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A spatially explicit population model of stoloniferous N-fixing legumes in mixed pasture with grass

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Summary

1 In a previous paper, we outlined the physiological prerequisites for population oscillations between a grass and a nitrogen-fixing legume, such as clover. Here, we examine the field-scale consequences of patch-scale oscillations in legume content, using a cellular automaton with variable hierarchy between the two species.

2 We define cell states in the automaton by species content and soil N status. Grass–legume oscillations at the patch scale are represented as an alternation between states of grass dominance (high N) and legume dominance (low N). To this physiologically based population oscillation, we add local extinctions of legume and state-dependent success in legume invasion.

3 Legume populations oscillate at the field scale, given arbitrary initial conditions. However, spatially random perturbations to the soil N status (e.g. urine) establishes a pasture structure that dampens the field scale oscillation. The stabilizing pasture structure comprises moving patches of legume dominance. This pattern was not predicted by our previous, purely physiological model.

4 The model highlights that a patchy species distribution does not in itself mean the species is dispersal limited. In this model, changing the dispersal ability of legumes plays only a limited role in determining their proportion in the mixture. Legume abundance depends as much on the rate at which favourable (low N) sites become available for invasion.

5 Seasonal disturbances that act uniformly across the field, such as winter (legume) mortality and/or springtime fertilizer application, can lead to sustained field scale variations in legume content that are only partly explained by the level of seasonal disturbance itself. Another large part is explained by previous years' legume contents. Pastures may therefore exhibit a 'memory' for legume performance which helps to explain the perceived 'unpredictability' of some grass–legume associations.

6 We argue that legume dynamics in mixed pastures cannot be fully understood without combining ecological and physiological concepts of species interactions at three different scales: competitive interactions at the patch-scale, dispersal at the between-patch scale, and seasonality at the field-scale.

Keywords: cellular automaton, metapopulation dynamics, pattern formation, population oscillations

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Introduction

In a previous paper (Schwinning & Parsons 1996), we used rye-grass/white clover associations as a 'model' system and showed that the coexistence of grasses and legumes may be based on exploitation, rather than on mutual competition. Grasses benefit from the ability

of legumes to introduce nitrogen (N) into the system, but simultaneously suppress legume growth through competition for light. This interaction provides the basis for large amplitude oscillations of grass and legume densities. We conjectured that this has important consequences at the field scale, but recognized that to scale up from the patch-scale to the field-scale, we need to consider spatial processes, such as local extinctions and invasions (Levin 1974; Wiens 1989; Kareiva 1990). In particular, our physiological model

did not give rise to the moving patches of legume in a background of grass, that are observed experimentally, e.g. by Cain *et al.* (1995). Moreover, the model did not explain persistent fluctuations in legume content at the field-scale, as observed in long-term field experiments (Steele & Shannon 1982; Rickard & McBride 1986).

If individuals interact and disperse only locally, highly complex spatial patterns of species distributions are known to emerge (Hassell *et al.* 1991; Nowak & May 1992). The spatial patterns of species distributions are likely to affect the dynamics of metapopulations (Britton 1989; Silvertown *et al.* 1992), and models indicate that the interaction of local dynamics, dispersal, and disturbance have diverse effects on metapopulation dynamics (Kareiva 1990; Pacala *et al.* 1990; Comins *et al.* 1992; Hastings 1993; Goldwasser *et al.* 1994; Molofsky 1994). A grazed grass–legume system has the properties required for pattern formation: local interaction and slow (vegetative) dispersal, but pastures are also frequently disturbed, for example, by animal excreta. Apparently unpredictable variation in the legume content at the field-scale is frequently reported (e.g. Steele & Shannon 1982; Lambert *et al.* 1986; Rickard & McBride 1986; Davies *et al.* 1993), but the reason for this is largely unknown. Extensive research has been conducted on the physiology and morphology of pasture species, not least to improve the reliability of this widespread, low input, low environmental impact land use system. All this makes grass–legume associations an appropriate and accessible study system for an exploration of metapopulation dynamics and pattern formation, and their relevance to the stability of plant communities.

To combine oscillatory local population dynamics and the dynamics of dispersal and extinction in one model, we chose the simple but powerful tool of cellular automata. Cellular automata have been successfully employed to examine the spatial dynamics of competition (Hassell *et al.* 1991; Silvertown *et al.* 1992) and exploitation systems (Comins *et al.* 1992). Although they are spatially and temporally discrete, they are able to reproduce, qualitatively, the spatial dynamics of continuous reaction-diffusion models (Tilman 1994).

In existing automata models of plant interactions (Silvertown *et al.* 1992; Molofsky 1994; Hendry & McGlade 1995; Moilanen & Hanski 1995), species have fixed competitive hierarchies. We assume that grasses and legumes can switch their competitive relation depending on the soil N status. The physiological prerequisites of this switching is explained in our previous paper (Schwinning & Parsons 1996). Here, we represent physiology merely as its dynamic result: periodic alternations between states of ‘grass dominance’ (and high soil N) and states of ‘legume dominance’ (and low soil N).

Spatial dynamics (extinctions and invasions) are

considered only for the legume. This is an approximation based on observations that grass is ubiquitous and has a comparatively low rate of local extinction. Typically, legumes (such as clover) are distributed patchily in a continuous background of grass (e.g. Edwards 1994; Cain *et al.* 1995).

The model

STRUCTURE

Simulated pastures comprise up to 90 000 interlocking hexagonal cells. The edges of the automaton are wrapped, so that all cells are surrounded by six neighbouring cells. Cells can be in one of four states (Fig. 1). Both species (grass and legume) are present in two of the cell states, but either grass or legume is dominant. In the other two cell states only grass is present: these cell states are distinguished by their N status.

Cells with grass dominance, legume dominance and cells in the pure grass/high N state are further classified by ‘age’, since these states have finite longevity. In general, ageing represents changes in the N status of cells. Legume-dominated cells age due to N-enrichment, grass-dominated and pure grass/high N cells age due to N-depletion. Cells in the pure grass/low N state do not age, because this state can continue indefinitely. The parameters of the model and default values are summarized in Table 1.

THE TEMPORAL AND SPATIAL SCALE

The iterative step size of the simulation is equal to the time necessary for the invasion of one cell. Thus, time scale and spatial scale are correlated. The average dispersal rate of the legume white clover (*Trifolium repens*) has been reported to be 10–15 cm per year (Sackville-Hamilton & Harper 1989b). However, under favourable conditions, clover can spread for short periods at a rate of up to 70 cm per year (Chapman 1983). We run the simulation with a 2-month time step, assuming that the invasion of an N-depleted cell from a clover-dominated cell is initiated and completed within this interval. This implies that each cell has a diameter of at least 3 cm.

DETERMINISTIC STATE TRANSITIONS

Deterministic state transitions are indicated in Fig. 1 by solid arrows. Grass-dominated cells become legume-dominated when they reach the age corresponding to their life span, T_G . Similarly, legume-dominated cells become grass-dominated when they reach age T_C . Hence, the period of the intrinsic grass–legume oscillation is $T_G + T_C$. The life span of pure grass/high N cells is T_D and when they reach this age they become pure grass/low N. T_G and T_D both express a rate of N-depletion and one would expect T_D (the time until a pure grass cell becomes N-

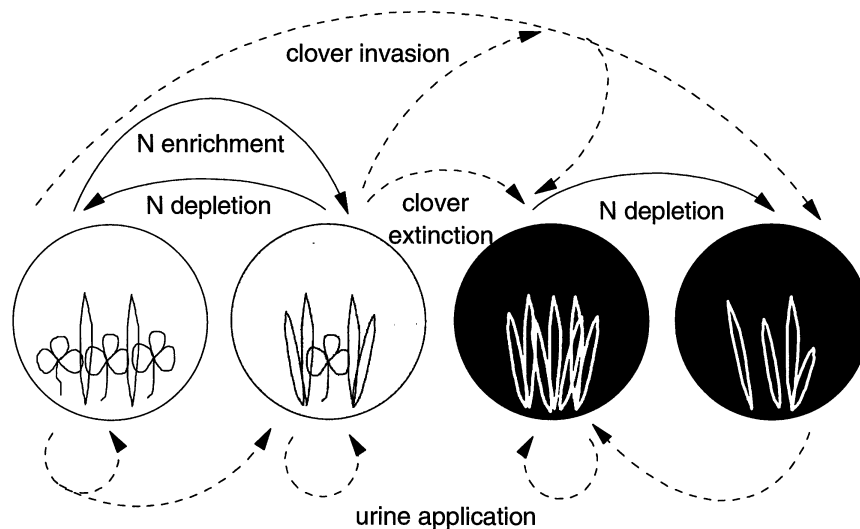


Fig. 1 Schematic representation of the four cell states in the automaton: white, legume dominance; light grey, grass dominance (with legume present); dark grey, pure grass at high soil N; black, pure grass at low soil N. State transitions are indicated by arrows. Solid arrows indicate deterministic transitions, broken arrows indicate stochastic transitions.

Table 1 Parameters and their meaning

Symbol	Description	Value
T_G	duration of the grass-dominated part of cycle	16 iterations (2.7 years)
T_C	duration of the legume-dominated part of the cycle	8 iterations (1.3 years)
T_D	time until pure grass becomes maximally N-depleted	12 iterations (2.0 years)
T_U	duration of the urine effect	1 iteration (2 months)
T_F	duration of the fertilizer effect	2 iterations (4 months)
p_e	legume extinction probability (per time step) for grass-dominated cells	0.3
p_i	probability (per time step) of legume invasion from a grass-dominated cell into a neighbouring legume-free cell	0.05
p_U	probability (per time step) of urine application to a cell	0.2
S	urine patch size	7 cells (diameter = 3 cells)

depleted) to be no greater than T_G (the time until a grass-dominated, mixed cell becomes N-depleted).

The default settings for T_G , T_C and T_D were derived from our previous physiological model (Schwinning & Parsons 1996). The period of the unperturbed cycle is four years and grass dominance lasts twice as long as legume dominance. Empirical data on the period of local population cycles suggest a cycle length with similar period (Cain *et al.* 1995).

STOCHASTIC STATE TRANSITIONS

There are three kinds of stochastic events (indicated in Fig. 1 by dotted arrows): legume extinctions, legume invasions, and N (urine) applications. During the phase of grass dominance, legume has a constant extinction probability per time interval, p_e . If legume becomes extinct, grass-dominated cells of age T_G become pure grass/high N cells. The age of the new grass cells depends on the age it had in its former state. For example, if legume becomes extinct in a grass-dominated cell half-way towards the beginning

of legume dominance, the new grass cell is also half-way towards becoming N-depleted.

Invasions can originate from all cells that contain legume into adjacent pure grass cells. When a pure grass/low N cell is invaded, a legume-dominated cell establishes and when a pure grass/high N cell is invaded, a grass-dominated cell emerges. Invasion from legume-dominated cells are certain within the time interval (i.e. $p_i = 1$), assuming that a dense legume population will necessarily spill into all adjacent invulnerable spaces. But invasions of legume from grass-dominated cells are uncertain (i.e. $0 \leq p_i < 1$). This assumes that a sparse legume population (with a small number of growing points) cannot disperse in all directions simultaneously.

To our knowledge, no empirical data are available for the local extinction and invasion probabilities of clover in relation to the local pasture state. We deal with this lack of information by varying p_i and p_e across their full range.

The probability of urine application into any cell during a time step, p_U , is constant. Urine events are

spatially random, but urine was applied over areas of 1, 3 or 5 cells in diameter, which for consistency with rates of clover invasion, corresponds to $\approx 3, 9$ and 15 cm. For reference, the urine patches of sheep have a diameter of ≈ 10 cm (Doak 1952; Wolton 1979). Urine instantaneously increases the nitrogen status of cells, but the duration of the urine effect, T_U , is relatively short. Urine adds the time T_U to the age of legume-dominated cells (moving them more quickly into the grass-dominated phase) and subtracts the same time from the age of grass-dominated cells (delaying their transition to legume-dominance). Urine also subtracts age from pure grass/high N cells and transforms pure grass/low N cells temporarily into high N cells.

We set the probability of urine application per time step $p_U = 0.2$. This corresponds to a daily application rate of $\approx 0.3\%$ of the total area, or a stocking rate of 20 sheep per ha with 15 urinations per animal per day (Doak 1952; Parsons *et al.* 1991; Orr *et al.* 1995). N levels stay elevated in the soil for only 30–50 days after urine application but N levels in plants may remain elevated longer. Therefore, we set the duration of the urine effect $T_U = 1$, equivalent to 2 months (Ryden 1984; Marriott *et al.* 1987).

QUANTIFICATION OF LEGUME DISTRIBUTION

It is useful to define a quantity to represent the average legume content of the automaton. Necessarily, this has to be an arbitrary measure, useful only for the purpose of comparing simulation results, but not to be taken as measures of biomass or biomass percentage. We express the legume content of cells as percentages based on their states (legume or grass dominance) and their ages as a .

For cells in legume dominance:

$$\text{legume content} = 50 \left(1 + \sin \left(\frac{a}{T_C} \pi \right) \right). \quad (1)$$

This formula says that legume dominance begins and ends with 50% legume content, and that it peaks at 100% half way through the phase of legume-dominance.

For cells in grass dominance:

$$\text{legume content} = 50 \left(1 - 0.8 \sin \left(\frac{a}{T_G} \pi \right) \right). \quad (2)$$

This formula says that the lowest legume content of grass-dominated cells is 10%. Thus, we assume that the minimal legume content of a cell in grass dominance is an order of magnitude smaller than the maximal legume content.

To characterize the spatial distribution of legume, we calculate a relative clumping index I_C after Hendry & McGlade (1995):

$$I_C = \frac{\frac{1}{6n_c} \sum_{i=1}^{n_c} N_i^C}{\binom{n_c}{n} \binom{n_c}{n}} \quad (3)$$

where n is the total number of cells, n_c is the number of cells containing legume and N_i^C is the number of cells, in the six cells adjacent to the i th legume cell, that also contain legume. Thus, the index is the ratio of the actual frequency of legume–legume interfaces to the expected frequency, if legume cells were distributed spatially at random. $I_C > 1$ indicates clumping.

Results

SPATIAL PATTERNS

The dynamic properties of this system are best illustrated by considering first the case of a single cell of legume spreading into a background of N-depleted pure grass. As one would expect, the periodic alternation between grass and legume dominance within cells produces waves of legume dominance followed by waves of grass dominance (Figs 2 and 3). In the absence of extinctions and urine applications (Fig. 2), spatial waves have a length that is simply the product of the invasion rate and the period of the grass–legume oscillation. If spatial waves remain undisturbed, they last indefinitely. Once established, these waves do not propagate by invasion (since, in this particular case, all cells contain legume), but simply by ‘ageing’. Because consecutive stages in the grass–legume cycle follow each other not only in time but also in space, waves of legume dominance appear to emanate from the original patch.

Spatial waves can also develop if there are random legume extinctions in grass-dominated cells. These waves are different, however, because they continue to propagate by invasion. Since extinctions and invasion are a stochastic processes, these waves do not remain static, but fragment, and can eventually dissolve into an apparently random pattern of legume distribution. Disturbance by urine facilitates the disintegration of spatial waves (Fig. 3). Across a range of extinction probabilities and rates of urine applications, there is a continuum of asymptotically approached spatial patterns, ranging from highly uniform distributions, to a pattern of moving mosaics, to distinct waves of legume dominance sweeping across a background of pure grass (Fig. 4).

One can characterize asymptotic pasture patterns using several statistics, for example, the frequencies of the four cell states, the average diameter of the patches they form and the clumping index I_C for the legume population. These statistics converge on constant values as the legume content converges on a

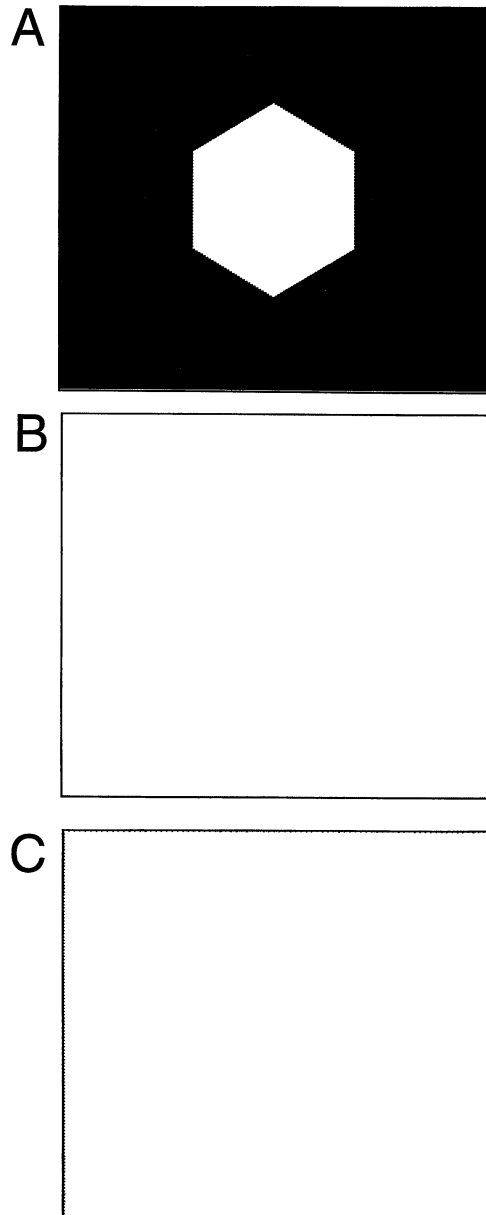


Fig. 2 The propagation of a single legume cell into N-depleted grass when there are no legume extinctions ($p_e = 0$) and no urine applications ($p_u = 0$). (A) after 5 years, (B) 30 years, (C) 100 years. White, legume dominance; light grey, grass dominance (with legume present). The parameters of the intrinsic grass–legume oscillation are set to default values. For reference, the waves of legume dominance are eight cells wide.

fixed value, although the precise spatial pattern is continually changing.

The stabilizing pasture state is determined by the complex interactions of the intrinsic dynamics of the grass–legume association, extinction and invasion probabilities, the frequency and urine application and even the sizes of urine patches. Table 2 illustrates the effects of extinction probability and urine patch sizes on the asymptotic pasture state. As is obvious from

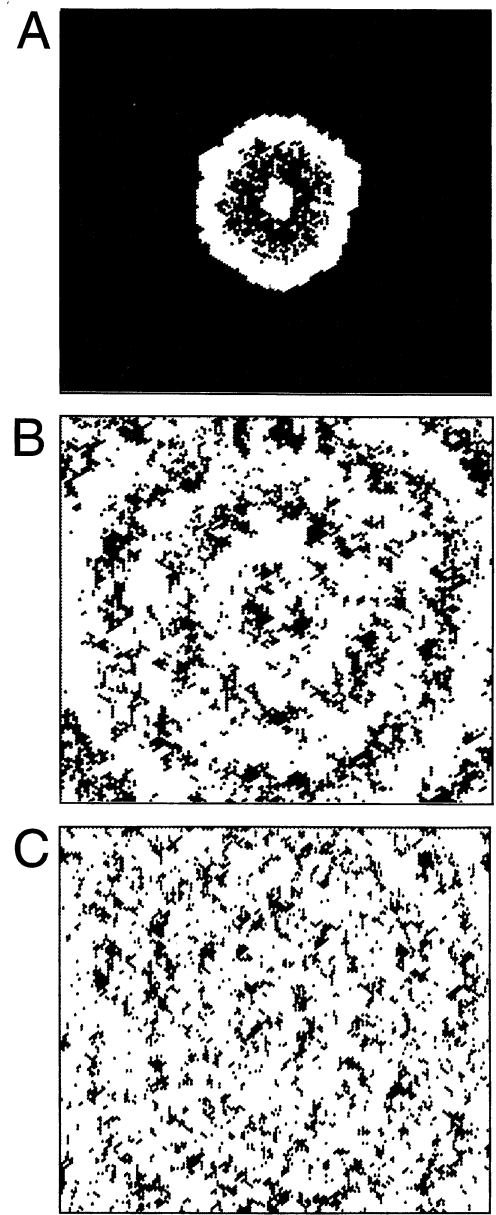


Fig. 3 The propagation of a single legume cell into N-depleted grass when the legume extinction probability (p_e) is 0.3 and the urine application probability (p_u) is 0.2. (A) after 5 years, (B) 30 years, (C) 100 years. White, legume dominance; light grey, grass dominance (with legume present); dark grey, pure grass at high soil N; black, pure grass at low soil N. The parameters of the intrinsic grass–legume oscillation are set to default values.

Fig. 4, larger extinction probabilities reduce the percentage area covered by legume. Urine also reduces the legume content, chiefly because it increases the time cells spend in grass dominance where legumes are vulnerable to extinction. Urine can increase the degree of clumping, particularly if extinction probabilities are high. Although the degree of clumping and the average legume patch diameter tends to increase with the diameters of urine patches, there is no simple correspondence between the diameters of

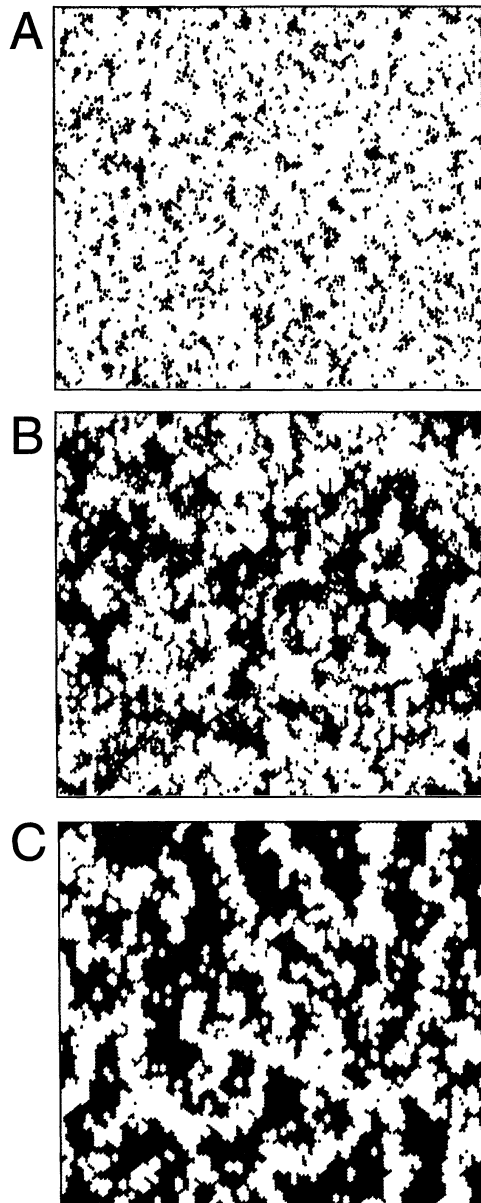


Fig. 4 Asymptotic pasture states for three extinction probabilities: (A) $p_e = 0.3$, (B) $p_e = 0.6$, (C) $p_e = 1.0$. White, legume dominance; light grey, grass dominance (with legume present); dark grey, pure grass at high soil N; black, pure grass at low soil N. The parameters of the intrinsic grass–legume oscillation are set to default values.

urine patches and the average diameters of legume patches.

2. FIELD-SCALE DYNAMICS AND EQUILIBRIA

Whenever pastures deviate from asymptotic structure, their legume content oscillates at the field scale. Two factors determine whether or how fast pastures converge on a stable state: initial conditions and the

level of random disturbances to the soil N status. Figure 5 illustrates the effect of initial condition if there are no random disturbances. A uniform initial condition gives rise to oscillations with maximum amplitude, because the entire pasture oscillates in concert with every cell in it. When the automaton is initialised with a spatially random distribution, with 50% of all cells containing legume, legume content oscillates with lower amplitude. This emphasizes that a random distribution of cell states does not necessarily produce field-scale stability. However, if the legume population is founded by a single cell via invasion, a stabilizing pasture state develops spontaneously.

Random perturbation of the cells' soil N status dampens field-scale oscillations by offsetting different areas with respect to the grass–legume cycle. In the model, this can be done in two ways (Fig. 6). The obvious way is the spatially random application of urine, since urine resets the soil N state instantaneously. The more frequently urine is applied, or the longer the urine effect lasts, the stronger is the dampening effect on pastures. Field scale oscillations are also dampened by legume extinctions alone. These affect the N states of cells in the long term, mainly by interfering with the rate of N depletion. Thus, the dampening effect of random legume extinctions is stronger, the greater the difference between the rate of N depletion in grass-dominated cells (T_G , here = 16) and in pure grass cells (T_D).

The legume content of a pasture at equilibrium is the result of the combined effects of patch-scale dynamics (expressed in the 'physiological' parameters T_C , T_G , T_D and p_U) and the dispersal ability of the legume (expressed in the 'dispersal' parameters p_e and p_i). Figure 7 shows how these parameters interact in setting the asymptotic legume content of pastures. Each line in Fig. 7 corresponds to a set of 'physiological' parameters, while the symbols scattered along each line indicate the solutions for a range of 'dispersal' parameters. We did not present the individual effects of extinction probability (p_e) and extinction probability (p_e), since they have the expected effects: increasing p_e reduces the number of cells containing legume, and increasing in p_i does the opposite.

Figure 7 highlights that p_e and p_i can affect the number of cells containing legume, but that this does not have a large effect on legume content. This is because in a more widely dispersed legume population, a greater proportion of area has grass as the dominant species. In short, an increase in legume cover tends to add only competitively suppressed sub-populations. It follows that the sensitivity of legume content to variation in legume dispersal ability depends on the density of legume in areas of grass dominance: the smaller this density, the less is gained by increasing legume dispersal.

Figure 7 also illustrates that the greater the physiological ability of the legume to compete against grass

Table 2 The effects of legume extinction probability (p_{α_e}) and urine patch diameter on pasture structure. Results are steady state solutions; variation between simulation runs was < 1%. D is the mean diameter of the legume-dominated patch (no. of cells)

p_e	Urine patch diameter (no of cells)	legume content	Cells with legume %	avg. diameter of legume-dominated patch (no of cells)	I_C
0.3	no urine	42	97	1.55	1.00
	1	37	90	1.44	1.03
	3	36	86	1.70	1.05
	5	35	81	1.98	1.09
0.6	no urine	41	94	1.60	1.02
	1	31	65	1.95	1.46
	3	31	65	2.27	1.30
	5	29	57	2.83	1.46
1.0	no urine	39	85	1.64	1.11
	1	28	51	2.69	1.74
	3	28	53	2.91	1.69
	5	28	48	3.19	1.82

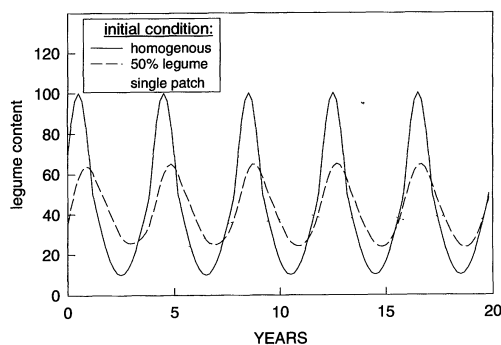


Fig. 5 Field-scale legume dynamics depend on initial conditions. There are no extinctions and urine applications ($p_e = p_U = 0.0$). The parameters of the intrinsic grass–legume oscillation are set to default values.

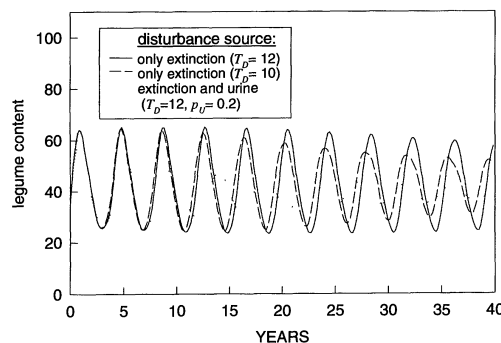


Fig. 6 Field-scale legume dynamics depend on the perturbation regime. The initial condition in all cases is a random cell state distribution with 50% of all cells containing legume. Parameters not referenced in the figure are set to default values.

(expressed, for example, by a shorter period of grass dominance or longer legume dominance), the less important is dispersal. Legumes can be widely dispersed in the equilibrium pasture state, purely because they perform well in competition with grass, and not

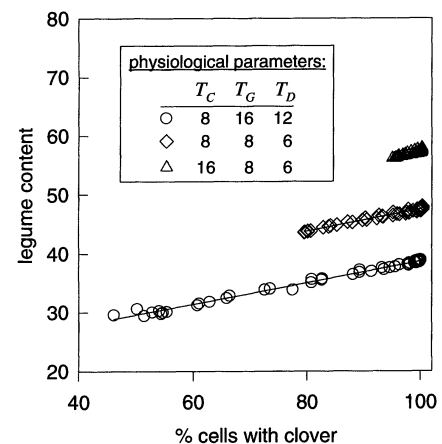


Fig. 7 The legume content of the pasture as a function of legume dispersal. Dispersal is measured as the percentage cells that contain legume. Linear regression solutions are shown for three sets of physiological parameters. Points represent asymptotic solutions for all combinations of a range of extinction probabilities $p_e = [0, 0.1, \dots, 0.9, 1.0]$ and invasion probabilities $p_i = [0.0, 0.3, 0.5, 0.7, 1.0]$. Parameters not referenced in the figure are set to default values.

because they are particularly good invaders or survivors.

3 SEASONALITY

Up to this point, we have not considered perturbations that act on the field-scale. Seasonal variation, such as winter mortality of legume or spring-time fertilizer application are real world examples of seasonal perturbations that act uniformly across pastures. We simulated winter mortality by subjecting *all* cells containing legume (including cells with legume dominance) to an additional extinction probability for one interval every year. If fertilizer was applied, it was applied to all cells in the interval following the

winter extinctions. The effect of fertilizer is similar to the effect of urine: it resets the soil N status instantaneously, but its effect lasts twice as long as the urine effect. Figure 8 illustrates some effects of such seasonal perturbations.

A constant rate of winter mortality (at 50%) can eliminate year-to-year variation in legume content more quickly than seen if only continual, spatially random extinctions of competitively suppressed subpopulations occur (compare Figs 8a,b). Still, in Fig. 8b, the end-of-season legume content stabilizes only after about 10 years. In contrast, if annual winter mortality is variable (between 20% and 80%), the legume content continues to vary greatly between years (Fig. 8c). If, additionally, fertilizer is applied at the beginning of the growing season, year-to-year legume variation appears more periodic, peaking about every seven years (Fig. 8d). Although winter mortality is the only source of variation between years, it explains only a minor proportion of the end-of-season variation in legume content (for the time series in Fig. 8c: 8.6%; in Fig. 8d: 34.6%).

Autocorrelation analysis of the end-of-season legume contents of the time series in Fig. 8c and 8d reveal significant periodicity in year-to-year variation (Fig. 9). The period in the time series of Fig. 8c is approximately four years, corresponding to the duration of an undisturbed population cycle at the cell scale. However, fertilizer application greatly prolongs the period of field-scale oscillations.

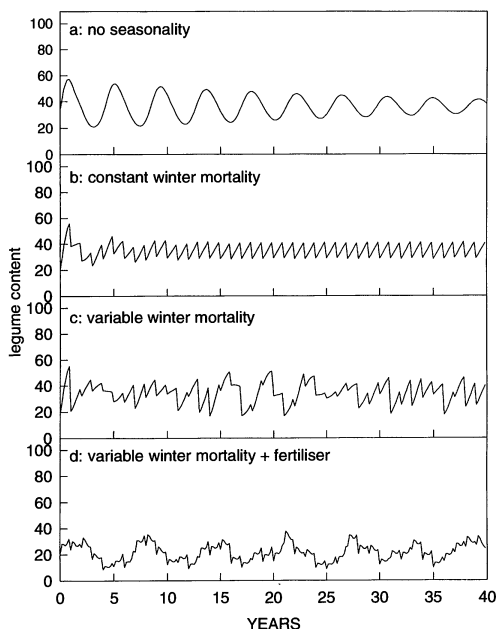


Fig. 8 Variable winter mortality leads to persistent fluctuation in legume content: (A) no seasonal perturbation; (B) constant winter mortality (50%); (C) uniformly random winter mortality (between 20% and 80%); (D) uniformly random winter mortality (between 20% and 80%) and constant springtime fertilizer application. All parameters are set to default values.

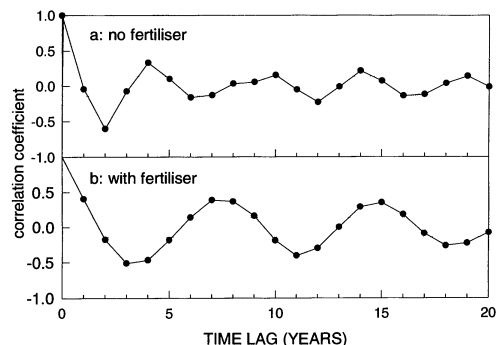


Fig. 9 Autocorrelation analysis reveals the intrinsic periodic component of between-year variation in legume content. Analysis corresponds to the time series in Figs 8c (a) and 8d (b) but is based on 200 years of data.

4. STABLE GRASS-LEGUME ASSOCIATIONS

Our results so far are based on the assumption that grass-legume associations are intrinsically unstable. However, one can envisage dynamically stable grass-legume associations (and we showed the conditions for this in the previous paper). We conclude our analysis by examining the spatial dynamics of stable grass-legume associations that do not oscillate at the patch scale.

To simulate stable grass-legume associations, we assumed that cells approach equilibrium proportion of legume monotonically, from any initial condition. In addition, we assumed, as in the unstable case, that urine input temporarily reduces the legume content of cells and that the legume can become extinct in cells (with a probability inversely proportional to legume content) if legume density is below the equilibrium density. By making the appropriate changes in the automaton, we can examine the spatial consequences of this scenario.

Not surprisingly, the stable grass-legume association does not generate travelling waves under any circumstance, nor oscillations at the field scale. Without perturbations by urine and extinctions, pastures become spatially uniform with equilibrium legume content. With increasing perturbation by extinction and urine, pastures become increasingly patchy. As in unstable grass-legume associations, high density legume patches form by successive invasions into N depleted pure grass. Thus, a patchy distribution of a legume in a grass pasture does not signify an unstable grass-legume association. However, different from unstable grass-legume associations, the stable pasture state is approached directly, without oscillations, from any initial condition (Fig. 10a).

From this, one should expect that stable grass-legume associations respond more predictably to seasonal variation. Indeed, legumes in stable associations with grass converge on the seasonal cycle almost immediately (Fig. 10b). Variable winter mortality, with and without fertilizer application (Fig. 10c,d), generates an apparently random temporal pattern

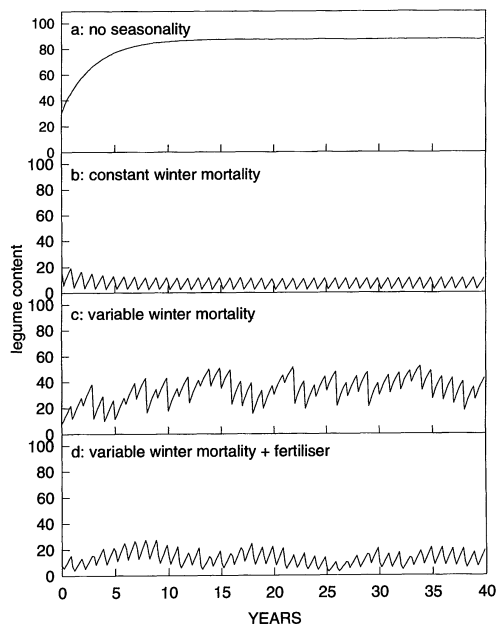


Fig. 10 Stable grass–legume association do not have long-term periodic trends. (A) no seasonal perturbation; (B) constant winter mortality (50%); (C) uniformly random winter mortality (between 20% and 80%); (D) uniformly random winter mortality (between 20% and 80%) and constant springtime fertilizer application. It is assumed that the legume populations of cells reach equilibrium density in 1 year if undisturbed. Local extinctions are inversely proportional to legume density.

where winter mortality explains by far the largest portion of the end-of-season variation in legume content. Autocorrelation analysis (not shown) reveals that the previous year's legume content has a small positive effect on the present year's legume content, but the effects of all earlier years are negligible.

Discussion

It is widely recognized that legumes such as clover are distributed patchily in mixed pasture with grass species (e.g. Cain *et al.* 1995) and that the average clover content of pastures can vary greatly from year to year (Steele & Shannon 1982; Rickard & McBride 1986). This spatial and temporal 'unpredictability' in legume content is seen to represent an element of risk in grassland systems. It discourages reliance on what has been proposed to be a valuable, sustainable alternative to fertilizer-based agriculture, with reduced environmental impact.

The scientific literature proposes several hypotheses about the causes of the apparent unpredictability of legumes in mixed pastures. Some hypotheses allude to physiological mechanisms, observing that legumes improve soil structure and fertility and reduce their own competitive ability in the long term (Turkington & Harper 1979). In the previous paper (Schwinning & Parsons 1996), we demonstrated how this hypothesis can explain legume instability at the patch scale,

but fails to explain field-scale fluctuations if spatially random perturbations allow pastures to become heterogeneous. Other hypotheses allude to legume's clonal growth habit. This is based on the largely unstated assumptions, first, that patchy distributions are somehow 'bad', and second, that legumes are dispersal-limited (Kessler & Nösberger 1994). Stoloniferous clonal growth may explain how patches evolve from isolated plants through clonal dispersal, but it does not explain why patchiness persists in the long term (Cain *et al.* 1995). After all, clonal growth does not prevent the widespread dispersal of legumes in monocultures.

In the present paper, we integrated the physiological, patch-scale explanation with the morphological, dispersal explanation of legume performance in mixed pasture. Furthermore, we added the effects of seasonal perturbation, which adds a third, field-wide scale. In agreement with other spatial models (e.g. Caswell 1991), we showed that only the combination of all three scales of interaction, and the integration of physiological and ecological concepts, can account for the observed spatial and temporal variability of legume in mixed pastures.

THE ORIGIN AND THE SIGNIFICANCE OF PATCHY LEGUME DISTRIBUTION

In our earlier, purely physiological model (Schwinning & Parsons 1996) we laid out the basis for patch-scale population fluctuations between grasses and N-fixing legumes. The model showed that the grazing system itself is a source of spatial variation. In both the previous physiological model and the present spatial model, spatially uniform pastures fluctuate at the field scale, but random urine applications dampen field-scale oscillations. The present spatial model adds that random local legume extinctions can have a similar stabilizing effect. Both events (urine application and local extinction) perturb the cycling of N and gradually randomize patch states by setting local population oscillations out of phase.

Thus, both models suggest that field-scale stability may actually depend on the establishment of a patchy pasture. In our purely physiological model, neighbouring patches had no effect on each other, and so only the frequency distribution of patch types mattered, not their spatial arrangement. In our spatial model, the pattern of legume distribution mattered as well. In general, population sizes in spatial models are constant when the rates of local extinctions are balanced by the rate of invasions. Since the rates of invasion in our model were determined by the number of cells containing legume *and* the number of invasion opportunities in the surrounding cells, a stable pasture had a specific cell frequency distribution *and* a specific spatial structure.

The spatial structure of grass–legume pastures has been a cause for concern, both in terms of identifying

the factors that limit legume performance and in terms of pasture utilization by grazing animals (Parsons *et al.* 1994). To many (e.g. Kessler & Nösberger 1994), a clumped distribution of legume in mixed pasture indicates that the legume has a dispersal problem and that the legume content of pastures can be increased therefore by finding ways to distribute legume more widely. However, our model indicated that the existence of a patchy distribution of clover is not, in itself, evidence that the species is dispersal limited. Improving the parameters for dispersal had little effect on species composition and may do little more than redistribute the legume from a clumped distribution (e.g. Fig. 4c) to a more uniform distribution where large portions of the pasture contain legume but at low density (e.g. Fig. 4a). In our model, pastures also became more clumped and formed larger patches of legume dominance if legumes had a higher risk of extinction in grass-dominated cells (Table 2). Some further practical implications of spatial heterogeneity in grass/legume pastures are discussed by Chapman *et al.* (1996).

AN EXPLANATION FOR SUSTAINED YEAR-TO-YEAR VARIATION IN LEGUME CONTENT

In the model, spatially random perturbation of the N status establishes a stable legume content. In real pastures, particularly if they are grazed, such perturbation should be quite common, and one would expect the legume content of pastures to be constant. This is not the case, however, and our model suggests an explanation for the persistence of periodic, and apparently unpredictable, year-to-year variation in legume performance.

The key to the persistence of year-to-year variation is that the establishment of a stabilizing pasture structure in unstable grass–legume associations is slow compared to the period of seasonal perturbation. Thus, pastures are unable to recover a stable state within a growing season and legume content maintains a tendency to oscillate at the field scale. It is well known that the interaction of intrinsic oscillatory dynamics and seasonal variation can generate complex dynamic patterns (e.g. May 1981).

In our model, the fluctuations in the legume content of pastures maintained a significant periodic component (the oscillation of around 4 years derived from their physiological interaction), even though there was great variation in annual mortality. Springtime fertilizer application delayed field-scale oscillations, by inhibiting the re-establishment of legume-dominated patches following winter. There are few published long-term data sets observing the average clover content of pastures (Steele & Shannon 1982; Rickard & McBride 1986). These clearly convey alternations of grass and legume dominance with an apparent periodicity of 3–4 years, but we are not aware of any formal time series analysis. Our own

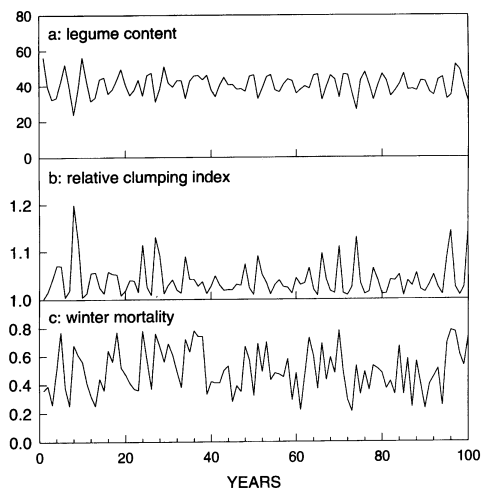


Fig. 11 The prominence of periodic fluctuation is associated with the degree of clumping. (A) the end-of-season legume content; (B) the relative clumping coefficient I_C ; (C) the rate of winter mortality. Winter mortality varies between 20% and 80%. There is no fertilizer application. All parameters are set to default values.

preliminary analysis confirms significant periodicity at 3–4 years in at least some empirical data. A publication is in preparation.

An interesting feature of the model-simulated time series (Fig. 11a) is that the temporal patterns appear to change over time, thus also predicting the uncertainty in legume content seen in the long term empirical data. In the model, relatively well-defined oscillations (e.g. for years 62–82) are interspersed with sequences with no apparent periodicity (e.g. years 30–50). These differences do not seem to be correlated with spurious patterns in winter mortality (Fig. 11c). We believe that differences in apparent pasture dynamics are related to pasture structure, in particular, the degree of legume clumping (Fig. 11b). Preliminary analysis suggests that episodes of large amplitude, regular oscillations appear to be induced by highly clumped legume distributions, while episodes of low amplitude, less regular variation are associated with a lower degree of clumping.

Clumped distributions arise when legumes recover from very low density (perhaps caused by a sequence of high-mortality winters). Recovery from low density is accomplished largely by invasion into N-depleted areas, and so many of the new subpopulations will be in similar phases of the intrinsic grass–legume oscillation. As a result, a large portion of the pasture will be synchronized and, as seen before, this causes field-scale population oscillations. In time, the pasture becomes randomized again through the effects of spatially random processes. In this way, pastures may drift in and out of periodic phases. To our knowledge, no experimental studies have been performed to test the association of pasture spatial structure and species dynamics for grass legume systems. However, there is circumstantial evidence that homogeneity may induce

instability in legume content. Field researchers frequently refer to a 'clover crash', which is the unexplained decline in clover populations some 2–3 years after sowing mixed pasture (Frame & Newbould 1986). This phenomenon is apparent in our models and it is possible that the pasture homogeneity, enforced by ploughing and re-sowing, is responsible for the sudden decline in clover content. Clearly, the general topic of long-term field-scale dynamics deserves further analysis.

Conclusions

The pasture legume white clover, in association with ryegrass, has been the subject of several decades of research in grasslands. This has led to a wealth of observations, but few formal analyses, of the spatial and temporal variability of legume content. Our model provides a testable hypothesis to explain many of the diverse phenomena observed.

Legume physiology, dispersal, and responses to seasonal variation are inseparable components of legume performance. We have argued that the legume's ability to fix atmospheric nitrogen may be exploited by grasses and that exploitation encourages population oscillations. Here we add that unstable dynamics at the patch scale can generate sustained and highly complex field-scale dynamics, when subject to seasonal perturbation. In addition, unstable local population dynamics may complicate the biological role of legume dispersal.

The 'ideal' legume should distribute patchily, be able to invade spaces where it will have high rates of growth, and avoid spaces where it would be competitively suppressed. So far, in our models, we have assumed that legumes disperse indiscriminately. But observations on stoloniferous, clonal legumes such as white clover indicate that their morphology is controlled by a combination of internal and external factors (Brock *et al.* 1988; Sackville-Hamilton & Harper 1989a; Robin *et al.* 1994), which give phenomena of branching as if plants were foraging for resources. To understand fully the function of branching and clonal integration, future research must address the relationships between morphology and intra- and interspecific interactions, as well as between morphology and the environment.

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