

# *Plants, soils and environment*

**Geoff Squire & Karl Ritz**

*The new structure of the Institute establishes the PSE Division as a major international research group specialising in the science of populations and element fluxes in arable fields. Its main practical aim is to understand and design multi-purpose arable ecosystems that satisfy requirements of food production, environmental safety and wildlife habitat.*

The central theme of research is how the number and type of organisms, their interactions and their spatial and temporal arrangement, give rise to the desired arable systems. The new grouping combines expertise in a wide range of taxonomic and functional groups, notably the primary producers in the mandate crops and arable flora, the omnivores, herbivores and predators among nematodes, insects and mites, and the microbial communities of the soil. Scales of study range over six orders of magnitude from the fine soil pores, through the plant, patch, and field to regional dispersion. Organisms and scales are all examined by methods that seek convergence of approaches within the Division and Institute.

The science base in the Division feeds a portfolio of policy-led research, mainly in areas of environmental risk. From an independent stance, we advise government, industry and the public on GM crops, biodiversity, nitrate pollution in water and other matters of ecological and economic importance. The Division

has continued the rapid expansion of externally funded work established by its component groups, recently winning contracts in soil-root interactions (BBSRC) and ecological risk (DETR). Our understanding of variability in populations and environment has been taken to the market place with computerised decision-support systems - notably the Management Advisory Package for Potatoes (MAPP) and (with nematologists) the Potato Cyst Nematode Model.

The aim of the Division in the next year is to weld the specialisms in its two Units – Soil Plant Dynamics and Vegetation Systems - through shared experiments and innovative mathematical and statistical techniques. Collaboration will be increased with organisations whose remit includes land use and advisory work.

## **Unit of Soil Plant Dynamics**

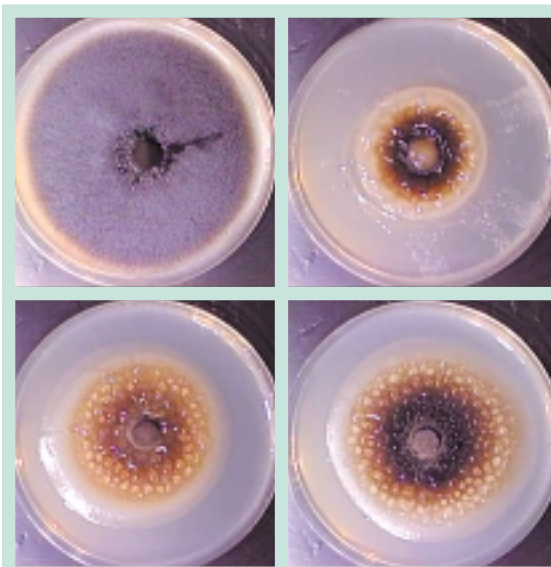
Soil is a difficult and intractable subject for scientific study at the fine scale, yet new experimental and theoretical approaches have enabled great progress in link-

ing biological, physical and chemical aspects of soils. We begin with some examples of fine-scale interactions, then show how the diversity of soil organisms affects the integrity and leakiness of soils at a wide range of scales.

**Volatile-mediated microbial interactions** Soil microbes produce volatile organic compounds (VOCs) that affect the way other microbes function. All of a random selection of over 100 soil bacteria produced VOCs that either stimulated, by up to 35%, or inhibited, by up to 60%, the growth rate of at least one fungal species. Four volatile compounds, 2-propanone, 2-methyl-1-butanol, heptanal and octanal were shown to be effective in the inhibition of basidiomycete growth at concentrations down to ppm levels. Further work showed that altering the amino acid content or concentration in the growth media resulted in significant changes in the VOC output. It might be feasible therefore to manipulate soil systems if the effect of VOCs on the interactions between organisms was better understood. The results are already finding a potential application in the biological control of fungi in order to prevent wood decay and the production of spoilage compounds such as sap-stains (with the University of Abertay Dundee and funding from the EU).

**Spatial organisation of soil communities** The spatial distribution of soil organisms and communities has a strong influence on how they function. At a microscale, organisms may be physically protected by residing in pores that are too small to allow access by larger predators, while an organism's position in the soil fabric relative to the pore network affects the movement of solutes and gases around it. Pioneering studies in the Unit are now enabling us to see soil microbial communities in their natural positions. The technique, described in an accompanying article, involves infiltration of soil cores, staining and thin sectioning to produce maps of biological material preserved within the solid phases and pore network of the original soil.

Communities are also being mapped at much larger size scales. For the first time in the British Isles, the distribution, shape and size of potato cyst nematode (PCN) foci in a previously designated seed potato field were quantified. Six years after the previous seed potato crop, foci of nematode populations were distributed in either a north/south or east/west direction, suggesting secondary spread had occurred due to cultivation in these directions. An individual focus measured approximately 30m in diameter. Future work will aim at confirming the above findings in other fields and devising optimum sampling strategies to detect early infestations of PCN in seed potato land. Similarly, the spatial distributions of both the New Zealand flatworm and earthworms within the same field have also been studied for the first time in the UK. Flatworms were confined to within 70-80 metres of the perimeter of the field where they had a statistically significant negative effect on the earthworm population. Future work will follow the progress of the infection in that field, and investigate the impact of temperature, soil moisture and availability of earthworms on the population dynamics of the flatworm.



Effect of VOCs derived from different bacteria on growth and morphology of the fungus *Sclerophoma pityophila*. Top left plate is the control.

**Root caps fuel the rhizosphere** Decaying roots and shoots provide the greatest input of carbon to soil, but the loss of substances from living root material is far from insignificant. The sloughing of border cells and exudation of mucilage from root tips make it easier for roots to penetrate compacted soils. Border cells can remain living in the rhizosphere for a week or more, and act as a source of carbon compounds to soil microorganisms. They might also act as 'decoys' for plant pathogens. We quantified the rate of sloughing of root cap cells in sand that was compacted to create mechanical impedance to root

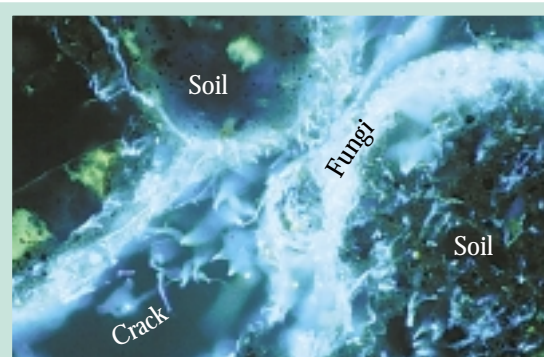
growth. This is the first time that border cell production has been quantified in a realistically abrasive medium. The number of root cap cells sloughed into sand increased twelve-fold as a result of compaction - from 60 to more than 700 per mm of root extension.

The whole of the cap surface area was covered with detached cells in compacted sand, compared with about 7% of the surface area in loose sand. This lubricating layer of border cells and mucilage still accounted for less than 10% of the total carbon deposited in the rhizosphere by living roots, the majority of carbon being contained in mucilage exudates elsewhere in the root system. The work was performed in a collaborative project between SCRI, IACR Long Ashton, and Nagoya University, Japan, and is continuing with the aid of a Royal Society Collaborative Research Grant and the addition of Tokyo University to the group.

**Soil community structure and resilience** The resilience of an ecosystem is a measure of whether and how fast it returns to its initial state after being disturbed. Measurements of the resilience of soil processes to persistent and transient stresses have confirmed the potential usefulness of resilience as an assay for 'soil health'. More specifically, a measure of resilience enables us examine how a microbial community's composition affects the processes that go on in soils. Comparisons were made of industrially polluted and non-polluted soils, and of intensively and organically managed agricultural soils. Standard biological indicators (protozoan populations, which are sensitive to environmental disturbance) and substrate utilisation kinetics (how well the soils use different substrates) could not distinguish the compromised soils. In contrast, resilience was a promising discriminator of the biological status of the soils. The accompanying article summarises recent developments. We are now examining the links between soil physical and biological resilience, the comparative resilience of soils to different stresses, and the effects of microbial diversity on resilience (NERC funding, in collaboration with the University of Aberdeen).

**Soil structural integrity** Arable soils need specific properties if they are to maintain their stability under repeated disturbance. Their fine structure should be undamaged when wetted, yet they should drain freely and not develop large cracks when dry. We are studying the biological processes that influence the ability of soils to buffer water absorption by their fine struc-

ture (water repellency) and so maintain cohesion under stress. As in other studies on soil, progress has been limited by being unable to measure at a fine enough scale. Now, a probe developed at SCRI is capable of measuring water repellency at the scale of a few millimeters. The measurement technique is based on soil transport properties that can be used directly to assess water flow in structured soil. The probe has shown that many British soils have low water repellency, and that the level of repellency diminishes if soil is disturbed and depleted of nutrients by intensive cultivation. A model study of soil structural genesis in the rhizosphere has shown that enhanced aggregation is a product of not only stronger interparticle bonds but also of higher levels of water repellency caused by root mucilage. Although cracking is one of the major processes in the structural genesis of soil, the physical conditions required for cracking to occur are poorly understood. We have adopted state-of-the-art approaches from fundamental fracture mechanics research to describe ductile crack growth in soil. This approach is now being used to assess how the biological properties of soil will affect cracking and hence soil structural genesis.



Thin section of soil showing fungi proliferating through a crack in soil.

**Nitrogen cycling in arable soils** Soil nitrogen is present as several different compounds, both inorganic (ammonium, nitrate and nitrite) and organic. Most chemical transformations in the N cycle are carried out by the action of soil organisms in a complex interdependent network of biological processes. A key compound in the N cycle is nitrate, which is important as a supply of N to plants and as a pollutant in ground and surface waters.

Soil nitrate can derive from fertilizer, but large quantities are also generated by the oxidation of ammonium, a process carried out predominantly by autotrophic soil bacteria. An important uncertainty is the large spatial and temporal variation in the rate at which nitrate is produced. Possible explanations have included variation in the distribution of bacterial nitrifier populations, in the sources of  $\text{NH}_4^+\text{-N}$  or in the substrates that the bacteria live on. We have examined these possibilities using an experimental protocol - the augmented nitrification assay - devised at SCRI. Briefly, a number of different carbon and

nitrogen compounds were added to soils during short term incubations in the laboratory at concentrations ranging from those that prevail in root exudates (very low concentration) to those previously determined as optimal for heterotrophic respiration. In many instances, the addition of a C-containing compound at a low concentration, including pure amino acids, resulted in significant increases in potential nitrification, often more so than corresponding effects at high concentration. These concentrations suggest a mode of action operating at a 'signal' rather than 'substrate' level. The findings suggest that stages within the nitrogen cycle are not simply determined by gross amounts of microbes, sources of N or substrates, but may be more interdependent and interlinked by subtle interactions than previously thought. The study indicates the potential for manipulation of biogeochemical nitrogen transformations by changing cultural and management practices.

Further detailed knowledge of N-cycling events at fine temporal resolution on a field scale was obtained from use of the natural abundance levels of the stable isotopes of N ( $\delta^{15}\text{N}$ ). Most chemical and biochemical transformations of N are accompanied by changes in the isotopic composition of both the substrate N and its product N. Work at SCRI aims to characterise the processes isotopically and use the resulting knowledge to model N transformations and pathways at a high temporal resolution in the field. The first step in achieving this has been to devise new chemical methods for isolating the target N pools from soil solutions, existing methods being inadequate for use with  $\delta^{15}\text{N}$ . We have developed a compound-specific technique that allows us to determine the  $\delta^{15}\text{N}$  of nitrate in soil solution, and in eutrophic and marine waters. The new method has been used with success in arable soils for 2 years and is revealing much new information about the generation of nitrate in these soils and the periods in which the system purges itself of excess nitrate through gaseous loss of N. The results of this work have potentially profound implications for the efficient use of fertiliser and the sustainability of agriculture.

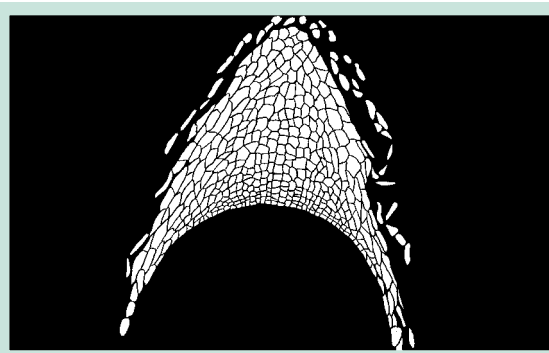
**Plant-soil interactions at the intra-specific level** The basis for plant biodiversity within species resides in the

functional life form and the genotype. The long-term goal of work in this area is to connect functional performance, through for instance a physiological indicator, to molecular information on a plant's genome. Progress was made with the realisation that the natural abundances of the stable isotopes of N ( $\delta^{15}\text{N}$ ) and C ( $\delta^{13}\text{C}$ ) could be used as indicators of plants' physiologies that discriminated their performances in nature.  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  are used alongside traditional plant physiological techniques,  $\delta^{15}\text{N}$  pointing to variations in the plants' N relationships, and  $\delta^{13}\text{C}$  to variations in the plants' C, water and N relations as well as indicating anatomical and structural differences. We can now assess and interpret variations in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  against a growing body of knowledge, much of which was pioneered at SCRI. We have now shown that while  $\delta^{13}\text{C}$  mainly reports on the conditions under which the plant gains and sequesters C, including the type of N nutrition,  $\delta^{15}\text{N}$  mainly reports on the conditions under which

plants lose N. Most of the N loss, and much of the C loss, is through the roots to the soil. As described above, such losses are a rich source of nutrition sustaining soil microbial communities. New work will continue to emphasise the functional diversity in the barley genome and investigate the chemical types and isotopic signatures of N lost from wild plant genotypes and life-forms, collected from English

chalk grasslands and investigated in collaboration with researchers at Sheffield University.

**Moving up a scale: soil heterogeneity in relation to transport processes and root uptake** The movement of pollutants to water is one of several issues that have to be considered on a scale much beyond the single field. Water quality is a topic of great public concern, and subject to increasingly strict environmental regulations. The concentrations of pollutants, including fertilizers, pesticides, and microbial organisms, in stream water are determined largely by farming practices and by the adsorption and desorption of chemicals as rain water percolates through the soil. Computer simulations are often used for predicting pollutant concentrations in stream water, but assume that soil has largely homogeneous transport properties – they ignore the fact that soil structure channels



Border cells detaching from maize root cap.



much of the flow through small fractions of the soil pore space. Therefore, to gain a more realistic appreciation of this complex subject, SCRI, with MLURI and Aberdeen University, are studying the effect of soil structure on solute transport processes at scales ranging from the individual soil pore (1  $\mu\text{m}$  or smaller) to that of a sub-catchment (1  $\text{km}^2$ ). The approach is to use detailed mathematical theory to generate hypotheses that can be tested experimentally at scales of the soil core, lysimeter, and field plot. So far, mechanistic models have been constructed of liquid flow and solute transport through complex three-dimensional fractal structures, which have transport properties that can be related to those of real soils, at the core scale. Input and test data are provided by experimental work at the project's contrasting test-sites at a low-input, upland sub-catchment near Aboyne, and an intensive lowland farm in the Ythan catchment. Geostatistical analyses of soil physical and chemical properties are used to identify the pattern of spatial variability at scales of 10 cm to 1 km. The advanced theoretical science in the project shows excellent promise for application to many problems, such as the relations between root uptake and soil structure, and the impact of soil structure on pollutant flow in soils.

## Unit of Vegetation Systems

The Unit examines the links between plant process, the structure and composition of vegetation, and the invertebrates that feed off and live in it. Given the great range of potential animal and plant subjects, the work seeks generic methods that can be applied to the Institute's mandate vegetation systems and more widely. Its broader practical aim is to help devise more efficient, integrated strategies for managing weeds and insect pests, which impose by far the costliest burden on crop protection.

**The relation between trait and community** Agricultural plant communities are repeatedly challenged by new crop varieties, by new weeds and by a range of management interventions, all of which act through the physiological traits that link a plant with its environment. Our main aim is to understand the links between trait and community so as to answer questions of two general types: how does an introduced trait, in a new crop cultivar for example, influence the composition of the arable community; and what combinations of traits and individuals can coexist in communities constrained by climate or management? The central theme taken to study these links is the expression of physiological trait space within real physical

space. Trait space is the many-dimensional, abstract space formed by the axes of botanical characters. While plants can be defined in this abstract space, they compete and otherwise interact through a physical, heterogeneous resource in a field. Progress has been made in defining trait space *ex situ* for both arable seedbanks and species-rich grassland (the latter with BioSS, MLURI and SAC in a SERAD FF project). The arable seedbank has been examined as sources of both weeds and floristic diversity, for which characteristics of germination and dormancy have received particular attention, since they determine seasonal growth cycles and longevity. A review of rate-temperature curves and secondary dormancy in the flora has been undertaken using data supplied mostly by external collaborators, the main finding being that germination in crops, weeds and wild species could be characterised by the same few parameters. Attention was then directed at germination and dormancy in feral oilseed rape, which is now an important member of the seedbank and a recipient of gene flow from new crop varieties. Seed lots and populations of oilseed rape were examined by statistical and molecular techniques that quantified the genetically based variability in germination.

Examination of the botanical trait space becomes exceedingly complicated as populations advance through their life cycle. As a way of understanding this, we have developed unique models that link plant traits and communities. The most important advance is a spatially explicit model based on real physiological processes rather than the simple decision rules that form the basis of most alternative approaches. Methods have been found to incorporate data on trait space and, from there, to show that wide-scale ecological metrics such as the species-abundance relation might exist on a small scale within populations. This conceptual framework is a particularly important achievement, since it enables us to transfer ideas between populations and ecosystems, to set up hypotheses that can be tested quantitatively in the field and ultimately, to incorporate further trophic layers. The developments are described in one of the accompanying articles.

**Tri-trophic systems** Biotechnology has the potential to provide new forms of pest control. It is possible to modify plants to express certain antifeedants which will either retard insect pest development or have a more harmful effect on the pest. Higher yield and the use of fewer chemicals might result. There are, however, potential side effects in that the pest might adapt to the toxin, and the toxin might be transmitted

through the food web to cause harm to insects that eat the pest. The potential for both side-effects is being examined by a mathematical approach to plant-pest-predator interactions (MAFF funding). A version of the Lotka-Volterra predator-prey model has been modified to explore the rate of adaptation of a herbivore to a transgenic crop, which has insect resistance determined by an allele at a single locus. The model accounts for the different palatability of the plant genotypes and for factors in the pest's life cycle. The model has been extended to consider the primary producer, herbivore and predator as three layers that interact through the transmission of food and toxin. The rate at which pests and their predators grow and move out from foci depends on the nutritional supply and architectural traits of the vegetation, while analysis of the physiological trade-offs between production and defence in plants provides potentially valuable guidance for plant improvement and habitat creation. The model will henceforth be fully integrated with the Unit's experimental programme, which has now tested prototype experimental systems for barley, oilseed rape and raspberry crops containing weeds and feral plants.

**Ecological risk and benefit of GM technology** Many of the Unit's skills have been brought to bear on the issue of GM risk assessment. The basis for GM technology is the introduction of a gene into a plant. The gene itself is not going to have any direct consequences on the environment. Instead it is the gene product, in most cases a protein, which is responsible for the direct physical effects of a gene or its phenotype. It is therefore important to understand the potential interactions of the gene products which are being considered for use in GM technology. In 1999, we were involved in a study to determine if the prospective anti-insect, toxin protein from the snow drop (GNA lectin) could interact with human white blood cells. The findings did indeed confirm that a number of human white blood cell glycoproteins (sugars linked to proteins) reacted with the toxin. It is highly likely that these interactions involve surface receptors, which are also part of the process of cell division. However, this research has ended and it has not been possible to identify these human receptors. These binding properties are consistent with the known activities of many other naturally occurring lectins in plants such as peas, beans, onions and leeks. The full consequences of these lectin molecules in diets is still not understood and they are likely to depend on many factors including digestibility,

uptake rates and the surface molecules with which they finally interact. The snow drop toxin is not part of any food plant and more independent research is required before it could ever be considered.

### **Impact of GM technology on farmland biodiversity**

Research on gene flow and plant demography in arable systems has continued on several fronts. In particular, progress has been made on factors that determine life cycle biology in feral oilseed rape and other weeds. A synthesis of seedbank records showed that feral brassicas (probably oilseed rape) decayed rapidly for a year or two after seed deposition, but thereafter existed at frequencies typically several hundred per square metre of soil down to plough depth. These are small frequencies compared to the seedbanks of many weeds, which can number in the 10,000s per square metre, but confirm persistence over several years. We then developed a life cycle model of feral oilseed rape that is based on physiological responses and driven by events in the arable calendar, such as cultivation and application of herbicide (MAFF funding). Given that many of the input variables are naturally stochastic, the model will be used to generate probability distributions of certain outcomes, such as specified percentages of mixing in seed or seedlings. The work is collaborative with CSL, York, who will help to implement its use in a range of experiments (e.g. the BRIGHT trials) and industrial applications.

The government's Farm Scale Evaluations of GM Crops, carried out jointly with the Centre for Ecology and Hydrology (CEH) and the Institute for Arable Crops Research (IACR), entered the first year of the scale-up phase (funding from DETR/MAFF/SERAD). The experimental protocols devised in the previous year were applied at farm sites to compare the effects of GM and conventional technology on plant and invertebrate diversity. Each partner has responsibility for one of the crops, certain experimental protocols and for measurements at farm sites near to the respective organisation. The work is tightly co-ordinated, the partner organisations having effectively combined their resources to tackle this major issue at a national scale. Nevertheless, these experiments are highly contentious and several experimental sites were damaged by people and groups opposed to them. The work has brought staff at SCRI into direct and regular contact with farmers, elected members of government, the industry and a range of other interests. The results of the evaluations will be complete in 2002 to 2003.