

ABSTRACTS OF COMMUNICATIONS

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

EDITED BY

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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-sixth meeting of the group, chaired by Professor R. J. Wilkins of the Institute of Grassland and Environmental Research, North Wyke, was held in the Wellcome Meeting Room at the Royal Society, 6 Carlton House Terrace, London on Friday, 7 April 1995, when the following papers were read.

Development and validation of a temperature-response model for apex diameter in calabrese (*Brassica oleracea* var. *italica*). K. PHELPS, R. J. READER, D. C. E. WURR AND J. R. FELLOWS. *Horticulture Research International, Wellesbourne, Warwick CV35 9EF, UK*

It is suggested that calabrese responds directly to relatively cold conditions by rapidly increasing the diameter of its apex from a smooth hemisphere in the vegetative state to a small multi-floreted head. Using data from an experiment in controlled environment cabinets, with temperatures ranging between 7 and 23 °C, a model has been developed which predicts the change in apex diameter with temperature (Wurr *et al.* 1995). The rate of increase of the diameter at any time, which is described by the product of the diameter and a 'wigwam' shaped temperature response function, is shown to be maximal at around 15 °C.

Different crop-covering treatments, generating a range of temperature conditions during growth from transplanting to head initiation, were used to test the model. There were four such treatments: covered throughout, open throughout and covered either before or after the time at which plants were estimated to have achieved half their expected weight at head initiation. Temperatures at plant height were measured hourly throughout the experiments. Samples were taken from each plot approximately twice-weekly and their apex diameters estimated from hourly temperature data. The model fitted the data extremely well.

In previous studies (Wurr *et al.* 1993) models were derived solely from field data. The problems of

developing and testing temperature-based models, both with and without controlled environment data, are discussed.

We thank the Ministry of Agriculture, Fisheries and Food for funding this work.

WURR, D. C. E., FELLOWS, J. R., PHELPS, K. & READER, R. J. (1993). Vernalisation in summer/autumn cauliflower (*Brassica oleracea* var. *botrytis* L.). *Journal of Experimental Botany* **44**, 1507–1514.

WURR, D. C. E., FELLOWS, J. R., PHELPS, K. & READER, R. J. (1995). Vernalisation in calabrese (*Brassica oleracea* var. *italica*) – a model for apex development. *Journal of Experimental Botany* (in press).

Effects of random variation in the timing and magnitude of stimulation on the paradoxical responses of a stimulated excitable system. J. P. A. FOWERAKER AND D. BROWN. *Department of Neurobiology, Babraham Institute, Cambridge CB2 4AT, UK*

Previous work on models of excitable, continuous-time systems of FitzHugh–Nagumo/Bonhoeffer–van der Pol (FHN) type has demonstrated complex responses to regular stimulation. The excited response (pulse) frequency exhibits a non-monotonic relationship with increasing stimulus frequency, typically consisting of sawtooth fluctuations (gradual rises, interrupted by sharp falls) increasing to an overall maximum, followed by a region of complete pulse suppression, comparable with frequency relationships observed in real neural systems (e.g. Brown *et al.* 1994). Poissonian patterns of stimulation show a

much smoother, monotonic relationship between the expected pulse and expected stimulus frequencies. Similar results hold for oscillatory models. Little has been done on the response of excitable FHN models between these extremes, i.e. for the case involving moderate random variation in interstimulus timing not as great as in the Poisson process; and also random variation in stimulus magnitude, except in the case of low amplitude noise. Previous work on the effects of random perturbations on nonlinear dynamical systems suggests that small departures from determinism result in slight variations in the overall response pattern.

Simulation results involving a wider range of the two types of randomness are presented here. Slight random variation in stimulus timing and size smooths the sawtooth fluctuations in the pulse/stimulus frequency relationship, whilst maintaining the overall non-monotonic nature. The existence of thresholds at which the non-monotonicity breaks down, at moderate levels of variation in stimulus size and timing, is demonstrated. When both types of variation are present, the thresholds are reduced. Descriptive statistical models of the interaction are provided.

BROWN, D., HERBISON, A. E., ROBINSON, J. E., MARRS, R. W. & LENG, G. (1994). Modelling the luteinizing hormone-releasing hormone pulse generator. *Neuroscience* 63, 869-879.

Turning a tomato crop simulation model into a procedure for computing a CO₂ set-point. D. P. AIKMAN. *Horticulture Research International, Wellesbourne, Warwick CV35 9EF, UK*

CO₂ enrichment improves yields of greenhouse tomato crops (Hand 1982). An environmental control computer can maintain a CO₂ concentration. The objective here is to provide the optimal set-point.

A simulation model consists of modules for leaf photosynthesis, canopy light interception, partitioning, and fruit growth, and for air exchange rate and glasshouse temperatures. Financial implications are covered by a cost for the CO₂ and a module for predicting fruit prices. The key consists of using the modules of the slower processes to compute, off-line, an anticipated worth per mole of carbon assimilated. This can be used by an associated on-line system that uses the modules of the faster processes.

The module for the fruit growth is used to predict the time distribution of photosynthate in subsequent harvests. Combined with predictions of future market prices, this provides initial estimates, one for each day from first anthesis, of a factor to convert the rates of CO₂ assimilation to expected financial values. A combination of the external climate and the crop regime predicts crop temperatures and hence allows for the temperature dependence of fruit growth. The conversion factors are revised to include the deferred

benefit given by additional photosynthesis in increasing early vegetative growth, and hence subsequent photosynthesis and yield. This revision ensures a supply of CO₂ even if no fruit is yet set.

A real-time system can use the crop photosynthesis model to predict the cash benefit for any CO₂ concentration, given inputs for the current environment and the conversion factor for that day. The cost of maintaining a concentration can be obtained from a prediction of the ventilation air exchange rate, the external concentration and the unit price of CO₂. The current CO₂ set-point can be quickly evaluated as the concentration that maximizes the net predicted profit rate.

The work was funded by the Ministry of Agriculture, Fisheries and Food as part of a joint project with Silsoe Research Institute.

HAND, D. W. (1982). CO₂ enrichment, the benefits and problems. *Scientia Horticulturae* 33, 14-43.

Modelling the economic consequences of adopting new reproductive technologies into the bovine industry.

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The adoption of new reproductive technologies such as improved oestrus detection, sexing, embryo transfer and multiple embryo transfer will have far-reaching consequences upon the bovine production industry. This potential impact on national production patterns has been assessed using a sequence of models. In the first instance, basic financial assessments were made for typical dairy, suckler and beef finishing enterprises using estimates of physical performance and market prices. For beef production the benefits associated with the new technologies were assumed to be improved meat quality, the sole production of male calves and/or the production of twin calves; therefore, the financial implications were assessed over one production cycle only.

For milk production, where a natural rate of genetic progress exists through 'genetic gain' from the use of artificial insemination, the full impact of the technologies will only become apparent over several years (e.g. embryo transfer where a 'genetic lift' in milk production can be achieved), therefore, the financial performance of the dairy herd is assessed over a 15 year period in order that the benefits of a technology be realised. To accomplish this a Markov chain model (Yates *et al.* 1995) using a discrete state space as a broad approximation of the continuous state space was constructed. States were defined in terms of an animal's parity (1, 2 or 3) and its genetic status (i.e. the multiplicative effect of successive lifts and gains from the original generation of cows).

The physical and financial results generated by these enterprise models then become one of the inputs

to a large scale linear programme constructed for estimating the likely changes to national production patterns due to the adoption of the new technologies (Yates *et al.* 1994). This model considers the interactions between specific farm types as well as restraints on national production. The model is constructed as a double staircase matrix, representing both the interaction of different farm types and the competition for resources between technologies within a farm type.

Future developments of this work will include the optimization of new technologies at an enterprise level, a higher degree of economic sophistication, the incorporation of uptake theory and the regionalization of the national model.

YATES, C. M., REHMAN, T. & CHAMBERLAIN, A. T. (1995). Evaluation of the potential effects of embryo transfer on milk production on commercial dairy herds: the development of a Markov chain model. *Agricultural Systems* (in press).

YATES, C. M., REHMAN, T. & CHAMBERLAIN, A. T. (1994). *The Socioeconomic Impact of New Breeding Technologies*. Final project report: Modelling the enterprise, 'farm-gate' and national consequences, The University of Reading.

The spread of viral infection in moths. T. ROOSE¹, P. K. MAINI¹, J. CORY² AND R. HAILS². ¹Centre for Mathematical Biology, Mathematical Institute, Oxford OX1 3LB, UK, ²NERC Institute of Virology, Oxford OX1 3SR, UK

To control insect pests with a virus, it is important to determine the optimum time for the treatment. However, before analysing this problem, a realistic model for the uninfected host must be developed. A model framework for this has been developed and applied to the pine beauty moth which is a major pest of lodgepole pine in Scotland.

The life cycle of the pine beauty moth is well documented. For much of the year the insect is dormant as soil-dwelling pupae. In spring, adult moths emerge from the pupae and migrate to the trees and lay eggs. The moths live for about a month but consume an insignificant amount of food. The larvae are the principal consumers of food in the population and are heavily predated. Larvae hatch from the eggs and develop through a number of instar stages before returning underground. The larvae require more virus to kill them as they age, although to some extent this may be compensated for by the greater feeding capacity of larger larvae and thus the greater probability of acquiring virus.

A simplified mathematical model which describes the evolution of the insect through the life cycle by a system of nonlinear ordinary differential equations has been constructed. Many of the key parameters of the model can be obtained from field experiments. The model poses several mathematical problems

which are of general interest in ecological modelling. The first concerns parameter sensitivity. A detailed parameter sensitivity analysis has been carried out to determine which parameters critically affect the behaviour of the system. This indicates which parameters require accurate experimental measurement and provides a model framework for investigating the effect of variances in parameter values. The second concerns the modelling of the seasonal cycles. This may be modelled either through introducing temporally-varying parameters, or through a discrete change, leading to the novel mathematical problem of solving a coupled model of continuous and discrete time equations. Our preliminary investigations show that, with realistic biological parameters, the model yields results consistent with experimental observations. The next step will be to simulate the introduction of the virus in order to predict when in the life cycle is the application of virus most effective, with a view to both short- and long-term control strategies.

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Modelling the role of roots in below-ground nutrient cycling. A. J. F. BUCKNER, K. E. BLACK AND J. E. HOOKER. *Soil Biology Unit, Land Resources Department, Scottish Agricultural College, Craibstone Estate, Aberdeen AB2 9TQ, UK*

Plant roots play a major role in the below-ground cycling of carbon and mineral nutrients, mainly by uptake, mortality and decomposition. There are potentially large root-mediated fluxes of carbon and nutrients within the soil, but accurate quantification of root dynamics has been hampered severely by the lack of methods of measurement and a suitable mathematical framework for interpretation and prediction. Recent developments in minirhizotron technology (Hooker & Atkinson 1992) mean that reliable measurements of root production and mortality can be obtained. Analysis of these data using a technique based on cohorts of roots (Hooker *et al.* 1995) and survival analysis (Lee 1980) has proved particularly useful. The data have highlighted the need for a rigorously-based modelling methodology which allows the impact of root turnover on nutrient cycles to be properly determined.

The mathematical techniques available for modelling the changing age structures of populations are reviewed. A technique used in studies of animal population dynamics (Hoppensteadt 1975) is suggested as a basis for developing an analytical root model. This will have the potential to be integrated with existing plant and soil models in order to improve their robustness.

HOOKER, J. E. & ATKINSON, D. (1992). Application of

- computer-aided image analysis to studies of arbuscular endomycorrhizal fungi effects on plant root system morphology and dynamics. *Agronomie* 12, 821-824.
- HOOKER, J. E., BLACK, K. E., PERRY, R. L. & ATKINSON, D. (1995). Arbuscular mycorrhizal fungi induced alteration to root longevity of poplar. *Plant & Soil* (in press).
- HOPPENSTEADT, F. (1975). *Mathematical Theories of Populations: Demographics, Genetics and Epidemics*. Philadelphia: SIAM Publications.
- LEE, E. L. (1980). *Statistical Methods for Survival Data Analysis*. Belmont CA: Lifetime Learning Publications.

- FRANCE, J., GILL M., THORNLEY, J. H. M. & ENGLAND, P. (1987). A model of nutrient utilization and body composition in beef cattle. *Animal Production* 44, 371-385.
- GERRITS, W. J. J., TAMMINGA, S. & SCHRAMA, J. W. (1995). The effect of protein and protein-free energy intake on protein and fat deposition in veal calves. *VII Symposium on Protein Metabolism and Nutrition*. Vale de Santarém, Portugal, 24-27 May 1995.
- MOUGHAN, P. J. & VERSTEGEN, M. W. A. (1988). The modelling of growth in the pig. *Netherlands Journal of Agricultural Science* 36, 145-166.

Modelling growth of pre-ruminant calves. W. J. J. GERRITS, J. DIJKSTRA AND J. FRANCE. *Institute of Grassland and Environmental Research, North Wyke Research Station, Okehampton, Devon EX20 2SB, UK*

During the last decade, emphasis in meat production has shifted from obtaining maximum growth of animals to production of lean meat and increased efficiency of nitrogen utilization. Simultaneously, interest in growth simulation models has increased, since they provide a tool for better understanding of complex growth processes (France *et al.* 1987). In pig production, such models are also used in the development of feeding strategies (Moughan & Verstegen 1988). Lack of information on the effect of nutrient intake on growth and growth composition of pre-ruminant calves led to a research programme comprising experiments and modelling. The experiments involved measurement of body composition of calves fed different amounts of protein and energy (Gerrits *et al.* 1995). The model currently being developed is a dynamic, mechanistic model which partitions nutrients from ingestion through intermediary metabolism to growth, consisting of accretion of protein, fat, ash and water. The intermediary metabolism is represented by four pools: fatty acids, glucose, amino acids and acetyl co-enzyme A equivalents. Turnover of protein and fat is represented.

New features are the explicit representation of muscle, bone, hide and visceral protein and their amino acid composition, endogenous protein secretion and the synthesis of non-essential amino acids. The development of hide, bone and visceral protein is made dependent on development of muscle protein, allowing slow growers to show priority for bone and hide growth especially. Distribution of energy to protein and fat retention is set to match the experimental data, as is the distribution of protein between accretion and catabolism. The assignment of an amino acid profile to each of the protein pools allows evaluation of the quality of the amino acid pattern of the feed offered. The model is developed in order to evaluate effects of different feeding strategies (protein and energy intake) on protein retention in hide, bone, viscera and muscle tissue, on fat deposition, and on ash deposition.

The presentation of model output. P. H. NYE. *Department of Plant Sciences, University of Oxford, Oxford OX1 3RB, UK*

This paper is about models having several input parameters and an output such as yield or pollutant concentration. Since few readers will want to run your model themselves, the published model should (a) show the general effects of the input parameters on the output, and thereby illuminate your system, and (b) enable easy calculation of the output for particular values of the input parameters.

I suggest the following minimum procedure. Further elaboration, e.g. by a full factorial survey, greatly increases the number of runs for small gain.

- If possible, reduce the number of variables by combining them.
- If sensible, linearize responses by transforming variables, e.g. $\log x$, $1/x$, $x^{\frac{1}{2}}$.
- Decide on practical limits to the domain of each parameter, remembering possible constraints on combinations.
- For publication, scale parameter values by their range, making their upper, mid-point and lower limits $+1$, 0 , -1 .
- Make a standard run with all scaled values $= 0$.
- Make runs with each parameter in turn at scaled values $+1$, $+\frac{1}{2}$, $-\frac{1}{2}$, -1 , with the rest at 0 . This will enable first-, second- and third-order derivatives of the responses to be calculated.
- Plot the response curves on a single normalized sensitivity diagram, so that the sensitivity to each parameter is scaled by its range. This conveys more than a conventional sensitivity diagram.
- For each pair of parameters make runs with scaled values $(+1, +1)$, $(+1, -1)$, $(-1, +1)$, $(-1, -1)$. This enables first-order interactions to be calculated. The total number of runs for n parameters is thus $1 + 4n + 4n(n-1)/2$.
- Display interactions in a normalized diagram of $(n-1) \times (n-1)$ sub-graphs to show the effect of one parameter on the response to another.
- Give a table from which the output for any given input values can easily be interpolated. Outputs may conveniently be calculated from a two dimensional Taylor approximation, at least to second-order accuracy.

The text of this talk is available, on receipt of an A4 stamped addressed envelope, from P. H. Nye, Hewel Barn, Common Road, Beckley, Oxon OX3 9UR.

Analysis of gas production curves from *in vitro* incubation of ruminant feeds. M. S. DHANOA¹, J. DIJKSTRA², J. FRANCE² AND J. H. M. THORNLEY³. ¹*Institute of Grassland and Environmental Research, Plas Gogerddan, Aberystwyth, Dyfed SY23 3EB, UK,* ²*Institute of Grassland and Environmental Research, North Wyke Research Station, Okehampton, Devon EX20 2SB, UK,* ³*Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK*

The drive towards non-invasive and inexpensive screening techniques has renewed interest in *in vitro* methods of ruminant feed evaluation. The *in vitro* digestibility procedure (Tilley & Terry 1963) is an end-point technique which does not provide information on the kinetics of degradation. Kinetics information is usually obtained using the dacron bag method (Ørskov & McDonald 1979). The fact that disappearance from the bag rather than degradation or fermentation of the substrate is measured, as well as the low capacity of the method for repeated measurement and replication, limits its utility. As a consequence, there is an upsurge in the use of *in vitro* gas production methods, where fermentation under controlled conditions allows the ranking of feedstuffs according to digestibility and the exploration of degradation kinetics.

Suitable mathematical models are needed to describe the resultant cumulative gas production profiles. The profiles vary in shape from a rectangular hyperbola (no inflexion point) to highly sigmoidal, thus requiring flexibility in the choice of an appropriate model. In this study, a variety of functions has been examined. These included standard growth functions (e.g. Richards or generalized logistic, modified Gompertz), enzyme kinetic equations, and a purpose-built gas production equation (France *et al.* 1993). Comparison of these functions was undertaken with gas production data generated using the pressure transducer technique (Theodorou *et al.* 1994). A range of substrates was used in this comparison, including straw, conserved forage and tropical forage trees.

The standard growth functions, which do not generally yield simple expressions for calculating the extent of ruminal degradation (ERD), presented convergence problems. The enzyme kinetic equations fitted the data very well, but they do not allow suitable interpretation in order to calculate ERD. The purpose-built gas production equation, which permits ERD to be calculated simply, was found to fit most of the profiles well.

FRANCE, J., DHANOA, M. S., THEODOROU, M. K., LISTER, S. J., DAVIES, D. R. & ISAC, D. (1993). A model to interpret

gas accumulation profiles associated with *in vitro* degradation of ruminant feeds. *Journal of Theoretical Biology* **163**, 99–111.

ØRSKOV, E. R. & McDONALD, I. (1979). The estimation of protein degradability in the rumen from incubation measurements weighted according to rates of passage. *Journal of Agricultural Science, Cambridge* **92**, 499–503.

THEODOROU, M. K., WILLIAMS, B. A., DHANOA, M. S., McALLAN, A. B. & FRANCE, J. (1994). A simple gas production method using a pressure transducer to determine the fermentation kinetics of ruminant feeds. *Animal Feed Science and Technology* **48**, 185–197.

TILLEY, J. M. A. & TERRY, R. A. (1963). A two stage technique for the *in vitro* digestion of forage crops. *Journal of the British Grassland Society* **18**, 104–111.

A simple computer model of predator-prey interactions.

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The two spotted spider mite (TSSM), *Tetranychus urticae*, is a serious pest of hops and widespread resistance to traditional pesticides has elevated its pest status. Hop growers are encouraged to adopt biological control strategies using the predatory mite *Phytoseiulus persimilis* (PP). Although successful control of TSSM is possible, it is highly dependent upon sufficient natural enemies being available at suitable stages in the life cycle of the pest.

Although much progress has been made in modelling predator-prey interactions, the developed models have been very demanding on computer resources and mathematical expertise. For the applied entomologist, a greatly simplified model is often required when assessing pest population outbreaks and suitable control strategies. A simple model of predator-prey interactions developed by Wyatt (1983) has been extended further to allow for delayed introduction of natural enemies. Input to the model are initial estimate of pest population numbers, pest increase rate, initial number of predators released, predator increase rate and predator release date.

A field experiment was carried out to investigate the impact of different densities of PP on populations of TSSM on hops. The model predicted accurately the dynamics of pest populations in three of four treatments. Experimentation with the model showed that the potential increase in pest numbers and timing of pest extinction was dependent upon the initial ratio of prey:predator numbers and timing of predator introductions.

WYATT, I. J. (1983). Simple calculator models of predator-prey interactions: exponential population growth. *Protection Ecology* **5**, 235–244.