

## SUMMARY

It is now four years since the establishment of the NERC Soil Biodiversity Thematic Programme, centred upon the intensive study of a large field experiment located at the Macaulay Land Use Research Institute's farm at Sourhope in the Scottish Borders. During this time, the site has been monitored to assess changes in aboveground biomass production (productivity), species composition and relative abundance (diversity). Three management processes are having major impacts upon botanical changes:

- Mowing effect - in April 1998 fencing was erected around the site, to protect it from all grazing animals, and a mechanical system of cutting (mowing) was implemented. The key change amongst the dominant plant species on the site is the promotion of *Festuca* spp. primarily at the expense of *Agrostis* spp., which appear to be comparatively intolerant of mowing. Stress tolerant plant species have expanded in unfertilised plots where, in contrast to those plots treated with nitrogen and/or lime, there is likely to be a gradual but on-going fall in available soil nutrients as grass clippings are deposited off-site. It is also likely that regular mowing is contributing to the expansion in bryophytes through the maintenance of a sward height of some 6cm.
- Fertilisation effect – productivity is significantly higher within those plots treated with nitrogen and/or lime although there are signs that productivity may have peaked in those plots treated with both nitrogen and lime where mean soil pH is now close to 7.0. Distinct differences in the functional structure of plant communities are apparent within lime-treated plots compared to all other treatments, probably resulting from the extremely high levels of lime applied (equivalent to 6 tonnes ha<sup>-1</sup> yr<sup>-1</sup>).
- Insecticide effect – plant species diversity, as measured by the Shannon Diversity Index, is highest within the insecticide-treated plots. Whilst it is recognised that the evidence is only circumstantial at this stage, the possible impact of the soil insecticide, Dursban 4 (Dow AgroSciences) upon plant diversity is discussed. In particular, consideration is given to the possible role of reduced plant herbivory.

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## INTRODUCTION

It is now four years since the establishment of the NERC Soil Biodiversity Thematic Programme, centred upon the intensive study of a large field experiment located at the Macaulay Land Use Research Institute's farm at Sourhope in the Scottish Borders. The primary aims of the Programme are to achieve simultaneously an understanding of the biological diversity of the soil biota and the functional roles played by soil organisms in key ecological processes. In seeking to achieve these aims 24 separate research projects have been funded to study soil structure, soil processes (such as the carbon and nitrogen cycles) and the roles of micro-fauna and flora (Bacteria, Nematoda, Protozoa and Fungi), microarthropods (including Collembola and Acari), invertebrate root feeders (Tipulid, Bidionid and Scarabeid larvae), meso-fauna (such as Enchytraeidae) and macro-fauna (including Megradili, Mollusca and Coleoptera). Sixteen of these projects were funded under Phase I (1998-2001) whilst the remaining eight projects have been funded under Phase II. Full details of the each project are available on the Soil Biodiversity website <http://www.nerc-merlewood.ac.uk/soilbio/index.html> or from the Centre for Ecology and Hydrology, Windermere Road, Grange-over-Sands, Cumbria LA11 6JU (Tel 01539 532264).

It is understandable that funded projects under the Soil Biodiversity Programme deal almost exclusively with below-ground activity. It was, nevertheless, recognised at the outset that there are close links to the above-ground vascular and non-vascular plant communities, and feedback mechanisms which are likely to result in concomitant changes within both systems. A botanical survey of the site, which was undertaken in 1998 prior to the start of the Programme, found that the site equated to NVC community U4d consisting of "*Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, *Luzula multiflora-Rhytidiadelphus loreus* subcommunity" (Kenny, 1998). Following this, broad scales of botanical monitoring have been undertaken as part of the site management with the work focussing, in particular, upon above-ground biomass production (productivity), species composition and relative abundance (diversity).

The site was grazed by sheep until April 1998, when fencing was erected to deny access to all grazing animals including deer and rabbits. In 1999 a management regime was put in place to carry out five summer cuts to 6cm every four weeks beginning in May each year. In addition there are five prescribed treatments which can essentially be separated between those plots to which nitrogen and/or lime are added (fertilised) and those to which nitrogen and/or lime have not been added (unfertilised). In broad terms it is expected that productivity in the fertilised plots will increase, but remain level or perhaps, even, fall in the unfertilised plots due to the loss of nutrients contained in the grass cuttings which are deposited off-site

The impact upon plant species diversity is less certain. In their study of *Agrostis/Festuca* plant communities under different sheep grazing management regimes at two sites in Scotland, Hulme *et al.* (1999) report that changes in botanical composition were small and few species invaded or were lost when grazing stock were excluded. However, in a separate study of a range of plant communities following cessation of burning and the reduction or elimination of grazing, Ball (1974) reports that changes in structure and floristics were least marked in species rich *Agrostis/Festuca* grassland and most marked in species poor *Agrostis/Festuca* grassland, with the number of species in ungrazed plots falling by about a half over 12 years. In contrast to these studies, however, the Soil Biodiversity site has been mechanically cut since grazing stopped.

Under the fertile treatments the impact of mowing is unlikely to have any particularly adverse effect upon those species which are able to make use of the greater availability of nutrients, since these species are likely to be more competitive with faster re-growth following cuts. Within these treatments it, therefore, seems likely that plant communities will become less diverse as a few plant species become dominant, displacing often slower growing and smaller species. Within the unfertilised plots growing conditions are likely to become less favourable over time, as nutrients are lost from the system in the grass cuttings, with the possible loss of certain species such as *Festuca rubra* and *Poa pratensis*, which are closely associated with improved pastures. It is likely, however, that this would be a long-term consequence and, in the shorter-term diversity is likely to

remain stable or perhaps increase a little as more nutrient-demanding species contract allowing other species to expand or establish in their place.

Whilst changes in species richness and diversity are of interest, it is perhaps of more relevance to the various Programme Research Groups to know whether there have been any changes to the functional nature of the plant communities. In seeking to answer this question it is important to recognise that plants may be separated into functional groupings or types using very different criteria. Population biologists, for example, seek to define functional types through the measurement of demographic patterns, particularly relating to the spatial and temporal distribution of reproduction, mortality, dispersal and dormancy (eg Harper 1977; Whittaker & Goodman, 1979). In contrast, physiologists define functional types by reference to those features of life history, physiology and biochemistry that determine the responsiveness of plants to soils, land-use and climatic factors (Grime *et al.*, 1996). These have resulted in the identification of functional types based upon factors such as differences in phenology (eg Raunkiaer, 1934; Al-Mufti *et al.*, 1977) and plant species' distribution relative to water supply (eg Ellenberg, 1988). The CSR system (Grime, 1979) is a comprehensive functional classification of common British vascular plants, which uses a mix of demographic and physiological information. This system identifies three permutations of environmental extremes and concludes that those species typically associated with these extremes all possess distinct sets of traits leading to characteristic ecological behaviour. In the case of low stress and low disturbance this is competitiveness (C), in the case of high stress and low disturbance this is stress-tolerance (S) and in the case of low stress and high disturbance this is ruderality (R). The fourth environmental contingency, that of high stress and high disturbance, does not support plant life. The initials of the three "primary" types give the CSR system its name. Intermediate types also exist within the system, with each representing a different intermediate combination of stress and disturbance.

Nutrient stress is likely to be reduced within the fertilised plots suggesting that there will be a functional shift from stress tolerators towards more competitive plant species. Within the unfertilised plots the removal of disturbance and spot fertilising, arising from

the presence of grazing livestock, is replaced by the more uniform disturbance of mowing coupled with a gradual reduction in fertility as nutrients are lost in clippings which are deposited off-site. In these circumstances stress tolerant species are likely to be the biggest beneficiaries.

## **METHODS (INCORPORATING SITE ACTIVITY)**

The Rigg Foot Experimental Site at Sourhope consists of 5 replicate blocks in downslope environmental gradients. Each block contains 6 main plots with treatments allocated at random. The main plots are subdivided into 10 sub-plots and areas are allocated to different research groups using a 0.5m x 0.5m cell system. Appendix 1 provides a map of the site, showing treatments allocated to each plot.

### *2.1 Site management and application of treatments.*

There are one site-level and three plot-level management tasks, which have been undertaken each year since 1999. Vegetation across the whole site is mowed monthly between May and September to a level of approximately 6cm using a Kubota riding grass mower. Immediately following these cuts Dursban 4 OPA insecticide (ex Dow AgroSciences), containing 44.6% chlorpyrifos w/w, is applied to the Insecticide plots (previously referred to as Biocide plots). Nitrogen and/or lime is added to designated plots during spring. Full details of the dates and, where appropriate, the application rates of these treatments are provided in Appendix 2.

### *2.2 Site data collection.*

- Regular temperature, rainfall and other weather data have been collected since February 1999 from an on-site Automatic Weather Station.
- Estimates of above-ground productivity involve the collection of vegetation samples from a randomly chosen 0.5m<sup>2</sup> cell within sub-plots S, T, U & V of every plot

immediately prior to each mow. The clippings are oven-dried at 80°C and subsequently weighed. Samples have been collected since 1999.

- Between 27<sup>th</sup> July and 7<sup>th</sup> August 1998 a baseline assessment of vegetation was undertaken using a 0.5m<sup>2</sup> point quadrat consisting of 25 points. In this survey five randomly selected sub-plots were surveyed in each main plot. Each point of the quadrat was followed down to the soil surface where a record was made of the single species which occurred at this precise point.

More extensive botanical surveys, using the point analysis technique, have subsequently been undertaken in July/August in the years 2000, 2001 and 2002. In these surveys a separate 0.5m<sup>2</sup> cell within each of sub-plots S, T, U & V has been used each year. A point quadrat frame, containing a grid of one hundred holes, is placed over the appropriate cell. A large pin is dropped through the same twenty five holes each time and a record made of each occasion a species is touched by the pin down the vegetation profile.

During the 2002 point analysis survey an effort was made to identify bryophytes to species' levels in contrast to previous years when they were only separated to *Rhytidiadelphus squarrosus*, other mosses and liverworts. Appendix 3 contains a full species list together with details of other species seen elsewhere on the site.

- Soil samples have been collected regularly since 1998 to monitor soil pH (measured in H<sub>2</sub>O) at approximately 5cm down the soil profile. During 2002 soil pH was measured in the centre of each plot in March and in the centre of each cell used in the botanical point analysis survey in July/August.
- On 16<sup>th</sup> August 2002 a theta probe was used to measure soil moisture content in each corner of every cell used in the botanical point analysis survey. These measures have not been taken as a specific management task in previous years, although it is recognised that some research groups regularly collect soil moisture measurements as part of their studies.

- Additional small-scale botanical surveys have been undertaken at various times:
  - vegetation cover estimates within nine separate 5cm x 5cm squares (0.0225m<sup>2</sup>) above buried minirhizotron tubes in Control 1, Insecticide and Nitrogen & Lime plots (2000, 2001 & 2002). Project 2113.
  - Biomass samples whereby vegetation was cut to ground level, sorted to species, dried and weighed. Year 2000 (excl. C2) samples 250mm x 250mm (0.0625m<sup>2</sup>). Year 2002 (C2, Insecticide, Nitrogen only and Lime only, blocks 1,2 & 3 only) samples 250mm diameter circles (0.049m<sup>2</sup>). Projects 2109 & 2115 respectively.
  - vegetation cover estimates in sub-plot Y disturbance:fertility gradients within C1 plots only. Year 2000 (all – 6.25m<sup>2</sup>) and 2001 (half – 3.25m<sup>2</sup>). Project 2133.

Full details of these surveys may be obtained from the Project PI's.

### *2.3 Research group site activity.*

Fieldwork associated with the sixteen projects funded under Phase I has largely finished, although there is still some occasional activity primarily from groups collecting samples and/or additional data to conduct further small-scale studies. Researchers from seven of the eight projects funded under Phase II have visited Sourhope during 2002 to undertake major fieldwork activities. Many of these have involved labelled <sup>13</sup>CO<sub>2</sub> pulses and/or the measurement of trace gases using two mobile laboratories from the Centre for Ecology and Hydrology (CEH), which were based on the Soil Biodiversity site for some 6 weeks at various times during June, July and September.

Research group activity on the site reverted to more normal levels, following the reduction in 2001 when restrictions upon site visits were imposed following the outbreak of foot and mouth disease (Appendix 4). Soil samples collected from the site since the start of the experiment now total 11621.

## RESULTS

### 3.1 Automatic Weather Station.

Appendix 5 provides headline weather data at the site since the start of the experiment. When compared to previous records the main points of note in 2002 were low rainfall in April and September offset by wet periods in February, July and the last 3 months of the year resulting in rather higher than average rainfall for the year. In temperature terms Winter 2001/02 was extremely mild, with an average air temperature of  $3.88^{\circ}\text{C}$  for the months of December to February compared to  $2.28^{\circ}\text{C}$  and  $2.86^{\circ}\text{C}$  for the same periods in 2000/01 and 1999/2000 respectively.

### 3.2 Above-ground biomass estimates.

As in previous years, there was a consistent hierarchy throughout the summer of biomass samples collected from plots subjected to the different treatments (Figure 1). Unlike

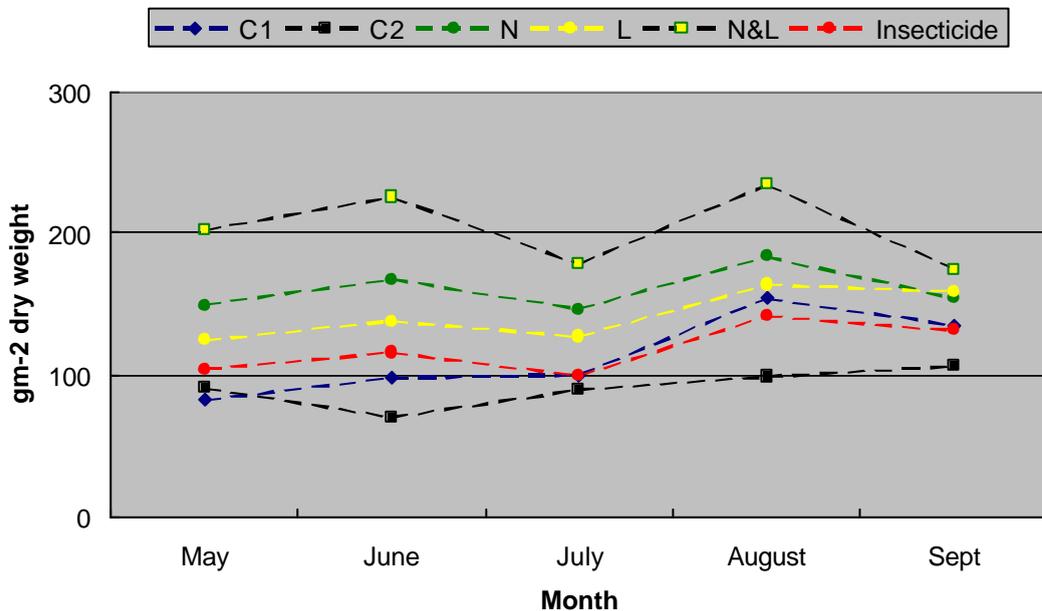
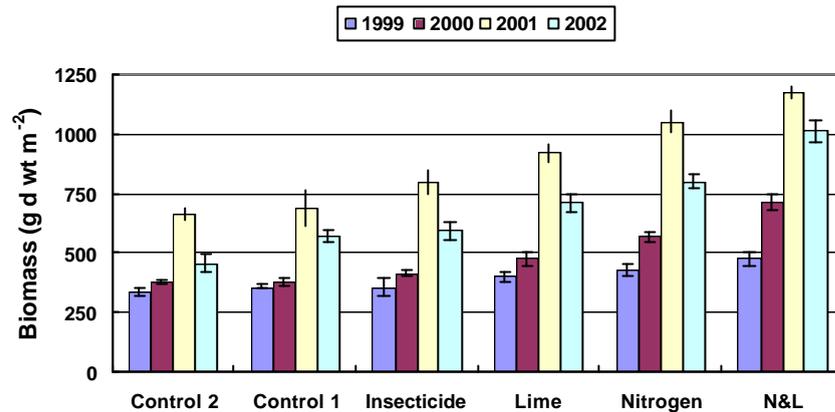


Figure 1 - Analysis of treatment differences between monthly above-ground biomass harvests (May-Sept 2002)

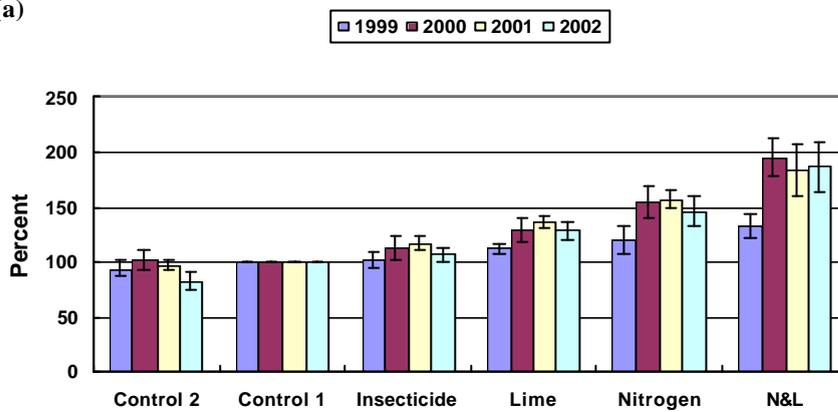
previous years, however, production in mid-summer fell across a number of treatments. Biomass samples collected from the Control 2 plots, which were used by research groups for sampling for the first time during 2002, often followed a different monthly pattern to that of the other treatments. In absolute terms biomass productivity fell in 2002 compared to 2001, but this does not deter from the longer-term trend of increasing biomass production across all treatments compared to their starting point in 1999 (Figure 2a). The positive impact of nitrogen and, to a lesser extent, lime upon productivity is clearly visible in Figure 2 (b), in which biomass samples from each treatment have been normalised against the corresponding Control 1 samples in each year. The most effective promotion of above-ground biomass continues to be seen within the plots in which nitrogen and lime have been applied together, whilst the Control 2 plots were less productive than the Control 1 plots for the third time in four years. Whilst productivity within the most fertile nitrogen and lime plots has marginally increased relative to the Control 1 plots in 2002 compared to 2001, it is apparent that all other treatments have reduced. Split-plot ANOVA's, using ln-transformed biomass dry weights, reveal statistically significant differences between a number of treatments in 2002 (Figure 2) and a significant interaction between treatment and year (Table 1).

**Table 1 Results of split plot ANOVA (Genstat 6) examining the effects of Treatment, Year and Interaction on shoot biomass harvested between May and September in 1999, 2000, 2001 and 2002. Estimates of shoot biomass were made at each of the five mowing occasions conducted during each summer, when vegetation was collected from random 0.5m<sup>2</sup> cells in each of 4 sub-plots in each plot. Dry weights were summed, to give annual biomass, and then ln-transformed for this analysis.**

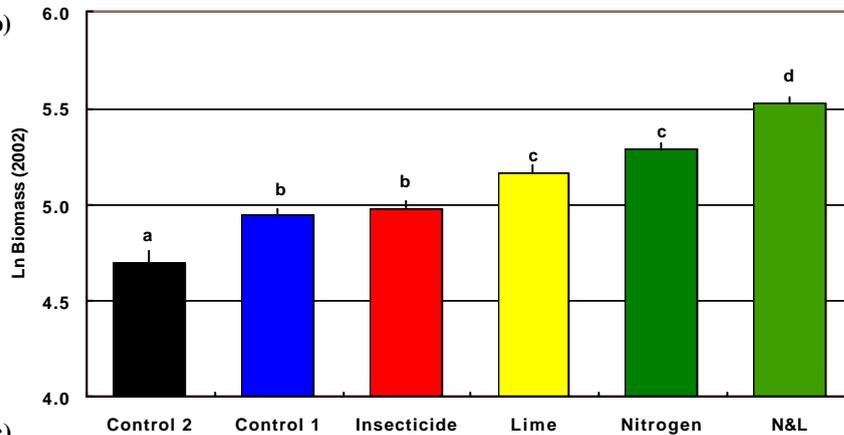
Source of variation	<i>df</i>	SS	MS	<i>F</i> -ratio	<i>P</i>
Block stratum	4	0.76	0.19	1.30	
Block.Plot stratum					
<b>Treatment</b>	5	20.72	4.14	28.38	<0.001
Residual	20	2.92	0.15	3.25	
Block.Plot.Subplot stratum	90	4.04	0.04	1.65	
Block.Plot.Subplot "Units" stratum					
<b>Year</b>	3	46.36	15.45	565.99	<0.001
<b>Treatment.Year</b>	15	2.00	0.13	4.89	<0.001
Residual	342	9.33	0.03		
Total	479	86.15			



(a)



(b)



(c)

**Figure 2 – (a) Above-ground biomass, summed from harvests made at each of the five cuts each summer from 1999 to 2002. (b) – Treatment biomass samples expressed as a percentage of Control 1 estimates in each year. (c) – Results of split-plot ANOVA (Genstat 6) showing effect of treatment on shoot biomass in summer 2002 (data ln transformed  $F=38.97$   $df=4,5,20,90$   $p<0.001$ ). Means with the same letter do not differ significantly (Isd test  $p>0.05$ ).**

Appendix 6 shows total biomass sampled within each plot since 1999, together with the mean within each block during the same period. Sampled biomass reduced across all treatments in 2002 compared to 2001. Reductions ranged from 13.7% in the N&L plots up to 31.2% in the Control 2 plots. Although there were no significant differences between blocks (ANOVA,  $F=0.34$   $df=5,4,20$   $p>0.05$ ) there was a clear negative relationship between location on the slope and productivity, with Block 5 recording a fall of 16% in sampled biomass whilst Block 1, at the bottom of the slope, recorded a fall of 30%. A similar pattern was also evident in 2001 when large increases in sampled biomass weights were observed across the site compared to 2000. On this occasion the lowest percentage increase was seen in Block 1.

Appendix 7 shows total estimates of annual biomass productivity within each plot in 2002 together with cumulative totals from 1999 to 2002.

### 3.3 The interaction between soil pH, moisture content and above-ground productivity.

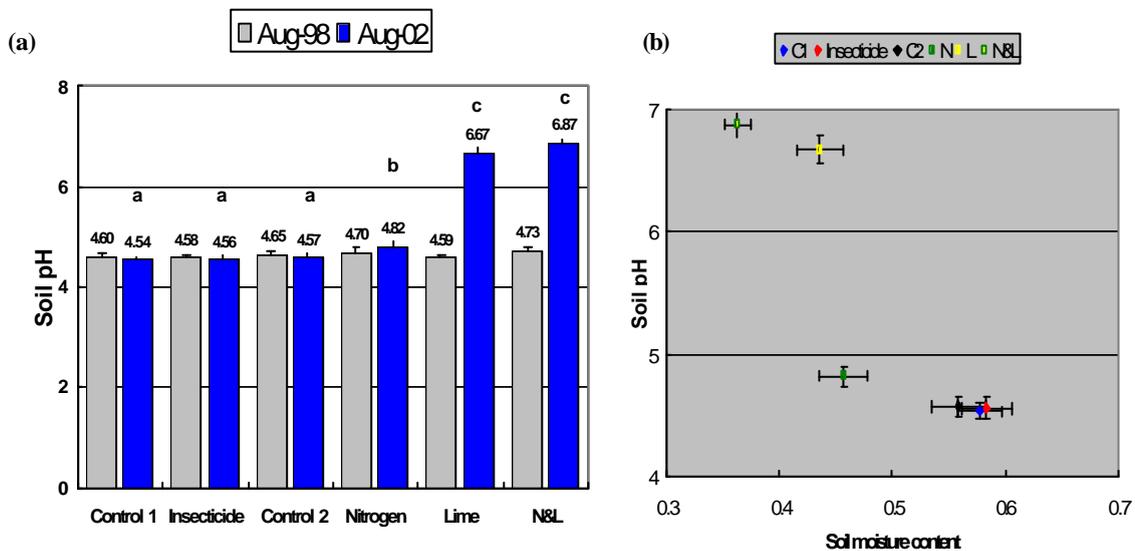


Figure 3 – (a) Changes in soil pH (5cm depth, measured in distilled water) across different treatments in August 2002 compared to baseline samples taken from the same plots prior to the start of the experiment in August 1998, at which time means were not significantly different. Letters are used to indicate treatments with significantly different means in 2002. Test by LSD after general ANOVA ( $F=230.79$   $df=4,5,110$   $p<0.001$ ). Four samples were collected from each plot during August 2002. Bars show +/- one standard error. (b) - Link between Soil pH, soil moisture content and treatments as measured in July/August 2002

Figure 3a shows that the addition of lime has had a highly significant positive effect on soil pH, at least in the upper section of the soil profile, with the result that average soil pH is now approaching seven within both limed treatments. Nitrogen has had a smaller, but still statistically significant positive impact whilst the controls and Insecticide treated plots are virtually unchanged from their 1998 starting points. There is a strong negative correlation between soil moisture content and soil pH (correlation coefficient,  $r=0.68$ ,  $n=120$ ) with a clear separation between the improved plots and the wetter, more acidic unimproved plots (Figure 3b).

Figure 4a shows strong positive linear ( $r=0.69$ ) and polynomial ( $r=0.73$ ) correlations between upper soil profile pH and biomass productivity when all treatments are included. However, if each treatment is considered in isolation (Figure 4b) this positive correlation becomes less significant within those plots to which nitrogen or lime have been added, whilst the relationship actually becomes negative in those plots to which both nitrogen and lime have been added, suggesting the polynomial relationship is more accurate.

### 3.4 Point Analysis survey

The Point Analysis survey in July/August 2002 was conducted by Graham Burt-Smith together with Willow Walker, a botanical surveyor employed specifically for this purpose. Each was responsible for 50% of all quadrats surveyed. There was no statistically significant difference between the total number of hits recorded by each surveyor (general blocked ANOVA  $F=0.31$ ,  $df=4,1,114$   $p>0.05$ ) and the total number of hits recorded in 2002 was similar to the previous year.

Appendix 8 reveals clear treatment differences in the frequency with which species were encountered in the 2002 point analysis survey. In particular, two grass species commonly associated with improved pastures (*Festuca rubra* and *Poa pratensis*) were relatively abundant within the improved plots, accounting for 53% of total hits within the Nitrogen and Lime-treated plots, 30% within the Lime-treated plots and 25% within the Nitrogen-treated plots, but failed to account for more than 10% of total hits within any of the

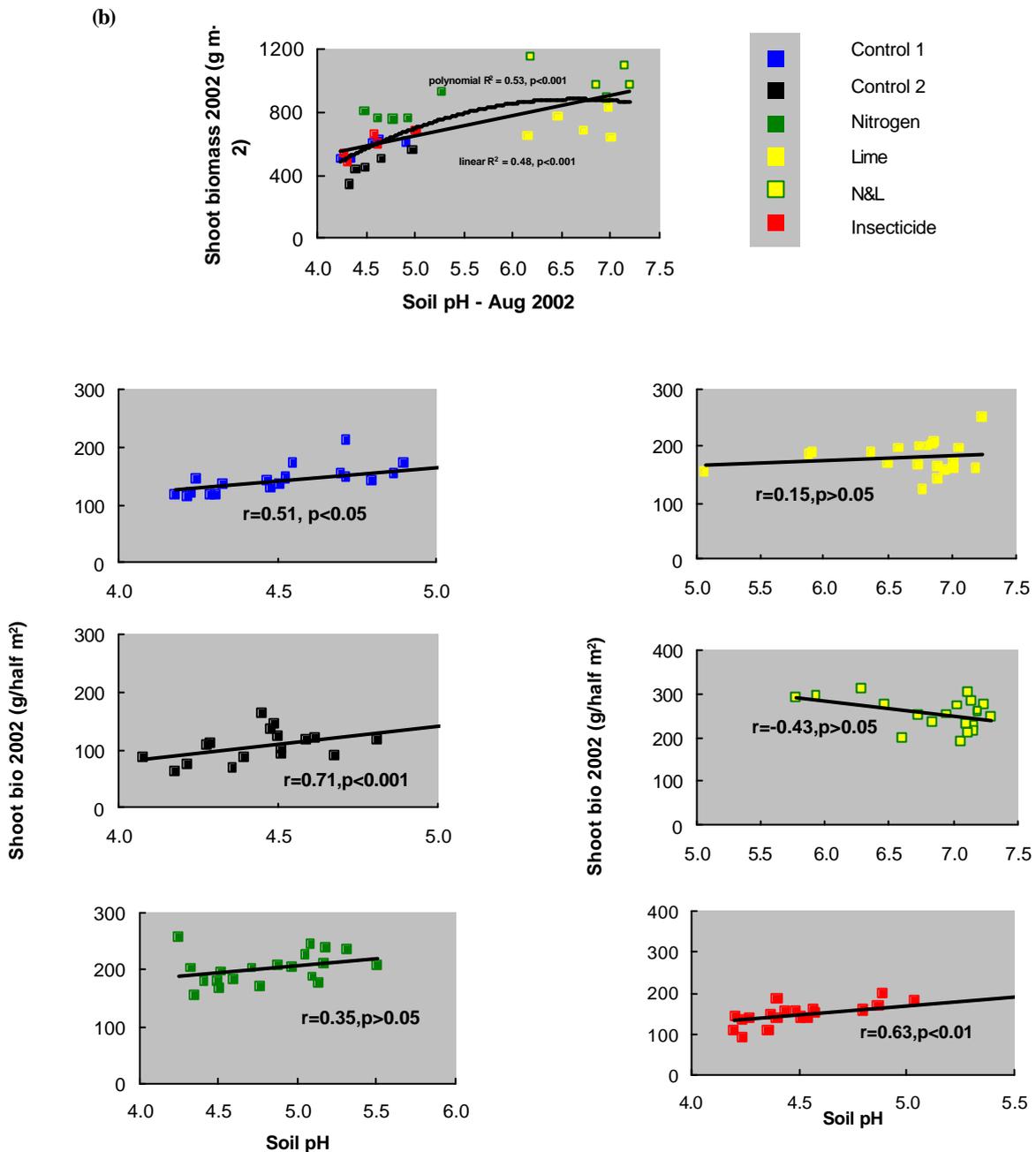


Figure 4 – Above-ground biomass sampled during summer 2002 plotted against soil pH measured during August 2002. (a) All plots (per plot). (b) Within treatments (4 samples per plot).

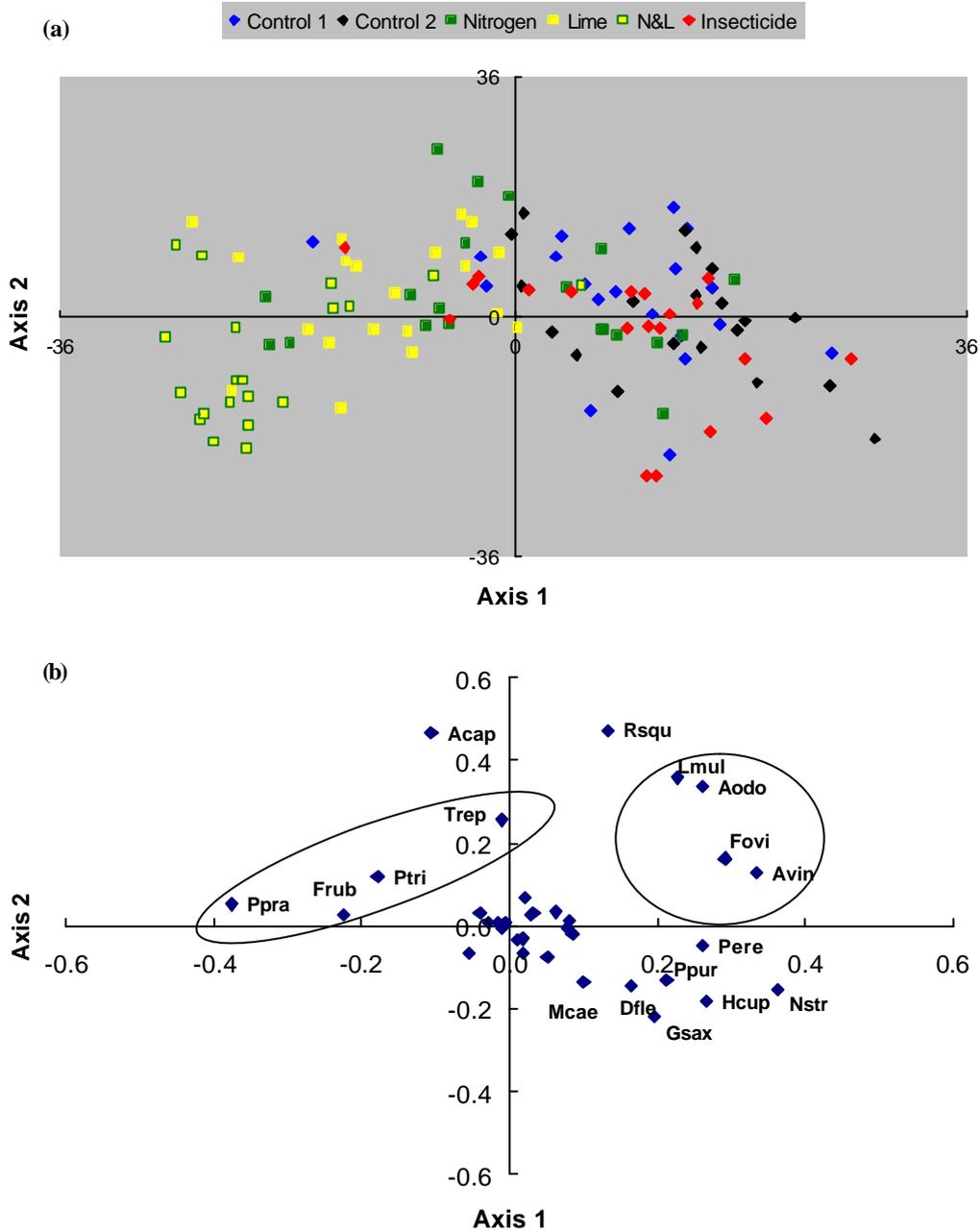
Control or Insecticide-treated plots. In contrast two grass species commonly associated with unimproved pastures (*Festuca ovina* and *Anthoxanthum odoratum*) accounted for just 9% of total hits within the Nitrogen and Lime treated plots whilst the total percentage

of hits in the other treatments ranged from 16% within the limed plots up to 30% within the Control 2 plots. *Agrostis* and *Festuca* spp. continue to be the dominant vascular plant species at the whole-site level. Although *Agrostis capillaris* remains the most abundant individual species the relative frequency of encounter with each of the two *Agrostis* spp. (both *capillaris* and *vinealis*) declined in 2002 compared to 2001 continuing the trend first noted in last year's Annual Report. In contrast a relative fall in *Festuca ovina* "hits" (down 25% in 2002 compared to 2001) was accompanied by a rise in *Festuca rubra* "hits" (up 43% over the same period), possibly reflecting identification difficulties in separating weak *rubra* and strong *ovina* specimens. The overall result is that the two *Festuca* spp. accounted for 30.76% whilst the two *Agrostis* spp. accounted for just 25.32% of total hits in the 2002 survey. This contrasts sharply with the corresponding figures in the 2000 survey (*Agrostis* spp. 43.28%, *Festuca* spp. 23.26%).

As in previous years, the Point Analysis data from the 2002 survey have been subjected to Principal Components Analysis (PCA). However, in contrast to previous years, when no statistical weighting was applied, species were first ranked within treatments before undertaking the PCA (Figure 5a). The results broadly separate improved and unimproved plots. In particular there is a clear grouping of those plots treated with lime. There is evidence that a number of nitrogen-treated samples, particularly from blocks one, two and five, share similar vegetation characteristics to the limed plots, although most of the nitrogen-treated samples from blocks three and four are more closely associated with the controls and insecticide-treated plots. A plot of latent vector loadings (Figure 5b) clearly separates groups of species such as *Poa pratensis*, *Festuca rubra* and *Trifolium repens*, which are commonly associated with more fertile growing conditions, from others such as *Festuca ovina*, *Agrostis vinealis*, *Luzula multiflora* and *Anthoxanthum odoratum*, which are usually associated with less fertile growing conditions.

Appendix 3 shows that six separate mosses and one liverwort were identified on the plots during surveys in 2002. Bryophytes, in particular *Rhytidiadelphus squarrosus*, continue to become more abundant across the whole site and account for 19.92% of total hits in

the 2002 survey compared to 10.82% in 2001 and 6.48% in 2000 (Appendix 8). Split-plot ANOVA reveals a highly significant difference between treatments in the frequency with



**Figure 5 – A Principal Components Analysis (PCA - Genstat 6) has been undertaken using data from the 2002 point analysis survey. Species were first ranked according to number of hits in each sample. Percentage variation explained by axis 1 is 24.4% and axis 2 is 11.1%. (a) PCA scores. (b) PCA latent vector loadings for each of the 34 vascular plant and bryophyte species recorded in the survey**

which bryophytes are encountered ( $F=6.43$   $df=4,5,20,90$   $p<0.001$ ). At the species level, the relative abundance of *Eurynchium praelongum* is similar in each treatment but other bryophyte species all appear to be negatively impacted by the application of nitrogen (especially *Rhytidiadelphus squarrosus* and *Pseudoscleropodium purum*) or lime (particularly *Hypnum cupressiforme*) with the result that bryophytes are particularly infrequent in the N&L plots. Compared to the year 2000, the percentage of total bryophyte hits has increased across all treatments in each of the 2001 and 2002 point analysis surveys (Figure 6a). This increase has been particularly marked within the unimproved plots (Control and Insecticide) where it has been coupled with an increase in dicot numbers which, together, have resulted in reductions of 24% (Control 1) and 18% (Insecticide) in monocot hits as a percentage of total hits during this period. Other surveys, in 2000 and 2002, in which small areas of vegetation were cut, sorted to species, dried and subsequently weighed reveal an even more dramatic increase in the contribution of bryophytes to the overall biomass in the unimproved plots (Figure 6b).

In 2000 there were no significant differences between treatments in the frequency with which dead vegetation (litter) was encountered in the point analysis survey (ANOVA  $F=0.13$ ,  $df=4,4,16$   $p>0.05$ ). Figure 7, however, shows that statistically significant differences between the various treatments have emerged in 2001 and 2002, with the N&L plots recording the highest mean number of hits whilst the Control 1 plots have recorded the lowest.

Shannon Diversity Indices have been calculated using the basic point analysis data from the initial baseline data survey in 1998 together with the subsequent more extensive point analysis surveys in 2000, 2001 and 2002 (Figure 8). Prior to the start of the experiment there were no statistically significant differences across the site (split-plot ANOVA,  $F=0.49$   $df=4,5,20,120$   $p>0.05$ ). Evidence of treatment differences became apparent in 2000 (split-plot ANOVA,  $F=3.72$   $df=4,4,16,75$   $p<0.05$ ) and became more pronounced in both 2001 (split-plot ANOVA,  $F=10.60$   $df=4,4,16,75$   $p<0.001$ ) and 2002 (split-plot

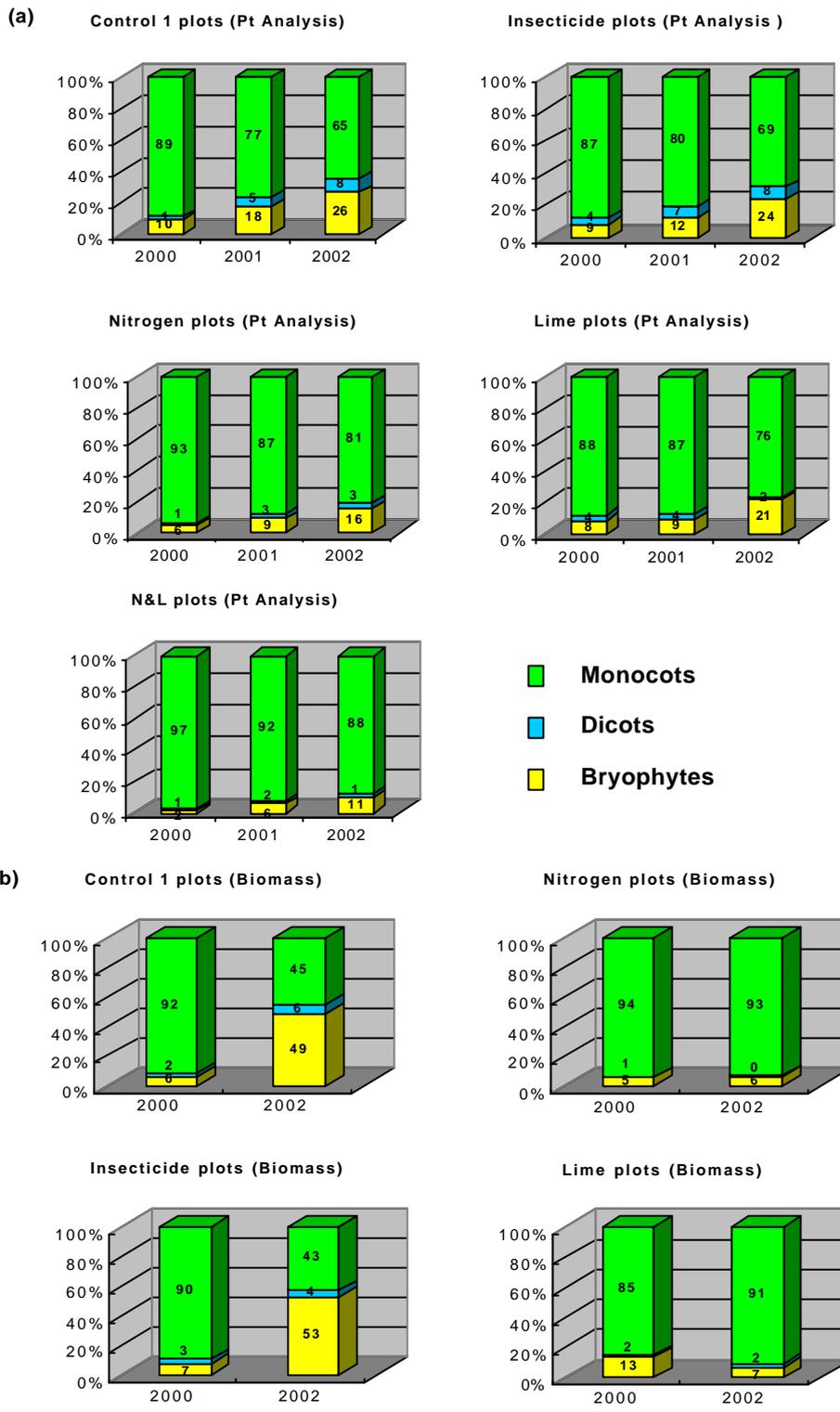
ANOVA,  $F=17.91$   $df=4,5,20,90$   $p<0.001$ ). When compared to the baseline data survey, the 2002 Shannon Diversity Index has fallen by 15% in the nitrogen and lime treated plots in contrast to all the other treatments which have seen increases in the Shannon Diversity Index ranging from a minimum of 2% in the limed plots up to a maximum of 29% in the Insecticide-treated plots.

There are three predominant functional groups - stress tolerant (S), C-S-R and SR/C-S-R species – which have, together, accounted for a minimum of 69% and a maximum of 95% of total vascular plant hits in any one plot in the various Point Analysis surveys which have been undertaken (Table 2).

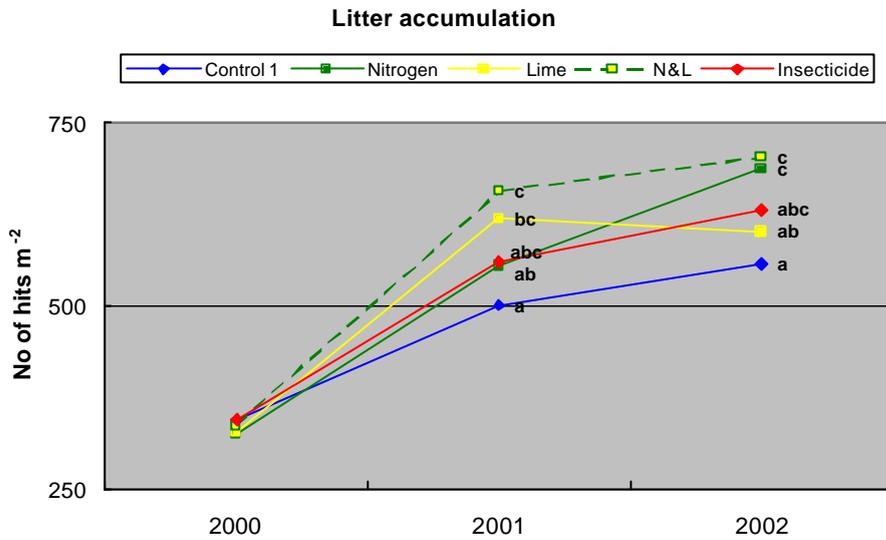
**Table 2 – Percentage of Point Analysis survey live vascular plant “hits” represented by stress tolerant (S), C-S-R and SR/C-S-R plant species prior to the start of the treatments (1998) and in subsequent years.**

	Minimum %	Maximum %
1998	69	95
2000	75	99
2001	76	99
2002	80	99

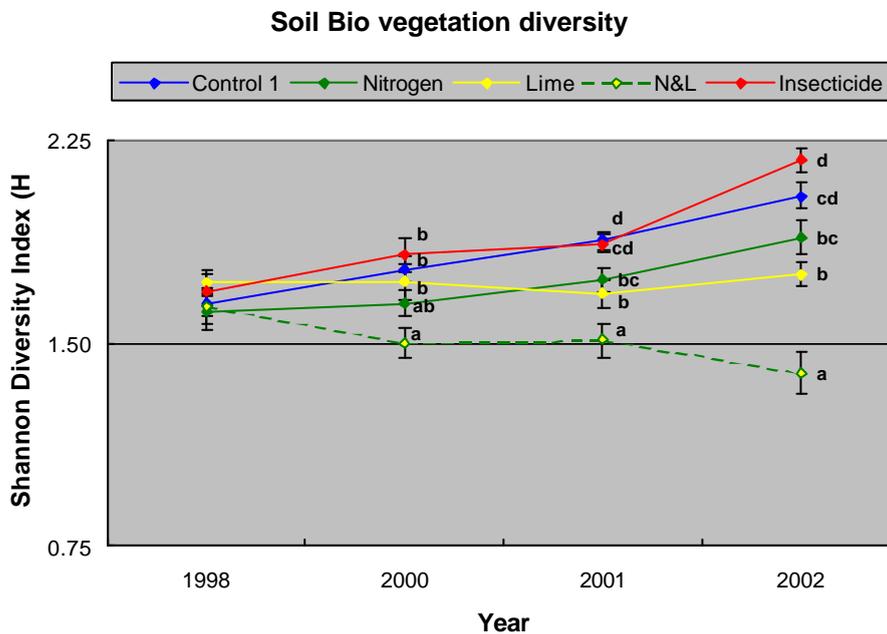
Within each of these functional groupings there were no significant differences between the plots allocated to each treatment prior to the start of the experiment in 1998 (Figure 9a). However, treatment differences within the SR/C-S-R functional group emerged in 2000 and, by 2002, each of the three functional groupings recorded highly significant statistical differences between treatments (Figure 9b-d). C-S-R species have greatly expanded to become dominant within the nitrogen and lime plots, whilst stress tolerant species are particularly benefiting within the unimproved plots, although they are also showing modest gains within those plots treated with nitrogen-only and lime-only. SR/C-S-R species are particularly reduced within the lime- (with and without nitrogen) and insecticide -treated plots.



**Figure 6 – Changes in fundamental botanical groupings within different treatments analysed from various surveys during 2000 to 2002. (a) Point analysis surveys – frequency within each group is expressed as a percentage of the total for that particular year. (b) Biomass surveys in 2000 (n=5, sample size 6250mm<sup>2</sup>) & 2002 (n=3, sample size 4900mm<sup>2</sup>).**



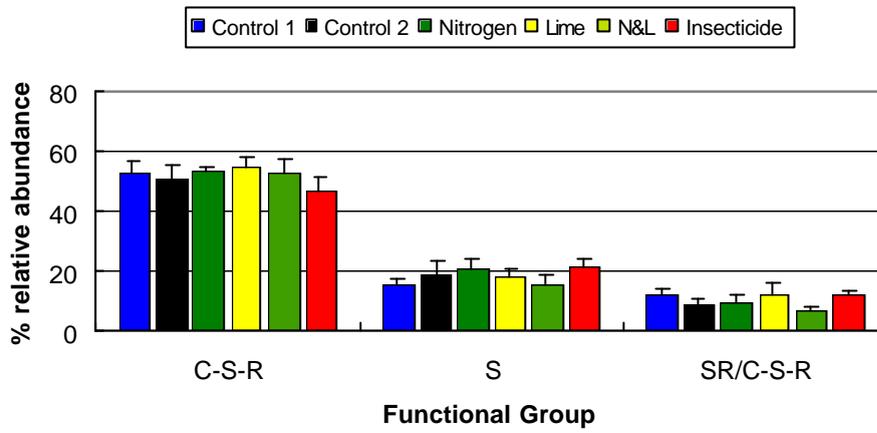
**Figure 7 – The mean number of litter hits m<sup>-2</sup> within each treatment from the point analysis surveys in each of the past 3 years (error bars omitted to aid clarity). ANOVA's have been undertaken for each year: 2000 F=0.13, df=4,4,16,75 p>0.05 2001 F=3.46 df=4,4,16,75 p<0.05 2002 F=3.52 df=4,5,20,90 p<0.05. In 2000 there were no statistically significant differences between means. Thereafter means with the same letter do not differ significantly within years (Isd test p>0.05). Control 2 plots are excluded.**



**Figure 8 - Mean Shannon diversity indices have been calculated for each treatment using data from the point analysis surveys. Standard error bars are shown. In 1998 there were no statistically significant differences between means. Thereafter means with the same letter do not differ significantly within years (Isd test p>0.05)**

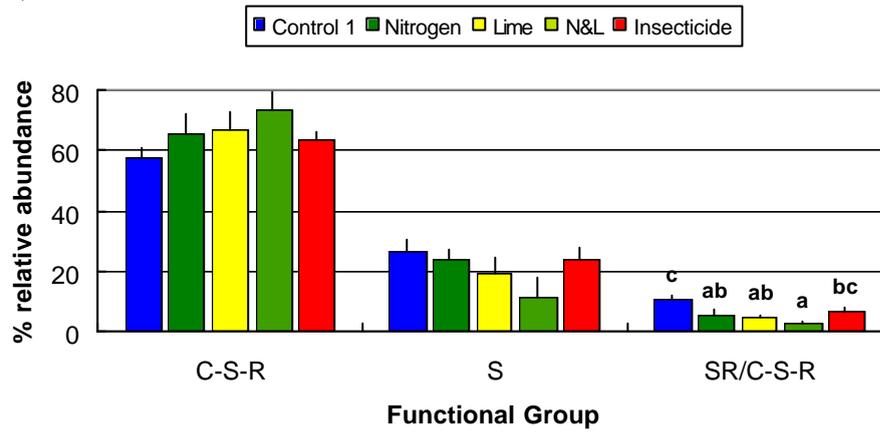
(9a)

1998



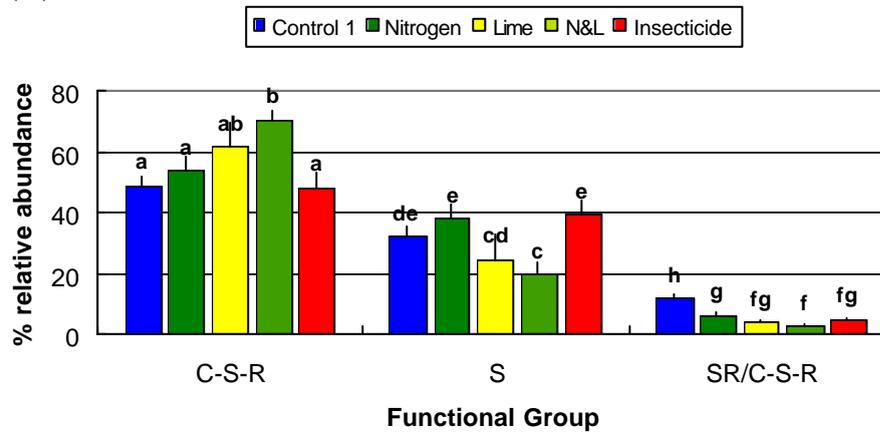
(9b)

2000



(9c)

2001



(9d)

2002

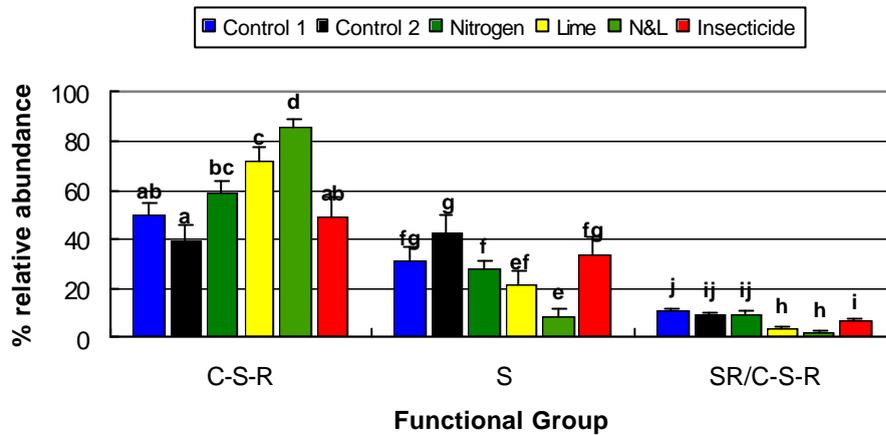


Figure 9 – Relative abundance of key functional groups of vascular plant species shown as percentage of total live vascular plant “hits” in point analysis surveys. S=stress tolerators, CSR=competitive stress ruderals and SR/CSR=stress ruderal/competitive stress ruderals (Grime, 1977). Means with the same letter do not differ significantly (Isd test  $p>0.05$ ). Bars indicate plus one standard error.

ANOVA's:

Fig	CSR	S	SR/CSR
9a	F=1.25 df=4,5,20 $p>0.05$	F=0.76 df=4,5,20 $p>0.05$	F=0.96 df=4,5,20 $p>0.05$
9b	F=2.03 df=4,4,16 $p>0.05$	F=2.10 df=4,4,16 $p>0.05$	F=4.94 df=4,4,16 $p<0.01$
9c	F=4.29 df=4,4,16 $p<0.05$	F=5.18 df=4,4,16 $p<0.01$	F=13.54 df=4,4,16 $p<0.001$
9d	F=12.86 df=4,5,20 $p<0.001$	F=6.12 df=4,5,20 $p<0.001$	F=11.43 df=4,5,20 $p<0.001$

## 4. DISCUSSION

Changes to plant productivity and botanical composition can be summarised under three main headings plus one supplemental heading:

### 4.1 Mowing effect

One of the most striking points to emerge from the Point Analysis surveys is the reduction in both *Agrostis capillaris* and *Agrostis vinealis* which have together declined by over 40% since 2000. This has occurred in approximately equal measures across all treatments, suggesting that the decline in these particular species does not result from the application of any particular treatment but is, rather, due to some site-level factor. One potential explanation is an adverse reaction of these species to the mowing, in particular the homogenous nature of the cuts which do, of course, differ considerably from the heterogeneous grazing of livestock. Other possibilities include climatic or biotic factors such as competitive exclusion by other species. The major vascular plant beneficiary is *Festuca rubra*, which is one of the group of species identified as being associated with plots to which lime and, to a lesser extent, nitrogen have been added. It is unsurprising therefore, that the expansion in relative abundance of this species has been particularly apparent within the more fertile plots.

The expansion of stress tolerant species across all treatments, with the sole exception of nitrogen and lime, suggests that this functional group has also benefited most from some general site-level factor, such as reduced levels of disturbance following the removal of grazing animals. It is suggested that this reduction in disturbance has also been responsible, at least to some extent, for the decline in SR/C-S-R species across all treatments, given the ruderal nature of this functional group of species. Treatment differences across both these functional groups reflect those attributes of stress tolerant species, such as long-living leaves, which enable them to cope more successfully with the lower soil pH and nutrient levels associated with the unimproved treatments.

The widespread expansion of mosses across the site generally supports the study by Hulme *et al.* (1999) who found that maintenance of an *Agrostis/Festuca* grassland sward height at some 4.5cm resulted in a higher content of mosses in the absence of the tussock grass *Nardus stricta*. It is possible that the maintenance of a sward height of approximately 6cm through regular mowing, possibly coupled with the absence of grazing animals for the past five years, has produced conditions enabling a rapid expansion in the relative abundance of bryophytes. This effect is somewhat reduced by the greater vascular plant productivity within the more fertile treatments.

#### *4.2 Fertilisation effect*

Since 1999 there has been an on-going positive effect upon aboveground vegetation biomass (productivity) of soil improvements, involving the addition of nitrogen and/or lime. However, whilst the most productive plots remain those to which both nitrogen and lime have been added, there are some signs that productivity may have peaked within these plots, possibly as a result of their increased soil pH linked with a comparatively low soil moisture content. Whilst it is generally accepted that a Soil pH of around 6.0 provides good growing conditions to optimise agricultural productivity within grasslands, it is apparent that the high annual rates of lime application to designated plots in the Soil Biodiversity project have resulted in their mean soil pH being closer to 7.0 by summer 2002. In graphical terms the relationship between above-ground biomass and soil pH is frequently normally distributed and it is possible therefore that productivity within these plots will continue to decline if soil pH rises again following another application of lime in spring 2003. It is also possible that the extra stimulation to plant growth within those plots to which Nitrogen has been added, in addition to lime, has significantly reduced soil moisture content. This has, in turn, caused the vegetation to be particularly susceptible to water stress during dry periods, probably leading to reduced plant growth. There was some visual evidence of plant stress in summer 2002 when large patches of vegetation suffered from chlorosis, particularly within those plots treated with lime.

The increase in C-S-R species, within those plots treated with both nitrogen and lime, supports the hypothesis that plant species within this functional group have been able to expand by using those attributes, such as growth rate, which enable them to make greater use of the more benign growing environment. For C-S-R species, a higher soil pH appears to be more important than the addition of nitrogen as evidenced by the relatively poor performance of C-S-R species within those plots fertilised with nitrogen only compared to those plots treated with lime only.

#### *4.3 Insecticide effect*

Interactions between plants and herbivores are numerous and extremely complex. Field experiments in grassland plant communities show that animals and birds often, but not always, increase plant diversity whilst plant diversity usually decreases when they are excluded. Studies have demonstrated clear effects of insect herbivory on plant species composition, vegetation cover and structure (Brown, 1982, 1985) although it is apparent that these vary according to the type of insecticide applied and the life history grouping of the plants. For instance, in their study into the differential effects of above- and below-ground insect herbivory during early plant succession Brown and Gange (1989) reported that plant species richness and diversity, in general, were increased by the application of soil insecticide but, by the second season, depressed by foliar insecticide whilst the responses differed between annual herbs, perennial grasses and perennial herbs.

According to the product label, Dursban 4 insecticide (Dow AgroSciences) is effective for controlling the agricultural pests frit fly and leatherjackets on pasture land, although other insects will also be susceptible. However, in the absence of information about the exact nature and levels of insect control, it would be unwise to report a direct link between reduced insect herbivory and a higher Shannon diversity index. It is nevertheless clear that the results mirror those of Brown and Gange (1989) and, if such a link does indeed exist, one possible explanation is that benefits are accruing to a number of more palatable plant species for which conditions are now suitable to survive whereas, previously, they would have been unable to sustain herbivore damage in the relatively

infertile environment at Sourhope. As long as the environment remains relatively infertile these plants should not become dominant and it is likely that plant diversity levels would therefore remain comparatively high.

#### 4.3 *Trampling effect*

Sampling within the C2 plots took place for the first time in 2002 and this probably accounts for the dramatic fall in productivity within these plots relative to the C1 plots. In particular, it is likely that vegetation growth in many of the C2 plots was suppressed by trampling during intense periods of activity associated with the application of labelled  $^{13}\text{CO}_2$  pulses on these plots.

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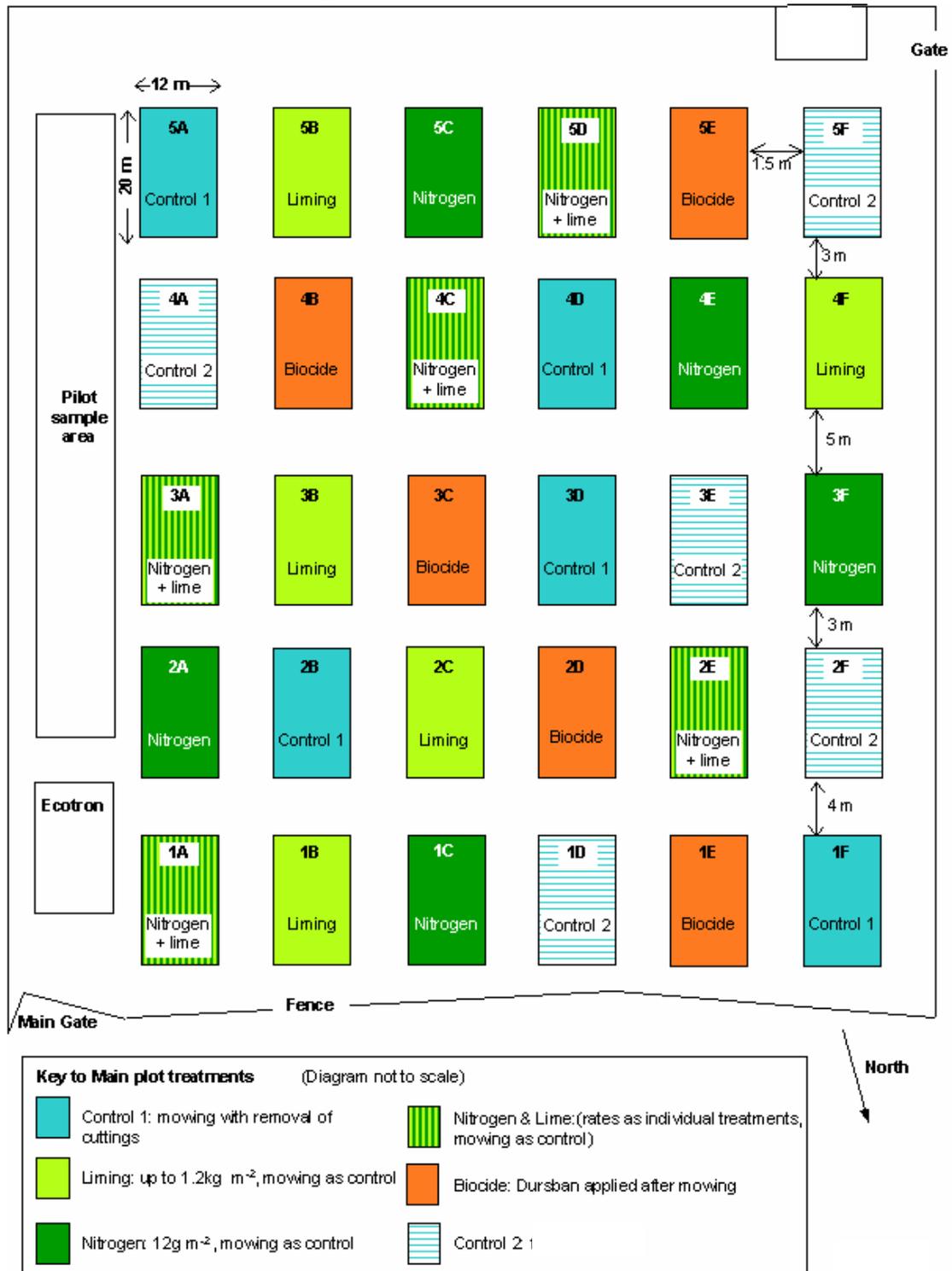
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**Appendix 1 – Soil Biodiversity site, Sourhope. Map showing orientation of site and treatments allocated to each plot (NB wef 2002 Biocide amended to Insecticide plots)**



## Appendix 2 – Summary of Soil Biodiversity site and plot level treatments

- **Site level treatment – vegetation cutting**

	1999	2000	2001	2002
Cut 1	1 <sup>st</sup> - 9 <sup>th</sup> Jun	8 - 12 <sup>th</sup> May	5 <sup>th</sup> - 18 <sup>th</sup> May (*)	20 <sup>th</sup> - 27 <sup>th</sup> May
Cut 2	29 <sup>th</sup> Jun - 5 <sup>th</sup> Jul	5 <sup>th</sup> - 9 <sup>th</sup> Jun	4 <sup>th</sup> - 8 <sup>th</sup> Jun	17 <sup>th</sup> - 26 <sup>th</sup> June
Cut 3	26 <sup>th</sup> - 29 <sup>th</sup> Jul	3 <sup>rd</sup> - 7 <sup>th</sup> Jul	3 <sup>rd</sup> - 18 <sup>th</sup> Jul (*)	15 <sup>th</sup> - 19 <sup>th</sup> July
Cut 4	23 <sup>rd</sup> - 26 <sup>th</sup> Aug	31 <sup>st</sup> July - 4 <sup>th</sup> Aug	6 <sup>th</sup> - 14 <sup>th</sup> Aug	19 <sup>th</sup> - 26 <sup>th</sup> August
Cut 5	21 <sup>st</sup> - 25 <sup>th</sup> Sep	28 <sup>th</sup> - 31 <sup>st</sup> Aug	4 <sup>th</sup> - 11 <sup>th</sup> Sep	24 <sup>th</sup> Sept - 1 <sup>st</sup> Oct

(\*) includes period where mower unavailable due to mechanical breakdown

- **Plot level treatments**

- Control 1 .....No treatment applied
- Control 2 .....No treatment applied
- Nitrogen .....Applied as NH<sub>4</sub>NO<sub>3</sub> (ICI NITRAM granular fertilizer; Total N (34%), Ammonical N (17.2), Nitric N (17.3%))  
Annual rate of application 24g m<sup>-2</sup> (5.76kg plot<sup>-1</sup>, 240kg ha<sup>-1</sup>)  
  
Applied in two doses  
Year 1 - 1999: Spring (2<sup>nd</sup>-3<sup>rd</sup> April) and Late Summer (28-29<sup>th</sup> Sept.)  
Year 2 - 2000: Spring (17-18<sup>th</sup> April) and Late Spring (16<sup>th</sup> May)  
Year 3 - 2001: Spring (11-12<sup>th</sup> April) and Late Spring (23-25<sup>th</sup> May)  
Year 4 - 2002: Spring (8-9<sup>th</sup> April) and Late Spring (1<sup>st</sup>-2<sup>nd</sup> May)
- Lime .....applied as CaCO<sub>3</sub> (powdered lime; 39.4% Calcium ASH insoluble in HC 1 0.5%)  
Annual rate of application 600g m<sup>-2</sup> (144kg plot<sup>-1</sup>, 6000kg ha<sup>-1</sup>)  
  
Applied in one dose  
Year 1 - 1999: Spring (7-20<sup>th</sup> May)  
Year 2 - 2000: Spring (5-10<sup>th</sup> May)  
Year 3 - 2001: Spring (17-26<sup>th</sup> April)  
Year 4 - 2002: Spring (10-17<sup>th</sup> April)
- Nitrogen and Lime .....N & L as above
- Insecticide .....Dursban 4 OPA insecticide (ex Dow Chemicals)  
Rate of application 0.15 ml m<sup>2</sup> (36ml in 10 litres plot<sup>-1</sup>, 1.5 litres ha<sup>-1</sup>)  
(Annual rate 7.5 litres ha<sup>-1</sup>)  
  
Applied after each mowing as soon as weather was permitting  
Year 1 - 1999: 16<sup>th</sup> July, 6<sup>th</sup> Aug., 3<sup>rd</sup> Sept. & 30<sup>th</sup> Sept.  
Year 2 - 2000: 15<sup>th</sup> May, 14<sup>th</sup> June, 18<sup>th</sup> July, 11<sup>th</sup> Aug., 1<sup>st</sup> Sept.  
Year 3 - 2001: not applied in May, 12<sup>th</sup> June, 21<sup>st</sup> July, 16<sup>th</sup> Aug., 13<sup>th</sup> Sept.  
Year 4 - 2002: 28<sup>th</sup> May, 27<sup>th</sup> June, 25<sup>th</sup> July, 27<sup>th</sup> August, 3<sup>rd</sup> October.

### Appendix 3 - Soil Bio species list - 2002

Acap	<i>Agrostis capillaris</i>	1
Avin	<i>Agrostis vinealis</i>	1
Aodo	<i>Anthoxanthum odoratum</i>	1
Cvul	<i>Calluna vulgaris</i>	2
Crot *	<i>Campanula rotundifolia</i>	2
Cpra *	<i>Cardamine pratensis</i>	2
Cpan	<i>Carex panicea</i>	1
Cpil	<i>Carex pilulifera</i>	1
Cfon *	<i>Cerastium fontanum</i>	2
Cpal	<i>Cirsium palustre</i>	2
Ccri *	<i>Cynosurus cristatus</i>	1
Dglo *	<i>Dactylis glomerata</i>	1
Dfuc *	<i>Dactylorhiza fuchsii</i> (?)	1
Dces	<i>Deschampsia cespitosa</i>	1
Dfle	<i>Deschampsia flexuosa</i>	1
Fovi	<i>Festuca ovina</i>	1
Frub	<i>Festuca rubra</i>	1
Gsax	<i>Galium saxatile</i>	2
Hlan	<i>Holcus lanatus</i>	1
Hmol	<i>Holcus mollis</i>	1
Hrad *	<i>Hypochoeris radicata</i>	2
Jeff *	<i>Juncus effusus</i>	1
Jsqu *	<i>Juncus squarrosus</i>	1
Llin	<i>Lathyrus linifolius</i>	2
Lpra	<i>Lathyrus pratensis</i>	2
Lper *	<i>Lolium perenne</i>	1
Lmul	<i>Luzula multiflora</i>	1
Lpil	<i>Luzula pilosa</i>	1
Mcae	<i>Molinia caerulea</i>	1
Nstr	<i>Nardus stricta</i>	1
Pann	<i>Poa annua</i>	1
Ppra	<i>Poa pratensis</i>	1
Ptri	<i>Poa trivialis</i>	1
Pere	<i>Potentilla erecta</i>	2
Racr	<i>Ranunculus acris</i>	2
Rrep	<i>Ranunculus repens</i>	2
Race	<i>Rumex acetosa</i>	2
Trep	<i>Trifolium repens</i>	2
Vmyr	<i>Vaccinium myrtillus</i>	2
Vcha *	<i>Veronica chamaedrys</i>	2
Epra	<i>Eurynchium praelongum</i>	3
Hspl	<i>Hylocomium splendens</i>	3
Hcup	<i>Hypnum cupressiforme</i>	3
Psch	<i>Pleurozium schreberi</i>	3
Ppur	<i>Pseudoscleropodium purum</i>	3
Rsqu	<i>Rhytidiadelphus squarrosus</i>	3
Lbid	<i>Lophocolea bidentata</i>	3

1 = MONOCOT      2 = DICOT      3 = BRYOPHYTE

\* indicates species seen on plot but not found in the point analysis survey

Other species seen on the site but off-plot: *Achillea millefolium*, *Chamaenerion angustifolium*

*Juncus conglomeratus*, *Trisetum flavescens*, *Viola lutea* plus mosses *Hypnum jutlandicum* and several *Polytrichum* spp

**Appendix 4 - Summary of site activity at Sourhope since the start of The Soil Biodiversity Thematic Programme**

	<b>1998</b>	<b>1999</b>	<b>2000</b>	<b>2001</b>	<b>2002</b>
Soil sampling	2	63	68	31	57
Measurement	1	13	33	12	26
Experimental set up/input	0	9	15	4	18
Other	0	5	12	9	9
<b>Total</b>	<b>3</b>	<b>90</b>	<b>128</b>	<b>56</b>	<b>110</b>

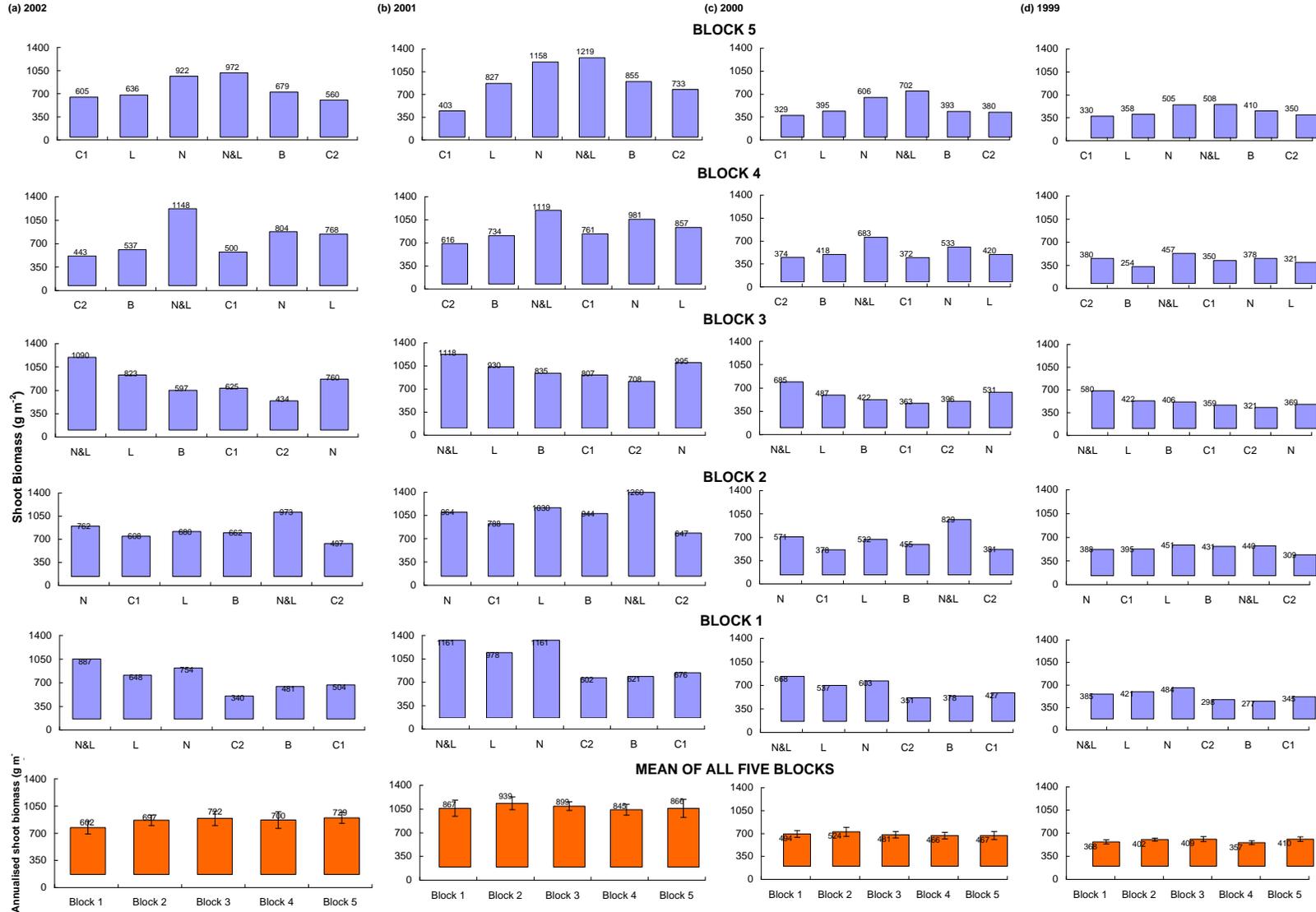
**Appendix 5 - Soil Biodiversity Site Automatic Weather Station – headline measures  
1999 to 2002**

	Total rainfall (mm)	Total radiation (MJ m <sup>-2</sup> )	Mn soil moisture (m <sup>3</sup> m <sup>-3</sup> )	Mn air temp 2m (°C)	Mn air temp 2cm (°C)	Mn soil temp 2cm (°C)	Mn soil temp 5cm (°C)	Mn soil temp 10cm (°C)	Mn soil temp 20cm (°C)
<b>1999</b>	845	3439	0.30	8.17	8.33	8.65	8.64	8.65	8.57
<b>2000</b>	1209	3472	0.35	7.47	8.00	8.12	8.08	8.07	8.04
<b>2001</b>	839	3473	0.37	7.28	7.66	7.72	7.67	7.66	7.62
<b>2002*</b>	1135	3559	0.38	7.96	8.54	8.62	8.58	8.55	8.37

\* Figures for 2002 include periods between July and November when the weather station malfunctioned. It is believed that this resulted from damage to software during an electrical storm. The problem was identified and rectified on 7th November. A total of some 6 weeks data was lost or failed to be recorded (30<sup>th</sup> July - 12<sup>th</sup> August plus 4<sup>th</sup> October - 7<sup>th</sup> November).

During this period rainfall, radiation and air temperature values from the nearby Konza plots weather station were substituted. The remaining 2002 values quoted above (soil moisture, air temp at 2cm and all soil temperatures) exclude data for those “missing” dates in July/August and October/November.

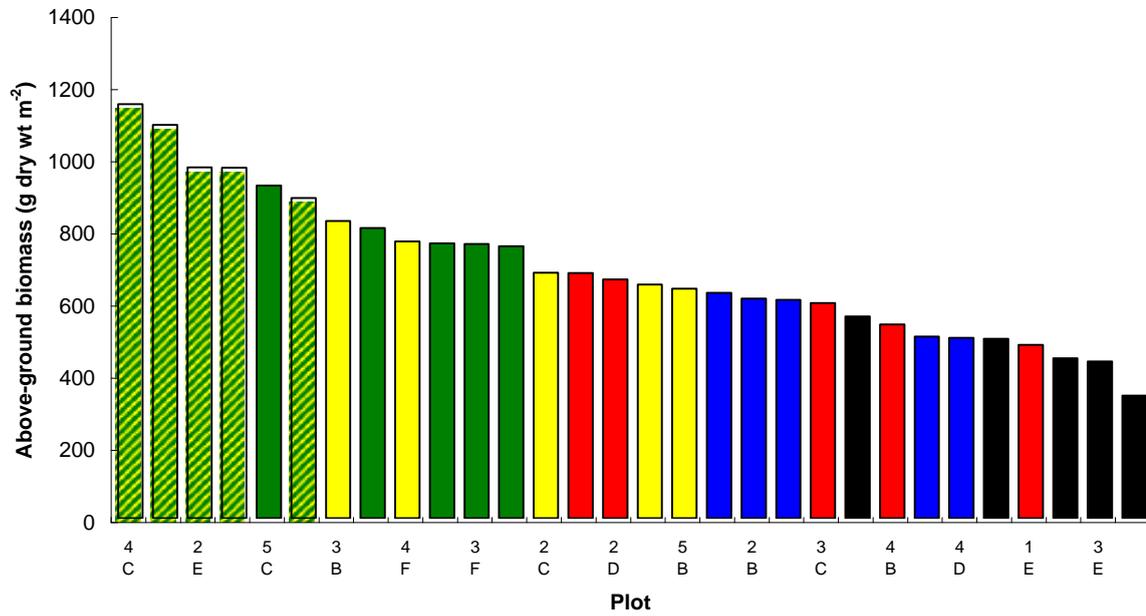
Appendix 6 Annualised above-ground biomass in each of the plots plus the mean of the five replicate blocks



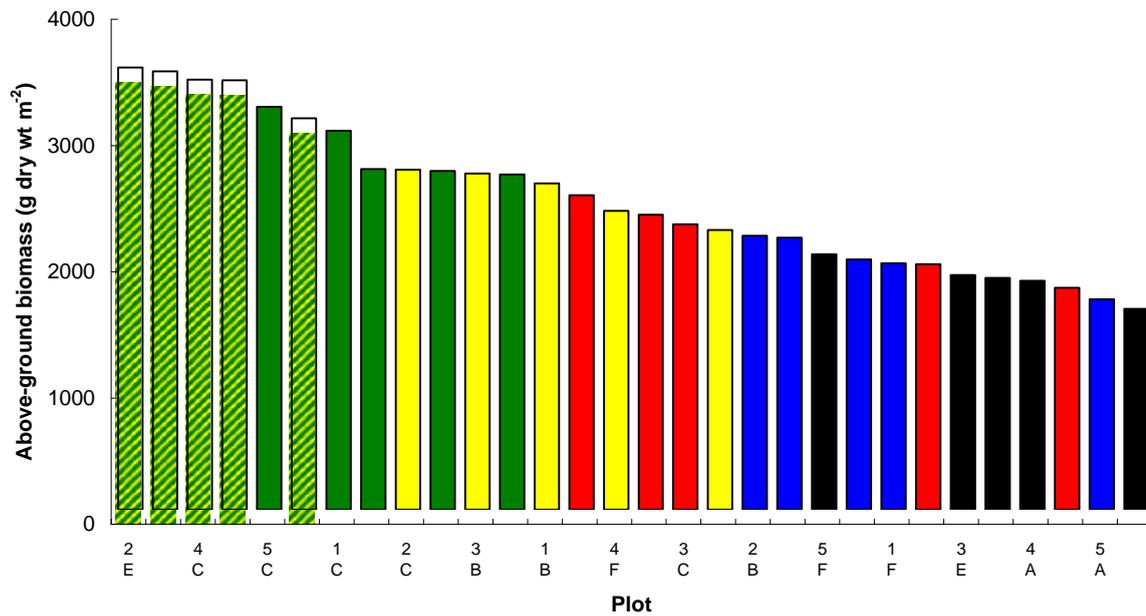
In the above treatments "B" refers to Biocide plots - now referred to as Insecticide plots (wef 2002/3)

Appendix 7 Rank in the above-ground biomass samples from each plot obtained from the sum of the five summer samples collected prior to each mowing. Colour coding: Blue = Control 1, Black = Control 2, Green = Nitrogen, Yellow = Lime, Green & Yellow = N&L, Red = Insecticide.

a) Biomass samples for 2002



b) Cumulative biomass samples 1999 to 2002



**Appendix 8 Comparison of the percentage rank abundance of species in the point quadrat botanical surveys conducted in 2000, 2001 & 2002. Species are ranked based upon the total number of hits per treatment. The total rank abundance of each species across the entire site is also shown. Litter is excluded.**

<b>Control 1</b>				<b>Control 2</b>			<b>Biocide</b>			
% of C1 hits 2000	% of C1 hits 2001	% of C1 hits 2002		* % of C2 hits 2000	* % of C2 hits 2001	% of C2 hits 2002	% of B hits 2000	% of B hits 2001	% of B hits 2002	
Rsqu	9.57	16.67	20.56	Fovi		23.01	Acap	26.78	21.88	20.31
Acap	33.39	23.48	20.41	Acap		16.20	Fovi	14.19	24.87	15.87
Fovi	15.99	17.68	14.92	Rsqu		16.18	Rsqu	8.70	12.15	13.46
Avin	11.11	10.36	8.45	Frub		7.40	Avin	18.96	9.47	7.08
Aodo	9.92	8.77	7.79	Aodo		6.70	Hcup			6.09
Frub	2.35	1.48	4.95	Avin		6.32	Frub	5.44	3.54	6.01
Trep	0.94	3.05	3.13	Nstr		5.05	Nstr	6.04	5.00	5.32
Nstr	7.73	5.81	2.96	Lmul		2.89	Aodo	5.89	4.21	5.02
Gsax	0.06	0.47	2.85	Gsax		2.35	Ppra	6.19	5.76	3.55
Ppra	5.16	3.26	2.72	Pere		2.15	Pere	1.02	2.36	3.28
Hcup			2.43	Ppur		1.80	Epra			2.41
Lmul	0.78	1.04	1.89	Trep		1.78	Lmul	1.66	1.32	1.93
Pere	0.31	1.30	1.84	Epra		1.56	Gsax	0.27	1.33	1.86
Epra			1.57	Hcup		1.53	Trep	2.29	2.26	1.71
Ppur			0.84	Ppra		1.34	Ppur			1.37
Hspl			0.64	Hmol		0.91	Dfle	1.27	0.29	1.31
Dfle	1.13	0.97	0.51	Dfle		0.62	Hlan		1.23	0.70
Llin	0.13	0.16	0.42	Mcae		0.58	Lpil	0.27	0.07	0.50
Mcae	0.19	0.70	0.24	Cpan		0.36	Mcae	0.17	0.07	0.35
Cpil	0.03	0.58	0.19	Hspl		0.32	Cpan	0.20	0.29	0.28
Ptri	0.16	0.08	0.15	Lpil		0.25	Hspl			0.25
Hlan			0.10	Cpal		0.19	Dces			0.20
Lpil	0.06	0.08	0.08	Cpil		0.13	Cpal		0.22	0.20
Cpan	0.03	0.27	0.07	Llin		0.13	Llin	0.12	0.18	0.18
Lbid		0.93	0.07	Ptri		0.09	Race	0.17	0.51	0.17
Race	0.03	0.39	0.07	Hlan		0.06	Cpil	0.25	0.14	0.17
Hmol	0.84	0.31	0.05	Rrep		0.05	Lbid			0.12
Psch			0.05	Race		0.03	Ptri	0.10	0.22	0.07
Vmyr			0.05	Lbid		0.02	Racr			0.07
Dces	0.09	2.10	0.02				Psch			0.07
Lsyl		0.08					Rrep			0.05
							Vmyr	0.51	0.03	
							Lsyl	2.13		
							Hmol	0.02		

<b>Nitrogen</b>				<b>Lime</b>			<b>N&amp;L</b>			<b>Total</b>					
% of N hits 2000	% of N hits 2001	% of N hits 2002		% of L hits 2000	% of L hits 2001	% of L hits 2002	% of N&L hits 2000	% of N&L hits 2001	% of N&L hits 2002	% of total hits 2000	% of total hits 2001	% of total hits 2002			
Acap	29.93	21.77	22.70	Acap	34.63	28.32	23.42	Frub	14.55	26.31	35.45	Acap	32.03	23.08	20.08
Fovi	20.24	27.61	18.83	Frub	7.19	10.90	19.91	Ppra	15.69	13.82	18.01	Fovi	14.85	20.87	15.76
Frub	10.00	10.22	16.87	Rsqu	8.21	9.07	19.14	Acap	35.78	20.40	17.59	Rsqu	6.48	10.64	15.39
Rsqu	5.65	9.47	14.13	Fovi	12.56	17.99	13.72	Rsqu	1.90	6.05	8.98	Frub	8.41	10.45	15.00
Aodo	5.52	5.15	7.44	Ppra	10.18	10.19	9.71	Fovi	11.08	14.63	7.44	Ppra	9.29	7.59	6.48
Avin	12.86	8.99	5.05	Avin	10.01	3.88	2.76	Hlan	0.52	0.30	3.21	Aodo	5.42	4.65	5.24
Ppra	7.74	5.39	4.13	Aodo	4.23	3.04	2.47	Aodo	2.71	2.08	1.70	Avin	11.25	7.26	5.22
Lmul	1.02	1.25	2.22	Lmul	1.16	0.72	1.87	Avin	4.00	3.14	1.54	Nstr	3.92	3.61	2.62
Nstr	2.06	3.12	1.38	Ptri	0.93	5.91	1.71	Epra			1.52	Lmul	1.11	0.98	1.93
Dfle	2.11	1.35	1.33	Epra			1.22	Ptri	4.37	3.82	1.35	Hcup			1.75
Epra			1.30	Trep	2.99	2.05	1.13	Race			0.71	Epra			1.59
Gsax	0.33	1.74	1.19	Ppur			0.84	Lmul	0.89	0.50	0.68	Pere	0.36	1.01	1.45
Pere	0.27	0.84	0.84	Nstr	3.80	2.28	0.77	Dces	0.19	2.35	0.64	Trep	1.42	1.82	1.41
Hcup			0.48	Pere	0.17	0.35	0.39	Hmol	5.67	2.81	0.35	Gsax	0.15	0.75	1.39
Trep	0.38	0.53	0.48	Lpra			0.24	Trep	0.87	1.44	0.27	Ppur			0.90
Ppur			0.41	Rrep		0.62	0.19	Pere	0.06	0.15	0.14	Hlan	0.12	0.31	0.67
Cpil	0.07	0.39	0.36	Hspl			0.14	Lpil			0.12	Dfle	1.11	0.55	0.64
Hmol	0.78	0.58	0.29	Lpil			0.07	Nstr	1.34	1.88	0.08	Ptri	1.29	1.99	0.58
Ptri	0.27	0.35	0.16	Cpil	0.15	0.08	0.07	Ppur			0.08	Hmol	1.90	1.03	0.28
Race	0.04	0.06	0.10	Cpal			0.07	Mcae	0.02		0.08	Hspl			0.23
Llin	0.27	0.19	0.08	Race	0.44	0.16	0.05	Rrep		0.08	0.03	Mcae	0.13	0.32	0.22
Cpal			0.08	Dces	0.17	1.72	0.03	Dfle	0.11		0.02	Race	0.14	0.22	0.18
Mcae	0.09	0.35	0.05	Cpan	0.29	0.16	0.03	Lsyl		0.15		Lpil	0.07	0.03	0.17
Cpan	0.38	0.19	0.05	Mcae	0.20	0.47	0.02	Pann		0.08		Cpil	0.10	0.24	0.15
Dces			0.03	Dfle	0.96		0.02	Cpil	0.02			Dces	0.09	1.17	0.15
Hspl			0.03	Hcup			0.02	Cpan	0.11			Cpan	0.21	0.18	0.13
Lbid			0.02	Hmol	1.51	1.56						Llin	0.15	0.18	0.13
				Llin	0.23	0.39						Cpal		0.04	0.09
				Vcha		0.16						Rrep		0.13	0.05
Lsyl		0.39						Gsax	0.04			Lpra			0.04
Vcha		0.06						Race	0.06			Lbid		0.18	0.04
												Psch			0.02
												Vmyr		0.10	0.01
												Racr			0.01
												Lsyl			0.56
												Vcha			0.04
												Pann			0.01

\* Control 2 plots were not surveyed in 2000 or 2001.

For species code see Species list (Appendix3)