Modelling Grassland Ecosystems

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Abstract

In this contribution a view of the promise and difficulties of modelling grassland is given. This is largely centred around work with a grassland ecosystem simulator known as the Hurley Pasture Model.

A brief introduction sets forth possible reasons for building a large ecosystem model, and stresses the importance of modelling objectives. It is suggested that a model is *de rigeur* for any research programme which aims to take a firm grasp of the complex responses of grassland. Mechanistic models are required to provide the understanding needed for intelligent and flexible management of grassland, whatever the prevailing environmental or economic objectives. The models are necessarily large, reflecting the complexity of the 'real' system, and, in a sense, are 'big' science. The challenge is to develop models of 'engineering strength'. This requires an appropriate research environment, which should be reasonably stable, multidisciplinary, well-connected to experimental programmes, and permit adequate support for the three essential legs of an ecosystem model: development, documentation, and application. Some modelling researchers are dismayed by the wasteful fragmentation of many plant ecosystem modelling research programmes.

Next an outline account of the Hurley Pasture Model (HPM) is given. Most plant ecosystem models are now quite similar at the qualitative level, and few would dispute the statement that a reasonable level of consensus is emerging. The HPM is a standard model of the genre. It comprises plant, animal, soil and water submodels. To-date there is no phenology submodel. There are environmental and management drivers, the former accepting monthly, daily or diurnal data, the latter permitting the simulation of fertilizer, grazing, and cutting scenarios, more or less *ad libitum*.

Recent developments of the HPM include a submodel to take account of acclimation of photosynthesis to light, nitrogen, carbon dioxide ('down-regulation') and temperature; and a simple method of using the HPM to simulate legume dynamics in a grass-legume pasture.

Finally, some applications of the model are presented, relating to fertilizer application, grazing, harvesting, and climate change. These are to illustrate the scope of the model, for both application and understanding. The last application shows that in grassland ecosystems climate change responses can be greatly affected by (i) a variable legume content; (ii) management, e.g. how the crop is grazed or cut; and (iii) water stress, as occurs in southern Britain. The impact of climate change on grassland ecosystems is of particular interest. It is known that, in a constant climate, a grassland ecosystem can take hundreds of years to come to equilibrium. Experiments cannot address the problem directly. Short-term experiments can give very variable responses, depending on conditions, which are often misleading, even opposite in sign from long-term responses. Mechanistic models provide a clear framework for unifying these variable results, understanding why they arise, and making predictions about the future time course of plant ecosystems. There seems to be no other way of doing this work..

Keywords: ecosystem, grassland, model

Introduction

First, some of the general principles of modelling in biology and agriculture are presented. These ideas can nearly all be traced back to de Wit (1970), who has largely pioneered the subject of crop simulation.

In any modelling project, the most important exercise is a clearly thought-through and consistent set of objectives. People build models for many different reasons, and with many different goals in mind. Much of the controversy which sometimes emerges in modelling discussions is rooted in differing objectives. Ecosystem modelling is essentially a long-term commitment of at least ten years and more. Short-term work is, almost inevitably, rather superficial. The learning curve is too long, and covers too many different areas (biology, mathematics, computing) for it to be otherwise. Because of the requirement for expertise in several different areas, team-work and collaboration are important. An agreed and coherent set of objectives provides motivation and direction to researchers. Some of the reasons why people build models are therefore considered.

Why build models?

Models are not necessarily, or even usually, mathematical, but here the concern is principally with mathematical models. The need for mathematical models is driven by the increasingly quantitative nature of many biological data, the requirement for integrating the behaviour of different parts of a complex system, and is facilitated by the rapid advances in computer technology. There are many possible reasons for building a model, just as there are several different types of model which can be built (see France and Thornley, 1984, or Thornley and Johnson, 2000, for a fuller discussion).

1. Models can provide a convenient data summary, which is useful for interpolation, cautious extrapolation, and prediction. "Empirical" models which essentially redescribe data are sometimes suitable for this purpose.
2. Modelling may lead to a reduction in the amount of *ad hoc* experimentation, because experiments can sometimes be designed to answer focussed questions.
3. A common reason for building a model is that there is above all a need to be able to make predictions. A model of some sort, not always mathematical, is needed to make predictions. However, it is not necessary to understand how something works in order to be able to predict its behaviour. Indeed, in some areas it has been common for man to be able to make predictions before an understanding is achieved.
4. Another potent reason for building a model is that an understanding of how (say) the grassland system works is wanted. That is, curiosity is the motivating impulse. "Understanding" is taken to mean defining the relationships between the responses of a system and the mechanisms that are assumed to operate within the system. For this purpose a "mechanistic" model is required (see below). If it is possible to both understand and predict, then the opportunities for intervention and influencing future events are maximized.

Although biologists and agronomists are sometimes wary of modelling, it has to be emphasized that modelling and mathematics are the servants of science. The hypotheses expressed in mathematics and computer programs are derived from biological concepts. The model and computer program provide a powerful framework for representing, exploring and applying ideas about how it is thought that the system works.

Types of models

Models can be deterministic or stochastic, dynamic or static, mechanistic or empirical. A *deterministic* model makes definite predictions for quantities such as plant dry mass or animal intake without any associated probability distribution. This may be acceptable in many instances. But for rather variable quantities or processes, such as rainfall, migration (of diseases, pests or predators) and death this may not be satisfactory.

Stochastic models include a random element as part of the model, so that the predictions have a distribution. A problem with stochastic models is that they can be technically difficult, and hard to test or falsify. The apparent stochasticity of a system may merely reflect current ignorance about what is going on. A deterministic simulator, such as the Hurley Pasture Model, is driven by determined inputs for rainfall, wind, radiation etc. These inputs can be given values that occur in actual weather, thus allowing unambiguous connections to be made between outputs (predictions) and inputs. It is usually worth building a deterministic model first, to see if this will give the desired results, before attempting what may be a difficult stochastic problem. After all, weather is mostly predicted by large deterministic simulators, in spite of the variability of the weather in many locations.

A *dynamic* model predicts how quantities vary with time, so the model is generally presented as a set of ordinary differential equations with time, t, as the independent variable, such as $dM_{sh}/dt = ...$, $dM_{rt}/dt = ...$, for e.g. the rates of change of shoot and root mass. Sometimes the model is presented as a set of difference equations, relating the (say) plant mass on day $i + 1$, M_{i+1}, to the plant mass on day i, M_i, thus $M_{i+1} = M_i + ...$.

A *static* model does not contain time as a variable and does not make time-dependent predictions, e.g. a model predicting the fruit dry mass at harvest, or the total animal input over the season may be a static model, and a static model is usually empirical (see below).

An *empirical* model aims principally to describe the responses of a system, often using mathematical or statistical equations without any scientific content, and unconstrained by any scientific principles. Depending upon one's objectives, this may be the best kind of model to construct. Generally, an empirical model describes the responses belonging to a single level of the descriptional or organizational hierarchy (see below).

A *mechanistic* model provides a degree of understanding or explanation of the phenomena being modelled. To achieve this, the model must be constructed on (at least) two levels of organization or description (e.g. the plant and organ levels). The approach of scientific reductionism is employed. The term "understanding" implies a causal relationship between the quantities and processes ("mechanisms") which are represented on the lower level, and the phenomena which are predicted/observed at the upper level. For example, plant/crop growth rates (upper level phenomena) can be interpreted in terms of the operation of the processes of photosynthesis, allocation of substrates, respiration, nitrogen uptake, and transpiration (lower level processes). The lowest levels in a model, where the processes are represented, are always empirical. A mechanistic model is a structure of empirical components. Any empirical component can be modelled mechanistically at still lower levels. However, any model or scientific explanation has to stop somewhere, and a mechanistic model is therefore always incomplete. However, a well-constructed mechanistic model is transparent and open to modification and extension, without practical limit. Also, it is best to use not more than two levels in the reduction process, otherwise the model tends to become unmanageable. The processes (with their mathematical equations) which describe the lower level can be regarded as "empirical": that is they should describe reasonably accurately the process being modelled at the lower level, and the equation describing the process might or might not have some theoretical basis from analysis at a still lower level. A mechanistic model is based on ideas about how the system works, what the important elements are, and how they relate to each other. As with other types of models, the careful formulation of

objectives is needed, and determines the scope of the model constructed. Mechanistic models tend to be more research-oriented than application-oriented, although this is changing as mechanistic models become more reliable. Mechanistic models represent what is known scientifically about the system and its components; this knowledge base is ever expanding; the models can be developed rationally and step-by-step, integrating different items/areas of knowledge. A mechanistic model, built using a lower level of assumptions, has the potential of providing a view of system behaviour which, compared to an empirical model constructed on a single level using mathematical/statistical relationships unconstrained by science, is richer and offers more possibilities.

Another issue which sometimes arises when developing models of complex systems is: 'How mechanistic?', or 'How complex?'. Einstein said: 'As simple as possible, but no simpler.' The modeller tries to include the important mechanisms in his model. In biology there are many processes which, although essential for function, are in a sense trivial. Some multi-enzyme processes may behave very similarly to a single-enzyme process. Transport from A to B to C to D to E may, phenomenologically, be simulated as A to E transport, with suitable transport coefficients. Such modelling simplifications can understandably infuriate those researching the assumed 'triviality', and modelling papers are sometimes rejected by reviewers because their *amour-propre* is threatened. The modeller must understand the detail, but know how and when to simplify. In the never-ending search for efficient and meaningful ways in which to join up the different levels of description, to span the range from the plant and ecosystem to the gene and protein, it may be necessary to construct, by conjecture or otherwise, new intermediate-level descriptors.

Evaluation and validation of models

Evaluation is the term I use to include all methods of critiquing a model. Evaluation of models is essential, although it is often rather subjective. Evaluating the model with respect to the objectives of the person(s) constructing the model is the first consideration, perhaps followed by evaluation using additional or alternative objectives. Evaluation of a mechanistic model should begin at the level of the assumptions (lower level) and proceed to the predicted outcomes (upper level). Parameters should be determined by investigations at the lower level, that is, at the level of the model's assumptions. Unfortunately this is not always possible, and some "tuning" or "calibration" of parameters is usually needed. The fact that evaluation is not a wholly objective process gives many problems between authors of modelling manuscripts and reviewers and editors, who often/usually are not hands-on modellers and therefore lack the perspective which that brings. Arguably, it is high time there was a 'code of conduct' for reviewers of modelling papers (Thornley and Johnson, 2000, pp. 31-32, 41-44, discuss these issues). As mentioned above, a mechanistic model is always incomplete, and therefore usually does some things well and other things badly or not at all. While an initial evaluation of a model should always start from the objectives of the modeller, and includes questioning the modelling objectives, it is reasonable to proceed to a wider evaluation. The wider evaluation may consider properties of the model such as: simplicity, plausibility of assumptions, elegance, generality, applicability, and the qualitative and quantitative accuracy of predictions. Note that some of these are properties of the model standing alone, whereas others depend on the relationship between the model and other issues. Applicability depends on the application being considered.

The quantitative accuracy of predictions, sometimes referred to as "validity", is usually concerned with a model's ability to predict results for some particular experimental or observational scenario accurately. Again, validity is not a property of the model alone, but of the model in relation to some application. Attempts to formally "validate" a mechanistic

model are not generally conclusive, and neither is using mechanistic models as gigantic regression equations. However both activities continue to attract some support, although not usually from the mechanistic modellers themselves. A model is often acceptable (or "valid") for certain situations (e.g. southern Britain), and not acceptable in other situations (e.g. northwest Africa). "Validity" is not an all-or-nothing concept, but may be regarded as lying in the range zero to unity. A grassland farmer, considering using a model for helping him take management decisions on his farm, is primarily concerned with an affordable and do-able applicability and acceptable predictions for his environment. These requirements are rightly far more important to him than the quality of the science represented in the model, or the elegance of the model.

The Hurley Pasture Model (HPM)

The HPM is mechanistic, dynamic, and deterministic. The principal modelling objective has been to obtain an understanding of the more important factors determining the responses of the grassland ecosystem in the British environment. The model is written on approximately two levels of description. The top level of the model is drawn in Figure 1, which gives the ecosystem components represented in the model. The model accounts for the pools and fluxes of carbon (C), nitrogen (N) and water in grassland. There are submodels for the plant (Figure 2), animal (Figure 3), soil (Figure 4) and water (Figure 5), where the pools and processes represented are indicated. Table 1 lists the environmental and management variables which drive the system.

The model is formulated using standard methods for modelling continuous dynamic systems. The rate-state approach is used. That is, there is a set of state variables which are assumed to define the system. The state variables represent quantitites of substance (where "substance" can include geometrical aspects such as area), and are shown in the rectangular boxes in Figures 2 to 5. The rate of change of a state variable Y is calculated by

$$\frac{dY}{dt} = I_Y - O_Y \qquad (1)$$

where I_Y and O_Y are the inputs and outputs of Y. The input and output fluxes to a box (state variable) are calculated using some assumed mathematical equations. E.g. photosynthesis in Figure 2, which is an input to the shoot C substrate box (labile carbohydrates), is calculated assuming that the rate of photosynthesis depends upon light, CO_2, and air temperature using an empirical hyperbolic relationship which is known to describe measured leaf photosynthetic responses rather accurately (Cannell & Thornley, 1998b). The processes and their equations represented in Figure 2 (and in Figures 3 to 5) can all be regarded as empirical relationships which supply the mechanisms used to interpret and provide an understanding to the level 1 description in Figure 1. The empirical leaf photosynthesis equation provides one of the contributing mechanisms when viewed from above, the ecosystem/plant level. Alternatively, in a different model, the leaf level could be regarded as the top level of a mechanistic model of leaf photosynthesis; this then has lower levels comprising perhaps the Calvin cycle and the light reactions (all of which are empirical constructs), which provide mechanistic explanation to the leaf level.

Key assumptions of the plant submodel (Figure 2)

M Plant dry matter is regarded as being "structural" (e.g. cellulose) and "storage" or substrates (mono- and di-saccharides, starch, fructans for C substrates; amino acids, nitrate, some labile proteins for N substrates). This assumption partially decouples "sources" from

"sinks", which have different environmental dependencies. It permits a more meaningful calculation of growth, and also allows realistic within-plant allocation patterns to be calculated mechanistically.

M Within-plant allocation (shoot:root ratio) is calculated using the mechanistic transport-resistance approach (Thornley, 1998c). This method allows the great plasticity of plant allocation patterns to be accurately and realistically simulated.

M Using a "photosynthetic" protein pool, a phenomenological algorithm simulates photosynthetic acclimation to light, nitrogen, CO_2 (down-regulation) and temperature (Thornley, 1998b).

M Shoot and root structural material are assigned an age structure. Tissue ageing and turnover is a key feature of grassland, allowing the plants to withstand repeated cutting and grazing.

M Simple dynamic representation of variable grass-legume mixtures. Legume content follows a target value determined by the carbon:nitrogen substrate ratio in the plant. Symbiotic N fixation is calculated (as is non-symbiotic N fixation in the soil, Figure 4) as depending on legume content (slow response) and carbon and nitrogen substrate concentrations in the root (fast response).

M Ammonia fluxes through the stomates. Although these fluxes are small, they can be significant in low N deposition grassland ecosystems close to equilibrium.

Weaknesses of the plant submodel

M No explicit representation of plant proteins, except for the "photosynthetic" protein pool (see above). The explicit consideration of plant proteins would allow variable plant nitrogen:carbon relations to be more realistically incorporated, including a further refinement of the way in which "maintenance" respiration is calculated (Cannell and Thornley, 2000; Thornley and Cannell, 2000b).

M No representation of reproductive growth. This limits applications to swards which are grazed or cut in such a way that reproductive growth does not occur to a great extent. But see Riedo *et al*. (1998), who modify the plant submodel for this purpose.

The implementation of the first item would seem to be relatively straightforward, whereas the second item is difficult to treat satisfactorily. The method used by Riedo *et al*. (1998) is valuable in that it increases the range of application of their model (which makes use of a version of the plant submodel of the HPM). They use a temperature sum to calculate a developmental stage. This can be reset by cutting (grazing is not considered). Developmental state affects photosynthesis and partitioning.

Animal submodel (Figure 3)

This is the simplest submodel; it is highly empirical and is without significant state variables. The equations used in this submodel relate animal inputs directly to outputs to the atmosphere and to the soil and litter submodel. Arguably, a plant ecosystem model does not need a sophisticated animal submodel (e.g. Baldwin and Donovan, 1998). A generic animal submodel to transform inputs of C and N into outputs, with most of the ingested C being respired may be sufficient for many purposes.

Key assumptions of the soil submodel (Figure 4)

The soil submodel standard in most respects. Where the present formulation departs from most other models is:

M Ammonium N and nitrate N pools are separately represented. This allows loss processes which act on these different substrates to be more realistically accounted for - e.g. volatilization and nitrification occur from the ammonium pool, whereas nitrate is the substrate for denitrification and leaching. Also, plant and microbes do not respond equally to the two substrates. Although these two pools are small, only their explicit representation allows N ecosystem losses to be sensibly calculated.

M A soluble carbon pool represents C substrates in the soil such as carbohydrates and organic acids in the soil. This pool drives C leaching, microbial growth, and non-symbiotic N fixation.

Just as with the plant submodel, it seems that representing the relatively small but able substrate pools allows the model to simulate alternative uses and changing priorities in a natural and flexible manner. The alternative, of omitting substrate pools, is to use clumsy and *ad hoc* devices which can block off further model development.

Weaknesses of the soil submodel

M Only a single soil horizon is considered.

M Only a single microbial pool is included. Perhaps as a result of this assumption, it was necessary to use linear kinetics for the soil organic matter transformations rather than more realistic non-linear expressions such as the Michaelis-Menten equation which has elsewhere been used extensively.

Key assumptions of the water submodel (Figure 5)

M A mechanistic physico-chemical basis is chosen for this submodel. Plant water potential and its components are represented. Soil water potential and soil hydraulic conductivity are calculated from soil relative water content. The plant cells are elastic. Osmotic effects are included. Water fluxes are driven by water potential gradients.

Weaknesses of the water submodel

M A single horizon for soil water in used.

M The soil is assumed homogeneous.

M Simply and quite widely used equations are used to calculate soil water potential and soil hydraulic conductivity from soil water content, which arguably, rarely apply to #real$ soils with their complex pore size distributions, worm-holes, and cracks.

The dilemma here is that a more empirical approach might give greater accuracy, but could close off some desirable possibilities for model development.

Environmental data (Table 1)

The model accepts a variety of environmental data inputs: diurnal data, daily data, and monthly data, on all of which can be imposed a slow year-to-year drift to represent climate change (Figure 10). There are also options by which components of the environment can be modified by multiplication or addition.

Diurnal data. Data required are: latitude and N deposition rate (constants), and then radiation (photosynthetically active), air and soil temperatures, rain, wind and relative humidity. The latter six quantities can be at an arbitrary time interval, although measurements less frequent than once per hour are not recommended. Linear interpolation between data time points is employed, so that the internal time step of the model (the integration interval -

typically about 20 minutes) is independent of the data time interval.

Daily data. Data required are latitude, and then daily radiation (photosynthetically active), daily air maximum and minimum temperatures, soil temperature (daily mean), daily rainfall, daily windrun, daily maximum and minimum relative humidities, and daily N deposition of ammonium and nitrate. The program calculates instantaneous values of radiation, air temperature and relative humidity through the day by assuming sinusoidal variation. Soil temperature, rain and wind are assumed constant through the day, as are N deposition rates.

Monthly data. Data required are latitude, coefficients for the Ångström formula for calculating radiation from bright sunshine hours (Martinez-Lozano *et al.*, 1984: these authors give estimates of coefficients for various locations), and N deposition rate (constants). Then follows monthly means of daily maximum and minimum air temperature and relative humidity, monthly rainfall and monthly bright sunshine hours. These are as listed in the tables given by Meteorological Office (1982) who give 30-year means. Using linear interpolation, daily values are calculated, and then instantaneous values assuming sinusoidal variation (see above).

Applications of the Hurley Pasture Model

Some applications of the HPM are described in order to show the range of applications that lie within the scope of this grassland ecosystem model as currently formulated. These applications extend those described by Thornley (1998a), but use the latest version of the model (The source program of the HPM is pasture.csl; the program is well-annotated; it is obtainable *gratis* from www.nbu.ac.uk/efm/). The model is programmed in ACSL (**A**dvanced **C**omputer **S**imulation **L**anguage), a software package designed for dynamic modelling problems (ACSL, 2000).

The initialization problem

A difficulty associated with using any plant ecosystem model to attempt to simulate reality is: how to initialize the model? This is sometimes referred to as the "spin-up" problem. The difficulty resides primarily but not entirely with the soil submodel. Most soil submodels use discrete pools which are not amenable to experimental characterization. An undisturbed grassland soil may take several hundred years to reach an equilibrium state, even given constant environment and management, which are unlikely to have occurred. The current soil state depends therefore on a long uncertain history. Any disturbance of the system, natural or man-made, causes increased respiration and mineralization, and the soil pools could be expected to be below, possibly far below, their equilibrium values.

Here a "pragmatic" recipe for initialization has been adopted. The HPM was run to equilibrium using an internally generated mean environment for southern Britain with constant N deposition of 30 kg N ha^{-1} y^{-1}, clay content of 0.1, variable legume content, without fertilizer inputs or harvesting, and grazed to a constant leaf area index (*LAI*) of about two by mature sheep so that 99% of the ingested N is returned to the soil (Thornley, 1998a, chapter 4). These equilibrium values were used to initialize the HPM, and then various 'treatments' were applied.

Response of harvested dry matter to N fertilizer

The seasonal response to harvesting, with and without fertilizer addition is illustrated in Figure 6 (Thornley, 1998a, pp. 169-172). Three runs were made: the equilibrium run (see

above), then grazing was switched off and harvesting was applied, and last fertilizer and harvesting were applied. The timing of the harvests and the timing and amount of the fertilizer applications are shown in Figure 6(a). The effects of the three treatments on leaf area index (*LAI*) are given in Figure 6(b). The equilibrium run demonstrates that the constant-*LAI* grazing algorithm succeeds in maintaining the *LAI* close to two. Harvesting gives a sawtooth pattern to *LAI*, which is repeated at higher values when fertilizer is applied. The consequences for the soil mineral N pool are drawn in Figure 6(c). The equilibrium run shows strong seasonal variation, with high winter values. Soil mineral N is decreased (as expected) by harvesting without fertilizer addition. The response of the accumulated dry matter is illustrated in Figure 6(d), showing a moderate response to the addition of 360 kg N fertilizer. The legume response [Figure 6(e)] is not untypical (Frame and Newbould, 1984), in terms of both its seasonal variation and its response to added N. With five harvests per year, the *LAI* is kept at a lower average value than in the equilibrium scenario, decreasing light interception and photosynthesis (Table 2), although transpiration and stomatal closure [Figure 6(f)] are also decreased. Table 2 summarizes the treatment effects on the annual C and N fluxes into and out of the system. In this simulated example for southern Britain, water stress greatly affects grassland performance, as it does in reality.

Figure 7 depicts the effects of total fertilizer addition on total yield over a season. Two further simulations show how the effects of immobilization caused by straw addition and of a poor soil can be simulated. Straw addition depresses yield even for quite high fertilizer applications. However, the effect of a poor soil is overcome and surpassed by fertilizer application of 320 kg N ha^{-1} or more.

Response of intake to grazing

There has been much discussion in the UK (Hopkins, 2000) and elsewhere about grazing managements which optimize dry matter intake. Any pattern of stocking can be specified in the model. Figure 8 illustrates the effect on intake of grazing the sward to a target *LAI*, *LAI*$_{target}$, which is constant through the year[1]. Maximum intake is given by an actual *LAI* between 1 and 1.4, which is achieved by taking a target *LAI* of a similar value (In the model, *LAI* = 1 corresponds to a sward height of 2.6 cm).. This value maximizes the net effects on growth of photosynthesis, respiration, shoot allocation and water stress. Note that to achieve an actual average *LAI* of 2 requires a target *LAI* of about 2.3 [Figure 8(a)]: the relationship between target and actual *LAI* becomes non-linear above *LAI*'s of about 1.8 . Figure 8(b) illustrates the fact that gross production is highest for *LAI* of c. 1.8, which is greater than the *LAI* for maximum intake. For *LAI* greater than 1.8, photosynthesis is increasingly decreased by increasing stomatal closure [Figure 8(b)]. Legume content [Figure 8(c)] increases with increasing average *LAI* and decreasing grazing severity, as is often observed (*loc.cit.*).

Climate change

The last application presented here is concerned with climate change, and suggests an answer to the question: what are the possible effects of climate change on the productivity of temperate grassland. Note that climate change experiments are almost invariably quite short term (of several years duration at best), and are often concerned with the responses to step-changes in environmental variables. It is dangerous to extrapolate such results to the reality

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[1]Intake is simulated by a quasi step function dependence on *LAI*, so that for *LAI* < *LAI*$_{target}$ intake falls quickly to zero, and rises to high values if *LAI* > *LAI*$_{target}$. This stabilizes *LAI* around *LAI*$_{target}$, so long as enough shoot growth occurs so that *LAI* can attain this value.

of climate change which is slow, may span centuries, and gives ecosystems much time to respond. Indeed, these and other simulation results indicate that the results of short-term experiments can be quite opposite to the long-term effects. Therefore first the simulated consequences of step changes to environmental factors are examined, before considering the simulated consequences of realistic climate change scenarios. The assumed climate change affects atmospheric CO_2, atmospheric N deposition and temperature only.

Figure 9 illustrates, for southern Britain equilibrium conditions with a grass-legume sward grazed to a constant leaf area index of about two, the effects over eight years of step changes to ambient CO_2 (+ CO_2: doubled, from 350 to 700 :mol mol^{-1}), N deposition (+ N: 30 to 100 kg N ha^{-1} y^{-1}) and temperature (+T: all temperatures increased by 5°C). The grassland model is, using the language of dynamic systems, a classical 'stiff' system: the carbon dynamics are relatively fast, whereas the longer-term behaviour depends on nitrogen, and its acquisition or loss by the ecosystem. This can be seen by comparing the ratio of carbon input, of order 1 kg C m^{-2} y^{-1}, to the carbon content, of order 8 kg C m^{-2}, giving a rate constant (by division) of 1/8 = 0.125 y^{-1}, with the ratio of nitrogen input, of order 0.0050 kg N m^{-2} y^{-1}, to the nitrogen content, of order 0.8 kg C m^{-2}, giving a rate constant (by division) of 0.0050/0.8 = 0.006 y^{-1}. The latter is over twenty times smaller, giving a correspondingly longer time constant. A more detailed explanation of grassland N dynamics is given by Thornley and Cannell (2000a). Note that a grass sward with no legume content can give more anomalous behaviour and is considerably slower to respond to environmental change than a grass-legume sward with its greater ability for regulating nitrogen inputs.

+CO_2 and + T (1st and 3rd columns of Figure 9) give some immediate responses which are partially or even completely reversed with the further passage of time: e.g. for net production (+T), legume fraction, soil mineral N, and specific leaf area. Responses to N are mostly simpler, but note that shoot:root ratio moves in the opposite direction to shoot:root growth ratio for a sward grazed to a constant height [Figure 9(e)]. These results, for a grass-legume sward grazed to a constant leaf area index (*LAI*), should be compared with those of Cannell and Thornley (1998a), who did a similar analysis for a grass-only sward with a 'free' LAI. Their results indicate more plainly the anomalous and possibly misleading responses which can be obtained from short-term experimentation on a grassland system.

The simulated effects of 250 years of climate change, from 1850 to 2100, are illustrated in Figure 10. The climate scenario is given in Figure 10(a), where ambient CO_2 concentration, N deposition rate, and temperature are drawn. The effects of different combinations of these climate change components on net primary production, total system C, soil mineral N and animal intake are illustrated in Figs 9(b) to 9(f). These calculations indicate that, for a grass-legume sward grazed to a constant height (leaf area index), CO_2 is the most important variable; N deposition is of minor important for a grass-legume sward; temperature only has large effects on system C [Figure 10(b)], legume fraction [Figure 10(g)], and shoot:root ratio [Figure 10(c)]. However, these results may be compared with Thornley (1998a, figure 8.17, p. 188) for a grass-only sward with a relatively 'free' leaf area index. Here, the impact of nitrogen and to a lesser extent temperature on *LAI* and thereby on gross production are substantial and significantly affect the outcome; the combination of increased atmospheric CO_2 and increased N deposition are powerful indeed, acting through the increased *LAI,* with very beneficial consequences for grassland productivity. The impact of climate change on grassland is therefore strongly dependent on grassland type, local conditions, and management. There are no universal answers.

Conclusions

The development of mechanistic models is an integral and essential part of the shift in

the research focus towards the need for quantitative explanation, integration of complexity, and prediction in the agricultural and ecological sciences. A grassland research program without a modelling component may be critically emasculated by this missing dimension. A plant ecosystem model is 'big' science, and to do such work successfully requires appropriate organization and commitment. While models are, rightly, only a part of the research scene, they provide a framework for ideas which can be helpful to all involved in grassland research and applications of that research.

For grassland ecosystems in particular, this work has shown that climate change responses can be greatly affected by (i) a variable legume content; (ii) management, e.g. how the crop is grazed or cut; and (iii) water stress, as occurs in southern Britain.

Acknowledgements

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Table 1 - Environmental and management variables used in the Hurley Pasture Model. By default a 22.5 minute (1/64 d) time step is used in the model. The model can be driven by diurnal, daily, or monthly data, or can generate its own environmental data assuming sinusoids.

Quantity	Units
Environment	
Atmospheric CO_2 concentration	vpm (:mol mol^{-1})
Environmental N input to soil ammonium pool	kg ammonium N m^{-2} d^{-1}
Environmental N input to soil nitrate pool	kg nitrate N m^{-2} d^{-1}
Photosynthetically active radiation J m^{-2} d^{-1}	
Air temperature ^{o}C	
Soil temperature	^{o}C
Rainfall	m d^{-1}
Wind speed at specified reference height	m s^{-1}
Relative humidity	
Reference height for meteorological measurements m	
Management	
Fertilizer	
N applied at each fertilizer application	kg N m^{-2}
Fractions of N fertilizer entering soil ammonium and nitrate pools	
Number of fertilizer applications y^{-1}	
Times of fertilizer applications	d
Harvesting	
Harvest height	m
Number of harvests y^{-1}	
Times of harvesting	d
Stocking	
Constant stocking density through year	sheep m^{-2}
Stocking densities for up to 26 periods of stocking	sheep m^{-2}
Times when stock are introduced	d
Duration of stocking periods	d

Table 2 - Annual carbon (C) and nitrogen (N) inputs (I) to and outputs (O) from the system

(*sys*). $I_{C,sys}$ is the photosynthetic input. The equilibrium scenario (top row) is grazed to a constant leaf area index of about two.

	$I_{C,sys}$	$O_{C,sys}$	$I_{N,sys}$	$O_{N,sys}$
	(kg C m^{-2} y^{-1})		(kg N m^{-2} y^{-1})	
Equilibrium	1.65	1.65	0.0063	0.0064
No grazing	1.30	1.38	0.0051	0.0078
Harvesting (no fertilizer)	1.30	1.54	0.0055	0.0172
Harvesting + fertilizer	1.32	1.62	0.0399	0.0460
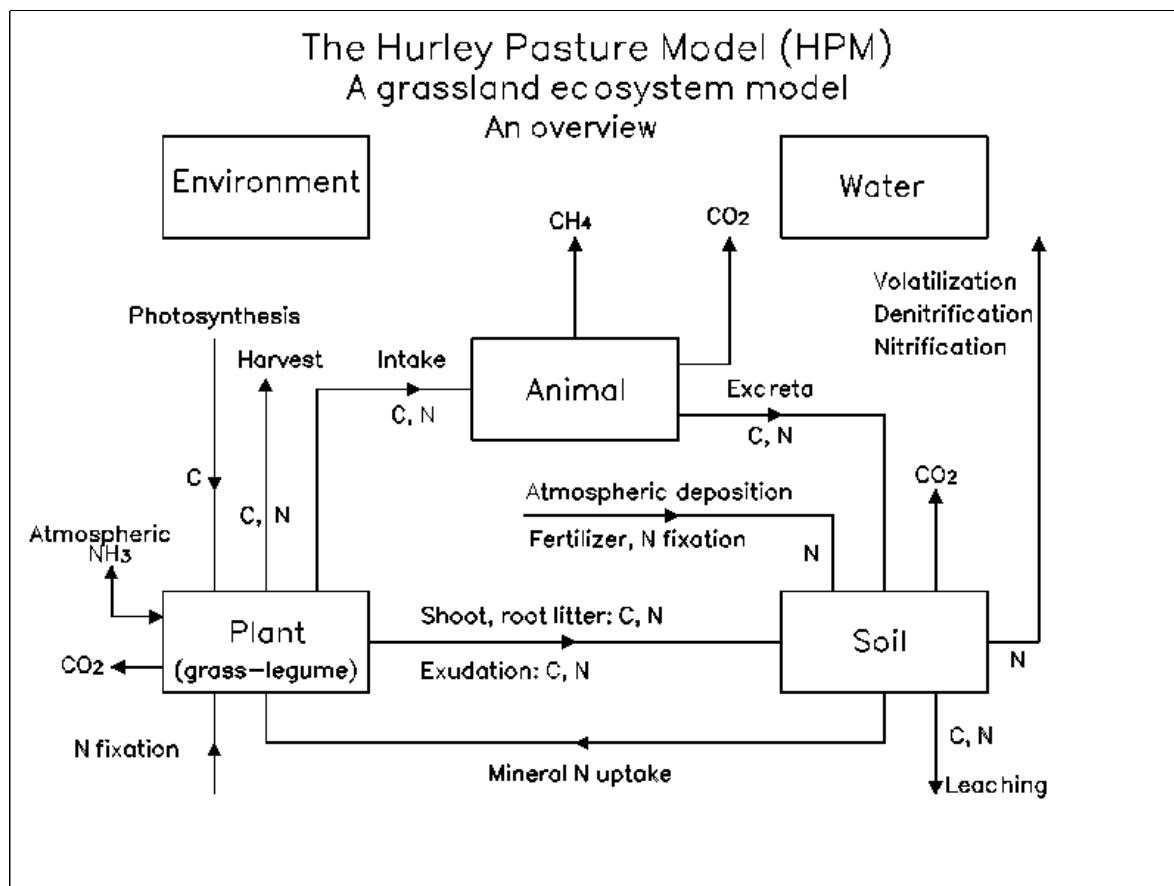
Figure 1 - Hurley pasture model: overview.
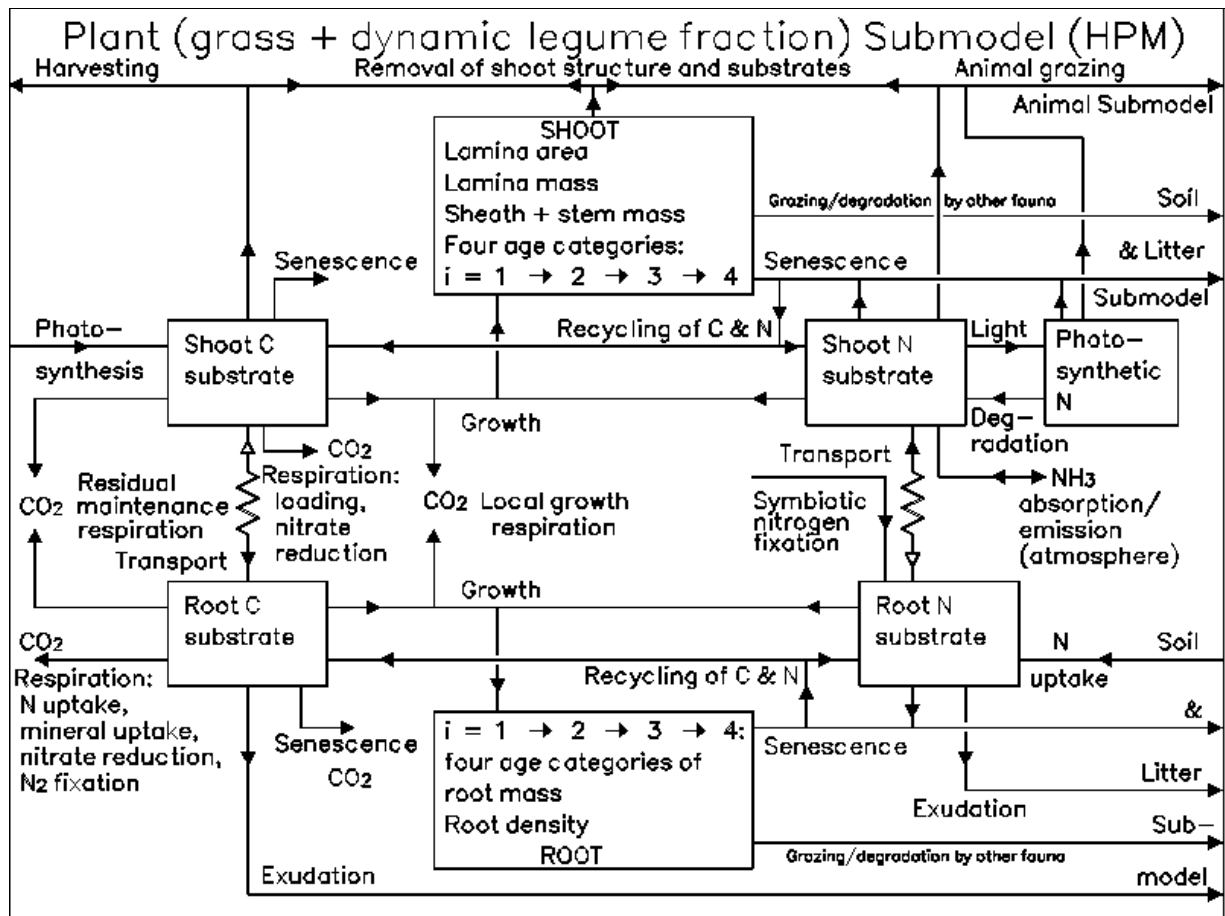
Figure 2 - Plant submodel.
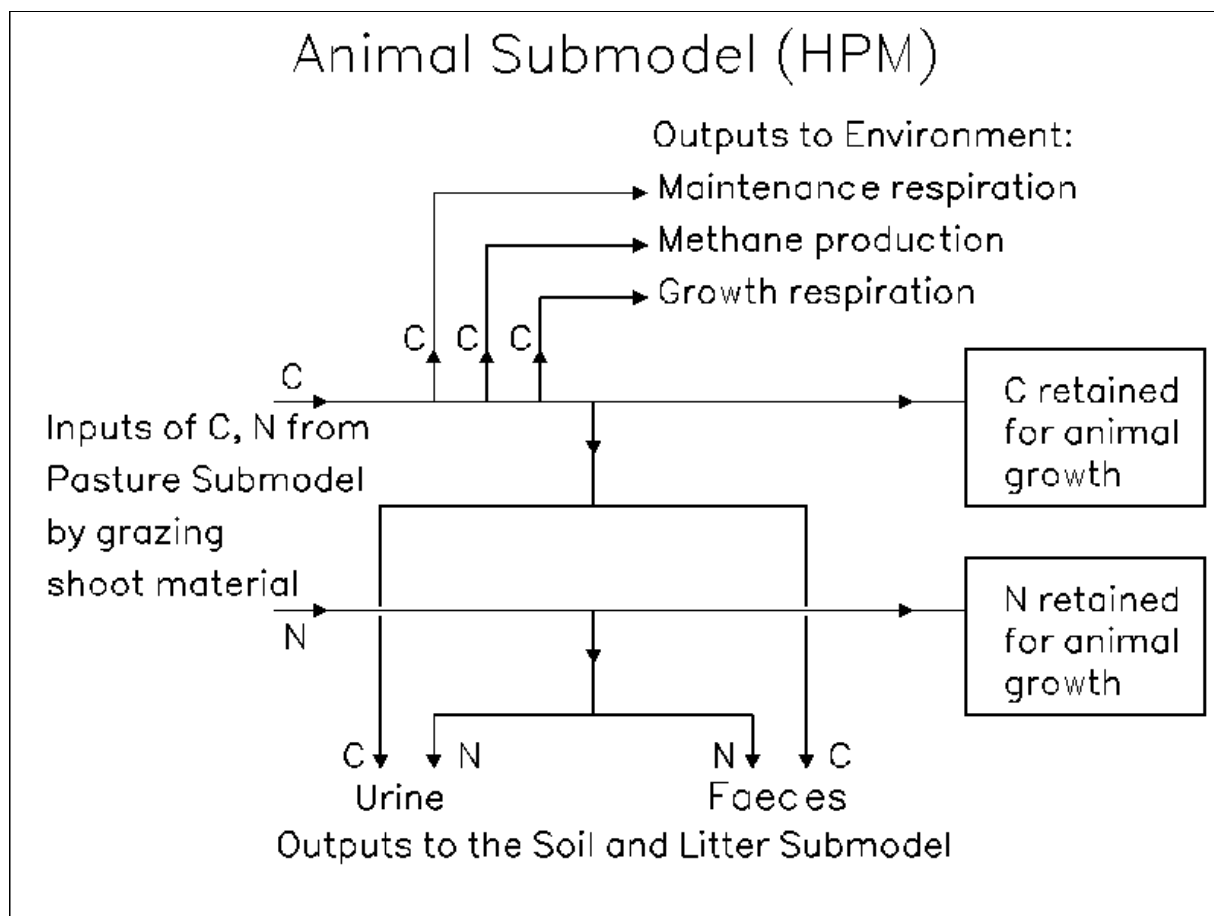
Figure 3 - Animal submodel.
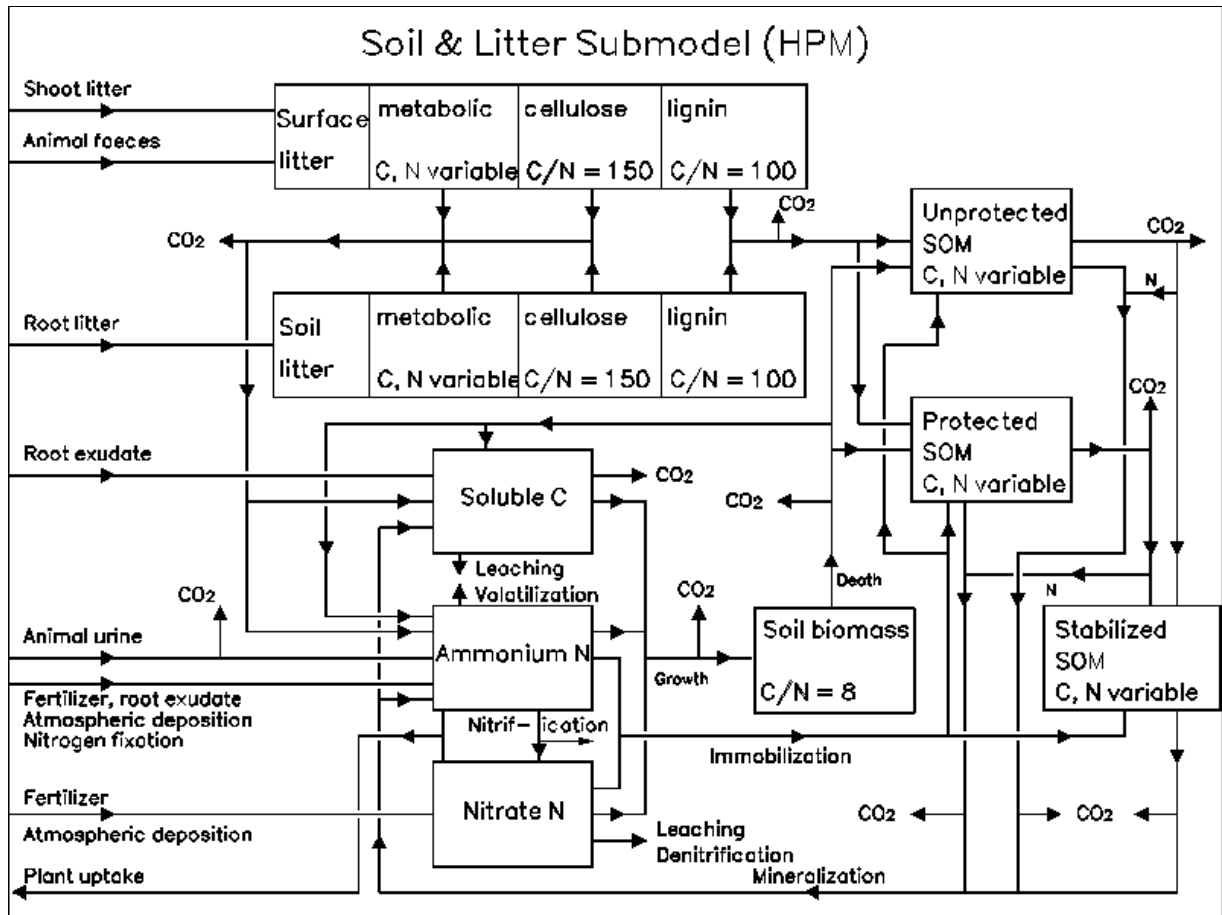
Figure 4 - Soil and litter submodel.
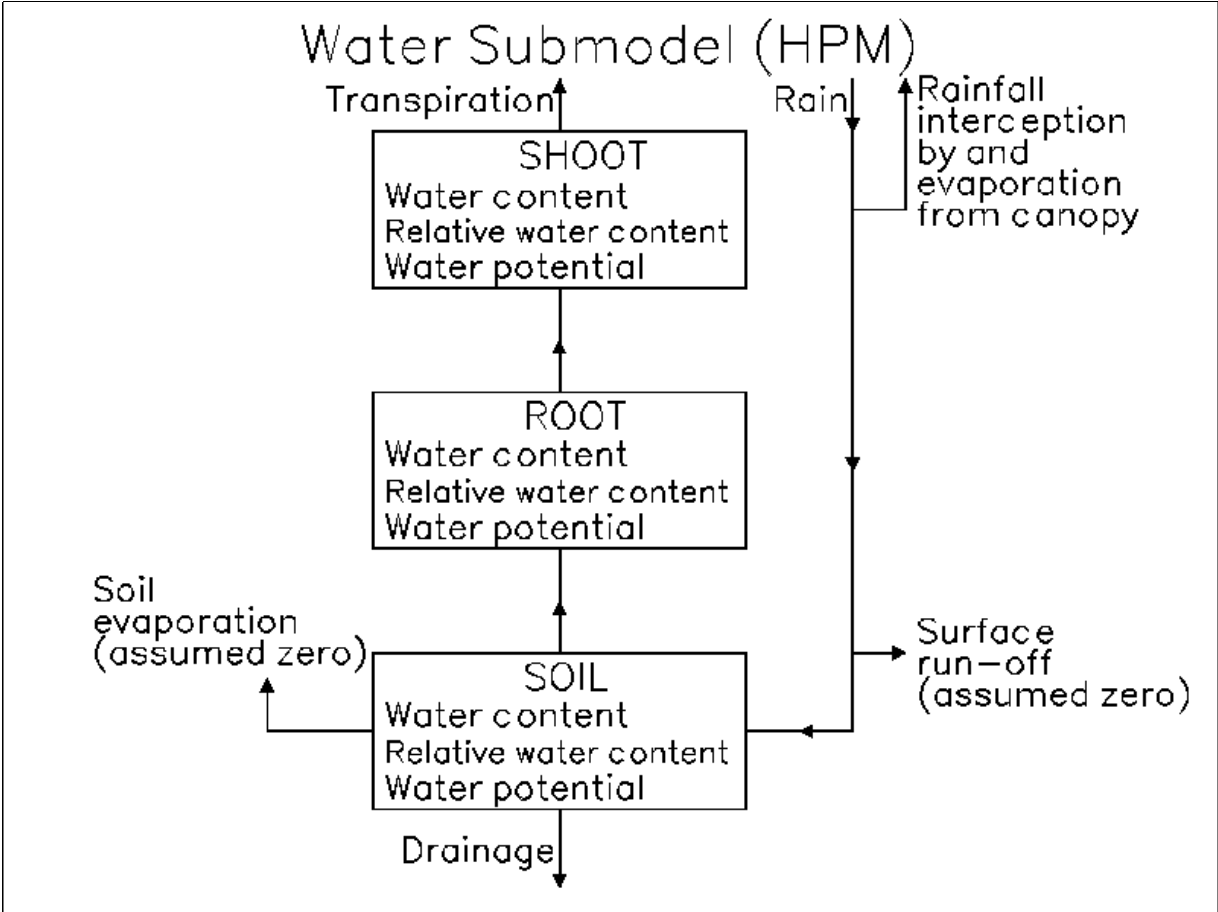
Figure 5 - Water submodel.
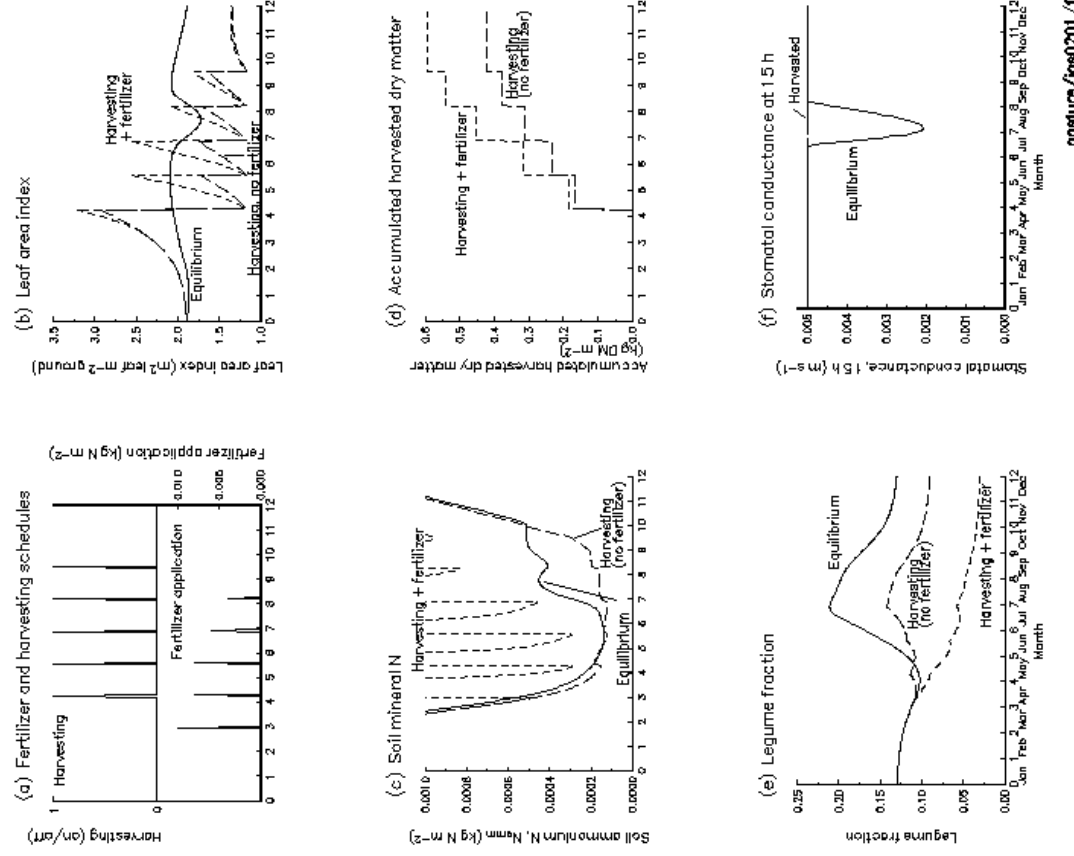
Figure 6 - Effects of N fertilizer application. 100, 80, 80, 60, 40 kg N ha^{-1} are applied on 1 Apr, 11 May, 20 June, 30 July, 8 September; 70% of the N is ammonium N, the rest is nitrate N. The sward is cut to 3 cm on 10 May, 19 June, 29 July, 7 Sep, 17 October. The three simulations are for the equilibrium grazed sward, then harvesting without fertilizer application, and last, fertilizer with harvesting. An average south Britain environment with grazing to a constant leaf area index of about two is used to determine the initial values on 1 January, which is the equilibrium state obtained by running the model for hundreds of years. (a) fertilizer application and times of harvesting. (b) leaf area index. (c) soil mineral N. (d) cumulative yield. (e) legume fraction. (f) stomatal conductance at 15 h.
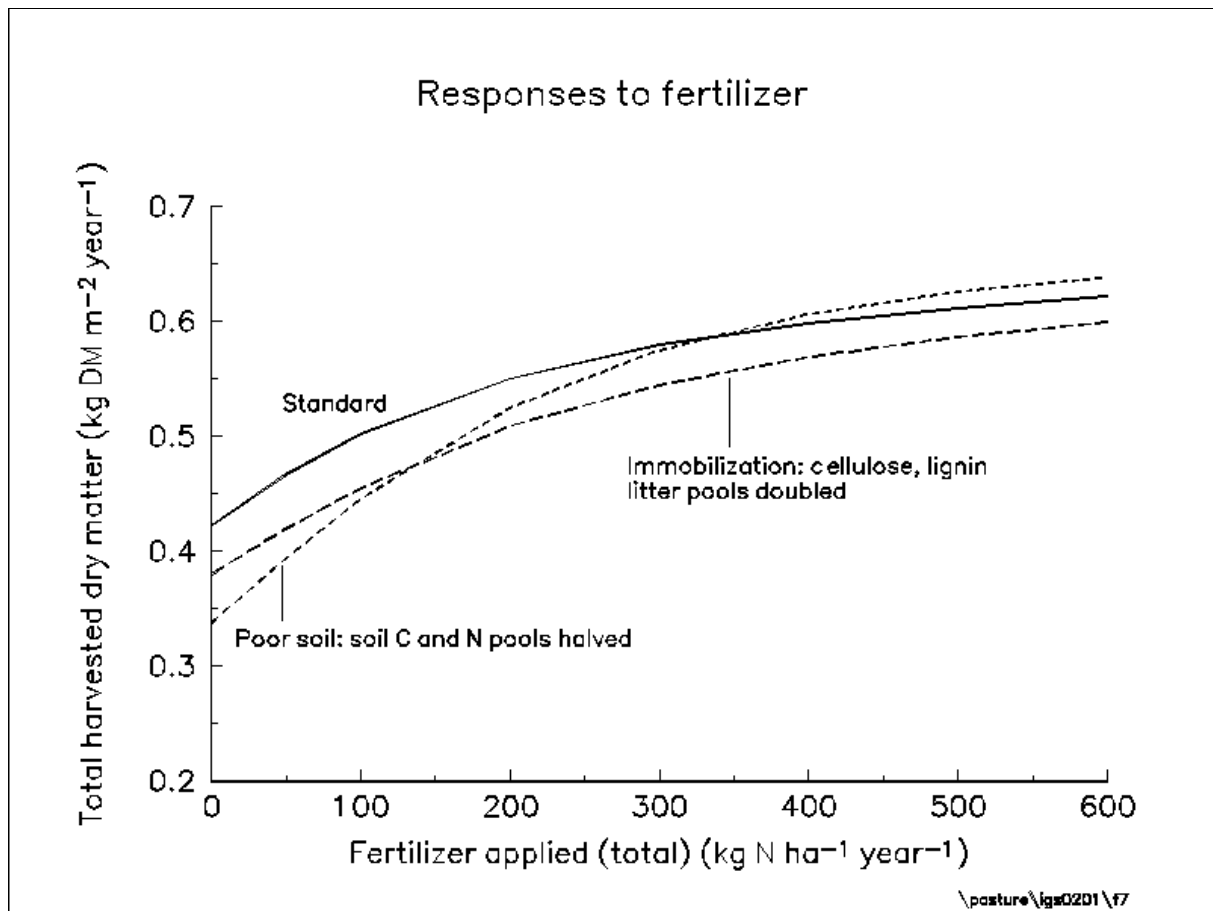
Figure 7 - Fertilizer responses. The environment, sward cutting and fertilizer regimes are as in Fig. 6 but using different total quantities of fertilizer. The standard curve is for the southern British environment equilibrium initial conditions with zero fertilizer application. For the second curve the initial values on 1 January of the litter cellulose and lignin pools are doubled relative to the equilibrium initial values to mimic the effects adding straw. For the third curve all the soil C and N pools have been halved from the equilibrium values on 1 January, to mimic the immediate effects of a poor soil.

Figure 8 – Responses to grazing intensity. The sward is grazed with a step-function intake equation with a target leaf area index (*LAI_target*), which is constant throughout the year. *LAI_target* is a maximum value which is not always achieved due to physiological or environmental constraints (e.g. for a *LAI_target* above about 1.8). Results are shown as a function of the average *LAI* actually achieved over the year (abscissa). Except for the target *LAI*, default values are used with equilibrium initial values and no fertilizer application. (a) animal dry matter intake. (b) gross production (*GP* = canopy gross photosynthesis) and the fractional decrease in *GP* from stomatal closure. (c) legume fraction.
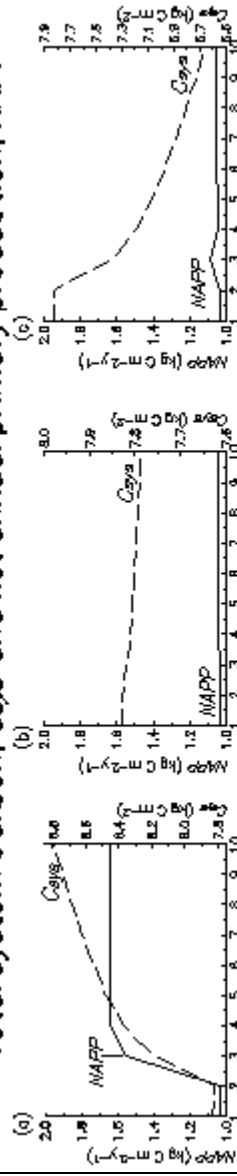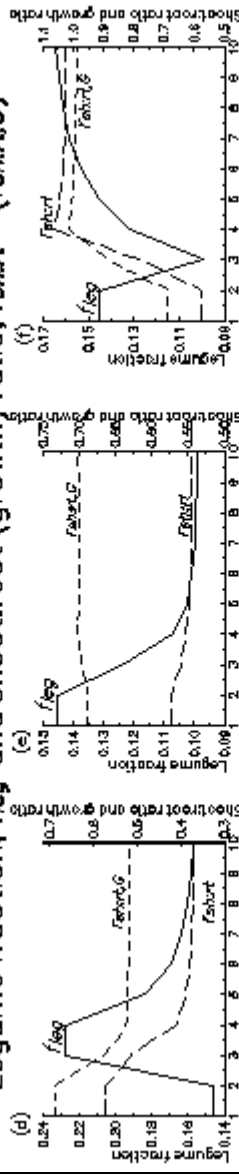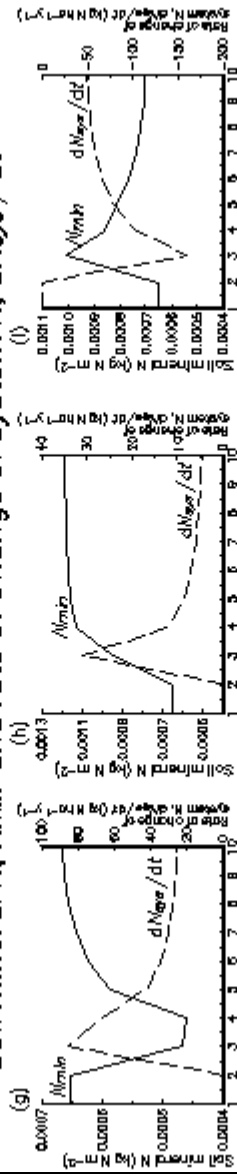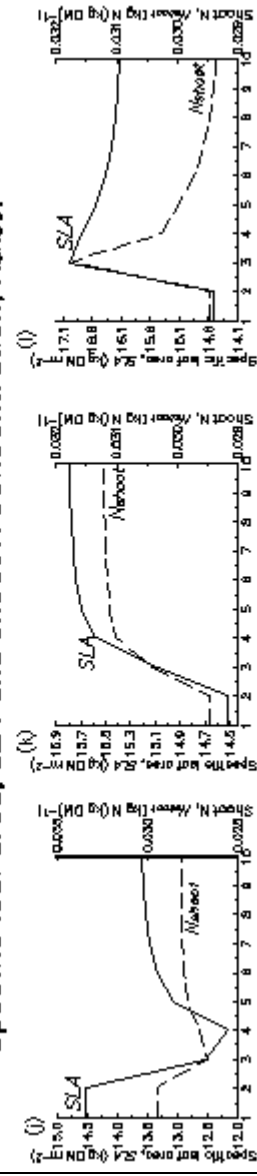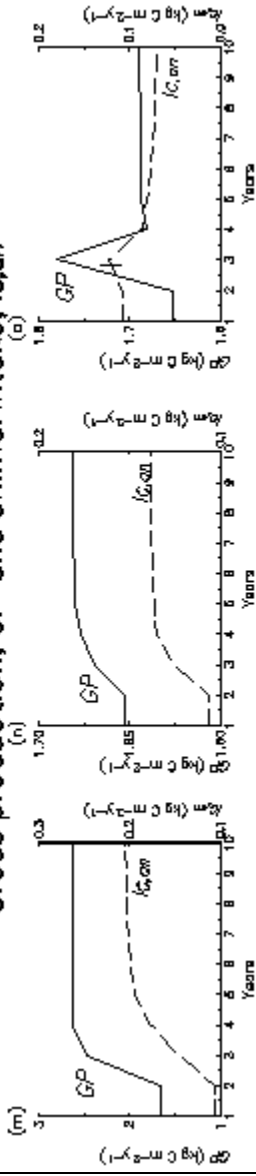
Figure 9 – Responses to step changes in ambient CO_2, N deposition and temperature. Ambient CO_2 is doubled, from 350 to 700 :mol mol^{-1} (left-hand column); N deposition is increased from 30 to 100 kg N ha^{-1} y^{-1} (centre column); all temperatures increased by 5°C (right-hand column). The environment is for southern Britain using equilibrium initial values for a grass-legume sward grazed to a constant leaf area index of about two.
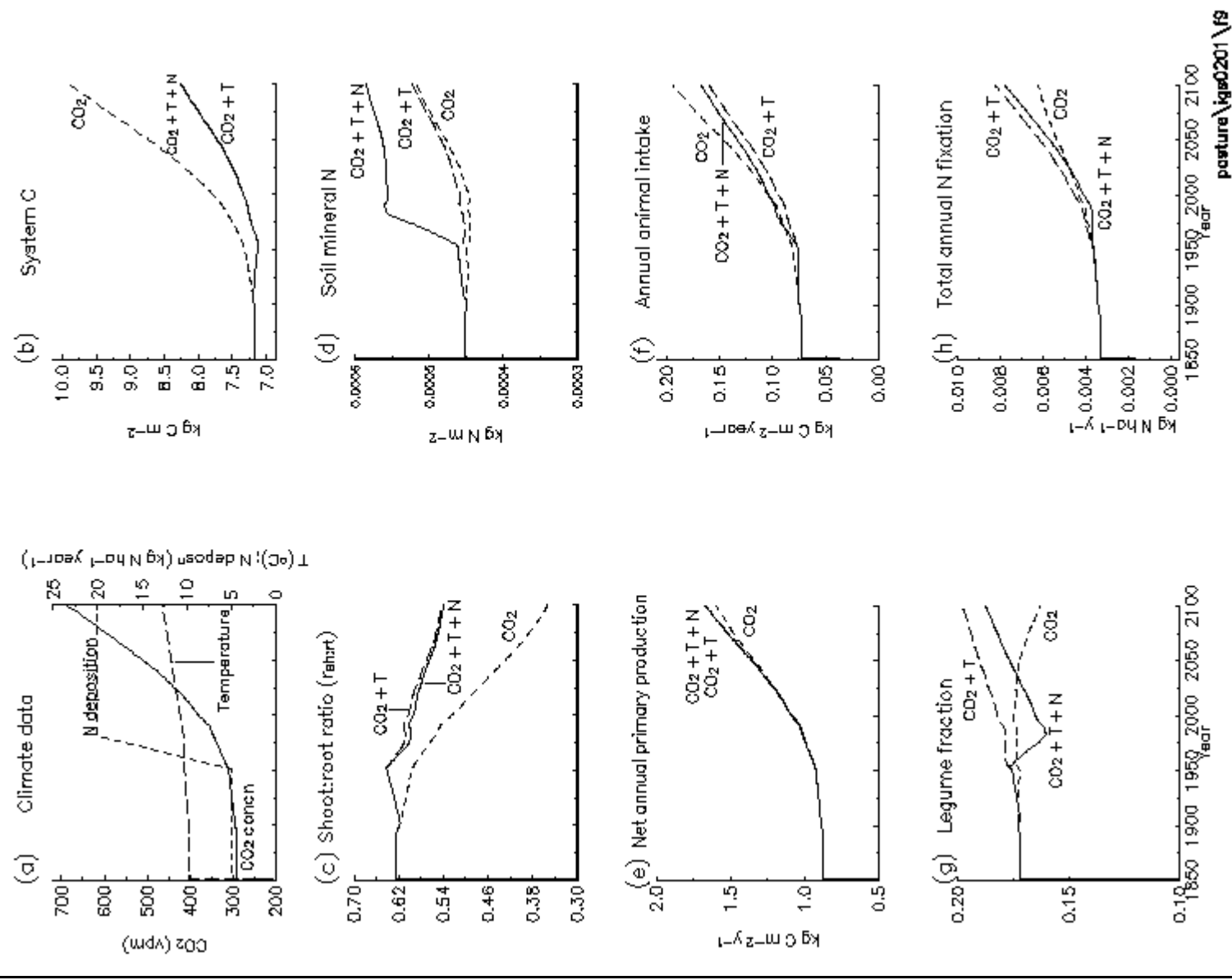
Figure 10 - Simulated climate change from 1850 (pre-industrial climate). Constant leaf area index grazing to an *LAI* of about two is applied throughout. The climate data shown in (a) are used to modify the standard southern Britain environment. Effects of climate components are shown: with CO_2 increase alone (CO_2), CO_2 increase + temperature increase ($CO_2 + T$), CO_2 increase + temperature increase + N deposition increase ($CO_2 + T + N$). N deposition is placed in the ammonium soil pool. Quantities shown are annual averages or sums.