
ABSTRACTS OF COMMUNICATIONS

Proceedings of the Twenty-Ninth 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-ninth meeting of the group, chaired by Professor R. H. Ellis of the Department of Agriculture, University of Reading, was held in the Wellcome Meeting Room at the Royal Society, 6 Carlton House Terrace, London on Friday, 21 March 1997, when the following papers were read.

Decoherence – A useful paradigm for modellers? T. M. ADDISCOTT. *IACR-Rothamsted, Harpenden, Herts AL5 2JQ, UK*

Classical physics is deterministic in nature, whereas modern quantum physics, which is concerned mainly with processes within atoms, is not. The Solar System behaves in an entirely determinate, Newtonian way, but particles within the atoms of which it is made up obey the laws of chance. That these vastly different hierarchical levels behave so differently is not surprising, but do we have a concept for the difference? This loss of indeterminacy by large quantum systems was described by Stewart (1995) as *decoherence*. It is a potentially useful concept for agricultural and environmental modellers, who also deal with processes at different hierarchical levels and for whom scaling up models is an increasingly important problem.

One implication of decoherence is that large areas of land should behave in a more determinate and therefore more predictable way than small areas. This may seem counter-intuitive, but denitrification provides an example. In small volumes of soil, active microsites or 'hotspots' control denitrification (Parkin 1987), and these are unpredictable with respect to their location and behaviour. The process remains difficult to predict at the scale of the field, but Groffman & Tiedje (1989) and Corre *et al.* (1996) have shown that predictive relationships for denitrification become easier to establish at the scale of the landscape.

The roots of decoherence can be found in the original statement by Laplace that underpins de-

terminism (see Stewart 1995). The concept should help modellers choose between deterministic and stochastic approaches on a rational basis, rather than that of personal preference, if it is used in conjunction with the scale diagram of Hoosbeek & Bryant (1992) to define the level of determinacy appropriate for modelling processes at particular scales.

CORRE, M. D., VAN KESSEL, C. & PENNOCK, D. J. (1996). Landscape and seasonal patterns of nitrous oxide emissions in a semiarid region. *Soil Science Society of America Journal* **60**, 1806–1815.

GROFFMAN, P. M. & TIEDJE, J. M. (1989). Denitrification in north temperate forest soils: spatial and temporal patterns at the landscape and seasonal scales. *Soil Biology and Biochemistry* **21**, 613–620.

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

PARKIN, T. B. (1987). Soil microsites as a source of denitrification variability. *Soil Science Society of America Journal* **51**, 1194–1199.

STEWART, I. (1995). *Nature's Numbers*. London: Wiedenfeld & Nicholson.

Interactions between defoliation, resource allocation to leaves, and plant growth. C. P. D. BIRCH AND B. THORNTON. *Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB15 8QH, UK*

A mathematical model was developed to investigate whether allocation patterns adapted to repeated, substantial defoliation may differ from those adapted

to other conditions. It considers the trade-off between production of leaf mass and other mass. Leaves are assumed to include all photosynthetic machinery and all tissue exposed to defoliation. Thus, allocation away from the leaves reduces growth before the next defoliation, but also increases the mass certain to survive defoliation. The net assimilation rate per unit leaf mass is allowed to change over time, but constant partitioning is assumed. When defoliation is frequent in an immediate neighbourhood and the leaf masses before and after defoliation are weakly related, low allocation to leaves maximizes the net increase in plant mass. This low allocation to leaves in the medium term contrasts with the rapid remobilization to shoots immediately after defoliation characteristic of grazing-tolerant grasses (Richards 1993). However, when leaf masses before and after defoliation are strongly related, the model predicts high allocation to leaves, suggesting that allocation may be mainly determined by the functional balance between root and shoot.

Results from the model were compared with measurements from an existing study of remobilization in four grass species (Thornton *et al.* 1993). After prolonged, weekly, severe clipping, dryland browntop (*Agrostis castellana*) and red fescue (*Festuca rubra*) allocated a smaller proportion of growth to leaves than ryegrass (*Lolium perenne*) or rough meadow-grass (*Poa trivialis*), indicating that different strategies of allocation after defoliation exist among grasses. Although leaf growth between defoliations of browntop and fescue was similar to that of ryegrass and meadow-grass (0.17 and 0.15 g v. 0.16 and 0.23 g), their total biomass was greater after a series of repeated weekly clippings (2.2 and 2.0 g v. 0.7 and 1.2 g). The model predicted that a low allocation to leaves would be optimum under the experimental conditions, so these observations were consistent with the model.

RICHARDS, J. H. (1993). Physiology of plants recovering from defoliation. In *Proceedings of the 17th International Grassland Congress, Hamilton, New Zealand*, pp. 85–94.
 THORNTON, B., MILLARD, P., DUFF, E. I. & BUCKLAND S. T. (1993). The relative contribution of remobilization and root uptake in supplying nitrogen after defoliation for regrowth of laminae in four grass species. *New Phytologist* **124**, 689–694.

The effect of the functional form of the photosynthesis equation: a comparison of four models. C. F. E. TOPP AND C. J. DOYLE. *Department of Applied Economics and Agricultural Systems, SAC Auchincruive, Ayr KA6 5HW, UK*

Currently there are a number of functional forms that have been used to represent the diurnal variation in radiation and temperature in the mathematical de-

scription of the photosynthesis process. This may have implications for the projected yields. Four models of the photosynthesis process which are all based on the non-rectangular hyperbola have been incorporated into a model of the grass-clover sward.

Daily values for the temperature and radiation are used in model 1 (Johnson & Thornley 1984). In contrast, in model 2 the temperature and radiation were approximated by sinusoidal time functions (Thornley & Johnson 1990) and were calculated every 20 min. The third model requires expanding the function describing canopy photosynthesis as a Taylor series about the mean value of the radiation and temperature (Thornley & Johnson 1990). The diurnal variations in the environmental variables are incorporated in this model by defining the coefficients of variation of radiation and temperature, and the correlation coefficient between radiation and temperature. In model 4, Sands (1995) assumed that the above canopy photosynthetically active radiation varies sinusoidally. The diurnal variation in the temperature is incorporated in the model by calculating the function for the average morning and afternoon temperatures.

The results for the sward indicated that in terms of the yield of the grass, white clover and the combined yield, photosynthesis sub-model 1 gave the highest production, followed by sub-models 2, 4 and 3. The differences between sub-models 3 and 4 were not significant. However, sub-model 1 resulted in significantly higher yields than sub-model 2, which was significantly higher than sub-models 3 and 4. There was no significant difference between the models in the proportion of white clover harvested.

JOHNSON, I. R. & THORNLEY, J. H. M. (1984). A model of instantaneous and daily canopy photosynthesis. *Journal of Theoretical Biology* **107**, 531–545.

SANDS, P. J. (1995). Modelling canopy production. II. From single-leaf photosynthetic parameters to daily canopy photosynthesis. *Australian Journal of Plant Physiology* **22**, 603–614.

THORNLEY, J. H. M. & JOHNSON I. R. (1990). *Plant and Crop Modelling: a Mathematical Approach to Plant and Crop Physiology*. Oxford: Clarendon Press.

Dynamics of soil water under temperature gradients. M. ASHRAF, D. A. ROSE AND M. A. ADEY. *Department of Agricultural & Environmental Science, University of Newcastle, Newcastle upon Tyne NE1 7RU, UK*

The movement of water and heat are closely coupled near the soil surface, especially in arid and semi-arid regions. The theory of Philip & de Vries (1957) has been used extensively to describe water movement in homogeneous soil under non-isothermal conditions in terms of gradients of temperature and of water

content. Their theory is: (i) recast in terms of gradients of temperature and of water potential to make it applicable to saline and heterogeneous soils; and (ii) extended to allow for the effects of temperature and salinity on relative humidity. Both theories were evaluated under five different experimental conditions in a controlled environment. Experiments were conducted on a sandy loam packed into vertical columns in which there were fluxes of non-saline water both into (from a water table at 55 cm depth) and out of the soil (evaporation to the atmosphere).

The original theory (Philip & de Vries 1957) predicted the measured soil-water flux well at low water contents but overpredicted by factors of 2–20 at intermediate and high water contents. The extended theory predicted the measurements well at low matric potentials but underpredicted by factors of up to 20 at intermediate and high matric potentials. These discrepancies may be due to the difficulty of calculating fluxes near the surface where moisture gradients are large and consequently transport coefficients vary rapidly. Under such circumstances it is uncertain what form of 'average' transport coefficient should be used to calculate the flux between successive depths at which potentials have been measured.

Temperature gradients had a significant effect on soil-water movement throughout the entire range of water content. Vertical temperature gradients aided the formation of a dry layer at the soil surface that decreased the evaporation rate. The steeper the temperature gradient, the sooner such a dry layer formed and the faster the evaporation rate fell to a steady value (generally $< 1 \text{ mm d}^{-1}$) compared to the evaporativity of the atmosphere ($c. 20 \text{ mm d}^{-1}$). The steeper the temperature gradient, the greater was the water-content gradient over the top few centimetres. The shallow water table contributed significantly to evaporation.

The evaporative flux within the soil is the resultant of five components. The *isothermal vapour flux* was negligibly small in all experiments. The *thermal vapour flux* was negligibly small below 10 cm but its magnitude at the soil surface increased with decreasing water content and increasing temperature. The *isothermal liquid flux* contributed significantly to the net soil-water flux except at very low water contents. *Thermal liquid flux* contributed significantly to the net soil-water flux except at very low water contents and was comparable in magnitude to both the isothermal liquid flux and net vapour flux. The downward *liquid flux due to gravity* was comparable in magnitude to those of the isothermal and thermal liquid fluxes, particularly at high water contents.

PHILIP, J. R. & DE VRIES, D. A. (1957). Moisture movement in porous materials under temperature gradients. *Transactions of the American Geophysical Union* **38**, 222–232.

Short-term and long-term responses to CO₂ fertilization in N-poor and N-rich grassland. J. H. M.

THORNLEY AND M. G. R. CANNELL. *Institute of Terrestrial Ecology, Edinburgh EH26 0QB, UK*

The Hurlley Pasture Model is a mechanistic grassland ecosystem simulator which represents the coupled fluxes and pools of C, N and water in the atmosphere, plant, animal, litter and soil system. The model has been used to address by means of simulation two questions which cannot be directly answered by experimentation: (i) are the long-term responses of commonly measured variables in N-poor grassland to CO₂ fertilization limited by lack of N? (ii) do short-term experiments on grassland responses to CO₂ fertilization give accurate or misleading information about the long-term responses?

N-poor and N-rich grasslands have experienced respectively annual N inputs of 5 and 100 kg N ha⁻¹ y⁻¹. They are in a steady-state with *c.* 2000 and 12000 kg N ha⁻¹ in the soil–plant system.

The answer given by the model to the first question is that, contrary to the view of some researchers, the long-term response of N-poor grassland to CO₂ fertilization can be very substantial indeed, often proportionately much higher than is attained in N-rich grassland. This effect can be traced back to the mechanisms represented in the model, and is mediated via increases in gross photosynthesis, plant sugar levels, root/shoot ratio and root activity, C exudation, giving decreased soil mineral N pools and N losses, leading to a slow accumulation of C and N in the system. An N-poor grassland is on the linear steep portion of an N fertilizer response curve (e.g. Whitehead 1995, p. 205); CO₂ enrichment tightens the system against N losses, improves N nutrition, so the response to CO₂ is amplified by the improved N nutrition. An N-rich grassland is on the flat asymptote of the fertilizer response, so the CO₂ response cannot be enhanced by a N nutrition effect.

The answer to the second question is that short-term and long-term responses can be very different in N-poor grassland, even of opposite sign for some variables, and this could be highly misleading since experiments are inevitably short-term. In N-rich grassland, short- and long-term responses are at least qualitatively similar, although it hardly seems possible to infer the long-term quantitative consequences from short-term data.

Our simulations suggest that plant ecosystem models, thoroughly evaluated in short-term experiments and by experiments at the process level, may now be giving more reliable answers to climate change questions than is directly given by the experimental results themselves.

WHITEHEAD, D. C. (1995). *Grassland Nitrogen*. Wallingford: CAB International.

A structure for modelling post-absorptive nitrogen metabolism in the lactating dairy cow. D. E. BEEVER¹, J. FRANCE², M. D. HANIGAN³, J. DIJKSTRA⁴ AND J. C. MACRAE⁵. ¹Centre for Dairy Research, University of Reading, Reading RG6 2AT, UK, ²Institute for Grassland and Environmental Research, North Wyke, Okehampton, Devon EX20 2SB, UK, ³Purina Mills Inc., P.O. Box 66812, St Louis, MO 63166-6812, USA, ⁴Wageningen Institute of Animal Sciences (WIAS), Animal Nutrition Division, Marijkeweg 40, 6709 PG Wageningen, the Netherlands, ⁵Rowett Research Institute, Bucksburn, Aberdeen AB21 9SB, UK

Whilst the several metabolizable protein schemes (e.g. AFRC 1992) now available for assessing the protein requirements of dairy cattle are considered adequate for predicting changes in amino acid supply to the duodenum following dietary manipulation, they are not good at predicting the responses in milk constituent output to these changes in amino acid absorption, possibly because their representation of post-absorptive metabolism is a fixed linear function. The modelling described in this paper forms part of a collaborative, industrially-funded research project concerned with improving quantitative understanding of the nutritional and physiological basis of post-absorptive amino acid utilization and milk protein synthesis in lactating dairy cows. As such, it impinges on UK government objectives in relation both to the effective use of feed resources and to the production of milk components in the required proportions. The primary goals of the modelling exercise are: (i) to develop simple, experiment-specific models of the mammary gland, liver, gastro-intestinal tract and blood flow; and (ii) to construct a dynamic, mechanistic model, which integrates information across experiments and from the literature, of post-absorptive nitrogen metabolism in the lactating dairy cow to study effects on the output of milk constituents (review Hanigan *et al.* 1997a).

The structure adopted for the modelling exercise comprises four biological compartments (i.e. mammary, liver, gut and blood) and four modelling phases (i.e. kinetic, dynamic, holistic and integrative modelling). The kinetic modelling phase concerns constructing and solving steady state, single amino acid, isotope dilution submodels for each of these biological compartments (e.g. France *et al.* 1995, 1997). The dynamic phase relates to developing dynamic, single amino acid submodels for each compartment (e.g. Hanigan *et al.* 1997b). The holistic phase concerns building independent models of the mammary gland, the liver, the gastro-intestinal tract and blood flow which represent explicitly all the significant amino acids and energy-yielding nutrients. The integrative phase relates to building the model of post-absorptive metabolism by integrating the holistic mammary, liver, gut and blood flow models. The

work presented in this paper focuses on aspects of the mammary and liver modelling.

The consortium comprising government (MAFF, BBSRC, SOAEFD) and agribusiness (MDC, Purina Mills, Hendrix) is thanked for funding this work.

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- FRANCE, J., BEQUETTE, B. J., LOBLEY, G. E., METCALF, J. A., WRAY-CAHEN, D., DHANOA, M. S., BACKWELL, F. R. C., HANIGAN, M. D., MACRAE, J. C. & BEEVER, D. E. (1995). An isotope dilution model for partitioning leucine uptake by the bovine mammary gland. *Journal of Theoretical Biology* **172**, 369-377.
- FRANCE, J., HANIGAN, M. D., BEQUETTE, B. J., METCALF, J. A., BEEVER, D. E., LOBLEY, G. E., MACRAE, J. C. & BACKWELL, F. R. C. (1997). A model for quantifying the contribution of extracellularly-derived peptides to milk protein synthesis in the ruminant mammary gland. *Journal of Theoretical Biology* **185**, 379-388.
- HANIGAN, M. D., DIJKSTRA, J., GERRITS, W. J. J. & FRANCE, J. (1997a). Modelling post-absorptive protein and amino acid metabolism in the ruminant. *Proceedings of the Nutrition Society* (in press).
- HANIGAN, M. D., FRANCE, J., WRAY-CAHEN, D., BEEVER, D. E., LOBLEY, G. E., REUTZEL, L. & SMITH, N. E. (1997b). Alternative models for analyses of liver and mammary transorgan metabolite extraction data. *British Journal of Nutrition* (in press).

Cellular automata simulation of cell wall degradation. M. J. METCALF¹, A. J. TRAVIS² AND A. CHESSON². ¹Biomathematics and Statistics Scotland, Rowett Research Institute, Bucksburn, Aberdeen, AB21 9SB, UK, ²Rowett Research Institute, Bucksburn, Aberdeen, AB21 9SB, UK

The kinetics of cell wall degradation by rumen micro-organisms *in vivo* are complex and difficult to model mathematically in a biologically meaningful way (Chesson 1993). Experimentally, degradation can be measured *in sacco*, providing information about the rate at which cell material is lost, and *in vitro*, where for example, measurement of gas production gives an indirect measure of such degradation. Analysis of the experimental observations then normally involves fitting exponential models. However, many factors combine to determine the overall shape of the degradation curve produced and it is almost impossible to assess their relative contribution by fitting curves using simple exponential models.

An alternative is to simulate the degradation process using an array of cellular automata. This approach examines the structure of the final degradation curve by starting to model degradation at a more fun-

damental level. Cellular automata process data in discrete steps or iterations, and the whole system evolves according to a simple set of rules which only apply in a local region around each automaton in the array. In the case of the cell wall degradation model, each automaton represents a small cube of cell wall material or enzyme solution (in which the plant material is incubated *in vitro*). The rules governing the behaviour of automata in the model have been defined to simulate the diffusion of cell-free enzymes and the loss of cell wall material, with both processes assumed to obey linear relationships. This model simulates the degradation of plant material using digitized images of actual tissue sections, which allows factors such as selection of different anatomical and chemical characteristics, diffusion rate of enzyme, and accessibility of the cell walls to be manipulated, and hence their importance to the degradation process to be evaluated.

Preliminary results have demonstrated the importance of anatomy and lignin distribution in determining the degradation characteristics of the tissue. For example, images of transverse sections from a newly extended maize internode were used to simulate degradation of sclerenchyma tissue using the cellular automaton model. The simulation revealed substantially higher rates of degradation for tissue from the youngest part of the internode, which also had the highest surface area to volume ratio.

CHESSON, A. (1993). Mechanistic models of forage cell wall degradation. In *Forage Cell Wall Structure and Digestibility* (Eds H. G. Jung, D. A. Buxton, R. D. Hatfield & J. Ralph), pp. 347–376. Madison WI: ASA-CSSA-SSSA.

An improvement to a simple and general model for plant competition. L. R. BENJAMIN. *Horticulture Research International, Wellesbourne, Warwick CV35 9EF, UK*

A simple empirical model using overlapping zones of influence can give fits to the growth of isolated carrot (*Daucus carota* L.) plants as good as those made by complex mechanistic models (Benjamin 1994). In further work on this model, the zone of influence has been equated to the shoot crowns. In using the model to simulate plant growth, the light extinction coefficient and the parameters relating leaf area, projected crown area and within-crown leaf area index to plant weight were obtained from independent observations. The conversion efficiency of light to dry matter was taken as a value typical for C₃ plants that form storage organs. For regions of crown overlap, three contrasting rules were used to quantify the partitioning of crop dry matter between individual plants.

The results of simulations based on these three rules were compared with: (i) the growth of individual

plants at different positions in imposed spatial planting patterns; and (ii) the growth of plants of contrasting pre-competitive weight planted in a uniformly-spaced array. The simulation that gave growth closest to that in the experimental data was based upon an equation that partitioned crop dry matter between plants according to the degree of 'crowding' each plant experienced. This supports the view that plants alter their morphology in response to the presence of neighbours, thereby modifying the extent of growth interactions due to competition. The time taken for calculating the areas of overlap remains an obstacle to the commercial exploitation of these models.

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

BENJAMIN, L. R. (1994). A simple and general model for plant competition. *Journal of Agricultural Science, Cambridge* **122**, 162.

Developing fertilizer recommendations for grassland based on modelling and soil testing. D. SCHOLEFIELD AND L. BROWN. *Institute of Grassland and Environmental Research, North Wyke, Devon EX20 2SB, UK*

Nitrogen use in intensively managed grassland agriculture is generally inefficient, with a large proportion of the N inputs being lost to the wider environment through volatilization and leaching (Jarvis 1993). Inefficient N use is associated with the accumulation of large amounts of mineral N (nitrate and ammonium) in the soil during the summer and autumn. Farmers have the opportunity to regulate the supply of mineral N when fertilizer is applied, but current recommendations are based mainly on economic criteria and include only general rules for taking account of the amount of N supplied through mineralization and other sources. New fertilizer recommendations are needed that enable the farmer to optimize mineral N supply to achieve a given economic target in relation to soil conditions, sward management and patterns of weather. Such recommendations should also enable economic targets to be linked with environmental impacts (N losses), so that any environmental constraints to production can be considered.

An existing model of the N cycle in grazed grassland (Scholefield *et al.* 1991) has been developed to enable the prescription of patterns of fertilizer N required to achieve any production target with optimum use of N, and calculates the associated N losses by ammonia volatilization, denitrification and leaching of nitrate. The original model is based on annual mass balance, assuming zero net flux of soil mineral N. A new version of this model has been produced (NFERT) with

shorter time-steps (e.g. 1 month) by applying weighting factors to obtain distributions of each annual pool and flux over the year. The weighting factors were derived from plant N-yield data obtained from multi-site grassland experiments, long term measurements of denitrification and mineralization and average monthly weather data for each climatic zone.

NFERT predicts the average annual soil mineral N profile for any location in the UK required for achieving the desired economic and/or environmental target. This profile is the sum of the leachable N and fertilizer N pools. The amount of mineral N measured in the soil profile just prior to each monthly top-dressing of fertilizer is assumed to be that predicted as leachable by the model. Fertilizer is then added according to that predicted to achieve the target. Thus, soil tests can be used to check the accuracy of model predictions and as a basis for regulating fertilizer supply for optimum efficiency of N use. A rapid test for soil mineral N has been developed for on-farm use, in tandem with the model (Scholefield & Titchen 1995).

A replicated cut-plot experiment is being conducted at three sites in order to test the model output. Three profiles of soil mineral N are imposed at each site for two growing seasons, calculated to achieve a range of herbage yields and associated N losses. Experimental data for the first year show that the model over-predicted herbage yield and denitrification while it under-predicted net mineralization of N. However, the model gave reasonably accurate predictions of N loss by leaching. Application of the model and integrated soil testing approach to improving the efficiency of N use on four commercial dairy farms has produced encouraging results: compared to conventional patterns of application, the model-generated fertilizer patterns produced equivalent amounts of herbage with 33% less fertilizer on average. NFERT is now being further developed for sensitivity to non-average weather and to enable different harvesting frequencies to be considered.

JARVIS, S. C. (1993). Nitrogen cycling and losses from dairy farms. *Soil Use and Management* **9**, 99–105.

SCHOLEFIELD, D., LOCKYER, D. R., WHITEHEAD, D. C. & TYSON, K. C. (1991). A model to predict transformations and losses of nitrogen in UK pastured grazed by beef cattle. *Plant and Soil* **132**, 165–177.

SCHOLEFIELD, D. & TITCHEN, N. M. (1995). Development of a rapid field test for soil mineral nitrogen and its application to grazed grassland. *Soil Use and Management* **11**, 33–43.

Analysis of eating patterns in silage-fed ruminants.

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The factors that control and limit the daily intake of conserved forages by ruminants are poorly understood. Full understanding of intake potential must be realised in order to achieve optimum animal performance. The ingestive behaviour of silage-fed cattle is dominated by non-eating periods of various durations between any two consecutive feeding bouts. The animals are unable to eat silage continuously. The relationships between patterns of intake and daily intake are examined in a current project. Also methods for summarizing patterns of intake data are evaluated to facilitate treatment comparisons.

In the study reported here, six lactating cows were housed individually indoors and monitored over 4 days. A grass-based silage was offered *ad libitum* with refusals lifted and fresh feed offered once daily following 5 kg of standard dairy concentrate. The silage offered was placed on individual electronic balance platforms and the weight of feed remaining was recorded automatically at a minimum of 30 sec intervals for the following 23.5 h. Cumulative loss of feed from the feed bin gave the cumulative intake pattern for each animal. The meal length was defined as the total duration of consecutive feeding bouts separated by < 10 min in which no feed was consumed.

Rook & Penning (1991) used a finite Markov chain to study transition among eating, ruminating and idling activities and explored whether these were time-dependent. Only eating activity was found to be sensitive to the preceding length of a given meal. In the present study, data were obtained for eating and non-eating only. Meal durations were split into four phases, i.e. < 5, 5–10, 10–15 and > 15 min duration. Non-eating periods too were divided into the same four phases. This generated a Markov chain with eight states. There were a large number of structural zeroes as movement is only to the next larger duration phase or the alternative activity.

As a summary of the eating pattern, an 8 × 8 matrix of counts was obtained for each of the grouping factors. These matrices can be compared, in pairs, using a chi-squared test devised by Billingsley (1961). This test can be applied to individual rows and to a group of rows, thus making treatment comparisons feasible. In addition, correlation between first meal size (kg of fresh silage) and daily intake was found to be very poor and the same was true of the intake rate (g/min) calculated from the first meal compared to the overall rate of cumulative intake over eating time. This observation was consistent with the findings of Gill & Romney (1994), where the hypothesis that factors limiting the first meal size dominate daily intake was discounted. Average length of meals, for the 23 data sets in this study, was < 5 min in 51% of

the cases and 54% of the non-eating intervals were < 5 min whilst 33% exceeded 15 min. For better understanding, non-eating intervals need to be subdivided into ruminating and idling components.

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

BILLINGSLEY, P. (1961). *Statistical Inference for Markov Processes*. Chicago: University of Chicago Press.

GILL, M. & ROMNEY, D. (1994). The relationship between the control of meal size and the control of daily intake in ruminants. *Livestock Production Science* **39**, 13–18.

ROOK, A. J. & PENNING, P. D. (1991). Stochastic models of grazing behaviour in sheep. *Applied Animal Behaviour Science* **32**, 167–177.