron commutatum* - *Festuca rubra* spring (Rodwell 1991). Eddy *et al.* (1969) recognise a species-rich calcareous community from Moor House NNR, the *Cratoneuron* - *Carex nodum*, which the *Cratoneuron commutatum* springs closely resemble. McVean & Ratcliffe (1962) and Ratcliffe (1964) describe the *Cratoneuron* - *Saxifraga aizoides* nodum, which is similar to this community, although *Saxifraga aizoides* is absent here. The *Cratoneurion* association, outlined by Jones (1973) is also similar except for the fact that *Saxifraga aizoides* is absent. *Cratoneuron* dominated springs can also be found in Scandinavia. Persson (1962) for example, noted that calcareous springs dominated by *Cratoneuron* spp. were the dominant spring vegetation in an area north of Lake Torneträsk, Sweden.

4.2: Detrended Correspondence Analysis

A standard run of DECORANA was performed and the resulting species scores (Figure 2) and sample scores, which are weighted means of the species scores (Figure 3) plotted. Thus samples with similar species compositions occupy similar positions in the ordination diagram. Certain species, found at the extremes of the axes, tend to be outliers in that they only occur in a few relevés and hence are not considered important eg. *Equisetum variegatum*, *Deschampsia flexuosa* and *Glyceria* seedling/sp. Other species, situated slightly nearer the centre such as *Polytrichum commune*, *Sphagnum recurvum*, *Ctenidium molluscum* and *Dicranella palustris* are common and can be considered to represent more useful limits in the direction of floristic variation. (A list of species along with their codes is given in Appendix II). Certain species, located in the middle of the plot, were common in several communities and ecological conditions, such as *Cerastium fontanum* and *Trifolium repens*.

Figure 3: DCA plot of sample scores

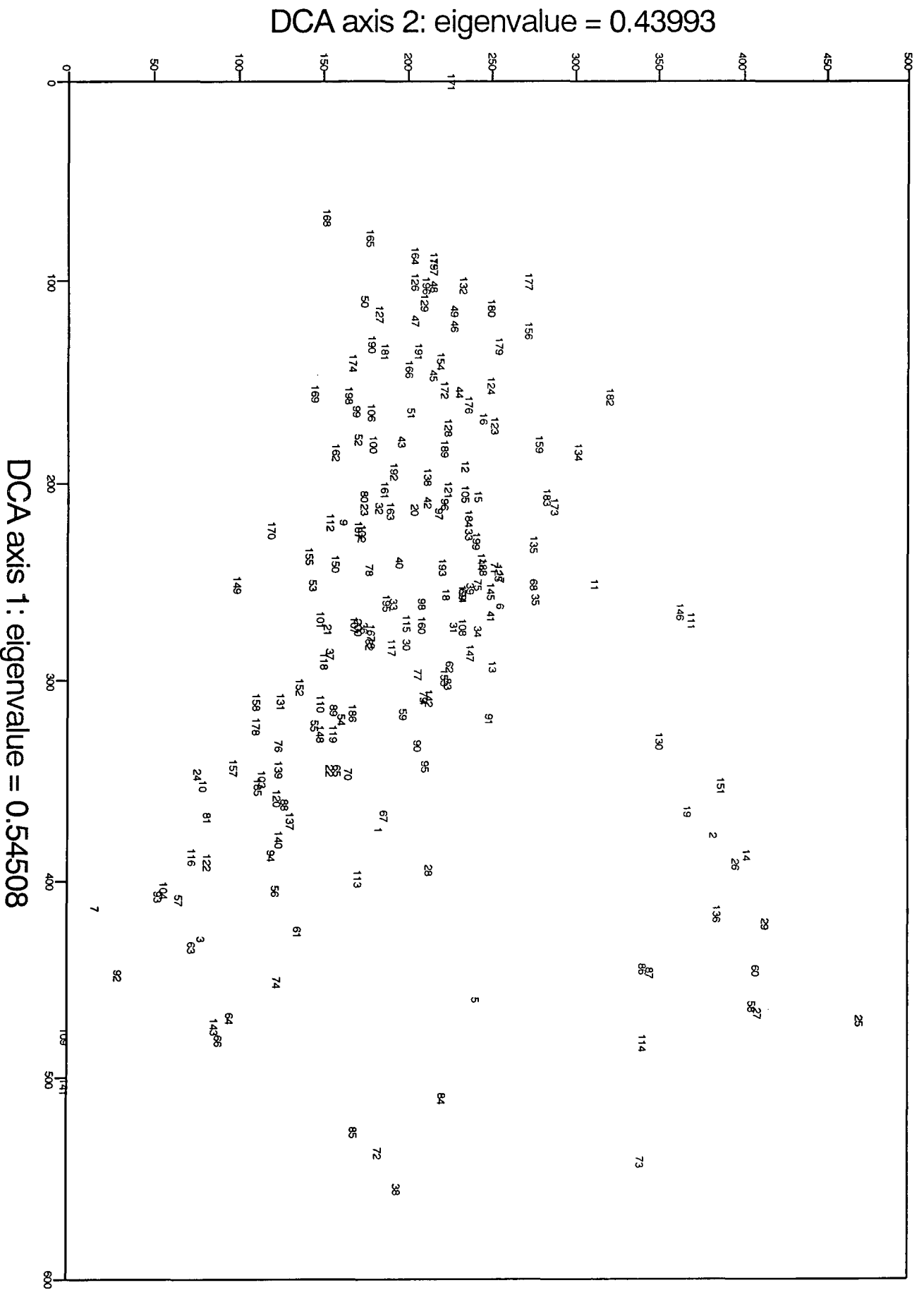


Figure 4: DCA plot of selected species

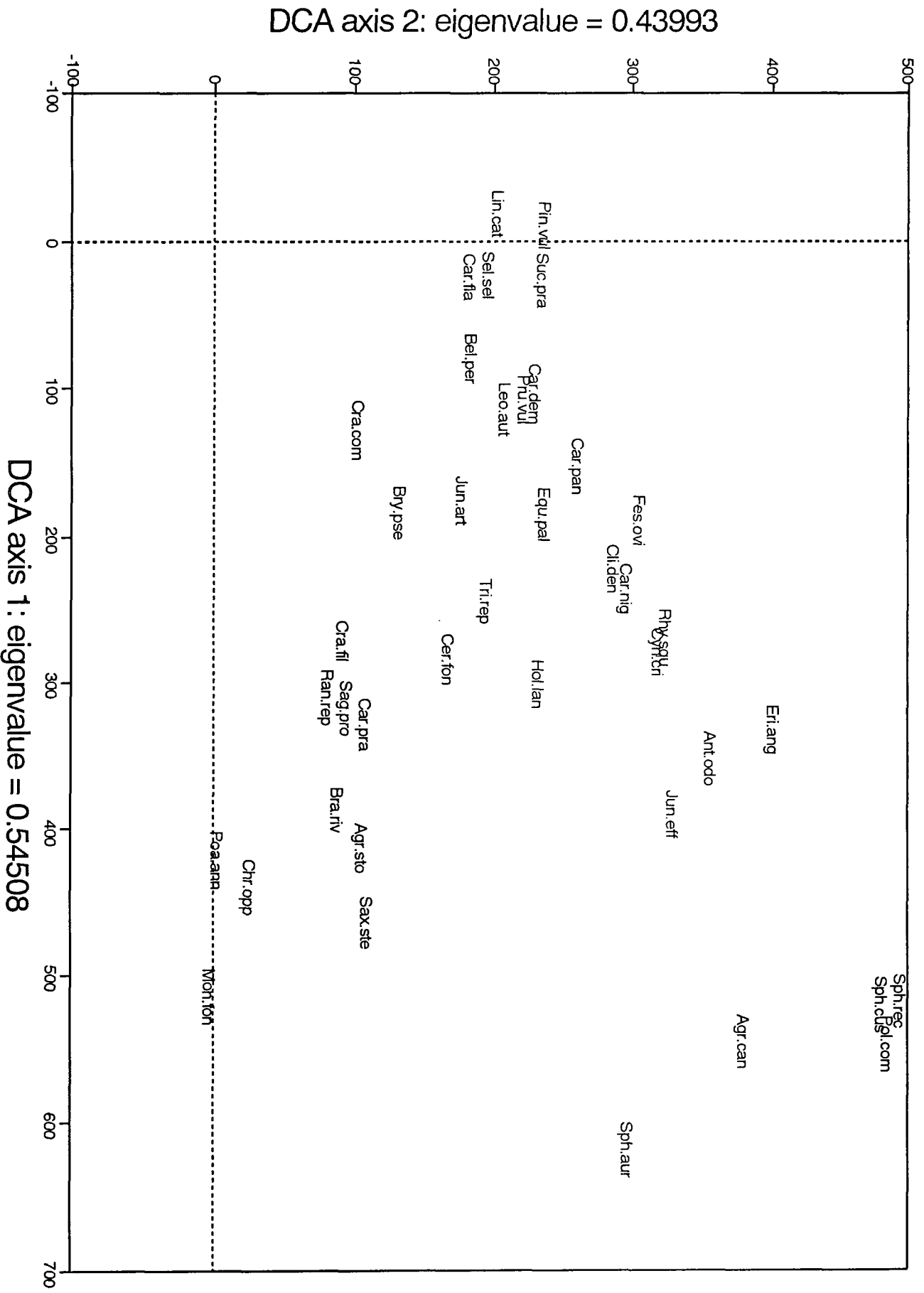


Figure 5: DCA plot of samples displayed as communities

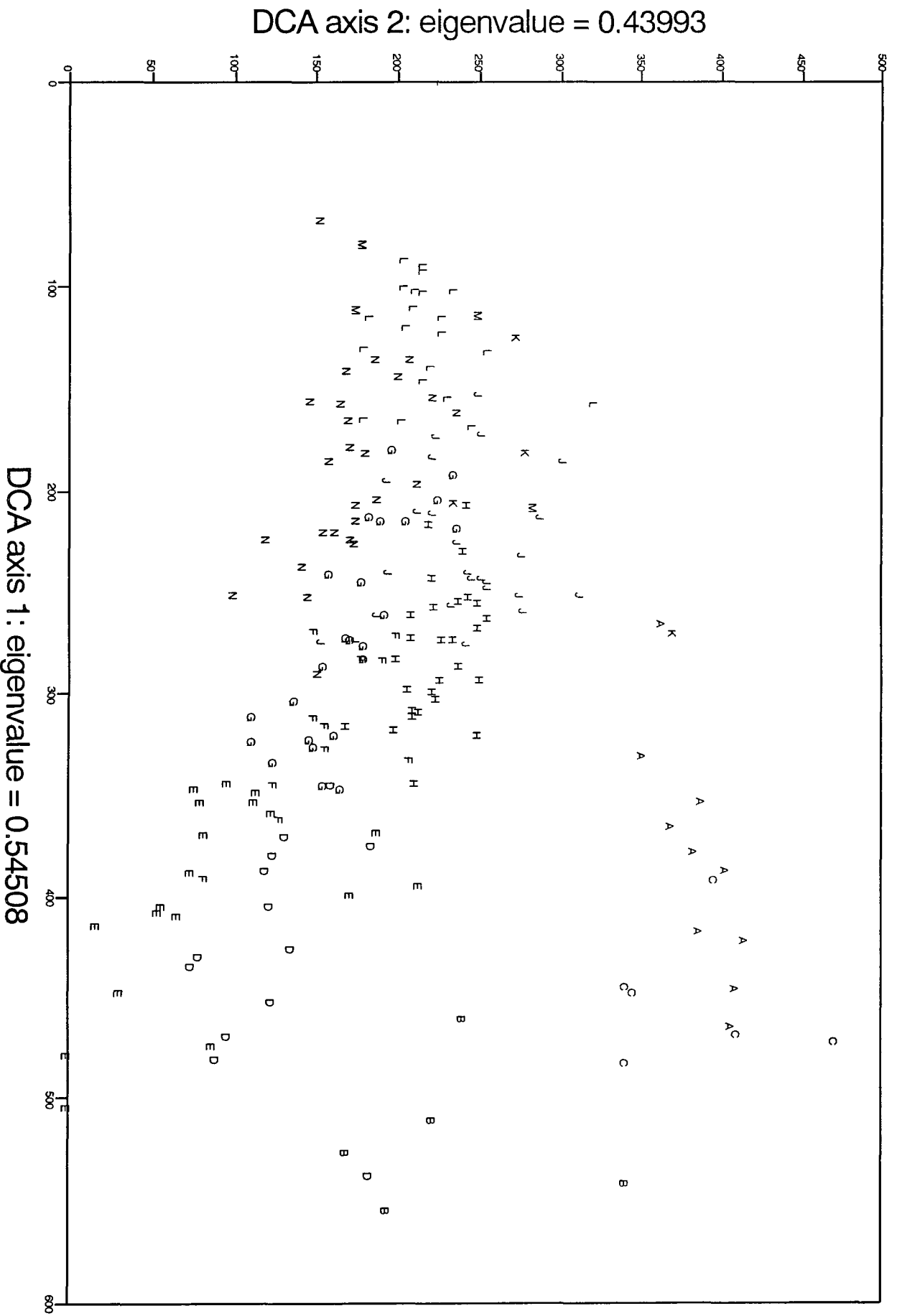


Figure 4 is a simplified plot, showing only the species which are common in a particular community. Species clustering together are found in similar associations and represent similar ecological conditions. For example the cluster at the bottom right of the plot contains *Montia fontana* and *Chrysosplenium oppositifolium* which are typical of wet, mesotrophic spring heads, whilst the cluster to the left of the diagram contains *Linum catharticum*, *Pinguicula vulgaris* and *Selaginella selaginoides* - species characteristic of eutrophic mires. Figure 5 is a plot of sample scores with each point denoted by the community that sample represents (a key to the species abbreviations and community codes is given in Appendix III). Here clusters of each community can be seen, with floristically similar communities close together and often overlapping, such as the *Montia fontana* - *Juncus effusus* spring and the *Montia fontana* - *Stellaria alsine* - *Cardamine pratensis* spring. This plot therefore indicates the floristic relationships between the communities.

Both the species and sample plots show a broad floristic gradient which appears to be related to the pH and conductivity of the samples, with those indicative of oligotrophic habitats such as the *Sphagnum* - *Polytrichum commune* community situated to the right of the plot, whilst eutrophic communities such as the *Carex flacca* - *Leontodon autumnalis* mire are situated to the left of the plot. This is not, however, a clear-cut linear trend and groups of species characteristic of less oligotrophic conditions such as the *Montia fontana* - *Juncus effusus* spring community occupy similar positions on the first ordination axis as the oligotrophic *Sphagnum* dominated communities. The second axis of variation is more difficult to distinguish but could be related to moisture status of the substrate, with species found where surface water is rarely present, such as *Rhytidiadelphus squarrosus* having more positive scores than 'wetter' species and samples. Again, this is not a simple linear trend - for example the damp *Sphagnum* dominated communities also have high second axis scores.

4.3: Canonical Correspondence Analysis

It was not possible to perform CANOCO on all the samples and environmental variables simultaneously since some samples had no soil present, or soil that was completely waterlogged and so lack soil pH values. Conversely, samples where no surface water was present lack data for surface water pH and conductivity. Therefore three separate runs of CANOCO were carried out with Run 1 using only the samples where surface water was present and omitting soil pH as a variable and Run 2 using only the samples with soil pH values and omitting water pH, conductivity and soil type 1 (no soil) as variables. Samples from which both soil and water pH values were obtained were included in both runs. Run 3 included all the samples, but omitted soil pH, water pH and conductivity as

environmental variables. This is not an ideal situation, in that the effects of pH are not directly comparable in all the sample set but if it is important in each of the first two runs, its importance can be inferred for the whole of the sample set. Aspect and herb height were not used in the analysis since it was felt that they showed no apparent trends and herb height appeared to be chiefly a function of the time of year. The environmental variables used in the analysis, together with their values for each sample are summarised in Table 15 (Appendix IV).

Standard runs of CANOCO were carried out in each case, with unrestricted Monte Carlo permutation tests used to test whether the species are significantly related to the environmental variables given. Monte Carlo permutation tests randomise species and environmental data separately between samples and calculate the first eigenvalue for each permutation, which allows a level of significance to be assigned to the first canonical axis (Ter Braak 1988). Species scores have been plotted for each run as have sample scores, which are linear combinations of environmental variables and environmental biplot scores, displayed as arrows. The scores have been multiplied by a multiplier chosen in such a way that the scores displayed lie between -999 and 999. The multiplier used for sample and species scores was 100 whilst that used for environmental biplot scores was 1000 so that the environmental variables were more clearly displayed. This has no effect on the interpretation of the results since it is the relative lengths of the arrows rather than their absolute lengths, which indicates their importance in relation to each other.

4.3.1: CANOCO Run 1 (samples with no surface water present omitted)

A preliminary run was carried out which gave soil type 1 (no soil) as having an inflation factor of 33.4. If the inflation factor of a variable is >20 , then the variable is almost perfectly correlated with the other variables and thus has no unique contribution to the regression equation and does not merit interpretation (Ter Braak 1986). A second run was therefore carried out omitting soil type 1 as a variable in addition to soil pH.

A Monte Carlo test on the first canonical axis gave a significant value ($P = <0.01$) and so it can be inferred that the environmental variables used in the analysis have a significant correlation with the vegetation.

The inter-set correlation values between the environmental variables and species axes consisting of sample scores (Table 16), indicate which variables are the most highly correlated with each axis. Their signs indicate the direction of the gradient. The t-values of the canonical coefficients (Table 17) indicate the significance of the influence of a particular environmental variable. If an environmental variable has both a high inter-set

correlation coefficient and a significant t-value on a given axis, then it can be inferred to have an important effect on the vegetation composition. If however, an environmental variable has a high inter-set correlation coefficient but a non-significant t-value, although a trend may be shown, it will not be significant, possibly because of a high degree of scatter in the data. A significant t-value but a low inter-set correlation coefficient implies that there is a small, but significant trend.

	Axis	1	2	3	4
t - value	Altitude	1.8	-0.2	12.5	-0.7
	Slope	-0.8	5.0	1.8	4.9
	% cover	-1.3	-0.2	-3.7	-3.6
	Limestone	0.8	-6.2	-4.2	-0.6
	Shale	0.4	-7.4	-4.8	-1.7
	Sandstone	2.8	-6.8	-4.0	0.6
	Clay	2.8	1.3	-0.8	-1.9
	Silt	3.0	0.7	0.4	-1.2
	Coarse	2.6	1.5	0.2	-0.7
	Peat	4.1	3.1	1.7	-1.8
	Soil moisture	-3.8	0.3	-0.8	0.7
	Water pH	-7.0	-3.4	3.2	-1.8

Table 16: t-values of canonical coefficients from Run 1 of CANOCO. Significant values (>2.5) are shown in bold. Environmental variables where no values are significant have not been shown.

	Axis	1	2	3	4
	Eigenvalue	0.47208	0.34135	0.29351	0.20899
Inter set correlation	Altitude	0.270	-0.271	0.649	-0.231
	Slope	-0.196	0.134	-0.130	0.393
	% cover	0.042	0.103	-0.086	-0.213
	Limestone	-0.361	0.140	-0.243	0.004
	Shale	0.193	-0.278	0.016	-0.238
	Sandstone	0.535	-0.119	0.048	0.216
	Whin sill	-0.143	0.198	0.385	0.164
	Gravel	-0.052	-0.062	-0.070	0.335
	Clay	-0.204	0.034	-0.203	-0.358
	Silt	-0.088	-0.130	0.223	-0.214
	Coarse	-0.192	0.166	-0.226	0.153
	Peat	0.471	0.485	0.044	-0.275
	Peaty gley	-0.036	-0.101	0.126	-0.091
	Soil depth	0.134	0.268	0.020	-0.587
	Soil moisture	-0.136	0.371	-0.097	-0.431
	Water pH	-0.841	-0.136	0.147	0.021
Conductivity	-0.603	0.139	0.208	-0.162	

Table 17: Inter set correlations from CANOCO Run 1

From the above tables it can be seen that the environmental variables with the highest inter-set correlation coefficients and significant t-values are: water pH, peat and

sandstone for axis 1 and peat for axis 2. Conductivity and soil moisture both have high inter-set correlation coefficients but non-significant t-values, for axis 1 and 2 respectively. Canonical axis 3 appears to be one of altitude. This is illustrated in the species-environment biplot Figure 6 and sample-environment biplot Figure 7 (Explanation of the environmental variable codes is given in Appendix V). Here, the longest arrows are those of water pH, conductivity, peat and sandstone. The close correlation of water pH, conductivity and sandstone with axis 1, is reflected in the biplot with the arrows lying in that direction. In contrast, moisture status is more closely correlated with axis 2 as can be seen from the biplot, whilst peat, important in both axes, lies approximately half way between the two. Axes 3 and 4 have not been shown, since their eigenvalues are lower and thus they are not considered as important.

Figure 8 is a simplified biplot showing only the most 'important' species, i.e., those that are common in a given community. Water pH and conductivity generally have similar effects on species distribution, with high pH values usually correlated with high conductivity values. Thus species characteristic of more eutrophic conditions such as *Selaginella selaginoides* and *Carex flacca* are found on the left hand side of the biplot, whilst those characteristic of more oligotrophic conditions such as *Sphagnum* spp. can be found to the right. Non-limestone bedrock such as shales and sandstone are commonly associated with more acidic conditions and appear on the right hand side of the biplot. Species more often found on peat such as *Sphagnum* spp. and *Eriophorum angustifolium* are grouped in that region. Since the scale used in assessing moisture status has the lowest value, 1 as the wettest, species grouped near the arrowhead can be inferred to be those most characteristic of the 'driest' conditions. Thus species characteristic of wet spring heads such as *Montia fontana* and *Myosotis scorpioides* can be found at the opposite end of the arrow on the biplot. It should be remembered that the environmental variables interact in affecting the distribution of a species and so species associated with a particular environmental factor such as high pH, are not necessarily displayed near the arrowhead because of the effects of other environmental factors.

Figure 9 shows the distribution of samples in relation to environmental variables in terms of the community they represent. (explanation of the community codes is given in Appendix III). The *Sphagnum* dominated communities are shown to be associated with peat and more oligotrophic conditions, whilst the more eutrophic communities such as the *Carex flacca* - *Leontodon autumnalis* flush occur in regions of higher pH and conductivity. 'Wetter' communities such as the *Montia fontana* - *Juncus effusus* spring head tend to cluster in the bottom right hand corner, i.e., at the opposite end of the moisture arrow.

Figure 6: CCA plot of species and environmental variables (Run 1)

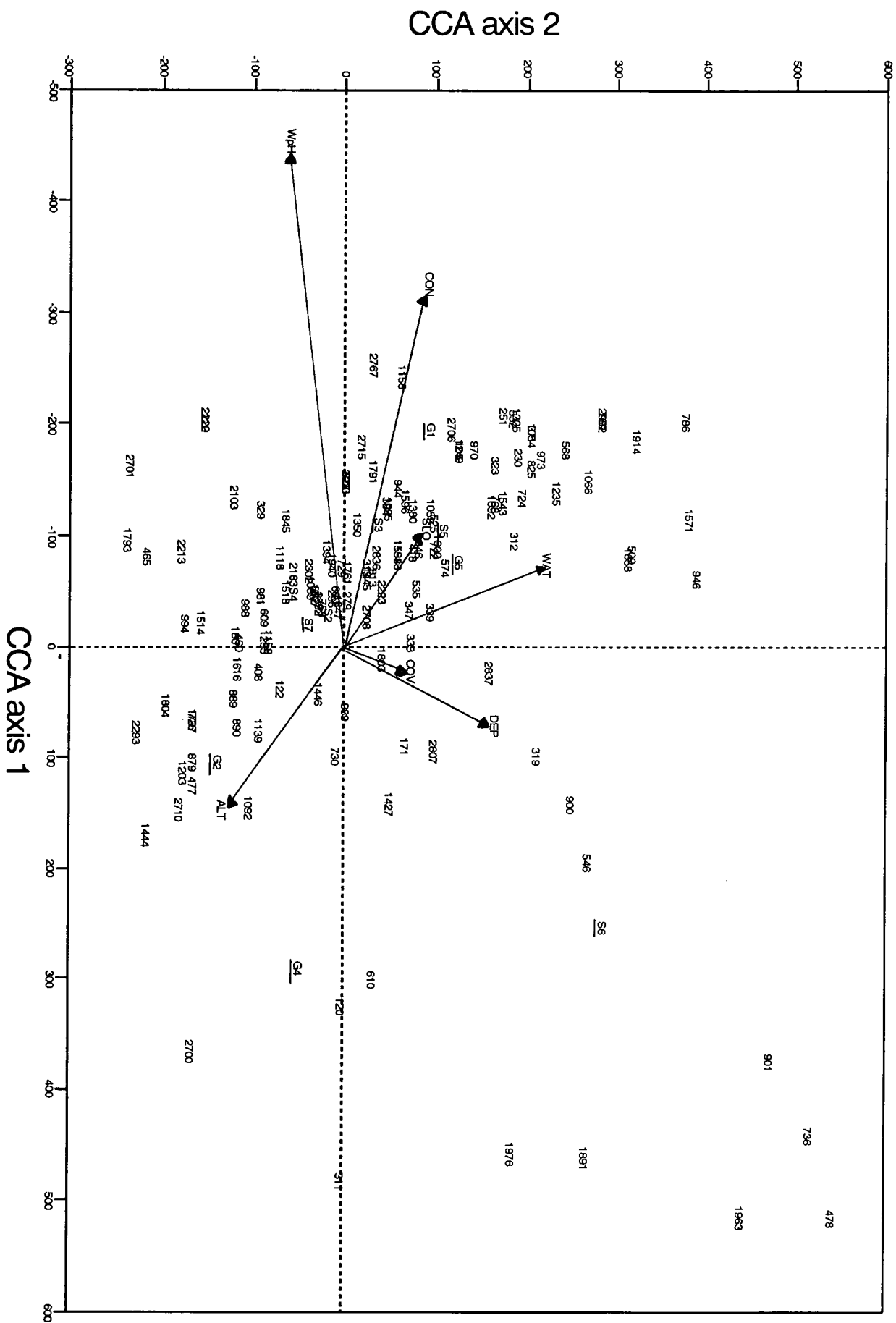


Figure 7: CCA plot of samples and environmental variables (Run 1)

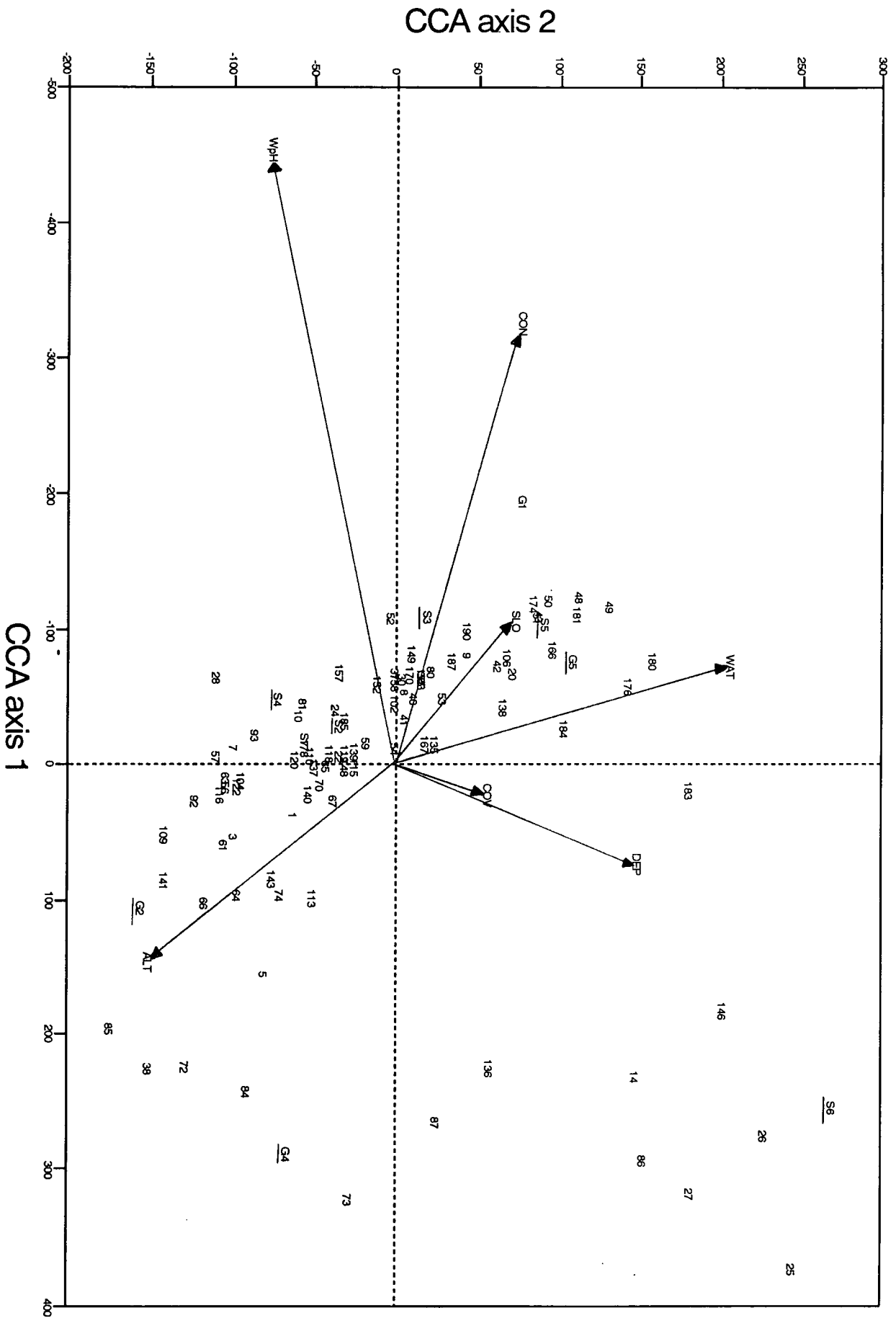


Figure 8: CCA plot of selected species (Run 1)

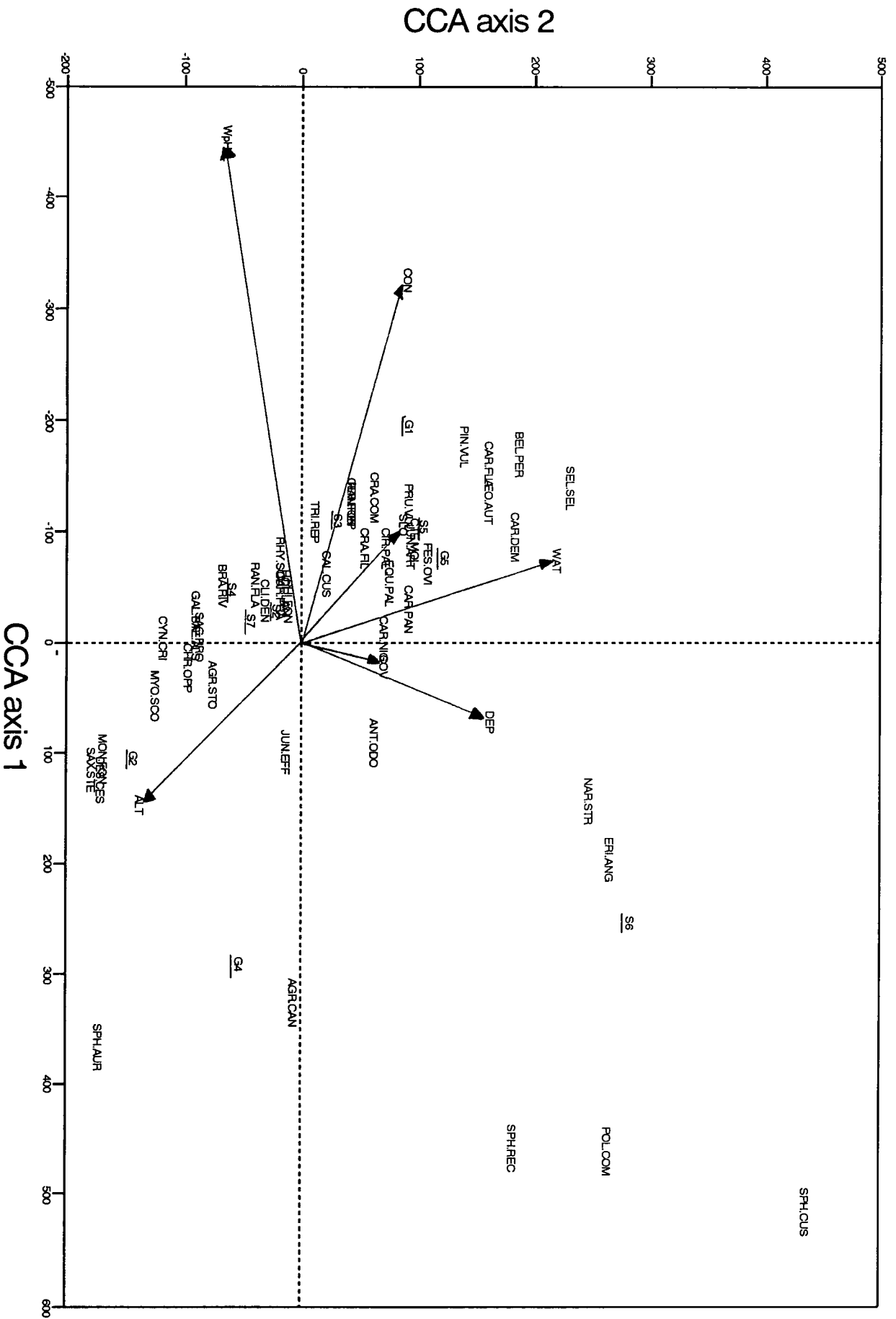
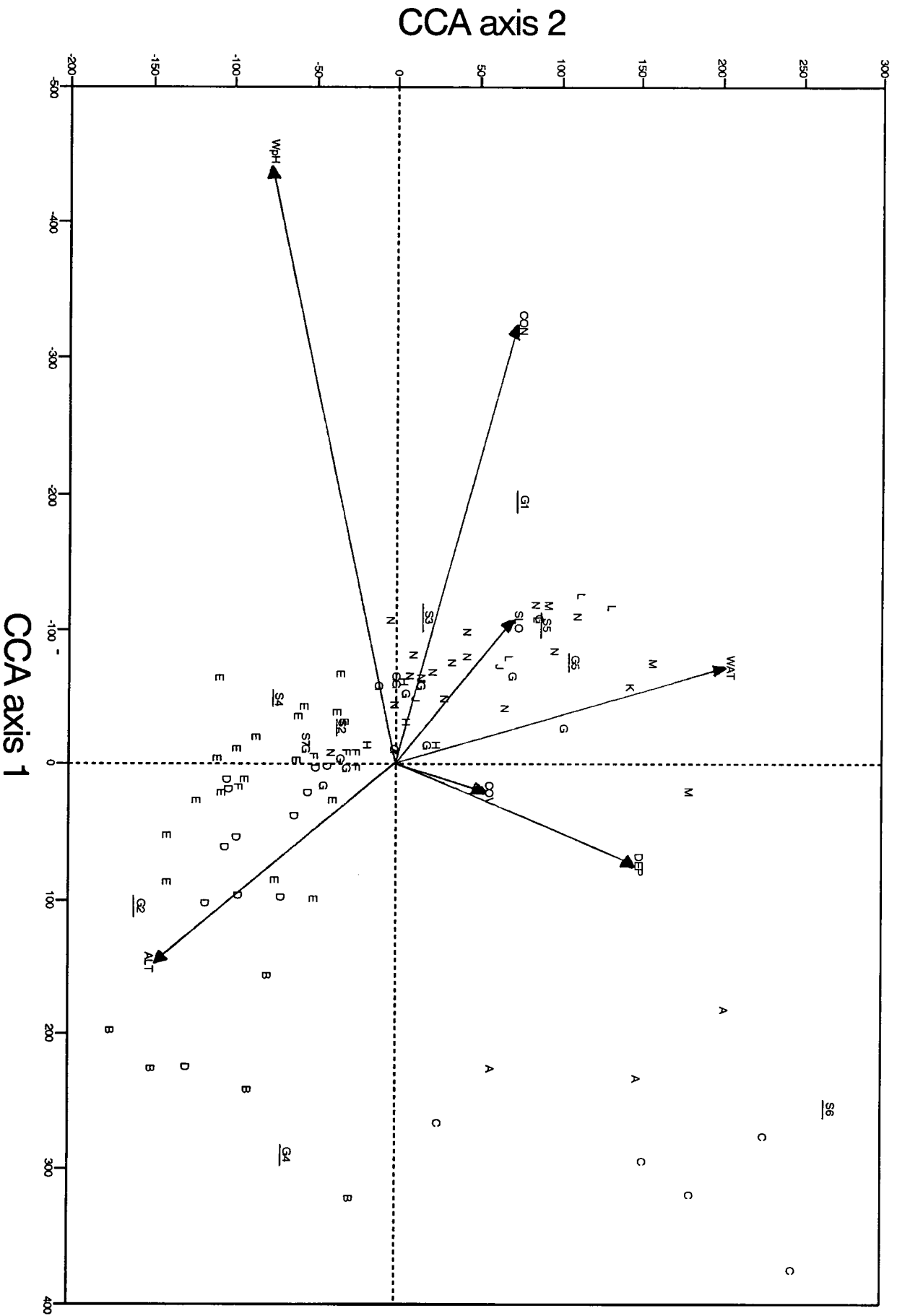


Figure 9: CCA plot of samples displayed by community (Run 1)



4.3.2: CANOCO Run 2 (samples with no soil pH data omitted)

In a preliminary run, soil types 3, 4, 5, 6 and 7 all came out with inflation factors of >20 and so a second run was carried out omitting these variables in addition to water pH, conductivity and soil type 1 (no soil).

A Monte Carlo permutation test on the first canonical axis gave a significant value ($P = <0.01$) and so it can be inferred that the environmental variables used in the analysis had a significant correlation with the vegetation.

t-value	Axis	1	2	3	4
	Altitude	6.0	-11.8	6.6	0.2
Slope	-4.8	2.3	-0.8	0.4	
Limestone	2.3	-3.6	-8.7	10.0	
Shale	2.5	-3.3	-8.1	10.0	
Mill grit	4.1	2.8	-4.0	10.5	
Sandstone	2.4	-2.7	-8.1	8.8	
Whin sill	-1.4	-1.9	-3.4	13.9	
Gravel	-3.8	-3.2	-3.2	2.7	
Soil depth	-0.3	-0.7	-4.7	-0.5	
Soil moisture	-3.8	4.8	-0.7	-0.3	
Soil pH	-12.8	-6.4	-3.5	0.4	

Table 18: t-values of canonical coefficients from Run 2 of CANOCO

	Axis	1	2	3	4
	Eigenvalue	0.35989	0.25395	0.21477	0.18429
Inter set correlation	Altitude	0.239	-0.675	0.249	0.092
	Slope	-0.261	0.063	-0.128	-0.015
	% cover	0.067	0.253	-0.120	0.018
	Limestone	-0.158	-0.103	-0.408	-0.200
	Shale	0.287	-0.074	0.065	0.058
	Mill grit	0.269	0.285	0.016	0.336
	Sandstone	0.142	0.010	-0.061	0.032
	Whin sill	-0.289	0.076	0.466	0.521
	Gravel	0.003	-0.025	0.078	-0.053
	Soil depth	0.327	-0.188	-0.258	0.002
	Soil moisture	-0.375	0.228	-0.055	0.009
	Soil pH	-0.689	-0.336	-0.141	0.001

Table 19: Inter set correlations of environmental variables from CANOCO Run 2

From the above tables, the environmental variables with the highest inter-set correlation coefficients and significant t-values (i.e., those that are most important) are soil pH and soil moisture on axis 1 and altitude on axis 2. Soil pH has a smaller but still significant influence on axis 2 as does altitude on axis 1. Geology appears to be more important in axes 3 and 4.

Figure 10: CCA plot of species and environmental variables (Run 2)

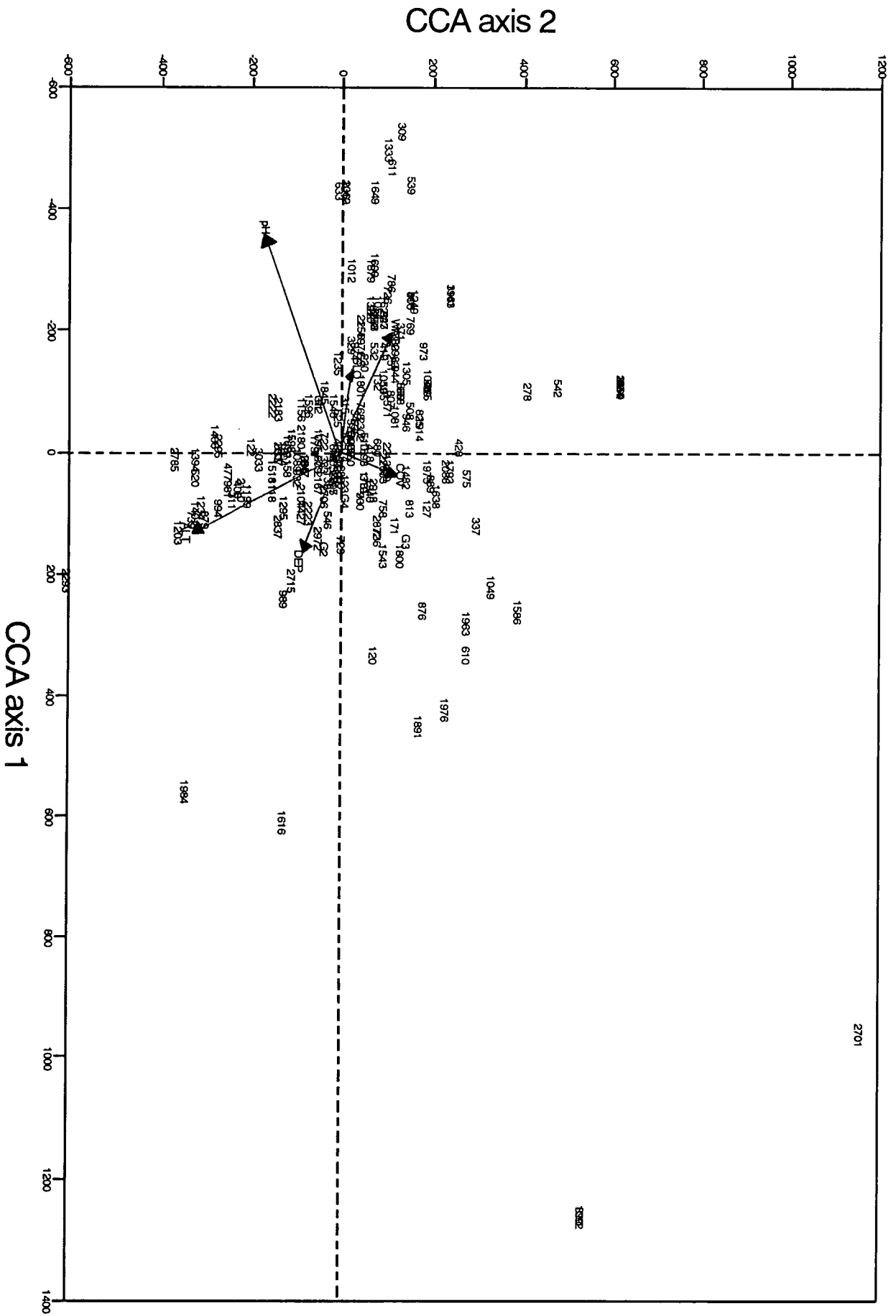


Figure 11: CCA plot of samples and environmental variables (Run 2)

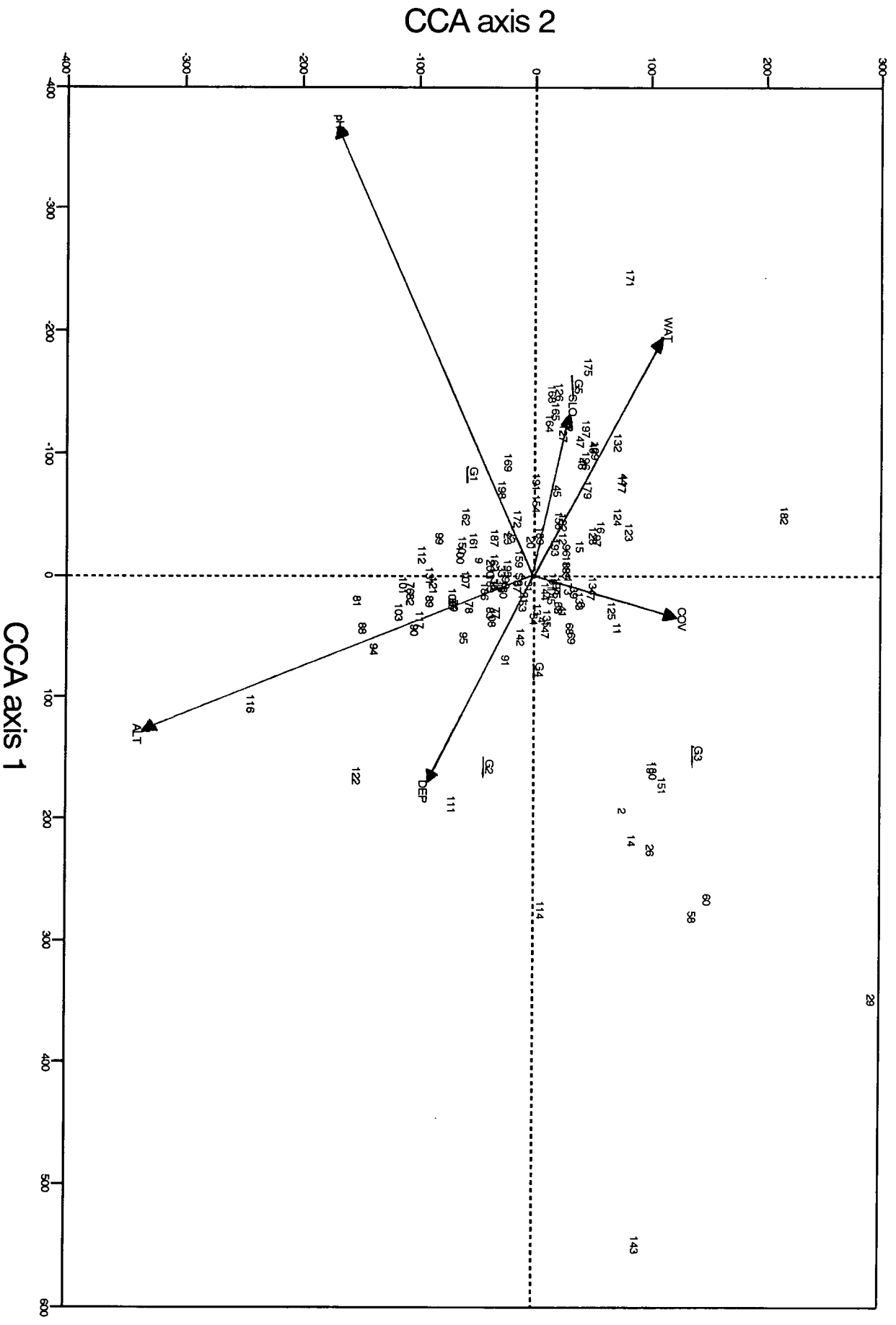


Figure 12: CCA plot of selected species (Run 2)

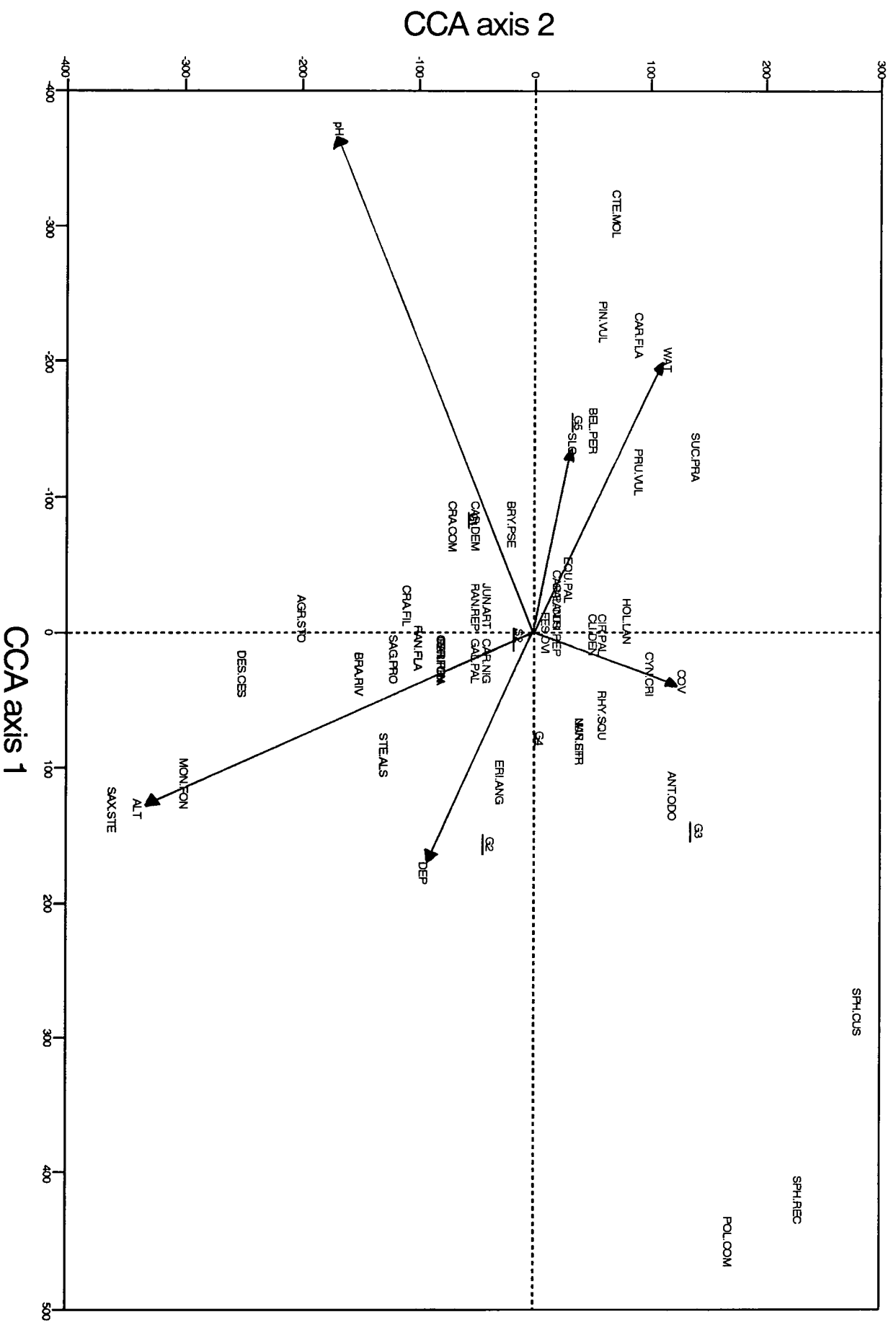
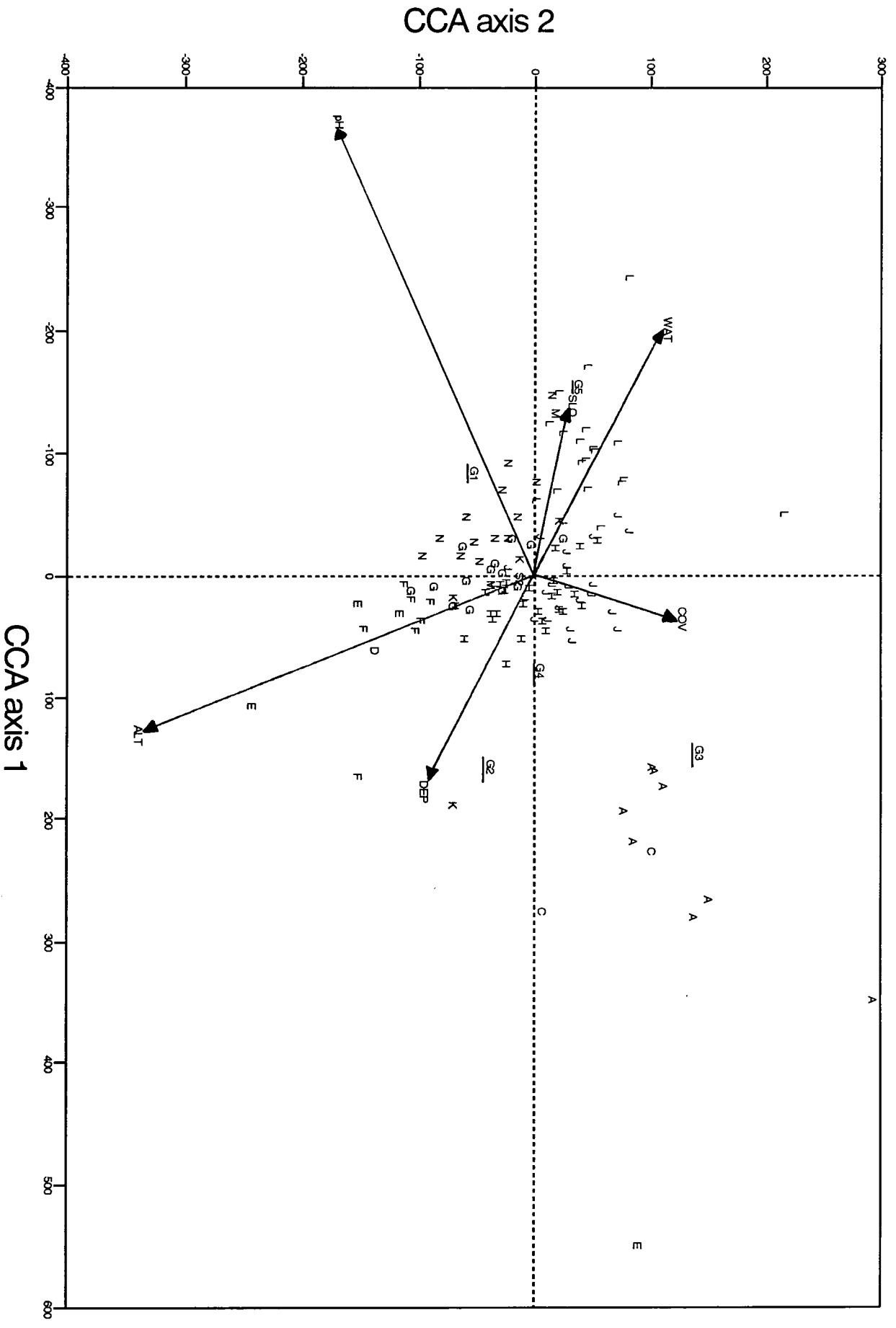


Figure 13: CCA plot of samples displayed by community (Run 2)



This is illustrated in Figure 10 for species and Figure 11 for samples, for the first two canonical axes. Soil pH and altitude have the longest arrows reflecting their importance, with soil pH lying more in the direction of axis 1, with which it is most strongly correlated and altitude lying more in the direction of axis 2.

Figure 12 is a simplified biplot, showing only the most 'important' species i.e., those that are common in a given community. *Sphagnum* spp. and *Polytrichum commune* cluster in the top right hand corner and are characteristic of the most acidic conditions i.e., are at the opposite end of the pH gradient. The presence of G3 (Millstone Grit) in this area is not important since only one relevé was taken from this type of bedrock. *Saxifraga stellaris* is located near the altitude arrowhead which reflects its high-altitude distribution throughout the samples. *Montia fontana* is also situated in this area although its location here reflects wet conditions (i.e., the opposite end of the moisture gradient) rather than high altitudes. Species commonly found in basic habitats which are often relatively 'dry' such as *Ctenidium molluscum* and *Succisa pratensis* form a group towards the top left of the diagram. These species are often found over relatively shallow soils and so also represent the shallow end of the soil depth axis.

A similar pattern is shown in Figure 13 illustrating the distribution of samples in relation to environmental variables in terms of the community they represent. Here the oligotrophic *Sphagnum* dominated communities are clustered at the opposite end of the soil pH axis to the more eutrophic *Cratoneuron commutatum* springs and *Carex flacca* - *Leontodon autumnalis* mires, which have negative first axis scores. Samples of the *Philonotis fontana* - *Saxifraga stellaris* community tend to be clustered towards the centre of the plot because of their generally intermediate moisture status and relatively mesotrophic nature, but nevertheless tend to be located in the bottom right hand section, reflecting the high altitude distribution of this community.

4.3.3: CANOCO Run 3

This run which excludes conductivity, soil pH and water pH as environmental variables, was carried out in order to look at the effects of other environmental variables in the whole sample set. A standard run was performed and a Monte Carlo test on the first canonical axis was significant ($P = <0.01$). Thus the environmental variables used were significantly correlated with the vegetation. The eigenvalues for each axis in Run 3 are slightly lower than for the other two runs, probably because of the omission of pH which emerged as the most important variable in each of the previous runs.

t-value	Axis	1	2	3	4
	Altitude	7.36	8.40	3.35	-9.27
Slope	-6.17	3.88	-0.81	0.15	
% cover	-0.55	-5.04	0.55	-1.47	
Limestone	4.51	-2.86	-7.28	-1.72	
Shale	5.35	-3.81	-6.24	1.97	
Mill grit	3.26	-2.99	-1.30	4.58	
Sandstone	6.06	-4.52	-5.21	3.38	
Whin sill	0.62	3.24	-2.99	2.98	
Peat	0.77	-1.87	4.56	1.49	
Soil depth	0.09	-2.70	-0.39	-4.04	
Soil moisture	-6.77	0.71	-0.74	0.32	

Table 20: t-values of canonical coefficients from CANOCO Run 3

	Axis	1	2	3	4
	Eigenvalue	0.35189	0.23093	0.17829	0.15438
Inter set correlation	Altitude	0.442	0.267	0.137	-0.531
	Slope	-0.206	0.119	-0.228	0.075
	% cover	-0.228	-0.284	0.126	-0.211
	Limestone	-0.286	-0.116	-0.377	-0.165
	Shale	0.323	-0.065	0.097	-0.018
	Mill grit	0.074	-0.142	0.138	0.194
	Sandstone	0.296	-0.128	0.112	0.131
	Whin sill	-0.174	0.450	0.289	0.169
	No soil	0.412	0.233	-0.143	0.286
	Gravel	0.165	0.072	-0.116	0.282
	Clay	-0.130	-0.193	-0.120	-0.364
	Silt	-0.178	0.161	-0.098	-0.158
	Coarse	-0.180	0.114	0.003	0.174
	Peat	0.070	-0.308	0.502	0.184
	Soil depth	-0.062	-0.412	0.231	-0.443
Soil moisture	-0.614	-0.151	0.038	-0.254	

Table 21: Inter set correlations of environmental variables from CANOCO Run 3

From the above tables the most important environmental variables, with the highest inter-set correlation coefficients and significant t-values are soil moisture, altitude and geology on axis 1 and soil depth and geology on axis 2. This is reflected in Figures 14 & 15, the biplots for environmental variables with species and samples respectively. Moisture status and altitude have the longest arrows and both lie in the direction of axis 1 indicating their significance on this axis. Similarly soil depth lies in the direction of axis 2 as does Whin Sill bedrock.

Figure 16 is a simplified biplot showing only the most 'important' species i.e., those that are common in a given community. Species with negative first axis scores are typically those

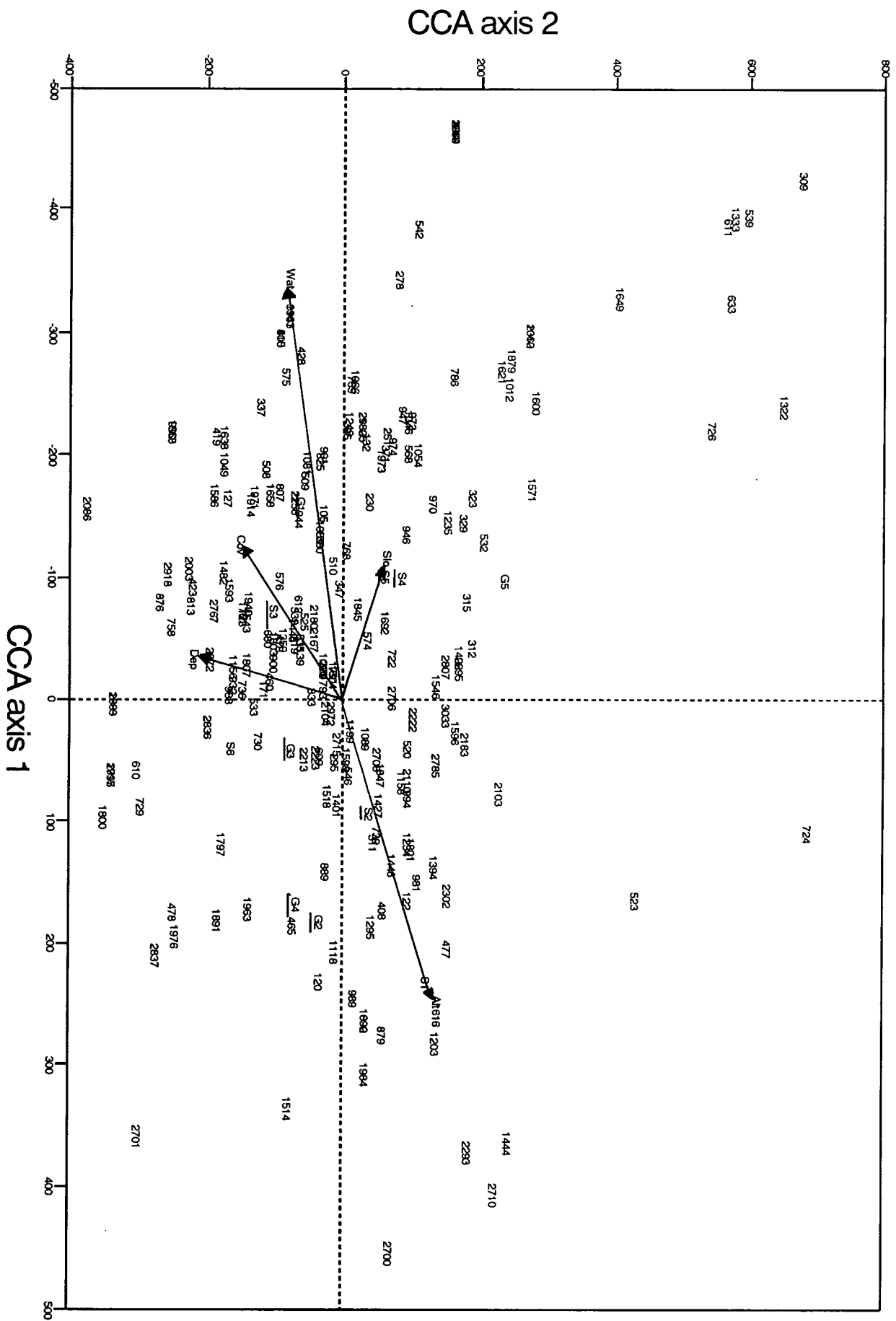


Figure 14: CCA plot of species and environmental variables (Run 3)

Figure 15: CCA plot of samples and environmental variables (Run 3)

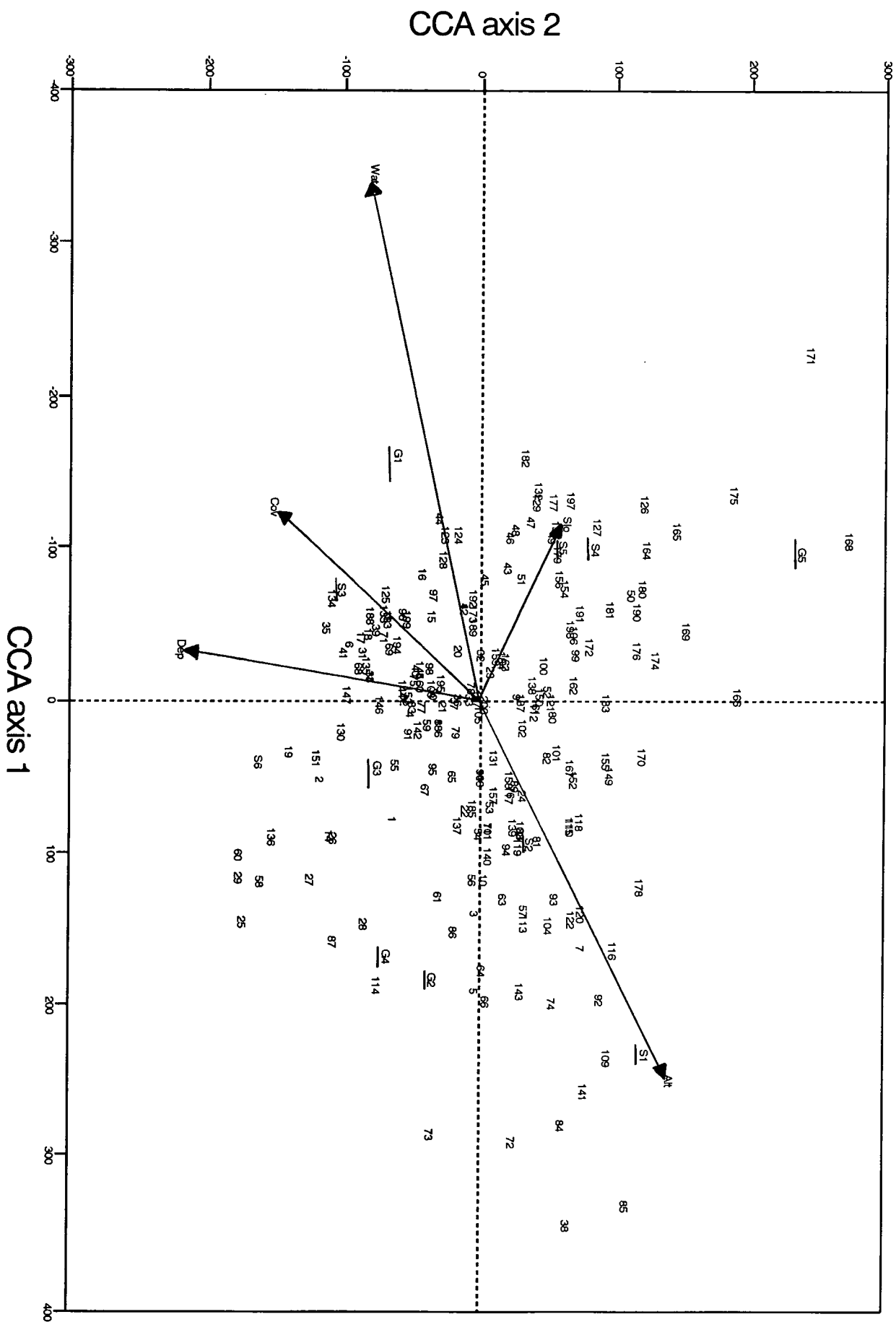


Figure 16: CCA plot of selected species (Run 3)

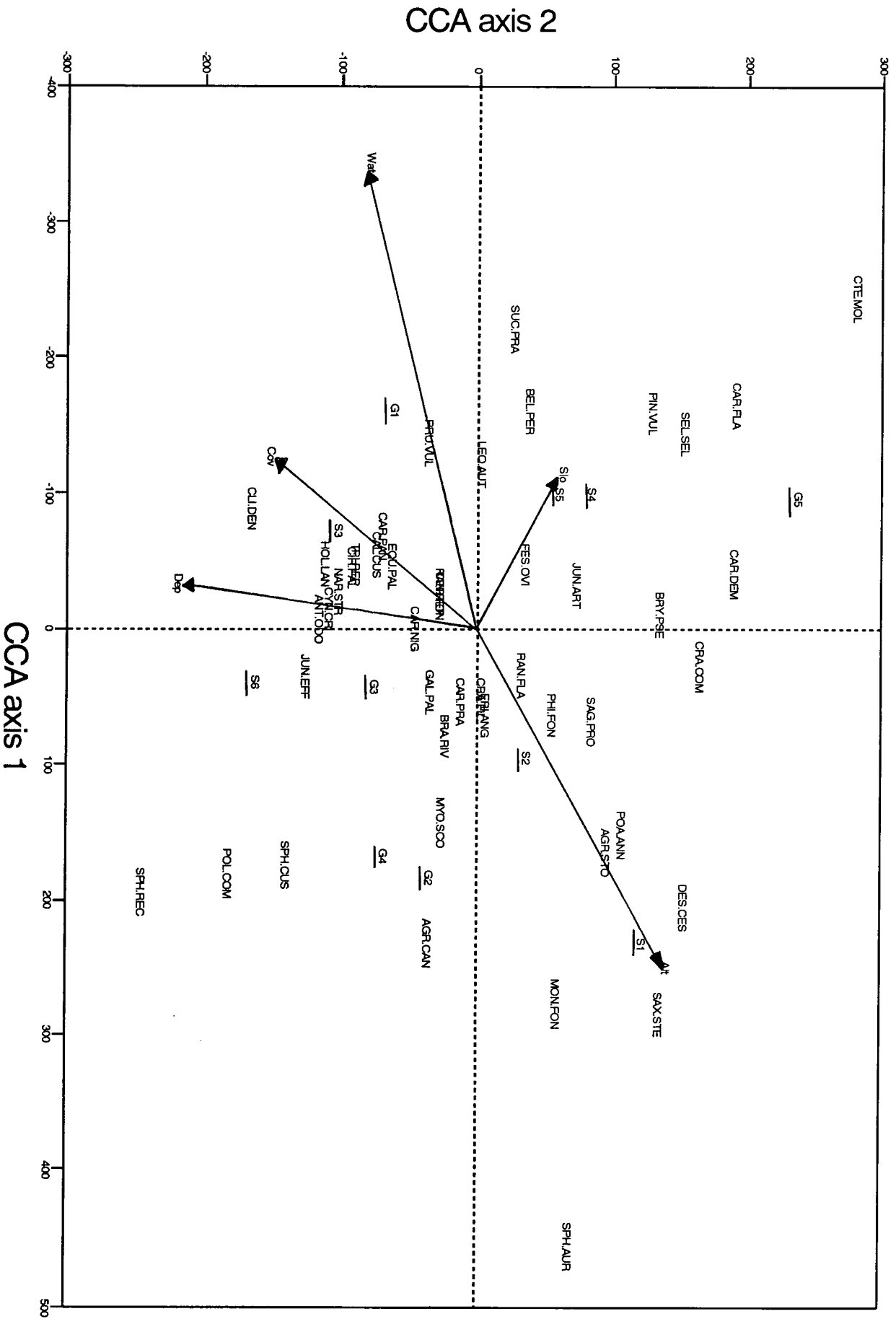
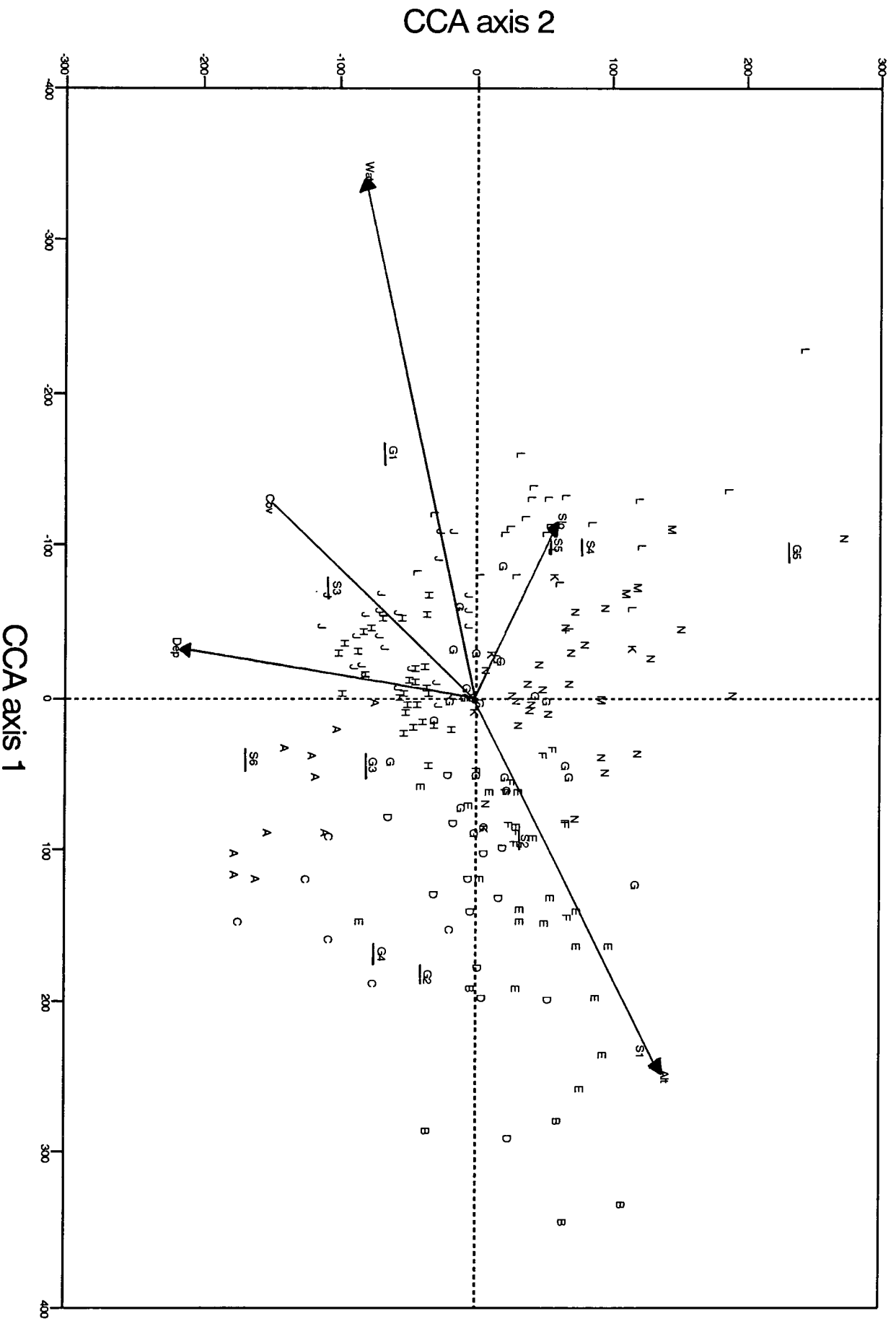


Figure 17: CCA plot of samples displayed as communities (Run 3)



characteristic of 'drier' conditions such as *Ctenidium molluscum* and *Climacium dendroides* whilst typical spring head species such as *Montia fontana* and *Myosotis scorpioides* lie at the opposite end of the arrow also associated with soil type 1 (no soil). *Sphagnum auriculatum*, a species always found in 'wet' habitats is located at the far end of the arrow. *Deschampsia cespitosa* and *Saxifraga stellaris*, both largely confined to high altitudes in the study, are located by the altitude arrow head. Despite the fact that pH was not used in this run of CANOCO, species characteristic of higher pH habitats are grouped in the top left section.

This pattern is reflected when samples are displayed according to the community they represent (Figure 17), with the 'wet' *Montia* dominated springs at the opposite end of the moisture gradient from the relatively 'dry' *Juncus effusus* - *Cardamine pratensis* and *Calliargon cuspidatum* - *Carex* mires. The high altitude *Philonotis fontana* - *Saxifraga stellaris* spring lies in the direction of the altitude arrow, but is not near the arrowhead, possibly because such springs are not necessarily as 'wet' as those dominated by *Montia* nor are they necessarily associated with soil type 1 (no soil). More oligotrophic *Sphagnum* dominated communities lie in the same direction as more acidic bedrocks such as sandstone. Conversely, the more eutrophic communities such as the *Carex flacca* - *Leontodon autumnalis* mire lie in the general direction of Whin Sill, commonly associated with relatively calcicolous communities in Upper Teesdale despite the fact that Whin Sill itself is not a calcareous rock type. Whin Sill is, however, impervious and so calcareous drainage water from the nearby limestone may be forced to 'flush out' on contacting the Whin Sill. Thus an indirect pH gradient could be said to operate in the form of associated bedrock, even though pH was not used as an environmental variable here.

5: DISCUSSION

5.1: The Plant Communities

A summary of the communities defined in the study is given in Table 22, which highlights the relationships between them. From this it appears that the vegetation is essentially a continuum, within which the delimitation of the vegetation types is inevitably somewhat arbitrary. This is supported by the ordination diagram of samples in terms of the communities they represent (Figure 5) which illustrates how certain communities which occupy a similar place in the multidimensional space, are essentially similar. As discussed by Poore (1955), McVean & Ratcliffe (1962), Birks (1973) and Huntley & Birks (1979), the vegetation types delimited should be regarded as convenient 'reference points' within

a field of more or less continuous variation and not as discrete units that can be traced from one area to another.

Some communities which have been described, such as the *Carex nigra* - *Eriophorum angustifolium* mire, have no direct equivalent in the literature. No prejudgement was made as to the nature of the vegetation in relation to that described in other studies nor was any attempt made to 'fit' it into any previously described unit. Since the delimitation of communities is somewhat arbitrary, it is thus not surprising that some of the communities are unique to this study. Although Eddy *et al* (1969) described the vegetation of Moor House NNR, and Pigott (1956) and Jones (1973) described that of Upper Teesdale, no previous studies have outlined the soligenous mire and spring vegetation of the whole of the North Pennines. Studies in other regions such as Cader Idris, Wales (Edgell 1969) and the Scottish Highlands (McVean & Ratcliffe 1962) may describe different mire and spring vegetation types because of differences between the regions, for example in geology, altitude and oceanicity of climate. Thus it is also possible that some of the communities outlined here simply may not occur in other areas.

5.2: Factors influencing vegetation composition

Although the Canonical Correspondence Analysis had to be carried out separately for samples with no surface water present and those with no soil, both showed pH as being the most important environmental variable and so it can be concluded that pH is of major importance in influencing the vegetation composition. Other factors that emerged as being important were: soil moisture status, altitude and to a lesser extent, bedrock and soil type.

Sjörs (1950) describes the variation in Swedish mire vegetation from 'poor fen' (oligotrophic) to 'rich fen' (eutrophic) as being closely related to the acidity and base content of the mire waters. Although he found a definite correlation between pH and vegetation composition, he did not take this to mean that the vegetation composition is strictly determined by pH. A high salt content, measured as electrical conductivity, was generally combined with 'rich fen' vegetation, but the latter was not always dependent on the former, and he concluded that salt content had a less direct influence on vegetation composition than pH.

Table 22: Summary of community data (translation of species abbreviations and community codes is given in Appendix III)

Community	A	B	C	D	E	F	G	H	J	K	L	M	N
No. Relevés	10	5	6	12	19	9	24	28	26	4	22	4	26
Mean sp/sam	9	5	6	11	11	21	15	20	21	8	23	4	13
Sph. rec	V	-	III	-	I	-	-	-	I	-	-	-	-
Pol. com	V	II	V	-	-	-	I	I	-	I	-	-	-
Jun. eff	IV	I	I	V	I	-	II	V	II	-	I	-	I
Sph. aur	-	V	-	I	-	-	-	I	-	-	-	-	-
Agr. sto	-	IV	III	II	II	II	II	II	I	-	I	-	III
Sph. cus	-	-	III	-	-	-	-	-	-	-	I	-	-
Agr. can	II	I	III	II	I	I	I	I	I	-	-	-	-
Mon. fon	-	-	I	V	III	IV	II	-	I	-	-	-	I
Ste. als	-	I	-	IV	IV	I	II	I	I	-	-	-	-
Chr. opp	-	-	-	III	III	II	I	II	I	-	-	-	I
Car. pra	-	I	-	III	III	V	V	V	IV	-	I	-	IV
Poa. ann	-	-	-	I	III	II	I	I	I	-	-	-	I
Bra. riv	-	-	-	II	III	II	I	III	I	-	-	-	-
Phi. fon	-	-	-	II	II	V	IV	III	III	-	I	-	II
Sax. ste	-	II	II	I	II	V	I	I	-	-	-	-	-
Fes. ovi	III	-	I	-	I	V	IV	III	III	III	IV	II	IV
Cer. fon	-	-	-	I	II	IV	III	V	IV	-	I	-	I
Car. nig	III	-	I	II	I	IV	IV	IV	IV	V	III	-	III
Des. ces	-	II	II	I	II	IV	I	I	I	-	I	-	I
Cra. fil	-	-	-	I	I	IV	II	I	I	-	I	-	II
Jun. art	I	-	-	I	II	III	IV	III	III	II	IV	IV	IV
Tri. rep	-	-	-	II	II	I	III	V	V	-	II	-	II
Bry. pse	-	-	-	-	II	II	III	I	I	-	III	-	IV
Ran. rep	-	-	-	II	-	II	III	IV	II	-	II	-	II
Sag. pro	-	-	-	-	I	II	III	I	I	-	I	-	-
Cal. cus	-	-	-	II	I	II	II	V	IV	-	II	-	I
Ant. odo	IV	I	II	II	II	II	II	IV	IV	-	I	-	I
Rhy. squ	I	-	-	I	-	-	I	IV	III	-	II	-	-
Gal. pal	-	-	-	III	II	II	I	III	I	-	-	-	I
Cli. den	-	-	-	-	-	-	I	III	III	-	I	-	I
Cir. pal	-	-	-	II	I	I	II	III	III	-	II	-	II
Equ. pal	II	-	-	-	II	III	II	III	III	III	IV	II	III
Hol. lan	I	I	-	II	-	I	II	III	III	-	II	-	I
Car. pan	I	-	-	-	-	I	I	I	IV	IV	II	-	II
Leo. aut	-	-	-	-	-	I	II	II	III	-	V	-	II
Cyn. cri	I	-	I	-	I	I	I	II	III	-	I	-	I
Pru. vul	-	-	-	-	-	-	II	II	III	-	IV	-	I
Eri. ang	I	-	II	I	-	I	I	I	I	IV	I	II	I
Car. fla	-	-	-	-	-	-	I	-	I	-	V	IV	II
Sel. sel	-	-	-	-	-	I	I	-	-	-	IV	-	I
Bel. per	-	-	-	-	-	-	II	I	--	-	III	-	I
Pin. vul	-	-	-	-	-	-	-	-	-	-	III	II	-
Suc. pra	-	-	-	-	-	-	-	-	-	-	III	-	-
Cte. mol	-	-	-	-	-	-	-	-	-	-	III	-	I
Lin. cat	-	-	-	-	-	-	-	-	-	-	III	-	I
Cra. com	-	-	-	-	I	II	II	I	I	II	II	II	V
Car. dem	-	-	-	-	-	I	II	I	I	III	II	III	III

It was beyond the scope of this study to conduct detailed analyses of soil chemistry and determine levels of nutrients such as Calcium, Magnesium, Nitrogen and Phosphorus, but several previous studies have measured these and discussed their effects on vegetation composition. In his examination of the distribution of Scottish mountain plants, Ferreira (1959) found that Calcium status was the most important soil factor. The available calcium status of a soil depends greatly on the speed with which calcium is released from the parent rock. Calcium is released most rapidly and is thus most readily available to plants when it is present as calcium carbonate (Ferreira 1959). McVean & Ratcliffe (1962) suggested that, subject to the occasional discrepancy, calcium status is closely correlated with pH. Geology is obviously important here and McVean & Ratcliffe (1962) showed the distribution of more eutrophic vegetation to virtually represent a map of the occurrence of calcareous bedrock in the Scottish Highlands. Therefore abundance of limestone as a bedrock offers some explanation as to the preponderance of relatively eutrophic mire and spring vegetation in the North Pennines.

Although some species such as *Carex nigra* and *C. panicea* have a wide ecological amplitude, being able to grow in a range of soil conditions, the presence in a stand of certain species which have a more restricted range of tolerance of pH and base status, can give an indication of the soil base status. A broad indication of the acidity and calcium status of mires can be given by their bryophyte flora. Poorer mires are generally dominated by *Sphagnum* spp. whilst those that are more eutrophic are characterised by large pleurocarpous mosses, the so-called 'brown mosses', such as *Cratoneuron commutatum* and *Drepanocladus revolvens* (Ratcliffe 1964).

Bryophyte flushes developed over rocky beds or springs have been used as a 'natural experiment' by Bell & Lodge (1963) to test the reliability of *Cratoneuron commutatum* as an indicator of base-rich conditions. *Cratoneuron commutatum* was found in waters of a wide range of calcium concentrations, but appeared to be limited below 0.5m.e./l. At Ca levels of <1.0m.e./l, the moss was more likely to be present at high rather than low magnesium levels. From this they concluded that the presence of the moss does indicate base-rich conditions, but does not necessarily indicate high levels of calcium.

'Exacting Calcicoles' have been defined by McVean & Ratcliffe (1962) as species confined to soils with a pH >6.0 and exchangeable calcium levels of >300mg/100g and include *Carex lepidocarpa*, *C. capillaris* and *Philonotis calcarea*, all species which were confined to the most eutrophic communities such as the *Carex flacca* - *Leontodon*

autumnalis mire in the present study. 'Calcicoles' require soils with a pH >4.8 and exchangeable calcium levels of >30mg/100g. Several species encountered in this study fall into this category, including, *Carex dioica*, *Ctenidium molluscum* and *Selaginella selaginoides*. Some species grow equally well where magnesium replaces calcium as the predominant cation and are termed 'basiphiles', in that they are restricted to base-rich soils (Ferreira 1959). Examples of these include *Carex flacca* and *Juncus triglumis*. Species defined by McVean & Ratcliffe (1962) as 'Calcifuges' indicate the poorest soils, with a pH usually of <4.5 and exchangeable calcium levels of <30mg/100g and include, *Carex curta*, *Sphagnum auriculatum* and *Sphagnum cuspidatum*.

Some species change their nutrient requirements in different parts of their range, generally tending to become more exacting and calcicolous towards their geographical limits (Ratcliffe 1964). For example, *Eriophorum angustifolium*, reported by Malmer (1962) to be limited to richer fen communities in Sweden, can be found in both oligotrophic bogs and eutrophic soligenous mires in the North Pennines. The causes of these differences in edaphic tolerances within the geographical range of a species are not fully established, but it is possible that different climatic areas may produce physiological adaptations in some species or that genotypic variation may produce locally adapted races (Birks 1973).

McVean & Ratcliffe (1962) and Brown *et al.* (1993a, 1993b) explain some of the principal vegetation gradients in the Scottish Highlands in terms of the oceanicity of climate, which increases westwards. Although no such gradient is obvious in the North Pennines, a smaller geographical area, small-scale differences in climate are nonetheless important. The altitudinal gradient detected in this study is related to climate, and the associated temperature decrease with an increase in altitude has several effects including a shortened growing season and longer period of snow lie (The mean lapse rate, that is the rate at which temperature decreases with an increase in altitude is given by the Meteorological Office as 6.0°C per 1000m elevation). The geographical and altitudinal distribution of many montane plants suggests that their lower limits result from an intolerance of a warm climate. Dahl (1951) correlated the lower limits of some arctic-alpine species in Fennoscandia with the isotherms of maximum summer temperature. Another possibility is that many montane plants are absent from lower ground not because of temperature intolerance but because they cannot withstand competition from tall shrubs and trees (McVean & Ratcliffe 1962).

According to Ratcliffe (1977), soligenous mires differ from lowland topogenous mires in having a vascular plant sward of much lower stature, which appears to be a result of the

heavy grazing that characterises the British uplands. The North Pennines are no exception, and evidence of grazing by sheep and occasionally cattle, noted as nibbled vegetation, the presence of dung, or the animals themselves, was observed in the vicinity of every stand sampled. Grazing was omitted as an environmental variable from the Canonical Correspondence Analysis, partly because it was a universal phenomenon and partly because grazing pressure was extremely difficult to quantify. Ratcliffe (1977) suggests that on poorer mountains, flushed sites may well carry the most palatable vegetation and be selectively grazed. He also notes that grazing tends to suppress shrub and tree growth and suggests that probably most British soligenous mires below the tree-line (640m in the Cairngorms and lower in more western areas) would carry growths of willow and possibly birch in the absence of grazing.

5.3: Conservation, threats and the future

The soligenous mires and springs of the North Pennines support several rare species. Species that are nationally scarce, occurring in 16-100 10km grid squares, found in the study are shown in Table 23. A list of all vascular plants and bryophytes found in the study is given in Appendix II.

Species	No. of 10km squares
<i>Carex capillaris</i>	70
<i>Equisetum variegatum</i>	89
<i>Galium sternerii</i>	81
<i>Juncus biglumis</i>	21
<i>Primula farinosa</i>	58
<i>Sedum villosum</i>	75

Table 23: Nationally scarce species found in the study

Although not recorded in this study, the Red Data Book species *Saxifraga hirculus* & *Kobresia simpliciuscula* have both been reported from localities in the North Pennines from which samples were taken. WiddyBank Fell in Upper Teesdale, which was not sampled because access permission was not granted, is renowned for its flush vegetation, playing host to several rarities, including *Minuartia stricta* for which there is no other British locality.

Several species found in the study (Table 24) are of phytogeographical interest and represent Northern montane, Arctic-alpine and Alpine elements. Northern montane species have their distribution centred on northern Europe and are restricted to sub-montane and montane zones in central and southern Europe. Arctic-alpine species are

found in arctic and sub-arctic regions in addition to high altitude areas of central Europe, whilst alpine species have their distribution centred on central European mountains and are mainly absent from northern European and arctic areas.

Upper Teesdale has been famed for over a century as a locality for several rare and phytogeographically disjunct species known as the 'Teesdale assemblage'. Reasons as to why species from widely different phytogeographical groups have been able to survive and flourish within this relatively small area have been under discussion for a considerable time. Godwin (1949) suggested that they might be the remnants of a late-glacial vegetation which had migrated northwards as the climate improved. Macrofossils of *Thalictrum alpinum* have been found in southern England, which provides evidence for the changing distribution of this species. Johnson *et al.* (1971) have explained the survival of the flora since then, as due to a combination of unique bedrock, the severe climate of the Teesdale fells and more or less continuous grazing of the area which has maintained areas free of trees suitable for these species which tend to be shade-intolerant. Jeffrey & Pigott (1973) suggested that the low level of phosphorus in the soils developed over limestone in Teesdale may contribute to the survival of the flora.

Phytogeographical element	Species
Northern montane	<i>Alchemilla glabra</i> <i>Carex ovalis</i> <i>Coeloglossum viride</i> <i>Equisetum variegatum</i> <i>Poa subcaerulea</i>
Arctic-alpine	<i>Carex capillaris</i> <i>Epilobium anagallidifolium</i> <i>Juncus triglumis</i> <i>Polygonum viviparum</i> <i>Saxifraga stellaris</i> <i>Selaginella selaginoides</i> <i>Thalictrum alpinum</i>
Alpine	<i>Cochlearia pyrenaica</i>

Table 24: Species of phytogeographical interest (from Graham 1988).

Soligenous mires and springs are not only significant in botanical terms but may also be important for upland birds. The presence of a spring and associated mire vegetation in an area of otherwise dry grassland or heather moorland may provide feeding sites for

waders such as Redshank and Curlew. The distribution of Snipe in Sutherland is affected by the distribution of suitable feeding habitats - wet rank flushes with an abundant cover of *Juncus* spp. (NCC 1987). Presumably this type of habitat is also important for Snipe in the North Pennines. Ratcliffe (1977b) noted that Golden Plovers breeding in montane terrain show some tendency to feed in flush bog and spring complexes, although they seldom nest on such ground and may fly some distance from their nests to reach the feeding ground.

Although the number of species found in a single stand may not be high, particularly in more oligotrophic mires, the total number of species associated with soligenous mire and spring vegetation is high in comparison with other vegetation types. Taking the study of the vegetation of Moor House by Eddy *et al.* (1969) as an example, from the species given, 189 out of a total of 234 species of vascular plant and bryophyte occur in the 8 mire & spring noda delimited by them: *Philonoto - Saxifragetum stellaris*; *Poa annua - Montia fontana*; *Cratoneuron commutatum - Carex*; *Carex panicea - Ctenidium molluscum*; Species-rich *Juncetum effusi*; *Sphagneto - Juncetum effusi* and *Sphagneto - Caricetum alpinum*. Thus a total of 81% of the species can be found in these communities, which only account for a small physical area of the reserve. These communities can be seen to represent 'hotspots' of biodiversity, and since biodiversity is often equated with conservation value (Brown and Thompson 1992) they are of high conservation value.

In addition to species also common in the grassland vegetation that often surrounds mires and springs, such as *Festuca ovina* and *Cerastium fontanum*, soligenous mires and springs contain species unique to these communities such as *Montia fontana* and *Chrysosplenium oppositifolium*. Although these species are presently common, if these habitats were lost they would become extremely rare in the uplands. Therefore, when considering the conservation of these habitats, it is not just species that are already rare that would be threatened.

According to Ratcliffe (1964), soligenous mires tend to be less affected by human disturbance than bogs since they are usually more difficult to burn and it is more difficult to alter their drainage regime. There is some truth in this, but it is rather a simplification. Soligenous mires and springs, in being typically developed as small stands, are particularly vulnerable, not just to destruction in their own right, but to damage to adjacent habitats. Although they may form small complexes, they are often fragmented habitats, with some distance between each area of soligenous influence, which makes it particularly difficult for the more specialist mire species to spread.

The activities of man have had a profound effect on upland vegetation, beginning with forest clearance in neolithic times and the subsequent expansion of agriculture, and many now threaten the communities in question. Overgrazing by stock could threaten certain mire communities, allowing grasses to become dominant at the expense of the forbs. However, Pigott (1956) discusses the importance of grazing in maintaining the open nature of some of the 'turfy marsh' communities in Upper Teesdale. He suggests that grazing suppresses competition from some of the more vigorous species and allows certain rarities to thrive. There is thus a fine balance that ought to be achieved between overgrazing and not undergrazing, which could result in scrub encroachment in zones below the tree line.

Agricultural improvement by drainage or the application of fertiliser is another threat. Although small mires and springs are unlikely to be drained specifically, drainage of surrounding areas will alter the hydrology of the catchment which may have an indirect effect on the moisture regime of these communities. Ratcliffe (1991) mentions *Carex capillaris*, *Primula farinosa* and *Polygonum viviparum* as plants that have had their populations reduced due the addition of nitrogen and phosphorus fertilisers to hill pastures. In a comparison of British calcareous mires, Wheeler (1980) notes that although the substrata of calcareous mire communities are undoubtedly rich in certain cations, they appear to be comparatively infertile and unproductive. He suggests that calcareous mires have only a low concentration of available phosphorus and possibly also of available nitrogen and that this provides some explanation for the open, low-growing character of many such mires and for their high species diversity (c.f. Grime 1973). The application of fertilisers not necessarily to the mire itself but to adjacent pasture, could well lower the overall diversity of certain mire communities in addition to threatening species which are 'stress-tolerant' (Grime 1979) and could not survive in the face of competition from the more competitive species favoured by fertiliser application.

Afforestation has had devastating effects on many areas of blanket bog such as the 'flow country' of Caithness and Sutherland and its ecological consequences have been discussed in several reports (e.g., NCC 1987). It is also a threat to other upland habitats and although many of the soligenous mires and springs developed on relatively steep ground may 'escape', the afforestation of nearby more level areas will affect the hydrology of the whole catchment.

Recreation is a more minor threat, but nevertheless one that is increasing in importance. Outdoor activities are becoming more popular, as the population and mobility of Britain

increases, and a network of footpaths, including the Pennine Way, dissect the North Pennines region. Some of these pass through particularly sensitive mires and flushes, and so increasing pressure on the footpaths can be seen as a threat.

Although changes in global environmental conditions have been occurring continually throughout history, the increasing levels of so-called 'greenhouse gases' in the atmosphere are expected to lead to an overall increase in global temperature at a rate more rapid than any time in the last 18 000 years. Global warming is likely to have serious implications for conservation at all scales. An increase in temperature, with its associated effects on precipitation will cause a geographical shift in optimum areas for various habitats. As a general rule, these optima will shift towards higher latitudes and altitudes. Thus communities typical of lower altitudes such as the *Sphagnum recurvum* - *Juncus effusus* mire, may find their optimum location in areas currently optimum for more montane communities, which will be forced to even higher altitudes.

Plants can respond to climatic change either by evolution or migration. Palaeoecological evidence indicates that evolutionary adaptation has played no more than a minor role and that migration is the usual response. Migration is likely to be particularly difficult where the habitats are fragmented. Because of the individualistic nature of plant taxa in responding to environmental conditions (Huntley 1991), different taxa will migrate at different rates. As a result, communities will not simply be duplicated at higher altitudes or latitudes, but new communities will form.

Conservation measures consist largely of trying to arrest, ameliorate or reverse the processes that have caused decline and loss of species and habitats in the past (Ratcliffe 1991). To some extent this can be achieved at a local scale, with the designation of protected areas. Two National Nature Reserves already exist in the North Pennines, but other areas are more vulnerable. The future of sheep farming will depend to a large extent on the level of European Community subsidies and the perceived viability of other concerns, notably forestry (Gimingham 1988). Action to prevent the addition of more greenhouse gases to the atmosphere must be taken at an international level. Thus the major threats to these communities are largely affected by political decisions.

In conclusion soligenous mires and springs can be viewed as specialised habitats with a high level of diversity. They are particularly fragile due to their typically small size and fragmented nature and vulnerable both to direct damage, and to indirect damage to the surrounding area. This will have severe consequences to the flora and associated fauna and some species may be lost altogether. The North Pennines has a variety of soligenous

mire and spring communities and is perhaps particularly significant in having an abundance of calcareous communities associated with the predominantly limestone bedrock. Data collected on these communities in Britain is rather scant and their extent is not known. It may turn out that there are areas particularly rich in soligenous mires and springs that have simply not been found yet. If, on the other hand, the areas for which data already exists turn out to be the only ones then this habitat is particularly threatened and in urgent need of protection. More information is needed regarding the extent of these communities in Britain - perhaps then their significance will be more widely realised.

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Appendix I: Vegetation tables

Table 2: *Sphagnum recurvum* - *Juncus effusus* mire

Relevé number	2	14	19	29	58	60	136	151	130	146	
Grid reference 100km square	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	
Grid reference easting	662	742	864	677	857	858	961	735	805	967	
Grid reference northing	530	522	533	427	478	479	349	256	341	355	
Altitude (metres)	340	470	370	530	450	450	490	580	470	490	
Slope (degrees)	0	0	5	9	12	8	10	10	12	24	
Aspect (degrees)	-	-	310	140	280	250	170	140	50	140	
Vegetation cover (%)	99	97	95	100	98	98	100	98	97	85	
Soil depth (centimetres)	70+	70+	70+	60	28	35	70+	30	70+	70+	
Soil pH	4.2	4.0	5.2	4.2	4.2	4.7	-	5.0	3.8	-	
Water pH	-	4.1	-	-	-	-	4.0	-	-	4.5	
Conductivity (µS/cm)	-	37	-	-	-	-	82	-	-	57	
Herb height (centimetres)	6	6	7	6	8	6	15	15	22	5	
<i>Sphagnum recurvum</i>	6	8	7	6	6	9	7	7	6	6	V
<i>Polytrichum commune</i>	6	4	4	4	3	4		2	4	1	V
<i>Juncus effusus</i>	6	3	6	1	6	4	5	7			IV
<i>Juncus articulatus</i>									7	4	I
<i>Anthoxanthum odoratum</i>	5		4	6	4	4	5	5	6		IV
<i>Carex nigra</i>	4	4	3				1	3		5	III
<i>Festuca ovina</i>	4	4	3	3				4	5		III
<i>Galium saxatile</i>			2	2	3		2	5	4		III
<i>Agrostis canina</i>					5		3	4			II
<i>Carex echinata</i>								4	3	5	II
<i>Equisetum palustre</i>			4				2		3		II
<i>Eriophorum angustifolium</i>		5								3	I
<i>Holcus lanatus</i>			3			3					I
<i>Juncus squarrosus</i>								5		4	I
<i>Nardus stricta</i>								2		5	I
<i>Aulacomnium palustre</i>	1		3								I
<i>Agrostis capillaris</i>			3								I
<i>Carex panicea</i>										5	I
<i>Cynosurus cristatus</i>				2							I
<i>Narthecium ossifragum</i>										4	I
<i>Potentilla erecta</i>								3			I
<i>Potentilla palustris</i>									2		I
<i>Rumex acetosa</i>									3		I
<i>Viola palustris</i>										3	I
<i>Rhynchospora squarrosus</i>	3										I
<i>Agrostis vinealis</i>				4							I
<i>Galium sp</i>	4										I
Number of species per sample	9	6	11	8	6	5	7	12	10	11	

Table 3: *Sphagnum auriculatum* - *Agrostis stolonifera* mire

Relevé number	5	38	73	84	85	
Grid reference 100km square	NY	NY	NY	NY	NY	
Grid reference easting	662	702	954	695	695	
Grid reference northing	528	463	442	341	341	
Altitude (metres)	360	450	500	830	830	
Slope (degrees)	0	5	13	12	10	
Aspect (degrees)	-	110	40	140	140	
Vegetation cover (%)	70	95	98	94	92	
Soil depth (centimetres)	10	0	60	5	4	
Water pH	5.3	4.8	4.6	5.6	5.7	
Water conductivity ($\mu\text{s}/\text{cm}$)	44	43	67	56	37	
Herb height (centimetres)	3	3	3	5	4	
<i>Sphagnum auriculatum</i> var <i>auric</i>	6	9	9	8	9	V
<i>Agrostis stolonifera</i>	5	2		5	3	IV
<i>Deschampsia cespitosa</i> <i>cespitosa</i>				4	2	II
<i>Saxifraga stellaris</i>				5	7	II
<i>Polytrichum commune</i>			5	6		II
<i>Scapania undulata</i>				4	5	II
<i>Agrostis canina</i>					2	I
<i>Anthoxanthum odoratum</i>	3					I
<i>Cardamine pratensis</i>	1					I
<i>Carex curta</i>				2		I
<i>Holcus lanatus</i>			3			I
<i>Juncus effusus</i>	5					I
<i>Ranunculus omiophyllus</i>	1					I
<i>Stellaria alsine</i>		4				I
Number of species per sample	6	3	3	7	6	

Table 4: *Sphagnum* - *Polytrichum commune* mire

Relevé number	25	114	87	26	27	86	
Grid reference 100km square	NY	NY	NY	NY	NY	NY	
Grid reference easting	643	705	686	643	643	686	
Grid reference northing	423	333	348	422	422	348	
Altitude (metres)	550	810	840	520	540	840	
Slope (degrees)	3	0	7	5	2	15	
Aspect (degrees)	270	-	300	270	270	300	
Vegetation cover (%)	95	92	96	90	95	90	
Soil depth (centimetres)	70+	35	0	50	70+	70+	
Soil pH	-	5.1	-	4.0	-	-	
Water pH	3.8	-	5.3	3.9	4.1	4.9	
Conductivity ($\mu\text{s}/\text{cm}$)	58	-	49	50	49	68	
Herb height (centimetres)	3	4	5	5	20	7	
<i>Polytrichum commune</i>	5	5		8	3	3	V
<i>Sphagnum recurvum</i>	8	9	10				III
<i>Sphagnum cuspidatum</i>				5	9	7	III
<i>Agrostis canina</i>			3		3	2	III
<i>Agrostis stolonifera</i>			3	3		5	III
<i>Eriophorum angustifolium</i>	3	3				7	III
<i>Anthoxanthum odoratum</i>				5	4		II
<i>Deschampsia cespitosa</i> <i>cespitosa</i>				3		2	II
<i>Saxifraga stellaris</i>		3				1	II
<i>Carex curta</i>						2	I
<i>Carex nigra</i>	3						I
<i>Cynosurus cristatus</i>			3				I
<i>Deschampsia flexuosa</i>	4						I
<i>Festuca ovina</i>				3			I
<i>Juncus effusus</i>					6		I
<i>Juncus squarrosus</i>				4			I
<i>Montia fontana</i>		3					I
<i>Nardus stricta</i>				4			I
<i>Poa subcaerulea</i>				4			I
<i>Galium</i> sp		2					I
Number of species per sample	5	8	4	7	5	8	

Table 5: *Montia fontana* - *Juncus effusus* spring

Relevé number	1	3	56	61	66	74	72	63	65	64	94	137	140	
Grid reference 100km square	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	
Grid reference easting	663	662	857	859	930	944	954	859	926	926	694	958	958	
Grid reference northing	529	528	477	483	408	433	442	484	413	413	356	350	350	
Altitude (metres)	340	350	440	430	470	420	500	420	480	480	670	520	520	
Slope (degrees)	3	0	4	5	2	25	13	43	17	25	10	5	10	
Aspect (degrees)	90	-	310	340	80	320	40	20	50	50	20	170	160	
Vegetation cover (%)	80	80	90	80	90	75	80	75	90	85	97	88	93	
Soil depth (centimetres)	4	0	10	0	0	2	5	3	60	10	33	0	0	
Soil pH	-	-	-	-	-	-	-	-	-	-	6.5	-	-	
Water pH	6.3	5.9	6.6	6.1	5.9	6.6	4.7	7.4	5.4	5.1	-	5.9	6.1	
Conductivity ($\mu\text{s}/\text{cm}$)	69	44	129	93	78	89	67	92	68	74	-	112	112	
Herb height (centimetres)	4	2	8	2	3	2	3	5	4	5	4	4	3	
<i>Montia fontana</i>	8	6	5	8	8	4	8	4	4	6	5	6	5	V
<i>Juncus effusus</i>	3	5	5	4	2	4	1	3	5	4	2	3	3	V
<i>Stellaria alsine</i>			5		3			4	2	3	2	4	3	IV
<i>Chrysosplenium oppositifolium</i>								5	2	5	3	4	7	III
<i>Cardamine pratensis</i>	2	2	4		1				4	3	4			III
<i>Galium palustre</i>		2	3	1				2	2	2			1	III
<i>Myosotis scorpioides</i>	2	6			4			3	3	3				III
<i>Anthoxanthum odoratum</i>	3								3		4	4	5	II
<i>Holcus lanatus</i>				4				3	3			3	3	II
<i>Brachythecium rivulare</i>	2		2					2	4			2		II
<i>Agrostis canina</i>					3		5			5				II
<i>Agrostis stolonifera</i>		3	3			4								II
<i>Carex nigra</i>	2								2			1		II
<i>Cirsium palustre</i>		1										1	1	II
<i>Ranunculus flammula</i>	2	3							3					II
<i>Ranunculus omiophyllus</i>		4				3				5				II
<i>Ranunculus repens</i>							2		2		3	2		II
<i>Trifolium repens</i>	3					2			3					II
<i>Calliergon cuspidatum</i>	3		3								4			II
<i>Philonotis fontana</i>								3		3			4	II
<i>Scapania undulata</i>				3		6		2						II
<i>Cerastium fontanum triviale</i>									1		3			I
<i>Cynosurus cristatus</i>				3					3					I
<i>Myosotis secunda</i>											1	2		I
<i>Poa annua</i>										5	3			I
<i>Prunella vulgaris</i>									1		2			I
<i>Cratoneuron filicinum</i>											2	2		I
<i>Dactylis glomerata</i>	1													I
<i>Deschampsia cespitosa cespitos</i>											4			I
<i>Eriophorum angustifolium</i>						5								I
<i>Galium saxatile</i>	3													I
<i>Juncus articulatus</i>									2					I
<i>Poa pratensis</i>	2													I
<i>Rumex acetosa</i>										3				I
<i>Saxifraga stellaris</i>										3				I
<i>Calliergon giganteum</i>												2		I
<i>Bryum pseudotriquetrum</i>												3		I
<i>Rhytidiadelphus squarrosus</i>	1													I
<i>Chiloscyphus pallescens</i>								2						I
<i>Chiloscyphus polyanthos</i>										6				I
<i>Nardia scalaris</i>				2										I
<i>Sphagnum auriculatum</i> var <i>auric</i>							4							I
<i>Glyceria seedling/sp</i>						2								I
<i>Bryum sp</i>									3					I
Number of species per sample	14	9	11	4	6	8	4	11	19	9	14	15	13	

Table 6: Montia fontana - Cardamine - Stellaria springs (continued)

Relève number	103	104	57	7	109	141	67	185	10	24	28	81	93	113	92	143	157	116	120	
Agrostis canina																				I
Carex nigra																				I
Cirsium palustre								3												I
Festuca ovina									1											I
Mysotis scorpioides		3	2	3	1															I
Mysotis secunda																				I
Rumex acetosa										1										I
Calliergon cuspidatum									3											I
Achillea ptarmica			1																	I
Carex demissa																				I
Cynosurus cristatus																				I
Dactylis glomerata																				I
Epllobium palustre									2											I
Ranunculus omlophyllus																				I
Brachythecium mildeanum																				I
Plagiomnium cuspidatum				2																I
Rhizomnium punctatum																				I
Plagiomnium ellipticum																				I
Sphagnum recurvum																				I
Nardia scalaris				2																I
Agrostis vinealis																				I
Callitriche seedling/sp																				I
Epllobium sp				1																I
Number of species per sample	18	12	17	9	5	4	10	17	11	9	8	12	9	9	8	8	14	13	12	

Table 7: *Philonotis fontana* - *Saxifraga stellaris* spring

Relevé number	82	88	89	90	101	110	115	117	119	122	139	
Grid reference 100km square	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	
Grid reference easting	696	694	694	694	705	708	706	705	705	705	958	
Grid reference northing	328	356	356	356	309	323	333	335	333	334	350	
Altitude (metres)	680	680	680	680	690	820	800	790	800	790	520	
Slope (degrees)	11	10	13	9	10	5	17	16	8	9	7	
Aspect (degrees)	260	20	20	20	310	340	50	50	50	50	160	
Vegetation cover (%)	97	96	97	95	95	90	96	90	95	92	75	
Soil depth (centimetres)	30	70+	50	60	70	70+	5	30	30	70+	33	
Soil pH	6.4	6.9	6.9	6.4	6.4	-	-	6.5	-	6.0	-	
Water pH	-	-	-	-	-	6.2	6.1	-	6.4	6.1	6.4	
Conductivity	-	-	-	-	-	181	115	-	108	125	113	
Herb height (centimetres)	5	3	4	6	4	3	4	6	4	3	5	
<i>Philonotis fontana</i>	4	3	8	1	3	6	3	3	7	4	7	V
<i>Saxifraga stellaris</i>	3	3	3	3	4	5	3	3	4	4	4	V
<i>Cardamine pratensis</i>	3	3	3	3	3	4	1	1	3	3	3	V
<i>Festuca ovina</i>	3	3	4	5	3	3	3	3	3		2	V
<i>Cerastium fontanum triviale</i>	2	3	3	3	3		1	1	2			IV
<i>Montia fontana</i>	1	7	3	3				2	3	3	1	IV
<i>Carex nigra</i>	6		1		4		5	8	4	2		IV
<i>Deschampsia cespitosa cespitos</i>	2	4	3		2	4	5			3		IV
<i>Cratoneuron filicinum</i>		2	1		3		2	4	6	2		IV
<i>Equisetum palustre</i>							1	1	3	1	1	III
<i>Juncus articulatus</i>	4		3		3					2	2	III
<i>Ranunculus flammula</i>		3	2	2	4					3		III
<i>Agrostis stolonifera</i>	3		3		2				4			II
<i>Chrysosplenium oppositifolium</i>					3		1			3	3	II
<i>Galium palustre</i>			2	2					2		2	II
<i>Ranunculus repens</i>	3			1	3						3	II
<i>Bryum pseudotriquetrum</i>			2			4	2	2				II
<i>Plagiomnium affine</i>		2	2				2	2				II
<i>Rhizomnium punctatum</i>						3	7	3	2			II
<i>Anthoxanthum odoratum</i>			2	3						2		II
<i>Poa annua</i>		4	2							2		II
<i>Poa subcaerulea</i>					1		3		4			II
<i>Sagina procumbens</i>	1				2	2						II
<i>Sedum villosum</i>	2			3				3				II
<i>Calliergon cuspidatum</i>			2	7					2			II
<i>Brachythecium rivulare</i>		3				3		2				II
<i>Cratoneuron commutatum</i>	3				4	2						II
<i>Bryum sp</i>	3	1			5							II
<i>Carex demissa</i>	2						3					I
<i>Cynosurus cristatus</i>			3						2			I
<i>Festuca rubra</i>		3	3									I
<i>Nardus stricta</i>				1						2		I
<i>Rumex acetosa</i>		3		3								I
<i>Stellaria alsine</i>		3								2		I
<i>Viola palustris</i>							4	3				I
<i>Dicranella palustris</i>									9	4		I
<i>Agrostis canina</i>								2				I
<i>Agrostis capillaris</i>		3										I
<i>Caltha palustris</i>								4				I
<i>Carex curta</i>				6								I
<i>Carex dioica</i>							1					I
<i>Carex panicea</i>					2							I
<i>Cirsium palustre</i>										3		I
<i>Epilobium anagallidifolium</i>					2							I
<i>Epilobium palustre</i>										1		I
<i>Eriophorum angustifolium</i>						1						I
<i>Galium uliginosum</i>					1							I
<i>Holcus lanatus</i>						3						I
<i>Juncus triglumis</i>								2				I
<i>Leontodon autumnalis</i>					4							I
<i>Polygala serpyllifolia</i>		3										I
<i>Selaginella selaginoides</i>					1							I
<i>Trifolium repens</i>	4											I
<i>Calliergon giganteum</i>										2		I
<i>Fissidens osmundoides</i>	2											I
<i>Plagiomnium elatum</i>												I
<i>Marchantia polymorpha</i>	1											I
<i>Jungermannia exertifolia var c</i>					1							I
<i>Galium sp</i>	3											I
<i>Pellia cf. endiviifolia</i>					2							I
Number of species per sample	20	18	20	15	24	12	17	19	13	14	18	

Table 10: Calliergon cuspidatum - Carex mire

Relevé number	21	40	42	96	123	124	125	128	133	144	188	189	192	195	36	69	68	134	194	17	34	35	71	135	11	173
Grid reference 100km square	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY	NY
Grid reference easting	864	744	743	742	811	811	811	806	864	958	904	903	903	904	704	930	931	962	903	864	674	674	928	962	797	845
Grid reference northing	531	404	404	399	335	335	342	313	349	252	253	253	253	466	412	409	357	253	533	445	444	413	357	513	288	513
Altitude (metres)	380	370	380	400	470	470	460	460	460	510	450	450	440	450	400	460	460	12	440	380	480	470	470	490	480	530
Slope (degrees)	6	0	40	9	26	25	19	15	10	13	10	18	10	9	21	20	9	0	13	3	5	3	15	12	18	0
Aspect (degrees)	340	-	90	320	50	50	50	50	230	120	50	50	50	50	90	40	160	20	50	120	340	340	40	20	270	-
Vegetation cover (%)	96	85	90	97	97	96	99	95	98	97	97	98	98	90	90	97	95	98	97	95	95	99	90	97	97	97
Soil depth (centimetres)	71	45	15	33	40	22	35	25	71	71	60	30	71	30	10	25	20	71	50	71	71	30	71	71	55	71
Soil pH	4.9	-	-	7.0	5.4	5.8	5.0	5.6	4.8	6.1	6.9	6.9	6.2	6.7	6.2	4.3	5.1	6.2	6.8	6.2	5.9	5.9	6.3	5.7	5.3	5.1
Water pH	-	6.6	7.1	-	-	-	-	-	-	-	-	-	-	-	7.6	-	-	-	-	-	-	-	-	-	-	-
Conductivity (µs/cm)	-	74	106	-	-	-	-	-	-	-	-	-	-	-	204	-	-	-	-	-	-	-	-	-	-	-
Herb height (centimetres)	3	6	6	6	10	20	13	26	20	30	7	6	9	5	4	5	4	4	4	8	5	3	6	4	4	11
Trifolium repens	5	2	3	5	3	3	2	4	3	3	2	4	3	3	3	2	3	3	3	3	3	3	2	3	4	3
Carex panicea	3	6	7	5	2	4	3	3	4	1	2	3	6	4	5	4	5	6	4	4	6	4	3	4	4	3
Calliergon cuspidatum	4	-	2	4	5	4	3	4	5	5	4	3	3	4	2	5	5	3	3	4	5	3	1	3	4	4
Anthoxanthum odoratum	2	-	2	4	5	4	3	4	5	2	3	3	3	4	3	3	3	3	3	3	4	3	3	1	3	4
Cerastium fontanum triviale	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cardamine pratensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carex nigra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ailacomium palustre	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Juncus squarrosus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sphagnum subnitens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Potentilla erecta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Equisetum palustre	1	3	3	5	3	1	3	3	3	2	4	3	3	3	3	3	3	4	4	1	1	3	2	3	3	2
Festuca ovina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holcus lanatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Juncus articulatus	1	4	3	3	5	3	3	5	7	3	5	2	3	3	3	5	3	3	3	3	4	2	2	2	3	3
Phlomis fontana	4	1	3	2	3	2	2	2	3	5	1	3	2	1	6	5	5	5	5	5	5	5	2	2	2	3
Leontodon autumnalis	2	1	3	2	3	2	2	2	2	2	2	4	1	3	3	3	3	1	3	3	3	3	1	1	1	2
Ranunculus repens	3	3	3	4	4	1	3	2	2	2	2	2	2	3	3	3	2	2	2	3	3	3	2	3	3	3
Rhytidadelphus squarrosus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladium palustre	3	1	1	1	4	4	4	2	2	3	2	2	2	2	1	2	3	3	3	1	1	1	1	1	1	3
Cynosurus cristatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prunella vulgaris	3	1	2	2	2	4	4	2	2	3	2	2	2	2	2	3	3	3	3	4	4	4	4	4	4	3
Climacium dendroides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nardus stricta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ranunculus acris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ranunculus repens	3	3	3	3	4	4	3	3	3	3	2	2	3	2	2	2	2	4	5	3	3	3	3	3	3	3
Juncus effusus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hylacomium splendens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caltha palustris	3	3	2	2	2	4	4	2	2	2	2	2	2	2	3	3	3	3	3	6	6	4	4	6	4	4
Rumex acetosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plagiomnium affine	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bellis perennis	3	2	2	2	1	3	2	2	2	2	3	3	2	2	4	4	4	3	3	3	1	1	3	2	2	2

Table 10: Calliergon cuspidatum - Carex mire (continued)

Relavé number	21	40	42	96	123	124	125	128	133	144	188	189	192	195	36	69	68	134	194	17	34	35	71	135	11	173	
<i>Agrostis canina</i>																											
<i>Agrostis capillaris</i>																											
<i>Carex ovalis</i>																											
<i>Chrysosplenium oppositifolium</i>																											
<i>Cirsium vulgare</i>																											
<i>Cochlearia pyrenaea</i>																											
<i>Coeloglossum viride</i>																											
<i>Deschampsia cespitosa cespitos</i>																											
<i>Eleocharis multicaulis</i>																											
<i>Juncus conglomeratus</i>																											
<i>Leontodon hispidus</i>																											
<i>Molinia caerulea</i>																											
<i>Montia fontana</i>																											
<i>Myosotis scorpioides</i>																											
<i>Oxalis acetosella</i>																											
<i>Pedicularis palustris</i>																											
<i>Poa pratensis</i>																											
<i>Poa subcaerulea</i>																											
<i>Potentilla palustris</i>																											
<i>Pteridium aquilinum</i>																											
<i>Campyllum stellatum</i>																											
<i>Ceratodon purpureus</i>																											
<i>Cratoneuron commutatum</i>																											
<i>Dicranum scoparium</i>																											
<i>Drepanocladus revolvens</i>																											
<i>Fissidens adianthoides</i>																											
<i>Fissidens osmundoides</i>																											
<i>Plagiomnium rostratum</i>																											
<i>Plagiomnium elatum</i>																											
<i>Sphagnum palustre</i>																											
<i>Sphagnum recurvum</i>																											
<i>Chiloscyphus polyanthos</i>																											
<i>Lophocolea bidentata</i>																											
<i>Lophozia ventricosa</i>																											
<i>Bryum sp</i>																											
<i>Pellia sp</i>																											
<i>Peltigera sp</i>																											
<i>Viola seedling/sp</i>																											

Number of species per sample 16 15 20 21 32 31 24 33 23 20 20 26 18 22 21 17 16 24 23 18 15 19 16 23 24 15

Table 11: *Carex nigra* - *Eriophorum angustifolium* mire

Relevé number	105	156	159	111	
Grid reference 100km square	NY	NY	NY	NY	
Grid reference easting	715	743	753	708	
Grid reference northing	306	265	268	323	
Altitude (metres)	690	590	570	820	
Slope (degrees)	0	8	0	0	
Aspect (degrees)	-	140	-	-	
Vegetation cover (%)	96	93	95	95	
Soil depth (centimetres)	70+	10	70+	35	
Soil pH	6.6	6.3	6.7	4.8	
Herb height (centimetres)	7	6	9	4	
<i>Carex nigra</i>	7	4	5	5	V
<i>Carex panicea</i>	3	5	6		IV
<i>Eriophorum angustifolium</i>	2		4	4	IV
<i>Carex demissa</i>			6	5	III
<i>Carex pulicaris</i>		4	2		III
<i>Equisetum palustre</i>	2		3		III
<i>Festuca ovina</i>		3		3	III
<i>Viola palustris</i>	1			3	III
<i>Caltha palustris</i>	2				II
<i>Carex dioica</i>		3			II
<i>Carex echinata</i>		4			II
<i>Carex lepidocarpa</i>		5			II
<i>Juncus articulatus</i>		3			II
<i>Juncus triglumis</i>	3				II
<i>Nardus stricta</i>				3	II
<i>Campyllum stellatum</i>		4			II
<i>Cratoneuron commutatum</i>	3				II
<i>Plagiomnium affine</i>	2				II
<i>Polytrichum commune</i>				4	II
<i>Sphagnum tenellum</i>				7	II
Number of species per sample	9	9	6	8	

Table 12: Open gravel flushes

Relevé number	50	165	180	183	
Grid reference 100km square	NY	NY	NY	NY	
Grid reference easting	742	848	845	846	
Grid reference northing	401	283	294	295	
Altitude (metres)	410	520	420	390	
Slope (degrees)	6	0	7	0	
Aspect (degrees)	310	-	50	-	
Vegetation cover (%)	30	40	60	50	
Soil depth (centimetres)	3	15	0	2	
Soil pH	-	7.2	-	-	
Water pH	7.4	-	7.5	6.7	
Conductivity (µs/cm)	375	-	160	178	
Herb height (centimetres)	3	4	5	3	
<i>Carex flacca</i>	4	4	4		IV
<i>Juncus articulatus</i>	4	5		3	IV
<i>Carex demissa</i>			6	5	III
<i>Carex lepidocarpa</i>		5			II
<i>Equisetum palustre</i>	2				II
<i>Eriophorum angustifolium</i>				5	II
<i>Festuca ovina</i>			3		II
<i>Nardus stricta</i>			2		II
<i>Pinguicula vulgaris</i>	1				II
<i>Cratoneuron commutatum</i>	3				II
Number of species per sample	5	3	4	3	

Table 13: *Carex flacca* - *Leontodon autumnalis* mire (continued)

Relève number	44	45	46	47	48	49	106	126	127	129	132	196	197	16	51	154	164	171	175	179	190	182	
<i>Bryum pallens</i>																							
<i>Dicranella varia</i>										1													
<i>Rhizomnium punctatum</i>										1													
<i>Pseudoscleropodium purum</i>																			4				
<i>Rhytidiadelphus triquetrus</i>	2																						
<i>Sphagnum cuspidatum</i>	1																						3
<i>Tortella tortuosa</i>										1													
<i>Chiloscyphus polyanthos</i>																							
<i>Leiocolea turbinata</i>					3																		1
<i>Lophozia ventricosa</i>					1																		
<i>Marchantia polymorpha</i>													1										
<i>Pellia endiviifolia</i>																							1
<i>Aneura pingula</i>					1																		
<i>Jungermannia atroviolens</i>										2													
<i>Agrostis sp</i>																							2
<i>Bryum sp</i>																							
<i>Scapania sp</i>																							2
<i>Juncus sp.</i>																							2
Number of species per sample	26	24	25	26	22	23	21	27	31	34	25	24	23	22	19	19	12	14	22	21	12	23	

Table 14: Cratoneuron commutatum springs (continued)

Relève number	9	23	53	80	99	100	102	112	118	138	149	161	162	52	155	166	168	169	170	172	174	181	187	191	198
<i>Pellia endiviifolia</i>																									
<i>Bellis perennis</i>		3						2					3	4											
<i>Carex echinata</i>								1																	
<i>Carex pullicaris</i>								2																	
<i>Epilobium anagallidifolium</i>																									
<i>Eriophorum angustifolium</i>					1			3																	
<i>Galium palustre</i>								1																	
<i>Galium lanatum</i>								1																	
<i>Juncus bulbosus</i>																									
<i>Linum catharticum</i>																									
<i>Polygala serpyllifolia</i>								3						2											
<i>Prunella vulgaris</i>																									
<i>Veronica beccabunga</i>		2																							
<i>Plagiomnium affine</i>																									
<i>Conocephalum concium</i>																									
<i>Lophozia ventricosa</i>					1			3						4											
<i>Alchemilla vulgaris agg</i>																									
<i>Pellia cf. endiviifolia</i>					1			4																	
<i>Briza media</i>					2																				
<i>Chrysosplenium oppositifolium</i>																									
<i>Cirsium vulgare</i>																									
<i>Cynosurus cristatus</i>																									
<i>Blechnum palustre</i>																									
<i>Equisetum arvense</i>		1																							
<i>Equisetum fluviatile</i>																									
<i>Euphrasia officinalis agg</i>																									
<i>Genum rivale</i>					1																				
<i>Juncus biglumis</i>					1																				
<i>Juncus triglumis</i>					3																				
<i>Lychnis flos-cuculi</i>																									
<i>Montia fontana</i>									2																
<i>Poa annua</i>																									
<i>Poa subcaerulea</i>					2																				
<i>Potentilla erecta</i>																									
<i>Ranunculus acris</i>					2																				
<i>Nasturtium officinale</i>																									
<i>Sagina nodosa</i>																									
<i>Thalictrum alpinum</i>																									
<i>Calliergon giganteum</i>																									
<i>Bryum pallens</i>																									
<i>Climacium dendroides</i>		1																							
<i>Ctenidium molluscum</i>					1																				
<i>Marchantia polymorpha</i>																									
<i>Jungfermannia exsertifolia var c</i>																									
<i>Carex seedling/sp</i>					3																				
<i>Galium sp</i>								2																	
<i>Equisetum sp</i>					3																				

Number of species per sample 17 15 8 10 25 20 18 26 13 13 9 11 14 10 6 10 8 12 7 11 7 8 14 18 19

Appendix II: Species list with species codes

Vascular plants

105	<i>Achillea ptarmica</i>	120	<i>Agrostis canina</i>
123	<i>Agrostis capillaris</i>	122	<i>Agrostis stolonifera</i>
2701	<i>Agrostis vinealis</i>	127	<i>Ajuga reptans</i>
132	<i>Alchemilla glabra</i>	251	<i>Briza media</i>
171	<i>Anthoxanthum odoratum</i>	230	<i>Bellis perennis</i>
2785	<i>Alchemilla vulgaris</i> agg.	2708	<i>Callitriche</i> seedling/sp.
278	<i>Calluna vulgaris</i>	279	<i>Caltha palustris</i>
295	<i>Cardamine pratensis</i>	2706	<i>Carex</i> seedling/sp.
309	<i>Carex capillaris</i>	311	<i>Carex curta</i>
312	<i>Carex demissa</i>	315	<i>Carex dioica</i>
319	<i>Carex echinata</i>	323	<i>Carex flacca</i>
325	<i>Carex hostiana</i>	329	<i>Carex lepidocarpa</i>
333	<i>Carex nigra</i>	339	<i>Carex panicea</i>
337	<i>Carex ovalis</i>	371	<i>Centaurea nigra</i>
347	<i>Carex pulicaris</i>	415	<i>Cirsium arvense</i>
384	<i>Cerastium fontanum trivale</i>	418	<i>Cirsium palustre</i>
408	<i>Chrysosplenium oppositifolium</i>	423	<i>Cochlearia pyrenaica</i>
419	<i>Cirsium vulgare</i>	460	<i>Cynosurus cristatus</i>
428	<i>Coeloglossum viride</i>	1249	<i>Danthonia decumbens</i>
465	<i>Dactylis glomerata</i>	478	<i>Deschampsia flexuosa</i>
477	<i>Deschampsia cespitosa cespitosa</i>	494	<i>Drosera rotundifolia</i>
508	<i>Eleocharis multicaulis</i>	509	<i>Eleocharis palustris</i>
510	<i>Eleocharis quinqueflora</i>	2836	<i>Epilobium</i> sp.
520	<i>Epilobium anagallidifolium</i>	523	<i>Epilobium nerterioides</i>
525	<i>Epilobium palustre</i>	532	<i>Equisetum arvense</i>
533	<i>Equisetum fluviatile</i>	535	<i>Equisetum palustre</i>
539	<i>Equisetum variegatum</i>	2837	<i>Equisetum</i> sp.
542	<i>Erica tetralix</i>	546	<i>Eriophorum angustifolium</i>
568	<i>Euphrasia officinalis</i> agg.	574	<i>Festuca ovina</i>
575	<i>Festuca pratensis</i>	576	<i>Festuca rubra</i>
2715	<i>Galium</i> sp.	609	<i>Galium palustre</i>
610	<i>Galium saxatile</i>	611	<i>Holcus lanatus</i>
722	<i>Juncus articulatus</i>	724	<i>Juncus biglumis</i>
726	<i>Juncus bulbosus</i>	729	<i>Juncus conglomeratus</i>
730	<i>Juncus effusus</i>	736	<i>Juncus squarrosus</i>
739	<i>Juncus triglumis</i>	3163	<i>Juncus</i> sp.
758	<i>Lathyrus pratensis</i>	768	<i>Leontodon autumnalis</i>
769	<i>Leontodon hispidus</i>	786	<i>Linum catharticum</i>
800	<i>Lotus corniculatus</i>	807	<i>Luzula campestris</i>
2872	<i>Luzula campestris/multiflora</i>	813	<i>Lychnis flos-cuculi</i>
825	<i>Lysimachia nemorum</i>	876	<i>Molinia caerulea</i>
879	<i>Montia fontana</i>	889	<i>Myosotis scorpioides</i>
890	<i>Myosotis secunda</i>	900	<i>Nardus stricta</i>
901	<i>Narthecium ossifragum</i>	1118	<i>Nasturtium officinale</i>
932	<i>Oxalis acetosella</i>	944	<i>Parnassia palustris</i>
946	<i>Pedicularis palustris</i>	947	<i>Pedicularis sylvatica</i>

970 *Pinguicula vulgaris*
974 *Plantago major*
988 *Poa pratensis*
990 *Poa trivialis*
1012 *Polygonum viviparum*
1049 *Potentilla palustris*
1059 *Prunella vulgaris*
1081 *Ranunculus acris*
1092 *Ranunculus omiophyllus*
1139 *Rumex acetosa*
1158 *Sagina procumbens*
1203 *Saxifraga stellaris*
1234 *Sedum villosum*
1295 *Stellaria alsine*
2982 *Taraxacum officinale* agg.
1333 *Thymus praecox arcticus*
1360 *Tussilago farfara*
1394 *Veronica beccabunga*
1401 *Veronica officinalis*
1427 *Viola palustris*

973 *Plantago lanceolata*
981 *Poa annua*
989 *Poa subcaerulea*
994 *Polygala serpyllifolia*
1046 *Potentilla erecta*
1054 *Primula farinosa*
1066 *Pteridium aquilinum*
1089 *Ranunculus flammula*
1095 *Ranunculus repens*
1156 *Sagina nodosa*
1199 *Saxifraga hypnoides*
1214 *Scirpus setaceus*
1235 *Selaginella selaginoides*
1305 *Succisa pratensis*
1322 *Thalictrum alpinum*
1350 *Trifolium repens*
1380 *Valeriana dioica*
1406 *Veronica serpyllifolia*
2999 *Viola* seedling/sp.

Mosses

1482 *Aulacomnium palustre*
1518 *Brachythecium rivulare*
1543 *Bryum pallens*
1444 *Calliergon cordifolium*
1446 *Calliergon giganteum*
1586 *Ceratodon purpureus*
1596 *Cratoneuron commutatum*
1600 *Ctenidium molluscum*
1621 *Dicranella varia*
1649 *Ditrichum flexicaule*
1683 *Fissidens adianthoides*
1761 *Hylocomium splendens*
1845 *Philonotis calcarea*
1791 *Plagiomnium affine*
1804 *Plagiomnium elatum*
1795 *Plagiomnium rostratum*
1879 *Pohlia carnea*
1914 *Pseudoscleropodium purum*
1801 *Rhizomnium punctatum*
1941 *Rhytidiadelphus triquetrus*
1963 *Sphagnum cuspidatum*
1976 *Sphagnum recurvum*
1984 *Sphagnum tenellum*
2012 *Tortella tortuosa*

1514 *Brachythecium mildaneum*
2807 *Bryum* sp.
1546 *Bryum pseudotriquetrum*
1445 *Calliergon cuspidatum*
1571 *Campylium stellatum*
1593 *Climacium dendroides*
1598 *Cratoneuron filicinum*
1616 *Dicranella palustris*
1658 *Dicranium scoparium*
1658 *Drepanocladus revolvens*
1692 *Fissidens osmundoides*
1797 *Mnium marginatum*
1847 *Philonotis fontana*
1793 *Plagiomnium cuspidatum*
1803 *Plagiomnium ellipticum*
1807 *Plagiomnium undulatum*
1891 *Polytrichum commune*
1800 *Rhizomnium pseudopunctatum*
1940 *Rhytidiadelphus squarrosus*
2700 *Sphagnum auriculatum*
1971 *Sphagnum palustre*
1973 *Sphagnum subnitens*
2003 *Thuidium tamariscinum*

Liverworts

2256 *Aneura pinguis*

2103 *Chiloscyphus pallescens*

- | | | | |
|------|---|------|---------------------------------------|
| 2104 | <i>Chiloscyphus polyanthos</i> | 2086 | <i>Cephalozia bicuspidata</i> |
| 2110 | <i>Conocephalum conicum</i> | 2302 | <i>Jungermannia atrovirens</i> |
| 155 | <i>Leicolea turbinata</i> | 2180 | <i>Lophozia ventricosa</i> |
| 2168 | <i>Lophocolea bidentata</i> | 2213 | <i>Nardia scalaris</i> |
| 2183 | <i>Marchantia polymorpha</i> | 3033 | <i>Pellia</i> cf. <i>endiviifolia</i> |
| 2222 | <i>Pellia endiviifolia</i> | 2917 | <i>Pellia</i> sp. |
| 2223 | <i>Pellia epiphylla</i> | 2969 | <i>Scapania</i> sp. |
| 2293 | <i>Scapania undulata</i> | | |
| 2295 | <i>Jungermannia exertifolia</i> var <i>cordifolia</i> | | |

Lichens

- 2918 *Peltigera* sp.

Appendix III

Key to species abbreviations

Ant.odo = <i>Anthoxanthum odoratum</i>	Pin.vul = <i>Pinguicula vulgaris</i>
Agr.can = <i>Agrostis canina</i>	Poa.ann = <i>Poa annua</i>
Agr.sto = <i>Agrostis stolonifera</i>	Pru.vul = <i>Prunella vulgaris</i>
Bel.per = <i>Bellis perennis</i>	Ran.fla = <i>Ranunculus flammula</i>
Car.dem = <i>Carex demissa</i>	Ran.rep = <i>Ranunculus repens</i>
Car.fla = <i>Carex flacca</i>	Sag.pro = <i>Sagina procumbens</i>
Car.nig = <i>Carex nigra</i>	Sax.ste = <i>Saxifraga stellaris</i>
Car.pan = <i>Carex panicea</i>	Sel.sel = <i>Selaginella selaginoides</i>
Car.pra = <i>Cardamine pratensis</i>	Ste.als = <i>Stellaria alsine</i>
Cer.fon = <i>Cerastium fontanum</i>	Suc.pra = <i>Succisa pratensis</i>
Chr.opp = <i>Chrysosplenium oppositifolium</i>	Tri.rep = <i>Trifolium repens</i>
Cir.pal = <i>Cirsium palustre</i>	
Cyn.cri = <i>Cynosurus cristatus</i>	Bra.riv = <i>Brachythecium rivulare</i>
Des.ces = <i>Deschampsia cespitosa</i>	Bry.pse = <i>Bryum pseudotriquetrum</i>
Equ.pal = <i>Equisetum palustre</i>	Cal.cus = <i>Calliargon cuspidatum</i>
Eri.ang = <i>Eriophorum angustifolium</i>	Cli.den = <i>Climacium dendroides</i>
Fes.ovi = <i>Festuca ovina</i>	Cra.com = <i>Cratoneuron commutatum</i>
Gal.pal = <i>Galium palustre</i>	Cra.fil = <i>Cratoneuron filicinum</i>
Hol.lan = <i>Holcus lanatus</i>	Cte.mol = <i>Ctenidium molluscum</i>
Jun.art = <i>Juncus articulatus</i>	Phi.fon = <i>Philonotis fontana</i>
Jun.eff = <i>Juncus effusus</i>	Pol.com = <i>Polytrichum commune</i>
Leo.aut = <i>Leontodon autumnalis</i>	Rhy.squ = <i>Rhytidiadelphus squarrosus</i>
Lin.cat = <i>Linum catharticum</i>	Sph.aur = <i>Sphagnum auriculatum</i>
Mon.fon = <i>Montia fontana</i>	Sph.cus = <i>Sphagnum cuspidatum</i>
Nar.str = <i>Nardus stricta</i>	Sph.rec = <i>Sphagnum recurvum</i>

Key to community abbreviations

- A = *Sphagnum recurvum* - *Juncus effusus* mire
- B = *Sphagnum auriculatum* - *Agrostis stolonifera* mire
- C = *Sphagnum* - *Polytrichum commune* mire
- D = *Montia fontana* - *Juncus effusus* spring
- E = *Montia* - *Stellaria* - *Cardamine* springs
- F = *Philonotis fontana* - *Saxifraga stellaris* spring
- G = *Cardamine pratensis* - *Philonotis fontana* mire
- H = *Juncus effusus* - *Cardamine pratensis* mire
- J = *Calliargon cuspidatum* - *Carex* mire
- K = *Carex nigra* - *Eriophorum angustifolium* mire
- L = *Carex flacca* - *Leontodon autumnalis* mire
- M = Open gravel flushes
- N = *Cratoneuron commutatum* springs

Appendix IV

Table 15: Summary of environmental variables used in CANOCO

Samp.	Altit.	Slope	% cov.	Geol.	Soil	Depth	Moist.	S.pH	W.pH	Cond.
1	340	3	80	Lime	Grav	2	1	-	6.3	69.1
2	340	0	99	Lime	Coar	70+	3	4.2	-	-
3	350	0	80	Lime	Bed	0	1	-	5.9	44.1
4	350	12	75	Lime	Clay	30	3	5.1	-	-
5	360	0	70	Lime	Bed	0	1	-	5.3	43.0
6	480	10	100	Lime	Peat	70+	4	6.2	-	-
7	490	15	90	Lime	Bed	0	1	-	6.8	283
8	480	14	95	Lime	Clay	70+	2	6.0	6.6	282
9	480	17	100	Lime	Coar	45	2	6.2	6.6	230
10	480	5	97	Lime	Grav	3	1	-	6.7	216
11	480	18	97	Lime	Clay	70+	4	5.3	-	-
12	480	20	97	Lime	Peat	25	4	6.3	-	-
13	470	0	100	Lime	PG	70+	4	5.9	-	-
14	470	0	97	Shale	Peat	70+	2	4.0	4.1	36.8
15	370	7	96	Lime	Clay	70+	3	5.9	-	-
16	370	5	98	Lime	Clay	70+	3	6.1	-	-
17	380	3	95	Lime	PG	70+	3	6.2	-	-
18	370	0	98	Lime	Clay	55	4	5.9	-	-
19	370	5	95	Lime	Peat	70+	3	5.2	-	-
20	380	10	85	Lime	Peat	70+	2	6.2	6.8	193.7
21	380	6	96	Lime	Peat	70+	3	4.9	-	-
22	380	3	80	Lime	Bed	0	1	-	6.6	200
23	380	0	95	Lime	Coar	10	4	6.8	-	-
24	400	0	70	Lime	Coar	30	2	-	6.4	112.4
25	550	3	95	Lime	Peat	70+	2	-	3.8	57.5
26	520	5	90	Lime	Peat	50	2	4.0	3.9	49.7
27	540	2	95	Lime	Peat	70+	2	-	4.1	48.7
28	530	4	90	Lime	Grav	5	1	-	7.6	293
29	530	9	100	MG	Peat	70+	3	4.2	-	-
30	470	13	97	Lime	Clay	70+	2	6.7	7.5	270
31	470	5	97	Lime	Clay	55	4	6.8	-	-
32	480	8	98	Lime	PG	70+	3	6.6	-	-
33	480	3	96	Lime	Coar	70+	2	6.5	6.9	268
34	470	5	95	Lime	PG	70+	3	5.9	-	-
35	480	3	95	Lime	Clay	70	4	5.9	-	-
36	400	21	90	Lime	Coar	10	2	6.2	7.6	204
37	390	10	90	Lime	Coar	10	2	6.1	7.6	204
38	450	5	95	Shale	Bed	0	1	-	4.8	43.0
39	370	3	95	Lime	Clay	40	4	5.8	-	-
40	370	0	85	Lime	Clay	45	2	-	6.6	73.9
41	370	0	94	Lime	Clay	33	2	5.7	6.5	89.0
42	380	40	90	Lime	Clay	15	2	-	7.1	105.6
43	400	55	90	Lime	Grav	10	2	-	5.8	37.3
44	400	13	99	Lime	Silt	25	5	6.8	-	-
45	410	18	95	Lime	Silt	40	3	6.9	-	-
46	410	25	95	Lime	Coar	25	3	7.2	-	-
47	410	25	98	Lime	Coar	10	4	7.0	-	-
48	400	10	75	Lime	Coar	10	2	-	7.0	274
49	400	30	90	Lime	Coar	10	2	6.8	7.0	262

50	410	6	30	Lime	Grav	2	1	-	7.4	374
51	400	42	85	Lime	Grav	10	1	-	7.4	177
52	420	22	90	Lime	Bed	0	1	-	7.9	169
53	570	8	90	Shale	Peat	70+	2	-	6.7	221
54	570	8	85	Shale	Peat	70+	2	-	6.7	221
55	570	5	95	Shale	Peat	40	3	6.2	-	-
56	440	4	90	Shale	Bed	0	1	-	6.6	129
57	440	24	85	Shale	Bed	0	1	-	7.1	128
58	450	12	98	Shale	Peat	28	3	4.2	-	-
59	450	12	85	Shale	Coar	20	2	-	6.6	215
60	450	8	98	Sand	Clay	35	3	4.7	-	-
61	430	5	80	Shale	Bed	0	1	-	6.1	93
62	420	13	96	Shale	Silt	20	4	5.9	-	-
63	420	43	75	Shale	Bed	0	1	-	7.4	92
64	480	25	85	Shale	Coar	10	1	-	5.1	74
65	480	17	90	Shale	Coar	60	2	-	5.4	68
66	470	2	90	Sand	Bed	0	1	-	5.9	78
67	460	5	97	Sand	Coar	25	2	-	5.6	117
68	460	9	95	Sand	Silt	20	3	5.1	-	-
69	460	20	97	Shale	Clay	25	4	4.3	-	-
70	470	10	50	Shale	Bed	0	1	-	5.7	76
71	470	15	99	Shale	Coar	30	4	6.3	-	-
72	500	13	80	Sand	Grav	5	1	-	4.7	67
73	500	13	98	Sand	Coar	60	2	-	4.6	67
74	420	25	70	Shale	Grav	3	1	-	6.6	89
75	420	10	90	Shale	Coar	30	3	5.6	-	-
76	690	15	97	Lime	Clay	45	4	6.8	-	-
77	690	5	98	Lime	Silt	71	4	6.0	-	-
78	680	3	97	Lime	Clay	70	4	6.1	-	-
79	690	9	97	Lime	Clay	60	4	6.3	-	-
80	690	10	90	Lime	Silt	20	2	-	7.2	532
81	700	0	90	Lime	Clay	70	2	6.6	7.0	376
82	680	11	97	Lime	Silt	30	3	6.4	-	-
83	680	7	98	Lime	Clay	70	3	6.8	-	-
84	830	12	94	Sand	Bed	0	1	-	5.6	56
85	830	10	92	Sand	Bed	0	1	-	5.7	37
86	840	15	90	Sand	Peat	70	2	-	4.9	68
87	840	7	96	Sand	Bed	0	1	-	5.3	49
88	680	10	96	Lime	Silt	70	4	6.9	-	-
89	680	13	97	Lime	Silt	50	3	6.9	-	-
90	680	9	95	Lime	Silt	60	4	6.4	-	-
91	670	10	97	Lime	Silt	50	3	6.0	-	-
92	670	10	90	Lime	Grav	20	1	-	6.9	195
93	670	20	85	Lime	Silt	50	2	-	7.0	136
94	670	10	96	Lime	Silt	33	3	6.5	-	-
95	670	9	97	Lime	Clay	50	4	6.3	-	-
96	400	9	97	Lime	Silt	33	3	7.0	-	-
97	410	12	99	Lime	Silt	12	4	6.7	-	-
98	690	25	97	Lime	Clay	40	3	5.9	-	-
99	690	28	92	Lime	Clay	41	3	6.4	-	-
100	690	25	96	Lime	Clay	70	3	6.0	-	-
101	690	10	95	Lime	PG	70	3	6.4	-	-
102	700	0	97	Lime	PG	70+	2	-	6.8	168
103	700	12	98	Lime	Clay	60	3	6.5	-	-

104	690	0	95	Lime	PG	70	2	-	6.6	160
105	690	0	96	Lime	Silt	70+	3	6.6	-	-
106	690	23	91	Lime	Clay	32	2	-	6.7	228
107	700	25	98	Lime	Clay	30	3	6.6	-	-
108	680	8	99	Lime	Silt	70+	3	6.1	-	-
109	820	0	90	Shale	Bed	0	1	-	6.0	55
110	820	5	90	Shale	Silt	70+	2	-	6.2	181
111	820	0	95	Shale	Clay	35	3	4.8	-	-
112	720	11	96	Lime	Clay	28	3	6.9	-	-
113	810	5	95	Shale	Bed	0	1	-	5.6	47
114	810	0	92	Shale	PG	35	3	5.1	-	-
115	800	17	96	Shale	Bed	0	1	-	6.1	115
116	790	10	60	Shale	Clay	42	2	6.1	6.5	88
117	790	16	90	Sand	Clay	30	3	6.5	-	-
118	790	15	95	Shale	Silt	20	2	-	6.7	110
119	800	8	96	Shale	Clay	30	2	-	6.4	108
120	800	10	80	Shale	PG	50	2	-	6.4	135
121	790	11	98	Shale	Clay	70+	4	6.0	-	-
122	790	9	92	Shale	Silt	70+	2	6.0	6.1	125
123	470	26	97	Lime	Clay	40	4	5.4	-	-
124	470	25	96	Lime	Silt	22	4	5.8	-	-
125	460	19	99	Lime	Clay	35	4	5.0	-	-
126	460	27	82	Lime	Coar	10	4	7.5	-	-
127	460	23	81	Lime	Coar	20	4	6.6	-	-
128	460	15	95	Lime	Clay	25	4	5.6	-	-
129	470	21	90	Lime	Silt	23	4	6.4	-	-
130	470	12	97	Lime	Peat	70+	4	3.8	-	-
131	480	13	90	Lime	Clay	40	3	6.5	-	-
132	460	15	95	Lime	Clay	30	5	6.8	-	-
133	460	10	98	Lime	Clay	70+	3	4.8	-	-
134	490	12	98	Shale	Clay	70+	3	6.2	-	-
135	490	12	90	Shale	Clay	70+	2	5.7	6.1	217
136	490	10	100	Sand	Peat	70+	2	-	4.0	82
137	520	5	88	Lime	Bed	0	1	-	5.9	112
138	520	11	85	Lime	Silt	55	2	-	6.2	148
139	520	7	75	Lime	Silt	33	2	-	6.4	113
140	520	10	93	Lime	Bed	0	1	-	6.1	114
141	530	8	70	Lime	Bed	0	1	-	5.7	71
142	530	5	97	Lime	Silt	28	3	5.9	-	-
143	520	15	97	Lime	Bed	-	1	-	6.0	69
144	510	13	97	Shale	Peat	70+	3	6.1	-	-
145	510	10	97	Shale	Peat	45	3	5.6	-	-
146	490	24	85	Shale	Peat	70+	2	-	4.5	57
147	490	5	95	Sand	Peat	70+	4	5.7	-	-
148	480	10	97	Shale	Silt	70+	2	-	5.8	75
149	500	6	50	Lime	Clay	20	2	-	7.6	339
150	570	8	90	Lime	Silt	13	5	6.7	-	-
151	580	10	98	Lime	Peat	30	3	5.0	-	-
152	590	35	80	Lime	Bed	0	1	-	7.6	204
153	610	21	96	Lime	Clay	33	4	6.4	-	-
154	600	25	90	Lime	Silt	23	4	7.1	-	-
155	600	19	90	Lime	Bed	0	1	-	7.2	372
156	590	8	93	Lime	Silt	10	4	6.3	-	-
157	570	5	96	Lime	Silt	28	2	-	7.1	398

158	570	0	97	Lime	Peat	70+	2	-	6.9	459
159	570	0	95	Lime	Peat	70+	3	6.7	-	-
160	570	0	98	Lime	Silt	40	4	6.6	-	-
161	570	0	97	Lime	Peat	70+	4	6.7	-	-
162	560	12	95	Lime	Silt	45	4	6.6	-	-
163	560	10	91	Lime	Silt	45	4	6.4	-	-
164	560	7	80	Lime	Silt	20	4	7.0	-	-
165	520	0	40	WS	Coar	15	3	7.2	-	-
166	520	0	92	WS	Bed	0	1	-	7.1	395
167	520	0	94	WS	Coar	12	2	-	6.7	251
168	520	0	98	WS	Coar	20	3	6.3	-	-
169	520	0	95	WS	Silt	10	4	6.2	-	-
170	520	0	90	WS	Bed	0	1	-	7.2	249
171	530	0	97	WS	Silt	33	5	6.8	-	-
172	530	0	95	WS	Peat	70+	3	6.0	-	-
173	530	0	97	WS	Peat	55	3	5.1	-	-
174	530	0	98	WS	Grav	10	1	-	6.8	231
175	520	15	96	WS	Silt	11	4	7.3	-	-
176	520	0	90	WS	Coar	25	2	-	6.8	227
177	420	15	90	Lime	Silt	25	4	6.1	-	-
178	420	7	30	Lime	Bed	0	1	-	7.5	164
179	420	10	97	Cong	Silt	35	3	6.3	-	-
180	420	7	60	Cong	Bed	0	1	-	7.5	160
181	400	13	90	Cong	Bed	0	1	-	7.6	155
182	390	0	99	Cong	Coar	20	4	5.7	-	-
183	390	0	50	Cong	Grav	3	1	-	6.7	178
184	380	0	88	Cong	Bed	0	1	-	6.6	183
185	460	6	90	Lime	Silt	15	2	-	7.5	313
186	460	8	95	Lime	Silt	25	3	6.6	-	-
187	450	13	96	Lime	Clay	45	2	6.8	7.4	306
188	450	10	97	Lime	Silt	60	4	6.9	-	-
189	450	18	98	Lime	Silt	30	4	6.9	-	-
190	450	15	55	Lime	Bed	0	1	-	7.3	290
191	450	16	97	Lime	Clay	20	3	6.7	-	-
192	440	10	98	Lime	Peat	70+	4	6.2	-	-
193	440	15	99	Lime	Clay	70+	4	6.9	-	-
194	440	13	97	Lime	Clay	50	5	6.8	-	-
195	450	9	90	Lime	Silt	30	3	6.7	-	-
196	480	5	94	Lime	Silt	20	4	6.3	-	-
197	480	5	90	Lime	Silt	10	5	7.2	-	-
198	490	9	97	Lime	Clay	50	3	6.5	-	-
199	490	2	96	Lime	Clay	40	3	6.5	-	-
200	490	0	92	Lime	Coar	26	3	6.6	-	-

Key to Table 15

Samp. = Sample number
Altit. = Altitude (m)
Slope = Slope (degrees)
% Cov = Vegetation cover (%)
Geol. = Bedrock
Soil = Soil type
Depth = Soil depth (cm)
Moist. = Soil moisture status
S.pH = Soil pH
W.pH = Water pH
Cond. = Conductivity ($\mu\text{s}/\text{cm}$)

Soil type:

Bed = Bedrock - no soil present
Grav = Shallow gravel
Clay = Clay - usually gleyed
Silt = Silt
Coar = Coarse grained
Peat = Peat
PG = Peaty gley

Geology:

Lime = Limestone
Shale = Shales
MG = Millstone Grit
Sand = Sandstone
WS = Whin Sill
Cong = Conglomerates

Soil moisture status:

1 = Surface water over bedrock
2 = Saturated soil - surface water present
3 = Saturated soil - water table below
4 = Moist but not saturated soil
5 = Relatively 'dry'

Appendix V

Key to environmental variable codes displayed on CANOCO plots

Alt = Altitude
Slo = Slope
Cov = % Cover
Dep = Soil depth
Wat = Soil moisture
SpH = Soil pH
WpH = Water pH
Con = Conductivity
G1 = Limestone
G2 = Shales
G3 = Millstone Grit
G4 = Sandstone
G5 = Whin Sill
G6 = Conglomerates
S1 = No soil
S2 = Shallow gravel
S3 = Clay
S4 = Silt
S5 = Coarse grained
S6 = Peat
S7 = Peaty gley

