

ABSTRACTS OF COMMUNICATIONS

Proceedings of the Thirty-third 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, was formed in 1970 and has since met at approximately yearly intervals in London for one-day meetings. The thirty-third meeting of the group, chaired by Professor P. K. Maini of the Mathematical Institute, University of Oxford, was held in the Kohn Centre at the Royal Society, 6 Carlton House Terrace, London on Friday, 6 April 2001 when the following papers were read.

A process-based model to predict rates of the ozone precursor isoprene emitted from leaves under varying environmental conditions. M. J. MARTIN¹, C. M. STIRLING², S. W. HUMPHRIES¹ AND S. P. LONG³. ¹*Department of Biological Sciences, University of Essex, Wivenhoe Park, Colchester, Essex CO4 3SQ, UK*, ²*School of Agricultural and Forest Sciences, University of Wales, Bangor, Gwynedd LL57 2UW, UK*, ³*University of Illinois, Departments of Crop Sciences and Plant Biology, 190 Edward R. Madigan Laboratory, 1201 West Gregory Drive, Urbana, IL 61801, USA*

Current knowledge of the biochemical pathway of isoprene synthesis was used to construct a new process-based model to predict isoprene emission rates from leaves. The objective was to produce a model to simulate the effects of environmental change on rates of isoprene emission, to enable the prediction of emission rates under future climates. The model assumes that the rate of isoprene synthesis will be controlled by the rate of the slowest reaction within its synthetic pathway. The model is therefore based on the three potentially rate-limiting processes underlying isoprene synthesis. These are: (1) pyruvate supply as the input to the biosynthetic pathway; (2) adenosine triphosphate (ATP) supply for phosphorylation to dimethylallyl pyrophosphate (DMAPP), the precursor of isoprene, and (3) isoprene synthesis from DMAPP, which is controlled by the temperature dependency of the isoprene synthase. Pyruvate supply is predicted using a modified Farquhar *et al.* (1980) biochemical model of leaf photosynthesis, allowing synthesis to be linked to photon flux density, carbon dioxide concentrations and temperature.

The model was used to predict the interactive effects of elevated concentrations of carbon dioxide and temperature on rates of isoprene emission. Simulations indicated that the effects of carbon dioxide and temperature on isoprene emission rates were complicated by the interactive effects of two of the controlling rate-limiting processes in the synthesis of isoprene, namely phosphorylation rates and isoprene synthase activity.

Under present concentrations of carbon dioxide and at photon flux density levels above *c.* 500 $\mu\text{mol}/\text{m}^2/\text{s}$, the controlling rate process is predicted to be the temperature dependency of isoprene synthase. A vegetation cover coefficient to simulate the dependency of isoprene emission on leaf cover variation during the year was included when scaling the model up to canopy level within WIMOVAC (Humphries & Long 1995; www.life.uiuc.edu/plantbio/wimovac).

This research was funded by the Natural Environmental Research Council under grant GT4/92/16/L.

FARQUHAR, G. D., VON CAEMMERER, S. & BERRY, J. A. (1980). A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta* **149**, 78–90.
HUMPHRIES, S. W. & LONG, S. P. (1995). WIMOVAC: a software package for modelling the dynamics of plant leaf and canopy photosynthesis. *CABIOS (Computer Applications in BioSciences)* **11**, 361–371.

Modelling lodging in cereal crops. M. STERLING¹, C. J. BAKER¹ AND P. M. BERRY². ¹*School of Civil Engineering, The University of Birmingham, Edgbaston, Birmingham B15 2TT, UK,* ²*School of Biosciences, Division of Agriculture and Horticulture, The University of Nottingham, Sutton Bonington Campus, Loughborough, Leicestershire LE12 5RD, UK*

Lodging, the wind induced permanent displacement of cereal stems from the vertical, can cut the profitability of a cereal crop drastically through lower yield, reduced grain quality and greater drying costs (Berry *et al.* 1998). Previous research (Baker *et al.* 1998) has modelled the lodging process by considering a wheat crop to act as a damped harmonic oscillator, subjected to a stepped input. The value of the wind induced base bending moment is then compared to both the soil and stem resistance moments, lodging being assumed to occur if either of these values are exceeded. This paper will highlight the subsequent developments that have occurred which enable the lodging model to produce a realistic prediction of yield loss for a wheat crop.

The wide spatial variability in both the plant and soil parameters has been modelled successfully from a pre-existing data-set of relevant measurements. This showed these parameters to be normally distributed (subjected to maximum and minimum physiological limits) and enabled any inter-dependence between plant parameters to be quantified. In addition, empirical relationships which define the changes in plant parameters with time have been incorporated, enabling temporal changes to be modelled. The realism of the model has been achieved using actual atmospheric data collected over a 20-year period. This enables both actual and average values of lodging to be determined.

The results are insensitive to the number of plants included in the model, provided that the number of plants exceeds 300, enabling a small sample area of a typical field to be modelled and the results interpreted for the whole field. Accounting for temporal changes to the plant parameters means that the crop becomes more lodging prone through time, and this increases yield losses by 50%. By varying the soil and plant parameters the effect of site and husbandry on both lodging and yield loss can be examined, thus enabling growers to make optimum use of their lodging control methods.

The fundamental assumptions embodied in the model are being addressed currently through a series of field experiments. In order to control the meteorological conditions, a portable wind tunnel has been constructed and placed over a specially grown wheat crop, enabling the effect of both realistic and non-realistic (extreme) conditions to be examined (for further details, see Sterling *et al.* 2001).

BAKER, C. J., BERRY, P. M., SPINK, J. H., SYLVESTER-BRADLEY, R., GRIFFIN, J. M., SCOTT, R. K. & CLARE, R. W. (1998). A method for the assessment of the risk of wheat lodging. *Journal of Theoretical Biology* **194**, 587–603.

BERRY, P. M., SPINK, J. H., GRIFFIN, J. M., SYLVESTER-BRADLEY, R., BAKER, C. J., SCOTT, R. K. & CLARE, R. W. (1998). Research to understand, predict and control factors affecting lodging in wheat. *Home Grown Cereals Authority Research Project No. 169*. London: HGCA.

STERLING, M., BAKER, C. J., BERRY, P. M., SPINK, J. H., WADE, A., SYLVESTER-BRADLEY, R. & SPARKES, D. (2001). Lodging: wind induced forces on cereal crops. *3rd European & African Conference on Wind Engineering, Eindhoven*. Submitted.

An isotope dilution model for partitioning phenylalanine and tyrosine uptake by the mammary gland of lactating dairy cows. L. A. CROMPTON¹, C. K. REYNOLDS¹, B. J. BEQUETTE², M. D. HANIGAN³, J. A. MAAS⁴, J. A. N. MILLS¹, E. KEBREAB¹, C. M. YATES¹ AND J. FRANCE¹.

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Current feeding systems for ruminants, based on either metabolizable energy or protein, cannot predict milk protein output. If future nutrient based feeding systems are to predict milk protein production, they will need to include a description of intracellular amino acid partition and metabolism within the mammary gland (MG). As part of this approach, an isotope dilution model describing the partition of phenylalanine (PHE) and tyrosine (TYR) uptake by the MG of dairy cows has been constructed and solved in the steady state. The model contains four intracellular pools representing free PHE and TYR and PHE and TYR in milk protein and four extracellular pools representing arterial and venous PHE and TYR. The scheme assumes that the only entry of label into the system is via the input fluxes to the extracellular pools and that, for the duration of the infusion, the enrichment of constitutive protein can be regarded as negligible. Within the scheme, conservation of mass principles were applied to each pool to generate two sets of balance equations (one set for total PHE/TYR and one set for labelled PHE/TYR) that describe the behaviour of the system in steady state. Algebraic manipulation of these equations enables the model to be solved for the unknown steady state fluxes.

The inputs required for model solution are (i) blood flow rate across the tissue, (ii) PHE, TYR and carbon dioxide concentrations and plateau isotope enrich-

	11.7% CP				16.5% CP			
	Saline	E600	S.E.D.	<i>P</i>	Saline	E600	S.E.D.	<i>P</i>
Plasma flow rate (l/min)	4.60	4.56	0.07	0.57	4.66	4.80	0.12	0.28
Net uptake	88.4	116	12.8	0.12	94.2	97.2	10.4	0.78
Influx	109	163	13.8	0.030	118	146	13.1	0.085
Efflux	20.1	46.9	4.99	0.013	24.2	49.3	13.0	0.11
Constitutive PS	67.7	98.9	19.3	0.21	79.3	89.0	10.5	0.40
Constitutive PD	70.9	86.1	11	0.26	72.2	84.8	7.08	0.14
Milk output	87.8	98.0	3.63	0.066	85.4	91.2	2.47	0.064

ment in the arterial and venous pools, and (iii) plateau PHE and TYR enrichment in the tissue intracellular free pool (or in milk which acts as the assumed proxy in this instance). Using these data and a limited number of assumptions, the model can be solved to calculate the steady state flux rates for PHE and TYR influx, efflux, oxidation and hydroxylation, and PHE and TYR fluxes representing protein synthesis (PS) and protein degradation (PD) in constitutive and export proteins. Using the model solutions and appropriate literature values for MG protein mass and PHE and TYR content of the tissue, total (constitutive and export) protein fractional synthesis rates can be estimated for the MG.

The model was used to resolve *in vivo* stable isotope data obtained from experiments with multi-catheterized dairy cows. Six Holstein–Friesian cows (600 kg) in mid-lactation, were fed hourly a diet of chopped lucerne hay and either a low or high protein concentrate (50:50 w/w DM basis), in a crossover design, resulting in mixed rations of 11.7 and 16.5% crude protein (CP) respectively. On each dietary CP level, animals received a constant jugular vein infusion of saline for 3 days followed by essential amino acids (EAA) for a further 3 days, at a rate equivalent to the EAA in 600 g of milk protein/day (E600; 312 g EAA/d; 232 $\mu\text{mol}/\text{min}$ PHE). On day 3 of each infusion, [^{13}C]PHE and [$^{2,3,4,5-2}\text{H}$]TYR were infused into the jugular vein at 35 and 9 $\mu\text{mol}/\text{min}$ respectively for 8 h. Plasma samples were taken hourly during the isotope infusion to measure PHE and TYR concentration and enrichment across the MG.

Milk yield and dry matter intake were not affected by either dietary CP level or EAA infusion and averaged 23 and 21 kg/day respectively. Milk protein yield (MPY; g/day) was unchanged by dietary CP level, averaging 845 and 848 for the 11.7% and 16.5% CP diets, respectively. However, the increase (E600-saline) in MPY in response to EAA infusion was 76 g/day ($P = 0.044$) on the low CP diet compared to 36 g/day ($P = 0.093$) on the higher CP diet. The PHE fluxes measured across half the MG are shown in the table with units of $\mu\text{mol}/\text{min}$ unless otherwise stated.

Plasma flow rate across half the MG was not affected by diet or EAA infusion. Conversion of PHE to TYR within the MG did not change with diet or EAA infusion and on average accounted for 6.1% of PHE influx. There was no detectable oxidation of PHE across the MG. On the low CP diet, EAA infusion caused a 30% increase in PHE net uptake, which not only accounted for the increase in PHE output in milk protein, but also stimulated the MG to gain constitutive protein. However, on the higher CP diet in response to EAA infusion, only 50% of the increase in PHE output in milk protein was attributable to the change in PHE net uptake and the remainder was due to a greater increase in constitutive PD relative to constitutive PS, probably as a result of changes in intracellular amino acid channelling.

Despite some limitations, the model described is a useful tool for partitioning the uptake of PHE and TYR by the ruminant MG. The level of representation adopted means that the model could be applied to other amino acids with similar metabolic fates within the mammary gland. If the model is to be rigorously applied, future *in vivo* studies must measure directly the intracellular free amino acid enrichment in conjunction with the measurements of plasma enrichments and flow rates.

This work was funded by a consortium of the MAFF, BBSRC, Milk Development Council, Purina Mills Inc. and Hendrix Voeders B.V.

Explaining rain forest diversity. C. J. BAMPFYLDE^{1,2,3}, N. D. BROWN², D. J. GAVAGHAN¹ AND P. K. MAINI³. ¹*Oxford University Computing Laboratory, Wolfson Building, Parks Road, Oxford OX1 3QD, UK*, ²*Department of Plant Sciences, South Parks Road, Oxford OX1 3RB, UK*, ³*Centre for Mathematical Biology, Mathematical Institute, 24–29 St. Giles', Oxford OX1 3LB, UK*

Rain forests exhibit enormous tree species diversity, but the mechanisms for establishing and maintaining such diversity are unknown. To explore this phenomenon, we have developed model frameworks which

allow us to investigate the interaction of different plausible ecological processes (Bampfylde *et al.* 2001). We first examine a simple competition–colonization model, consisting of a coupled system of non-linear ordinary differential equations. The model describes the time evolution of the population density of different tree species competing for light and space and interacting in a variety of ways, including recruitment, establishment, growth and death. The aim of this simple model is to try to identify the mechanisms that drive species diversity. In the second model, competition is removed entirely and tree species are assumed to colonize sites depending on whether or not they are present, rather than on their position in the competition hierarchy. Mathematical analysis shows that neither model can exhibit species diversity for realistic parameter values. Hence we need to search for an additional mechanism.

Another mechanism observed in the rain forests of South-East Asia is random mast fruiting events. Tree species do not all flower and fruit annually, but instead gregarious fruiting events occur when the majority of species fruit at the same time. The frequency of the events is connected to the El Niño Southern Oscillation, which occurs about every 3–11 years. In order to incorporate this effect into the models the colonizing ability of a tree species is made to decay exponentially with time after a fruiting event. Field observations indicate that there is a trade off between producing many fast growing seedlings and fewer long-lived seedlings.

Within this model framework, we find that the inclusion of random fruiting events is the crucial factor necessary to predict successfully species co-existence and mimic correctly the field observations of rain forest tree dynamics.

C. B. acknowledges the financial support of the following organisations: a research studentship from EPSRC and from NERC; and D. G. a Career Development Fellowship from the Medical Research Council; which has allowed them to undertake this research. We also thank Dr Jonathan Whiteley for helpful discussions.

BAMPFYLDE, C. J., BROWN, N. D., GAVAGHAN, D. J. & MAINI, P. K. (2001). Modelling rain forest diversity: The role of competition. *American Naturalist*, submitted.

Model for ammonia systems transfers at the farm scale – MAST. C. A. ROSS, D. SCHOLEFIELD AND S. C. JARVIS. *Institute of Grassland and Environmental Research, North Wyke, Okehampton, Devon EX20 2SB, UK*

Atmospheric deposition of ammonia (NH₃) to land and aquatic surfaces can have eutrophication and acidification effects. Agricultural sources account for approximately 90% of the UK emission (Sutton *et al.*

1995), associated mainly with losses from livestock production systems and fertilizer application.

The UK is bound by 3 European directives: (1) The Gothenburg Protocol, (2) The National Emissions Ceilings Directive and (3) The EU Integrated, Pollution, Prevention and Control Directive, all directives aimed at controlling NH₃ emissions. In order to comply with the directives better prediction of losses from the main NH₃ source, livestock production systems, is required.

MAST (Model for Ammonia Systems Transfers) was developed to examine the reduction in NH₃ loss that can be achieved from the various stages in dairy, beef, pigs, sheep and poultry production systems. The user enters basic farm data on animal numbers, farm size housing and storage systems to give a baseline NH₃ emission for the farm for the year. This baseline can then be compared with a range of different mitigation options to determine the most effective strategy to reduce the NH₃ emissions on the farm. Emission for a common slurry based system was predicted to be 107 kg NH₃-N/ha/year, however, this could be reduced to 27 kg NH₃-N/ha/year using a combination of different abatement strategies. For farmyard manure the predicted range was between 86 and 33 kg NH₃-N ha/year, respectively, for the worst and best abated scenarios. The greatest reductions were achieved by manipulating options linked to manure application and fertilizer usage. MAST was written in Borland's Delphi 5.

This work was funded by the Ministry of Agriculture, Fisheries and Food (Project WA0705).

SUTTON, M. A., PLACE, C. J., EAGER, M., FOWLER, D. & SMITH, R. I. (1995). Assessment of the magnitude of ammonia emissions in the United Kingdom. *Atmospheric Environment* **29**, 1393–1411.

Modelling nitrogen utilization in dairy cows – the impact of diet on losses of nitrogen. C. F. E. TOPP AND C. J. DOYLE. *Management Division, SAC Auchincruive, Ayr KA6 5HW, UK*

The nitrogen excreted by the dairy cow impacts not only on pasture production, but also on the environment through the nitrogen losses from the system. To consider the efficiency of nitrogen use by dairy herds, a dynamic and deterministic model of the dairy cow (Topp & Doyle 1996), developed in visual basic, has been extended to cover nitrogen utilization, as well as the partitioning of energy within the grazing dairy cow. Thus the losses of nitrogen from the grazing animal and the returns of nutrients to the soil via urine and faeces, which are a function of the diet and the requirements of the dairy cow, can be explored. The sub-model describing the nitrogen flows is based on the model developed by the Agricultural and Food Research Council (1993). Essentially, the

model describes: (1) metabolizable protein requirements for protein; (2) protein intake; (3) utilization of protein; (4) microbial protein synthesis within the rumen, a function of the fermentable metabolizable energy; (5) determination of metabolizable protein; (6) faecal losses of nitrogen; and (7) urinary losses.

The inputs to the model are the crude protein content of the components of the diet, the water soluble fraction, the potentially degradable fraction and the fractional rate of degradation of the potentially degradable fraction, as defined by the AFRC (1993). In addition, the nitrogen content of the milk is a required input. There is a tendency for the model to under-predict faecal nitrogen and over-predict urinary nitrogen when the outputs of urinary and faecal nitrogen are compared with those observed by Castillo *et al.* (2001*a, b*).

The impact of changing the diet of the dairy cow from a grass-based silage to one based on a grass-white clover or lucerne silages on nitrogen excreted has been explored, using the model. Losses of urinary and faecal nitrogen were predicted to increase when the diet was based on forage legumes as opposed to grass silage (indexed nitrogen losses from the dairy cow are given in the table below). Thus, though forage legume swards are often considered more environmentally friendly because they do not require applications of inorganic nitrogen, they apparently have higher potential losses of nitrogen from the system.

Diet	Faecal N	Urinary N	Total N
Grass*	100	100	100
Grass-white clover	113	126	122
Lucerne	101	167	147

* Nitrogen losses from the grass diet are assumed to equal 100.

SAC receives financial support from the Scottish Executive Rural Affairs Department and the LEGSIL project is funded by the European Union (Contract FAIR CT96-1832).

AGRICULTURAL AND FOOD RESEARCH COUNCIL (1993). *Energy and Protein Requirements of Ruminants*. An advisory manual prepared by the AFRC Technical Committee on Responses to Nutrients. Wallingford: CAB International.

CASTILLO, A. R., KEBREAB, E., BEEVER, D. E., BARBI, J. H., SUTTON, J. D., KIRBY, H. C. & FRANCE, J. (2001*a*). The effect of energy supplementation on nitrogen utilization in lactating dairy cows fed grass silage diets. *Journal of Animal Science* **79**, 240–246.

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TOPP, C. F. E. & DOYLE, C. J. (1996). Simulating the impact of global warming on milk and forage production in Scotland: 2. The effects on milk yields and grazing management of dairy herds. *Agricultural Systems* **52**, 243–270.

A model for estimating endogenous nitrogen losses across the rumen. G. ZUUR¹, D. R. OUELLET², H. LAPIERRE² AND G. E. LOBLEY³. ¹*Biomathematics and Statistics Scotland, Rowett Research Institute, Bucksburn, Aberdeen AB21 9SB, UK*, ²*Agriculture and Agri-Food Canada, Dairy and Swine R&D Research Centre, CP 90 Lennoxville, Quebec J1M 1Z3, Canada*, ³*Rowett Research Institute, Bucksburn, Aberdeen AB21 9SB, UK*

Endogenous nitrogen (N) secretions into the gut can be determined after long-term isotopic labelling of body proteins and measuring differences in the enrichment (*E*) of digesta between sites in the digestive tract. For ruminants, the traditional isotope dilution model applied to the rumen includes recycled urea-N as endogenous loss, but this leads to overestimates of endogenous amino acid losses. The contribution of endogenous protein loss is important in prediction schemes, such as the NRC system (National Research Council 2001), which need to define the sources of amino acids that flow into the duodenum.

An isotope dilution model was constructed to separate the flow of duodenal N (F_{duo}) into undigested feed N ($F_{duo, feed}$), free endogenous N ($F_{duo, end}$) and bacterial N ($F_{duo, bac}$), with the latter subdivided into N from endogenous ($F_{bac, end}$), feed ($F_{bac, feed}$) and urea ($F_{bac, urea}$) sources:

$$F_{duo} = F_{duo, feed} + F_{duo, end} + F_{duo, bac}$$

$$F_{duo, bac} = F_{bac, feed} + F_{bac, end} + F_{bac, urea}$$

$$E_{duo} F_{duo} = E_{feed} F_{duo, feed} + E_{end} F_{duo, end} + E_{bac} F_{duo, bac}$$

$$E_{bac} F_{duo, bac} = E_{feed} F_{bac, feed} + E_{end} F_{bac, end} + E_{urea} F_{bac, urea}$$

$$F_{bac, urea} = p F_{duo, bac}$$

where $F_{duo, feed}$, $F_{duo, end}$, $F_{bac, feed}$ and $F_{bac, end}$ are unknown.

This model was applied to data from lactating (220 days) dairy cows labelled with [¹⁵N]L-leucine (8 day continuous intra-jugular infusion at 13.7 mmol/day), and assumes that 12% of bacterial N is derived from urea-N ($p = 0.12$), with E_{urea} and E_{end} given by urine and intestinal mucosa ¹⁵N enrichments, respectively. Results for high fibre (HF) and low fibre (LF) diets are given in the table (mean values for three (HF) and four (LF) cows; DM intake: 14.2 kg/day, N intake: 398 g/day, mean body weight: 607 kg):

Composition of duodenal N flow (g N/d)	HF	LF	S.E.D.
Duodenal N flow (F_{duo})	398	434	15.6
Feed N ($F_{\text{duo, feed}}$)	79	53	3.6
Free endo N ($F_{\text{duo, end}}$)	36	36	5.8
Bacterial N ($F_{\text{duo, bac}}$)	282	345	14.4
Urea N ($F_{\text{bac, urea}}$)	34	41	1.7
Feed N ($F_{\text{bac, feed}}$)	217	272	10.6
Endo N ($F_{\text{bac, end}}$)	32	31	3.4
Total endogenous N ($F_{\text{end}}; F_{\text{end}} = F_{\text{duo, end}} + F_{\text{bac, end}}$)	68	67	9.0

The calculated value for $F_{\text{duo, end}}$ of 2.5 g N/kg dry matter/day is approximately 30% greater than the 1.9 currently used by NRC.

Sensitivity analysis was used to examine the importance of E_{urea} , p and E_{end} measurements. An error of +50% or -50% on either E_{urea} or p gives a -12.2 to +12.2% error on F_{end} , whereas an error of +50% or -50% on E_{end} has a much larger effect on F_{end} , namely -33.3 to +100%. Thus accurate measurement of E_{end} is more important than either E_{urea} or p in definition of endogenous flows through the rumen.

The Scottish Executive Rural Affairs Department and the Dairy Farmers of Canada are thanked for funding this research.

NATIONAL RESEARCH COUNCIL (2001). *Nutrient Requirements of Dairy Cattle, 7th Revised Edition*. Washington, DC: National Academic Press.

Analysing the efficiency of energy utilization for milk production in dairy cows. E. KEBREAB¹, J. FRANCE¹, C. M. YATES¹, J. A. N. MILLS¹, L. A. CROMPTON¹, R. E. AGNEW² AND T. YAN². ¹The University of Reading, Department of Agriculture, Earley Gate, Reading RG6 6AR, UK, ²The Agricultural Research Institute of Northern Ireland, Hillsborough, Co Down, Northern Ireland, BT26 6DR, UK

The energy requirements of dairy cows in the UK are calculated according to the metabolizable energy (ME) feeding system for ruminants, based on studies conducted more than four decades ago. Various revisions have been made since then, with the most recent working version published in 1993 (AFRC 1993). The ME system relies on key parameters such as efficiency of utilization of ME intake for maintenance (k_m), for milk production (k_l), for growth (k_g) and efficiency of utilization of tissue energy for milk production (k_b). Similarly, the American system (NRC 1989) is based on calorimetric data reported by Moe *et al.* (1971).

A database of calorimetric data containing 465 energy balance observations was constructed from

experiments conducted at the Agricultural Research Institute of Northern Ireland (ARINI) and the Centre for Dairy Research (CEDAR), The University of Reading. These were used to compare results of analysis made using the classical method, based on multiple linear regression, and a new approach employed in this study. The new approach uses zero (± 5 MJ) energy balance data to estimate k_l , and the estimate of k_l is then used to estimate k_g and k_b from positive and negative energy balance data, respectively.

A direct comparison between nationally recommended values of efficiencies of energy utilization and values obtained from our set of data using the classical method of analysis showed significant differences in key parameters. For example, the estimate of maintenance requirement (0.51 MJ/kg LW^{0.75}/day; Moe *et al.* 1971) is much lower than the value obtained from our data (0.73 MJ/kg LW^{0.75}/day). However, using the new method of analysis, by taking the zero balance data only and estimating k_l , maintenance requirement is calculated to be 0.60 MJ/kg LW^{0.75}/day and k_l 0.61. The recommended value for k_b is 0.84 (Moe *et al.* 1971; AFRC 1993), but our results show a much lower value of 0.69. The recommended value for k_g is 0.6 (AFRC 1993) and 0.75 (Moe *et al.* 1971), but our results show the value is 0.86, which is closer to the value estimated using the new method of analysis. These significant differences suggest that the national recommendations for efficiencies of energy utilization need to be revised.

This research was funded through the MAFF Link project Feed-into-Milk.

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NATIONAL RESEARCH COUNCIL (1989). *Nutrient Requirements of Dairy Cattle*. Washington, DC: National Academic Press.

Differential equation models for biological data dependent on functions of environmental variables. S. J. POWERS, P. BRAIN AND P. W. BARLOW. *IACR-Long Ashton, Department of Agricultural Sciences, University of Bristol, Bristol BS41 9AF, UK*

Day-degrees (units of thermal time) are often used in place of simple time units, as a basis for modelling the development of organisms. Examples include: studies of leaf development (Wurr *et al.* 1998), seed germination (Grundy *et al.* 2000) and the assessment of disease risk (Zijp & Blommers 1997). However, the development of an organism may be influenced

significantly by additional factors such as day-length (Scaife *et al.* 1987), or moisture (Gummerson 1986). These lead to composite units such as hydrothermal time. Organism development can therefore be modelled in terms of functions of one or more external stimuli.

In the present paper, day-degrees and hydrothermal time are seen as special cases of 'developmental units', which are the monotonically increasing functions of the external stimuli regarded as critical in a given developmental process. A method is proposed whereby developmental units are used to model organism development which, at the same time, requires the solution of differential equations. As in day-degrees modelling, the rate parameters in the equations are proposed to be dependent on the environment. Thus, the equations are derived with functions of external stimuli regulating the current state of the system components. Consequently, if the environment at time t is denoted by $E(t)$, then a general differential equation for a biological system with only one component, describing some measure, W , of organism development, would be of the form:

$$\frac{dW}{dt} = f(E(t)) \times g(W),$$

where $g(W)$ is a function of the current state of the organism. This equation can be rewritten as:

$$\frac{dW}{d(\int^t f(E(u))du)} = g(W)$$

so that the 'time' variable, t , in the differential equation is replaced by $DU(t) = \int^t f(E(u))du$, where $DU(t)$ are the developmental units for the organism. Hence, developmental units arise naturally in simple differential equations where the rate parameter is dependent on the environment.

For systems of equations with inter-linked components, the concept of developmental units is relevant, but the relationship between the rate parameters and the environment may be different for different components. In this case, the resulting solution for each component may depend on some combination of different types of developmental units. These are employed in the system, with time being replaced by all relevant combinations of developmental units. The estimates of the parameters in the functions allow closer interpretation of the critical environmental influences on development.

To illustrate the approach, data from an experiment that investigated stem growth in aspen trees over two years were modelled. The numbers of three types of inter-related cells (cambial, xylem fibre and vessel) and those cells pertaining to a growth ring after the first year's growth, as seen in cross-sections of the stem, were counted at monthly intervals. The cambial cells divided to produce more cambial cells, but also

differentiated to give xylem fibre, vessel and growth ring cells. The system was modelled using simultaneous differential equations, one for each type of cell, but with different types of developmental units relating to specified environmental conditions.

The form of the relationship between the development rate parameters and the environment (the developmental units) was investigated. Estimation of the parameters was achieved by minimizing the weighted residual sum of squares between the predicted cell numbers and the observed cell numbers, where the predicted numbers were obtained by numerical solution of the differential equations.

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Quantifying lodging resistance of cereal cultivars: a field-based approach. M. J. CROOK. *Crop and Environmental Research Centre, School of Agriculture, Harper Adams University College, Newport, Shropshire TF10 8NB, UK*

Lodging has always been a serious problem to growers and can cost the UK wheat industry up to £120 million per year (Berry *et al.* 1998). One reason for its persistence is that resistance is difficult to select for. This is because of the unpredictability of lodging: in some years no lodging will occur in field trials whilst in others all cultivars will fall over, making it difficult to grade different cultivars for lodging resistance.

An advance is to devise a method of assessing lodging susceptibility of cultivars even when lodging does not occur. Here, a field-based method to do this is examined. This method (Crook & Ennos 2000) is based upon an established model of lodging failure (Crook & Ennos 1994, 1995; Crook *et al.* 1994) in which the anchorage moment (M , Nm) provided by a plant is given by:

$$M = (9/8)\tau\pi D^3$$

where τ (Pa) is the shear strength of the soil and D (m) is the diameter of the plant's root-cone. The forces,

which the plant must resist if it is to remain upright, are estimated by calculating the 'self-weight' moment generated by the plant's stems and ears.

Field measurements are made using a 'lodging meter' which measures the most important characteristics of the plant in keeping it upright: stem strength, anchorage moment and self-weight moment. Together these measurements allow the lodging resistance between cultivars to be quantified by calculating factors of safety against both stem (SF_{SL}) and root lodging (SF_{RL}), where:

$$SF_{SL} = \text{Tiller bending strength/Tiller self-weight moment}$$

$$SF_{RL} = \text{Anchorage moment at } x^\circ \text{ lean/Plant self-weight moment at } x^\circ \text{ lean.}$$

Tests show that the meter is able to quantify differences in lodging resistance of wheat cultivars. However, the technique was not successful in quantifying differences between barley cultivars. Why this is so is discussed.

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An integrated modelling approach to providing cost-effective means of reducing methane emissions from dairy cows. C. M. YATES, J. A. N. MILLS, E. KEBREAB, L. A. CROMPTON AND J. FRANCE. *The University of Reading, Department of Agriculture, Earley Gate, Reading RG6 6AR, UK*

The UK government, along with its EU partners, is committed to a 12.5% reduction in methane emissions by 2010. Emissions from dairy cows account for 10–15% of total UK methane output. The objectives

of this study were (i) to predict levels and variability of methane emissions from dairy cows using statistical and mechanistic modelling, and (ii) to develop cost-effective strategies to reduce emissions using operational research techniques. A database was constructed with 143 measurements of feed composition, nutrient intakes and methane production for lactating dairy cows from seven calorimetry trials. Total mixed rations consisted of whole-crop wheat, fresh grass, grass silage, maize silage and concentrates. In the first instance, statistical models were developed using multiple regression techniques to predict methane emissions from nutrient intakes. An overall prediction equation was constructed ($R^2 = 0.54$) for all diets; however, for silage-based diets an alternative equation was also constructed ($R^2 = 0.72$). Subsequently, a detailed mechanistic model of ruminant methanogenesis, developed from an existing model of rumen function, was used to extend the results of the statistical modelling analysis (Mills *et al.* 2001). In the final phase of this study, operational research techniques were used to explore potential strategies for reducing methane emissions. A linear programming (LP) model was constructed at the herd level to examine the effects of dietary composition on milk production. The results of the simulations were assessed on their implications for production economics and management, such as milk quota allocation, resource use and milk quality. Tables 1 and 2 show that feeding increased levels of maize silage not only reduced methane emissions but also is profitable. The use of high-starch concentrates also reduced emissions whilst remaining economically viable. At the national level, an improvement in herd fertility would not only increase farm incomes but would also reduce methane production. These results show the trade-offs between methane emissions and profitability, and the importance of considering this problem at a herd level.

Table 1. Methane production ($MJ CH_4$ per litre milk) for a range of diets, milk yields and fertility using the LP model

	LCR	GS	MS	M × G	HSC	LSC
Base run	1.30	1.51	1.24	1.36	1.24	1.32
Low milk production	1.42	1.61	1.37	1.48	1.38	1.51
High milk production	1.18	1.45	1.13	1.27	1.13	1.23
Low fertility	1.22	1.42	1.16	1.29	1.17	1.30
High fertility	1.37	1.62	1.31	1.45	1.31	1.46

Diets: least cost ration (LCR); grass silage (GS); maize silage (MS); mixed silage (M × G); high-starch concentrate (HSC); low-starch concentrate (LSC).

Table 2. Changes to herd gross margins (%) for a range of diets, milk yields and fertility using the LP model

	LCR	GS	MS	M × G	HSC	LSC
Base run	0.0	-1.0	-0.2	-0.5	-0.4	-0.7
Low milk production	-4.4	-4.6	-3.9	-3.0	-3.0	-3.3
High milk production	-0.2	-0.1	-0.1	-0.1	-0.1	-0.2
Low fertility	-2.6	-2.1	-2.0	-2.1	-2.0	-2.3
High fertility	3.2	2.4	2.8	2.6	2.5	2.4

Diets: least cost ration (LCR); grass silage (GS); maize silage (MS); mixed silage (M × G); high-starch concentrate (HSC); low-starch concentrate (LSC).

The Ministry of Agriculture, Fisheries and Food is thanked for funding this research under grant CC0239.

MILLS, J. A. N., DIJKSTRA, J., BANNINK, A., CAMMELL, S. B., KEBREAB, E. & FRANCE, J. (2001). A mechanistic model of whole tract digestion and methanogenesis in the lactating dairy cow. Model development, evaluation and application. *Journal of Animal Science*, in press.

Modelling rain splash and predicting vertical splash height using raindrop kinetic energy. S. PIETRAVALLE. IACR-Rothamsted, Harpenden, Hertfordshire AL5 2JQ, UK

Rain splash is the most important factor in the spread of conidiospores in splash-dispersed diseases such as Septoria leaf blotch (*Septoria tritici*) and Stagonospora blotch (*Stagonospora nodorum*) on winter wheat. Dispersal of such diseases is usually predicted using simple rainfall characteristics such as the amount, the duration or the rate. However, significant differences in splash height can occur between rainfalls with similar characteristics (Shaw 1991). A 'splash-meter' (Shaw 1987) was developed to observe splash height, but although giving good measurements, it proved too labour-intensive to enable effective crop spray decisions. Secondly, it could not associate splashes with time and only gave a summary of splashes during the exposure period. Thirdly, it is too large to be used practically in a crop for research purposes.

Lovell (1999) showed that kinetic energy of the impacting drops is related to splash height for drops at terminal velocity. Therefore, an 'impact sensor' was developed (Aardware design) to record the kinetic energy of an impacting drop.

We derived a mechanistic model that describes the trajectory of splashing droplets as a function of the kinetic energy of the impacting drops. We ignored in-flight evaporation and approximated droplet trajectories using simple parabolas that underestimate the initial velocity (Allen 1987). For any given impacting kinetic energy, a Gamma distribution was fitted to the initial droplet velocity (Allen 1987; Yang

et al. 1991) and the angle of release of droplets was assumed constant (Allen 1987). Rain tower experiments were used to estimate the three model parameters.

This model allows us to predict, for any raindrop kinetic energy, the vertical distribution of splashes at any given distance from the impacting point of the raindrop. Combining these distributions with records from the impact sensor allows prediction of splash height distribution for any given rainfall. The model was used on 21 natural rainfalls and predictions were compared with observations from the splashmeter. The overall splash height distribution was well predicted except at lower heights. The distance between the centre of the impact sensor and the drop impacting point, the time-period of the impact sensor and 'secondary' splashes may explain these differences.

This work can be used, subject to corrections due to canopy architecture, in relation with 'lesion proximity' (distance between highest lesion and emerging leaves) to predict risks of spread of disease within a crop.

This talk arises from work done in collaboration with F. van den Bosch, S. J. Welham, S. R. Parker and D. J. Lovell. This work was funded by the UK Ministry of Agriculture, Fisheries and Food. IACR Rothamsted receives grant-aided support from BBSRC.

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Graphical modelling of nitrogen response in crops. C. J. HINDE¹, A. J. ESCOBAR-GUTIERREZ², R. J. READER², K. PHELPS² AND I. G. BURNS². ¹Department of Computer Science, University of Loughborough, Loughborough, Leicestershire LE11 3TU, UK, ²Horticulture Research International, Wellesbourne, Warwick CV35 9EF, UK

NABLE (Greenwood *et al.* 1996) is a widely used N response model developed over a number of years at HRI to predict the effects of mineral N from soil and fertilizer on the growth and final yield of a range of vegetable and some arable crops. It takes account of

daily changes in the weather, the properties of the soil and the characteristics of the crop to predict the cycling of N in the soil, its uptake by the crop and its effect on growth. It assumes that the plants are grown in rows, with the soil profile divided into a series of separate horizontal and vertical zones in order to take account of within- and between-row spatial variation in soil processes on the redistribution and uptake of mineral N. Simulated response curves are used to predict the optimum N fertilizer requirement of the crop.

N_ABLE consists of a number of separate but highly integrated sub-models describing the various component processes involved. As such, it provides a valuable resource for other models (e.g. plant competition and weed models) through its component sub-models. The associated FORTRAN program is complex with approximately 20,000 lines of source code.

Use of the modelling tool HIPPO (Hinde *et al.* 2000) allows N_ABLE to be represented in a form that is readily comprehensible to other scientists. It can be readily extended and modified without knowledge of the underlying HIPPO generated computer code. This representation is presented and some of its implications discussed.

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Modelling the sorption and degradation of pesticides: a laboratory study. C. D. BROWN¹ AND D. A. ROSE. ¹*Department of Agricultural & Environmental Science, University of Newcastle, Newcastle upon Tyne NE1 7RU, UK, ¹Now Cranfield Centre for EcoChemistry, Cranfield University, Silsoe, Bedfordshire MK45 4DT, UK*

A field experiment (Brown *et al.* 1995) at Cockle Park, Northumberland, on a clay loam soil cropped with winter wheat explored the effects of drainage and season of application on the movement of four pesticides (fonofos, isoproturon, mecoprop, trifluralin) in drainage water and sorbed to sediment. In order to understand better the environmental behaviour of these pesticides, standard sorption and

degradation incubations were performed in the laboratory on three soils having contrasting physical properties.

Sorption was described by Freundlich isotherms having coefficients ranging between 0.8 and 1.0, in good agreement with many previous studies. These isotherms reduced to linear relations at the low solution concentrations typically found in the field, with distribution coefficients that depended strongly on the organic-matter content of the soil. These distribution coefficients were compatible with estimates from an equation of Briggs (1981), which also requires a knowledge of the octanol-water partition coefficient of the pesticide.

Degradation was studied in closed and open incubators, the closed system limiting air supply to the microbial population of the soil and eventually inducing anaerobic conditions, the open system remaining aerobic at all times. The experiments were factorials, e.g. 3 soil types \times 3 temperatures (T) \times 3 soil-water contents (θ) \times 4 pesticides, with replicate containers sampled at 10 different times up to 250 days. In closed systems, degradation was well fitted by dual first-order kinetics, an initial rapid degradation (presumably aerobic) with half-lives typically 10–20 days followed by slow degradation (presumably anaerobic) with half-lives of the order of 200–2000 days, the half-lives generally decreasing as both T and θ increased. In open systems, degradation followed simple first-order kinetics, with the first-order rate coefficients, k , being related to environmental conditions by best-fit multiple regression equations of the form:

$$\sqrt{k} = a + b\sqrt{\theta} + cT^2.$$

Using these equations, diagrams of the effect of environmental conditions on degradation rates, drawn as contours of k (or half-life) on a graph of T against θ , were produced. Such a representation (i) allows a clear visual display of the effect of environmental conditions on pesticide degradation and (ii) demonstrates, from the spacing of the contours, the sensitivity of individual soil–pesticide pairs to change in environmental conditions.

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