ABSTRACTS OF COMMUNICATIONS
Proceedings of the Twenty-Third Meeting of the AFRC Modellers' Group

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This group, which is concerned with the applications of mathematics to agricultural science, is sponsored by the Agricultural and Food Research Council. It was formed in 1970, and has since met at approximately yearly intervals in London for one-day meetings. The twenty-third meeting of the group, chaired by P. H. Nye of the Department of Plant Sciences at the University of Oxford, was held in the Wellcome Meeting Room at the Royal Society, 6 Carlton House Terrace, London on Friday, 7 May 1993, when the following papers were read.

Phosphorus metabolism in the sheep: a balance model.
J. M. FORBES[1] AND J. H. TERNOUTH[2]. [1] *Department of Animal Physiology and Nutrition, University of Leeds, Leeds LS2 9JT, UK,* [2] *Department of Agriculture, University of Queensland, St Lucia, Queensland 4067, Australia*
Phosphorus (P) is an essential nutrient and is involved in most of the metabolic activities of the body as well as in the formation of bone. Because of the large amount of recycling between digesta and blood to saliva in ruminant animals, it has proved difficult to determine the requirements for phosphorus, and many studies have been performed using sheep in order to improve our understanding of the control of phosphorus balance. In the model presented here, the digestive system is represented by rumen, abomasum, duodenum, nine segments of small intestine, and large intestine. Extracellular fluid (ECF) is used as the body fluid compartment. Food type and rate of intake determine the rate of saliva production, while saliva P concentration depends on ECF-P concentration. Absorption from the rumen depends on P concentration in rumen fluid, while P is secreted into the abomasum and duodenum at fixed rates. P absorption from each segment of small intestine is proportional to the concentration of P in the lumen, and P is also absorbed from the large intestine at a constant rate. Excretion of P in urine is related to ECF concentration. Running the model predicts that increasing the level of feeding with a constant P concentration in the feed results in decreasing concentrations of P in ECF and saliva, while rumen concentration and faecal excretion are increased. Increasing the concentration of P in the feed results in increasing concentrations of P in ECF, saliva and rumen fluid, together with increased faecal excretion: these predic-

tions agree with reality. The model is relatively insensitive to changes in ECF volume and rumen P absorption, but is very sensitive to the rate of saliva production and the relationship between P concentration and absorption in the small intestine. In simulations of several published experiments, the model performed well in qualitative terms and was quantitatively appropriate as long as conditions were close to 'normal'. The absence of any endocrine representation prevented it responding appropriately to conditions outside the normal range.

A model of the phasic behaviour of vasopressin neurosecretory cells. D. BROWN, G. LENG, J. P. A. FOWERAKER AND R. W. MARRS. *AFRC Babraham Institute, Babraham Hall, Cambridge CB2 4AT, UK*
Vasopressin (AVP) neuronal cells typically fire in asynchronous bursts of duration from 5 s to *c.* 1 min at firing rates of 3–15 spikes/s, separated by periods of inactivity. The durations of bursts and silences are variable over a short time scale, with little clear relationship between adjacent burst and silences. A typical single spike of such a neurone consists of an initial depolarization of duration *c.* 3 ms, immediately followed by a hyperpolarization (duration *c.* 30 ms), and finally a further depolarization (duration 10–20 ms) due to a calcium current. The opioid dynorphin has recently been shown to be co-localized with AVP, and to be released during AVP cell activity. If such dynorphin release elevates the cell threshold for firing, and the dynorphin decays slowly in the absence of further release, this, together with the calcium after-current, provides a possible mechanism for phasic firing of AVP cells. Once an AVP cell begins to fire, due to the combined effect of incoming

random excitatory and inhibitory potentials causing the membrane potential to exceed the firing threshold, the calcium after-currents facilitate a continuation of the activity. On the other hand, the slow build-up of dynorphin concentration ensures that, after some time, the cell stops firing, and is not able to recommence firing until the local dynorphin concentration declines back to a low level. The choice of model type (*a*) between deterministic and stochastic, and (*b*) between linear and nonlinear, is discussed in terms of degree of realism and insight into the mechanism.

Travelling waves in density-dependent dispersion models. P. K. MAINI[1] AND F. SÁNCHEZ-GARDUÑO[1,2]. [1] *Centre for Mathematical Biology, Mathematical Institute, 24–29 St Giles, Oxford OX1 3LB, UK*, [2] *Departamento de Matemáticas, Facultad de Ciencias, UNAM Circuito Exterior, CU, México 04510, DF Mexico*

Many models have been proposed to account for the spatial dispersion of populations of insects, bacteria, etc. Some species migrate from densely populated areas into sparsely populated regions to avoid overcrowding, while other species have a tendency to aggregate. Hence, density-dependent dispersion is a common phenomenon in ecology and has been studied in several different contexts. For example, nitrogen fixation in some plants is facilitated by the bacterium *Rhizobium*, which diffuses through the plant roots according to a non-linear diffusive law. A variety of authors have studied models in one spatial dimension in which dispersal of the species is modelled by a density-dependent diffusion coefficient, and growth is modelled by a non-linear function which increases at low population density, but decreases at higher population densities.

The analysis of this type of reaction–diffusion model is extended to include several different types of density-dependent diffusion coefficient (Sánchez-Garduño & Maini 1993). It is shown that, depending on the values of the parameters and the specific behaviour of the diffusion coefficient, the model can exhibit waves of population invasion, which may be of smooth or sharp travelling-front type. The speed of these waves is calculated in terms of the parameters of the model. Furthermore, the region in parameter space for which this type of behaviour occurs can be predicted, and outside this region the model does not exhibit travelling waves.

SÁNCHEZ-GARDUÑO, F. & MAINI, P. K. (1993). Wave patterns in one-dimensional nonlinear degenerate diffusion equations. In *Experimental and Theoretical Advances in Biological Pattern Formation* (Eds H. G. Othmer, P. K. Maini & J. D. Murray). New York: Plenum Press (in press).

A model of the interaction between grazing mammals and a two-species sward. J. A. NEWMAN[1] AND A. J. PARSONS[2]. [1] *AFRC Unit of Ecology and Behaviour, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK*, [2] *AFRC Institute of Grassland and Environmental Research, North Wyke Research Station, Okehampton, Devon EX20 2SB, UK*

A teleonomic model of foraging behaviour (grazing time, daily intake and diet selection) is combined with a physiologically based model of plant growth and competition in a mixed-species sward. It considers the impact of selective defoliation by herbivores, interacting with differences (growth rate, capacity for competition and spread) between plant species on the stability of composition of a mixed-plant community. The model is demonstrated using parameters based on sheep grazing a ryegrass–clover sward, but is easily modified to consider other animal types and plant communities. The model considers spatial aspects of the presence of species. It considers separately the horizontal availability of species (their cover and spread) and their vertical availability (height and upward growth), and their effect on both selection and interspecific competition. When the model is run for situations in which the relative horizontal availability of each species is fixed, and the relative vertical availability is free to change dynamically, the prediction depends strongly on how the two species are distributed spatially in the sward. When grass and clover are highly aggregated in the sward (low interspecific competition), the grazing system (plants and animals) is more stable at high or low initial proportions of clover, but not at intermediate levels. When the plants species are completely intermixed spatially (high interspecific competition) the system is far more stable at all initial levels of clover. When the relative vertical availability of each species is fixed and the relative horizontal availability of each species is allowed to vary dynamically, the system is more stable. This model highlights the deficiency of characterizing a sward in terms of a simple proportion. As agricultural models come to address environmental issues, the need for a combination of ecological and physiological approaches is apparent.

Modelling the soil–plant system in terms of entropy production. T. M. ADDISCOTT. *Soil Science Department, AFRC Institute of Arable Crops Research, Rothamsted Experimental Station, Harpenden, Herts AL5 2JQ, UK*

Thermodynamic models have been used in soil science since the time of Schofield (1955), and possibly earlier. More recently Runge (1973) proposed a model for soil profile development that explained the process in terms of the ordering brought about by the flow of water through the soil. His basic concept was that entropy was lessened and the profile therefore made

more ordered by the input of energy provided by the flow of water through the soil. Hoosbeek & Bryant (1992) pointed out, however, that Runge used equilibrium thermodynamics, which are appropriate to closed systems, whereas the soil is an open system. An open system tends towards a steady state rather than an equilibrium and is therefore described by non-equilibrium, or irreversible, thermodynamics (Prigogine 1947), in which the steady state is characterized by minimum production of entropy (e.g. Katchalsky & Curran 1967). The latter authors commented on 'several remarkable analogies' between an open system approaching a steady state and the development of living systems towards maturity. It seems reasonable to extend the analogy to soil–plant systems, in which ordering (entropy-lessening) and dissipative (entropy-increasing) processes are discernible. Using non-equilibrium thermodynamic theory relating to steady states as an analogue of the soil–plant system provided some interesting but non-quantitative descriptions, in terms of entropy production, of long-term changes in soil and vegetation at Rothamsted. In the agricultural context, entropy production can involve both the net production of small molecules such as NO_3^-, N_2O and CO_2, which cause environmental concern, and the de-ordering of the soil profile. It is therefore suggested that minimum production of entropy may be a useful criterion of sustainable agriculture.

Hoosbeek, M. R. & Bryant, R. B. (1992). Towards the quantitative modelling of pedogenesis – a review. *Geoderma* 55, 183–210.

Katchalsky, A. & Curran, P. F. (1967). *Non-equilibrium Thermodynamics in Biophysics*. Cambridge, MA: Harvard University Press.

Prigogine, I. (1947). *Etude Thermodynamique des Processus Irréversibles*. Liège: Desoer.

Runge, E. C. A. (1973). Soil development sequences and energy models. *Soil Science* 115, 183–193.

Schofield, R. K. (1955). Can a precise meaning be given to available soil phosphorus? *Soils and Fertilizers* 18, 373.

A model for plant growth under environmental variation and competition for light. D. P. AIKMAN, L. R. BENJAMIN AND A. SCAIFE. *Horticulture Research International, Wellesbourne, Warwickshire CV35 9EF, UK*

A new model for plant and crop growth is proposed. In an isolated plant, it is assumed that foliage, whose total leaf area is proportional to the plant mass, is contained within a crown whose projected zone area is proportional to the $\frac{2}{3}$ power of the plant mass. If light were the sole limiting growth resource and were constant, one can derive a growth equation, $dw/dt = rw\phi = rw[1 - \exp(-\kappa w^{\frac{1}{3}})]/(\kappa w^{\frac{1}{3}})$, which approximates to a particular case of the Richards (1959) growth equation. The differential equation integrates over time to give $w^{\frac{1}{3}} = \kappa^{-1} \ln\{1 + [\exp(\kappa w_0^{\frac{1}{3}}) - 1] \exp(rt/3)\}$.

This self-shading equation would describe growth of plants prior to canopy closure. In a crop of density n plants per unit area, canopy closure is assumed to occur when the zone area per plant reaches space available per plant, $1/n$, when the zone areas are assumed to merge and the within-plant Leaf Area Index becomes a crop Leaf Area Index. Thereafter, the foliage would form a uniform canopy, and mutual shading gives the expolinear equation of Goudriaan & Monteith (1990).

In practice, light is not the sole environmental limitation to growth, nor is it constant. It is proposed that the effects of a set of environmental variables on plant growth may be described in terms of conductances in series, and that the conductances are dependent on each of the environmental variables that limit the growth rate of plants. For example, temperature, T, photosynthetically active radiation, I, and carbon dioxide, C, would result in a growth rate given by $dw/dt = w/([a(T-T_0)]^{-1} + [b\phi I]^{-1} + [c(C-\Gamma_*)]^{-1})$, where the efficiency with which plant foliage intercepts light, ϕ, is obtained from the self- or mutual-shading relations described above. The model fits closely to data from a number of monocrop experiments over a range of densities and over different periods of varying environmental conditions. It can be extended, successfully, to fit data from mixed-aged monocrop experiments.

Goudriaan, J. & Monteith, J. L. (1990). A mathematical function for crop growth based on light interception and leaf area expansion. *Annals of Botany* 14, 605–614.

Richards, F. J. (1959). A flexible growth function for empirical use. *Journal of Experimental Botany* 10, 290–300.

Models to provide planting plans for Brussels sprouts. P. J. C. HAMER AND E. AUDSLEY. *AFRC Silsoe Research Institute, Wrest Park, Silsoe, Bedford MK45 4HS, UK*

A major objective in commercial vegetable production is to market a steady supply of produce over a long period. This requirement can be planned by using different varieties, or by sowing or planting the crop at different times and at different spacings. Using Brussels sprouts as an example, planting plans and a harvesting strategy to maximize profit are determined, which satisfy demand for buttons in specified size ranges.

The progress of button yield (Y_b) is represented by a logistic curve where the asymptote (Y_m) represents the maximum yield the crop can produce and the dependent variable is thermal time (degree days). Each variety can be described by Y_m and τ, the period from establishment to $Y_b/Y_m = 0.5$. The progress of waste yield (Y_w) through unacceptable quality is also represented by a logistic curve. A single parameter [the time from $(Y_b/Y_m = 0.5)$ to $(Y_w/Y_m = 0.5)$] describes the time trend in the loss of yield through

Y_w. The yield of quality buttons in specified size ranges can be satisfactorily described by a normal distribution. The mean button diameter is related to yield and the number of buttons on a stem (N_b), and the standard deviation is empirically related to N_b for a range of sites and varieties. The effects of sowing date and plant density on the marketable yield is modelled in relation to Y_m, τ and N_b. The maximum yield is considered in relation to the total solar radiation intercepted by the crop canopy during the main periods of growth. The period τ is related to thermal time and photoperiod time units, and N_b is modelled by specifying the maximum yield and button number for known sowing date and plant density.

Varieties which have poor plant or sprout characteristics such as colour or shape are eliminated. A scheduling model determines the optimum area of which variety to harvest each week to satisfy the demand from a number of customers for a given weight of sprouts within specified size ranges. Hence the area of each variety to plant is calculated. The linear programming model consists of weekly constraints that the demands must be satisfied plus constraints which determine the amount of each size harvested each week. Sprouts surplus to demand can, at best, be sold at a lower price. The objective is to maximize profit.

A mathematical model of the aerobic deterioration of silage within an opened silo.

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When silage is stored within a closed silo the anaerobic conditions prevent yeasts and moulds from flourishing. When opened, however, oxygen is free to permeate the silage and aerobic deterioration commences. Yeasts and moulds develop, consuming nutrients, heating the silage, and making it less palatable for animal consumption. Moreover, the subsequent rise in pH creates an environment in which harmful pathogens, such as *Listeria monocytogenes*, can flourish (Fenlon *et al.* 1989). There is a need to understand the deterioration process so that effective counter-measures can be designed.

A simplified, nonspatial model for the aerobic deterioration of silage is described. The model assumes that the process is initiated by yeasts which metabolize lactate and acetate in the silage. The dynamics of the yeast population, substrate concentrations and temperature are described by a system of ordinary differential equations, which is then used to predict the stability of a number of silages, as measured in experiments reported in the literature. Although requiring only one-third as many parameters as previous models (Courtin & Spoelstra 1990; Muck *et al.* 1991) the model is shown to be as effective a predictor of stability.

A spatial model of the aerobic deterioration of silage in an opened silo, based on the above, is then described. Diffusion is taken to be the transport mechanism of both heat and oxygen, and the inhibition of microbial activity at low oxygen concentrations is assumed to be governed by a Michaelis–Menten relationship, in common with previous spatial models (Pitt & Muck 1993). This model is then used to investigate the effectiveness of spraying the open face of a silo with propanoic acid as a method of limiting deterioration. Simulation results are presented which suggest that this counter-measure will be effective only if usage rates are high, and offers little advantage otherwise.

FENLON D. R., WILSON, J. & WEDDELL, J. R. (1989). The relationship between spoilage and *Listeria monocytogenes* contamination in bagged and wrapped big-bale silage. *Grass and Forage Science* **44**, 97–100.

COURTIN, M. G. & SPOELSTRA, S. F. (1990). A simulation model of the microbiological and chemical changes accompanying the initial stage of aerobic deterioration of silage. *Grass and Forage Science* **45**, 153–165.

MUCK, R. E., PITT, R. E. & LEIBENSPERGER, R. Y. (1991). A model of aerobic fungal growth in silage. 1. Microbial characteristics. *Grass and Forage Science* **46**, 283–299.

PITT, R. E. & MUCK, R. E. (1993). A diffusion model of aerobic deterioration at the exposed face of bunker silos. *Journal of Agricultural Engineering Research* **55**, 11–26.

Economic effects of restricting carbon emissions.

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The argument proceeds from an identity:

$$C = EFWP \qquad (1)$$

where C = annual emission of carbon into the atmosphere, E = energy used to produce unit gross domestic product (GDP), F = fraction of carbon emitted as a result of energy use, W = GDP *per capita* and P = population. Variables E and F are the efficiency of converting energy to wealth and the carbon efficiency of energy use, respectively. The units are chosen to be self-consistent; energy is expressed in terms of oil-equivalent, and GDP in some deflated common unit of value, e.g. 1985 US dollars.

Taking logarithms of Eqn (1), differentiating with respect to time, t, and rearranging enables the relative rate of change of wealth, $W^{-1}(\mathrm{d}W/\mathrm{d}t)$, to be found from the relative rates of change of C, E, F and P.

Using the compound interest law, we may estimate relative rates of change of C over various numbers of years, n. If emissions are allowed to double, then $C^{-1}(\mathrm{d}C/\mathrm{d}t) = 0.007$ a^{-1} (i.e. 0.7% a^{-1}) if $n = 100$ years, 0.010 a^{-1} if $n = 70$ years and 0.023 a^{-1} if $n = 30$ years. If emissions are cut by one-quarter by 2005 ($n = 12$), $C^{-1}(\mathrm{d}C/\mathrm{d}t) = -0.024$ a^{-1}.

The model can be operated for the entire world, for an economic grouping or for an individual country.

For OECD, over the period 1973–85, relative rates of change were -0.010, -0.003 and $+0.005$ a^{-1} for E, F and P respectively. Doubling carbon emissions in 100 years will slow the post-1945 increase in wealth to 1·5% a^{-1}; decreasing emissions by 25% by 2005 implies a decrease in wealth of 1·6% a^{-1} unless improvements in E and F accelerate, e.g. by moving away from energy-intensive industry and replacing fossil fuels by other sources of energy. For developing countries with rates of population increase of 3·0% a^{-1} or more, restricting carbon emissions will deepen poverty.

Optimizing weed management using stochastic dynamic programming. J. E. SELLS. *Silsoe Research Institute, Wrest Park, Silsoe, Bedford MK45 4HS, UK*

Farmers are under pressure to operate in more environmentally acceptable ways and to maintain an efficient arable cropping industry. One aspect of this is weed control using cultivation techniques as well as herbicides at various application rates. To this end, stochastic dynamic programming is used to optimize the farmer's management of weeds over the long term. It is necessary to consider a long-term time scale because of the nature of weed populations. This year's actions have repercussions for years to come.

The model determines the optimum strategy of weed control which minimizes the long-term cost, including weed competition and contamination. A strategy includes decisions on crop, autumn cultivation, timing of planting and herbicide treatments. The efficacy of the herbicide treatments is considered uncertain. The performance of a herbicide for a given week will vary for different years and soil types, and is described by a log-normal distribution. The states of the dynamic programme are defined as ranges of the number of weed seeds in the soil. The one-year probabilities and costs of moving between states for each decision option are calculated from the relationships between annual weed seedbanks and crop yield, and the log-normal distribution describing the herbicide performance. The model for wild oats in continuous winter wheat is compared with the results of a simulation using single-value herbicide performances. The dynamic programme gives similar optimum spray thresholds to the simulation when either full- or half-rate Difenzoquat is sprayed. These are about 2 seedlings/m² for full-rate Difenzoquat and zero for half-rate.

Including the variability of herbicide performance increases the threshold and thus reduces the amount of herbicides used compared to the optimum calculated with a fixed performance. The model shows that combining all cultural and herbicide control gives an optimum strategy where half-rate Difenzoquat is used below 5 seedlings/m² and full rate above. For an average farmer there is an 18% reduction in the amount of Difenzoquat used compared with using a full rate above 2 seedlings/m² or a 34% reduction from using full rate every year. The optimum spray thresholds for each cereal year of a rotation can be calculated. A break crop every 4 years requires less herbicide than one every 5 years. Increased herbicide prices or reduced cereal prices have little effect upon the optimum spray strategy.