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South Somerset SSSIs

A study of neutral grassland succession

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SOUTH SOMERSET SSSIs: A STUDY OF NEUTRAL GRASSLAND SUCCESSION

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1 SUMMARY

1.1 This report details studies of fields of known ages and past treatment within a narrow compass of countryside in Somerset, near the border with Dorset. The ancient grasslands studied were previously identified as among the richest MG5 communities known, supporting up to 47 species in a square metre. This diversity is in part attained through a mixture of species characteristic of all MG5 subcommunities growing together.

1.2 Analysis revealed predictable effects of past ploughing and disturbances such as reseeding with ryegrass and cropping. Sowing with hay-seed however has produced a very rich grassland in all senses within only a few decades.

1.3 Despite this, differences are detectable between grasslands to the oldest studied (not ploughed since before 1808). Younger grasslands can be very rich in species, including those regarded as indicators of unimproved grassland. However, the full mixture of subcommunity preferentials, most notably the full range of MG5c species present, continues to develop for well over a century.

1.4 Possible explanations for the richness of these grasslands and the time they take to develop lie in the nature of the associated soils and their development. The mixture of calcareous and acidophilous species found in these grasslands may be the result of natural soil processes causing micro-spatial variation in the mottled and partly gleyed heavy soils where they are found.

1.5 These studies suggest that the time taken for species-rich mesotrophic grassland communities to develop is a similar order of magnitude to that reported for species-rich calcareous grasslands, i.e. well over a century. These findings must be treated with caution because they are effectively based on a single site in unusually favourable circumstances for the late 20th century. Despite this caution, a preliminary description of the mesotrophic grassland succession has been developed to stimulate its testing by observation and experiment elsewhere.

2 INTRODUCTION

Calcareous grasslands are the best known species-rich open ground communities to most British ecologists. Ancient chalk grasslands in particular are often cited as examples of communities which have dense species packing within small areas as well as being rich in species on a larger scale (e.g. Tansley 1939, Rodwell 1992 ed.).

In consequence a great deal of attention has been paid to the mechanisms by which diversity in calcareous grasslands is generated and maintained. One particular focus has been the generation of this diversity through ecological succession, and the typical time-scales on which ancient species-rich communities develop from arable farmland or other origins (Tansley and Adamson 1925, Wells *et al* 1976, Gibson and Brown 1991, Gibson 1995).

The consensus is that ancient calcareous grasslands, in all but the most exceptional circumstances, take at least a century to develop, i.e. reach a stage where a recognisable plagioclimax vegetation is present. Knowledge of this timescale has been important both in informing attempts to re-create these grasslands and in safeguarding existing ancient grassland sites.

Calcareous grasslands are not the only British plant communities with this exceptional diversity in ancient communities. Among the grassland communities described in Rodwell (1992 ed.), there are a number of mesotrophic and acid grassland communities for which some samples used in generating the National Vegetation Classification contained 45 or more species in the 2x2m quadrats used for the surveys, i.e. comparable with the richest ancient calcareous grasslands. These include communities such as MG2 (*Filipendulo-Arrhenatheretum* tall-herb grassland), and U4 (*Festuca ovina-Agrostis capillaris-Galium saxatile* grassland), the latter having as many as 62 species per sample. Outside grasslands, some flush and small-sedge mire communities can be equally rich.

Despite the recognition of the nature conservation value of these other species-rich grasslands (NCC 1989, Jefferson & Robertson 1996) and their rapid decline, virtually nothing is known about the time it takes for them to develop or the processes involved. Experimental work has been limited to quantifying the deleterious effects of agricultural improvement (e.g. Mountford et al 1993) or documenting the slow process of recovery after the application of modern agricultural fertilisers ceases (Olff and Bakker 1994).

In these circumstances, the only option has been to assume that these other species-rich communities take a similar time to develop as species-rich ancient calcareous grasslands. While this may be a plausible assumption, it would be much better to base site safeguard and defence and more general ecological knowledge on a sounder footing.

This report documents a first attempt at assessing the timescale of succession in a single type of one of these other species-rich grasslands. In the course of work on the different effects of horse and cattle grazing on MG5 (*Centaureo-Cynosuretum* grasslands) neutral grasslands in England, it emerged that these grasslands, in contrast to the (with hindsight) relatively species-poor examples used for the NVC, could have species packing as dense as any other ancient grassland community (Gibson 1996). Species rich examples, containing 35-45 species in one square metre (more than any MG5 sample in the NVC did in four square metres) and up to over 60 in the 2x2m area most nearly comparable with NVC samples, were scattered between Somerset and Worcestershire. Since then, the author has become aware of equally rich examples in Wales (D Stephens, personal communication).

The richest single site included in Gibson's (1996) study was at Grove Farm, just within Somerset on the Dorset border near Hardington Mandeville. Inspection of this site and conversation with the owner revealed that it formed part of a network of MG5 fields, many but not all of which had been ploughed and sometimes reseeded during the memory of the owner and his family. Taken together, these fields provide a unique opportunity to observe vegetation composition in fields of known age on the same soils and otherwise with the same treatment. Later, discussions with English Nature staff revealed another pair of fields suitable for the same study nearby, at Hardington Moor National Nature Reserve.

The analysis below is designed to extract a best estimate of the successional changes in the MG5 grasslands in this area of the Somerset border, assuming that the fields are representative of others of their age. The conclusions derived are strictly limited but are presented to provide a start of understanding in the hope that it will stimulate further refinement through both observation and experiment. In particular the following limits should be noted.

- Most successional ages and treatments are represented by only one field. The fields may not be representative of similar situations elsewhere.

- Unusually for the late 20th century, the Grove Farm grasslands when disturbed have always remained adjacent to other species-rich ancient grassland patches. The potential for recolonisation is at a maximum, unlike in most other sites in Britain.

- Despite choosing only those fields with relatively simple management and past history, there may be unknown or unreported factors complicating the results in individual fields.

- The ancient grasslands within this study are unusually species-rich. The conclusions may not apply to less rich or otherwise different sites.

3 METHODS

3.1 The sites

1 Site locations are shown on Figure 1 and the layout of the fields at Grove Farm and Hardington Moor on Figure 2. The fields included in the study were selected because they appeared to have had relatively simple treatments. Further fields of MG5 grassland and/or with known history were available but rejected because of complex or uncertain past management or (sites remote from the main group on Pen Hill) they did not have suitable paired controls of undisturbed ancient grassland. The fields studied comprise the following.

GF76R Southeastern part of Plain Close pasture. Arable on 1808 estate map, but pasture on 1844 tithe map. Ploughed in 1976 and immediately reseeded with ryegrass mixture. Since then, grazed as cattle pasture with the other fields on Pen Hill.

GFCRR Barley Plot, but recorded as pasture in both 1808 and 1844. Ploughed post-World War II, with 2-3 years crops in the 1970s, followed by reseeding as a ryegrass pasture. Since then, cattle pasture.

GF60R Higher Dampier's Ground. Arable in 1808 and 1844, followed by a long period of pasture until approximately 1960 when it was ploughed and then reseeded, not with ryegrass but with "hayseed", i.e. from the indigenous hay crop. Used as cattle pasture since.

GF52TS Ope Field. Pasture in both 1808 and 1844, but ploughed and subsoiled in 1952, subsequently cattle pasture with the rest.

GFU1 Southeastern field of Plain Close. Pasture in 1808, 1844 and subsequently. Now grazed with cattle with the remaining Pen Hill fields. High density of large anthills.

GFU2 Northwestern part of Plain Close. Arable in 1808 but pasture by 1844 and subsequently. Grazed by cattle with the remaining fields, but with evidence of recent poaching not seen elsewhere in the selected fields. High density of large anthills.

GFU3 Field east of Higher Dampiers Ground separated from it by large ancient hedgerow. Estate map of 1808 labels "arable" over Higher Dampiers Ground and this field, but likely to refer to only Higher Dampiers Ground because of separation. Pasture by 1844 and subsequently. High density of large anthills.

HNU Hardington Moor NNR. Southern portion of Hawkins Hill pasture. Pasture on 1843 tithe map and no record of ploughing or other disturbance. Reported by English Nature staff to be the part of the NNR most similar to HNP before the latter was ploughed. Managed as HNP, except that it received farmyard manure in 1996.

HNP Hardington Moor NNR. Coker Hill. Arable on 1843 tithe map, but described as ancient species-rich grassland until ploughed and cropped for 2 years until 1984. Since then has been allowed to tumble down to grassland (i.e. no reseeding) within the NNR, put up for hay and aftermath grazed by cattle.

2 Within each field the sampling methods below were applied only to areas of MG5 grassland or its assumed precursors in early successional fields. The following features, all restricted to ancient grassland fields, were excluded.

- Patches which were not MG5 grassland.

- Anthills.

- Patches of scrub.

3.2 Site environmental factors

From the descriptions above, values were given to a series of "environmental" variables" for analysis and attempted explanation of the vegetation encountered. The environmental variables used were as follows.

- Age since last ploughing in years.

- Reseeding with a "modern" ryegrass mixture with fertiliser, or not.

- "Hayseed" reseeding or not.

- Subsoiling or not.

- Evidence of poaching or not.

- Percentage of bare ground in a quadrat.

- Average vegetation height in quadrat.

3.3 Quadrats

Quadrats were located within fields by the same "random walk" method used by Gibson (1997), described below.

1 Pick a random position within the patch from a pair of random distances, walked at right angles into the patch. This becomes the starting point for a random walk.

2 Pick a random distance and a random angle (compass direction from 1 to 8 (north round clockwise to north-west).

3 Travel at this angle for the indicated distance. If an edge is encountered, bounce off the edge as if bouncing light off a mirror.

4 The point found becomes the south-west corner of a quadrat.

5 After recording the quadrat, pick another random angle and distance to find the next quadrat from the last recorded.

6 Repeat until six quadrats have been recorded.

7 No quadrat may lie within two metres of another (because of possible interference effects from recording the first one). Should this happen, the random walk continues, ignoring the "illegal" position.

The quadrat used was 1m square, divided into 25 square 20x20cm cells. Before placing the physical quadrat, three height estimates were made by the dropped-disc method, followed by recording a full vascular plant species list for each cell. The percentage of bare ground was also recorded.

4 ANALYSIS

4.1 Analysis strategy

Data analyses carried out are described below in the order in which they were done. The order as well as the nature of the analysis is important because it was designed to avoid formal statistical and probability problems as far as possible.

4.2 Multivariate assessment procedure

1 DECORANA

DECORANA (also called DCA) stands for detrended correspondence analysis, a standard ordination method originally developed by MO Hill (1973). It describes vegetation in terms of the most important independent patterns (axes) of variability in species composition between samples (here quadrats). By itself, it cannot identify the causes of variability.

Here, DCA was used to explore the data structure and check for anomalies which might suggest the need for data transformation, exclusion of outlier samples or species, or any other modifications.

This operation cannot test the influence of environmental variables: it is merely a data exploration technique used to check that the data structure was suitable for the subsequent analyses, which used DCCA (detrended canonical correspondence analysis) to test the influence of environmental variables including age.

2 DCCA - investigating the effects of key variables

The core of DCCA is a double ordination in which an ordination of species composition is constrained to devise the most likely relationship between the species composition data and linear combinations of the environmental variables.

Although more robust than older methods which make many assumptions about the underlying structure of the data, DCCA is still sensitive to sets of variables which are highly intercorrelated and explain little variation independently of each other. With each ordination carried out, DCCA provides summary statistics which were inspected to ensure that only variables which did have independent explanatory power were included.

An explanatory model was then built and tested using CANOCO's facility for forward selection of environmental variables. Relations between environmental variables and vegetation have been built up stepwise, for instance by first taking the variable with the greatest explanatory power and testing the significance of its effect by Monte Carlo permutations, followed by repeating the process for each variable in turn. If the effect of a variable is significant, it is retained, otherwise it is left out of the model.

Variables were only included if they had an individual effect at a significance level of at least 0.01: this superficially "conservative" procedure is the correct one where a sequence of variables is being tested.[1]

3 "Partial" DCCA - a best estimate of successional age categories

Although the effects of reseeding and other past treatments are of interest, it was considered important to derive as good an estimate as possible of the species which might characterise different successional ages, without the confounding effects of other variables. Accordingly, a partial DCCA analysis was run which factored out the effects of all variables except age as "covariables", leaving an estimate of the patterns at different ages without the effect of the other variables.

4.3 Species, categories and other attributes

By testing ordinations and environmental variables, CANOCO identifies significant effects of variables of interest. Plant species and species groups which are associated with their effects can be identified from their positions relative to the effects of variables. Attention is drawn to particular species in this report which appear to be characteristic of, for instance, reseeding, but the main analysis has been a direct division of the "age" axis derived from partial DCCA (above) to show different successional stages.

It is also of interest to examine effects of age and other variables with reference to simpler aspects of the vegetation, such as species richness, abundance of mesotrophic grassland indicators and similar categories derived from independent studies, i.e. outside the particular data studied here. Strictly, a probability level, and therefore significance tests, cannot be assigned to such effects because testing them is not independent of the statistical tests already carried out by CANOCO. However, if for instance there are many fewer indicator species in younger fields, this means that such indicators have made an important contribution to the high significance level shown by CANOCO for the effects of age since ploughing on the vegetation. Demonstration of the effects on such categories is therefore illustrative, not formal, but is essential for forming hypotheses about the nature of succession towards ancient mesotrophic grasslands.

Attributes of the vegetation chosen for such illustration were as follows.

1 Species richness.
2 Species diversity (Williams' alpha) to show evenness as well as richness.
3 Indicator species scores as supplied to Bioscan by English Nature (Rowell and Robertson 1994), in which species are scored from 1 to 8 with increasing

[1] For instance, if one does a sequence of 20 tests, an average of one of them would be expected to be "significant" at the p=0.05 (1 in 20) level by chance alone.

strength of restriction to unimproved mesotrophic grasslands.

4 CANOCO indicators of successional age derived from partial DCCA analysis.

4.4 Graphics conventions

In all the multivariate analyses described above, it is a common convention to show the more important axis being plotted (usually the first axis) as the horizontal or x-axis and the axis of lesser importance as the vertical or y-axis. Species and/or samples are plotted simply in the positions indicated by their scores on each axis, labelled by a shortened form of their names. A full list of plant names and abbreviations is given in Appendix 1 and of quadrats (samples) in Appendix 3.

The plotting of environmental variables is a little more complex. If a variable can only take one of two values (i.e. presence or not, such as "hayseed") it is a "nominal" variable and its influence on the analysis is conventionally represented by a single point - its centroid. If an environmental variable is quantitative, such as "age" and could take many values, its influence is best represented by its biplot arrow, which in DCCA arises from the origin and passes in a direction which shows its relative influence on each axis (acute angle means strongly associated) for a distance proportional to the strength of its effect (long arrows mean a strong effect).

5 FINDINGS

5.1 Richness, diversity and indicators

Tables 1 to 3 show the total vascular plant species richness per 1m square, Williams alpha diversity and the number of mesotrophic indicator species per square metre average in fields or groups of fields with particular past histories. These incomplete (not all ages had all factors) matrices of values are arranged so that the central row shows fields of a known age with no additional factors affecting them. The top row shows the field subject to a factor (hayseed) which would be expected to accelerate development towards an ancient unimproved grassland community. The bottom row shows fields with additional factors which would be expected to have a negative effect on unimproved grasslands.

Table 1: Species richness in fields of different history

Last ploughed	1984	1976	1960s	1952	>150
Assumed positive factor			Hayseed		
			39.8		
No additional factor	28.0	34.7			36.8(3)
		20.7		31.7	37.7
Assumed negative factor		Ryegrass & crop		Subsoiled	Poaching

All fields contain species-rich vegetation by most standards of comparison. The hayseeded field and the oldest fields are the richest by a relatively small margin. The only field with markedly lowered richness (just over half that in the best fields) is the one subject to cropping followed by reseeding and improved grassland management. The poaching in one field had no effect on richness.

Table 2: Species diversity (Williams alpha) in fields of different history

Last ploughed	1984	1976	1960s	1952	>150
Assumed positive factor			Hayseed		
			11.2		
No additional factor	7.6	9.6			10.1
		5.5		8.6	10.5
Assumed negative factor		Ryegrass & crop		Subsoiled	Poaching

Patterns in species diversity are almost identical to those for overall richness, with the hayseeded field having the highest diversity.

Table 3: Indicator species richness in fields of different history

Last ploughed	1984	1976	1960s	1952	>150
Assumed positive factor			Hayseed		
			18.8		
No additional factor	8.2	13.5			17.9
		2.2		13.2	17.8
Assumed negative factor		Ryegrass & crop		Subsoiled	Poaching

The greatest difference between fields is shown in the mesotrophic indicator species richness per 1m square. Indicators were virtually absent from the 1976 reseeded field and show a clear successional trend, although the hayseeded field is again the richest overall. Poaching had no effect.

5.2 Multivariate analyses

1 DCA analysis arranged quadrats (Figure 3) in a pattern on the first two axes which suggests a contrast between successional age or other disturbance and between the two groups of fields at Hardington Moor NNR and at Grove Farm (Pen Hill). The Hardington fields score low on both axes, but the ploughed field quadrats there scored higher on axis 2 and lower on axis 1 than the ancient grassland.

Grove Farm quadrats form a similar and parallel but more extensive series on Figure 3, with disturbed and/or young fields scoring high on axis 2 and low on axis 1 and the ancient grasslands there scoring lower on axis 2 but with much higher axis 1 scores than the equivalent Hardington Moor field.

Examination of the species patterns involved (Figure 4) fits well with the interpretation of disturbance. Species scoring high on axis 2 but low on axis 1 are all species characteristic of early succession or disturbance in mesotrophic or calcareous grassland (e.g. *Senecio jacobaea* SENJACO, *Cirsium vulgare* CIRVULG, *Poa trivialis* POATRIV (Gibson and Brown 1991), *Lolium perenne* LOLPERR - Gibson 1997). The Hardington Moor grasslands are more characterised by species which are shared with calcareous grasslands such as *Avenula pubescens* AVEUPUB and *Sanguisorba minor* SANGMIN in the ancient grassland and *Daucus carota* DAUCARO in early succession. Conversely, MG5c preferentials such as *Succisa pratensis* SUCCPRA, *Genista tinctoria* GENTINC and *Potentilla erecta* POTEREC score high on axis 1, appearing to be associated with the Grove Farm grasslands.

This separation is far from complete however. Indeed, the Grove Farm grasslands are striking by their combination of species preferential to different MG5 subcommunities growing together.

2 DCCA analysis identified grassland age, sward height, reseeding, subsoiling and seeding with hay-seed as having significant effects on species composition (Figure 5). Increasing age was closely associated with low scores on axis 1 and less so with low scores on axis 2 (note direction of arrow). The reseeding effect has a high score on both axes (represented as a point - centroid - because it is a nominal variable). The effect of hay-seeding is associated with low scores on canonical axis 2 and taller swards are indicated with high scores on axis 1 and low scores on axis 2. Note that the youngest field (HNP) was also put up for hay so is inevitably taller.

Examination of the species concerned (Figure 6) shows that the formal explanation of DCCA largely reflects the informal interpretation from the illustrative DCA analysis above. Species in the upper right quadrant of Figure 6 are virtually all ones well known to be associated with disturbance or agricultural improvement (e.g. *Bromus mollis* BROMOLL and *Taraxacum* agg. TARXOFF as well as the examples cited for Figure 4 above. Conversely the taller swards include species (e.g. *Vicia cracca* VICICRA, *Lathyrus pratensis* LATHPRA) also associated with hay management by Gibson (1996).

Individual effects of the remaining variables are more difficult to disentangle, although the apparent association of *Trifolium medium* TRIFMED with the hay-seeded field is of note.

Examination of species associated with different aged fields is left to the partial DCCA analysis described in the next section.

5.3 Successional categories

Partial DCCA analysis to factor out the effects of all variables with age results by definition in only one canonical axis: plotted as the first or horizontal axis in Figure 7. Older grasslands are to the right and younger ones to the left. The spread of species on the second axis reflects residual variation not explainable by any of the environmental variables or covariables, i.e. the first axis of a DCA ordination of the remaining variability in species composition which is unexplained. The patterns of species on this axis do not suggest an obvious or simple explanation.

Division of axis 1 produces the best approximation to a simple successional series which can be gathered from the data. Any division is arbitrary but seven groups have been derived to make as even a division as possible while retaining enough species in each group to give a meaningful interpretation. The groups are shown in full in Table 4, arranged in order from group 1, the species most associated with the oldest grasslands, to group 7, the species most associated with the youngest grasslands.

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Table 4: Species in different successional stages from division of Figure 7 Axis 1

Axis 1 score	Species
Species shown in **bold underline** occurred in ten or more of the 54 quadrats, those in **bold** in five or more quadrats. Sparser species cannot be presumed to be reliably associated with particular stages: they merely happened to be found there in this study. Woody plant seedlings are omitted.	
1: >3.0 Oldest	Arrhenatherum elatius, **Avenula pubescens**, Blackstonia perfoliata, Carex pulicaris, Convolvulus arvensis, **Festuca pratensis**, **Leontodon autumnalis**, **Oenanthe pimpinelloides**, Oenanthe silaifolia, **Orchis morio**, Plantago media, Potentilla sterilis, Sanguisorba minor, **Serratula tinctoria**, **Silaum silaus**, Stachys officinalis, **Tragopogon pratensis**, **Trisetum flavescens**.
2: >2.0	**Avenula pratensis**, Brachypodium sylvaticum, **Briza media**, **Cirsium acaule**, **Danthonia decumbens**, Hieracium pilosella, **Polygala vulgaris**, **Ranunculus acris**, **Succisa pratensis**.
3: >1.0	**Achillea millefolium**, **Agrimonia eupatoria**, **Ajuga reptans**, **Anthoxanthum odoratum**, **Carex caryophyllea**, **Carex panicea**, **Centaurea nigra**, **Cirsium dissectum**, **Dactylis glomerata**, Deschampsia caespitosa, **Festuca rubra**, **Galium verum**, **Genista tinctoria**, Heracleum sphondylium, **Hypochaeris radicata**, **Lotus corniculatus**, **Plantago lanceolata**, **Potentilla erecta**, **Primula veris**.
4: >0	**Agrostis capillaris**, **Carex flacca**, **Cirsium palustre**, **Cynosurus cristatus**, Elymus repens, Euphrasia officinalis agg, **Holcus lanatus**. Hordeum secalinum, **Lathyrus pratensis**, **Leontodon hispidus**, Leontodon taraxacoides, **Linum catharticum**, **Luzula campestris**, Pedicularis sylvatica, **Poa trivialis**, Potentilla anserina, **Ranunculus bulbosus**, **Taraxacum agg.**, Trifolium medium, **Trifolium pratense**, **Trifolium repens**, Veronica officinalis, **Viola hirta**, **Viola riviniana**,
5: >-1.0	Alchemilla vulgaris agg., **Bellis perennis**, **Bromus hordeaceus hordeaceus**, **Cirsium vulgare**, **Gaudinia fragilis**, **Leucanthemum vulgare**, **Lolium perenne**, Mentha arvensis, **Phleum pratense**, **Potentilla reptans**, **Prunella vulgaris**, **Pulicaria dysenterica**, **Ranunculus repens**, **Senecio erucifolius**, **Senecio jacobaea**, **Trifolium dubium**.
6: >-2.0	**Agrostis stolonifera**, **Cerastium fontanum**, Cirsium arvense, Festuca x loliacea, Geranium dissectum, Juncus acutiflorus, **Medicago lupulina**, **Poa pratensis**, Rumex acetosa, **Sagina procumbens**,.
7: <-2.01 Youngest	**Centaurium erythraea**, **Daucus carota**, Hypericum maculatum, Hypericum perforatum, Hypericum tetrapterum, **Juncus inflexus**, Veronica serpyllifolia, **Vicia cracca**.

Figure 8 shows the relative contributions which each of the seven groups make to the vegetation in fields of different ages sampled, irrespective of other treatments. Grasslands not ploughed since at least 1808 have been given a notional age of 250 years.

Group 1 is almost wholly restricted to the oldest grassland, where it forms a minor (less than 10%) component. Examples of the two commonest species involved are shown in Figure 9. The grass *F.pratensis* is a surprising member of this group as it is widespread in grasslands elsewhere not noted for their age, but the restriction of *S.tinctoria* is less surprising.

Group 2 contains species which are virtually absent from the youngest grasslands and only become an important component of the vegetation in grasslands over a century old. It contains several strong indicators of ancient unimproved grasslands (calcareous and/or mesotrophic, exemplified in Figure 10 by *S.pratensis* and *B.media*.

Group 3 are species already present as a significant component in early succession. Their contribution doubles between 20 and 35 years old but changes little thereafter. Individual common species were sometimes erratic in their relationship, such as the grass *A.odoratum* shown as an example in Figure 11, perhaps as a result of particular conditions in individual fields. Other common species showed a much more even increase (*P.erecta* - Figure 11).

Group 4 species are a major component throughout the age range studied although overall their contribution decreases slightly from the youngest to the oldest fields. The large number of common individual species in this group show no particular trend with age (e.g. *T.pratense* and *C.flacca* in Figure 12).

Groups 5 to 7 clearly define early succession, with groups 6 and 7 only a noticeable component in the youngest grassland sampled, at Hardington Moor. Group 5 species make up approximately half the vegetation there, but decline steadily until they are only a minor component of the oldest grasslands. It is notable that this group contains species which are commonly (and perhaps mistakenly) regarded as signs of "success" in wildflower grassland creation, such as *Leucanthemum vulgare* and *Prunella vulgaris*. Examples of the more frequent species involved are shown in Figures 13 and 14. Notable among these is the rare and restricted grass *G.fragilis*, an annual suspected to be an ancient introduction. Although present at low frequency at any age, it is ubiquitous in the youngest field studied being present in all cells of all quadrats (average cells occupied 25 out of 25).

5.4 Succession and the MG5 subcommunities

The grasslands at Grove Farm and Hardington Moor are unusual in containing all the MG5 constant species and all preferentials of all subcommunities except that the grass *Koeleria macrantha* (MG5b) and the herb *Pimpinella saxifraga* (MG5c) have not been seen by the author. The remaining subcommunity preferential species are often mixed together in a single quadrat, and 20 out of the 25 preferentials were abundant enough to be encountered in at least one quadrat.

All the MG5 constant species fall in groups 4 and 5 in Table 4, i.e. they are species which are widespread throughout the age range studied. It is in the subcommunity preferentials that a successional pattern appears to emerge (Figure 15). MG5a species as a group can be nearly twice as common in the early successional fields as in the oldest ones. MG5b species show no particular pattern, but MG5c preferentials show a very strong successional trend. They form only a minor component of the youngest grassland and steadily increase to peak in fields over 100 years old.

6 DISCUSSION

6.1 Age and other variables

In these studies, successional age is partly linked to other disturbances such as reseeding with ryegrass mixtures, subsoiling and cropping. Despite this it has been possible to derive a preliminary view of the mesotrophic grassland succession. The results reinforce other studies (Olff & Bakker 1991, Mountford et al 1993) which have shown that reseeding and improvement causes damage which is long-term and difficult to reverse.

Conversely, hay-seeding at Grove Farm has produced a grassland which in only a few decades has become as rich in species, including mesotrophic grassland indicators, and has equivalent diversity to the most ancient fields. This outcome is similar to Gibson and Brown's (1991) failure to distinguish the wartime ploughed Stony Piece chalk grassland at Aston Rowant NNR from adjacent ancient chalk grassland by analysis of species composition. The hayseed field did however emerge as a distinct cluster here in DCA ordination (Figure 3).

Unlike that situation, the hay-seed field remains different in one aspect from the ancient grasslands, i.e. in the cover of MG5c preferential species, which continue to increase (Figure 16) until fields are over a century old. In combination, this strongly suggests that significant vegetation change is still taking place in such grasslands for well over a century, just as is usually the case in calcareous grasslands.

A further natural part of the development of these grasslands is the growth and density of anthills, which were outside the scope of this study. The development of these structures, their vegetation and fauna, adds another dimension to the development of the grassland community which has not been addressed at all here.

It must also be remembered that the situation at Grove Farm and Hardington Moor is exceptionally favourable for the recovery of species-rich grasslands. As in the early 19th century, when the oldest ploughed grassland studied here were starting to revert from arable, there remains a framework of existing species-rich grassland surrounding any small field disturbance or ploughing. This is wholly unlike the usual late 20th century situation where surviving patches of species-rich grassland are usually well isolated from other sources of colonisation.

The situation at Grove Farm is also unusual in that the grasslands are richer in species than any MG5 areas used in the NVC studies. They are not exceptionally rich, as revealed by studies in 1995 and 1996 (Gibson 1997) and surveys of grassland in Wales (D Stephens pers. comm.), but they are outside the range of variation often encountered in England.

6.2 Why are the ancient grasslands so rich?

The immediate pattern behind this richness is the mixture of species supposedly preferential to several MG5 subcommunities in the same place, often including both calcicoles and supposedly calcifuge plants. Patches at Grove Farm can readily be found where *Genista tinctoria*, *Sanguisorba minor*, and *Leucanthemum vulgare* grow intertwined in the same few square centimetres.

Without specific information, one must assume some temporal and/or spatial variation on a very small scale which allow such plants to coexist. The cause is less obvious than the clear vertical stratification found in chalk heaths, where sand layers over chalk allow both calcicoles and calcifuges to coexist on a small scale (Watt 1936).

The Soil Survey of England and Wales (SSEW 1984) maps the local soils as Evesham I Association. The deeper soils within this association are Evesham series, calcareous pelosols in clay shales. The essential characteristic of these soils is that they are only slowly permeable and, despite having calcareous layers, develop mottling and can readily develop a spatial mosaic of different pH on a very small scale.

Given the baseline calcareous nature of these soils, it may well be that the spatial component which takes time to develop after deep ploughing or other disturbance is patchy acidity. This would be a plausible explanation of the continued increase in MG5c species over a very long period, but one which would need specific research to test.

The particular richness of these MG5 grasslands is therefore likely to be a combination of the necessary time for plant succession combined with soil development.

6.3 The workings of MG5 succession

The studies reported here did not include any fields in the first few years after ploughing. Aside from this, the patterns seen reflect those reported in calcareous grassland successions, with one important difference. There appear to be no species which are rare in both early succession and in ancient grasslands but common components in the middle decades. There is a strong component of this nature in calcareous grassland succession (Gibson and Brown 1992), comprising mainly robust but relatively short-lived species such as *Pastinaca sativa, Knautia arvensis, Silene vulgaris* and others. There are few such species in the fields studied, one being *Daucus carota* which was restricted to the youngest fields examined.

In contrast, there is a strong component of species which are already present in the youngest grasslands studied and remain a significant proportion of the vegetation throughout. These include the great majority of the MG5 constant species, as well as subcommunity preferentials such as *Leucanthemum vulgare*. Part of this result may be because the youngest grasslands studied here were only under the plough for a short time, so species from the original grassland may have survived in the buried seed bank or even as vegetative fragments.

Although species preferential to the oldest grasslands include many MG5c preferentials (Figure 16), they also include species more characteristic of calcareous conditions such as *Avenula pratensis* and *A.pubescens*. The ancient grasslands are thus characterised by a mixture of species of varied ecological requirements which have in common only their status as long-lived perennials and their observed slowness in colonising the grasslands.

Species of nature conservation interest in their own right such as *Orchis morio* and *Oenanthe pimpinelloides* tend to be associated with late successional groups (see Table 4). However this restriction is not absolute: individual species can often be encouraged quite quickly in contrast to the particular vegetation mixture which characterises ancient species-rich grasslands (reviewed in Gibson 1995).

6.4 Conclusions and consequences

Assuming that the findings from Grove Farm and Hardington Moor can be used as a start for developing a more general knowledge about mesotrophic grassland succession, there are significant consequences for site safeguard and for restoration studies and others which depend on manipulating succession.

With respect to site safeguard, it is clear that the ancient grassland MG5 community takes a similar order of time to develop as that seen in calcareous grasslands, i.e. well over a century. This is a minimum estimate, as in calcareous grasslands, because it takes no account of the development of specialised fauna and of biological / structural components such as anthills. This puts the value of real ancient grasslands sharply into perspective: they have a special interest which cannot be repaired or re-created on normal human timescales such as the typical lifetimes of planning obligations.

With respect to restoration, the results have identified the existence of circumstances (rarely occurring in modern Britain because surviving sites are usually small and/or isolated) when attractive grasslands can re-appear after only a few years and (the hay-seed field) attain many but not all of the attributes of ancient grasslands over a few decades. Conversely, the presence of a wide range of MG5 constant species does not mean that an ancient grassland has been recreated: this aspect and therefore the "fit" to an NVC community is revealed as one of the easier aspects of ancient grassland to re-create.

Despite the above, the limits of this study to a small geographical compass and a small number of fields mean that the conclusions are only preliminary. It is hoped that they will form a foundation stone for others to extend the observations to other grasslands of known age and treatment and, hopefully, stimulate experimental tests of the findings.

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APPENDIX 1
PLANT SPECIES ACRONYMS

Acronym	Latin name
ACERCAM	Acer campestre
ACHIMIL	Achillea millefolium
AGRCAPI	Agrostis capillaris
AGRIMEU	Agrimonia eupatoria
AGRSTOL	Agrostis stolonifera
AJUGREP	Ajuga reptans
ALCHVES	Alchemilla vulgaris agg.
ANTHODO	Anthoxanthum odoratum
ARRELAT	Arrhenatherum elatius
AVEUPRA	Avenula pratensis
AVEUPUB	Avenula pubescens
BELPERR	Bellis perennis
BLACPER	Blackstonia perfoliata
BRASYLV	Brachypodium sylvaticum
BRIMEDI	Briza media
BROMOLL	Bromus hordeaceus hordeaceus
CARECAR	Carex caryophyllea
CAREFLA	Carex flacca
CAREPAN	Carex panicea
CAREPUL	Carex pulicaris
CENTERY	Centaurium erythraea
CENTNIG	Centaurea nigra
CERFONT	Cerastium fontanum triviale
CIRACAU	Cirsium acaule
CIRARVE	Cirsium arvense
CIRDISS	Cirsium dissectum
CIRSPAL	Cirsium palustre
CIRVULG	Cirsium vulgare
CONVARV	Convolvulus arvensis
CRATMON	Crataegus monogyna (g)
CYNCRIS	Cynosurus cristatus
DACGLOM	Dactylis glomerata
DANTDEC	Danthonia decumbens
DAUCARO	Daucus carota
DESCAES	Deschampsia caespitosa
ELYREPE	Elymus repens
EUPHRAS	Euphrasia officinalis agg
FESLOLI	Festuca x loliacea
FESPRAT	Festuca pratensis
FESRUBR	Festuca rubra
FRAXEXC	Fraxinus excelsior (g)
GALVERU	Galium verum
GAUDFRA	Gaudinia fragilis
GENTINC	Genista tinctoria
GERDISS	Geranium dissectum
HERASPH	Heracleum sphondylium
HIERPIL	Hieracium pilosella
HOLCLAN	Holcus lanatus
HORDSEC	Hordeum secalinum
HYPMACU	Hypericum maculatum

Acronym	Latin name
HYPORAD	Hypochaeris radicata
HYPPERF	Hypericum perforatum
HYPTETR	Hypericum tetrapterum
JUNCACU	Juncus acutiflorus
JUNCEFF	Juncus effusus
JUNCINF	Juncus inflexus
LATHPRA	Lathyrus pratensis
LEONAUT	Leontodon autumnalis
LEONHIS	Leontodon hispidus
LEONTAR	Leontodon taraxacoides
LEUCVUL	Leucanthemum vulgare
LINUCAT	Linum catharticum
LOLPERR	Lolium perenne
LOTCORN	Lotus corniculatus
LUZCAMP	Luzula campestris
MEDILUP	Medicago lupulina
MENTARV	Mentha arvensis
OENPIMP	Oenanthe pimpinelloides
OENSILA	Oenanthe silaifolia
ORCHMOR	Orchis morio
PEDISYL	Pedicularis sylvatica
PHLEPRA	Phleum pratense
PLANLAN	Plantago lanceolata
PLANMAJ	Plantago major
PLANMED	Plantago media
POAPRAT	Poa pratensis
POATRIV	Poa trivialis
POLVULG	Polygala vulgaris
POTANSE	Potentilla anserina
POTEREC	Potentilla erecta
POTREPT	Potentilla reptans
POTSTER	Potentilla sterilis
PRIMVER	Primula veris
PRUSPIN	Prunus spinosa (g)
PRUVULG	Prunella vulgaris
PULIDYS	Pulicaria dysenterica
QUERCRO	Quercus seedling/sp
RANACRI	Ranunculus acris
RANBULB	Ranunculus bulbosus
RANREPE	Ranunculus repens
ROSACAN	Rosa canina (g)
RUMACET	Rumex acetosa
SAGPROC	Sagina procumbens
SALCINE	Salix cinerea
SANGMIN	Sanguisorba minor
SENERUC	Senecio erucifolius
SENJACO	Senecio jacobaea
SERRTIN	Serratula tinctoria
SILASIL	Silaum silaus
STACOFF	Stachys officinalis

SUCCPRA	Succisa pratensis
TARXOFF	Taraxacum seedling/sp
TRAGPRA	Tragopogon pratensis
TRIFDUB	Trifolium dubium
TRIFMED	Trifolium medium
TRIFPRA	Trifolium pratense
TRIFREP	Trifolium repens
TRISFLA	Trisetum flavescens
VEROFFI	Veronica officinalis
VERSERP	Veronica serpyllifolia
VICICRA	Vicia cracca
VIOHIRT	Viola hirta
VIORIVI	Viola riviniana

APPENDIX 2
SUMMARY OF DATA BY FIELDS

Each figure represents the mean cells occupied over six quadrats

Species	HNU	HNP	GFCRR	GF76R	GF60R	GF52TS	GFU3	GFU2	GFU1
ACERCAM				.166					
ACHIMIL			.166		.5	4	3.66		3.33
AGRCAPI	25	17.5	25	25	25	25	24.833	25	25
AGRIMEU	8.13		.333	5	18.833	7.66	6	5.33	11.17
AGRSTOL			.166	3	.333	.166	1.8333		.833
AJUGREP			.333		1.13	.166	.166	.333	.5
ALCHVES				.166	.333				
ANTHODO	24.166	6.33		4.13	13.833	1.13	11.833	10.3	5.66
ARRELAT	1.33								
AVEUPRA	3.66			.3					1.33
AVEUPUB	8.8333								
BELPERR	.3	.833	3.33	9	1	.166	4.13	1.33	2
BLACPER								.166	
BRASYLV					.333			.833	.333
BRIMEDI	8.8333			.5	9.33	4.5	20.5	20.833	22.83
BROMOLL		1.33	2.33						
CARECAR	.5	.166		1.5	3.33	7	7.8333	10.3	7.5
CAREFLA	8.66	20.5		20.166	16.833	13	14	21.3	23.33
CAREPAN				.333	.5	1	10	5.5	
CAREPUL								.833	.5
CENTERY				2.5	.166		.166		.166
CENTNIG	17	11.333		5	8.8333	15.3	8.5	4.66	13.33
CERFONT	1.13	1.13	1.13	3.66	.3	1.13	.166		
CIRACAU	4.13			.166	.833		1.8333		.833
CIRARVE		.333			.166				
CIRDISS	.166						3.33	3.13	
CIRSPAL				.166		1.66			.333
CIRVULG		.166	.166	1.13	.166	1.5	.166		.5
CONVARV	3								

Species	HNU	HNP	GFCRR	GF76R	GF60R	GF52TS	GFU3	GFU2	GFU1
CRATMON	.166				.833			.333	.166
CYNCRIS	24.833	17	20.166	21.5	22	24	23.3	25	22.83
DACGLOM	8.5	7	3.5	1.13	13.5	11.3	5.33	.5	11.83
DANTDEC	5.13	2		1	7.33	3.33	17.833	24.3	19.33
DAUCARO	.5	5.33							
DESCAES							.166	.166	
ELYREPE					.166				
EUPHRAS					1				
FESLOLI				.333					.166
FESPRAT	14.833			.833	1.8333	.333			1.833
FESRUBR	24.3	2.33	24.833	24.166	20.833	24.3	24.333	25	25
FRAXEXC						.333		.166	
GALVERU	.166				4.13	3.66	4	1.13	7
GAUDFRA	14	25	19.5		3.8333		.166	.5	.333
GENTINC	10			2	23.166	1.8333	4.8333	13.3	3.833
GERDISS		.333			.166				
HERASPH					.5				
HIERPIL	3.33					3.5			
HOLCLAN	15	15.3	21.166	9.13	3.13	5.8333	2.8333	.5	1.13
HORDSEC			.333						
HYPMACU				.333					
HYPORAD	8		3.33		2.8333	10.333	11.5	6.5	6
HYPPERF				.333	.166				
HYPTETR		.333							
JUNCACU				.3			1.13		
JUNCEFF				.333					
JUNCINF		1					.166		
LATHPRA	4.33	4.66			1.8333				
LEONAUT	1.8333				.3				2.13
LEONHIS	8.8333	.333	5.13	18	12.166	2.8333	7	.5	15.3
LEONTAR				.333					.5
LEUCVUL	8.13	24.333	.166	21	15.166	16.3	10.166	3.33	12.5

Species	HNU	HNP	GFCRR	GF76R	GF60R	GF52TS	GFU3	GFU2	GFU1
LINUCAT				3.33	4		1.13	5.8333	.833
LOLPERR	3.66	.833	25	23.333	4.8333	10.5	3.8333	.333	2
LOTCORN	21.5	11	2.8333	18	21.3	24	16.5	14.5	20.17
LUZCAMP	1.13	.333		2	.5	6.33	1	.166	.333
MEDILUP	1.33	5			.333				
MENTARV				1.13			1	1.33	
OENPIMP	2.8333	.166							
OENSILA	.3								
ORCHMOR	3.8333								
PEDISYL						3.66			
PHLEPRA	.833		1.66	4.8333	2.13	7	2.66		1
PLANLAN	12	5.8333	.166	5.13	13.5	1.13	1.66	4.13	3.833
PLANMAJ				.166					
PLANMED	.833								
POAPRAT	2.8333	8.8333		1.5	.5	.333	.166		
POATRIV		.166	9			.333			
POLVULG				.166		1.13		1	2.13
POTANSE							1.833		
POTEREC				8.33	10	9.33	15.3	21.5	21
POTREPT	1.33	12.333	12.166	17.5	12.5	8.33	16.833	9	8
POTSTER									.166
PRIMVER	3.33	1.33			1		1.13		.3
PRUSPIN					.3		.166		1.33
PRUVULG	4.5	5	2.66	19.333	9.5	9.33	11.5	4.13	11.83
PULIDYS	2.33	22.3		9.66	10.5	1.33	4	7.33	4
QUERCRO								.166	
RANACRI	10.833	.833		.833	4		3.5	.5	6.833
RANBULB	1.5			3.33	3	1.33		1.13	2.33
RANREPE	1.66	17.333	9	6.13	6.33	12.166	6.33	.833	
ROSACAN				.166					.166
RUMACET			.166	.5		.333			
SAGPROC				.833	.166		.5		

Species	HNU	HNP	GFCRR	GF76R	GF60R	GF52TS	GFU3	GFU2	GFU1
SALCINE		.166							
SANGMIN	3.33								
SENERUC		.333		1.13	2.33		.5	1.13	
SENJACO	.833		.166	1.833		.3			.166
SERRTIN					.5		.166	15.3	1
SILASIL	7.13	.833			.166				
STACOFF							.166		2.33
SUCCPRA	.833			.5	5.833	11.5	17.5	24.5	24.83
TARXOFF	7.66	1	11	6.66	1.833	3.833	6.66	2.33	2.5
TRAGPRA	1.5								
TRIFDUB	.333	1.33	1.66	.166		.333			
TRIFMED					3.66		.333		
TRIFPRA	18.833	24.333	13.833	8.833	8.66	8.5	5.33	10.833	9.33
TRIFREP	9		15	17.166	8.66	13.833	11.5	6.33	6.833
TRISFLA	11.166								.333
VEROFFI					.333		.166		
VERSERP				1.13			.5		
VICICRA		12.3							.333
VIOHIRT		.333			1.66		.333		.3
VIORIVI				1.66	2	2	1.13		2.66

APPENDIX 3
QUADRAT ENVIRONMENTAL DATA

No.	Name	Set	Age	Reseed	Hayseed	Subsoil	Poach	Bare %	Height cm
1	HNU1____	HNU	250	0	0	0	0	0	19
2	HNU2____	HNU	250	0	0	0	0	0	15.3
3	HNU3____	HNU	250	0	0	0	0	0	19
4	HNU4____	HNU	250	0	0	0	0	0	18.3
5	HNU5____	HNU	250	0	0	0	0	0	15
6	HNU6____	HNU	250	0	0	0	0	0	19.3
7	HNP1____	HNP	12	0	0	0	0	0	19
8	HNP2____	HNP	12	0	0	0	0	0	27.7
9	HNP3____	HNP	12	0	0	0	0	0	23.3
10	HNP4____	HNP	12	0	0	0	0	0	17
11	HNP5____	HNP	12	0	0	0	0	0	19.3
12	HNP6____	HNP	12	0	0	0	0	0	26
13	GFCRR1__	GCR	20	1	0	0	0	0	7.7
14	GFCRR2__	GCR	20	1	0	0	0	0	6.3
15	GFCRR3__	GCR	20	1	0	0	0	0	7.3
16	GFCRR4__	GCR	20	1	0	0	0	0	9.3
17	GFCRR5__	GCR	20	1	0	0	0	0	6.3
18	GFCRR6__	GCR	20	1	0	0	0	0	5.3
19	GF76R1__	G76	20	0	0	0	0	3	2
20	GF76R2__	G76	20	0	0	0	0	1	2
21	GF76R3__	G76	20	0	0	0	0	.5	1.7
22	GF76R4__	G76	20	0	0	0	0	.5	2.7
23	GF76R5__	G76	20	0	0	0	0	3	2.3
24	GF76R6__	G76	20	0	0	0	0	0	4
25	GF60R1__	GHS	35	0	1	0	0	0	5
26	GF60R2__	GHS	35	0	1	0	0	0	9
27	GF60R3__	GHS	35	0	1	0	0	3	5
28	GF60R4__	GHS	35	0	1	0	0	1	6.7
29	GF60R5__	GHS	35	0	1	0	0	2	6
30	GF60R6__	GHS	35	0	1	0	0	0	10

No.	Name	Set	Age	Reseed	Hayseed	Subsoil	Poach	Bare %	Height cm
31	GF52TS1_	GSU	45	0	0	1	0	0	3
32	GF52TS2_	GSU	45	0	0	1	0	.5	3.3
33	GF52TS3_	GSU	45	0	0	1	0	1	2.3
34	GF52TS4_	GSU	45	0	0	1	0	2	3.7
35	GF52TS5_	GSU	45	0	0	1	0	0	1.3
36	GF52TS6_	GSU	45	0	0	1	0	0	1.7
37	GFU21___	GPO	160	0	0	0	1	0	1.7
38	GFU22___	GPO	160	0	0	0	1	2	2.3
39	GFU23___	GPO	160	0	0	0	1	7	3
40	GFU24___	GPO	160	0	0	0	1	0	2.7
41	GFU25___	GPO	160	0	0	0	1	0	4.3
42	GFU26___	GPO	160	0	0	0	1	8	2.3
43	GFU31___	GU3	250	0	0	0	0	0	4
44	GFU32___	GU3	250	0	0	0	0	4	3.3
45	GFU33___	GU3	250	0	0	0	0	1	3.7
46	GFU34___	GU3	250	0	0	0	0	0	3.7
47	GFU35___	GU3	250	0	0	0	0	0	6.7
48	GFU36___	GU3	250	0	0	0	0	0	4.3
49	GFU11___	GU1	250	0	0	0	0	0	4.3
50	GFU12___	GU1	250	0	0	0	0	0	4.7
51	GFU13___	GU1	250	0	0	0	0	0	4.7
52	GFU14___	GU1	250	0	0	0	0	3	4.3
53	GFU15___	GU1	250	0	0	0	0	6	2.7
54	GFU16___	GU1	250	0	0	0	0	0	5.3

APPENDIX 4
QUADRAT DATA FOR DIVERSITY MEASURES

Quadrat	Total species	Summed cell frequencies	No. of indicator species
GF52TS1_	28	286	11
GF52TS2_	31	330	12
GF52TS3_	33	344	13
GF52TS4_	34	319	14
GF52TS5_	28	321	11
GF52TS6_	36	381	18
GF60R1__	44	444	24
GF60R2__	37	350	20
GF60R3__	46	439	22
GF60R4__	34	338	15
GF60R5__	39	341	16
GF60R6__	39	358	16
GF76R1__	33	350	15
GF76R2__	35	368	16
GF76R3__	32	329	14
GF76R4__	41	412	13
GF76R5__	40	370	16
GF76R6__	27	265	7
GFCRR1__	19	221	2
GFCRR2__	21	237	4
GFCRR3__	19	222	1
GFCRR4__	21	241	2
GFCRR5__	24	253	2
GFCRR6__	20	239	2
GFU11___	40	372	18
GFU12___	38	426	18
GFU13___	42	403	20
GFU14___	38	367	19
GFU15___	36	371	18

Quadrat	**Total species**	**Summed cell frequencies**	**No. of indicator species**
GFU16___	36	386	20
GFU21___	36	398	17
GFU22___	41	365	17
GFU23___	37	351	18
GFU24___	41	399	21
GFU25___	36	336	17
GFU26___	35	347	17
GFU31___	29	344	17
GFU32___	35	377	19
GFU33___	28	367	17
GFU34___	33	308	18
GFU35___	32	353	18
GFU36___	29	326	17
HNP1____	29	330	8
HNP2____	26	273	8
HNP3____	29	301	9
HNP4____	28	304	7
HNP5____	26	302	7
HNP6____	30	276	10
HNU1____	39	429	15
HNU2____	38	393	14
HNU3____	42	414	18
HNU4____	39	366	18
HNU5____	42	446	19
HNU6____	47	384	20

Figure 1: Site location

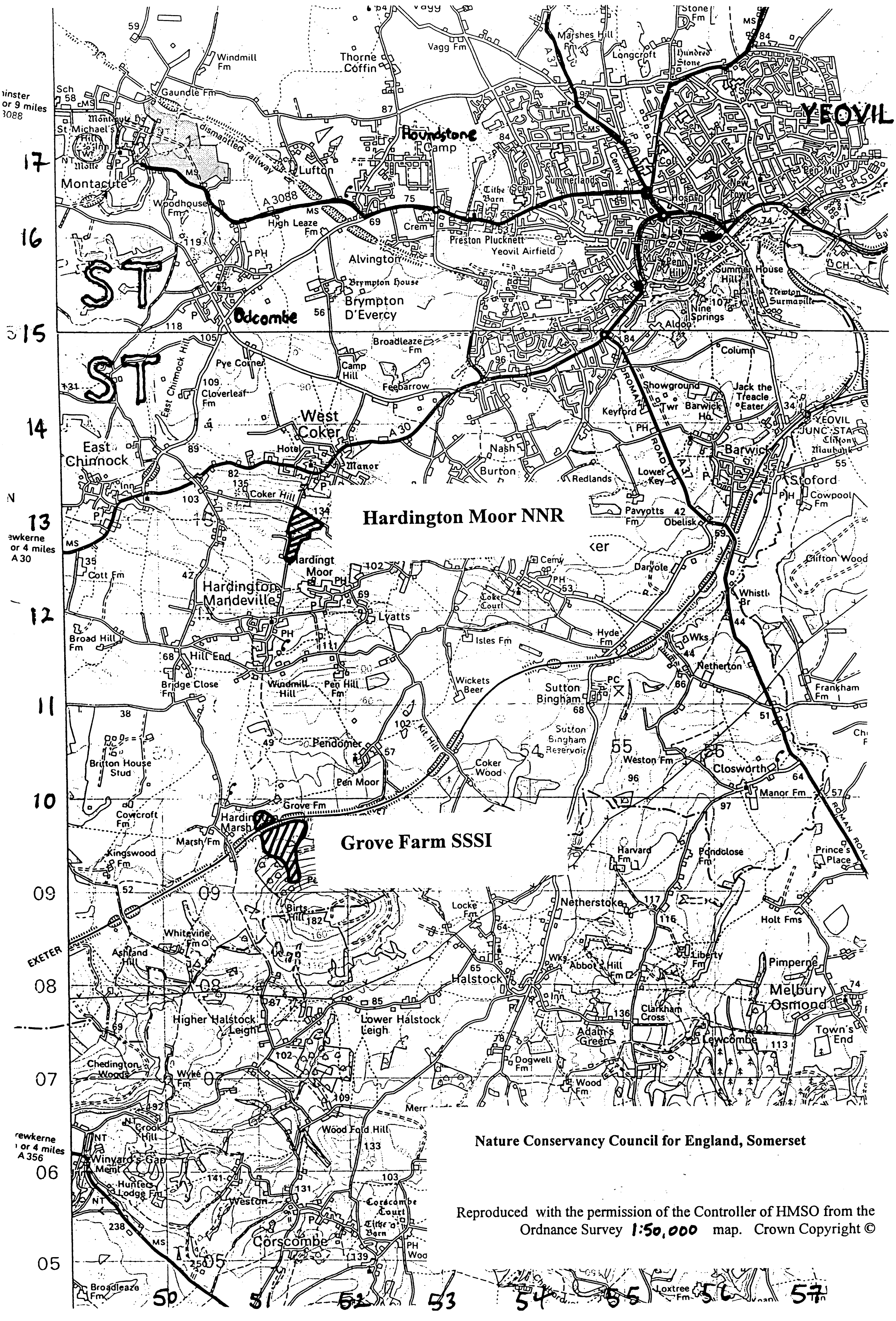
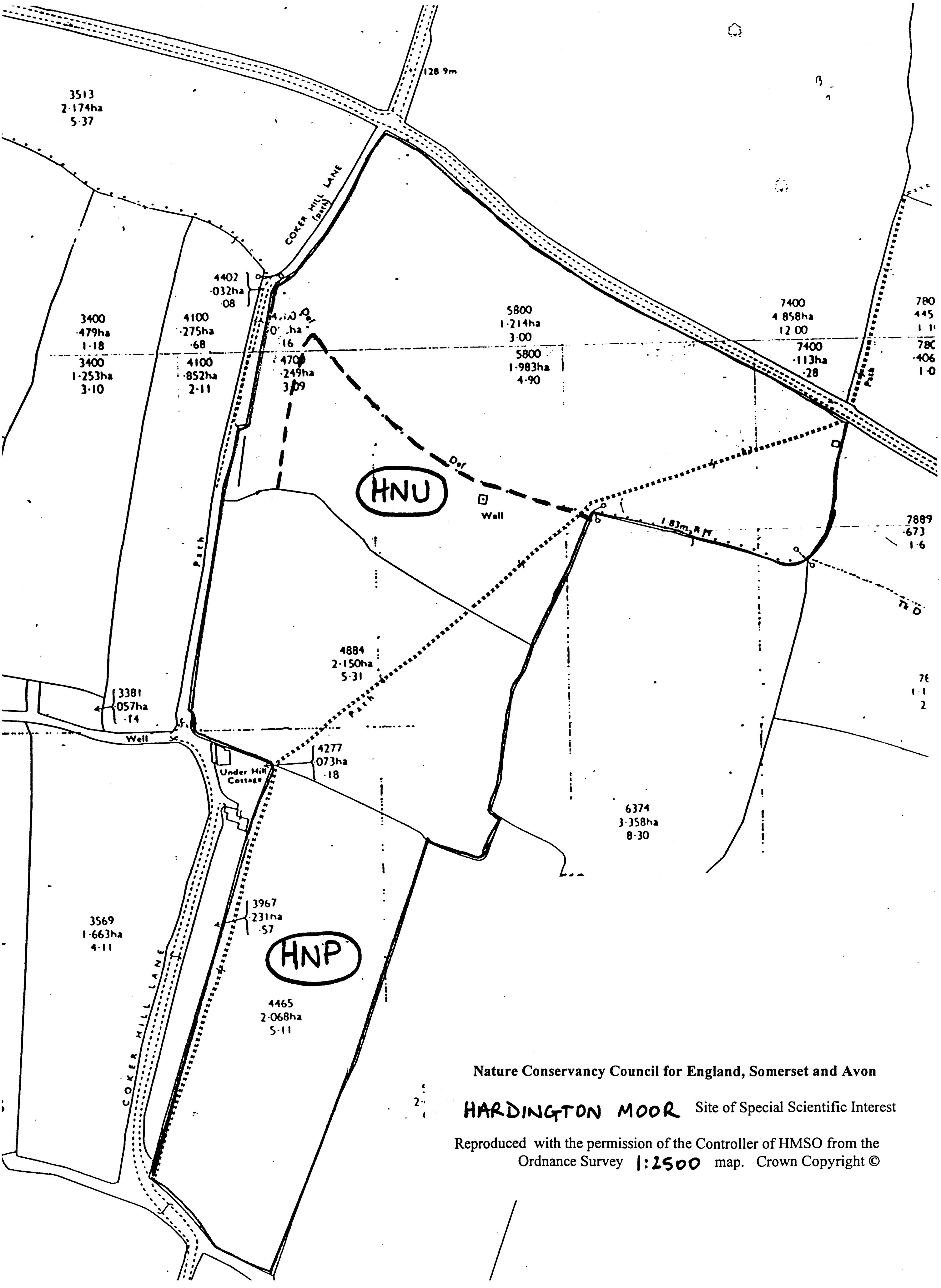


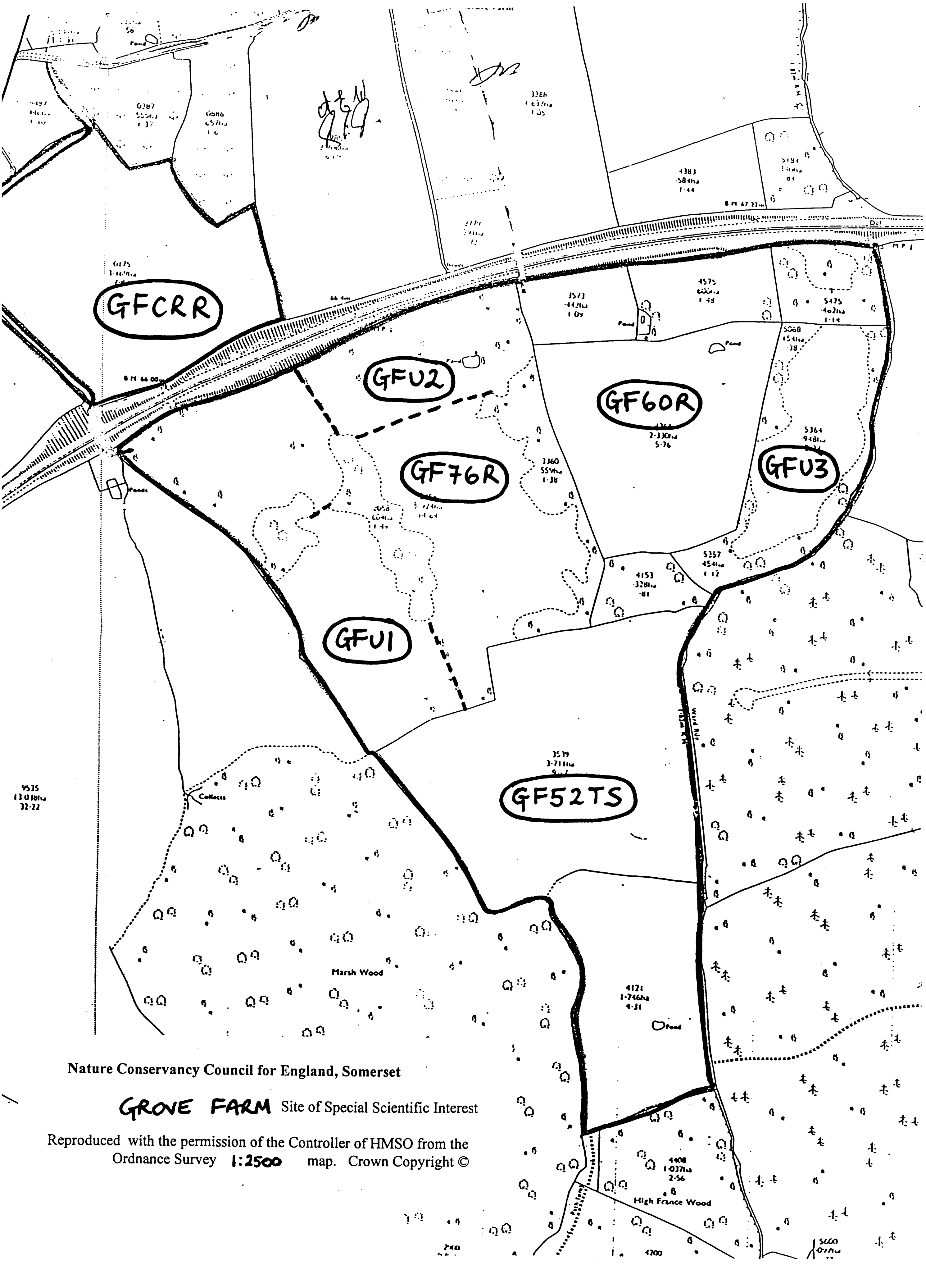
Figure 2b: Layout of fields at Hardington Moor



Nature Conservancy Council for England, Somerset and Avon

HARDINGTON MOOR Site of Special Scientific Interest

Figure 2a: Layout of fields at Grove Farm



Nature Conservancy Council for England, Somerset

GROVE FARM Site of Special Scientific Interest

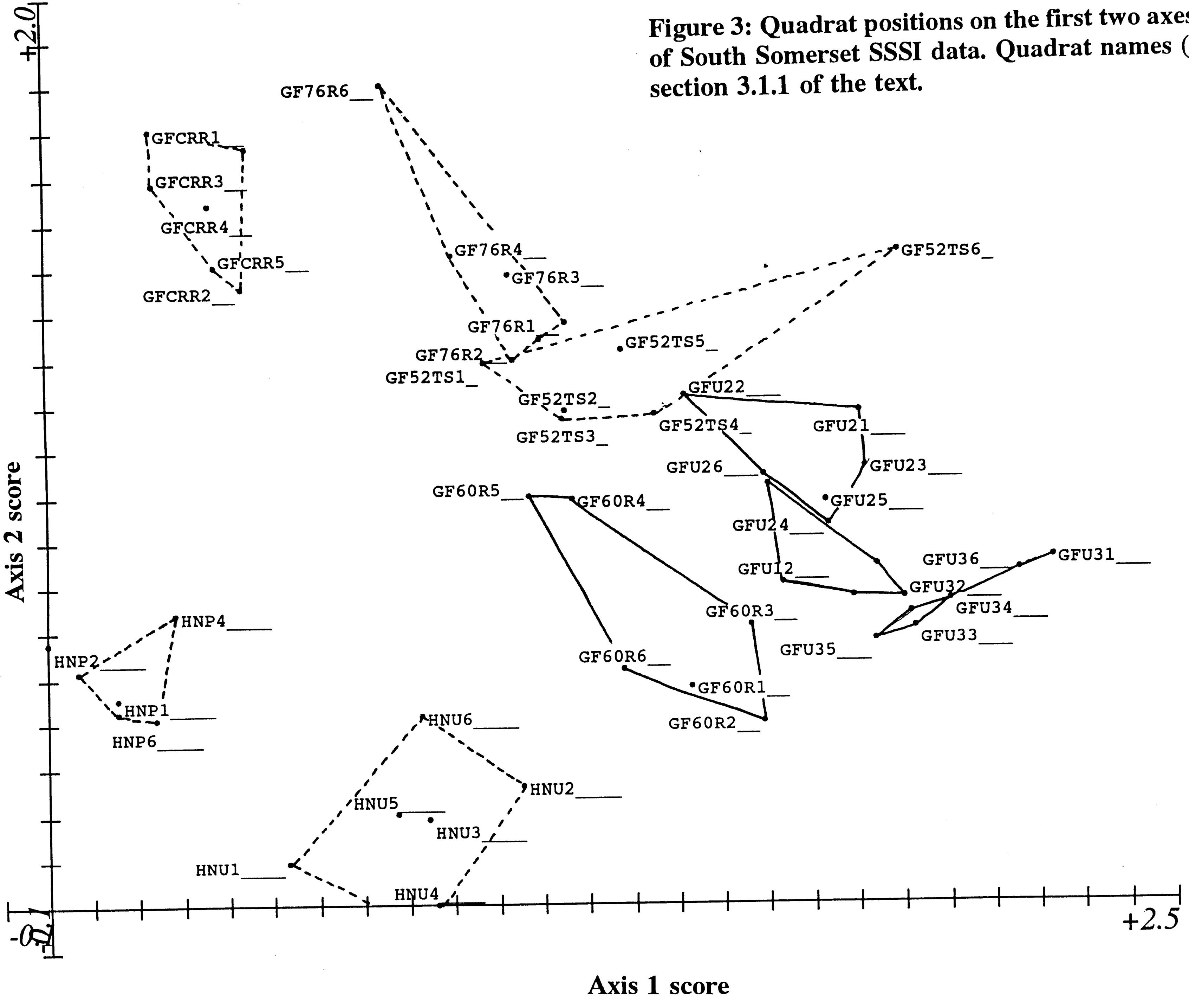
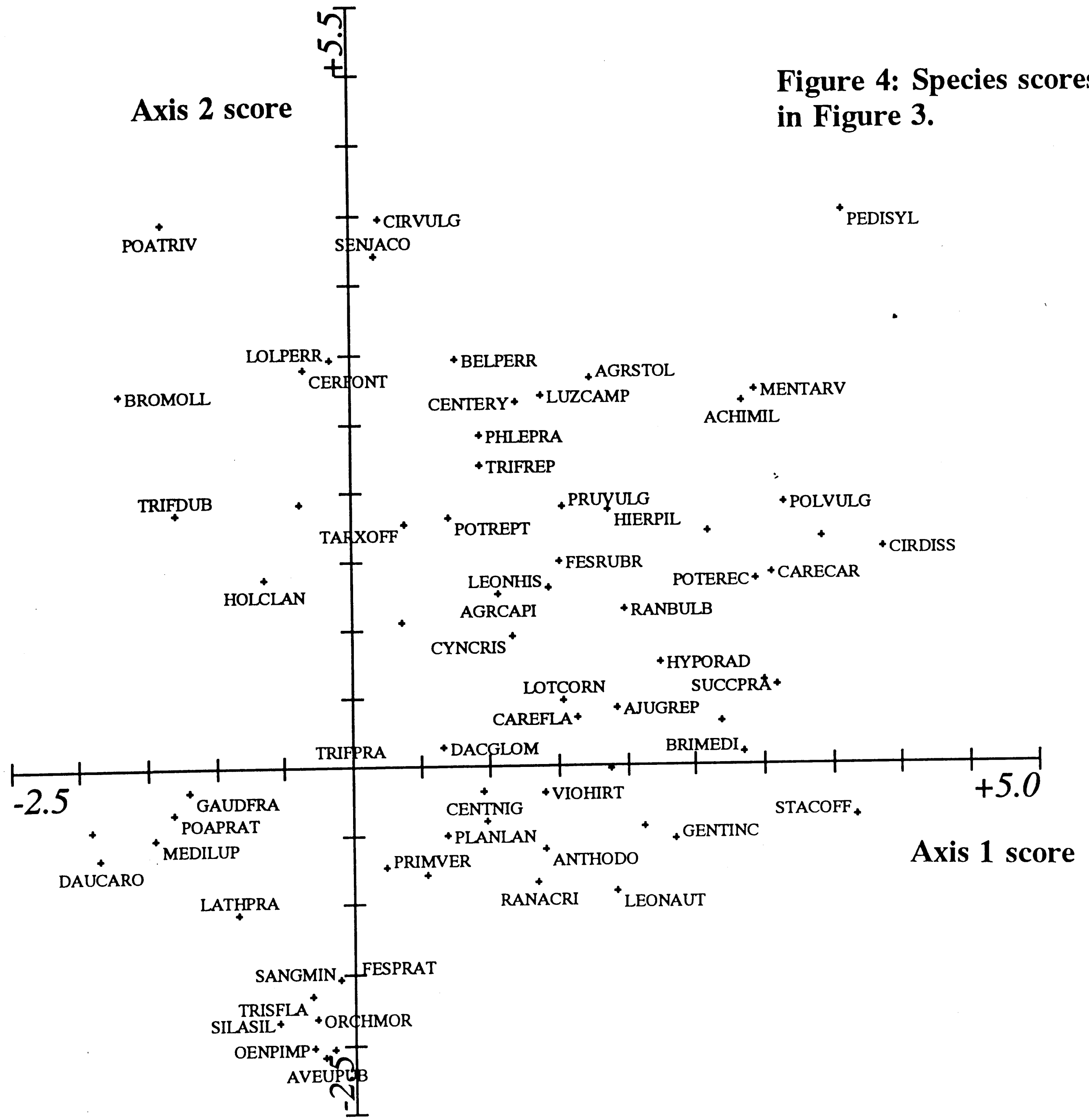


Figure 3: Quadrat positions on the first two axes of a DCA ordination of South Somerset SSSI data. Quadrat names (with numbers) follow section 3.1.1 of the text.

Figure 4: Species scores on the same DCA ordination plot as shown in Figure 3.



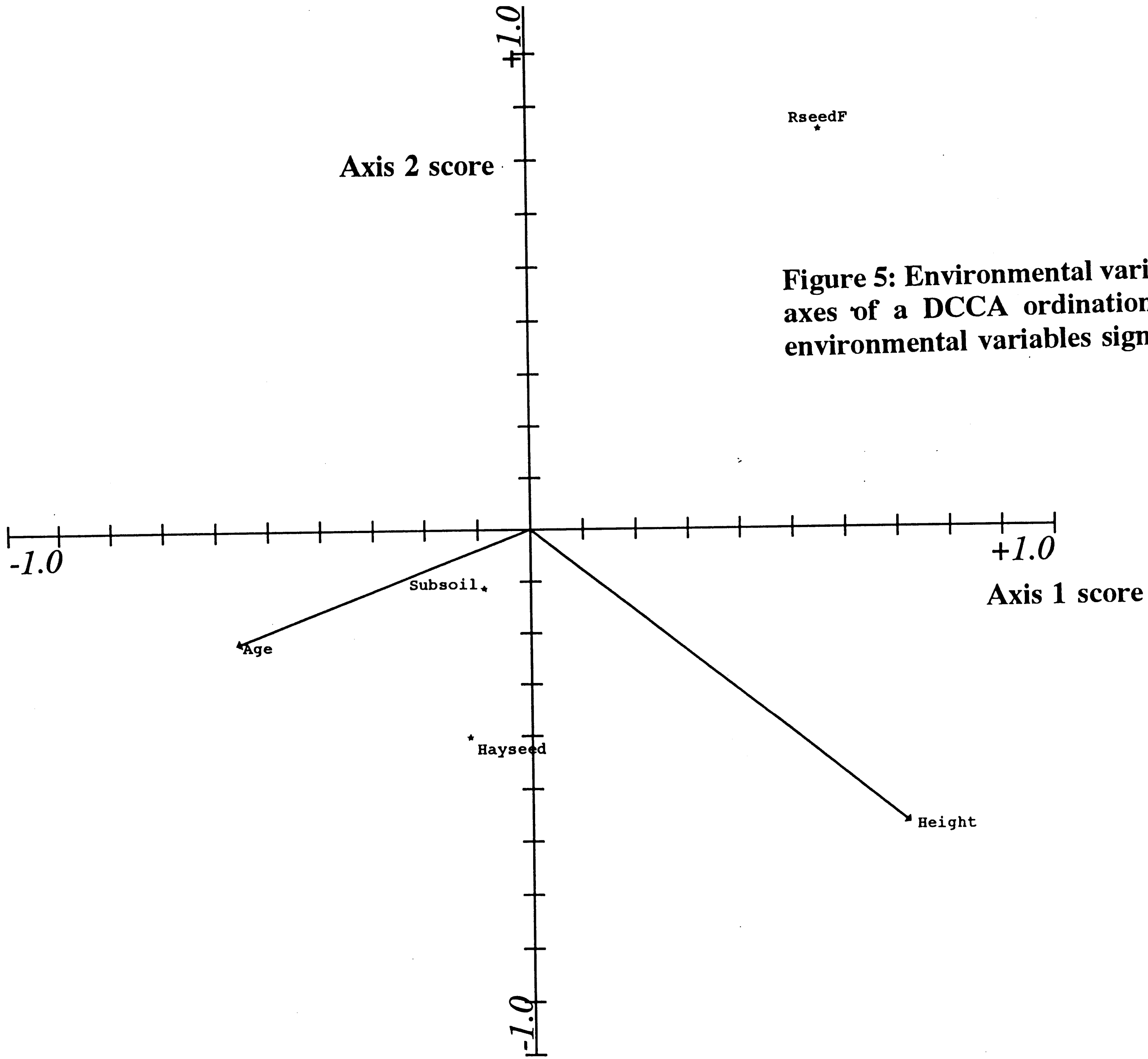


Figure 5: Environmental variable influences on the first two canonical axes of a DCCA ordination of South Somerset SSSI data. [Only environmental variables significant at $p < 0.01$ are included.]

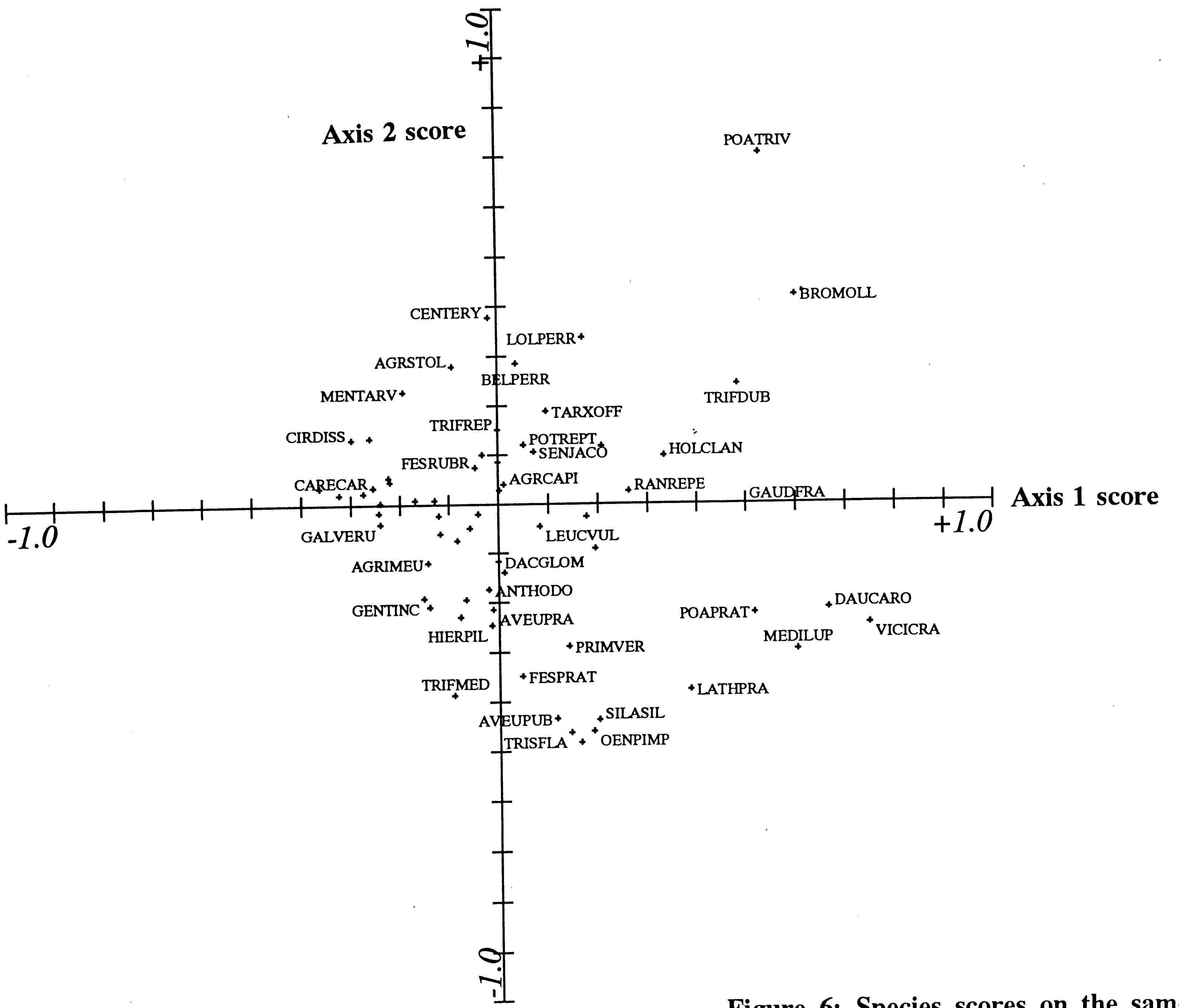


Figure 6: Species scores on the same DCCA ordination shown in Figure 5.

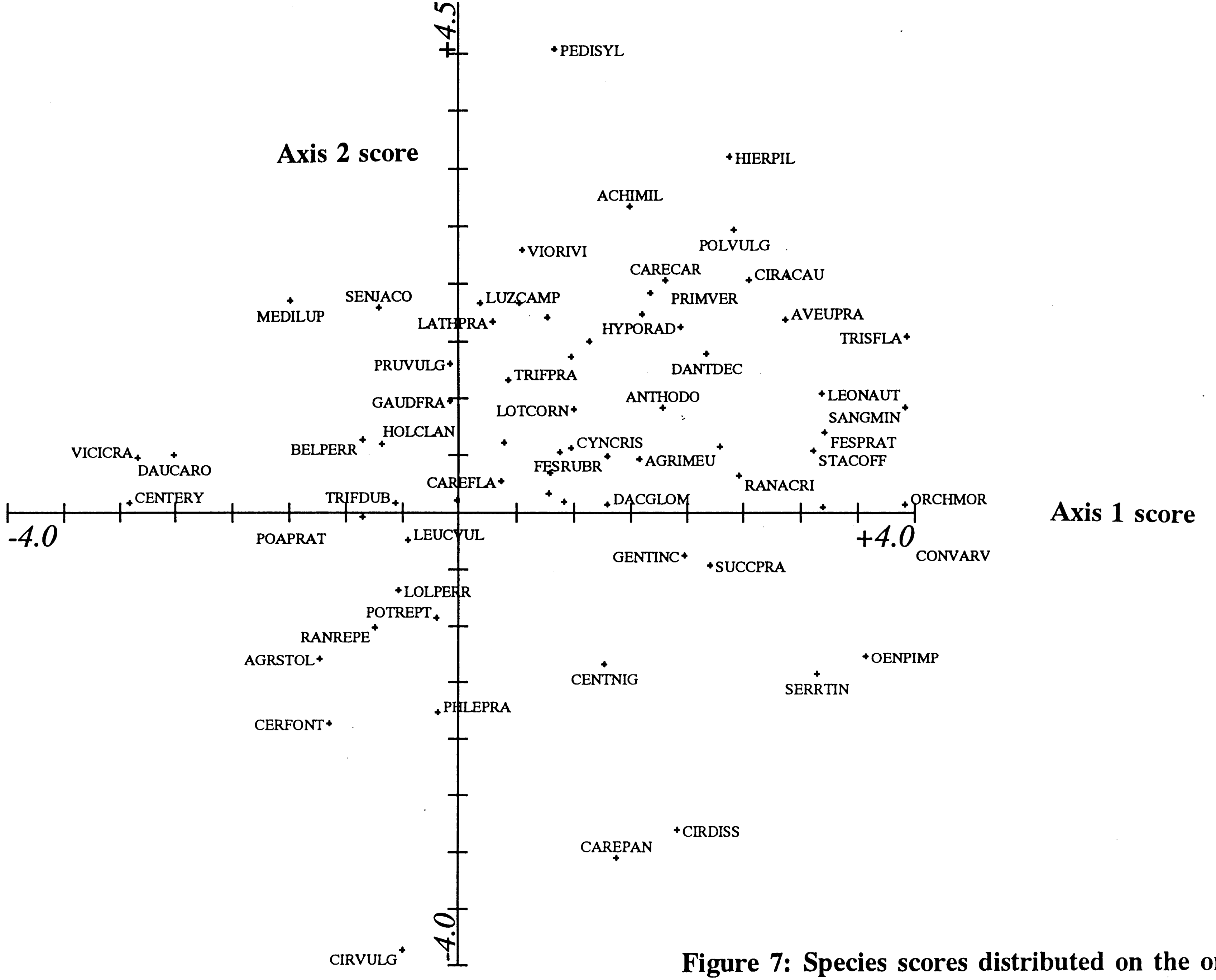
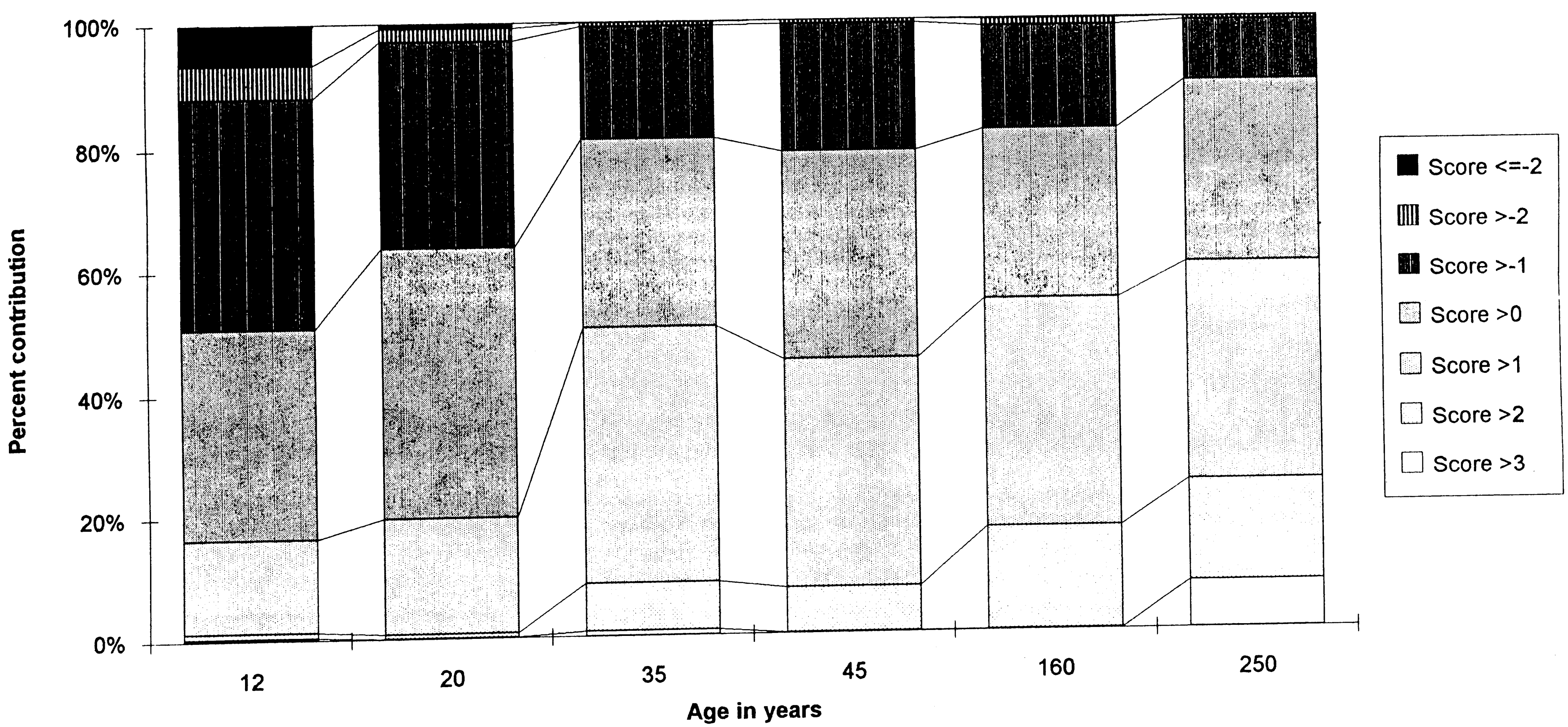
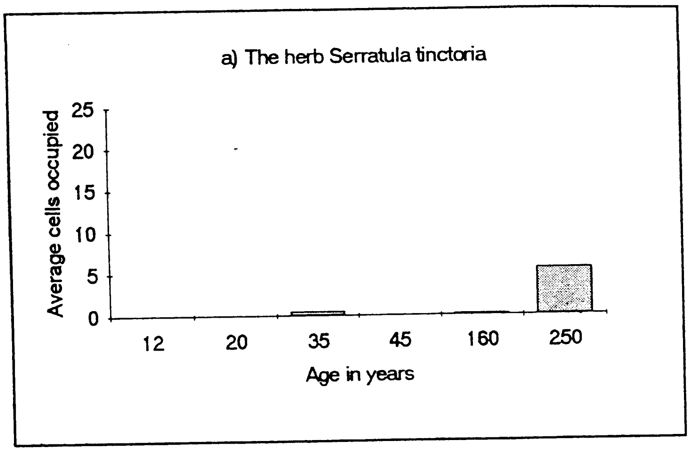


Figure 7: Species scores distributed on the only canonical axis of a partial DCCA ordination examining age alone (Axis 1). Axis 2 variation is not related to any measured environmental variable.

Figure 8: Grove Farm successional groups derived from Figure 7 Axis 1





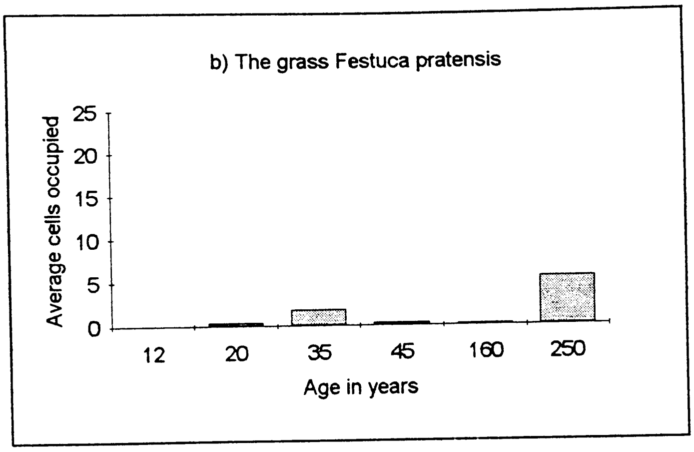
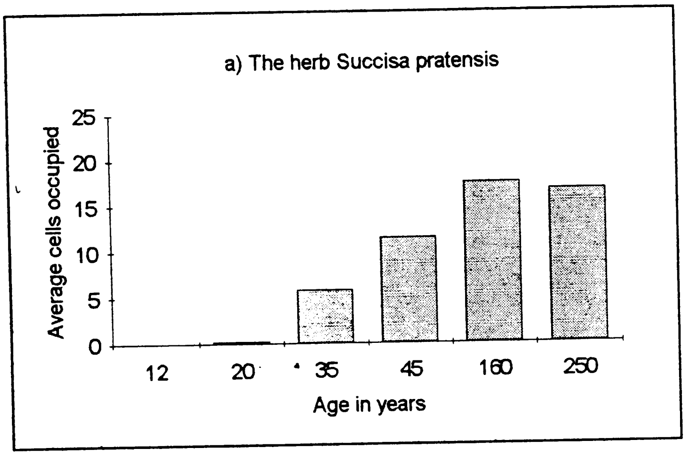


Figure 9: Examples of individual species distribution with field age I: Late successional: score >3



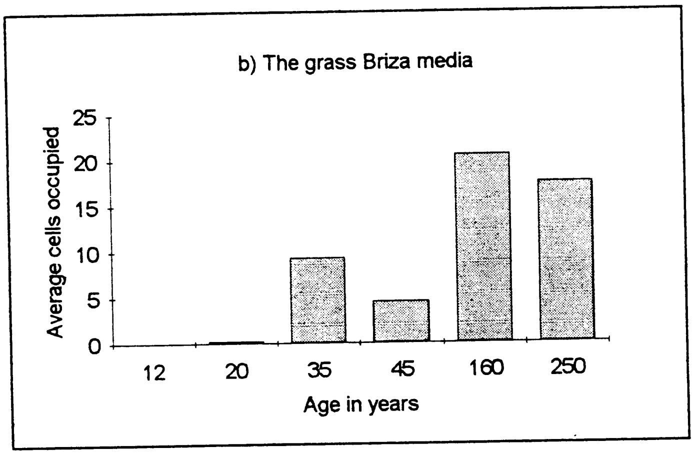
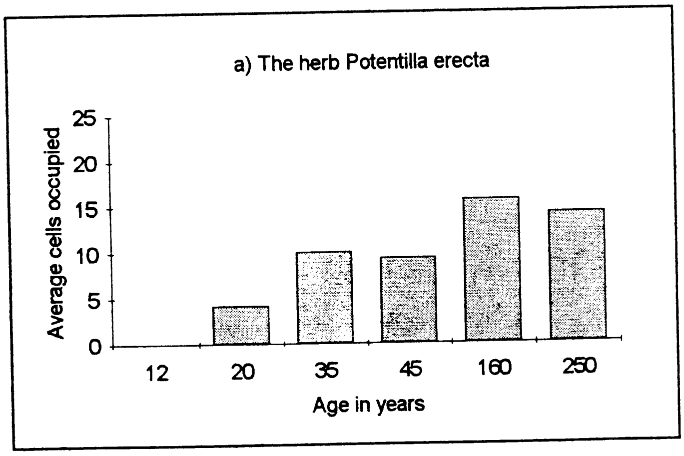


Figure 10: Examples of individual species distribution with field age II: Late successional: score >2



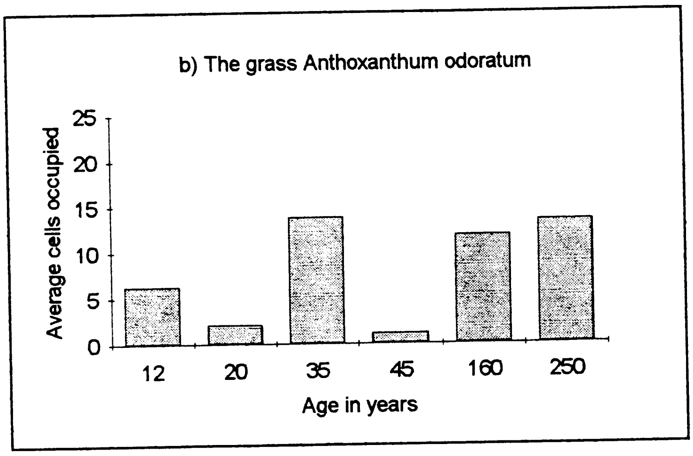


Figure 11: Examples of individual species distribution with field age III: Mid successional: score >1

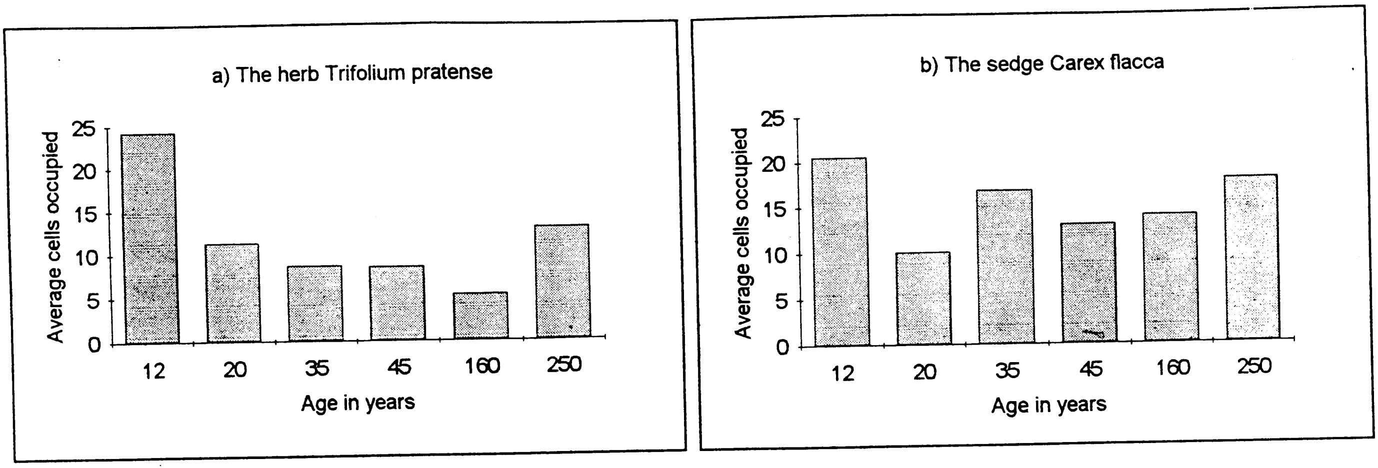


Figure 12: Examples of individual species distribution with field age IV: Mid successional: score >0

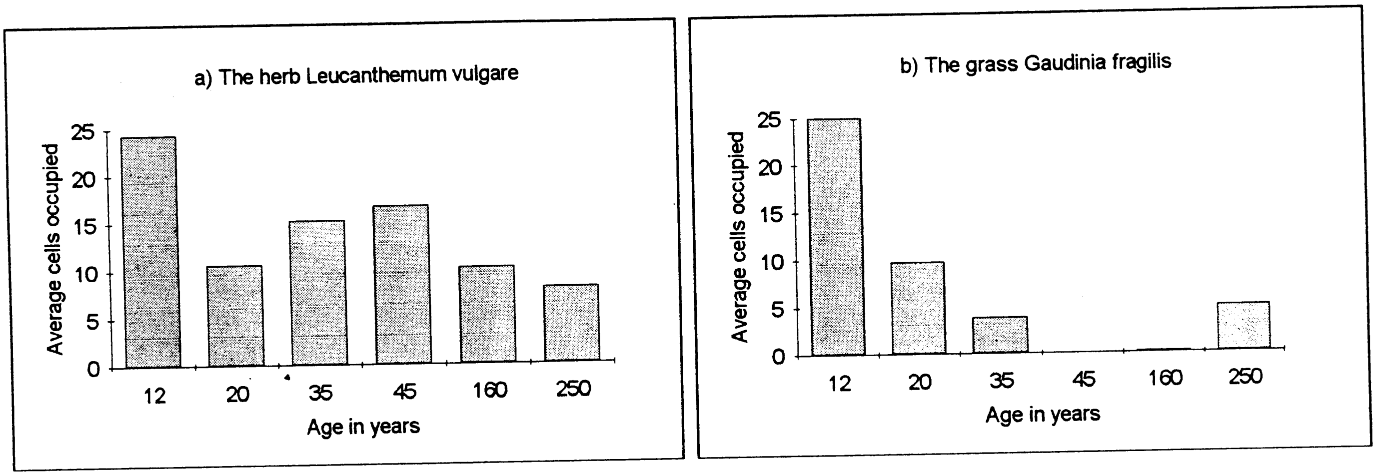


Figure 13: Examples of individual species distribution with field age V: Earlysuccessional: score >-1

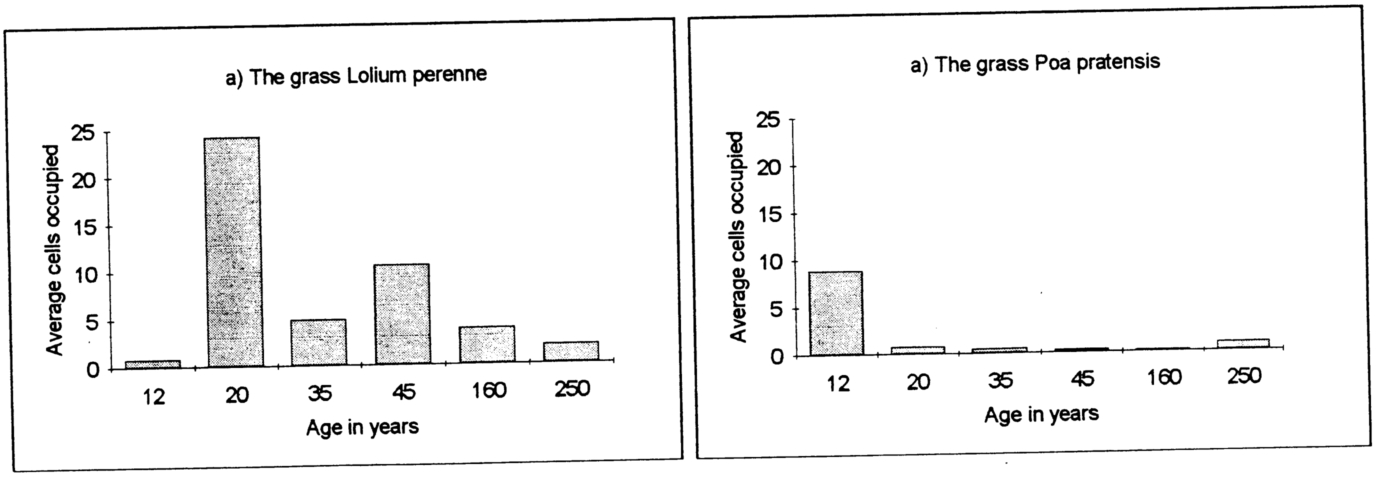


Figure 14: Examples of individual species distribution with field age VI: Early successional: score -1 to 0 (a) and <-1 (b)

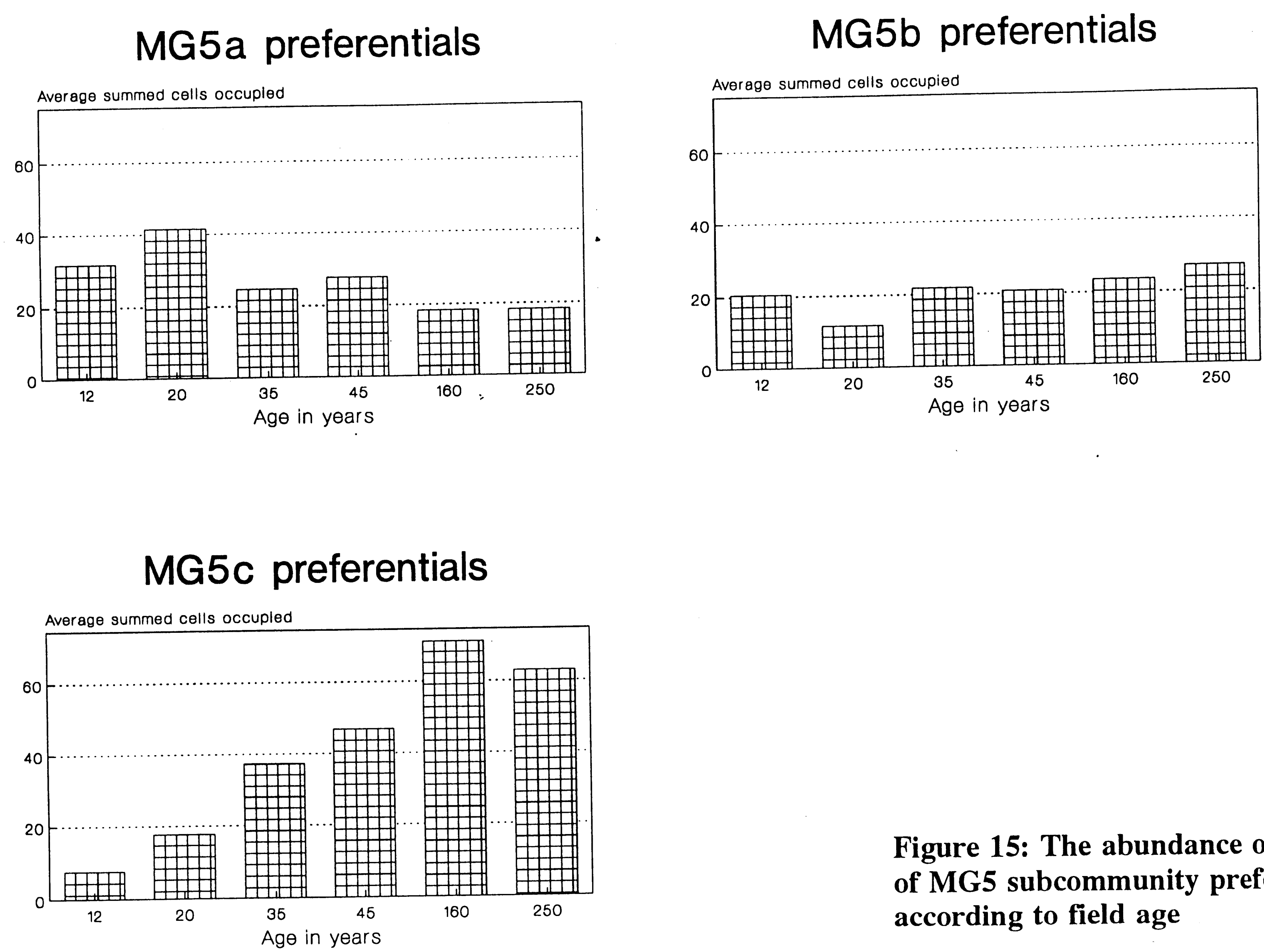


Figure 15: The abundance of groups of MG5 subcommunity preferentials according to field age

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Somerset Team Distribution List (Total 10)

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