Analysis of the Coexistence Mechanisms for Grasses and Legumes in Grazing Systems

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S. SCHWINNING and A.J. PARSONS*

Institute of Grassland and Environmental Research, North Wyke, Okehampton, Devon EX20 2SB, UK

Summary

1 It is widely assumed that grass–legume associations offer a way to sustainable, low input land use, with reduced environmental impact. However, a combination of both ecological and physiological principles may be needed to understand the sustainability of species balances.

2 To increase understanding of grass–legume dynamics, we developed a model that extends a recently proposed pasture model (Thornley, Bergelson & Parsons: *Annals of Botany* 1995, **75**, 79–94) by including selective grazing and spatial considerations. Population oscillations were shown to stem from the way grasses can exploit leguminous N fixation. If the legume is a relatively good competitor for light, populations do not oscillate near equilibrium, but in the converse case, populations do oscillate.

3 Large amplitude oscillations can arise when there are sufficiently long time delays in the plant populations' responses to changes in the competitive environment. In the present model, these stem from variable internal substrate pools (of C and N), which uncouple biosynthesis from resource uptake, but other time delay mechanisms are easily envisaged.

4 Urine deposits prevent the establishment of equilibrium within patches, but spatially random urine deposition stabilizes population fluctuations at the field scale. This is because perturbations to local N cycles desynchronize patches with regard to the grass–legume population cycle.

5 Differences in the soil N environment (fertilizer input, leaching rate) determine whether the species can coexist, but where coexistence is possible, species composition regulates soil mineral N.

6 Selective grazing (herbivory) does not essentially alter the grass–legume interaction, but complex foraging trade-offs lead to herbivory effects that may seem counter-intuitive. The model has important implications for attempts to control the legume content of mixed species communities.

Keywords: diet selection, nitrogen cycle, pasture composition, plant population dynamics, spatial heterogeneity

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Introduction

Low-input grazing systems based on mixtures of grasses and legumes (e.g. clover) have long been proposed as a sustainable alternative to intensive N-fertilizer based grassland. But these systems are perceived as inherently unpredictable and difficult to manage (Frame & Newbould 1986; Kessler & Nösberger 1994). Where long-term studies on pasture composition have been conducted, clover proportions have fluctuated widely over time (Steele & Shannon

* Present address: AgResearch, Grassland Research Centre, Tennent Drive, Palmerston North, New Zealand.

1982; Rickard & McBride 1986). In addition, clover is typically patchily distributed (Cain *et al.* 1995). The causes and consequences of clover variability in time and space are not fully understood. Indeed, few accounts explain the coexistence of these species at all. Apart from its relevance to agriculture, the association between rye-grass (*Lolium perenne*) and white clover (*Trifolium repens*) provides a useful 'model' system to study the temporal and spatial behaviour of plant communities in general (Newton *et al.* 1994) because much is known about the physiology of these species (Baker & Williams 1987; Jones & Lazenby 1988).

Recently, Thornley *et al.* (1995) introduced a model

predicting the coexistence of vegetatively propagating grass and clover. The model also predicted that grass and clover can engage in large scale population fluctuations with a period of 5–10 years before settling into a coexistence equilibrium. The key element of the model was a nitrogen-based competitive trade-off between grass and clover. The existence of this trade-off has been suspected for many years (see Harper 1977; Turkington & Harper 1979; Begon *et al.* 1990; Turkington & Jolliffe 1996), but Thornley *et al.*'s model is the first formal hypothesis on the consequences for population dynamics. The trade-off is essentially this: when soil mineral nitrogen (N) is low, clover has a greater relative growth rate than grass, since it can supplement mineral N uptake with N fixation. When soil N is high, grass has the greater relative growth rate, because mineral N uptake is more efficient than the combination of N uptake and N fixation. Through N cycling (between the plants and the soil), the two species establish an intermediate soil mineral N level at which their competitive advantages are balanced and thus they can coexist.

Thornley *et al.*'s model is an important step towards understanding temporal fluctuations in grass–legume mixtures. However, the model is too complex for comprehensive analysis. Thornley *et al.* (1995) noted that their model had more than enough complexity (with 22 state variables, five nonlinear functions and 52 parameters) to permit complex dynamics. It was left unclear which elements of model structure generated population cycles and if the dynamic system was capable of generating any dynamics other than damping oscillations. In addition, herbivory had not been explicitly included by Thornley *et al.* (1995). Selective defoliation by animals modifies the balance of competition between grass and legume, and so their contribution to N cycling. Herbivory also interferes directly with the cycling of N by short-cutting the slow return of leaf N through decomposition and instead, returning leaf N quickly in the form of animal waste. By removing N from everywhere in the pasture, but returning it locally in highly concentrated form, herbivory generates a patchy distribution of N. Therefore, to understand fully the effects of grazing, it is necessary to formulate a spatial pasture model.

Below, we present several modifications of Thornley *et al.*'s original model with the aim to improve understanding of the dynamics of grass–legume systems, and to examine the effects of herbivory. First we simplified Thornley *et al.*'s model. By ignoring age categories and the distinction between shoot and root biomass, we cut the number of state variables from 22 to 8. This allowed us to perform some formal analyses and to examine the origin and prerequisites for population oscillations in grass–legume systems. Then we added herbivory and extended the model spatially. Using the spatial model, we examined the effects of soil fertility, grazing pressure

and diet preference on pasture and diet composition.

The model

The model is described schematically in Fig. 1. The model is a synthesis of understanding gained from previous physiological models by Thornley and colleagues (Johnson & Thornley 1983, 1985, 1987; Thornley & Johnson 1990; Thornley & Verberne 1991) and models of herbivore foraging in ryegrass/white clover (Parsons *et al.* 1994b; Newman *et al.* 1995). Parameter values for our simplified model were derived from those detailed and comprehensive texts, and the biological information referred to within them. Where a single parameter in the simplified model is necessarily a composite of several parameters in the detailed literature (representing several component processes), we ensured further that our model demonstrated the appropriate basic phenomena, e.g. that the growth curves for each species at a range of fixed soil N levels were quantitatively realistic. The parameters describing composite soil processes are less certain, as in many cases the parameters for individual processes have not been estimated definitively in the experimental literature. But, to address this uncertainty, we explore the solutions for the model across a wide range of soil parameter space. State variables are defined and default parameter values given in Table 1. We approximated continuous dynamics using small discrete time steps (0.2 days). We found that this step size was adequate, while greatly reducing computation time.

GROWTH AND SENESCENCE

Grass and legume biomass densities are described in units of structural carbon (XC_1, XC_2 in g C m^{-2} ground area, where species 1 = grass: 2 = legume). Structural carbon is associated with structural N (XN_1, XN_2 in g
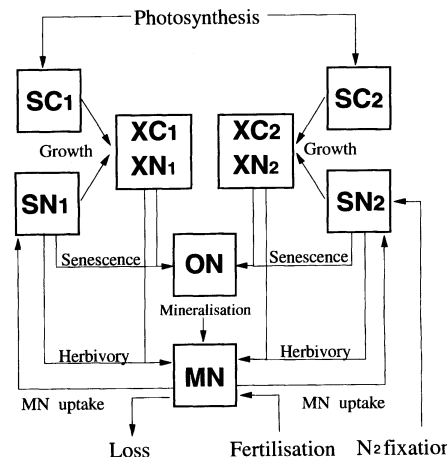
Fig. 1 Flow chart of the 8SV model. State variables are boxed.

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Table 1 Definition of state variables and parameters

Symbol	Description	Unit or parameter value
XC_i	structural carbon density (i = 1 for grass, i = 2 for legume)	g C m^{-2}
SC_i	substrate carbon density	g C m^{-2}
SN_i	substrate nitrogen density	g N m^{-2}
MN	mineral nitrogen content of the soil	g N m^{-2}
ON	organic nitrogen content of the soil	g N m^{-2}
g_i	maximal intrinsic growth rate of species i	0.3 day^{-1}
k_N	Michaelis–Menten constant for substrate N in growth	0.12 g SN g^{-1} XC
k_C	Michaelis–Menten constant for substrate carbon in growth	1.2 g SN g^{-1} XC
d_i	relative rate of senescence	0.03 day^{-1}
p_1	maximal rate of net carbon assimilation for grass	20 g SC m^{-2} day^{-1}
p_2	maximal rate of net carbon assimilation for clover	14 g SC m^{-2} day^{-1}
l_i	leaf area per structural carbon	0.025 m^2 g^{-1} XC
k_L	leaf area index at which the rate of canopy net assimilation is half-maximal	2 m^2 m^{-2}
c_{U_i}	specific rate of N uptake for species i	0.008 g MN m^{-2} day^{-1} XC
k_{U_i}	mineral soil N content at which the specific rate of nitrate uptake for species i is half-maximal	2 g MN m^{-2}
f	maximal fraction of clover's N uptake via nitrate	0.85
e	relative efficiency of N fixation vs. nitrate uptake	0.6
$imax$	maximal rate of herbivory	1.0 g XC m^{-2} day^{-1}
T_1	relative preference for grass	0.3
T_2	relative preference for clover	0.7
k_I	structural carbon density at which the rate of herbivory is half-maximal	50 g XC m^{-2}
r_i	ratio of structural N to structural carbon in biomass	0.1 g XN g^{-1} XC
c_{min}	relative rate of mineralization	0.05 day^{-1}
c_{loss}	relative rate of mineral N loss from the soil	0.05 day^{-1}
c_{fert}	absolute rate of mineral fertilization	0.02 g MN m^2 day^{-1}
$urine$	N application in single urination event	50 g MN m^{-2}

N m^{-2} ground area) in fixed ratios, but *substrate* C and N (SC_1, SC_2; SN_1, SN_2 in g C and g N m^{-2} ground area, respectively) are variable within tissues. *Sensu* Thornley & Johnson (1990, p49), 'structural' C and N represent components such as cell walls and proteins. 'Substrate' C and N represent more labile components, such as sugars and amino acids.

The daily gross growth rate of each species depends on the current biomass density (XC_i) and is a saturating function of the concentrations of substrate C (c_i) and N (n_i):

$$growth_i = g_i XC_i \frac{c_i}{c_i + k_C} \frac{n_i}{n_i + k_N} \qquad (1)$$

where

$$c_i = \frac{SC_i}{XC_i} \quad n_i = \frac{SN_i}{XC_i} \qquad (2)$$

and k_C, k_N are the substrate concentrations that give half-maximal growth rates.

The relative rate of tissue senescence (d_i) is constant:

$$senescence_i = d_i XC_i \qquad (3)$$

We assume that abscised tissues contain the same substrate concentrations as live tissues. Thus, not only structural C and N are lost with rate d_i, but also substrate C and N. We set $d_i = 0.03$ for both species, based on the observed leaf turnover rates of rye-grass and white clover (Grant *et al.* 1983; Parsons *et al.* 1983; Parsons *et al.* 1991a).

RESOURCE ACQUISITION

Plants assimilate resources into their substrate pools. The daily rate of net C assimilation by each species is determined by light interception, which is a hyperbolic function of leaf area index, *LAI* (e.g. see Johnson & Thornley 1984). Leaf area is a linear function of plant structural C with conversion factor l_i. The proportion of light intercepted by each species is assumed to be proportional to the *LAI* of species, so that:

$$assim_i = \frac{p_i l_i XC_i}{\sum_{j=1}^{2} l_j XC_j + k_L} \qquad (4)$$

where p_i is the maximum rate of net C assimilation (g C m^{-2} ground area day^{-1}) for each species and k_L is the *LAI* (m^2 leaf m^{-2} ground) that gives half-maximal carbon assimilation. We set $l_i = 0.025$ for both species, on the basis that about 40% of structural C is leaf lamina with a mean specific leaf area of 0.06 m^2 g^{-1} C (Parsons *et al.* 1991a). Observed differences between species in their ability to capture and utilize light are explored in the p_i parameters. With $k_L = 2.0$, growth curves match those demonstrated, e.g. by Robson (1973a,b).

In grass, the daily rate of N uptake into the N substrate pool is a saturating function of mineral N (MN; g N m^{-2}) in soil:

$$mineral\ N\ uptake_1 = c_{U_1} XC_1 \frac{MN}{MN + k_{U_1}} \qquad (5)$$

where c_{U1} is the maximum specific rate of N uptake (g N m^{-2} day^{-1} (g XC)$^{-1}$) and k_{U1} is the mineral N concentration (g N m^{-2} soil) at which the specific uptake rate is half-maximal. These kinetics have been characterized in flowing solution culture (MacDuff *et al.* 1996) as well as in soil.

In clover, total N uptake is the sum of two processes: mineral N uptake and N$_2$ fixation. We assume (unlike Thornley *et al.* 1995) that these processes do not occur in a fixed ratio. When soil mineral N content is low, clover obtains most of its N by fixation. As soil mineral N increases, clover obtains an increasing amount (and proportion) of N from soil nitrate. However, even at high mineral N, some N$_2$ fixation ($\approx 15\%$ of total N uptake) may remain engaged (Davidson & Robson 1985, 1986a,b). Hence for clover:

$$mineral\ N\ uptake_2 = c_{U2}XC_2 f\frac{MN}{MN+k_{U2}} \quad (6)$$

$$N_2\ fixation_2 = ec_{U2}XC_2\left(1-f\frac{MN}{MN+k_{U2}}\right) \quad (7)$$

where f is the maximal fraction of N uptake from the soil. The parameter e explores the efficiency of N uptake by fixation relative to mineral N uptake. When $e = 1$, the fixation rate is as efficient as the rate of mineral nitrate uptake and clover always achieves the maximal specific rate of total N uptake (i.e. c_{U2}). From the literature, we estimate that $e = 0.6$. Two costs of N fixation have to be taken into account: the direct metabolic cost of N fixation itself and the indirect cost of an increased root-shoot ratio. Ryle *et al.* (1979) measured an increase in respiratory costs, equivalent to 11–13% of total daily gross carbon uptake (i.e. $\approx 24\%$ reduction in net carbon uptake), in clover plants that were dependent on N$_2$ fixation compared to clover plants that were provided with ample nitrate. Also, Arnott (1984) observed a 10% increase in root : shoot ratio in N$_2$ fixing plants. With $f = 0.85$, $e = 0.6$, the specific rate of N (uptake + fixation) by clover growing in the absence of soil nitrate is 64% of that achieved under nonlimiting soil nitrate levels. This agrees well with the observed data comparing the growth rates and ceiling yields of clover, reliant on N$_2$ fixation, with clover grown at high mineral N (see Ryle *et al.* 1979). In Fig. 2a, the specific rates of N

(uptake + fixation) for each species (eqn 5–7) are plotted as a function of mineral N.

HERBIVORY

The daily rates of intake for each species ($herbiv_1$, $herbiv_2$) depend on the total and the relative abundance of each species in the pasture and on the fractional diet preference (T_1, T_2) of the grazers, according to:

$$herbiv_1 = imax\frac{XC_1^2}{XC_1^2+k_I^2}\left(1-T_2\frac{XC_2^2}{XC_2^2+k_I^2}\right) \quad (8)$$

$$herbiv_2 = imax\frac{XC_2^2}{XC_2^2+k_I^2}\left(1-T_1\frac{XC_1^2}{XC_1^2+k_I^2}\right) \quad (9)$$

$imax$ (g C m^{-2} day^{-1}) is the maximal rate of structural C consumption by a fixed number of animals when pasture biomass density or composition are non-limiting, and k_I is the biomass density of each species at which intake is half-maximal. Equations 8 and 9 contain a type III functional relationship (Holling 1959; Murdoch 1969) between intake and biomass availability. This function ensures that neither species can be eaten to extinction (Parsons *et al.* 1994b; Thornley *et al.* 1994). The terms in brackets describe how the intake of any one pasture component is influenced by the abundance of the alternative. When neither pasture density nor composition are limiting, animals take grass in proportion T_1 and clover in proportion T_2 (where $T_1 + T_2 = 1$). However, when the combined density is high, but one pasture component is limiting, the animals give up their preference and eat more of the alternative species in an attempt to sustain total intake. Equations 8 and 9 emulate many of the complex features of preference and value trade-off presented in more detailed, but less tractable, accounts of optimal foraging (e.g. Parsons *et al.* 1994b; Newman *et al.* 1995). In Fig. 2b, eqns 8 and 9 are illustrated for $T_1 = 0.3$ and $T_2 = 0.7$, the observed partial preferences for grass and clover by sheep (Newman *et al.* 1992; Parsons *et al.* 1994a). Similar preferences are observed for goats and cattle (Penning *et al.* 1995a,b).

Fig. 2 Two important functions in the model. a: specific N uptake rate (from mineral N and N-fixation) as a function of soil mineral N for grass (solid line) and legume (broken line), b: % legume in the diet as a function of the percentage legume available in the pasture at different *LAI* values.
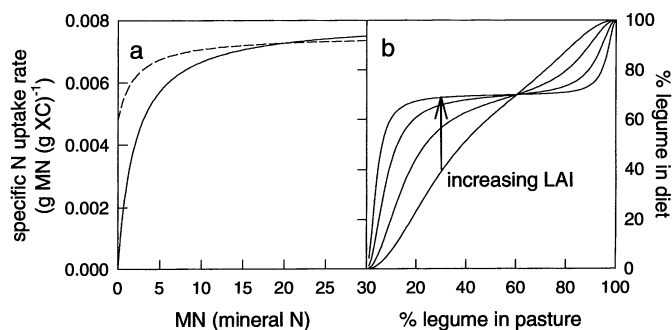
N enters the soil organic N pool, *ON*, as organic matter in litter at a daily rate:

$$litter = \sum_{i=1}^{2} senescence_i(r_i + n_i) \qquad (10)$$

where r_i is the fixed ratio of N to C in structure, and n_i is the substrate concentration of N (eqn 2). Organic N, *ON* (g N m^{-2}), is transformed into inorganic N through mineralization at a rate:

$$miner = c_{mn}ON \qquad (11)$$

where c_{min} is a rate constant of mineralization (day^{-1}). As a default setting, we chose $c_{mn} = 0.05$ to reflect a typical litter decomposition rate for leaf material under favourable conditions (e.g. Hunt 1977; Franzluebbers *et al.* 1994).

Mineral N may also be added directly as fertilizer at a constant rate:

$$fert = c_{fert} \qquad (12)$$

Mineral N is lost from the soil by various processes, for example, leaching and volatilization. After Thornley *et al.* (1995) we combine all losses in a single parameter c_{loss}:

$$loss = c_{loss}MN \qquad (13)$$

Note, this does not imply that the N loss rate is a linear function of N *input* (this would clearly be wrong), but a linear function of the current mineral N content which interacts with all components of the plant-soil system. As a result of the dynamic interactions described in this model, the relationship between N loss and N input is indeed nonlinear.

Finally, mineral N can be added by grazing animals as urine. The rate of ingestion of N depends on how much of each species is eaten (and so diet selection), and the species N contents. We assume that all N consumed in herbage is returned as urine-N, which is tantamount to mineral N, although cycling of organic N via dung can be considered readily. N retention by mature animals is negligible. Urine-N is added to the system irregularly and in high doses following rules that we explain further with the simulations below. The longevity of elevated mineral N after urine application (for the default parameter settings) is in keeping with observations (Ryden 1984; Marriott *et al.* 1987; Thomas *et al.* 1988) and is about 30–50 days.

GOVERNING EQUATIONS

Together, eqns 1–13 define the dynamic system:

Grass state variables:

$$\frac{dXC_1}{dt} = growth_1 - senescnece_1 - herbiv_1 \qquad (14)$$

$$\frac{dSC_1}{dt} = assim_1 - growth_1 - c_1(senescence_1 + herbiv_1) \qquad (15)$$

$$\frac{dSN_1}{dt} = N\,uptake_1 - r_1\,growth_1$$
$$- n_1(senescence_1 + herbiv_1) \qquad (16)$$

Clover state variables:

$$\frac{dXC_2}{dt} = growth_2 - senescence_2 - herbiv_2 \qquad (17)$$

$$\frac{dSC_2}{dt} = assim_2 - growth_2 - c_2(senescence_2 + herbiv_2) \qquad (18)$$

$$\frac{dSN_2}{dt} = N\,uptake_2 + N_2 fixation_2$$
$$- r_2\,growth_2 - n_2(senescence_2 + herbiv_2) \qquad (19)$$

Soil state variables:

$$\frac{dMN}{dt} = miner + fert + urine - N\,uptake_1$$
$$- N\,uptake_2 - loss \qquad (20)$$

$$\frac{dON}{dt} = litter - miner \qquad (21)$$

ISOCLINE ANALYSIS

In population ecology, plots of zero net growth isoclines (in short: isoclines) have long been used to visualize the nature of interactions between populations (see Begon *et al.* 1990; Murray 1989), but this approach has received little attention in applied plant ecology, or agriculture, despite the increasing interest in mixed species communities. Here we use the approach to explore the bases for the coexistence of grasses and legumes.

In two-dimensional (2D) systems (e.g. classic, two-species 'Lotka–Volterra' competition; Volterra 1926; Lotka 1932), isoclines are curves (drawn in species 1/species 2 state space) that represent all the combinations of the density of species 1 and the density of species 2 that give rise to zero net growth in each species. Thus, the species 1 isocline is the set of density combinations that give rise to zero net growth in species 1, and the species 2 isocline is the set of density combinations that give rise to zero net growth in species 2. Where the isoclines intersect, neither species is changing and the mixture is at equilibrium. Both graphical (Rosenzweig & MacArthur 1963) and for-

mal mathematical techniques (May, 1974) can be used to analyse the local stability of these equilibria.

For systems with a greater number of state variables, isoclines are not simply curves on a plane, but objects with higher dimensionality. In this case, the XC_1 isocline, for example, is a 7D object in 8D space. Clearly, such isoclines cannot be represented graphically and therefore do not aid the conceptual understanding of the system. However, in an attempt to generate a visual characterization of this system of two interacting species, we found that a certain representation in the XC_1 and XC_2 plane captured some important features of the interaction. We generated this representation in two steps. First, we identified a 2D manifold by determining, for any fixed pair of grass (XC_1) and legume (XC_2) densities, the values for the other six state variables, that set the rate of change for substrate concentrations and soil N pools to zero. For a wide range of parameter values, this criterion defines points on the manifold uniquely (i.e. the manifold has no folds with respect to the XC_1 and XC_2 plane). Second, we identified zero net growth isoclines for XC_1 and XC_2 on the manifold by approximating, for a range of values of XC_2, the values of XC_1 that set the net growth rate for one of the species to zero. These two curves on the manifold were then projected onto the XC_1 and XC_2 plane (e.g. Fig. 3). (Further details about the method are available from the authors).

We note that the manifold is not attracting and that therefore the isoclines on the manifold do not delineate the dynamics of the unconstrained 8D system. Nevertheless, we found this two-dimensional representation of the system to be useful (e.g. as compared to dynamic simulation alone) for two reasons. First, it helped to portray the nature of the interaction between grasses and legumes in a simple visual manner. Second, all equilibria – whether they are stable or unstable – are identified by isocline intersections.

Results

We present the analysis in two parts. In the first part, we consider the population dynamics of a single, homogeneous patch. We begin by examining the dynamic properties of equilibria and illustrate the role of environmental N sources and sinks. Then, we discuss the effects of urine-N and show how locally, urine applications perturb the system away from equilibrium. In the second part, we examine the spatial consequences of perturbation by urine-N and explain the generation and maintenance of spatial heterogeneity. Finally, we examine the effects of soil fertility, grazing pressure and the grazer's diet preference on pasture and diet composition.

PART I: WITHIN-PATCH DYNAMICS

Grass–legume equilibria and their stability

Grass and legume isoclines are shown in Fig. 3 for a situation without herbivory (no defoliation or urine). One notable feature of the system is the 'n' shaped isocline for grass. In simple two-species (e.g. Lotka–Volterra) systems, the isoclines of competing species have negative slopes throughout, reflecting the detrimental effect that each species has on the other. The shape of the grass isocline in Fig. 3 suggests that, at low legume density, an improvement in the growing conditions of the legume can actually lead to a substantial *increase* in the equilibrium density of grass, without much effect on the equilibrium density of legume. This form of interaction indicates not 'competition' but 'exploitation': grass exploits the legume by taking advantage of the additional N which the legume brings into the system, while suppressing legume growth through competition for light.

In Fig. 4, we introduce one aspect of herbivory, selective defoliation (but as yet, no urine return), and demonstrate two generalizations about the system. First, selective herbivory alters the shape of the isoclines (compare Figs 3 and 4a), but does not essentially modify the interaction between the two species. Secondly, several different dynamic behaviours exist in grass–legume systems (illustrated by sample trajectories). In all cases in Fig. 4, biomass densities oscillate near the equilibria if the equilibria are located on the left side of the grass isocline 'hump' (these equilibria are called 'foci', they are associated with a pair of imaginary eigenvalues). If they are located on the right side of the 'hump', populations do not oscillate, but approach equilibria monotonically (these equilibria are called 'nodes', they are associated only with real eigenvalues). Equilibria on the left side are governed by exploitation interaction and are akin to those seen in predator–prey systems (see May 1981b). Equi-
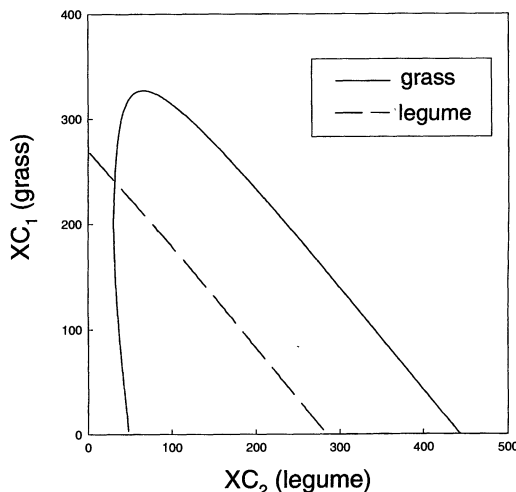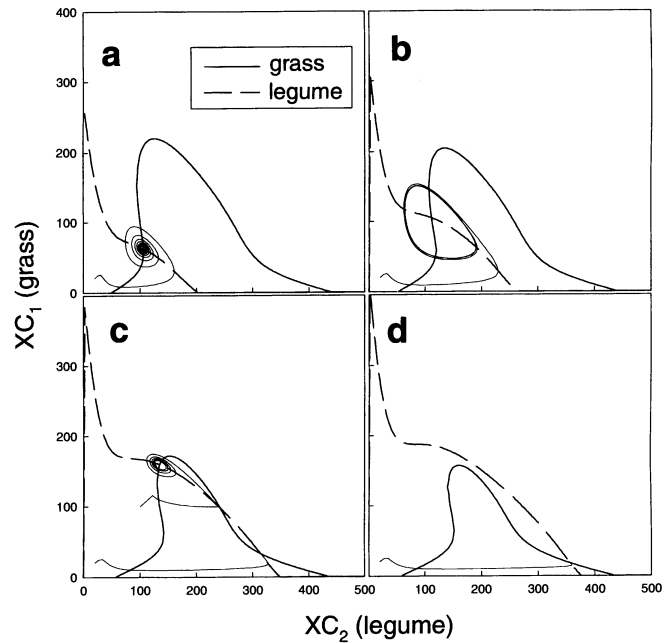
Fig. 3 Grass and legume isoclines in the 8SV model without herbivory (*imax* = 0).

Fig. 4 Grass and legume isoclines with *herbivory* (*imax* = 1) for different assimilation capacities for the legume. (a) $p_2 = 14$; (b) $p_2 = 16$; (c) $p_2 = 19$; (d) $p_2 = 20$. Dynamic solutions are superimposed as thin lines. In (c) two dynamic solutions converge on different attractors.

libria on the right side are more typical of competition interaction. For a wide range of parameter values, we have found no exceptions to the rule that solution curves oscillate on the left, and approach equilibria monotonically on the right side of the grass isocline hump.

The isoclines in Figs 3 and 4 illustrate another point: the grass isoclines are slightly folded and there is a range of XC_2 where the zero growth condition for grass has three positive solutions. For other parameter values (particularly different diet preference parameters T_1 and T_2), grass isoclines can be more folded, and even contain two separate curves.

Between Figs 4a–d, just one parameter of the dynamic system was varied: the legume's maximal rate of net carbon assimilation (p_2). In Fig. 4a, for the lowest assimilation capacity, the equilibrium is a stable focus and is approached by damping oscillations. In Fig. 4b the focus is unstable and the population oscillations do not dampen, but converge on a stable limit cycle. In Fig. 4c, there are three equilibria: one stable focus to the left of the grass isocline 'hump', and two nodes to the right. The first node (along the legume-axis) is unstable (a 'saddle point'), the second is stable. Finally, in Fig. 4d, for the highest assimilation capacity, there is just one equilibrium: a stable node. We confirmed the apparent stability properties of all equilibria by checking the eigenvalues of the linearized system.

The role of N input and losses and the capacity for self-regulation

An example of the three-dimensional approach to equilibrium (XC_1, XC_2 and MN) is shown in Fig. 5, for a situation in which the trajectory (previously
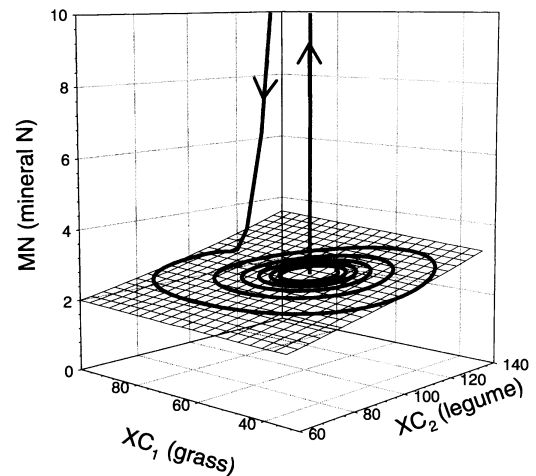

Fig. 5 Dynamic solution shown in three dimensions with mineral N as the third variable for $p_2 = 14$ ('clover'). The solution is identical to the one shown in 4a. The surface indicates the location of the 2D manifold (see section on 'isocline analysis').

shown in grass–legume state space; Fig. 4a) exhibits damped oscillations, after perturbation from equilibrium by a single pulse of mineral N. The shaded surface in Fig. 5 represents the 2D manifold that contains the isoclines of Fig. 4a. The figure illustrates that soil mineral N falls back quickly to near steady state levels. In contrast, the return of organic N to equilibrium values is comparatively slow. This is primarily due to a relatively low rate of mineralization, c_{min}. Simulations in which c_{min} was varied across a wide range of values (including outside reasonable limits) indicated that c_{min} can have large effects on the system's dynamics. For example, increasing c_{min} increased the damping of oscillations, reduced the

Fig. 6 Coexistence regimes as affected by the environmental N fluxes c_{loss} and c_{fert}. Solid lines bracket the region of coexistence, the dotted line indicates the transition between exploitation and competition: (a) no herbivory (*imax = 0*); (b) with herbivory (*imax = 1*). The inserts illustrate typical isoclines found in the different regions of parameter space.
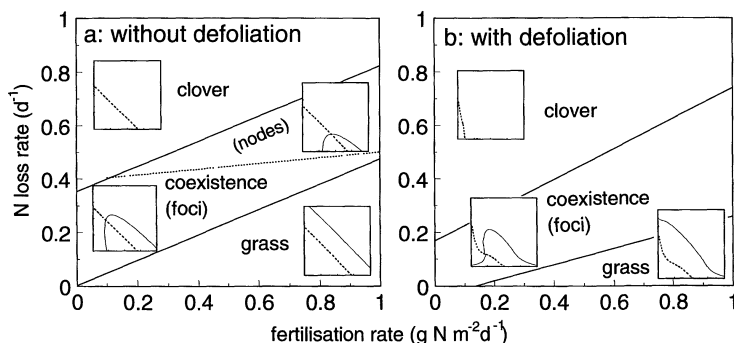

occurrence of limit cycles and the period of the oscillations. Decreasing c_{min} tended to do the opposite. For biologically reasonable variation in c_{min} (e.g. 0.01–0.1 day^{-1}), population cycles were pronounced and their periods varied between seven and four years.

The impact of the other parameters of the N environment on the grass–legume system is shown in Fig. 6, either in the absence of defoliation (Fig. 6a) or with selective defoliation (Fig. 6b; still no urine). From now on, we will return to the default setting for p_2 and call the legume component of the mixture 'clover'. As one would expect, high fertilizer input combined with low N loss rates (bottom right of graphs) discourage N-fixation and clover is excluded by grass (typical isoclines are shown in insets). Conversely, low fertilizer input and high leaching losses (top left of graphs) necessitate N-fixation for survival and clover monocultures arise.

Between these extremes, grass and clover coexist. As in Fig. 4, there are two coexistence types. Typically, foci (signifying exploitation) are associated with low equilibrium clover densities and high grass densities while nodes (signifying competition) are associated with the converse. Selective defoliation (Fig. 6b), despite the assumed preference for clover, actually extends coexistence into the region where grass alone would otherwise prevail (at the bottom of the graphs). In this case (but not generally) selective defoliation also removes the occurrence of stable nodes.

Intuitively, one would expect that pasture composition and external N inputs and losses have large effects on the equilibrium values of mineral N in the soil. But this is not the case. Figure 7 shows how mineral N is affected by a large range of relative N loss rates (in essence, Fig. 7 comprises cross-sections through Fig. 6 at $c_{fert} = 0.5$). Without defoliation (Fig. 7a) mineral N stays fixed over the entire coexistence region, as in Thornley *et al.*'s model. Even with selective defoliation, mineral N still stays within narrow limits in this region (Fig. 7b). The capacity to regulate soil N depends on the presence of both species. If the model is run for grass or clover monocultures, soil mineral N declines dramatically with increasing relative N loss rates. Moreover, soil mineral N for clover monocultures is greater than for grass monocultures or mixtures.
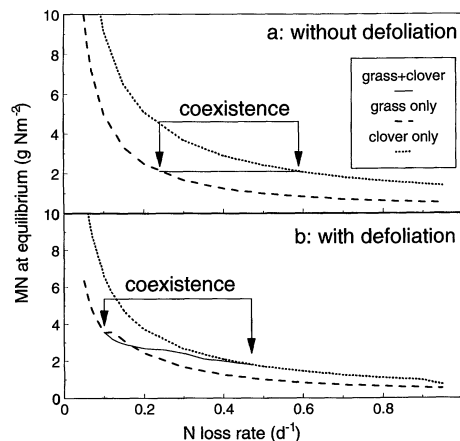
Fig. 7 Equilibrium values of mineral N as a function of N loss rate for simulations that were initialised with both species, only with grass, or only with clover. $c_{fert} = 0.5$: (a) no herbivory (*imax = 0*); (b) with herbivory (*imax = 1*).

These results can be understood largely in terms of the N balance for the entire system. In equilibrium (without defoliation), the rate of N loss from the system equals the rate of N gain, or:

$$c_{loss}MN^* = c_{fert} + N_2 fixation_2 \qquad (22)$$

(eqns 7, 13), where * indicates the equilibrium value. Thus,

$$MN^* = \frac{c_{fert} + N_2 fixation_2}{c_{loss}} \qquad (23)$$

Equation 23 explains that in grass monocultures (i.e. $fixation_2 = 0$), MN^* is simply an inverse function of c_{loss} and that in mixtures or clover monocultures (i.e. $fixation_2 > 0$), MN^* is larger than in grass monocultures. Furthermore, algebraically one can derive the value(s) of MN^* at which grass and clover can coexist. The exact formula is too long to be shown here, but the important aspect is that MN^* is the root of a third-order polynomial with coefficients that are composed only of plant parameters. Thus, MN^* is constant and independent of soil properties (i.e. c_{loss}, c_{fert} and c_{min}). This implies for eqn 23 that every change in environmental N inputs and losses applied to mixtures will be exactly compensated by N-fixation, i.e. by adjustment of the clover content. Put simply, if

more N is leached, there will be more clover, if soil fertility is greater, there will be less. With selective defoliation, the algebra becomes more complicated (because defoliation without urine return is an additional form of N loss), but many of the conclusions remain essentially the same (see Fig. 7b).

In summary: in the present model, as in Thornley *et al.*'s model, N losses and inputs to the system are important in determining whether coexistence is possible at all. But where coexistence is possible, the plant-soil system regulates itself and the physiological characteristics of the species in the mixture are more important in determining soil N than factors of the external N environment.

Urine N perturbs the grass–legume system

Most biological systems are disturbed at random by events which can shift the system away from equilibrium. Therefore, biological models should explain not only the approaches to equilibria, but also the dynamic responses of systems to random perturbations. In many cases, the sources of random perturbations are ill-defined, biologists using statistics to encompass but not explore perturbations, and their sources are set arbitrarily in many models. In the present system, the rate and magnitude of perturbation by urine-N is predictable: urine-N must equal the amount of N in harvested biomass. Furthermore, urine is discharged in reasonably fixed 'quanta' of known size (see Doak 1952; Wolton 1979). This means that, in any one patch, urine is not received continuously, but in some temporal pattern. Here we assume that it is received at irregular intervals, consistent with a spatially random urine application.
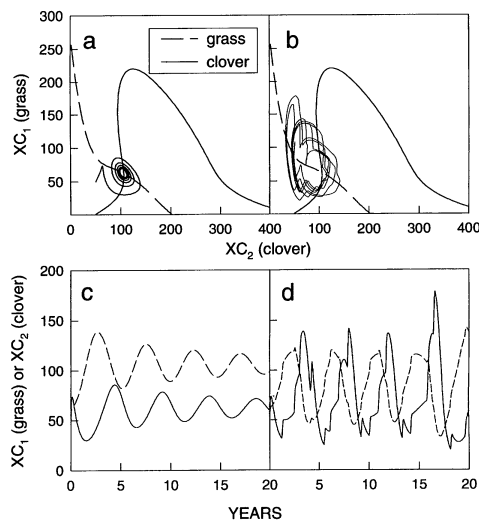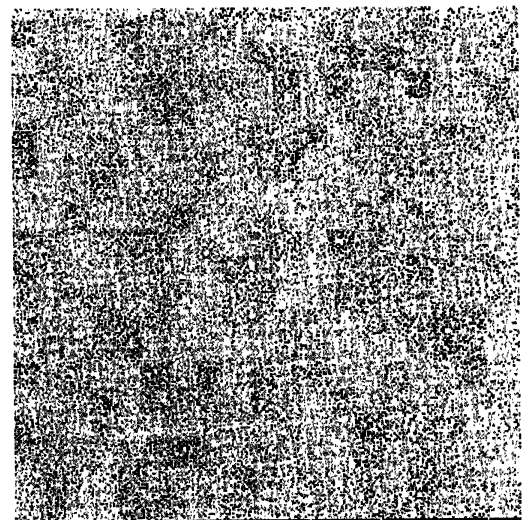
The result of perturbation by urine-N is shown in Figs 8b and d, and contrasted with the behaviour of the system in the absence of perturbation (Figs 8a and c). Urine input not only prevents the damping of the population oscillations, but exaggerates the oscillations. Most importantly (since the effect of urine may easily be misconceived), the frequency of the large scale population fluctuations does not reflect the average frequency of the urine inputs, but the frequency of the *intrinsic* grass–clover oscillation.

PART II: SPATIAL SIMULATIONS

When combining the effects of both aspects of grazing, selective defoliation and urine input, the problem becomes largely a spatial one. To run the model spatially, we constructed an array of patches with the 8SV model run independently for each patch. We assumed that animals foraged over the entire array of patches. Consequently, N was ingested from across the field, but returned to single, randomly selected patches at an application rate of 50 g N m^{-2} per event. Thus, patch sizes matched the size of the area covered by one urination (which may differ between animal species).

Heterogeneity of species abundances

Figure 9 gives an example of the spatial heterogeneity generated by random urine application. The figure shows a collection of 20 × 20 patches. Local grass and clover densities are indicated by the density of black and white dots, respectively. The simulated pasture is in steady state, i.e. average grass and clover densities are constant. Areas with a high concentration of black dots mark patches where urine-N

Fig. 8 Grass and clover isoclines (a,b) with dynamic solutions and the corresponding time courses (c,d) with herbivory (*imax* = 1). (a,c) No urine application; (b,d) random urine application.

Fig. 9 An example of the spatial heterogeneity generated by the model for default parameter settings. The density of black dots is proportional to local grass biomass, the density of white dots is proportional to local clover biomass.

has been deposited and subsequently given rise to high grass densities.

Intuitively, one may expect that grazing should maintain a relatively high soil N content, since herbivores continually return ingested N to the field. But Fig. 9 illustrates that grazing can actually lead to widespread N-depletion and the maintenance of a high average clover content. This is because the N collected widely is returned to very few patches at any one time. Also, Fig. 9 shows that spatially random urine input leads to spatial heterogeneity in clover density. Figs 8b and 8d showed how urine input can lead to temporal variability of clover. The patchy distribution of clover in Fig. 9 is merely a spatial expression of this. Spatially random urine application continually sets patches out of phase with respect to the grass–legume cycle.

Spatial herbivory and diet selection

Spatially explicit foraging models are not well developed but are becoming a topic of increasing interest (Dunning *et al.* 1995). In our model, there is no explicit *between-patch* selection. Animals eat from the entire area, but forage selectively *within patches* using the trade-offs shown in Fig. 2b. This generates many phenomena that could be misinterpreted in the field as between-patch selection. Some recent studies suggest that in confined, intensive grassland systems, foraging behaviour does approximate to this, even over relatively short time intervals (7–10 days; see Edwards 1994; Wallis de Vries & Dalebouldt 1994).

It is widely believed that herbivory, particularly with selective defoliation, is a major force in the balance of plant species. However, it is increasingly well documented that many paradoxes can arise. Many of these are apparent in the present model, despite its simple structure. The combined effects of grazing pressure, diet preference and the mineral N environment on pasture composition are summarized in Fig. 10. The results are spatial means obtained in field-scale steady states.

First, in many cases diet composition differs relatively little from pasture composition, despite large variation in the diet preferences of animals (Figs 10a–c, compare the curves with similar open and closed symbols). This is because, in the steady state, diet compositions reflect largely the rates of replacement of the two food resources (see also Parsons *et al.* 1991b). Regardless of preference, clover can *continue* to predominate in the diet only in situations where clover has a higher (absolute) growth rate than grass.

Secondly, there are circumstances where animals that show a strong preference for one species may end up eating less of that species than if they showed a weaker preference for it initially (Fig. 10a–c, look for negative slopes in open-symbol curves). This is the 'paradox of imprudence' (Slobodkin 1974; Parsons *et al.* 1991b).

Thirdly, higher grazing pressure generally increases

the clover percentage in the sward and in the diet, although more animals may exhibit clover preference (Fig. 10a–c, compare solid-circle and solid-triangle curves). This can be understood in terms of the N balance, which applies not only at the patch-scale (eqn 23), but also at the field-scale. Herbivory increases the rate of N loss even if N is returned as urine, because within urine patches, the plant uptake capacity for mineral N is far exceeded. Therefore, the greater the rate of herbivory, the more N is lost through leaching and volatilization, and the more clover there will be to balance this loss. Diet selection also affects the equilibrium balance between grass and clover. Because of the type III intake response to biomass density, which gives relatively more protection to the less abundant species, an increase in grazing pressure tends to increase the proportion of the less abundant species.

Finally, the effects of the N environment (e.g. the spatially homogeneous soil fertility) can be seen by comparing Figs 10a–c and d–f. Soil fertility can have a surprisingly small effect on total biomass density and total intake (Fig. 10d,e). This, again, is a consequence of the N dynamics of the mixture (eqn 23), where a change in fertility will be compensated by a change in the clover content. A further increase in fertility permits an increase in stocking density without reduction of biomass density (compare the solid-triangle curve in Fig. 10e at *imax* = 0.5 with the solid-triangle curve in Fig. 10f at *imax* = 1.0), as one would expect. However, total animal intake is not necessarily increased by increasing the stocking density, if animals have a strong preference for clover (Fig. 10e, compare open-circle and open-triangle curves). It is obvious from Fig. 10 that the interaction between the system's N balance, stocking density, and the dietary choices made by animals can be quite complex.

Discussion

Biological models differ substantially in complexity and the concepts that support them. To great effect, ecologists have used simple, general models to explain population interactions (for review see Begon *et al.* 1990). But these models contain little detail of the physiological processes that facilitate the fluxes of energy and matter which sustain any ecological system. By contrast, physiologists have developed detailed process-based models to analyse quantitatively the cycling of energy and matter (see Thornley & Johnson 1990). These models do not lend themselves easily to general interpretation and often defy application in ecological contexts. Our aim is to integrate these approaches. Above, we presented a simple pasture model that explained complex dynamic and spatial phenomena, but was based on fundamental physiological properties of species. Such models can not only improve our understanding of
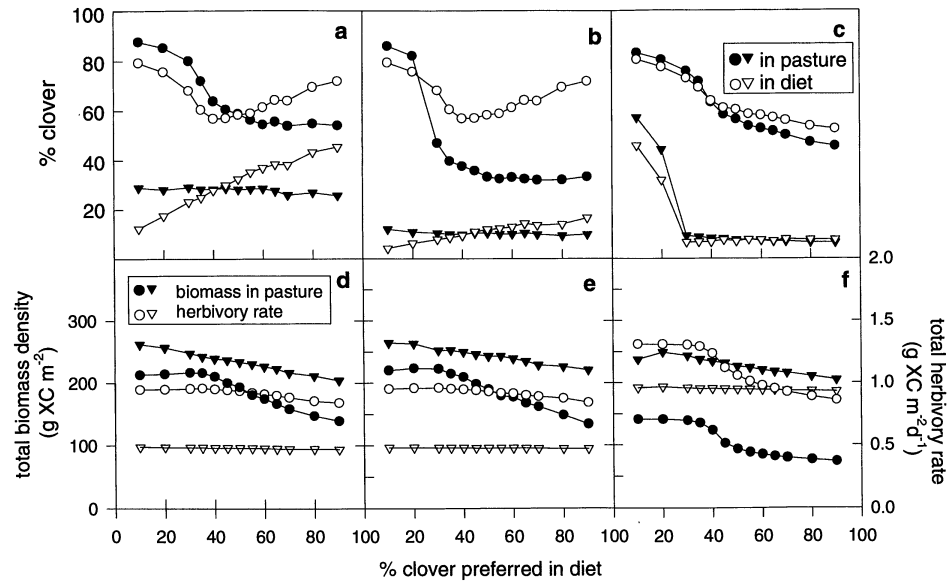
Fig. 10 The effects of diet preference, grazing pressure, and soil fertility on the clover percentage in the pasture and in the diet (a–c) and on total biomass density and rate of intake (d–f). Lower grazing pressure is indicated by triangles, higher grazing pressure by circles. There are three fertility regimes: (a,d) $c_{fert} = 0.01$ g N day^{-1}; (b,e) $c_{fert} = 0.1$ g N day^{-1}; (c,f) $c_{fert} = 0.2$ g N day^{-1}. In (a,b,d,e) the lower grazing pressure is *imax* = 0.5 g XC m^{-2} day^{-1} and the higher grazing pressure is *imax* = 1.0 g XC m^{-2} day^{-1}. In (c,f) the lower grazing pressure is *imax* = 1.0 g XC m^{-2} day^{-1} and the higher grazing pressure is *imax* = 1.5 g XC m^{-2} day^{-1}. Data are the field averages across 400 patches under steady state conditions.

ecological systems, but suggest specific strategies for manipulation and control.

GRASS–LEGUME CYCLES AND MODEL STRUCTURE

Having simplified and explored the behaviour of a model system, we conclude that population oscillations in grass–legume systems are of general ecological relevance, and are not specific to the model structure chosen by Thornley *et al.* (1995). The 8SV model generated dynamic phenomena which were largely equivalent to its 22 state-variable predecessor.

This begs the question if the 8SV model could be simplified further without losing physiological interpretation. Our analysis of the system in just 2 dimensions (for the depiction of isoclines) suggests that a two state variable model is unlikely to explore the systems dynamics adequately because of the comparatively slow rate of N recycling from plant litter to mineral N. This suggests that soil organic N would be a valuable component of a simplified model. However, plants do not take up organically bound N, so a four state variable (4SV) model, containing soil organic *and* mineral N, appears to be the least complex, physiologically descriptive alternative.

We formulated such a model (available from the authors) by abandoning variable substrate pools and fixing C and N concentrations in biomass. This model had similar isoclines (compared to the 8SV model)

and the same kinds of equilibria (foci and nodes) under very similar circumstances. However, the amplitudes, the periods and the durations of population oscillations were greatly diminished. Furthermore, we found no parameter settings that produced limit cycles. All equilibria were approached rapidly, perturbations (by urine) did not have long-term effects and did not produce large-amplitude variation in species content.

Previous work by Thornley and colleagues showed that the separation of structure and substrate pools of biomass is paramount to producing realistic plant growth dynamics (e.g. Thornley & Johnson 1990). Since the dynamic response to perturbation is an important aspect of pasture ecology, we decided that the 8SV model was the simplest useful representation of a grass–legume system. Nevertheless, the exercise of reducing the 8SV model to 4SV was informative. First, the 4SV model demonstrated that the existence of two forms of interaction between grasses and legumes – exploitation and competition – does not depend on the physiological structure of a model. Second, comparing the behaviours of the two models suggested that variable substrate pools may play a role in delaying resource-mediated population interactions.

In general, time-delays in the feedback mechanisms that control population densities increase the tendency of populations to oscillate (May 1981a,b). Thornley *et al.* (1995) used several more sources of time delay than we did, in particular, age structure,

dynamic root-shoot partitioning and an explicit time ('pipe') delay for the mineralization of litter. These are all biologically realistic but make a comprehensive analysis almost impossible. Thornley *et al.*'s model did generate erratic dynamic behaviour, but our relatively simple 8SV model generated similar (if not greater) complexity of behaviour. We conclude therefore that the potential for oscillation is an intrinsic property of grass–legume systems.

EXPLOITATION AS A SOURCE OF POPULATION CYCLES

Only a few examples of oscillations in plant populations are known (see reviews by Crawley 1990 and Stone & Ezrati 1996) and, to our knowledge, just two mechanisms that generate such oscillations have been put forward. Both mediate delayed density-dependence, one through the effect of previous generations' biomass on present germination rates (Symonides *et al.* 1986; Tilman & Wedin 1991) and the other through maternal effects (Crone & Taylor 1996). This study adds a third possible mechanism of delayed density-dependence, capable of producing oscillations in plant populations.

Plotting zero net growth 'isoclines' for the 8SV model reveals what it is about the nature of the interaction between the grass and legume populations that leads to the potential for population cycles. If legume biomass density is low, an increase in legume leads to an increase in the steady state density of grass (e.g. Figure 4a and b). But an increase in grass density does not lead to an increase in the steady state density of legume. We called this (+,–) interaction 'exploitation' and it has indeed many similarities with predator–prey interactions. Like a predator, grass improves its own net growth rate by associating with the other species, but the legume, like a prey, suffers a reduction in its net growth rate by the association. Systems of exploitation are well known to oscillate and are (in comparison to competition systems) more unstable (Rosenzweig & MacArthur 1963; May 1974, 1981a;b). We find that this result extends to the grass–legume system. The presence, in some cases, of two attractors (for example, a focus and a node, see Fig. 4c) adds complexity and could help to explain spontaneous dramatic transitions in pasture composition (clover 'outbreaks' and 'crashes').

Being able to categorize the grass–legume system as belonging to a general class of biological interactions allows us to connect with a large body of existing theory. The value of this is obvious: we can, for example, look for the presence of other general properties of exploitation systems. One such property is the' paradox of enrichment' (Rosenzweig 1977) which says that improvement of the prey ('clover') conditions can actually increase the predator population ('grass') and lead to greater instability. We do see this effect in Fig. 4a and b.

In those instances where the legume density is high, the grass–legume interaction is of the (–,–) type, expected of competition systems (e.g. Figure 4d). The key to understanding this fundamental transformation in species interaction is a shift in the relative importance of N limitation compared to light limitation. Grasses can exploit legumes only if the grasses are highly N-limited, i.e. if soil fertility is low and leguminous N-fixation is a major source of N for grass. Otherwise, i.e. if soil fertility is high, grasses and legumes compete predominantly for light and there is no opportunity for exploitation.

In equilibrium communities, N-fixing legumes can therefore be facilitators or competitors of grass populations. To be facilitators (and to elicit population oscillations), they must have some physiological disadvantage when N is not strongly limiting. In Thornley *et al.*'s model (1995), clover was disadvantaged only by its lower N (uptake plus fixation) efficiency. In the 8SV model, where we assumed that legumes adjust to high N levels by switching off most N fixation, another aspect of competitive disadvantage must be invoked. (With few options in a simplified model, we use a lower assimilation capacity in the clover canopy). If the legume has no or only a small disadvantage, it acts simply as a competitor of grasses. In this situation, grass can often be maintained in the mixture only by the presence of herbivores (with type III functional response, Holling 1959) which reduce competition but eat neither component to extinction (Parsons *et al.* 1991b).

Thus, herbivory increases the opportunity for coexistence if one species has an overall disadvantage. But if the species trade-off their competitive advantages, herbivory is not essential for coexistence. Herbivory can also affect the system's stability. For example, differences in diet preferences alone can alter the shapes and locations of isoclines and change the dynamic properties of equilibria. Although the foraging algorithm used in this study describes well-known herbivore behaviour, many of the predictions for different grazing scenarios may be seen as counter-intuitive.

In summary, there appear to be two fundamental requirements for coexistence with major population fluctuations in legume-grass (i.e. nonlegume) associations. First, the legume must be disadvantaged in competition with N-saturated grass. This generates the opportunity for exploitation, so that in a poor N environment, populations oscillate. Secondly, oscillations are accentuated if species' density responses are delayed. We argue that the uncoupling of the growth rate from immediate changes in the environment is one of many realistic delay mechanisms.

IMPLICATIONS FOR PLANT BREEDING AND MANAGEMENT

Although it may not be widely accepted that grasses and legumes oscillate in abundance, both patch scale

(Cain *et al.* 1995) and long-term field scale fluctuations (Steele & Shannon 1982; Rickard & McBride 1986) in legume content have been observed, and with similar period as predicted by the 8SVmodel. Considerable research effort is expended seeking ways to manipulate genotypes and manage land, often with the explicit purpose of increasing pasture homogeneity in space and time. But it is not obvious which plant characteristics must be altered for that purpose. Our results have several implications for the research necessary to 'improve' the performance of legumes to grasslands.

First, spatial heterogeneity in legume content may be a benefit, not a problem, for legume performance. In our model, heterogeneity reduced *field-scale* fluctuations in species densities. Heterogeneity arose spontaneously because local density oscillations were continually set out of phase by random urine input. By contrast, when the simulated pasture was uniform, all patches oscillated in synchrony and density fluctuation at the field scale were maximal. Therefore, management interventions that impose uniformity (ploughing and reseeding, periods of no grazing, spatially uniform fertilizer application) may invite field scale fluctuations and promote long-term uncertainty. In general, inappropriate attempts to control periodic systems can exacerbate oscillations and may even induce chaotic fluctuations (May 1981b).

Secondly, if grass–legume systems are self-regulating with respect to soil mineral N, then attempts to manipulate the contribution of the legume to the community, e.g. by breeding novel genotypes with greater competitive ability, or more effective rhizobial associations, may fail to have the expected result. By the 'paradox of enrichment', attempts to stimulate the growth of clover (the 'prey' in the predator-prey or exploitation system) can lead to as much increase in the growth of the 'predator', the grass. For example, in the model an increase (e.g. by plant breeding) in the capacity for N fixation in clover would be counterbalanced by a reduction in clover content, as the system maintains the same soil N status. Furthermore, increased capacity for N fixation may result in greater instability.

Lastly, if population cycles are indeed an intrinsic property of the grass–clover system, then differences in clover performance observed between years in agronomic experiments ('good clover years' and clover 'crashes') could be falsely attributed to uncontrolled year-type variation. We propose that research should be focused more on testing the existing hypotheses of grass–legume interaction, than on measuring the short-term (i.e. 1–3 years) responses of pastures to environmental and management variables, as these may be uninterpretable.

Some further practical implications for plant breeding and management are discussed by Chapman *et al.* (1996).

FURTHER DEVELOPMENT: THE ROLE OF DISPERSAL

Although the model accounts for the origins and the dynamics of spatial heterogeneity in species content, we do not believe that the model generates sufficiently flexible spatial *patterns*. In particular, the model does not predict patches of clover, of a scale larger than a urine patch, in a background of grass (Cain *et al.* 1995). There are two reasons for this: the absence of local clover extinctions and consequently, the absence of clover invasions. Although clover in the model can become quite rare in patches, it never disappears completely. This is a failing of most physiological models, as they are not individual-based and do not contain demographic effects. Therefore, clover is always available to re-establish once a patch has become N-depleted. In reality, clover can become extinct in patches. When it does, patches will remain longer in a state of N depletion until they are repopulated by invading clover plants. Clearly, local extinctions and invasions can generate more contrasting patterns of species densities.

Theoretical ecology offers alternative approaches to modelling plant population dynamics; some explain the coexistence of species entirely through the balance of local extinction and invasion (Levin, 1974; Nee & May 1992; Tilman 1994). Cain *et al.* (1995), for example, attempted to explain the observed pattern of clover distribution purely in terms of density-dependent stolon birth (invasion) and death (extinction) rates, but were unsuccessful. These authors argued the need for a physiological basis to drive alternating competitive advantage – possibly based on N cycling – as in our present model.

In the following paper (Schwinning & Parsons 1996) we link the results of the physiological model with spatial extinction and invasion dynamics, using a cellular automaton approach. This differs from other applications of cellular automata in plant ecology (Silvertown *et al.* 1992), because, based on our analysis here, we assume that species can alternate competitive hierarchies within patches. By combining the physiological and the explicitly spatial approach, we can consider the relative importance and possible interaction of physiological and (vegetative) dispersal characteristics for these species in mixed communities.

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