ABSTRACTS OF COMMUNICATIONS

Proceedings of the Twenty-Fifth Meeting of the Agricultural Research Modellers' Group

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This group, which is concerned with the applications of mathematics to agricultural science, is sponsored by the Biotechnology and Biological Sciences Research Council. It was formed in 1970, and has since met at approximately yearly intervals in London for one-day meetings. The twenty-fifth meeting of the group, chaired by Dr T. M. Addiscott of the Institute of Arable Crops Research, Rothamsted Experimental Station, was held in the Wellcome Meeting Room at the Royal Society, 6 Carlton House Terrace, London on Friday, 15 April 1994, when the following papers were read.

Concentration fluctuations of particulates in turbulent flows. A. M. REYNOLDS. *Silsoe Research Institute, Wrest Park, Silsoe, Bedford MK45 4HS, UK*
Much progress has been made in understanding many of the properties of particulates dispersing in turbulent flows. Among the fundamental problems that remain, however, is an understanding of particulate concentration fluctuations. Such an understanding is essential to the prediction of many agricultural situations, including the toxic effects of certain airborne substances, malodour perception, dust concentrations within livestock buildings and the coagulation of droplets from crop sprayers.

Particulate concentration fluctuations were investigated numerically using simulations of turbulence. It was necessary only to simulate turbulence kinematically as the turbulent dispersion of particulates is insensitive to the dynamics of turbulence (Batchelor 1953). Following Fung *et al.* (1992), isotropic homogeneous turbulence was simulated kinematically using random Fourier modes. The modes were chosen so that the turbulent velocity field was incompressible and so that the wavenumber–energy spectrum had the experimentally observed form (Kolmogorov form). Pairs of particulates were tracked, by numerically integrating their equations of motion, to obtain two-particle Lagrangian statistics. These statistics were then used to obtain the statistics of particulate concentration fluctuations.

The effects of particulate inertia and particulate drift velocity (resulting from body forces, typically gravity) on particulate concentration fluctuations were studied separately. Particulate concentration fluctuations were found to decay to zero with increasing time, with those of light particulates decaying more rapidly than those of heavy particulates. Particulate drift velocity was found to reduce turbulent mixing unequally in directions parallel and normal to the drift direction thereby making concentration fluctuations more persistent than those of non-drifting particulates. These effects were found to become more pronounced with increasing Reynolds number.

Standard models for particulates dispersing in turbulent flows predict only mean particulate concentrations. Research in progress is attempting to use the results presented here to construct a model of particulate concentration fluctuations.

BATCHELOR, G. K. (1953). The theory of homogeneous turbulence. *Cambridge Science Classics*.
FUNG, J. C. H., HUNT, J. C. R., MALIK, N. A. & PERKINS, R. J. (1992). Kinematic simulation of homogeneous turbulence by unsteady random Fourier modes. *Journal of Fluid Mechanics* **236**, 281–318.

Estimation of the distribution of protozoa in the rumen by linear programming. J. DIJKSTRA AND J. FRANCE. *Institute of Grassland and Environmental Research, North Wyke Research Station, Okehampton, Devon EX20 2SB, UK*
Ciliate protozoa in the reticulo-rumen associate with fresh rumen digesta (Orpin 1985) or the reticulo-rumen wall (Abe & Iriki 1989), presumably in order to allow their survival in this organ. However, unlike the numbers of protozoa in the rumen liquid phase, the numbers or biomass of protozoa not in the liquid

phase remain largely unknown. In this paper, a linear programming model is presented to estimate the proportion of protozoa in both the liquid and non-liquid phase in the reticulo-rumen, and some preliminary results are given.

A compartmental scheme was adopted to represent rumen protozoa, with two differential equations describing the system dynamics. The two state variables P_1 and P_2 denote protozoal biomass in the liquid phase and the non-liquid phase respectively. In each phase, growth, death and outflow from the rumen are represented, as well as exchange of protozoa between the phases. All these processes are assumed to be first order. Addition of appropriate slack variables allows the equations to equal to zero. The objective function Z denotes the deviation from steady state, calculated as the sum of the slack variables. Minimization of Z is undertaken by imposing a number of linear constraints on the rate constants and multipliers, based on observations on protozoal dynamics *in vitro* or *in vivo*. A general linear programming package is used to solve the model.

Four diets (high roughage or high concentrate diets fed at low or high intake levels) were simulated and the overall fractional growth rate of protozoa assigned values of 0·02, 0·04 or 0·06 per hour. The solutions for the possible range of protozoal biomass in each phase were obtained by minimizing Z, giving a minimum of Z equals zero (i.e. steady state). The solutions indicate a lower limit of *c*. 5% for P_1 in line with experimental results (Orpin 1985). This proportion is higher (up to 15%) when the fractional growth rate is increased, reflecting the shift in protozoal species and their properties (Williams & Coleman 1992). At the lowest fractional growth rate, an upper limit for P_1 of between 41 and 87% was obtained, whereas at the highest fractional growth rate, the protozoal biomass could be entirely in the liquid phase. The upper limit for P_1 is lower when liquid outflow rates are increased (i.e. on high roughage diets or high intake levels), because a high degree of attachment is necessary in order to avoid a too rapid passage with the liquid phase. The sensitivity of the solutions to perturbations in the constraints will be examined in future work.

ABE, M. & IRIKI, T. (1989). Mechanism whereby holotrich ciliates are retained in the reticulo-rumen of cattle. *British Journal of Nutrition* **62**, 579–587.

ORPIN, C. G. (1985). Association of rumen ciliate populations with plant particles *in vitro*. *Microbial Ecology* **11**, 59–69.

WILLIAMS, A. G. & COLEMAN, G. S. (1992). *The Rumen Protozoa*. New York: Springer-Verlag.

A mathematical model for chemotactic movement and aggregation in cellular slime moulds. T. HÖFER[1], P. K. MAINI[1] AND J. A. SHERRATT[2]. [1] *Centre for Mathematical Biology, Mathematical Institute, Oxford OX1 3LB, UK*, [2] *Nonlinear Systems Laboratory, Mathematics Institute, University of Warwick, Coventry CV4 7AL, UK*

The cellular slime mould *Dictyostelium discoideum* (Dd) is a widely studied organism. In starvation conditions, Dd amoebae aggregate into a slug-like body which can crawl some distance before forming a fruiting body. The spores at the top of the body are scattered and amoebae emerge from them to feed in their new environment. Aggregation occurs in response to periodic waves of the chemoattractant cyclic adenosine 3′,5′-monophosphate (cAMP), emanating from the centre of the aggregation territory, which organize waves of cell movement towards the centre. To date, mathematical models focus on the dynamics of cAMP in a homogeneous layer of stationary amoebae and, although they yield a valid description of the cAMP wave phenomena observed at the onset of aggregation, they do not consider cell movement.

Modelling of slime mould chemotaxis has so far been hampered by the 'chemotactic wave paradox'. Briefly, assuming that cells move up gradients of chemoattractant, intuitive considerations suggest that a pulse of chemoattractant will cause cell movement in the direction of the pulse. This is opposite to the observed direction of motion. Recently, it has been shown that the explicit consideration of the adaptation dynamics of cell receptors in response to cAMP can resolve the chemotactic wave paradox in a natural way (Höfer *et al*. 1994).

An integrated mathematical model of slime mould aggregation reflecting the intrinsic coupling between biochemical signalling and evolving cell density patterns is derived by coupling this chemotaxis-adaptation model to a model of the dynamics of cAMP. From simulations of the model, it is found that concentric or spiral waves of cAMP travelling through the cell layer stimulate the formation of a cell stream pattern perpendicular to the direction of wave propagation. The patterns are consistent with those observed experimentally. Variations in the initial cell density lead to a number of experimentally well-documented phenomena concerning the structure of the core region, and the growth rate and wave length of the stream pattern. Such phenomena are also exhibited by the model.

It is concluded that the complex spatio-temporal patterns seen during slime mould aggregation can be explained by a sequence of patterning events arising from the interaction of (excitable) chemoattractant production and diffusion with cell chemotaxis and adaptation.

HÖFER, T., MAINI, P. K., SHERRATT, J. A., CHAPLAIN, M. A. J., CHAUVET, P., METEVIER, D., MONTES, P. C. & MURRAY, J. D. (1994). A resolution of the chemotactic wave paradox. *Applied Mathematical Letters* **7** , 1–5.

The effect of temperature variation on the rates of biological and chemical processes in the environment.

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It is conventional to study rates of reaction at a series of constant temperatures (e.g. Johnson & Thornley 1985), and to relate these rates to temperature via the Arrhenius equation (chemistry: activation energy, k J/mol) or a Q_{10} relationship (biology), both non-linear. However, the temperature in the environment is not constant, but cyclic, with a daily wave superimposed upon an annual wave. This paper examines the effects of such cycling by combining the Arrhenius and Q_{10} relations with a square temperature wave (as might be imposed in an incubator or a growth chamber) and a sine wave (as observed, to a good first approximation, in the atmosphere and the soil) to calculate average rates of reaction over a complete temperature cycle.

The results are startling. The average rate of reaction at a given average temperature is not constant, but increases steeply both as the amplitude of the cycle and as the values of k and Q_{10} increase. This increase is approximately double for a square wave compared to a sine wave, and large. For example, for a Q_{10} of 3, the average reaction rate with an amplitude of 10 K is 1·7 times that at constant temperature, and equivalent to a reaction at a constant temperature almost 5 K higher.

Two implications of the analysis are: (i) experiments at a constant temperature equal to the 'average' temperature gave the wrong answer, delivering rates of reaction that are too small and predictions that are too conservative; (ii) a rise in temperature as a result of global warming will not, other factors being unchanged, necessarily lead to an increase in reaction rates if, for example, an increase in cloudiness causes the amplitude of the temperature wave to decrease (this is important for the evolution of CO_2 from oxidized Arctic peats).

The model explains (i) the failure of attempts to measure average or accumulated temperatures by the inversion of sucrose (Jones 1972), (ii) why seeds germinate faster in fluctuating than at constant temperatures (Harrington 1923), and (iii) why crop models often require different thermal-time sums for completing growth stages or triggering developmental changes when the same crop is planted at different times of the year (see Hanks & Ritchie 1991).

HANKS, J. & RITCHIE, J. T. (Eds) (1991). *Modelling Plant and Soil Systems*. Madison, WI: American Society of Agronomy.

HARRINGTON, G. T. (1923). Use of alternating temperatures in the germination of seeds. *Journal of Agricultural Research* **23**, 293–332.

JOHNSON, I. R. & THORNLEY, J. H. M. (1985). Temperature dependence of plant and crop processes. *Annals of Botany* **55**, 1–24.

JONES, R. J. A. (1972). The measurement of mean temperatures by the sucrose inversion method: a review. *Soils and Fertilizers* **35**, 615–619.

Predictions of the effects of climate and management change on temperate grassland.

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A temperate grassland model based on C and N pools and fluxes (the Hurley pasture model: Thornley & Verberne 1989) has been extended and used to simulate pasture performance and carbon sequestration (C_{seq}) in the plant–soil system under various environmental, management and land-use scenarios.

Multiple-harvest cutting experiments may give positive or negative responses to CO_2 enrichment, depending on conditions.

The model predicts that the 'business-as-usual' scenario for the CO_2 and temperature components of climate change may be neutral in terms of C_{seq}: the effects of the expected CO_2 increase (+3 vpm per annum) and temperature increase (+0·035 °C per annum) cancel each other out.

Steady-state results (obtained by running the model for hundreds of years) provide a tentative ranking for the way in which long-term climate and management parameters affect the amount of carbon sequestered by grassland. The responses of C_{seq}, net annual primary productivity (NAPP), leaf area index (LAI), animal production and leaching to temperature, radiation, ambient CO_2, rainfall, stocking density and fertilizer application have been examined. The results are sometimes counter-intuitive, revealing the complexity of the interactions between atmospheric CO_2 concentration, radiation, sward growth, transpiration, leaching and nitrogen. For example, even in environments as similar as southern (lowland) and northern (upland) Britain, a given change in climate may produce opposite effects on sequestered carbon. Adding fertilizer N may under some conditions reduce N leaching losses and under other conditions increase them.

Some current experimental research programmes, aimed at obtaining quick answers to climate impact questions, are perhaps misdirected, as it appears that reliable predictions of long-term ecosystem responses are not possible without a better physiological/biochemical understanding of the plant–soil system at a level to underpin process-based models, since these are essential to evaluate and extrapolate the results of experimental investigations. In the meantime, models may be giving better indications of the consequences of climate/management change by pointing unambiguously to the complexity and variety of the responses that may be obtained, than may be more directly suggested by limited experimentation.

THORNLEY, J. H. M. & VERBERNE, E. L. J. (1989). A model of nitrogen flows in grassland. *Plant, Cell and Environment* **12**, 863–886.

Modelling the impact of climate change on grass–clover swards. K. TOPP AND C. J. DOYLE. *Department of Economics, Marketing and Management, Scottish Agricultural College, Auchincruive, Ayr KA6 5HW, UK*

It is anticipated that global warming, with the associated increase in temperature and changes in rainfall pattern, will directly affect the production potential of grassland in the UK. Under present climatic conditions, the growth of white clover in spring is poor and the yield is generally inconsistent. This paper outlines the underlying assumptions of a mechanistic model of a grass–clover sward capable of responding to changes in temperature, radiation, rainfall and their associated interactions with soil type. In the model, forage production is calculated on a daily basis and is dependent on the herbage mass, and the available water and nutrients as well as the climatic factors. The grass and clover components are separately distinguished within the model and are divided into leaf stem, root and dead material. The canopy photosynthesis for each component is calculated using a formula derived by Johnson *et al.* (1989) and is dependent on both the grass and clover leaf area indices. As clover tends to predominate in the upper layers of cut grass–clover swards (Woledge *et al.* 1992), the vertical distribution of the sward has to be defined. The effect of water and nutrient stress is incorporated into the model by reducing the gross photosynthesis in proportion to the stress experienced by each crop component. The respiration requirement of each component is divided into the growth and maintenance elements. The respiration requirement is deducted from the gross photosynthate before the assimilate is partitioned between the leaf, stem and root material. Losses, through senescence, offset the production of new leaf and stem material. The senescent material passes into the pool of dead material, where it remains until it decomposes. The model has been used to assess the yields of a grass–clover sward under present climatic conditions and a warmer, wetter climate.

JOHNSON, I. R., PARSONS, A. J. & LUDLOW, M. M. (1989). Modelling photosynthesis in monocultures and mixtures. *Australian Journal of Plant Physiology* **16**, 501–516.

WOLEDGE, J., REYNERI, A., TEWSON, V. & PARSONS, A. J. (1992). The effect of cutting on the proportions of perennial ryegrass and white clover in mixtures. *Grass and Forage Science* **47**, 169–179.

Mathematical modelling of ammonia loss from slurry stores and its effect on *Cryptosporidium* transmission. G. D. RUXTON. *Scottish Agricultural Statistics Service, The King's Buildings (JCMB), Mayfield Road, Edinburgh EH9 3JZ, UK*

Nitrogen loss through ammonia volatilization from slurry is important ecologically and economically. Whilst losses after application have been studied intensively, storage losses have not received such close attention, with the only published model being due to Muck & Steenhuis (1982). This very simple model, using only four parameters, was able to give good predictions of several laboratory experiments. Whilst the model is able to produce predictions of the time course of volatilization, only its prediction of the cumulative loss has been tested against experimental data. Recent experiments (Sommer *et al.* 1993) have produced time series of the rate of volatilization over several months from large scale storage. These data were used to investigate the ability of the model to predict the time course of ammonia loss in the study reported here, and although the model captured the trend of the data qualitatively, it consistently overestimated ammonia loss in the initial period. A modification to the model (at the cost of an extra parameter) improves model performance in this respect.

Cryptosporidium is a protozoan parasite which completes its life cycle in the intestinal and respiratory systems of mammals. Infection causes high mortality in calves and lambs and can also be fatal in humans. The disease is transmitted by oocysts, an environmentally robust stage in the life cycle of *Cryptosporidium*. Infected animals can excrete up to 10^{10} oocysts per gram of solid waste. If consumed, these oocysts can initiate infection, hence there is considerable interest in understanding their likelihood of survival in waste stores, because of their potential for transfer to water catchments after waste application to land. Experiments have suggested that prolonged exposure to ammonia above a critical threshold concentration can render oocysts non-viable (Campbell *et al.* 1982; Sundermann *et al.* 1987; J. Kemp, unpublished). The model, in its modified form, was used to investigate the likelihood of oocyst survival at various depths in a slurry store, demonstrating that survival is highly sensitive to the threshold ammonia concentration assumed. However, if the results of Kemp are used to relate ammonia concentration to oocyst viability, the model predicts that oocysts are unlikely to be able to survive in a slurry store under even the most favourable conditions.

CAMPBELL, I., TZIPORI, S., HUTCHISON, G. & ANGUS, K. W. (1982). Effect of disinfectants on survival of oocysts. *Veterinary Record* **111**, 414–415.

MUCK, R. E. & STEENHUIS, T. S. (1982). Nitrogen losses from manure storages. *Agricultural Wastes* **4**, 41–54.

SOMMER, S. G., CHRISTENSEN, B. T., NIELSEN, N. E. & SCHJØRRING, J. K. (1993). Ammonia volatilization during storage of cattle and pig slurry: effect of surface cover. *Journal of Agricultural Science, Cambridge* **121**, 63–71.

SUNDERMANN, C. A., LINDSAY, D. S. & BLAGBURN, B. L. (1987). Evaluation of disinfectants for ability to kill avian *Cryptosporidium* oocysts. *Companion Animal Practice* **1**, 36–39.

Modelling radiocaesium dynamics in upland farm systems. N. CROUT[1], J. ABSALOM[1], S. YOUNG[1], A. GALER[1], N. BERESFORD[2] AND B. HOWARD[2]. [1] *University of Nottingham, Sutton Bonington Campus, Loughborough, Leicestershire LE12 5RD, UK*, [2] *Institute of Terrestrial Ecology, Merlewood Research Station, Grange-over-Sands, Cumbria LA11 6JU, UK*

There was widespread environmental contamination by Cs-137 and Cs-134 in many areas of western Europe following the Chernobyl accident in April 1986. The main regions affected in the UK were North Wales, North West England and some areas of Scotland. Upland areas within these regions were particularly affected due to localized rainfall. The main land use in the uplands is sheep farming and in some areas the movement of sheep was restricted to prevent contamination of the human food chain. Modelling work has been undertaken, in parallel with experimental and field studies, to improve the understanding of radiocaesium behaviour in these upland farm systems. This has led to the development of a model (RUINS – Radiocaesium Uptake in Natural Systems) which has the following main components:

(i) A description of the soil kinetics of radiocaesium in the acidic, highly organic soils typical of upland regions. The approach used divides the soil into a number of pools with differing availability to plants. Transfers occur between these pools, representing processes of absorption and fixation. Kinetic parameters were obtained by fitting model equations to experimental data.

(ii) The transport of radiocaesium down the soil profile, and out of the rooting zone, by leaching and diffusion.

(iii) The simulation of radiocaesium uptake from the soil by vegetation and its subsequent recycling to the soil via senescence and litterfall.

(iv) The removal of radiocaesium from the sward by grazing sheep, its subsequent metabolism in the animal, and recycling to the soil via excreta.

The principles behind RUINS and its development will be outlined and the main components described. All of the modelling work was undertaken using the simulation software system ModelMaker (SB-Technology 1993).

SB-TECHNOLOGY (1993). *ModelMaker 1.0 User Guide*. Basingstoke: SB-Technology.

Modelling the population dynamics of coccinellids and aphids. D. J. SKIRVIN. *Department of Entomology and Nematology, Institute of Arable Crops Research, Rothamsted Experimental Station, Harpenden, Herts AL5 2JQ, UK*

A model describing the population dynamics of the cereal aphid *Sitobion avenae* (Carter *et al*. 1982) was extended to another model describing the population dynamics of the aphid and its predator *Coccinella septempunctata*. The biological realism of the original model was improved by altering the equations used to describe the development and reproduction of *S. avenae*. For nymphal development, a sigmoid curve relating the development rate of each instar to temperature was used instead of accumulated hour–degrees. Reproduction, which depended only on the hour–degrees for each time step, was assumed to occur between 10 and 30 °C in the original model, with a maximum reproductive rate at 20 °C. This was changed to allow reproduction to occur between 0 and 30 °C, and the reproductive rate was allowed to vary with temperature. Since there was no evidence of curvilinearity, a linear relationship was assumed. These changes resulted in a closer fit to field data for some years, but the modified model was no better than the original in other years.

Representation of the coccinellids consisted of four submodels: development, reproduction, predation and immigration. The development of the larvae was related to temperature by a sigmoid curve and that of the adults was by means of hour–degree accumulation. Reproduction in coccinellids is more complicated with the reproductive rate being related to aphid consumption as well as temperature. Using data from A. F. G. Dixon & Y. Guo (personal communication) and Ghanim *et al*. (1984), a reproductive surface was produced. Predation was based on a temperature-mediated functional response (Mack *et al*. 1981; Mack & Smilowitz 1982) as this incorporates effect of temperature on the time taken to consume an aphid and searching rate. Immigration was calculated from counts of the number of insects in the field, since there is no other accurate way of measuring coccinellid immigration.

Several problems were encountered in the model building exercise, but the most common was the lack of data.

CARTER, N., DIXON, A. F. G. & RABBINGE, R. (1982). *Cereal Aphid Populations: Biology, Simulation and Prediction*. Wageningen: Centre for Agricultural Publishing and Documentation.

GHANIM, A. E. B., FREIER, B. & WETZEL, T. (1984). Zur nahrungaufnahme und eiblage von *Coccinella septempunctata* (L.) bei unterschiedlichem angebot von aphiden der arten *Macrosiphum avenae* (Fabr.) und *Rhopalosiphum padi* (L.). *Archiv für Phytopathologie und Pflanzenschutz* **20**, 117–125.

MACK, T. P., BAJUSZ, B. A., NOLAN, E. S. & SMILOWITZ, Z.

(1981). Development of a temperature-mediated functional response equation. *Environmental Entomology* **10**, 573–579.
MACK, T. P. & SMILOWITZ, Z. (1982). Using a temperature-mediated functional response model to predict the impact of *Coleomegilla maculata* (DeGeer) adults and third-instar larvae on green peach aphids. *Environmental Entomology* **11**, 46–52.

A mechanistic simulation of the action of fungal pathogens, used as an introduction to the underlying mathematical description of crop disease epidemics.

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An appreciation of epidemiological principles is a prerequisite of a comprehensive understanding of the interaction between pathogen and crop populations, but the mathematical nature of epidemiology can be intimidating to many students and might inhibit their intuitive appreciation of the biological processes which govern plant disease epidemics. A potentially useful approach is to introduce the subject, without specific reference to mathematics, through a computer model which simulates the spread of a fungal pathogen. Once a graphical introduction has been concluded, the mathematical description of disease progress becomes more readily understandable by reference to the previously observed spatial and temporal patterns.

An interactive computer simulation model, demonstrating the spread of fungal pathogens in crop populations, has been developed. Taking a series of user-defined values for model parameters, the model presents a graphical summary of the patterns of pathogen spread through a crop population. Disease progress data are fed to an output file, where they can be used as the starting point for a mathematical description of the epidemic.

Despite having been developed primarily for use as an educational tool, it is anticipated that the model will find research applications. For example, in the evaluation of sampling plans and monitoring protocols for patchy diseases of crops, it is necessary to know the true values for disease intensity and the extent of patchiness, and to compare the performance of sampling plans in estimating these. By adopting a simulation approach, the exact distribution of disease is known, allowing the validity of a sampling plan to be assessed.

Although the model is of a mechanistic nature, with no internal reference to observationally-derived empirical functions, correlations demonstrated between simulated epidemic patterns and accepted empirical descriptions support the use and continued development of the model.