
ABSTRACTS OF COMMUNICATIONS

Proceedings of the Thirty-second 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-second meeting of the group, chaired by Professor D. Scholefield of the Institute of Grassland and Environmental Research, North Wyke, was held in the Kohn Centre at the Royal Society, 6 Carlton House Terrace, London on Friday, 14 April 2000 when the following papers were read.

A mathematical model of plant nutrient uptake. T. ROOSE¹, A. C. FOWLER¹ AND P. R. DARRAH².

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The classical model of plant root nutrient uptake due to Nye, Tinker and Barber (Nye & Tinker 1977; Barber 1984) is developed and extended. We provide the derivation of an explicit closed formula for the uptake by a single cylindrical root for all cases of practical interest by solving the absorption-diffusion equation for the soil nutrient concentration asymptotically in the limit of large time (Roose *et al.* 2000). The analytical formula for nutrient flux enables a more advanced sensitivity study of the Nye–Tinker–Barber model to be carried out.

Using this single root model as a building block, we then construct a model which allows for root size distribution in a more realistic plant root system, and include the effects of root branching and growth (Roose *et al.* 2000). We are able to solve this model analytically and hence estimate the effect on nutrient uptake by a branching system of roots in the absence of competition. This enables us to estimate the possible error arising from the averaging of the root radius over the root population, which is commonly used in experimental validation of the standard Nye–Tinker–Barber model. The results of those models are compared with previous theoretical and experimental studies.

At the next stage we develop a model for the spatial root distribution development and the resulting nutrient uptake by it. This enables us to investigate the development of local nutrient concentration profiles within the root branching structures.

We have also derived a closed form expression for nutrient uptake by a cylindrical root with root hairs. Based on this analytical formula we propose new experiments for quantifying the importance of root hairs in comparison to lateral branches. We will also discuss a model for nutrient uptake by root with mycorrhizal symbiosis and the experiments required for its validation.

BARBER, S. A. (1984). *Soil Nutrient Bioavailability. A Mechanistic Approach*. New York: Wiley-Interscience Publications.

NYE, P. H. & TINKER, P. B. (1977). *Solute Movement in the Soil-Root System*. Oxford: Blackwell Scientific Publications.

ROOSE, T., FOWLER, A. C. & DARRAH, P. R. (2000). Mathematical model of plant nutrient uptake. *Journal of Mathematical Biology*, submitted.

Green area decline of wheat flag leaves. J. P. R. E. DIMMOCK, M. J. GOODING AND J. FRANCE. *Crops Research Unit, The University of Reading, Department of Agriculture, Reading RG6 6AT, UK*

The effects of disease on yield of wheat grain can be related to effects on green leaf area and interception

of photosynthetically active radiation (Bryson *et al.* 1997). The yield of wheat in the UK is closely related to leaf area duration following ear emergence, with the flag contributing approximately 45% of grain carbohydrate (Lupton 1972). Protection of the flag leaf also provides over half of all yield response to fungicides (Cook & Thomas 1990).

Studying the effects of fungicides on green leaf area duration in field experiments led to the derivation of a modified Gompertz model to describe this decline. Using the formula where green leaf area percentage at time $t = 100 \exp[-\exp(-k(t-m))]$, curves fitted over time to visual assessments of green leaf area throughout flag leaf life accounted for more than 98% of variation in 45 of 48 wheat cultivar \times fungicide treatment comparisons.

This data set spanned 17 years and therefore included cultivars of contrasting parentage and age. In the absence of fungicide, green leaf area decline was associated with drought or infection with a number of foliar pathogens including *Septoria tritici* (sexual stage *Mycosphaerella graminicola*), *Erysiphe graminis* and *Puccinia striiformis*. Fungicides applied to the flag leaf included propiconazole, propiconazole plus tridemorph, flusilazole or azoxystrobin. Fungicide effects on the variable m (i.e. time to 37% green area) were closely related to fungicide effects (as percentage of untreated) on mean grain weight and grain yield (variation accounted for 80 and 85% respectively) (Gooding *et al.* 2000).

This work demonstrates the efficacy of visual estimation of green leaf area, with the associated advantages of rapidity and non-destructiveness. Targeting fieldwork to estimate the variable m can significantly reduce the number of assessments necessary to quantify fungicide effects on green leaf area decline of flag leaves.

The Ministry of Agriculture, Fisheries & Food and DuPont (UK) Ltd. are thanked for funding this research.

BRYSON, R. J., PAVELEY, N. D., CLARK, W. S., SYLVESTER-BRADLEY, R. & SCOTT, R. K. (1997). Use of in-field measurements of green leaf area and incident radiation to estimate the effects of yellow rust epidemics on the yield of winter wheat. *European Journal of Agronomy* **7**, 53–62.

COOK, R. J. & THOMAS, M. R. (1990). Influence of site factors in responses of winter wheat to fungicide programmes in England and Wales, 1979–1987. *Plant Pathology* **39**, 548–557.

GOODING, M. J., DIMMOCK, J. P. R. E., FRANCE, J. & SMITH, S. A. (2000). Green leaf area decline of wheat flag leaves: the influence of fungicides and relationships with mean grain weight and grain yield. *Annals of Applied Biology* **136**, 77–84.

LUPTON, F. G. H. (1972). Further experiments on photosynthesis and translocation in wheat. *Annals of Applied Biology* **71**, 69–71.

Modelling the dispersal of linyphiid spiders using alternating renewal processes. P. BRAIN AND C. F. G. THOMAS. *IACR-Long Ashton, Department of Agricultural Sciences, University of Bristol, Long Ashton, Bristol BS41 9AF, UK*

The aerial dispersal of linyphiid or money spiders (Araneae, Linyphiidae) by ballooning on silk threads is recognized as an adaptation for survival in disturbed habitats (Duffey 1978). Several species of linyphiid spider are abundant in agricultural land, where they are important predators of crop pests (Alderwielde 1994). Increasing interest in developing sustainable agriculture has emphasized the need to understand the dynamics of spatially structured patchy populations and metapopulations (Gilpin & Hanski 1991). In spatially dynamic models of species in fragmented habitats, dispersal distance is a critical parameter affecting the success of an organism in locating a suitable new patch (Moloney *et al.* 1992). In these models the relationship between dispersal distance and the scale of spatial fragmentation of the environment, can be explored theoretically by describing dispersal distance as a function of spatial scale (Doak *et al.* 1992; Moloney *et al.* 1992). However, in real systems, spatial scale is an environmental constant, and actual dispersal distances need to be known. Dispersal distances, however, are amongst the most difficult parameters to quantify for many invertebrate organisms. Linyphiid spiders display a relatively simple system of windborne dispersal, which because of its passive nature, and its dependence on meteorological conditions, is amenable to analysis by simulation modelling (Halley *et al.* 1996). An existing model of this dispersal process has been extended and improved in this present work. The theoretical derivation of the model will be presented, some of the problems of model parameter estimation stated, and examples of the predictions given. The dispersal model will, in future, be incorporated into a more complex model of dispersal in fragmented landscapes, which will include varying point mortality, so that the effects of different landscape management systems can be studied. Further details of the experiments are given in Thomas (1992).

The model describes the dispersal process of the spider as two alternating stages; the airborne stage and the grounded stage. The following assumptions are made:

(i) The airborne stage. The spider is relocated to a random initial height by a wind thermal, before falling, drifting downwind as it descends. The horizontal distance moved can then be estimated. When the spider lands it enters the grounded stage.

(ii) The grounded stage. The distribution of the length of the grounded phase has been determined experimentally. At the end of the resting period it starts the next airborne stage. We assume that the length of the flight does not affect the length of the

grounded period, and that there is no interaction between the spiders.

The dispersal process is an example of an alternating renewal process, as described in, for example, Cox (1967), as it consists of two independent stages, in this case, airborne and grounded. Estimates of the model parameters were obtained from experimental results, and this estimation process itself involved the use of probabilistic models. The airborne/grounded process was simulated using these estimated parameters for each of a large number of individual spiders to obtain the distributional properties of the number of flights and the distance moved.

The predicted mean distance moved in an eight-hour day under typical weather conditions is about 30 km, as would be expected, with a maximum distance of about 70 km. The model is a simplified description of the dispersal process and needs to be extended to deal with more realistic landscape scenarios to give a detailed picture of the dispersal of these spiders.

- ALDERWIERELDT, M. (1994). Prey selection and prey capture strategies of linyphiid spiders in high-input agricultural fields. *Bulletin of the British Arachnological Society* **9**, 300–308.
- COX, D. R. (1967). *Renewal Theory. Methuen's Monographs on Applied Probability and Statistics*. London: Methuen Science Paperbacks.
- DOAK, D. F., MARINO, P. C. & KAREIVA, P. M. (1992). Spatial scale mediates the influence of habitat fragmentation on dispersal success: Implications for conservation. *Theoretical Population Biology* **41**, 315–336.
- DUFFEY, E. (1978). Ecological strategies in spiders including some characteristics of species in pioneer and mature habitats. *Symposium Zoological Society London* **42**, 102–123.
- GILPIN, M. & HANSKI, I. (1991). Metapopulation dynamics: empirical and theoretical investigations. *Biological Journal of the Linnean Society* **42**, nos. 1 & 2. London: Academic Press.
- HALLEY, J. M., THOMAS, C. F. G. & JEPSON, P. C. (1996). A model for the spatial dynamics of spiders in farmland. *Journal of Applied Ecology* **33**, 471–492.
- MOLONEY, K. A., LEVIN, S. A., CHIARIELLO, N. A. & BUTTEL, L. (1992). Pattern and scale in a Serpentine Grassland. *Theoretical Population Biology* **41**, 257–276.
- THOMAS, C. F. G. (1992). *Spatial Dynamics of Spiders in Farmland*. PhD thesis, University of Southampton.

DESSAC: a decision support system for arable crops.

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Advances in computer technology have enabled the development of sophisticated decision support systems (DSS) for use in agriculture. DESSAC will provide an integrated suite of DSS modules covering the main decision areas confronted by farmers. The

first of these modules aims to enable the user to take decisions on fungicide application to winter wheat, based on optimizing the economic margin. This module is called the Wheat Disease Manager (WDM).

Farmers typically spray a wheat crop two or three times during April to June to control fungal diseases. Different varieties have different susceptibilities and some of the highest yielding varieties are particularly at risk from the major diseases. The farmer has a choice of about 20 fungicide active ingredients that can be mixed in various combinations and applied at different timings. Because of the complexity of the problem and the variability in disease attacks, there is a perception that farmers use too much chemicals as insurance. WDM thus seeks to improve chemical use.

The WDM module consists of a suite of simulation models. These include a canopy growth model, a model of the development of four foliar fungal diseases which incorporates the effect of any sprays applied, and a yield loss model, based on light interception. The models used are semi-mechanistic and are driven by disease inoculum, weather and cultivar resistance. The disease models have been fitted to data sets from experiments to investigate the effects of climate on disease growth, and spray application data from experiments to investigate the effects of spray dose and timing.

A sophisticated user interface allows the user to experiment with a number of spray applications, chemical, timing and dose, or request an optimum treatment. Treatment optimization is achieved by comparing the value of the predicted disease induced yield loss, against treatment cost, for a range of optimal spray programmes.

A model for amino acid transport between plasma and red blood cells.

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Studies *in vitro* indicate that transport of amino acids between plasma and red blood cells is limited (Young *et al.* 1976). From studies *in vivo*, however, much higher rates of transfer have been observed (Elwyn *et al.* 1972). Two hypotheses for possible transport routes *in vivo* are that exchange of amino acids between plasma and red blood cells occurs via (i) shape changes of the red blood cells coming out of the capillaries, (ii) direct exchange between the red blood cells and the tissues (intermediary pool) when going through the capillaries.

To investigate the validity of these hypotheses, a

tracer kinetic experiment was conducted in sheep. A single dose of labelled amino acids was administered to the plasma pool, and for four amino acids (glycine, valine, leucine and phenylalanine), the enrichments in plasma and red blood cells were monitored for 30 minutes.

Two-compartmental models, based on first order differential equations and assuming steady state conditions for tracee (Shipley & Clark 1972), were developed that reflect the hypothesized amino acid transport routes between plasma and red blood cells. These models were fitted to the plasma enrichment data (sampling from the primary pool), using non-linear regression. To investigate the validity of the hypotheses, for each model the predicted red blood cell enrichment was compared to the observed red blood cell enrichment. It was found that the model reflecting hypothesis (ii) gave the better fit (prediction error sum of squares for glycine, valine, leucine and phenylalanine of 0.23, 0.73, 0.39, 0.26 v. 0.13, 0.0058, 0.0041, 0.0049 for (i) and (ii), respectively). The models were also fitted to the red blood cell enrichment data (sampling from the secondary pool). Model (i) underestimated, by 10–100-fold, the fractional turnover rate constant for inflow into the red blood cells from plasma. In contrast, model (ii) gave reasonable agreement for the fractional turnover rate constants (within two-fold for glycine, valine and phenylalanine).

There is evidence of transport from the tissues to the red blood cells. This study suggests that this transport of amino acids between plasma and red blood cells does not occur via changes in the shape of the red blood cells. Whether red blood cell enrichments could be used to reflect tissue intracellular enrichments for protein turnover studies requires further examination.

The Scottish Executive Rural Affairs Department is thanked for funding this research. Dr Lapiere was collaborator via a fellowship under the OECD Co-operative Research Programme.

ELWYN, D. H., LAUNDER, W. J., PARIKH, H. C. & WISE, E. M. (1972). Roles of plasma and erythrocytes in interorgan transport of amino acids in dogs. *American Journal of Physiology* **222**, 1333–1342.

SHIPLEY, R. A. & CLARK, R. E. (1972). *Tracer Methods for In Vivo Kinetics, Theory and Applications*. London: Academic Press.

YOUNG, J. D., ELLORY, J. C. & TUCKER, E. M. (1976). Amino acid transport in normal and glutathione-deficient sheep erythrocytes. *Biochemical Journal* **154**, 43–48.

Modelling herbicide and nitrogen effects on crop-weed competition for decision support in weed management. DO-SOON KIM, P. BRAIN, J. MARSHALL AND J. CASELEY. *IACR-Long Ashton, Department of Agricultural Sciences, University of Bristol, Long Ashton, Bristol BS41 9AF, UK*

Current weed management strategies rely heavily on the extensive use of herbicides. Manufacturers' recommended doses are generally high as a fail-safe measure. However, detailed knowledge of local edaphic or climatic conditions may allow for reductions in application levels, valuable both economically and environmentally. Brain *et al.* (1999) developed a model of the interaction between crop-weed competition and herbicide dose based on a rectangular hyperbola (Cousens 1985) and the dose-response curve (Streibig 1980). Recently, Kim (1999) extended this model to include weed density, different crop cultivars, multiple weed species infestation and different nitrogen levels.

Basic mathematical models were developed by combining the standard herbicide dose-response curve and the rectangular hyperbolic competition model to describe the effects of weed density and herbicide doses on crop yield and weed seed production. The models were also extended to include multiple weed species infestation, and different nitrogen levels. To describe the effects of multiple weed species competition and a range of herbicide doses on crop yield and weed biomass, the herbicide dose-response curves of the weed biomass and the weed competitiveness for two weed species were independently incorporated into a multivariate hyperbolic curve. To incorporate the effects of changing applied nitrogen levels, the parameters of the basic combined models for crop yield and weed biomass were described by functions of the applied nitrogen.

The models developed in this study require extensive validation under a range of edaphic and climatic conditions. When suitably validated they have the potential to be used to estimate the herbicide doses required to restrict crop yield loss and weed biomass to less than an acceptable level. The multiple weed competition model can also be used to recommend not only the dose of the herbicide mixture, but also the ratios of the herbicides in the mixture. The models can then be incorporated into decision support systems for optimizing herbicide and nitrogen inputs.

BRAIN, P., WILSON, B. J., WRIGHT, K. J., SEEVERS, G. P. & CASELEY, J. C. (1999). Modelling the effect of crop and weed on herbicide efficacy in wheat. *Weed Research* **39**, 21–35.

COUSENS, R. (1985). An empirical model relating crop yield to weed and crop density and a statistical comparison with other models. *Journal of Agricultural Science* **105**, 513–521.

KIM, D. S. (1999). *Modelling Herbicide and Nitrogen Effects on Crop-Weed Competition*. Ph.D. thesis, University of Bristol.

STREIBIG, J. C. (1980). Models for curve fitting herbicide dose response data. *Acta Agriculturae Scandinavica* **30**, 59–64.

Efficient specification of biological and ecological models. G. J. S. ROSS. *Statistics Department, IACR-Rothamsted, Harpenden, Hertfordshire AL5 2JQ, UK*

Complex multiparameter models for biological processes are easily specified, but the practical problems of fitting parameters to real data are given little attention. Re-examination of published analyses of various experimental data sets shows that there is often scope for improvement.

Attention will be given both to the parameterization of the models and to the assumed error distribution. The analysis should also indicate how the design of similar experiments could be improved in order to determine the parameters more precisely.

The first example concerns a study of germination rates as a function of time and of temperature. The proposed surface to be fitted involves exponentials of exponentials (Gompertz curves with respect to time, whose parameters are functions of temperature). The published analysis (Payendah *et al.* 1980), assuming normally distributed errors, is far from optimal because the data as originally scaled require parameter values computably indistinguishable from unity. Rescaling the data allows the best fit to be obtained, but the parameters are still too highly correlated for practical use. A stable parameterization (Ross 1990) making use of selected expectations as parameters provides a satisfactory set of parameters. A further improvement is to treat the observations as binomial variables, as they are given as percentages, although the actual counts are not provided.

The second example re-examines the classical competition experiments of Gause (1934) in which two species of *Paramecia* are subsampled over a number of days. The simple Lotka–Volterra differential equations involving six parameters are fitted. The published analysis (Pascual & Kareiva 1996) assumes a lognormal distribution for the counts, although this exaggerates the importance of the early observations in which numbers are small. The experimental technique suggests the Poisson distribution, although the results are more heterogeneous than expected. The parameterization can also be stabilized by choosing as parameters the expected rates of change of each species count at three different times. These six parameters can be converted to the defining parameters of the differential equations by solution of linear simultaneous equations. The results show that the analysis would have been helped if the experiments had been allowed to continue for a longer period.

This work arises from a collaborative project with

Professor Chris Gilligan and Dr Keith Briggs of the Department of Plant Sciences, University of Cambridge.

GAUSE, G. F. (1934). *The Struggle for Existence*. Baltimore: Williams & Wilkins.

PASCUAL, M. A. & KAREIVA, P. (1996). Predicting the outcome of competition using experimental data: maximum likelihood and Bayesian approaches. *Ecology* **77**(2), 337–349.

PAYENDAH, B., WALLACE, D. R. & MACLEOD, D. M. (1980). An empirical regression function suitable for modelling spore germination subject to temperature threshold. *Canadian Journal of Botany* **58**, 936–941.

ROSS, G. J. S. (1990). *Nonlinear Estimation*. New York: Springer.

Application of a mechanistic model of methanogenesis in the lactating dairy cow. Nutritional strategies to reduce methane emissions and increase dietary energy availability. J. A. N. MILLS¹, J. DIJKSTRA², A. BANNINK³, E. KEBREAB¹, S. B. CAMMELL¹

AND J. FRANCE¹. ¹*The University of Reading, Department of Agriculture, Earley Gate, Reading RG6 6AT, UK*, ²*WIAS Animal Nutrition, Wageningen University, Marijkeweg 40, PO Box 338, 6700 AH Wageningen, The Netherlands*, ³*ID-Lelystad, Department of Animal Nutrition, PO Box 65, NL 8200 AB Lelystad, The Netherlands*

Dietary intervention to reduce methane emissions from lactating dairy cattle is both environmentally and nutritionally desirable due to the importance of methane as a causative agent in global warming and as a significant loss of feed energy. This investigation involved the development of a dynamic mechanistic model of whole rumen function (Dijkstra *et al.* 1992). The model incorporates modifications to certain rumen fermentation parameters and the addition of a post-ruminal digestive element. Regression analysis showed good agreement between observed and predicted results for experimental data taken from the literature ($R^2 = 0.76$, root mean square prediction error (MSPE) = 15.4%). Evaluation of model predictions from five calorimetry studies (67 observations) with lactating dairy cows at the University of Reading showed an under-prediction of mean methane production of 2.1 MJ/day ($R^2 = 0.46$, root MSPE = 12.4%). The reasons for this under-prediction include erroneous feed characterization and under-prediction of total volatile fatty acid (VFA) production in the rumen for dairy cows with high dry matter (DM) intakes.

Application of the model to develop diets to minimize methanogenesis demonstrates a need to limit the concentration of soluble sugars in the concentrate. Complete replacement of sugars in concentrate DM (from 250 to 20 g/kg DM) led to a 3.5% increase in diet metabolizability (metabolizable energy (ME)/gross energy (GE)). Substitution of grass silage with maize silage may significantly reduce the environmental impact of dairy farming through

methane pollution whilst increasing the dietary energy available to the dairy cow. On a herd basis, the model predicts that increasing dietary energy intake per cow can minimize the annual loss of feed energy through methane production. Model simulations for lactating cows fed *ad libitum* v. restricted (78% of *ad libitum*) DM intake showed a 0.25% decline in the GE lost as methane, equivalent to a saving of 5070 L methane for a 305 day lactation at 244 MJ/day GE intake. These simulations indicate that intensive dairy farming operations designed to fill quota with the least number of cows, produce less methane per litre of milk than regimes that are more extensive.

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

DIJKSTRA, J., NEAL, H. D. St. C., BEEVER, D. E. & FRANCE, J. (1992). Simulation of nutrient digestion, absorption and outflow in the rumen: model description. *Journal of Nutrition* **122**, 2239–2256.

Stomatal changes caused by acute ozone exposure can be predicted by changes occurring in the mesophyll in wheat. M. J. MARTIN¹, P. K. FARAGE¹, S. W. HUMPHRIES² AND S. P. LONG³. ¹Department of Biological Sciences, University of Essex, Wivenhoe Park, Colchester, Essex CO4 3SQ, UK, ²Brookhaven National Laboratory, Upton, New York, 11973, USA, ³University of Illinois, Department of Crop Sciences and Plant Biology, 190 Edward R. Madigan Laboratory, 1201 West Gregory Drive, Urbana, IL61801, USA

Robust models based on the mechanistic understanding of how ozone and CO₂ affect photosynthesis will be required to predict the complex interactive effects of rising concentrations of these two gases on vegetation. The development of a model of acute ozone exposure effects on wheat leaf photosynthesis is described, based on reactive oxygen scavenging processes. Using the experimental data of Farage *et al.* (1991), the dose of ozone to the leaf above a threshold flux, here termed the effective ozone dose, was found to be linearly related to the decline in the *in vivo* maximum rate of carboxylation. The proposed mechanism is that ozone damage to the photosynthetic apparatus will only occur above a critical rate of ozone delivery.

By combining the model of the response of photosynthesis to ozone exposure with both a mechanistic biochemical model of leaf photosynthesis (Farquahar *et al.* 1980) and a phenomenological model of stomatal conductance (Ball *et al.* 1987; Harley *et al.* 1992), within WIMOVAC (Humphries & Long 1995; www.life.uiuc.edu/plantbio/wimovac), it was possible to investigate the degree of dependency of ozone-induced stomatal closure on changes in the mesophyll. The model closely predicted the measured

decline in stomatal conductance. These results indicate that stomatal changes caused by acute ozone exposure in wheat can be predicted from changes in the mesophyll, rather than direct effects on the stomata.

The findings that the effects of ozone on photosynthesis can be predicted by an effective ozone dose to the leaf, and that the resulting reduction in CO₂ assimilation rate can, in turn, predict stomatal closure, greatly simplifies modelling the effects of elevated concentrations of ozone and CO₂ on wheat photosynthesis. Future work should determine whether the model can be adapted to predict chronic ozone exposure effects on photosynthesis, and whether it can be applied to other species by adjusting the values of threshold flux. This threshold would be related to the maximum scavenging capacity within the leaf. The ozone slope coefficient of the model represents the inherent sensitivity of the photosynthetic apparatus to ozone, which may also vary with genotype.

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

BALL, J. T., WOODROW, I. E. & BERRY, J. A. (1987). A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In *Progress in Photosynthesis Research, Vol. IV. Proceedings of the International Congress on Photosynthesis* (Ed. I. Biggins), pp. 221–224. Dordrecht: Martinus Nijhoff.

FARAGE, P. K., LONG, S. P., LECHNER, E. G. & BAKER, N. R. (1991). The sequence of change within the photosynthetic apparatus of wheat following short-term exposure to ozone. *Plant Physiology* **95**, 529–535.

FARQUAHAR, G. D., VON CAEMMERER, S. & BERRY, J. A. (1980). A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* **149**, 78–90.

HARLEY, P. C., THOMAS, R. B., REYNOLDS, J. F. & STRAIN, B. R. (1992). Modelling photosynthesis of cotton grown in elevated CO₂. *Plant, Cell and Environment* **15**, 271–282.

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.

Coupling crop and soil models to simulate methane emissions from rice fields in Asia. R. B. MATTHEWS¹, R. WASSMAN^{2,3} AND J. W. KNOX¹. ¹Institute of Water and Environment, Cranfield University, Bedfordshire MK45 4DT, UK, ²International Rice Research Institute, P O Box 933, 1099 Manila, Philippines, ³Fraunhofer Institute for Atmospheric Environmental Research, Garmisch-Partenkirchen, Germany

The CERES-Rice crop simulation model (Ritchie *et al.* 1998) was used as a basis to develop a model to simulate methane emissions from rice-fields, and was linked to an existing sub-model calculating fluxes and concentrations of methane and oxygen in submerged

soils (Arah & Kirk 2000). The latter requires as inputs the amount of methanogenic substrate available and the profile distribution of root length, both of which are supplied by the crop model.

The crop model calculates the supply rate of substrate used by the methanogenic bacteria from (i) the rate of decomposition of soil organic matter (SOM), (ii) root exudates, and (iii) the decomposition of dead roots from the current crop. The SOM decomposition rate is calculated by assuming that there are two main pools—the fresh organic matter (FOM) which includes previous crop residues and green manure, and a more stable organic pool. The FOM pool is further divided into three arbitrary pools corresponding approximately to the carbohydrate, cellulose, and lignin fractions. Each of these pools has a different potential relative decay rate which may be modified by soil temperature, soil moisture, and the C/N ratio of the decaying material. Root death rate is assumed to be a constant fraction of existing root dry weight. Laboratory data showed that exudation rate per unit of root weight is a constant up until the time of flowering, and again constant but with a higher value from flowering to maturity.

Account was also taken of a pool of alternate electron acceptors, which can also be reduced by various bacteria during the final degradation of organic substrate producing CO₂ rather than CH₄.

The model was used to evaluate various agronomic practices to mitigate methane emissions from rice fields and to upscale field-level measurements to estimate methane emissions at the national level for a number of rice-producing countries in Asia.

ARAH, J. R. M. & KIRK, G. J. D. (2000). Modelling rice-plant-mediated methane emission. *Nutrient Cycling in Agroecosystems* (in press).

RITCHIE, J. T., SINGH, U., GODWIN, D. C. & BOWEN, W. T. (1998). Cereal growth, development and yield. In *Understanding Options for Agricultural Production. Systems Approaches for Sustainable Agricultural Development* (Eds G. Y. Tsuji, G. Hoogenboom & P. K. Thornton), pp. 79–98. Dordrecht: Kluwer Academic Publishers.

Modelling the progress of light leaf spot (*Pyrenopeziza brassicae*) on winter oilseed rape (*Brassica napus*) in relation to leaf wetness and temperature. K. PAPASTAMATI¹, S. J. WELHAM¹, B. D. L. FITT¹ AND P. GLADDERS². ¹IACR-Rothamsted, Harpenden, Hertfordshire AL5 2JQ, UK, ²ADAS Boxworth, Cambridge CB3 8NN, UK

Light leaf spot (*Pyrenopeziza brassicae*) is a polycyclic disease of winter oilseed rape (*Brassica napus*). Airborne ascospores are thought to start the epidemics, which then progress through repeated infections caused by secondary production of inoculum (conidiospores) subject to appropriate weather conditions.

Severity of light leaf spot epidemics differs between seasons and regions in the UK and between crops within the same region (Fitt *et al.* 1996). Understanding the mechanisms of epidemic development can contribute to prediction of risk of severe epidemics, but little work has been done to model the effects of environmental factors on disease progress in individual crops. Previous research has determined some factors affecting epidemic progress. Figueroa *et al.* (1995*a*, 1995*b*) suggested that 16 hours of leaf wetness was required for infection, followed by a latent period of 150–250 degree-days (above 0 °C) before sporulation. The interval from infection to appearance of necrotic lesions is usually much longer and has not been determined.

A compartmental model was developed to describe the progress of light leaf spot within one growing season on leaves of winter oilseed rape during the autumn in the UK. Differential equations described transition between healthy susceptible leaves L_s , infected symptomless leaves L_p , sporulating symptomless leaves L_l and leaves with necrotic light leaf spot lesions L_d , respectively. The model was fitted using ModelMaker software to data for progress of light leaf spot on winter oilseed rape at ADAS Bristol during the autumn of the 1990/91 season, for which daily *P. brassicae* ascospore concentrations were also available. Daily data for temperature and rain duration at local meteorological stations were used. Model parameters described rates of leaf appearance, leaf death, infection by air-borne ascospores (primary inoculum) and infection by splash-dispersed conidiospores (secondary inoculum). Infection was dependent on sufficient rain duration. The model gave a reasonable fit to the experimental data ($R^2 = 0.86$). Use of ascospore counts from different years showed variation in spore release patterns sufficient to affect model predictions. Assessment of incomplete data sets from other years suggested that improvements were required to make the model applicable across years and generally more flexible. The model could be improved by making infection criteria a function of temperature, use of non-constant latent and incubation periods and if possible, separate criteria for infection by ascospores and conidia.

FIGUEROA, L., FITT, B. D. L., SHAW, M. W., McCARTNEY, H. A. & WELHAM, S. J. (1995*a*). Effects of temperature on the development of light leaf spot (*Pyrenopeziza brassicae*) on oilseed rape (*Brassica napus*). *Plant Pathology* **44**, 51–62.

FIGUEROA, L., FITT, B. D. L., WELHAM, S. J., SHAW, M. W. & McCARTNEY, H. A. (1995*b*). Early development of light leaf spot (*Pyrenopeziza brassicae*) on winter oilseed rape (*Brassica napus*) in relation to temperature and leaf wetness. *Plant Pathology* **44**, 641–654.

FITT, B. D. L., GLADDERS, P., TURNER, J. A., SUTHERLAND, K. G. & WELHAM, S. J. (1996). Predicting risk of severe light leaf spot (*Pyrenopeziza brassicae*) on winter oilseed

rape in the UK. 1996 Brighton Crop Protection Conference, Pests and Diseases, 239–244.

Investigating the use of two simulation models of potato. J. A. CARRILLO-SALAZAR AND K. GREGSON. *Division of Environmental Science, University of Nottingham, Sutton Bonington Campus, Loughborough LE12 5RD, UK*

Simulation models are used in diverse areas such as forecasting, management and as a means to understanding the processes involved in the systems. However, how reliable are models for such purposes? In the process of optimizing two simulation models of potato growth (POTATOS, based on the model by Kooman & Spitters 1995, personal communication from J. Wolf, 1999; SIMPOTATO, from Hodges 1999) by fitting them to observed data, evidence was found of unusual behaviour in both models.

POTATOS is a relatively simple model that estimates biomass by applying light use efficiency factors. This model produced discontinuous biomass and tuber dry weight estimations when the parameter representing the temperature sum required for emergence of 50% of plants was changed, even in the sixth significant digit, similar to results found in other simulation models (Metselaar 1999). This can be explained by the fact that a conditional is used to estimate changes in phenological stages. Similar effects can be generated as a result of other phenological trigger parameters. The remaining parameters appear to behave in a continuous way.

SIMPOTATO is a complex model, which involves several subprograms and simulates physiological processes in order to estimate leaf area index, biomass and tuber dry weight. Very small changes in some of the parameters of the model, such as maximum potential tuber growth, plant density and daily mean temperature effect on tuber initiation, generate large differences in the prediction of crop variables. This may be explained by the non-linearity of the sub-models which, when interacting with each other, produce chaotic behaviour (Morrison 1991). Other possible factors involved are phenological switches, logic errors, domain errors and rounding errors. The effect of this behaviour is processes such as sensitivity analyses and optimization become difficult or impossible, which casts doubt both on the validity of the models and on the use of physiological models as management tools.

HODGES, T. (1999). SIMPOTATO model V 1.61. Available at <URL <http://www2.jps.net/~hodges/simpot.html>>. Accessed 25 February 2000.

KOOMAN, P. L. & SPITTERS, C. J. T. (1995). Coherent set of models to simulate potato growth. In *Modelling and Parameterization of the Soil-Plant-Atmosphere System. A Comparison of Potato Growth Models* (Eds P. Kabat, B. Marshall, B. J. Van den Broek, J. Vos & H. Van Keulen), pp. 179–210. Wageningen: Wageningen Press.

METSELAAR, K. (1999). *Auditing Predictive Models: A Case Study in Crop Growth*. Ph.D. thesis, Wageningen Agricultural University.

MORRISON, F. (1991). *The Art of Modeling Dynamic Systems. Forecasting for Chaos, Randomness and Determinism*. New York: John Wiley & Sons, Inc.

Modelling climate impacts for sugar beet production in Europe – radiation interception and radiation use efficiency. G. M. RICHTER¹, R. A. C. MITCHELL¹ AND A. R. WERKER². ¹IACR-Rothamsted, Harpenden, Hertfordshire AL5 2JQ, UK, ²IACR-Broom's Barn, Higham, Bury St. Edmunds, Suffolk IP28 6NP, UK

A model for sugar beet yield (Werker & Jaggard 1998) was used to predict climate change impacts on sugar production across Europe (Pidgeon *et al.* 2000). It simulates ground cover to estimate intercepted radiation and potential production rates using a constant light conversion coefficient (RUE). Drought effects on production rates are accounted for by using relative evapotranspiration ($E_{\text{actual}}/E_{\text{potential}}$). Water deficit is also likely to affect leaf area and light interception, and further, a changing fraction of diffuse radiation may affect RUE. The objective was (i) to account for the variation in fraction of diffuse radiation, and (ii) to relate the parameters of canopy dynamics to water stress. The magnitude of these two modifications was tested across Europe for baseline weather during a 35-year period.

The variability of RUE was generated using the physical principles described in SUCroS (Goudriaan & van Laar 1978) and deriving the fraction of diffuse radiation from atmospheric transmission (Spitters *et al.* 1986). The exponential decline of RUE with increasing direct radiation was parameterized for the UK, assuming isothermal conditions and a fraction of 0.7 diffuse radiation. Generalized across Europe, the simulations showed small overall effects for northern temperate zones. Yields were predicted to decrease by 4% only during very sunny years. Under continental conditions (e.g. Austria, Ukraine), average yield reductions of 7% were predicted.

Foliage cover was described originally by parameters of a dynamic differential equation averaged over several years (Werker & Jaggard 1997). Maximum foliage cover, final relative growth rate (μ_{min}) and the rate of change (k_r) at which initial relative growth rate decreases and approaches μ_{min} are now related to relative water content in the soil profile using a simple exponential model (Sinclair 1986). The most sensitive parameter for a drought response of foliage proved to be k_r . On average, simulated drought effects on foliage cover reduced predicted yields by 0.5 to 2%. Individual years showed a yield decrease of 3.5%.

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- GOUDRIAAN, J. & VAN LAAR, H. H. (1978). Calculation of daily totals of the gross CO₂ assimilation of leaf canopies. *Netherlands Journal of Agricultural Science* **26**, 373–382.
- PIDGEON, J. D., WERKER, A. R., JAGGARD, K. W., LISTER, D. H. & JONES, P. D. (2000). Past, present and future comparative advantage in Europe for sugar beet crop production. *Proceedings of the 63rd Congress of the Institut International de Recherches Betteravières*. Inter-laken, Switzerland, February 2000. (in press).
- SINCLAIR, T. R. (1986). Water and nitrogen limitations in soybean grain production. I. Model development. *Field Crops Research* **15**, 125–141.
- SPITTERS, C. J. T., TOUSSAINT, H. A. J. M. & GOUDRIAAN, J. (1986). Separating the diffuse and direct component of global radiation and its implication for modeling canopy photosynthesis. Part I. Components of incoming radiation. *Agricultural and Forest Meteorology* **38**, 217–229.
- WERKER, A. R. & JAGGARD, K. W. (1997). Modelling asymmetrical growth curves that rise and then fall: Applications to foliage dynamics of sugar beet (*Beta vulgaris* L.) *Annals of Botany* **79**, 657–665.
- WERKER, A. R. & JAGGARD, K. W. (1998). Dependence of sugar beet yield on light interception and evapotranspiration. *Agricultural and Forest Meteorology* **89**, 229–240.