Complex Dynamics in a Carbon–Nitrogen Model of a Grass–Legume Pasture

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A physiologically based model of a grass–legume pasture is used to study the dynamics of these competing species. In our model, we consider carbon and nitrogen pools and fluxes, incorporating competition for light and soil mineral nitrogen, and including the processes of nitrogen fixation, nitrogen losses and dry matter allocation. First, the steady-state responses of each species to nitrogen deposition, to leaching rate, and to other nitrogen losses are examined. We then consider the dynamic behaviour of these species when there is no time delay for nitrogen cycled through the soil organic matter pool. Next, the effects of various time delays associated with the soil organic matter nitrogen pool on the system dynamics are examined: the behaviour becomes complex, non-linear and exhibits lightly or heavily damped oscillations at two frequencies. The high sensitivity of the system both to the initial value of the soil organic matter nitrogen pool, and to any photosynthetic competitive advantage, is investigated. The implications of these results in relation to observations and experiments on grass–legume pastures are discussed.

Key words: Model, grass, legume, competition, co-existence, carbon, nitrogen, fixation, instability, chaos.

INTRODUCTION

The distribution and abundance of legumes in grazed mixtures, such as the perennial ryegrass–white clover swards found in cool temperate regions, demonstrate spatial and temporal fluctuations which are neither understood nor easy to manage in an agricultural context (e.g. for the UK see Frame and Newbould, 1984, 1986; Wilkinson, 1984). Clover can exhibit a dynamic instability, with patches appearing and disappearing, yet with the species persisting at low mean levels in the field. The dynamic behaviour of grass–legume mixtures raises many interesting questions about the coexistence of competing plants, and in the case of ryegrass–white clover swards, there is a unique opportunity to answer these questions mechanistically since much is known about the physiology of both species (e.g. Baker and Williams, 1987; Jones and Lazenby, 1988). It is hoped that a mechanistic understanding of the dynamics of grass and legume mixtures may enable improved management of this important agricultural system (Robson, Parsons and Williams, 1989, p. 47), and may help alleviate current concerns about their sustainability, particularly in relation to environmental change.

Although much work has been done on mixtures (e.g. Parsons, Harvey and Johnson, 1991*a*; Parsons, Harvey and Woledge, 1991*b*), the theoretical work to-date has focused largely on competition for light and the supply of carbon substrates for growth (Ross, Henzel and Ross, 1972; Thornley and Johnson, 1990, pp. 258–262), with little

attention paid to competition for nitrogen (but see Ross *et al.*, 1972; McMurtrie and Wolf, 1983). In the studies not incorporating nitrogen, stable persistence of ryegrass and clover has generally been unachievable except in the special case where the competitive advantage of clover is exactly balanced by the feeding preference of the grazing mammals (e.g. Parsons *et al.*, 1991*a, b*), or where environmental conditions are made to fluctuate. This has led to the suggestion that perennial ryegrass–clover mixtures are intrinsically unstable (Parsons *et al.*, 1991*a*), although the cause of such instability remains unclear. Furthermore, everyday experience indicates that perennial ryegrass–clover mixtures may persist for long periods. To date, no-one has explored the role of processes such as senescence, mineralization, competition and nitrogen fluxes in determining the dynamics of grass–clover mixtures.

The objective of the work described here is to explore the properties of a grass–legume model that incorporates the fluxes and pools of both carbon and nitrogen in order to investigate the implications for the steady states, stability, and dynamics of species composition in a mixed community. First, the steady-state solutions of grass alone, legume alone, and grass with legume are determined. Then, the dynamic behaviour of the system is studied with various time lags in the cycling of N. It is found that the time lag inherent in the cycling of N between plants and soils is sufficient to cause complex dynamics, possibly leading to chaos. Although this model is developed without any explicit spatial component, the relationship between erratic behaviour in time and space is discussed.

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FIG. 1. Grass–legume C–N competition model. The N losses from the system may include volatilization, nitrification, denitrification and leaching, and are of two types, parameterized by $f_{SOM, N, l}$ [eqn (3f)] and k_{leach} [eqn (3h)].

THE MODEL

The model proposed has been made as simple as possible, although it contains 22 state variables: ten of which describe the grass (shoot and root structure each with four age categories, C and N substrates), similarly ten describe the legume, and two describe soil conditions (N in soil organic matter, and mineral N) (see Fig. 1). Our experience here and elsewhere (Johnson and Thornley, 1985; Thornley and Verberne, 1989) is that the inclusion of tissue age categories makes a substantial and important difference to dynamic behaviour (see pp. 176–180 of Thornley and Johnson, 1990, for a general discussion of this point). All variables are per unit of ground area (m^{-2}), and are defined in Table 1. Standard parameter values are also given in Table 1. These parameter values were chosen from within the range of observed values whenever relevant values exist; no attempt was made to adjust or fit parameters in relation to observational data. The model is described in two sections. First we detail the physiology of the plants by considering photosynthesis, nitrogen uptake, total growth (in terms of substrate carbon and nitrogen utilization), allocation of carbon to roots and shoots, and the production of litter. This is followed by a description of the soil submodel.

Plant physiological submodel

Photosynthesis and competition for light. Rather than use a detailed mechanistic representation of sward structure, light interception and photosynthesis (e.g. Thornley and Johnson, 1990, pp. 258–262), we decided that a simpler empirical approach would be adequate for the current purpose.

It is assumed that competition for light is a function of the leaf area indices, L_{gr} and L_{le} , of the grass and the legume, and their relative capacities to generate new leaf area over time. Effective leaf area indices (total, grass, legume) are defined by

$$L_{eff} = L_{eff, gr} + L_{eff, le} \quad \text{where} \quad L_{eff, gr} = k_{LA, gr} L_{gr} \quad \text{and} \quad L_{eff, le} = k_{LA, le} L_{le}. \quad (1a)$$

Competition between the grass or legume can be applied by weighting with the dimensionless functions $k_{LA, gr}$ and $k_{LA, le}$ which encapsulate competitive advantages which arise from differences in leaf photosynthetic efficiency, sward structure, or aspects of age-related factors. We assume

$$k_{LA, gr} = \left(\sum_{i=1}^4 w_{gr, sh, i} M_{gr, sh, i} \right) / M_{gr, sh}; \quad (1b)$$

$$k_{LA, le} = \left(\sum_{i=1}^4 w_{le, sh, i} M_{le, sh, i} \right) / M_{le, sh}.$$

TABLE 1. Definitions of symbols and numerical values. *C* and *N* (Roman) denote carbon and nitrogen (the SI symbols for coulomb and newton are not used here). *XC* and *XN* denote structural *C* and *N*; *SC* and *SN* denote substrate *C* and *N*. [*C*] and [*N*] denote units of substrate *C* and *N* concentrations: kg *SC* (kg *XC*)⁻¹ and kg *SN* (kg *XC*)⁻¹, respectively

Symbol	Definition	Initial value
State variables of the grass–legume model		
Grass (subscript, <i>gr</i>)		
$M_{C,gr}$	Mass of substrate <i>C</i> (2o)	0.02 kg <i>SC</i> m ⁻²
$M_{gr,rt,i}$, $i = 1-4$	Mass of structural <i>C</i> in four age categories of the root [(2a), (2o)]	0.025, 0.025, 0.025, 0.025 kg <i>XC</i> m ⁻²
$M_{gr,sh,i}$, $i = 1-4$	Mass of structural <i>C</i> in four age categories of the shoot [(1c), (2o)]	0.025, 0.025, 0.025, 0.025 kg <i>XC</i> m ⁻²
$M_{N,gr}$	Mass of substrate <i>N</i> (2o)	0.002 kg <i>SN</i> m ⁻²
Legume (subscript, <i>le</i>)		
$M_{C,le}$	Mass of substrate <i>C</i> (2p)	0.02 kg <i>SC</i> m ⁻²
$M_{le,rt,i}$, $i = 1-4$	Mass of structural <i>C</i> in four age categories of the root [(2a), (2p)]	0.025, 0.025, 0.025, 0.025 kg <i>XC</i> m ⁻²
$M_{le,sh,i}$, $i = 1-4$	Mass of structural <i>C</i> in four age categories of the shoot [(1c), (2p)]	0.025, 0.025, 0.025, 0.025 kg <i>XC</i> m ⁻²
$M_{N,le}$	Mass of substrate <i>N</i> (2p)	0.002 kg <i>SN</i> m ⁻²
Soil		
N_{min}	Mass of soil mineral <i>N</i> (3i)	0.0005 kg <i>N</i> m ⁻²
N_{SOM}	Mass of <i>N</i> in soil organic matter pool [(3d) and (3e)]	0 kg <i>N</i> m ⁻²
Other significant variables of the grass–legume model		
C_{gr} , C_{le}	<i>C</i> substrate concentrations in grass and legume (2c)	kg <i>SC</i> (kg <i>XC</i>) ⁻¹
$F_{gr,rt,1}$, $F_{gr,sh,1}$, $F_{le,rt,1}$, $F_{le,sh,1}$	Fluxes of structural <i>C</i> allocated to root and shoot (2j)	kg <i>XC</i> m ⁻² d ⁻¹
$f_{a,gr,rt}$, $f_{a,gr,sh}$, $f_{a,le,rt}$, $f_{a,le,sh}$	Allocation fractions for new structural dry matter (2i)	
$f_{gr,rt}$, $f_{gr,sh}$, $f_{le,rt}$, $f_{le,sh}$	Fractions of structural matter in root and shoot (2h)	
$f_{L,gr}$, $f_{P,gr}$, $f_{L,le}$, $f_{P,le}$	Fractions of total LAI, total photosynthesis in grass and legume (1f)	
$G_{gr,XC}$, $G_{le,XC}$	Gross structural <i>C</i> growth rates (2e)	kg <i>XC</i> m ⁻² d ⁻¹
$G_{gr,XN}$, $G_{le,XN}$	Gross structural <i>N</i> growth rates (2g)	kg <i>XN</i> m ⁻² d ⁻¹
$I_{N,min,SOM}$	Input of <i>N</i> to the mineral <i>N</i> pool from soil organic matter (3f)	kg <i>N</i> m ⁻² d ⁻¹
L_{eff}	Effective LAI (1a)	m ² leaf (m ² ground) ⁻¹
L_{gr} , L_{le}	Leaf area indices of grass and legume [(1a), (1d)]	m ² leaf (m ² ground) ⁻¹
M_{gr} , M_{le}	Grass and legume total structural dry masses (2e)	kg <i>XC</i> m ⁻²
$M_{gr,sh}$, $M_{gr,rt}$, $M_{le,sh}$, $M_{le,rt}$	Grass and legume shoot and root structural dry masses (2e)	kg <i>XC</i> m ⁻²
N_{gr} , N_{le}	<i>N</i> substrate concentrations in grass and legume (2e)	kg <i>SN</i> (kg <i>XC</i>) ⁻¹
$O_{gr,XC}$, $O_{gr,XN}$, $O_{le,XC}$, $O_{le,XN}$	Total structural <i>C</i> , <i>N</i> litter fluxes (21)	kg <i>XC</i> , <i>XN</i> m ⁻² d ⁻¹
$O_{gr,SC}$, $O_{gr,SN}$, $O_{le,SC}$, $O_{le,SN}$	Total substrate <i>C</i> , <i>N</i> litter fluxes (2m)	kg <i>SC</i> , <i>SN</i> m ⁻² d ⁻¹
$O_{gr,C}$, $O_{gr,N}$, $O_{le,C}$, $O_{le,N}$	Total <i>C</i> , <i>N</i> litter fluxes (2n)	kg <i>C</i> , <i>N</i> m ⁻² d ⁻¹
P_{total} , P_{gr} , P_{le}	Photosynthetic rate: total gross (1e), grass and legume (1g)	kg <i>C</i> (m ² ground) ⁻¹ d ⁻¹
R_{soil}	Soil respiration (3a)	kg <i>C</i> m ⁻² d ⁻¹
$U_{N,fix}$	<i>N</i> fixation rate (2b)	kg <i>N</i> m ⁻² d ⁻¹
$U_{N,gr}$, $U_{N,le}$	Root uptake rates (2a)	kg <i>N</i> m ⁻² d ⁻¹
$\phi_{pa,gr}$, $\phi_{pa,le}$	Partitioning functions (2i)	
Parameters		
$c_{SLA,gr}$, $c_{SLA,le}$	Specific leaf area parameters (1d)	62.5, 62.5 m ² (kg <i>XC</i>) ⁻¹
$c_{LWR,gr}$, $c_{LWR,le}$	Leaf weight ratios (1d)	0.4 kg lamina <i>XC</i> (kg shoot <i>XC</i>) ⁻¹
$f_{SOM,N,1}$	Fraction of <i>N</i> leaving N_{SOM} box (Fig. 1) which is lost (3f)	0.02
$I_{N,min,af}$	Mineral <i>N</i> input from atmospheric deposition or fertilizer application (3i)	0 kg <i>N</i> m ⁻² d ⁻¹
$I_{N,SOM}(t \leq 0)$	Initial value for the pipe delay compartment [Fig. 1 and (3e)]	0.0002 kg <i>N</i> m ⁻² d ⁻¹
K_L	Photosynthesis constant (1e)	2 m ² leaf (m ² ground) ⁻¹
$K_{GC,gr}$, $K_{GC,le}$, $K_{GN,gr}$, $K_{GN,le}$	Growth Michaelis-Menten constants [(2e), (2f)]	0.1, 0.1 [<i>C</i>]; 0.01, 0.01 [<i>N</i>]
$k_{G,gr}$, $k_{G,le}$	Growth rate constants [(2e), (2f)]	0.1, 0.1 d ⁻¹

TABLE 1. (cont.)

Symbol	Definition	Initial value
$k_{i,rt,age}, k_{i,rt,lit}$ $k_{i,sh,age}, k_{i,sh,lit}$ k_{leach} k_p $k_{UN,fix}$ $k_{UN,gr}, k_{UN,le}$ $r_{NC,gr}, r_{NC,le}$ t_{delay}	Plant tissue ageing, litter rate constants [$i = gr$ (grass), le (legume)] (2k) Leaching constant (3h) Photosynthesis parameter (1e) N fixation parameter (2b) Root uptake parameters (2a) N:C ratios in grass, legume structure (2g) Delay time in passing through the litter/soil organic matter processes [(3c), (3d)]	0.03 (all) d^{-1} 0.02 d^{-1} 0.02 $kg\ C\ m^{-2}\ d^{-1}$ 0.002 $kg\ N\ (kg\ XC)^{-1}\ d^{-1}$ 3, 2 $m^2\ (kg\ XC)^{-1}\ d^{-1}$ 0.1, 0.1 $kg\ N\ (kg\ C)^{-1}$ 0 d
$w_{gr,rt,i}, w_{gr,sh,i}$ $w_{le,rt,i}, w_{le,sh,i}$ $i = 1-4$	Dimensionless tissue-age dependent weighting factors for photosynthesis and N uptake [(1b), (2a)]	1 (16 times)

FIG. 2. A, Relative nitrogen uptake/fixation efficiency of grass and legume. The quantities $k_{N,gr} = k_{UN,gr}N_{min}$ and $k_{N,le} = k_{UN,le}N_{min} + k_{UN,fix}$ are plotted against the soil mineral N concentration, N_{min} , for the standard parameter values (Table 1). B, Steady-state leaf area indices for grass and legume growing alone when soil mineral N concentration, N_{min} , is held at a constant level.

Here, $M_{gr,sh,i}$ and $M_{gr,le,i}$ ($i = 1-4$) are the shoot structural dry masses in each of the four tissue age categories. Competition may thus be modified by defoliation management as this can affect the age structure of the canopy (e.g. see Parsons, Johnson and Williams, 1988). The dimensionless constants $w_{gr,sh,1-4}$ and $w_{le,sh,1-4}$ permit the age categories of the grass or legume canopies to be made more or less effective (as these constants deviate from unity),

although in our standard simulations these are all equal to unity for convenience. The total grass and legume shoot and root structural dry masses, $M_{gr,sh}$ and $M_{le,sh}$, are obtained by:

$$M_{gr,sh} = \sum_{i=1}^4 M_{gr,sh,i}, \quad M_{gr,rt} = \sum_{i=1}^4 M_{gr,rt,i}, \quad (1c)$$

$$M_{le,sh} = \sum_{i=1}^4 M_{le,sh,i}, \quad M_{le,rt} = \sum_{i=1}^4 M_{le,rt,i}.$$

The formulation of eqns (1b) ignores any direct dependence of photosynthetic efficiency on plant nitrogen status, although the effects of N on growth (which may lead to competition for light) are considered later [eqns (2e) and (2f)].

The leaf area indices are defined as

$$L_{gr} = c_{SLA,gr} c_{LWR,gr} M_{gr,sh}, \quad (1d)$$

$$L_{le} = c_{SLA,le} c_{LWR,le} M_{le,sh},$$

where $c_{SLA,gr}$, $c_{SLA,le}$ are specific leaf area (SLA) constants which have been shown to differ between grass and clover (Parsons *et al.*, 1991b). [In our 'standard' simulations (Table 1) equal values are used for the SLA constants so that the simulation results can be more easily related to the structure and physiology of the system, and the consequences of differences between the two species can be examined separately.] $c_{LWR,gr}$, $c_{LWR,le}$ are leaf weight ratios, and $M_{gr,sh}$ and $M_{le,sh}$ are grass and legume shoot structural dry masses [eqn (1c)]. Differences in SLA may profoundly affect the dynamics of leaf area expansion in a species, and hence the outcome of inter-species competition (Parsons *et al.*, 1991a).

Total canopy photosynthetic rate of the grass and the legume combined, P_{total} ($kg\ C\ m^{-2}\ d^{-1}$), is assumed to be

$$P_{total} = \frac{k_p L_{eff}}{L_{eff} + K_L}, \quad (1e)$$

where the parameters k_p and K_L (Table 1) are taken as constant. Photosynthetic responses to irradiance and/or CO_2 concentration are subsumed in the k_p parameter. Total canopy photosynthesis, P_{total} [eqn (1e)], is apportioned between grass and legume according to their effective leaf

areas. Thus, the fraction of photosynthesis allocated to the grass is given by

$$f_{P,gr} = \frac{L_{eff,gr}}{L_{eff}}, \quad (1f)$$

and the photosynthetic inputs to the grass and legume shown in Fig. 1 are:

$$\begin{aligned} P_{gr} &= f_{P,gr} P_{total}, \\ P_{le} &= (1 - f_{P,gr}) P_{total}. \end{aligned} \quad (1g)$$

Nitrogen uptake. N uptake in grass and legume is assumed to be directly proportional to the amounts of root structural dry matter and the soil mineral N pool:

$$\begin{aligned} U_{N,gr} &= k_{UN,gr} \left(\sum_{i=1}^4 w_{gr,rt,i} M_{gr,rt,i} \right) N_{min}, \\ U_{N,le} &= k_{UN,le} \left(\sum_{i=1}^4 w_{le,rt,i} M_{le,rt,i} \right) N_{min}, \end{aligned} \quad (2a)$$

where the w s are dimensionless tissue-age-dependent weighting factors, and N_{min} (kg N m⁻²) denotes the soil mineral N pool from which uptake occurs. The weighting factors are set equal to unity in the ‘standard’ simulations for convenience, and because their value does not affect the results greatly. The root uptake constants ($k_{UN,gr}$, $k_{UN,le}$, Table 1) differ between the grass and the legume because it is assumed that the efficiency of uptake (kg N per kg root dry matter per day) of the nodulated legume root is less than that of the grass root. Legume N fixation is assumed to be directly proportional to legume root mass:

$$U_{N,fix} = k_{UN,fix} M_{le,rt}. \quad (2b)$$

This equation ignores any direct effect of a high mineral N level (N_{min}) in suppressing N fixation.

Note that, when root dry masses are equal ($M_{gr,rt} = M_{le,rt}$), and when the w s are set to unity, then if $N_{min} = k_{UN,fix} / (k_{UN,gr} - k_{UN,le}) = 0.002$ kg N m⁻², $U_{N,gr} = U_{N,le} + U_{N,fix}$ and the total N inputs to both grass and legume are equal. The relative N uptake/fixation efficiency of grass and legume is illustrated in Fig. 2A, where $k_{N,gr} = k_{UN,gr} N_{min}$ and $k_{N,le} = k_{UN,le} N_{min} + k_{UN,fix}$ are plotted. For N_{min} below the cross-over point, the legume has the advantage and *vice versa*. For the parameters in Table 1, $N_{min}(\text{crossover}) = 0.002$ kg N m⁻².

Growth of structural C (XC) and nitrogen utilization. The carbon and nitrogen substrate concentrations in the grass and the legume, with units of kg substrate carbon (nitrogen) (kg structural dry matter)⁻¹, using an obvious notation, are defined by

$$C_{gr} = \frac{M_{C,gr}}{M_{gr}}, \quad N_{gr} = \frac{M_{N,gr}}{M_{gr}}, \quad C_{le} = \frac{M_{C,le}}{M_{le}}, \quad N_{le} = \frac{M_{N,le}}{M_{le}}. \quad (2c)$$

The total structural dry masses of the grass and legume are [using eqns (1c)]

$$M_{gr} = M_{gr,rt} + M_{gr,sh}, \quad M_{le} = M_{le,rt} + M_{le,sh}. \quad (2d)$$

Growth of structural C (XC) in the grass is assumed to be proportional to total structural dry matter (i.e. meristem

mass and/or activity remain constant per unit structural mass), and a saturating function of C and N substrate levels:

$$G_{gr,XC} = k_{G,gr} M_{gr} \frac{C_{gr}}{K_{GC,gr} + C_{gr}} \frac{N_{gr}}{K_{GN,gr} + N_{gr}}, \quad (2e)$$

where $k_{G,gr}$, $K_{GC,gr}$ and $K_{GN,gr}$ are constants which determine the maximum rate of growth (C_{gr} and $N_{gr} \rightarrow \infty$) and the half-maximal response points with respect to C_{gr} and N_{gr} .

The equation for legume growth is identical to that for the grass:

$$G_{le,XC} = k_{G,le} M_{le} \frac{C_{le}}{K_{GC,le} + C_{le}} \frac{N_{le}}{K_{GN,le} + N_{le}}. \quad (2f)$$

The standard parameter values are taken to be the same in both species (Table 1). However, differences in N concentration between species can affect their relative capacity for leaf area expansion.

The rate of N utilization from the substrate N pool [gross growth rate of structural N (XN)] is

$$\begin{aligned} G_{gr,XN} &= r_{NC,gr} G_{gr,XC}, \\ G_{le,XN} &= r_{NC,le} G_{le,XC}. \end{aligned} \quad (2g)$$

The constants, $r_{NC,gr}$ and $r_{NC,le}$ are the N:C ratios in the grass and legume structural components.

Allocation of new structure to roots and shoots. The fractions of total structural dry matter in the shoot and root in the grass and legume are defined by

$$\begin{aligned} f_{gr,sh} &= \frac{M_{gr,sh}}{M_{gr}}, \quad f_{gr,rt} = \frac{M_{gr,rt}}{M_{gr}}, \\ f_{le,sh} &= \frac{M_{le,sh}}{M_{le}}, \quad f_{le,rt} = \frac{M_{le,rt}}{M_{le}}. \end{aligned} \quad (2h)$$

The allocation of new synthesized structural C and N between root and shoot is determined by the teleonomic partitioning method (Thornley and Johnson, 1990, p. 372; equations 13.5n and 13.4d), which maximizes plant specific growth rate during balanced exponential growth, giving

$$\begin{aligned} \phi_{pa,gr} &= \frac{f_{gr,rt} N_{gr} (1 + C_{gr})}{f_{gr,sh} C_{gr} (N_{gr} + r_{NC,gr})}, \quad \phi_{pa,le} = \frac{f_{le,rt} N_{le} (1 + C_{le})}{f_{le,sh} C_{le} (N_{le} + r_{NC,le})}, \\ f_{a,gr,rt} &= \frac{1}{1 + \phi_{pa,gr}}, \quad f_{a,gr,sh} = \frac{\phi_{pa,gr}}{1 + \phi_{pa,gr}}, \\ f_{a,le,rt} &= \frac{1}{1 + \phi_{pa,le}}, \quad f_{a,le,sh} = \frac{\phi_{pa,le}}{1 + \phi_{pa,le}}. \end{aligned} \quad (2i)$$

Here $\phi_{pa,gr}$ and $\phi_{pa,le}$ are partitioning functions for the grass and legume; the allocation fractions, $f_{a,gr,rt}$ etc., determine the allocation of eqns (2e) and (2f) between root and shoot, giving the flux of structural carbon into youngest tissue compartment (1), with

$$\begin{aligned} F_{gr,rt,1} &= f_{a,gr,rt} G_{gr,XC}, \quad F_{gr,sh,1} = f_{a,gr,sh} G_{gr,XC}, \\ F_{le,rt,1} &= f_{a,le,rt} G_{le,XC}, \quad F_{le,sh,1} = f_{a,le,sh} G_{le,XC}. \end{aligned} \quad (2j)$$

Tissue ageing and litter fluxes. The structural carbon fluxes between the tissue age compartments (1–4) and from compartment 4 to litter (li) are

FIG. 3. Response to atmospheric/fertilizer deposition of nitrogen [$I_{N_{min},af}$, eqn (3i)]. The results shown are steady-state solutions. L_{gr} , L_{le} and L are the leaf area indices [m^2 leaf (m^2 ground)⁻¹] for grass, legume and total in (A), (B) and (C). N_{min} is the soil mineral nitrogen concentration [kg nitrogen (m^2 ground)⁻¹]; and $f_{gr,rt}$ and $f_{le,rt}$ are the fractions of grass and legume dry matter in the root in (A) and (B). All other parameters are set to their standard values (Table 1). A, Grass alone. B, Legume alone. C, Grass and legume in competition for light and soil mineral nitrogen; $f_{L,le}$ is the legume fraction of the total LAI.

$$\begin{aligned}
 F_{gr,rt,1 \rightarrow 2} &= k_{gr,rt,age} M_{gr,rt,1}, & F_{gr,rt,2 \rightarrow 3} &= k_{gr,rt,age} M_{gr,rt,2}, \\
 F_{gr,rt,3 \rightarrow 4} &= k_{gr,rt,age} M_{gr,rt,3}, & F_{gr,rt,4 \rightarrow lit} &= k_{gr,rt,lit} M_{gr,rt,4},
 \end{aligned}
 \quad (2k)$$

$$\begin{aligned}
 F_{gr,sh,1 \rightarrow 2} &= k_{gr,sh,age} M_{gr,sh,1}, & F_{gr,sh,2 \rightarrow 3} &= k_{gr,sh,age} M_{gr,sh,2}, \\
 F_{gr,sh,3 \rightarrow 4} &= k_{gr,sh,age} M_{gr,sh,3}, & F_{gr,sh,4 \rightarrow lit} &= k_{gr,sh,lit} M_{gr,sh,4}.
 \end{aligned}$$

$k_{gr,rt,age}$, $k_{gr,sh,age}$, $k_{gr,rt,lit}$ and $k_{gr,sh,lit}$ are root and shoot ageing and litter rate constants (Table 1). Replacing the subscript *gr* by *le*, an analogous set of equations applies to the legume ageing and litter fluxes. In this equation tissue removal to litter or grazing only occurs from the oldest age category.

The litter fluxes can be used to calculate the output fluxes

of structural C (XC) and structural N (XN) from the grass and the legume:

$$O_{gr, XC} = F_{gr, rt, 4 \rightarrow li} + F_{gr, sh, 4 \rightarrow li}; \quad O_{le, XC} = F_{le, rt, 4 \rightarrow li} + F_{le, sh, 4 \rightarrow li}; \quad (2l)$$

$$O_{gr, XN} = r_{NC, gr} O_{gr, XC}; \quad O_{le, XN} = r_{NC, le} O_{le, XC}.$$

Here, $r_{NC, gr}$ and $r_{NC, le}$ are again the N:C ratios in the grass and legume structural components.

These structural litter fluxes carry with them substrate C and N (SC, SN) fluxes of

$$O_{gr, SC} = C_{gr} O_{gr, XC}; \quad O_{gr, SN} = N_{gr} O_{gr, XC}; \quad (2m)$$

$$O_{le, SC} = C_{le} O_{le, XC}; \quad O_{le, SN} = N_{le} O_{le, XC};$$

such that the total C and N fluxes to the litter and soil organic matter pools are

$$O_{gr, C} = O_{gr, XC} + O_{gr, SC}; \quad O_{gr, N} = O_{gr, XN} + O_{gr, SN}; \quad (2n)$$

$$O_{le, C} = O_{le, XC} + O_{le, SC}; \quad O_{le, N} = O_{le, XN} + O_{le, SN}.$$

Any endogenous recycling of substrate C or N to the younger tissues is neglected.

Compilation of the model. These components are combined to give the differential equations for the ten grass state variables:

$$\frac{dM_{C, gr}}{dt} = P_{gr} - G_{gr, XC} - O_{gr, SC};$$

$$\frac{dM_{N, gr}}{dt} = U_{N, gr} - G_{gr, XN} - O_{gr, SN};$$

$$\frac{dM_{gr, rt, 1}}{dt} = F_{gr, rt, 1} - F_{gr, rt, 1 \rightarrow 2};$$

$$\frac{dM_{gr, sh, 1}}{dt} = F_{gr, sh, 1} - F_{gr, sh, 1 \rightarrow 2};$$

$$\frac{dM_{gr, rt, 2}}{dt} = F_{gr, rt, 1 \rightarrow 2} - F_{gr, rt, 2 \rightarrow 3};$$

$$\frac{dM_{gr, sh, 2}}{dt} = F_{gr, sh, 1 \rightarrow 2} - F_{gr, sh, 2 \rightarrow 3}; \quad (2o)$$

$$\frac{dM_{gr, rt, 3}}{dt} = F_{gr, rt, 2 \rightarrow 3} - F_{gr, rt, 3 \rightarrow 4};$$

$$\frac{dM_{gr, sh, 3}}{dt} = F_{gr, sh, 2 \rightarrow 3} - F_{gr, sh, 3 \rightarrow 4};$$

$$\frac{dM_{gr, rt, 4}}{dt} = F_{gr, rt, 3 \rightarrow 4} - F_{gr, rt, 4 \rightarrow li};$$

$$\frac{dM_{gr, sh, 4}}{dt} = F_{gr, sh, 3 \rightarrow 4} - F_{gr, sh, 4 \rightarrow li}.$$

Similarly, the differential equations for the ten legume state variables are

$$\frac{dM_{C, le}}{dt} = P_{le} - G_{le, XC} - O_{le, SC};$$

$$\frac{dM_{N, le}}{dt} = U_{N, le} + U_{N, fix} - G_{le, XN} - O_{le, SN};$$

$$\frac{dM_{le, rt, 1}}{dt} = F_{le, rt, 1} - F_{le, rt, 1 \rightarrow 2};$$

$$\frac{dM_{le, sh, 1}}{dt} = F_{le, sh, 1} - F_{le, sh, 1 \rightarrow 2};$$

$$\frac{dM_{le, rt, 2}}{dt} = F_{le, rt, 1 \rightarrow 2} - F_{le, rt, 2 \rightarrow 3};$$

$$\frac{dM_{le, sh, 2}}{dt} = F_{le, sh, 1 \rightarrow 2} - F_{le, sh, 2 \rightarrow 3}; \quad (2p)$$

$$\frac{dM_{le, rt, 3}}{dt} = F_{le, rt, 2 \rightarrow 3} - F_{le, rt, 3 \rightarrow 4};$$

$$\frac{dM_{le, sh, 3}}{dt} = F_{le, sh, 2 \rightarrow 3} - F_{le, sh, 3 \rightarrow 4};$$

$$\frac{dM_{le, rt, 4}}{dt} = F_{le, rt, 3 \rightarrow 4} - F_{le, rt, 4 \rightarrow li};$$

$$\frac{dM_{le, sh, 4}}{dt} = F_{le, sh, 3 \rightarrow 4} - F_{le, sh, 4 \rightarrow li}.$$

Soil submodel

This is greatly simplified, in accordance with the objectives discussed in the Introduction. It is assumed that all the litter carbon flowing from grass and legume is respired, giving a soil respiration of

$$R_{soil} = O_{gr, C} + O_{le, C}. \quad (3a)$$

All the nitrogen flows in a ‘pipe delay’ box representing nitrogen in soil organic matter (N_{SOM}), with input

$$I_{N, SOM} = O_{gr, N} + O_{le, N}. \quad (3b)$$

This box gives a delay, t_{delay} , between input and output, which represents the processes of litter decay, incorporation into soil organic matter, and soil organic matter turnover. Thus the output from this box is

$$O_{N, SOM}(t) = I_{N, SOM}(t - t_{delay}). \quad (3c)$$

The quantity of N in the box and its rate of change are

$$N_{SOM}(t) = \int_{t-t_{delay}}^t I_{N, SOM}(\tau) d\tau;$$

$$I_{N, SOM}(t) = 2 \times 10^{-4} \text{ kg N m}^{-2} \text{ d}^{-1}, t \leq 0; \quad (3d)$$

$$\frac{dN_{SOM}}{dt} = I_{N, SOM}(t) - I_{N, SOM}(t - t_{delay}).$$

A constant input of N is assumed prior to the start of the

simulation. The initial value of soil organic matter N depends on t_{delay} , and is

$$N_{\text{SOM}}(t=0) = t_{\text{delay}} I_{N,\text{SOM}}(t \leq 0). \quad (3e)$$

The 'standard' value of $t_{\text{delay}} = 0$ (Table 1) gives $N_{\text{SOM}}(t=0) = 0$; this value is not intended to be realistic, but rather a convenient base value from which the effects of the SOM pool and the length of the delay can be investigated (Figs 7 and 8). For steady-state solutions (Figs 3, 4 and 5), initial values are unimportant.

It is assumed that there are losses of nitrogen from the system between the soil organic matter N box and the mineral N box; these are due to processes such as volatilization, nitrification, and denitrification. Thus, a fraction $f_{\text{SOM},N,l}$ of the output flux, $O_{N,\text{SOM}}$, is lost to the atmosphere, and the flux into the mineral N box from the soil organic matter box is

$$I_{N_{\text{min}},\text{SOM}} = (1 - f_{\text{SOM},N,l}) O_{N,\text{SOM}}. \quad (3f)$$

Each time nitrogen circulates round the system, a fraction $f_{\text{SOM},N,l}$ is lost; the faster N circulates, the faster it is lost. There is also an input of N to the mineral N box of $I_{N_{\text{min}},af}$, which is from N deposition from the atmosphere or fertilizer application (assumed continuous).

The outputs from the N mineral pool result from uptake by grass and legume [eqns (2a)]:

$$O_{N_{\text{min}},U} = U_{N,gr} + U_{N,le}, \quad (3g)$$

and to leaching:

$$O_{N_{\text{min}},le} = k_{leach} N_{\text{min}}, \quad (3h)$$

where k_{leach} is a rate constant. The leaching loss occurs in competition with the nitrogen uptake fluxes to grass and legume. Thus k_{leach} is to be compared with $k_{UN,gr} M_{gr,rt}$ and $k_{UN,le} M_{gr,le}$ [see eqns (2a)]. The differential equation for the mineral N pool is therefore

$$\frac{dN_{\text{min}}}{dt} = I_{N_{\text{min}},\text{SOM}} + I_{N_{\text{min}},af} - O_{N_{\text{min}},U} - O_{N_{\text{min}},le}. \quad (3i)$$

SIMULATIONS

Two kinds of simulation are reported: those that give rise to stable steady states, and those that give rise to oscillations in the grass–legume composition. Parameters have their standard values (Table 1) unless stated otherwise. The differential equations were integrated using Euler's method with a time interval of 0.5 d. The results did not change significantly with the use of shorter integration steps.

Steady-state solutions

A steady-state solution can be obtained when there is no time delay associated with the soil organic matter transformations (i.e. when $t_{\text{delay}} = 0$ d), and typically after 20 years simulation. In this section, we explore the response of this steady-state solution to variation in the nitrogen input and output parameters (atmospheric/fertilizer input of N; leaching, volatilization, nitrification and denitrification; see Fig. 1). In each case, the solutions were obtained for grass and legume growing separately, and for grass and legume in

competition. While some predictions of the model, e.g. concerning leaf area index or soil mineral N, may be thought to be rather high or low, the values predicted are easily altered by adjusting parameters for growth, ageing/litter or uptake.

Figure 2B shows the steady-state leaf area index (LAI) for grass or legume growing alone when the soil mineral N level (N_{min}) is held at each of a range of constant values. In this simulated situation, it is not possible for the soil mineral N level to be raised by N cycling through the litter and soil organic matter pools; neither does the model allow for the possibility of N recycling within the plants. Below a certain value of N_{min} (0.0011 kg N m⁻² for the legume, 0.0014 kg N m⁻² for the grass) growth cannot be sustained in either species. The cross-over point in LAI occurs where the specific N input rates to the root cross, as in Fig. 2A. Both species respond sigmoidally to N_{min} and share a common asymptotic LAI of 11.3. With regard to the death of the legume for low values of N_{min} , it may be noted (see Fig. 3B) that with zero externally applied N and allowing litter/soil recycling of N, the steady-state solution has a finite legume LAI of about 10; that is, Fig. 3B is not inconsistent with Fig. 2B, for setting $N_{\text{min}} = 0$ is not the same as applying zero external nitrogen.

In Fig. 3A, for grass growing alone, $I_{N_{\text{min}},af}$, the atmospheric deposition/fertilizer flux of nitrogen into the soil mineral N pool (Fig. 1) is varied over a range equivalent to 0–300 kg N ha⁻¹ year⁻¹, with all other parameters held at their standard values, there are large responses of the grass LAI (L_{gr}), the soil mineral nitrogen concentration (N_{min}) and the fraction of dry matter in the root ($f_{gr,rt}$). In contrast, the legume alone (Fig. 3B) shows a very small response to the application of nitrogen; this is because the nitrogen fixation rate for the legume monoculture only varies from 880 to 803 kg N ha⁻¹ year⁻¹ when the atmospheric deposition/fertilizer flux of nitrogen into the soil mineral N pool varies from 0–300 kg N ha⁻¹ year⁻¹. With a mixture of legume and grass (Fig. 3C), total LAI increases slightly with increasing nitrogen application. The model predicts a sustained (steady-state) co-existence of species across this range of N input, but the legume fraction in the pasture ($f_{L,le}$) at steady state drops from 18% to about 1% as fertilizer application is increased.

In Fig. 4, the leaching constant, k_{leach} , is varied. With grass alone (Fig. 4A), a constant nitrogen input ($I_{N_{\text{min}},af}$) equivalent to 100 kg N ha⁻¹ year⁻¹ is applied. The steady-state values of LAI (L_{gr}), soil mineral nitrogen (N_{min}) and the fraction of dry matter in the root ($f_{gr,rt}$) all respond quite strongly to leaching rate. For the legume alone (Fig. 4B) with no applied nitrogen, the responses to leaching are smaller than in the grass (Fig. 4A). When the grass and legume compete (Fig. 4C) in the absence of added nitrogen, the total LAI (L) is hardly affected by leaching rate, but the legume fraction in the pasture ($f_{L,le}$) at steady state increases steadily as leaching rate is increased. In Fig. 4C, the increasing leaching rate is exactly equal to the increased N fixation rate in the steady state, as required by nitrogen mass balance.

In Fig. 5, the parameter that represents nitrogen losses from volatilization, nitrification and denitrification (Fig. 1),

FIG. 4. Response to leaching rate [k_{leach} , eqn (3h)]. The results shown are steady-state solutions. L_{gr} , L_{le} and L are the grass, legume and total leaf area indices [m^2 (m^2 ground) $^{-1}$] respectively in (A), (B) and (C). N_{min} is the soil mineral nitrogen concentration [kg nitrogen (m^2 ground) $^{-1}$]; and $f_{gr,rt}$ and $f_{le,rt}$ are the fractions of grass and legume dry matter in the root in (A) and (B). A, Grass alone (with $100\text{ kg N ha}^{-1}\text{ year}^{-1}$ added). B, Legume alone (no added N). C, Grass and legume in competition for light and soil mineral nitrogen; $f_{L,le}$ is the legume fraction of the total LAI.

$f_{SOM,N,l}$, is varied over the range 0 to 1 while leaching is held constant at $k_{leach} = 0.02\text{ d}^{-1}$. For the grass alone (Fig. 5A), a constant nitrogen input ($I_{N_{min,af}}$) equivalent to $100\text{ kg N ha}^{-1}\text{ year}^{-1}$ is again assumed. As in Fig. 4A, the steady-state values of LAI (L_{gr}), soil mineral nitrogen (N_{min}) and the fraction of dry matter in the root ($f_{gr,rt}$) respond modestly to the range of nitrogen losses. In Fig. 5B, for the legume alone with no applied nitrogen, the responses to

non-leaching N losses are more similar to those in the grass (Fig. 5A), than was the case for leaching (Figs 4A, B). This is due to the fact that, in the simulations, the legume receives only recycled mineral N from litter, which is susceptible to non-leaching loss processes, whereas the grass is provided with an external N input ($100\text{ kg N ha}^{-1}\text{ year}^{-1}$) directly into the mineral N pool. When the grass and legume compete in the absence of added nitrogen (Fig. 5C), the total LAI (L)

FIG. 5. Response to nitrogen losses caused by volatilization, nitrification and denitrification [$f_{\text{SOM}, \text{N}, 1}$, eqn (3f)]. The results shown are steady-state solutions. L_{gr} , L_{le} and L are the grass, legume and total leaf area indices [$\text{m}^2 (\text{m}^2 \text{ground})^{-1}$] respectively in (A), (B) and (C). N_{min} is the soil mineral nitrogen concentration [$\text{kg nitrogen } (\text{m}^2 \text{ground})^{-1}$]; and $f_{\text{gr}, \text{rt}}$ and $f_{\text{le}, \text{rt}}$ are the fractions of grass and legume dry matter in the root in (A) and (B). A, Grass alone, with an atmospheric/fertilizer nitrogen input equivalent to $100 \text{ kg N ha}^{-1} \text{ year}^{-1}$. B, Legume alone (no added N). C, Grass and legume in non-dynamic competition for light and soil mineral nitrogen, with no atmospheric/fertilizer nitrogen input; $f_{\text{L}, \text{le}}$ is the legume fraction of the total LAI.

is hardly affected up to a certain level of nitrogen losses where the grass fraction in the pasture reaches zero, and thereafter the LAI of the all-legume sward declines monotonically. The soil mineral nitrogen level (N_{min}) behaves similarly.

Origins of co-existence. Before we consider more complex solutions to the model, particularly with respect to fluctu-

ations in the composition of a mixed community, it is necessary to understand how the model predicts co-existence at all. In the model, the co-existence of species depends on the assumptions regarding the efficiency of nutrient uptake in the grass relative to the legume (as illustrated in Fig. 2A), and the implications of this dynamically on plant growth and N cycling. Ecologists will recognise the basis for co-

FIG. 6. Dynamic solutions with no soil organic matter delay: $t_{\text{delay}} = 0$ d (3c). Parameters have their standard values (Table 1) unless stated otherwise. A, Grass alone with an atmospheric/fertilizer nitrogen input equivalent to $150 \text{ kg N ha}^{-1} \text{ year}^{-1}$. The grass LAI (L_{gr}) and the soil mineral nitrogen level (N_{min}) are shown. B, Legume alone with no atmospheric/fertilizer nitrogen input. The legume LAI (L_{le}) and the soil mineral nitrogen level (N_{min}) are shown. C, D, Grass and legume in competition for light and soil mineral nitrogen, with no atmospheric/fertilizer nitrogen input. The grass and legume leaf area indices (L_{gr} and L_{le}) are shown with the soil mineral nitrogen level (N_{min}). The nitrogen loss parameters are: A, B and C, $f_{\text{SOM}, N, l} = 0.02$ and $k_{\text{leach}} = 0.02 \text{ d}^{-1}$ (standard values); D, $f_{\text{SOM}, N, l} = 0.1$ and $k_{\text{leach}} = 0.1 \text{ d}^{-1}$.

existence portrayed here as being similar in principle to that argued theoretically by Lotka–Volterra (see Lotka–Volterra model with interspecific competition, e.g. Begon, Harper and Townsend, 1986) and by Tilman (see ‘differential resource utilization’ of Tilman, 1982). The present model is mechanistic in that it represents physiological processes, but it has no explicit tracking of individuals or spatial components. It is also unique in considering the interesting situation where one plant species has the capacity to ‘manufacture’ (by N fixation) one of the major limiting resources.

We consider the way in which N_{min} varies with time as the model runs dynamically. Note that, referring to Fig. 2A, if the model is started as a mixed community with a small proportion of legume and with low N_{min} ($0.001 < N_{\text{min}} < 0.002 \text{ kg N m}^{-2}$), the legume component of the sward will increase. This is because at $N_{\text{min}} < 0.002 \text{ kg N m}^{-2}$, the legume has an N uptake advantage, and we may state (consistent with Tilman, 1982) that ‘the legume may survive and achieve a given growth rate at lower levels of soil N than grass can’. However, as the legume component and its N fixation increases, N_{min} increases, and the grass benefits more per unit increase in N_{min} than the legume does. As high N_{min} is attained ($N_{\text{min}} > 0.002 \text{ kg N m}^{-2}$ in Fig. 2A), grass

now has the advantage and the legume content of the community begins to decline. However, ‘grass has the capacity to draw down the resource (N) that limits itself more than it limits the legume’. Unless a high level of N_{min} is sustained by large external applications of N, and/or low rates of N loss, then following the decline in the legume component, N_{min} declines and the grass advantage decays. As N_{min} falls below $N_{\text{min}} = 0.002 \text{ kg N m}^{-2}$ the advantage reverts to the legume. Thus across a range of intermediate N_{min} , and in a decaying N environment, the model dynamically approaches steady-state solutions with sustained co-existence, at which N_{min} approaches $0.002 \text{ kg N m}^{-2}$ (see parts of Figs 3C, 4C, 5C). At sustained low N_{min} , the mixed community is unstable and the legume alone may survive (see solutions at high $f_{\text{SOM}, N, l}$ in Fig. 5C). At sustained high N_{min} (high N inputs; low losses) the community is again unstable and grass alone may survive (see solutions at high N inputs in Fig. 3C).

It is important to note that the N loss parameters k_{leach} , $f_{\text{SOM}, N, l}$ can determine not only whether co-existence is achievable, but they can also determine the proportions of grass and legume in the community at equilibrium (see Fig. 6). This is true even though, in all cases, steady-state co-existence is achieved at the same value of N_{min} .

FIG. 7. Effect of different time delays, t_{delay} (3c). The initial values of the state variables are set to the steady-state values with the exception of the mineral N pool, where $N_{\text{min}}(t=0) = 0.025 \text{ kg N m}^{-2}$. The grass and legume leaf area indices (L_{gr} and L_{le}) are shown with the soil mineral nitrogen level (N_{min}). A, $t_{\text{delay}} = 0 \text{ d}$. B, 60 d. C, 180 d. D, 365 d. E, 730 d. F, 1825 d.

Dynamic solutions with no soil organic matter delay

Although steady-state solutions are obtained with no time delay ($t_{\text{delay}} = 0 \text{ d}$), it is useful to examine the approach to equilibrium for this case, as this reveals the dynamics of the grass–legume system alone without a soil contribution. For grass alone (Fig. 6A), and assuming a constant nitrogen input ($I_{N_{\text{min}}, \text{af}}$) equivalent to $150 \text{ kg N ha}^{-1} \text{ year}^{-1}$, the time constant for the approach to equilibrium is about 30 d with an overshoot (the time constant is the time taken for the variable to cover half the distance towards its equilibrium value). This contrasts with Fig. 6B for legume only with no external nitrogen inputs where the system is much slower to approach the steady state and the time constant is about 120 d. The longer time constant may be due to the fact that leaf area and soil mineral N are less tightly coupled in the

legume than in the grass (due to N fixation), so they take longer to come into equilibrium with each other. In Fig. 6C with the grass and legume competing for light and nitrogen, the dynamics is more complex with the system showing at least two time constants (as shown by the maxima in N_{min} and L_{le}), and taking many years to approach equilibrium after a substantial overshoot. It can be seen that, even without the addition of soil-organic-matter delays, the system is quite unstable, giving damped oscillations. Here the longer time constant of the system is determined by the nitrogen loss rate from the system with the two N loss parameters set to $f_{\text{SOM}, N, i} = 0.02$ and $k_{\text{leach}} = 0.02 \text{ d}^{-1}$ (their standard values). In Fig. 6D, these two parameters are increased to $f_{\text{SOM}, N, i} = 0.1$ and $k_{\text{leach}} = 0.1 \text{ d}^{-1}$. The effects of increasing these nitrogen loss constants are to modify the steady-state values (the grass:legume equilibrium ratio, cf.

FIG. 8. Effect of different initial values of soil nitrogen. Dynamic solutions with time delay $t_{delay} = 730$ d (2 years). Parameters have their standard values (Table 1) and the initial values are set at their steady-state values unless stated otherwise. A, With a soil organic matter N level $I_{N,SOM}(t \leq 0) = 0.00002$ kg N m⁻² d⁻¹ [see eqn (3e)]. B, 0.00005 kg N m⁻² d⁻¹. C, 0.0002 kg N m⁻² d⁻¹. D, 0.002 kg N m⁻² d⁻¹.

Figs 4 and 5), to decrease the long time constant (the time it takes the sward to respond to climate/land-use/management changes), and to lessen the oscillatory overshoots (reduced sward patchiness—see later).

Dynamic solutions with a soil organic matter delay

In Fig. 7, the consequence of a wide range of time delays associated with the soil organic matter dynamics is shown. The initial values are set to their steady-state values, which includes the initial flux into the SOM nitrogen pool, N_{SOM} , of $I_{N,SOM}(t \leq 0) = 0.00132$ kg N m⁻² d⁻¹. The system is then perturbed from equilibrium by making the value of N_{min} , the soil mineral N pool (Fig. 1), equal to 0.025 kg N m⁻²; this value is typical for a single deposition of urine in a patch in a sheep-grazed pasture (Cuttle and Bourne, 1993; see also Doak, 1952; Wolton, 1978). Comparing Fig. 7A ($t_{delay} = 0$ d) with Fig. 7B ($t_{delay} = 60$ d), shows that the oscillatory nature of the system increases as t_{delay} is increased. When $t_{delay} = 180$ d (Fig. 7C), the slow-oscillation period increases to 15 to 20 years, but rapid oscillations of period about 200 d appear (this is the time taken for N to cycle round the soil–plant system). Increasing the time delay to 1 year (Fig. 7D) and 2 years (Fig. 7E) makes the rapid oscillations more pronounced. Further increase to 5 years makes the oscillations appear self-sustaining (Fig. 7F), although running the simulation over 200 years shows that these oscillations eventually die out.

The effect of different initial values of soil nitrogen and a 2-year delay is shown in Fig. 8. In Fig. 8A, the system is deprived of nitrogen by putting the initial value of the pipe soil organic matter to the small value of $I_{N,SOM}(t \leq 0) = 0.00002$ kg N m⁻² d⁻¹ [see eqn (3e)]. Neither grass nor legume are viable, and both components of the sward die out. In Fig. 8B, the system is primed with more nitrogen by putting $I_{N,SOM}(t \leq 0) = 0.00005$ kg N m⁻² d⁻¹ [a poor soil with 0.037 kg organic N m⁻², see eqn (3e)]. There are damped oscillations with period t_{delay} , as the N pulse cycles round the system, and the oscillations die out as the pulse spreads out. The legume has the early growth advantage, although the grass component of the sward eventually recovers (see Fig. 9A). In Fig. 8C, with $I_{N,SOM}(t \leq 0) = 0.0002$ kg N m⁻² d⁻¹, the soil is modestly supplied with organic N with $N_{SOM}(t = 0) = 0.15$ kg N m⁻² [see eqn (3e)] and the grass sward recovers after some 30 years (this time period is unrealistically long and is due to the fact that in the model, the grass crop dry matter falls to very low values when the mineral N level is small). In Fig. 8D, for a rich soil with $N_{SOM}(t = 0) = 1.5$ kg N m⁻², the situation is reversed with the grass growing strongly early on, and it takes many years before sufficient N is lost from the system for the legume component to recover.

Figure 9 shows the effect of arbitrarily making the grass 20% more efficient photosynthetically than the clover. This is achieved by setting the weighting factors, $w_{gr,sh,i}$, $i = 1$ to 4 of eqn (1b) equal to 1.2 (instead of 1). Comparing Fig. 9A

Fig. 9. Effect of competition for light/photosynthesis, introduced by changing the grass $w_{gr,sh}$ factors of (1b). Time delay, $t_{delay} = 730$ d (2 years), and the initial soil organic matter N level $I_{N,SOM}(t \leq 0) = 0.0005 \text{ kg N m}^{-2} \text{ d}^{-1}$ [see eqn (3e)]; otherwise, parameters have their standard values (Table 1) and the initial values are set at their steady-state values. A, $w_{gr,sh,i} = 1$, $i = 1$ to 4. B, $w_{gr,sh,i} = 1.2$, $i = 1$ to 4.

to Fig. 9B shows the large effect this change has on the outcome: the fast oscillations are now well-sustained over 200 years, and the frequency, amplitude and decay rate of the slow oscillations are also much altered.

DISCUSSION

The model can only be used to address questions that lie within the framework shown in Fig. 1. Also, spatial aspects are ignored. While this is an important limitation, we felt that it was reasonable, in a first investigation of the problem, to attempt to describe the physiology of the system fairly realistically, and to see what can be deduced without treating the spatial aspects. Including spatial considerations would introduce a further dimension of complexity and difficulty, but will permit other problems to be addressed—further work is proceeding in this direction, using information gleaned from this study. Because the model also ignores leaves, tillers, stolons and plants as entities, it is not applicable on a small scale—the pasture is treated as a horizontally homogeneous soup.

The model is mechanistic but is necessarily based on much simplified physiology and biochemistry (Fig. 1), so that the origins of complexity in the dynamics of the system can be explored. A simplified model can not be expected to

give predictions which agree quantitatively with observations reported for grass–legume systems, which are in any case highly variable, but viewed qualitatively, Figs 3, 4 and 5 give acceptable predictions. Depending on certain parameters, some of which can be regarded as internal to the model and others of which can be regarded as belonging to the environment or management, it can produce a wide variety of steady-state solutions. It demonstrates not only the competition between these two contrasting plant species, but also their co-existence at a range of grass–legume ratios, depending on simple aspects of the N cycling process. However, stable co-existence is not only possible at the cross-over point on Fig. 2, where the acquisition of a single resource, nitrogen, is involved. A stable equilibrium can also be obtained if the legume N uptake parameter, $k_{UN,le} = 3$ [eqn (2a), Table 1], so that in Fig. 2, the legume line is always above the grass line giving the legume an advantage in N acquisition per unit of legume root dry mass; a counterbalancing advantage must be given to the grass—for instance, an increase in specific leaf area [$c_{SLA,gr}$, eqn (1d), Table 1], but other ways of advantaging the grass would do as well; in equilibrium the root fractions are different, as are the C and N substrate concentrations. However with present assumptions of equal litter/grazing loss rates, the grass and legume specific growth rates are equal at equilibrium: $G_{gr,xc}/M_{gr} = G_{le,xc}/M_{le}$ [see eqns (2e) and (2f)].

Figure 6 shows some basic aspects of the system dynamics without the soil delay function, which illustrates the sensitivity of the grass–legume system to the N loss rate. The variety and complexity of the periodic dynamic solutions generated when a soil organic matter delay is introduced is striking (Fig. 7). Small changes in the initial value of the soil organic matter N level greatly affect the outcome (Fig. 8). In Fig. 9 a 20% photosynthetic advantage is arbitrarily assigned to the grass component of the sward, and this also greatly modifies the dynamics of the system. The complexity of these results may be compared to the wide range of behaviour that has been observed in grass–legume swards, ranging from stability to instability, uniformity to patchiness (see below), and perhaps contributing decisively to the agricultural difficulties in controlling species composition in grass–legume swards discussed in the Introduction.

In the agricultural literature, one widespread explanation for the difficulty in establishing and sustaining high clover contents is that inputs of mineral N (including urine) disadvantage clover relative to grass. This may explain why clover content may become low, but few accounts proceed to explain how co-existence is achieved; that is, how a range of mixtures of low clover content are nonetheless sustained. Studies of the dynamics and the cycling and fate of N from urine patches (temporally and spatially heterogeneous environments) have been made (see Ryden, 1984; Bristow, Ryden and Whitehead, 1987; Marriott, Smith and Baird, 1987), and these clearly relate to the perturbation and alternation of species advantage explored here. However, the model predicts co-existence even with constant N inputs. As described earlier, this depends on the assumptions (illustrated in Fig. 2A) which encompass all features of the interaction of these species with mineral N implicit in the verbal accounts in the literature. Despite the emphasis on N

inputs as the basis of these species' interaction, in the literature, we are unaware of studies that test the suggested assumption of a cross-over in Fig. 2A, or that seek to elucidate other mechanisms to explain co-existence in typically *interspersed* grass/clover communities. In this case we have shown that stable co-existence may be a consequence of varying competitive ability for a single substrate (N; see Fig. 2A), or different competitive abilities for two substrates—e.g. N in Fig. 2A with no cross-over, compensated by the other species being more efficient at C acquisition.

None of our simulations has shown chaotic (i.e. non-periodic) dynamics convincingly, in the manner of, say, Duffing's oscillator in Fig. 1.1 (page 3) of Thompson and Stewart (1986); also, the results were not sensitive to small changes in initial values (changes larger than the accuracy afforded by the wordlength of 4 bytes). Nevertheless, the sensitivity to initial conditions and physiological factors, some of which may be easily changed as a result of management or environment is apparent. Thus there are several features which suggest to us that in practical terms, the grass–legume system may appear to be chaotic in some environments.

Our system fulfils all the requirements for chaos as outlined by Olsen and Degn (1985, p. 184) for a differential equation system. These are: there must be at least one non-linear term [e.g. (2a), (2e)]; and there must be at least three state variables (this is a 22-state-variable system, see Fig. 1, Table 1). Additionally we have represented the dynamics of soil organic matter by a simple time delay; in reality, there is a spectrum of time delays in the soil organic matter system, as discussed by Jenkinson (1990), Parton *et al.* (1987), and many others. A time delay increases the tendency towards chaos (Olsen and Degn, 1985). Tentatively, it may be concluded from the current study that the system's sensitivity to parameters is such that it may appear chaotic on time scales of practical interest (≤ 10 years), even though it is periodic in the long term for environments and managements that are strictly constant, although these will not occur in practice.

The model can give rise to a stable steady state, oscillations maintained over a long time, and unstable behaviour. Kauffman (1992), considering self-organization in complex dynamical systems, remarks that, by tuning the parameters of the system, it may exist in one of three states: rigid order; chaos; or a state of complexity balanced between rigid order and chaos. He suggests that systems existing close to the edge of chaos are most flexible and adaptable in terms of survival.

It is commonplace that an extension of a temporal oscillator (whether chaotic or otherwise) to one or two spatial dimensions can generate patterns in space (e.g. travelling waves on a rope, spatial patterns on a drumskin, Coulson, 1941). The Turing-type (Turing, 1952) of reaction-diffusion models is able to give rise to complex or simple patterns, whether on animal coats (Murray, 1981) or in phyllotaxis (Thornley, 1975). The model described here gives rise to the same general class of reaction-diffusion equations when extended into the spatial dimension. Spatial propagation of plants may occur by means of tillers,

stolons, rhizomes, and seeds, and of other influences by means of shading, soil mineral N pools, and possibly mycorrhiza. The dynamics of clover in pastures and simulated swards have been studied by Sackville Hamilton and Harper (1989), Sackville Hamilton (1990), and Thórhallsdóttir (1990*a, b*). Sackville Hamilton (1990) reports a speed of movement of white clover from stolon extension of 13 cm per year. This coupled with a 10-year oscillation period (say) could give rise to moving clover patches of order 130 cm. Patches of this order of magnitude can be easily observed in eastern Scotland and elsewhere (Thórhallsdóttir, 1990*a, b*).

Recently, Tilman and Wedlin (1991) reported results of a 5-year study of perennial grass dynamics, which they stated 'exhibited numerous traits associated with chaotic dynamics'. In their model, litter produced a delayed inhibition of growth by intercepting light; delays are required for chaotic dynamics. In the present study, delays are generated by the soil organic matter dynamics, and the mechanistic nature of the model allows the contribution of particular processes to be recognized and investigated. We believe that the best way to study these systems theoretically is to use models which represent known processes or mechanisms, and examine the role these processes play in the generation of complex and possibly chaotic behaviour.

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