Journal of Agricultural Science, Cambridge (1991), **117**, 129–133. Printed in Great Britain

ABSTRACTS OF COMMUNICATIONS

Proceedings of the Twenty-First 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-first meeting of the group, chaired by Professor B. J. Legg of the Silsoe Research Institute, was held in the Wellcome Meeting Room at the Royal Society, 6 Carlton House Terrace, London on Friday, 12 April 1991, when the following papers were read.

A model of the operation of a milking machine teatcup.

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The milking machine teatcup applies a vacuum to the cow's teat in order to open the teat duct and extract the milk. However, to prevent the applied vacuum from damaging the teat and to make the milking process acceptable to the cow, the teat is massaged by an oscillating teatcup liner at the same time. This liner is a thin-walled cylinder of flexible rubber of approximately the same internal diameter as the teat. The movement of the liner walls, which collapse and open cyclically, is controlled by a differential pressure across them. The liner movement interrupts the flow of milk and provides partial relief from the milking vacuum. There is a complicated interaction between the flow of milk away from the teat, the pressures in the teatcup and the oscillation of the liner which can be described by a mathematical model based on the laws of motion of the fluid.

The model has been developed for hydraulic milking, where air is excluded from the system and ball-valves present milk flowing back into the teatcup. This produces a second-order non-linear differential equation of motion, with coefficients based on empirical data describing the liner. The equation can be solved numerically to predict flow rates and pressure fluctuations and to estimate the effectiveness of massage. The results can be used to compare the effect of different milking machine components or different pressure settings on a particular animal, or the effect of different flow rates or teat sizes which occur with a variety of cows. Ultimately, the model may be used to optimize machine operation for all animals. Further developments will extend the model to describe conventional milking techniques where an air-bleed creates two-phase flow in the milk tubes.

Empirical models of the lactation curve in dairy cattle.

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Wood (1967) proposed the equation $Y = At^{b}e^{-ct}$ to describe the lactation curve of dairy cattle, where t is time from calving and Y is daily milk yield. Neal & Thornley (1983) proposed a mechanistic model of the lactation curve based on the premise that the lactation curve arises from the growth of secretory cells and their subsequent death. Empirically this may be represented by a general equation of the form $Y = A\phi_1(t)\phi_2(t)$, where $A (> 0)$ is a scalar, $\phi_1(t)$ is a monotonically increasing function with a positive initial value and an asymptote at $\phi_1 = 1$, and ϕ_2 is a monotonically decreasing function with an initial value of unity and an asymptote at $\phi_2 = 0$. The following functions were considered as candidates for ϕ_1: (1) $1 - b_0 e^{-b_1 t}$ (Mitscherlich), (2) $1/[1 + b_0/(b_1 + t)]$ (Michaelis-Menten), (3) $1/[1 + b_0/(b_1 + t^{b_2}]$ (generalized saturation kinetic), (4) $1/(1 + b_0 e^{-b_1 t})$ (logistic), (5) $b_0 \exp[(-\ln b_0)(1 - e^{-b_1 t})]$ (Gompertz), (6) $[1 + \tanh(b_0 + b_1 t)]/2$ (hyperbolic tangent). Candidates for ϕ_2 were (7) e^{-ct} and (8) $1/(1 + ct)$. The 12 models obtained from these functions, together with Wood's model, were fitted to whole lactation data from 18 cows fed a variety of diets. Models utilizing function (7) generally fitted better than those utilizing (8). Using (7) for the declining phase, (1) was found to fit better than Wood's model in most cases, whereas the remaining models were generally poorer. The model formed from (1) and (7) has the additional advantage over all other models (including Wood's) that analytical solutions exist for important summary statistics of the lactation curve including time to peak, maximum yield, total yield over a finite lactation and relative decline at the midway point of the declining phase. In conclusion, a general form for the lactation curve has been proposed, and the use of the Mitscherlich equation to describe the increasing phase of lactation has been shown to offer advantages over Wood's model.

NEAL, H. D. St. C. & THORNLEY, J. H. M. (1983). The lactation curve in cattle: a mathematical model of the mammary gland. *Journal of Agricultural Science, Cambridge* **101**, 389–400.

WOOD, P. D. P. (1967). Algebraic model of the lactation curve in cattle. *Nature, London* **216**, 164–165.

Diet selection by sheep: a teleonomic approach. J. A. NEWMAN. *AFRC Unit of Ecology and Behaviour, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK*

There is a great deal of interest in understanding why sheep eat what they eat. Sheep behaviour represents a complex series of tradeoffs regarding the costs and benefits of different fitness-enhancing activities. Hence, diet selection can be understood as a consequence of these tradeoffs. To do this, a teleonomic model of foraging behaviour is developed using stochastic dynamic programming. Sheep grazing a mixed-species sward are continuously faced with the decision of whether to eat, rest or ruminate. When the animal 'decides' to eat, it must decide which of several species it should graze, and at what depth to graze that particular species. The model assumes that the animal's body condition at the terminal time period is related to its ability to survive and reproduce in the future (i.e. its fitness). Decisions are modelled with the view that sheep behave in such a way that they maximize their expected fitness. Further, sheep behaviour is modelled as a state-dependent process using three physiological state variables: blood energy level, and the levels of digestible and indigestible gut fill. Using Bellman's principle of optimality, the model is solved for the optimal policy (state- and time-dependent strategy of behaviour). The model predicts, among other things, the following quantities: (i) diet composition, (ii) daily intake, (iii) daily time budget, (iv) bout length, number and timing, and (v) the distribution of grazing depths. The model can also be used to calculate the multidimensional indifference manifolds which quantify the behavioural tradeoffs. The model can be sequentially coupled with dynamic models of sward growth, whether mechanistic or teleonomic. In this way, answers regarding questions of species coexistence and community structure can be found, and the essence of the dynamic feedback system present in natural grassland communities can be represented.

Quantification of anaerobic fungi in the rumen ecosystem. D. DAVIES, J. FRANCE AND M. K. THEODOROU. *AFRC Institute of Grassland and Environmental Research, Hurley, Maidenhead, Berks SL6 5LR, UK*

Until the mid-1970s, microbial biomass in the rumen was assumed to consist of a mixed population of anaerobic bacteria and protozoa. Evidence has accumulated since then which leaves little doubt as to the presence and involvement of anaerobic fungi in the rumen ecosystem. These micro-organisms have a fermentative (mixed-acid) metabolism and contribute to the dissolution of plant biomass by producing a wide range of plant cell-wall-degrading enzymes. The fungal life cycle essentially consists of two stages in which motile zoospores in rumen liquid alternate with substrate-associated (particle-attached) fungal thalli. Thus, because of the difference in size of zoospores and thalli, fungal biomass is largely substrate-associated. However, whilst the population density of motile zoospores is fairly readily determined, that of the fungal thalli is much more difficult to assess, due to the practical difficulties of measuring amounts of substrate-associated fungal biomass in a mixed-population ecosystem.

Enumeration procedures used to date generally rely on counting either zoospores or developing zoosporangia (the sac-like organs producing zoospores). However, a 'most probable numbers' technique has been adapted for enumerating fungi, which relies on an endpoint dilution procedure (Theodorou *et al.* 1990). The method uses the ability of fungi to degrade plant cell walls to enumerate zoospores and thalli as thallus-forming units. It does not, however, distinguish between different stages of the life cycle nor account for the number of thalli associated with each particle. Therefore, a set of differential equations was postulated to describe the life cycle of anaerobic fungi in the rumen (France *et al.* 1990). From this model – and with information on rumen volume, the outflow of liquid and particulate matter from the rumen, and the concentration of motile zoospores in rumen liquid – a method for calculating the population density of fungal thalli in the rumen has been derived. The life-cycle model is presented and discussed in relation to other methods of enumeration of anaerobic fungi.

FRANCE, J., THEODOROU, M. K. & DAVIES, D. (1990). Use of zoospore concentrations and life cycle parameters in determining the population of anaerobic fungi in the rumen ecosystem. *Journal of Theoretical Biology* **147**, 413–422.

THEODOROU, M. K., GILL, M., KING-SPOONER, C. & BEEVER, D. E. (1990). Enumeration of anaerobic chytridiomycetes as thallus-forming units: novel method for quantification of fibrolytic fungal populations from the digestive tract ecosystem. *Applied and Environmental Microbiology* **56**, 1073–1078.

The spatial spread of the grey squirrel in Britain. P. K. MAINI[1], A. OKUBO[2], M. H. WILLIAMSON[3] AND J. D. MURRAY[4]. [1]*Centre for Mathematical Biology, Mathematical Institute, 24–29 St Giles', Oxford OX1 3LB, UK.* [2]*Marine Sciences Research Center, State University of New York, Stony Brook, New York 11794-5000, USA.* [3]*Department of Biology, University of York, York YO1 5DD, UK.* [4]*Department of Applied Mathematics FS-20, University of Washington, Seattle, WA 98195, USA*

Around the turn of the century the North American grey squirrel, *Sciurus carolinensis*, was released from various sites in Britain. Since then the grey squirrel has successfully spread to colonize much of England, Wales and the Scottish lowlands. Simultaneously, the indigenous red squirrel, *Sciurus vulgaris*, has disappeared from these localities. Three hypotheses have been put forward to account for this phenomenon: (i) competition between the reds and the greys, (ii) environmental changes that reduced the red squirrel population independent of the grey squirrel population, and (iii) introduction of diseases by the greys.

A deterministic competition–diffusion model to describe the interaction between the grey squirrel and the red squirrel is presented (Okubo *et al.* 1989). The model parameters are estimated from field data, and the random introduction of grey squirrels into red squirrel territory is simulated to show how colonization might spread. The solutions give population distributions qualitatively similar to those observed. The model predicts waves of grey squirrel invasion with speed of invasion typical of that observed in the field.

It is shown that competition alone could account for the observed displacement of the red squirrel by the grey in large areas of Britain. It is concluded that the spread of one species competitively overcoming another is not very different qualitatively from the spread of one without interaction. The quantitative difference is because competition slows down the speed of advance of the invading species.

OKUBO, A., MAINI, P. K., WILLIAMSON, M. H. & MURRAY, J. D. (1989). On the spatial spread of the grey squirrel in Britain. *Proceedings of the Royal Society of London* B **238**, 113–125.

A transport-resistance model of forest growth and partitioning. J. H. M. THORNLEY. *Institute of Terrestrial Ecology, Edinburgh Research Station, Bush Estate, Penicuik, Midlothian EH26 0QB, UK*

The transport-resistance approach to dry matter partitioning is used to construct a model of forest growth (J. H. M. Thornley, in press). The model is at the stand level for a monoculture of identical trees of the same age. There are five major tissue compartments in the model: foliage, branches, stem, coarse roots, and fine roots and mycorrhizas. The matter in each compartment is further subdivided into meristem, structure, carbon substrate and nitrogen substrate. The model is driven by daily radiation including day length, ambient CO_2 concentration and daily means of air and soil temperature. The fine roots are provided with constant values of soil mineral nitrogen pools (ammonium and nitrate) from which uptake occurs. Structural growth is a result of meristem activity, which is driven by the local concentrations of carbon and nitrogen substrates. Forest growth over about 100 years is simulated for various environmental conditions and soil mineral nitrogen levels; thinning is also simulated. Natural tree death occurs within the model. Particular attention is paid to dry matter partitioning patterns, and to the dry matter per stem when death occurs. The model is robust and responsive, and provides a framework for further development and application to many ecological and environmental scenarios, as well as to some forest management problems.

THORNLEY, J. H. M. A transport-resistance model of forest growth and partitioning. *Annals of Botany* **68**.

Using a diffusion model to explain the dispersal of pollutants in soil due to cultivation. P. W. LANE AND S. P. MCGRATH. *AFRC Institute of Arable Crops Research, Harpenden, Herts AL5 2JQ, UK*

One method of disposal of sewage sludge is to use it as fertilizer on agricultural land. Long-term experiments have been conducted to monitor the effect of this practice on the soil – particularly the effect of heavy metals present in the sludge. These experiments have indicated that the metal introduced in the sludge is somehow lost from the soil in the treated area of plots in the course of time. In this study, the movement of soil by cultivation during an experiment was investigated. Samples were taken from a treated plot and neighbouring untreated plots, and analysed for metal content; these showed considerable movement of metal across plot boundaries. A two-dimensional model based on classical diffusion theory fitted well to the observation of metal content. The model approximates the mechanical movement of soil particles due to discrete cultivation treatments, by a continuous diffusion process. Dispersion coefficients were 0·24 and 0·13 m^2 per tillage operation in directions parallel and perpendicular to the direction of ploughing. The model was tested by predicting concentrations of six metals in specific areas and times at which soil samples had been taken; the predictions agreed well with the concentrations found in the samples. Finally, the model was used to estimate the proportion of metals still present in the soil. More than 80% of the metals originally added was accounted for, 25 years after the last application of sludge. The remaining 15–20 % could not be accounted for, either by the model for dispersion or by alternative hypotheses for loss of metal from soil.

Modelling vernalization in wheat. J. CRAIGON, J. G. ATHERTON AND N. SWEET. *University of Nottingham School of Agriculture, Sutton Bonington, Loughborough, Leics LE12 5RD, UK*

Vernalization, a response to low temperatures which influences when or if plants subsequently become reproductive, is common to many crop species. Craigon *et al.* (1990) have shown that a simple laboratory-based model can successfully predict the vernalization response of carrots under field conditions. When applied to predicted warmer climatic conditions, the model has indicated that the changes in the vernalization stimulus perceived by non-juvenile plants would vary in size and direction, with time of year and degree of warming. Other crops having similar vernalization responses would therefore be expected to vary in a similar and, once quantified, ultimately predictable manner. Much of the variation in predicted phenology of winter wheat produced by using different models or different climatic data sets can be explained by the vernalization responses built into the models.

In the present work, the principles of the carrot model have been applied to suitable controlled environment data for winter wheat taken from the literature. The resulting model accurately predicted the development rate of specific varieties of wheat following a number of different vernalizing treatments. The results of testing the models against field data from the UK are discussed. As it has been shown that the stimulus perceived by plants is sensitive to small temperature changes, the consequences of predicted climatic change for wheat vernalization are considered.

CRAIGON, J., ATHERTON, J. G. & BASHER, E. A. (1990). Flowering and bolting in carrot. II. Prediction in growthroom, glasshouse and field environments. *Journal of Horticultural Science* **65**, 547–554.

Reconciling expert systems and crop models through model abstraction. J. SMART. *Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, UK*

Expert systems have an important contribution to make in augmenting conventional decision-making aids such as models. Expert systems can help interpret simulation results and they can model less precise information with which mathematical models cannot cope. However, developing an expert system to work alongside a model has its difficulties. A clear boundary between model and expert system is artificial, and some inconsistencies and duplication will be introduced when adding an expert system component to an existing model.

Our solution to these problems is to limit the role of the rule-based system to that of a more abstract form of the model, which mirrors the model but at lower resolution and detail. The model is first written in a modular form to expose all relations and variables, and rules written for each relation to turn model execution into an inference process. Then, a process of exhaustive simulation generates abstract rules from the quantitative model. These rules are in turn simplified for readability, to reduce redundancy and to save space.

Just as humans choose the appropriate level of detail to solve a problem depending on the quality of the available information, so the software should be able to use the form of the model appropriate to the situation. There are three main benefits to be gained from this approach. First, if detailed information is not available, the more abstract model may be used to give a (less precise) answer. Secondly, an explanation of the system's reasoning at an abstract level may be easier for the user to understand, since some complexity is hidden. Thirdly, an abstract model may be used to guide more detailed computation, by quickly eliminating irrelevant areas of the search space. Mozetic (1990) has demonstrated this by modelling the heart at varying levels of abstraction in order to speed up heart disorder diagnosis.

The technique is being tested on a model to calculate potato tuber size distribution and determine optimum seed planting rate (Marshall 1986). It will then be extended to a model of potato yield constrained by water availability (Jeffries & Heilbronn 1991).

JEFFRIES, R. A. & HEILBRONN, T. D. (1991). Water stress as a constraint on growth in the potato crop. 1. Model development. *Agricultural and Forest Meteorology* **53**, 185–196.

MARSHALL, B. (1986). Tuber size. *Aspects of Applied Biology* **13**, 393–396.

MOZETIC, I. (1990). *Hierarchical Model-based Diagnosis*. Technical Report TR-90-3. Austrian Research Institute for Artificial Intelligence.

Testing goodness-of-fit. D. A. ROSE. *Department of Agricultural and Environmental Science, The University, Newcastle upon Tyne NE1 7RU, UK*

Goodness-of-fit is often quoted as R^2, the proportion of the variance that is accounted for by the model, but this is often of limited value. A simple, but useful, test of a model is to perform a linear regression between the n model outputs, y, and data, x, as paired observations: $y = a + bx$. The value of R^2 remains the same, and the null hypothesis is that $a = 0$ and $b = 1$. The parameters a and b can then be tested separately by t-test with $(n-2)$ degrees of freedom, or simultaneously by F-test, as described by Dent & Blackie (1979, pp. 100–104). This technique is used to examine the goodness-of-fit for four models from soil science.

(1) The winter drainage predicted by the MAFF drainage model (MAFF 1971) was compared with that observed over 27 winters from the three turfed percolation gauges at Farlington, Hants (Rose 1991). Model and reality agreed well for the 61 cm gauge, but differed significantly for the deeper gauges, implying either that the model failed to account for transpiration from deep-rooted grass or that the deeper gauges leaked.

(2) Smith & Stewart (1989) related the nitrate loading of Lough Neagh to fertilizer usage, summer rainfall, summer temperature and winter stream flow via four simple or multiple regression equations. Although each equation produced a statistically significant correlation, only two, which included three or four variables, satisfy the criteria of Dent & Blackie (1979).

(3) The mortality of genetically engineered strains of *Pseudomonas putida* in soil can be modelled assuming that the population contains a large proportion of short-lived (half-life 1–2 days) and a small proportion of longer-lived (half-life 10–20 days) individuals. By contrast, the indigenous microbial population of the same soil does not change over a period of 90 days.

(4) Rose (1991) fitted normal distributions to annual estimates of winter drainage and Type 1 extreme-value distributions to annual estimates of winter leaching for five locations in England and Wales. The data do not differ significantly from the fitted distribution, except where there is an extreme outlier.

DENT, J. B. & BLACKIE, M. J. (1979). *Systems Simulation in Agriculture*. London: Applied Science Publishers Ltd.
MINISTRY OF AGRICULTURE, FISHERIES AND FOOD (1971). *The Significance of Winter Rainfall over Farmland in England and Wales*. Technical Bulletin 24. London: HMSO.
ROSE, D. A. (1991). The variability of winter drainage in England and Wales. *Soil Use and Management* **7**, 115–122.
SMITH, R. V. & STEWART, D. A. (1989). A regression model for nitrate leaching in Northern Ireland. *Soil Use and Management* **5**, 71–76.