Biological Diversity and Ecosystem Function in Soil

Soil **Biodiversity**

NERC Thematic Programme

Newsletter - Issue number 10

Inside the world of soils: new understanding of soil biodiversity and function

In 1997 the Natural Environment Research Council initiated its £6 million thematic research programme, Biological Diversity and Ecosystem Function in Soils and a large team of scientists rolled up their sleeves to find out more about life in the soil. Now that the Programme is drawing to an end, what have we learned?

The Programme was, we believe, unique in bringing together over 120 researchers to study the soil biota at a single

location. The field site at Sourhope (pronounced 'sirrup'), an upland grassland in the Cheviot Hills of southern Scotland has at times been swarming with activity in an effort to unlock its secrets. By studying the soil ecosystem in details we now facts about so know far more about life below ground than we did before the Programme began, and we have made Sourhope's soil possibly the best-studied in the world.

It is impossible in a single article to cover all the studies that have been undertaken in the Bateria mar Cereal bar Programme, but we've tried to pick out some of deartonic to holiday the major findings. All the projects have contributed to deepening our understanding of the soil ecosystem at Sourhope, and all have yielded important outputs in the form of published

papers.

New ways to study diversity Scientists have long known that soils teem with life. Bacteria, protozoa, fungi, nematodes, springtails, mites, worms, slugs and beetles are just some of the taxonomic groups that coexist in the soil and on its surface.

They interact in a complex food web with different groups of organisms performing different functional roles, such as herbivores, predators or decomposers. Unravelling these complex interactions is a scientific challenge, but doing so allows us to better understand how soils behave. For example, understanding the role of soil biology in controlling carbon flow from the atmospheric carbon dioxide pool through plants and into the soil allows us to develop better predictions of the soil response to climate change.

An important step in studying the below-ground biota is to determine the actual diversity of key functional groups of organisms; unless we know what it is there we cannot properly study their functions. To get a handle on soil

Website: http://soilbio.nerc.ac.uk



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biodiversity at Sourhope we have used both traditional field ecology and taxonomic methods as well as novel molecular techniques.

For larger organisms such as slugs and earthworms it is relatively easy to sample the soil and produce a catalogue of the species present. However, for microorganisms such as bacteria, the task is much more difficult. A range of techniques has been developed to determine the diversity of bacteria, protozoa and fungi. For example, we have developed a molecular method for more rapidly determining the diversity of nematodes in soil samples. The approach

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uses the sequence of a small fragment of a nematode gene. Each individual is classified into a Molecular Operational Taxonomic Unit (MOTU) based on this sequence. These MOTU compare well to recognized species determined by traditional taxonomy and thus the sequence is a kind of 'molecular barcode', allowing rapid taxonomic classification of nematodes.

We have also developed molecular approaches for determining how microbial diversity relates to functional diversity. Thus, not only do we know more about the diversity of Sourhope's soil, but we also have improved the techniques available for analysing other soils.

The Programme has revealed some fascinating aspects of the biological diversity of the Sourhope soil. For example, we have shown that soil organism abundance varies between soil horizons. Move just a few centimetres down through the soil into the next horizon and the range of organisms present will be quite different from the previous horizon. We've also recorded 365 species of a single group of protozoan species living in the soil at the field site. This is about one third of the global diversity of this group (as distinguished by morphology).

Coping with stress

Ecologists have long-recognised that co-existing species occupy different ecological niches, for example, by exhibiting different feeding habits. This means that if the numbers of a given organism, say a predatory mammal, are dramatically altered there is a knock-on impact further down the chain. Is this also the case below ground? What happens when species are removed from the system, or their abundance

continued on page 2

continued from Page 1

or diversity is affected by an applied stress? A number of projects on Sourhope soil have addressed these questions.

One study found that soil microbes are highly resilient to transient stresses. This suggests that there is overlap in functional roles; more than one species is able to perform a single function in soils. However, the situation is not quite so simple. True, some soil organisms appear to be resilient to some applied stresses but the impacts of chronic stresses, such as an elevated concentration of a heavy metal, could be damaging and long-lasting. Research suggests that soil organisms can probably switch activity on and off in response to changes in a stress.

At the Sourhope field site areas of soil were treated in different ways. The treatments applied to plots and subplots included reseeding the sward and additions of either sewage sludge, a biocide, or nitrogen plus lime. Soil from the treated areas did not recover as well from an applied heat stress as that from untreated areas, suggesting that the way in which land is used affects the resilience of soil microbial communities to environmental stress.



Other studies on model soil systems have shown that removing groups of organisms from the soil can have a marked impact on things like grass yield, forage quality and the capacity for the soil to store carbon. This work suggests that changes to soil organism diversity, as a result of environmental pressures, could have profound effects on soil ecosystems that are not readily predictable from previous research.

Tracing carbon

An important component of the Soil Biodiversity Programme has been the study of carbon pathways through the soil ecosystem. Understanding the fate of carbon dioxide absorbed by plants from the atmosphere is important because it can help us determine whether soils act as net sources or sinks of carbon dioxide, the main greenhouse gas. This knowledge allows us to determine under what circumstances a soil may switch from being a sink to a source of carbon. Such information is needed to refine models that are used to predict the extent and magnitude of climate change.

Studies at Sourhope have shown that carbon taken up by plants is transferred in a matter of hours to the soil in the form of root exudates. This carbon is rapidly available to a wide range of organisms including bacteria, protozoa, collembola, mites, enchytraeids, nematodes and earthworms. Some of these were previously thought of as detritivores; clearly soil food webs need to be rethought in the light of these results.

Arbuscular-mycorrhizal (AM) fungi are a key link in the transfer of recent root carbon from plant to soil biota, and an ingenious study at Sourhope showed that removal of

the hyphae greatly reduced this carbon transfer. Another study has shown that the AM fungal community at Sourhope is very diverse. The fungal species clearly exhibit differing host-plant preferences as well as different responses to applied changes.



The larger soil biota are crucial in processing older soil carbon; 90% of soil organic matter had been ingested and excreted by earthworms or enchytraeid worms. However, smaller organisms such as collembola and nematodes were responsible for processing more recently exuded carbon from plant roots. Several studies in the Programme looked at Sourhope's worms. Earthworms are important because they effectively 'churn up' the soil they inhabit, making the carbon they process more readily available to other organisms.



Enchytraeid worm

Another kind of worm, the pot worms or enchytraeids has also been studied at Sourhope. Distinct functional groups of enchytraeids have been identified at the site. These process carbon at differing rates. Furthermore, land improvement by nitrogen fertilisation and liming changes the balance between functional groups with impacts on carbon cycling.



Soil coring at Sourhope

Modelling Soil Biodiversity

In January 2003 a group from York and Cambridge set forth to synthesise the results of the Soil Biodiversity Programme into a theoretical framework and a computer model. The result is called SIM (Stable Isotope Model).

SIM uses well known food web methodology (Hunt *et al.* 1987) which assumes biomasses are constant, and infers flow through a food web by a series of simple carbon balances based on knowledge of the organisms' production and assimilation efficiencies and feeding preferences. The key advance is the incorporation of stable isotope dynamics into this static setting; this leads to a set of linear differential equations which can be solved numerically, but which also allow analytical progress in identifying the key carbon flows within the web. The model's output can then be validated against detailed pulse data from the Soil Biodiversity Programme, rather than simply validating against the global carbon budget of the system (Berg *et al.* 2001).



Workshop

In July 2003 the leafy glades of York were filled with a volatile mixture of applied soil scientists, soil biologists and mathematicians. The aims of this five day hands-on workshop were:

- to elicit feedback on the software from potential end users,
- to develop a consensus of what the Sourhope food web should look like, with validation against stable isotope pulse data,
- to address the most pressing theoretical limitations of the model.

The enforced interdisciplinary atmosphere was surprisingly productive; concrete progress was made, with the potential for ongoing collaborations and publications. A follow-up meeting in December consolidated this progress.

Model development

The July workshop showed that the model was highly sensitive to the values of production efficiencies for each group of organisms. Reduction of detrital feeding preferences dramatically changed the movement of the ¹³C pulse through the biota, producing far more realistic dynamics. Amendment of linkages using expert

knowledge of trophic interactions at Sourhope produced a ¹³C labelling sequence similar to that observed in field studies.

Following the recommendations arising from the workshop, a graphical user interface for the SIM model has been developed. This allows users to view and manipulate the soil food web at the click of a mouse. Output is displayed graphically, in a number of user-selectable ways e.g. pulse data can be shown as changes in ¹³C or concentration values. A command-line driven version of SIM is also available for users wishing to implement batch-mode simulations e.g. for comprehensive sensitivity analyses.

Theoretical advances

Adam Kleczkowski and Chris Gilligan at Cambridge are working to simplify, and then to generalise, the model using the eigensystem of the stable isotope pulse dynamics to identify its key components and pathways.

This simplification allows progress in quantifying the consequences of heterogeneity (spatial and temporal) and connectivity within the soil, using recently developed theories of quenched disequilibrium borrowed from theoretical physics.

The July workshop produced new theory to track stable isotope pulses in non-equilibrium (and therefore more realistic) food webs. Simulations show that oscillatory or chaotic population dynamics can have a massive effect on the observed fate of the pulse, warning that the limited replications and coarse temporal resolution of most stable isotope experiments might be insufficient to give a reliable picture of carbon dynamics. Fortunately (and to the profound disappointment of the mathematicians involved) when a simple five compartment oscillatory model is parametrised using Sourhope data, the low amplitude and high frequency of any oscillations are insufficient to perturb the isotope fluxes to any degree from those derived from a static model. Put simply, the Hunt modelling framework and its implementation in SIM seems to be

appropriate for Sourhope.

Future developments

We hope that this short project has made useful progress in understanding the impact of biodiversity at a functional level, and that its outputs will be carried forward into future theoretical and experimental work. We propose that future research should focus on the importance of spatial heterogeneity and connectivity, and of microbial diversity, and their impact on overall carbon flux.

Jon Pitchford, University of York

Berg, M., de Ruiter, P. C., Didden, W. A. M., Jansen, M. P. M., Schouten, A. J. and Verhoef, H. A. (2001) Community food web, decomposition and nitrogen mineralisationin a stratified Scots pine forest soil. Oikos 94:130-142.

Hunt, H. W., Coleman, D.C., Ingham E. R., Ingham R. E., Elliott, E. T., Moore, J. C., Rose, R. C. and Morely, C. R. (1987) The detrital foodweb in a shortgrass prairie, Biology and Fertility of Soils 3: 57-68.

SIM can be downloaded from:

www-users.york.ac.uk/~kh25/SIM

select 'SIMinst.exe'

3

Insect root herbivores, plants and microbes

Despite the fact that root-feeding invertebrates are a major component of the soil biota in grassland ecosystems little is known of their role in ecosystem functioning. In a study at Sourhope we monitored population changes in the major root herbivores at the site *Tipula paludosa*, (Diptera; Tipulidae,) and cutworms (*Agrotis* spp., Lepidoptera; Noctuidae.) in the Control (C), Nitrogen and Lime (NL) and Pesticide (P) treatments over a three year period. The regular application of the insecticide Chlorpyrifos (Dursban 4, Dow agrochemicals) reduced the *Tipula* and cutworm populations after the first summer.

There were no treatment differences between the C and NL plots. However, what was interesting was a switch in species dominance of the main root feeding species. At the outset of the study the most abundant were the Tipulids with populations in the order of 120 m^2 . Over time their numbers declined to zero in the C plots. Conversely, the populations of the *Agrotis* spp. increased with time from zero in the first year to around 80 m⁻² by March 2002 (Figure 1).

Both species have annual life-cycles and it appears that the change in the management at the field site from fairly lax grazing by sheep and goats, to a more intensive cutting regime influenced the recolonisation of the site in the second and third years. The Tipula prefer to lay eggs under the longer herbage available under the grazing regime located outside the fenced experimental area, whereas cutworms prefer to lay eggs in the shorter mown grass in the plot area. However, although there was a change in the dominant species, the function was maintained. There were no treatment differences (but there were temporal differences) in root turnover between the C and NL plots, but root turnover was significantly reduced in the P treatment, reflecting the reduced pressure on the plants from root herbivory by insects.

In addition to the more obvious impact of root herbivory (i.e. removal of plant tissue) root feeding has a number of other more subtle effects, both on the plant and on other members of the soil community.



Figure 1. Relative populations of insect root feeders in Contol plots at Sourhope from June 1999 to March 2002 (March 2001 was not sampled due to Foot & Mouth Disease regulations).



Figure 2. Canonical variates of metabolic profiles (Community Level Physiological Profiles, CLPP) of soil microbial communities under three plant species with and without *Tipula* spp. larvae present.

The detachment of large quantities of root material puts severe pressure on the plants and demands reallocation of resources for root maintenance and replacement. This is important in determining the fitness of individual plants with implications for plant diversity. Plant species richness was greater in the P plots than in the C plots and this may be a consequence of the removal of the root herbivores, particularly as the overall numbers of the major above ground herbivores (slugs) were not reduced by the pesticide. The removal of large amounts of plant tissue by root herbivores increases the inputs to the detrital pool in the soil and provides an energy source for the soil micro-organisms.

The soil microbial community is also influenced by changes in root exudation patterns, mediated by root feeding. This was demonstrated in a series of microcosm experiments, where changes in soil microbial communities were determined when *Tipula* were feeding on different grass species, either *Agrostis capillaris, Lolium perenne* or *Trifolium repens* (Figure 2).

This project highlights the effects of root feeding in the Sourhope system and in grassland systems generally. Investigations of plant/ soil interactions are important when considering ecosystem processes, however, it must be remembered that root herbivory is the norm and its effects must always be taken into account in such studies.

Phil Murray, IGER

Linking rhizosphere carbon flow to soil biodiversity- how has our research in the Soil Biodiversity programme addressed this fundamental issue?

Many of the projects in Phase II of the Soil Biodiversity Programme have studied the flow of carbon through the soil ecosystem, making use of a novel mobile facility developed by CEH to deliver pulses of isotopically-labelled carbon dioxide to vegetation and soils at Sourhope. Here one such group of researchers at the University of Aberdeen report on their work.

We are now in the final six months of our two year research programme and at an appropriate stage to report on what inroads we are making with respect to cracking one of the main fundamental issues that constrains our understanding of ecosystem ecology-how does rhizosphere carbon flow relate to soil biodiversity?

Our work complements the research being carried out by our colleagues at CEH Oxford, led by Mark Bailey. We have worked together both in the field and laboratory, successfully overcoming a number of technical problems, to address this key aspect of the Soil Biodiversity Programme.

While soil ecologists have some knowledge of the relationship between some components of carbon flow and soil biodiversity in managed systems, almost nothing is known of natural systems, where carbon flow through the rhizosphere is often from a mixed vegetation community. Recent studies suggest that differences in soil microbial community structure, as a function of above ground species diversity, may be associated solely with the rhizosphere as there is no association between plant and microbial species diversity in bulk soil. This is critical to our understanding of the linkage between carbon flow and rhizosphere microbial diversity and hence to our understanding of fundamental ecosystem processes.

Lack of information to date on how rhizosphere carbon flow relates to the diversity of the soil microorganisms on natural ecosystems, and of the interrelationships between this diversity and carbon cycling processes, has largely resulted from an inability to dissect the components of soil communities in a way that can be related to their competitive sink strength for carbon. The availability and conjunction of isotopic and molecular approaches provide the potential for a breakthrough in linking diversity and function.

Ecosystem function in the form of carbon-cycling pathways can be determined by using an isotope of carbon (¹³C) added to soil-vegetation system in the form of a 'pulse' of labelled carbon dioxide (¹³CO₂). It is possible to track the labelled carbon which is 'fixed' by plants into the different soil organic carbon compartments. These compartments include a total soil fraction, following removal of roots, soil microbial biomass and specific, extractable pools (e.g. lipids and nucleic acids). This has been the approach used in our soil biodiversity work based at Sourhope where we have exploited the ¹³CO₂ pulse labelling carried out by CEH (thanks to Nick Ostle and his team at Lancaster) to follow recent photoassimilate from the sward of the limed and unlimed grassland plots. The key to the exercise is stable isotope probing (SIP) to distinguish the phospholipids and nucleic acid pools associated with microbes (fungi and bacteria) which are major sinks for the photoassimilated carbon.

SIP is carried out by extraction of nucleic acids and separation of ¹³C-labelled and ¹²C nucleic acid pools. After

quantifying carbon assimilation by the soil microbial biomass (Figure 1), molecular analysis is carried out using techniques such as Denaturing Gradient Gel Electrophoresis (DGGE; Figure 2), cloning, and sequencing to determine the diversity of the active population. While published applications of this method have amplified DNA, methods are now available for analysis of RNA. This greatly increases sensitivity and is likely to be necessary for detection of active microbial populations where ¹³CO₂ pulses to vegetation are brief and/or involve lower ¹³C enrichments.



Figure 1. Percent (from total assimilated ¹³C by plant-soil system) of ¹³C assimilated as chloroform-labile carbon after pulse labelling of limed and un-limed grassland plots with ¹³CO₂

The data in figure 1 highlight in particular the rapid soil microbial assimilation of root-released photoassimilate and the increased turnover of carbon in upland, acid organic soils following lime treatment.

The DGGE gels that are now being generated from ¹³C enriched from the Sourhope nucleic acid pool point towards an exciting final six months in the laboratory where we



¹³C RNA

¹²C RNA

Figure 2. Section of DGGE gel profiles generated from ¹³C and ¹²C RNA derived from Sourhope soil amended with ¹³C-CO₂. Each zone is composed of fractions obtained from an equilibrium density gradient loaded with RNA derived from pulse labelled soil samples in the field.

can now achieve our goal of addressing the issue targeted in our research programme. For the first time, we will identify microbial groups which are the active sinks for the rhizosphere carbon flow in UK upland grass ecosystems, establishing a platform for further investigations of the link between rhizosphere carbon flow and soil biodiversity.

Ignacio Rangel Castro, Andy Meharg, Jim Prosser & Ken Killham, University of Aberdeen

Publications resulting from the research to date

Standing, D.E., Rangel Castro, I., Prosser, J.I., Meharg, A. and K. Killham 2003. Rhizosphere carbon flow- a driver of soil biodiversity? Soil Biodiversity, BES Special Publication (In press).

The Soil Biodiversity Database

The Soil Biodiversity Database is an important component of the Programme. From the outset it has been the ambition of the Steering Committee to collate the results of the research into a centrally managed database which could serve both the needs of the Programme's researchers and be a valuable data resource for further work.

Throughout the previous year, datasets from Phase 1 projects have been steadily integrated into the database, which currently holds 70 project datasets. More are expected and research groups are being encouraged to submit their datasets so as to build a comprehensive resource of information from the Programme. Additional data collected at the field site, including soil pH, vegetation biomass, vegetation survey (for 2001 and 2002) and Automatic Weather Station data, have been included in the database. These datasets may also be accessed directly from the Soil Biodiversity web site. During 2004 we will be asking Principle Investigators of Phase 2 projects to submit datasets to the database.

Most sampling and experimentation at the site has taken place in 50 x 50 cm 'cells' within the larger treatment blocks. Detailed records are kept of the use made of each cell, to avoid conflicts. In July 2003, a Site Usage Audit was undertaken.

The audit was based on information stored in the database. It is presented as a site map displaying all the recorded site activity since the start of the Programme and indicating the current status of the soil in each cell. The map gives a good reflection of site usage and plot cell availability for future work. The map can be viewed on the web site.

Despite the intensity with which the site has been studied during the Soil Biodiversity Programme, a surprisingly large number of cells are still available for further research. Any work carried out at the site will continue to be logged (see box).

In order to provide access to the wealth of data collected by researchers in the Programme, a data discovery web application is being developed (first reported in Issue 9 of the Soil Biodiversity newsletter). Work on this has been progressing and a pilot version is planned for release in April 2004. The system is being developed using Microsoft .NET software. The interface will enable users to view information about the projects and the







project outputs. It will also feature a Data Search option which scans the meta-data for selected keywords, or a user specified search string, and displays the meta-data description of Project datasets that meet the search criteria. The physical dataset itself is not shown, as access is restricted to registered users who have requested authorisation to download the data.

A security gateway will be implemented later this year that will permit authorised and licensed users to access the datasets

Although the interface is still in development, the screenshots above show how the system might look. It is anticipated that the final version will be available via the Soil Biodiversity web site (http://soilbio.nerc.ac.uk) by the end of 2004.

Effects of Treatments on Soil Microbes

It doesn't take a trained scientist to see some effects of the applied treatments on the Sourhope field site. Nitrogen or lime treated plots exhibit high yields of lush green biomass, whilst the application of biocide has had a lesser effect on plants and these plots appear similar to the control plots. Whilst the benefits of such practices to farmers are obvious, what is less certain is the impact of these additions on diversity of soil organisms, and the overall ecosystem consequences in terms of carbon storage. We have been addressing these questions by examining the impacts of these treatments on the diversity and activities of soil microbial communities using molecular, physiological and stable isotope techniques. We hypothesised that the physiological and functional activities of microbes would be increased in the nitrogen and lime plots due to greater plant carbon inputs. Furthermore, we predicted that higher plant biomass would impact on the diversity of microbial communities through increased competitive interactions due to greater nutrient availability.

Surprisingly, initial results revealed no overall differences in the quantity of total or active cells between treatments. A possible explanation for this finding may be a "hidden treatment" in the lime and nitrogen plots resulting from the greater plant biomass. Both these treatments had lower soil moisture contents, a factor which will decrease the physiological activity of soil microbes. However, when examining the speed of carbon movement from plants into active soil microbial pools using a 3-day ¹³CO₂ pulse, differences were apparent between the treatments (Figure 1). In particular, RNA extracted from limed soils became more highly enriched in ¹³C over a shorter time period compared to the other plots. Interestingly, the data did not show a corresponding decrease in the ¹³C signal over time, possibly due to microbial utilisation of ¹³C labelled plant material.

To assess whether the changes in microbial community functioning were accompanied by difference in community structure, the extracted RNA was profiled using DGGE. Analysis of profiles revealed that limed soils possessed the most distinct profiles (Figure 2), indicating that the higher pH in these plots may be a critical factor in influencing the diversity and functional activity of microbial communities. Of course there are many unanswered questions. For instance, are the organisms represented

laintaining site usage records

n order to ensure that the site is properly managed nd available for future sampling/experimentation, is very important that visitors to Sourhope continue to d submitted from the Soil Biodiversity web site see http://soilbio.nerc.ac.uk/soilbio/Visit_form.htm formed of all site activity, and the sampling an m, to ensure that this vital information is stored ir database, and made available for reference by re scientists. The forms can be downloaded, ir format, from the web page http://soilbio.nerc.ac.uk bio/coordination-documentation.htm.

Lynne Irvine, CEH Lancaster

in the limed DGGE profiles the ones responsible for the more rapid flow of carbon from the plant to the soil, and are we neglecting the fungal contribution? Also, in quantitative terms what can the data tell us about the effects of the land improvements on the overall biodiversity of soil microbes (increased or reduced)? We are hoping to answer some of these questions through the use of hierarchial and recently developed isotope probing techniques.



Figure 1. ¹³C content of soil RNA before during and after *in*situ ¹³CO₂ pulse labelling (3 day pulse). RNA was extracted, purified and analysed by GC-IRMS to determine ¹³C content. Error bars represent standard errors from analysis of three replicate blocks for each treatment.



Figure 2. Cluster analysis of ¹⁶SrRNA DGGE profiles based on presence/absence of brands.

continued from Page 2

Using what we have learned

The main purpose of the Soil Biodiversity Programme was to better understand the soil ecosystem, and particularly to explore the link between diversity and function. At the same time the results have potential in a number of applications. For example, the results could contribute to the selection of biological indicators of soil quality. This is important at a time when Defra is drawing up a soil strategy for England, similar strategies are being considered in Wales and Scotland and the EU is developing a European soils strategy.

The improved food webs and greater understanding of the functional role of organisms will allow more realistic assessment of the impacts of environmental stresses on carbon and energy flows, and on overall system resilience. For instance, the knowledge of the overall diversity of the soil biota provides the basis for examining the impacts of known and potential contaminants, such as dioxins, on biota and biologically mediated processes.

The information on carbon pathways and flows will help us to better understand the impacts of climate change on carbon turnover in soils and the role of soil biota in the production of carbon dioxide. It will also enable us to target future research on possible methods of increasing carbon sequestration. The improved understanding of the link between soil biology and plant productivity will contribute to the development of sustainable grassland management systems.



The Programme has yielded several new techniques or improved approaches to studying soil biodiversity and function.



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These include new molecular tool-kits, the study of carbon in soil thin sections using laser ablation and the development of mobile laboratories for delivering pulses of isotopically labelled CO_2 to vegetation and soils. Molecular and isotopic techniques have also been combined to allow the identification of functional groupings of soil organisms, and their response to environmental stresses.

The Programme has two other important outputs; the huge amount of data on the Sourhope soil ecosystem is being gathered into a web-based data discovery facility (see page 6), and Programme researchers have worked together to produce a model of carbon fluxes in soil food webs using the knowledge gained from the Sourhope studies.

What next?

There's no doubt we know far more now about the diversity of life in Sourhope's soil than we did in 1997 when the Programme began, and we've shown that there is an incredible diversity of organisms below the surface of what to many may appear an unremarkable patch of grassland, typical of British uplands. So where do we go from here? Well, there is plenty more science to do. We need to build on these results, extending them to other soil types, refining our knowledge and our models of soil food webs and soil carbon dynamics.

We also need to encourage more research at Sourhope. There is plenty of space there to carry out further work, and the site will be managed as a research facility (maintaining the treatments applied during the Programme) at least until 2006. We also need to apply the new techniques and methods developed in the Programme to a wider range of soils. Thankfully, as a result of the Soil Biodiversity Programme we have the trained ecologists ready and able to meet new challenges.

> Andrew Sier, Mike Hornung & Nick Ostle, CEH Lancaster

This will be the final issue of the Soil Biodiversity Newsletter. Many thanks to all those who have contributed.

Issues 1-10 are available in PDF format from the website.

The Soil Biodiversity Programme is also featured in the Spring 2004 issue of *Planet Earth*, published by NERC.