Interactions between Grasses and Legumes: Understanding Variability in Species Composition.

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ABSTRACT

Variability in the legume content of unfertilized pastures is perceived as a risk to herbage production. However, the link between herbage production and legume content is not well understood. To clarify the issue, we distinguish between intrinsic and external sources of variation and examine the effects of each on herbage production. Models and observations suggest that there is an intrinsic, oscillatory component of variation in grass-legume (e. g. clover) systems, with a period of 3-4 years. External sources of legume variation, or 'stresses', interact with these oscillations and introduce a random element to variation. In a spatial pasture model, we show that stress severity affects the pattern of annual legume yield: when annual legume mortality is low, the legume content of pastures oscillates between years, as legumes are limited primarily by a time-delayed interaction with grasses. When legume mortality is large, there are no oscillations and annual legume performance depends on the ability to invade into nitrogen-deficient grass. We argue that legume oscillations signify that legumes contribute substantially to soil fertility and herbage yield. The absence of oscillations signifies the opposite. We present an analysis on one of the few published, long-term data sets to support this hypothesis.

INTRODUCTION

It has long been recognised that unfertilised pastures can sustain soil fertility and a high level of sward production, despite continual losses of nitrogen through cutting or leaching, because they contain plant species capable of fixing atmospheric nitrogen. These species are typically legumes, and the most dominant pasture legume in the temperate zone is white clover (*Trifolium repens*). White clover is reported to contribute up to 342 kg N/ha/yr in mixed swards world wide (Ledgard and Steele, 1992). In a New Zealand pasture, about 50% of the nitrogen demand of grasses was met by the transfer of fixed nitrogen from white clover (Ledgard, 1991). Thus, white clover is considered a low-cost alternative to industrial nitrogen fertilizer.

However, unfertilized pasture is not the preferred system of herbage production in Europe and USA. One reason for the reluctance to rely on clover for maintaining soil fertility is the perception of risk. Unlike industrial nitrogen fertilizer, which can be administered at almost any time according to demand, biological nitrogen fixation is highly variable and largely uncontrollable. Most variation in the annual nitrogen fixation can be related to the white clover content of pastures and the availability of mineral nitrogen in the soil (Crush, 1987). Understandably, farmers are concerned that clover variability translates into uncertainties in herbage production.

The fact is that the link between the clover content of pastures and herbage production is not well understood (Harris, 1987; Chapman *et al.*, 1996). Although various authors have argued that there may be an "optimal" clover content and have speculated what its value may be (Martin, 1960; Curll, 1982), there have been no rigorous tests of this hypothesis. One difficulty in determining the optimal clover content is the inability to manipulate clover content as a fixed and independent treatment variable. While clover content responds predictably to many management interventions (e.g. fertilizer application usually decreases clover content; Ledgard and Steele, 1992), manipulating the clover content *per se* has proved exceedingly difficult (P.D. Penning, personal communication).

In addition, we do not fully understand the reasons behind clover variability. Long-term records from New Zealand and the U.K. (e.g. Steele and Shannon, 1982; Rickard and McBride, 1986; Tyson *et al.*, 1990) give evidence of persistent and substantial variation in annual white clover yield (between 10% and 40% on a biomass basis), despite consistent management practices. Such variability in the annual clover performance is often attributed to **external**, i.e. environmental factors. For example in the UK, two major factors limit annual clover performance: winter mortality of stolons and the rate of recovery during spring (Crush, 1987). In New Zealand, summer droughts are largely responsible for poor clover performance (Hutchinson *et al.*, 1995). But recent models suggest that there may also be **intrinsic** causes for variability in species mixtures containing legumes (Thornley *et al.*,1995; Schwinning and Parsons, 1996a;b). These models, which are based on fundamental physiological properties of grasses and legumes and their capacity for dispersal, predict that legume and grass populations should oscillate with periods of 4-10 years.

Thus, variation in the average legume content and the annual legume yield of pastures may have two components: one random, caused by variation in the external environment, and another deterministic, caused by intrinsic interactions between grasses and legumes. It stands to reason that these different sources of variation have different implications for the risk associated with herbage production on unfertilized pastures and the breeding and management strategies aimed at alleviating that risk.

Below, we briefly review recent models of grass-legume interaction and suggest an explanation for spontaneous population oscillation in grass-legume systems. We then discuss how externally imposed variation may interact with intrinsic oscillations. Lastly, we will argue that the pattern of observed temporal variation may contain clues that help to identify the main limitations to legume performance.

THE SOURCE OF INTRINSIC VARIATION

The key to understanding the intrinsic source of variability in mixtures of grasses and legumes is the difference in their growth response to the availability of nitrogen (N) in the soil. Grasses supply their demand for N almost entirely through the uptake of mineral N in the soil. Thus, if there is very little N in the soil, N uptake (and thus growth) rates are also small. In contrast, legumes can supplement mineral N uptake with N fixation, and so retain relatively high growth rates even in a low N soil environment. However, there are also drawbacks to N fixation: first, the metabolic costs of N fixation are higher than those

of mineral N uptake. Ryle *et al.* (1979) found that the daily growth rate of white clover seedlings (*Trifolium repens*) depending totally on N fixation, was c. 60% that of clover seedlings grown with ample mineral N supply. Second, even though legumes, such as clover, are known to adjust the rate of N fixation with the availability of N in the soil, they have been seen to retain some N fixation activity, even at high soil N. In white clover, this minimal activity (measured at high soil N) was shown to provide 15% of all N within tissues (Davidson and Robson, 1985; 1986a; 1986b). Thus, legumes such as clover always pay a higher price for N (in terms of metabolic energy) than grasses and other species that do not fix atmospheric N.

The contrasting response of grasses and legumes to the availability of soil N provides one explanation for their sustainable coexistence, as was recently shown in a dynamic growth model (Schwinning and Parsons, 1996a). At low soil N, legumes have a growth advantage and so legumes should exclude grasses, but at higher soil N, grasses have the growth advantage and should exclude legumes. If one assumes that soil N levels are constant, the two species do not coexist. To get coexistence, one must assume that soil N is also a dynamic variable, i.e. that soil N not only affects the plants, but also is affected by them. At low soil N, when legumes dominate, N accumulates in the soil through the accumulation of legume litter containing fixed N. Conversely, at higher soil N, when grasses dominate, soil N is depleted, because of diminishing input of legume litter. These negative feed-back controls of the soil N status not only maintain the competitive balance between the two species, but also keep soil N within narrow boundaries; this is the very attribute that makes grass/legume pastures attractive in terms of low environmental impact.

However, the control of soil N is a relatively slow process, and models show that grasses and legumes can therefore oscillate in dominance for many years before they reach an equilibrium mixture (Fig. 1; Thornley *et al.*,1995; Schwinning and Parsons, 1996a). The damping oscillations in Fig. 1 have a period of 4-5 years. This means that average clover content and annual herbage yields may differ between years, even though the environment is perfectly constant (as in the model). Fig. 1 also indicates that the relationship between the clover content of pastures and herbage yield is not simple: peaks in total yield do not coincide with peaks in legume percentage, but follow some 1-2 years later.

These are the results of models, but there is good empirical evidence that the proportions of white clover in mixed pasture oscillate. Cain *et al.* (1995) recently reported that neither clover patches, nor clover gaps persisted in a pasture, suggesting that there are indeed cyclic changes in grass and clover abundance at the patch scale.
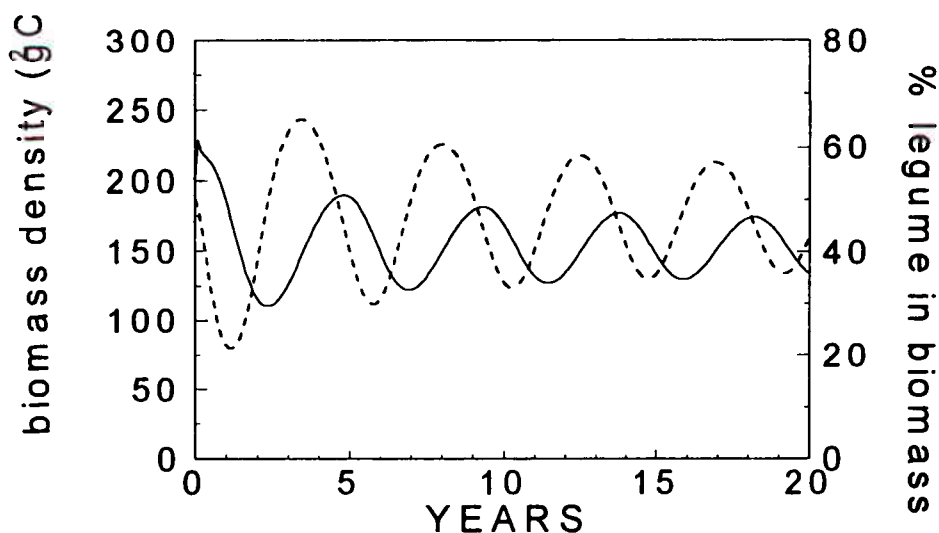
Figure 1. A grass-legume model predicts damping oscillations in total biomass density (solid line) and legume percentage (broken line).

Cycles of grass and clover abundance have also been proposed, and observed, at the **field scale** (e.g. Ledgard and Steele, 1992). But it has been unclear how cycles in species composition at the patch scale can generate cycles at the field scale. After all, species composition could oscillate at every point in the field, but averaged across the field, species composition could remain constant.

The circumstances that may lead to cycles, and so legume variability, at the field scale were recently examined by Schwinning and Parsons (1996b) using a spatial model (a cellular automaton model or 'CAM'). In this model, oscillating legume abundance at the patch scale was an *a priori* assumption. To make the model more realistic, it was also assumed that legumes were at risk of becoming extinct in places where they were at low density, and that legumes were able to spread into adjacent legume-free spaces. The spatial simulations showed that legume populations oscillated at the field scale when pastures were spatially uniform. This makes sense: if all patches in the pasture are 'in phase' with respect to the grass-legume cycle, the entire pasture oscillates. Conversely, a spatially heterogeneous pasture had a less variable average clover content. A typical picture of a heterogeneous pasture with constant average legume content is shown in Fig. 2. This spatial structure, one of moving patches of legume in a background of grass, arose spontaneously. As it did, field-scale oscillations in legume content died out. The slow transformation from spatially uniform legume content to patchy legume content was mediated by local perturbations in the form of legume extinctions and urine input. These local disturbance factors dampened variability in the average legume content by setting the different areas in the field 'out of phase'.
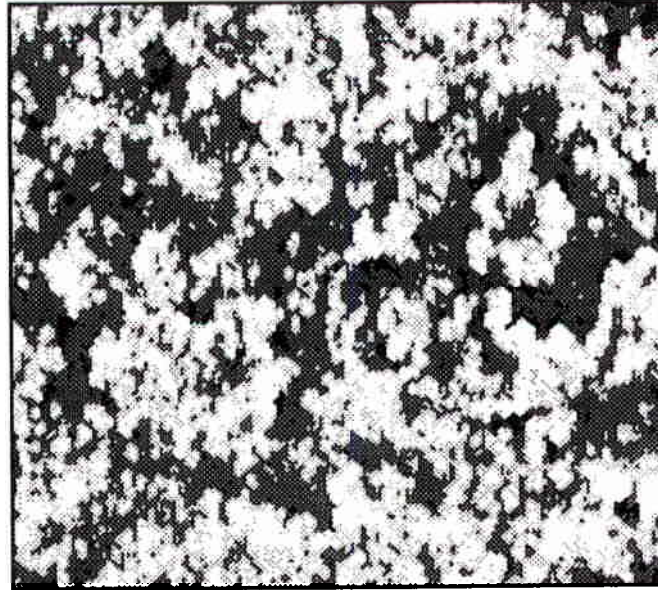
Figure 2. A spatial pasture model predicts the spontaneous formation of legume patches. White: legume dominance (low soil N), light grey: grass dominance (high soil N) dark grey: no legume (high soil N), black: no legume (low soil N). All patches contain grass.

EXTERNAL SOURCES OF VARIATION

It is well known that legume densities are affected by a wide range of external factors, some working at the local scale, for example, impacts caused by grazing animals, and some working on the pasture scale, such as weather conditions and seasonal variation.

At a small scale, the application of high dosages of N as animal excreta is probably the most common source of disturbance in grazed pastures. Since animals retain only a small portion of the N they consume, the frequency with which excreta are applied is closely related to the rate of herbivory. At intermediate stocking densities, approximately 0.3% of the total pasture area receives N input from urine every day (Orr *et al.*, 1995). Put differently, every patch in a pasture is fertilized by urine once every 300 days, on average.

Simulations (Schwinning and Parsons, 1996a) and data (Ledgard, 1991) suggest that N input by excreta does not contribute substantially to average soil fertility and pasture growth. N levels in the soil stay elevated locally for only 30-50 days after urine application (Wolton, 1979). Significant amounts of urine N are lost by leaching and volatilisation and are not utilised by plants (Steele, 1982). Thus, excreta have little effect on average species composition. However, they can be very effective at accentuating the intrinsic oscillations between grasses and legumes in patches, as models indicate (Schwinning and Parsons, 1996a). Even infrequently applied excreta disrupt the approach to equilibrium mixtures in patches. But since the inputs of excreta are largely random in space and time, they help stabilise the **average** species composition of pastures by setting local patches in the pasture out of phase with each other (Schwinning and Parsons, 1996b).

Perturbations at the pasture scale (such as weather) should have different effects than perturbations at the local scale (such as urine). Typically, pasture-scale perturbations, or "stresses", are caused by management practices (e.g. fertilizer application) or by random and seasonal variation in the weather. To understand the effects of these sources of variation, we continue to examine the spatial pasture model, the CAM. Since a CAM must simplify all matters pertaining to physiology, it cannot keep track of the various and complex effects that fertilizer or weather may have on plant populations. Instead, all external sources of perturbation are represented in the CAM by their ultimate effect on populations: to reduce local legume density or to set it to zero.

First, we examine the effects of seasonal variation. White clover biomass in pastures varies greatly over the course of a year, usually being at its lowest in spring, after the death of stolons during the cold season and before recovery. In the CAM, the annual die-back of legumes is mimicked by reducing the number of patches containing legume by some fraction once a year. To fully recover from this setback, legume populations must use the remainder of the year to re-invade the areas from which they were lost.
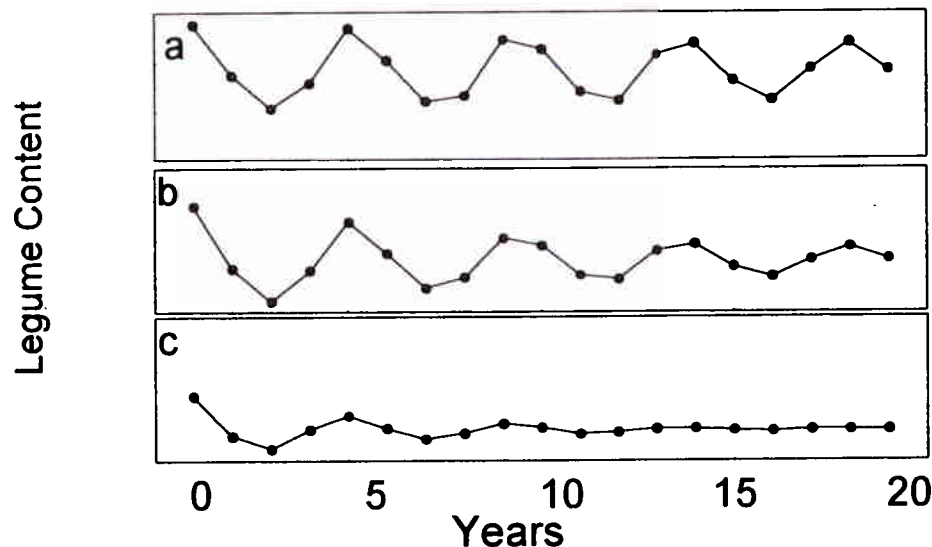

Figure 3. Fluctuations in the end-of-year legume content as predicted by the spatial pasture model. Annual rate of legume mortality is 0% (a), 20% (b) and 50% (c).

The spatial model shows, not surprisingly, that the greater the annual die-back, the less legume there is at the end of the year (Fig. 3). More interestingly, the degree of annual legume loss also influences the pattern of fluctuation between years. If annual legume loss is zero (Fig. 3a), an initially homogeneous pasture oscillates with declining amplitude for many years. If 20% legume cover is lost every winter (Fig. 3b), legume dynamics remain oscillatory for at least 20 years. If the annual legume loss is 50% (Fig. 3c), between-year oscillations disappear almost immediately.

In reality, the effect of year types on legume populations also varies, i.e. legume mortalities are different in different years. When one considers this further complication

(Fig. 4), the pattern of legume variation becomes highly complex - and quite realistic. Some long intervals can appear periodic, but these are inevitably terminated by intervals without apparent pattern.
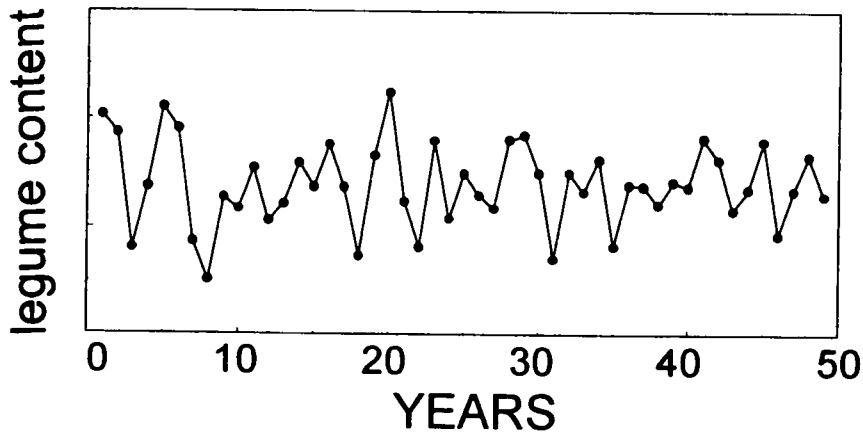

Figure 4. Fluctuations in the end-of-year legume content as predicted by the spatial pasture model when the annual rate of legume mortality varies between 20% and 80%.

Figs. 3 and 4 illustrate that legume variation **between years** can be dominated by two, qualitatively different, dynamic patterns. Under environmental conditions that are favourable to legumes (here: low losses during winter/early spring), legume populations are checked primarily by their interactions with the other pasture species. We have argued above that these interactions promote population oscillations (at the patch- and the field-scale). Therefore, one would expect pastures with relatively high legume content to have periodic variation in annual legume yield. In contrast, when the environment is unfavourable to legumes (high losses during winter/early spring), legume content should be slaved to the environmental stresses. As a consequence, the effects of other species on legume growth may be negligible and one would not expect to see periodic variation in annual legume yield.

In short, these simulation results suggest that the different sources of variation in legume content of pastures have distinguishable dynamic signatures. In the next section we test if this hypothesis is supported by field data.

CASE STUDY: WHITE CLOVER DYNAMICS IN CUT PASTURE AT WINCHMORE, N.Z.

Winchmore is the site of a long-term strip irrigation trial that has run uninterrupted from 1957 to the present. Pastures were subjected to 5 different irrigation regimes, ranging from a fixed irrigation interval of 3 weeks to no irrigation. Since 1962, all treatments were cut 9 times per year: in monthly intervals from September to March (spring and summer) and two times in the period between. Species compositions for the first 23 years of the experiment were summarised by Rickard and McBride (1986) and the following analysis is based on data shown in this report.

Moisture stress is regarded as a major limiting factor to clover (Hutchinson *et al.*, 1995). Therefore, it is not surprising that the non-irrigated pasture in Winchmore usually had a much lower clover percentage than irrigated pasture (Fig. 5). The lack of water also reduced total herbage yield by approximately 40%. Casual inspection of clover variation in the fully irrigated pasture (Fig. 5a) suggests that clover proportions oscillated with a period of approximately three years. The pattern of variation is less obvious for the non-irrigated pastures (Fig. 5b).
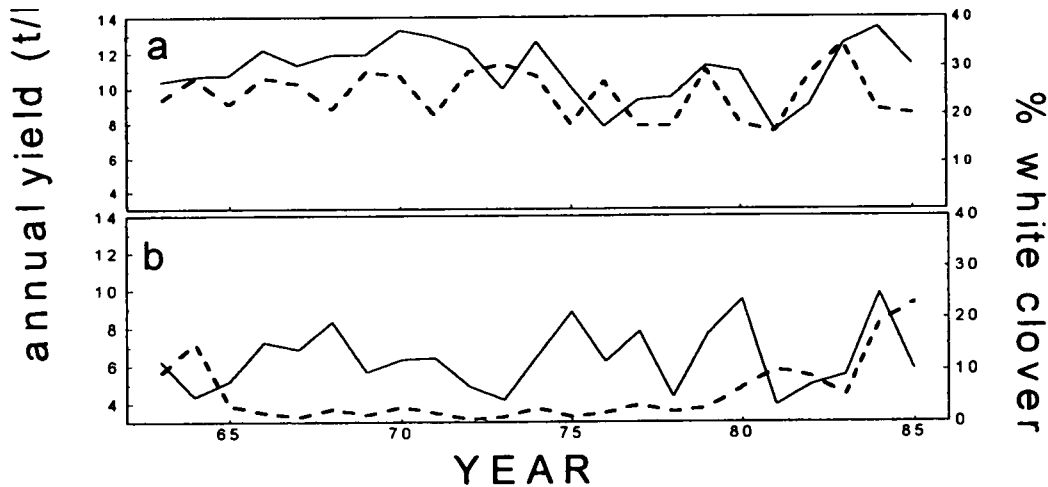

Figure 5. Variation in the total annual yield (solid lines) and the white clover percentages (broken lines) in cut pastures at Winchmore over the course of 23 years. a) pasture was irrigated every 3 weeks, b) non-irrigated pasture.

A more rigorous way to test for patterns in time series is autocorrelation analysis, where the degree of correlation between the present and past values of variables is determined. Table 1 shows the autocorrelations of clover percentage in annual yield. In irrigated pasture, the largest amount of variation is explained by the legume content of two years ago (lag=2), but the correlation is negative. This means that high legume content was often followed by low legume content two years later and vice versa. The negative autocorrelation (although just below the confidence limit) suggests a periodic process with a period of 3-4 years, and therefore supports the impression of periodicity in the time series. We analysed the legume variation in non-irrigated pasture only for the years 1965-1979, because clover percentages were consistently low during that time. All correlations were weak, i.e. there was no evidence that clover percentage had any effect on the clover percentages of following years.

Table 1. Autocorrelation for clover percentage in annual herbage yield. Confidence intervals around zero are ±0.417 for Irrigated and ±0.516 for Non-irrigated.

Lag (yrs)	Correlation coefficients	
	Irrigated	Non-irrigated
0	1.000	1.000
1	-0.065	-0.120
2	-0.369	-0.179
3	0.257	0.178
4	0.109	-0.161
5	-0.262	-0.048

Table 2. Crosscorrelations between annual herbage and past clover yield. Confidence intervals around zero are as in Table 1.

Lag (yrs)	Correlation coefficients	
	Irrigated	Non-irrigated
0	0.318	0.229
1	0.552	0.085
2	0.059	-0.130
3	-0.214	0.050
4	0.035	-0.261
5	0.081	0.190

In Table 2 we examine the crosscorrelations between clover percentage and total herbage yield, i.e. we ask if yield is affected by present and previous years' clover percentages. In irrigated pasture, present clover percentage had a relatively strong effect on yield. Surprisingly, the effect of the previous year's clover percentage was even greater and was highly significant. This suggests, again, that performance of irrigated pasture may be dominated by time-delayed and periodic processes. In non-irrigated pasture, cross-correlations were generally lower, suggesting that factors other than past or present clover percentages dominated herbage yield.

CONCLUSIONS

From an ecological point of view, the existence of intrinsic, periodic fluctuations in a plant population - moreover, one that is generated by plant-plant interactions rather than plant-animal interactions - is interesting in its own right. But how can this information be used by an agronomist concerned with herbage production?

First, we suggest that the pattern of annual clover yields gives clues that help to identify the main constraints to clover populations. In models, local population oscillations occur when pastures regulate soil fertility through shifts in the proportions between grasses and legumes. This implies that attempts to stimulate clover performance (e.g. by breeding) could be down-regulated (Chapman et al., 1996). We suggest therefore, that periodicity

(or negative autocorrelations) in the legume content of real pastures indicates that legume content is primarily limited by the companion species, i.e. by clover's paradoxical ability to improve the conditions for its competitors. Thus, oscillations are produced by the very characteristic of clover which makes it such a valuable pasture component: the ability to fix atmospheric nitrogen and make it available to other species.

If, on the other hand, no periodic element can be found in a time series, and instead, clover performance shows a large correlation with weather factors, it is reasonable to assume that the legume content of pastures is primarily limited by environmental conditions. In this case, there would be room for improving clover performance, for example, by increasing clover's tolerance for environmental stress (Ledgard and Steele, 1992).

Second, the Winchmore data illustrate that, in irrigated pasture, herbage production greatly depends on legume content, but that the main effect of clover content may be time-delayed. Ignoring time-delayed effects may partly explain why no clear-cut relationship between clover content and herbage yield have been identified (Harris, 1987). However, when the environmental stresses are severe, as in the non-irrigated pasture at Winchmore, total yields and legume content may not be strongly correlated at all.

For future research, it is essential to understand what limits clover content in a particular target population (Chapman et al. 1996). In general, clover content is not easy to control, as it is an integral part of a complex plant-soil-animal interaction. Contrary to popular belief, stability of herbage yield and pasture uniformity are not necessarily the measure of success. The results presented here suggest that periodic oscillations in legume content and herbage yield may actually be an indication that the system is working well, i.e. that pasture grasses receive the full benefit of clover nitrogen fixation. Conversely, the absence of periodic oscillations may indicate that clover is not well suited to cope with the current environmental constraints and that consequently, the benefit of having clover in pasture is small.

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