Management of clover in grazed pastures: expectations, limitations and opportunities

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Abstract

The value of white clover as a component of New Zealand pastures is undeniable, but it is also widely recognised that clover has limitations as a pasture plant and that these can lead to inefficiencies in the performance of grass/clover associations. This paper identifies some of the limitations to optimising the contribution of clover in complex soil/pasture/animal systems, within the context of the expectations commonly held of clover. Limitations to exploiting the greater digestive efficiency and short-term intake rate of clover compared to grass when they are grown in a mixture include animal behaviour responses that sometimes impose a restriction on total daily intake of nutrients, and the fact that clover often constitutes less than 20% of the pasture. Nitrogen inputs and yield advantages are also restricted by the low clover content of pastures. A simulation model is used to analyse the co-existence of grass and clover as influenced by N dynamics. This model explains the basis for self-regulation by grass/clover mixtures of the amount of mineral N in the soil. Self-regulation minimises N losses from mixtures, but the dynamic response of grass and clover to N availability also means that there may only be limited scope for increasing the overall clover content, or decreasing the spatial heterogeneity in clover distribution, of a mixture. Managing grass/clover associations to realise the benefits of white clover therefore means manipulating a complex system, where the outcomes of manipulation depend as much on the response of the companion grass as on the response of the clover itself. Opportunities for attaining a higher clover content in pastures include: manipulating the preferences of animals for clover versus grass; spatially separating grass and clover within fields; increasing the metabolic efficiency of N fixation in clover; uncoupling the apparent link between rhizobium symbiosis and the N content of clover leaves; and modifying the stolon morphology of clover as a way of increasing clover presence in favourable microsites within the pasture.

Keywords: genetic improvement, grass/clover competition, grazing behaviour, intake, models, N fixation, nitrogen dynamics, nutritive value

Introduction

The productive features of white clover are well known, and it is easy to nominate the advantages that clover brings, or is perceived to bring, to a mixed pasture. It is also widely recognised, however, that clover has limitations as a pasture plant, and that these can lead to inefficiencies in the performance of grass/clover associations. Our aim is to identify some of the limitations to optimising the contribution of clover within the context of complex soil/pasture/animals systems. In doing so, we will attach considerable importance to the role of interactions between the grass and the clover in governing the performance of clover, and the balance of grass and clover, in mixtures. In discussing limitations, our intention is not to dismiss the advantages of clover as a pasture species, or devalue the role that clover plays in pastoral production systems in New Zealand. Rather, our premise is that by identifying more precisely the limitations which restrict our ability to capitalise on the benefits of clover in grazing systems, we are in a stronger position to pinpoint opportunities for research that can help overcome these limitations.

Management manipulation and germplasm improvement

Previous research and on-farm development has been spectacularly successful in raising the productivity of grass/clover pastures in New Zealand. For example, at the Ruakura No. 2 Dairy Unit, milk solids production per hectare increased by 250% between 1940 and 1970 (475 to 1190 kg per hectare) due to the effects of phosphatic fertiliser inputs, drainage, improvements in pasture species, and improved pasture management and utilisation (Bryant 1993). However, the contribution of germplasm improvements to this advance is small relative to the contribution of other inputs. For instance, during approximately the same period when 250% increases in milksolids output per hectare were being recorded at Ruakura (above), the rate of gain in the agronomic performance of clover through breeding was estimated (from diverse studies) to be about 30% (Caradus 1993; Woodfield & Caradus 1994).

The benefits of genetic improvement, and other management inputs, for yield of grass/clover mixtures have been quantified by Chapman et al. (1993) in a single experiment in New Zealand comparing lamb liveweight gain on pastures based on different clover genotypes, or receiving different rates of phosphatic fertiliser application (Table 1). Here, the introduction of an improved clover cultivar yielded a 12% increase in liveweight gain over pastures based on the resident clover ecotype, whereas fertiliser application gave an 80% increase compared to unfertilised pastures. These results were obtained using a variable stocking rate approach, and in this respect the experiment represented a test of the potential of cultivar introduction for improving animal performance. This experiment, and a theoretical analysis of the improvements in yield possible from manipulating attributes of clover, highlight one very important point: if the genetic merits of clover (or other pasture species) are to be realised in improved animal output, stocking density must be adjustable so that any additional herbage produced is utilised by animals. The theoretical analysis (Figure 1) compares the relationship between stocking density and yield of animal product per hectare for pastures based on a proposed increase in the efficiency of nitrogen fixation, as predicted by a computer model. This analysis clearly shows that the gains in animal yield that are theoretically available from manipulation of the efficiency of N fixation will not be captured if stocking density remains fixed at a low level. Exactly the same principle applies for other input manipulations, as in the work of Bryant (1993), cited above.

Table **1:** Main effects of introducing an improved clover cultivar (Grasslands Tahora), or applying phosphatic fertiliser (37 kg P/ha/yr), on lamb production from a hill pasture. Data are means for four years, collected from self-contained grazing systems.

	----- Pasture type -----		━ Fertiliser application ━	
	Resident	Grasslands Tahora-based	Unfertilised	+P fertiliser
Lamb liveweight gain (kg/ha/yr)	380	425	243	428
	P<0.05		P<0.001	

Expectations of clover in a pasture mixture

Pasture management and plant breeding strategies for improving the yield of animal product from pastures should be formulated to achieve an optimum balance of grass and clover in a mixture. But it is not clear what the optimum clover content of a pasture is. Various authors have speculated on what it might be (Martin 1960;

Figure 1: Effect of a theoretical increase in nitrogen fixation efficiency in white clover on the relationship between stock density and yield of animal product per hectare as predicted by a model of soil/plant/animal interaction (Schwinning & Parsons 1996a; 1996b). Nitrogen fixation is assumed to be either 60% (e=0.60) or 80% (e=0.8) as efficient as mineral N uptake, in terms of energy costs of assimilation.
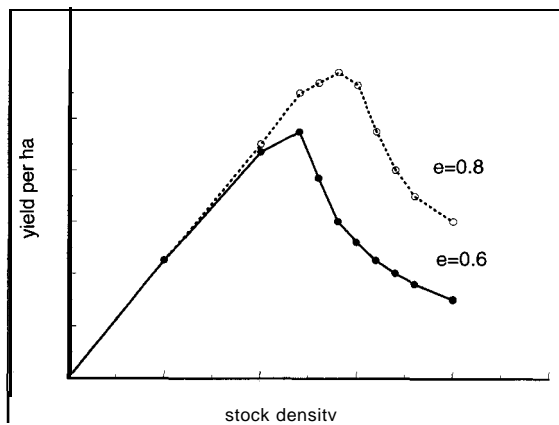
Curll 1982), but there have been no rigorous tests of their assumptions. Clearly, neither clover or grass monocultures are considered to provide optimum clover content because they are not commonly used in New Zealand agriculture (though pure grass swards are used extensively in other parts of the world, and monocultures of legumes such as lucerne are also common).

The optimum clover content is therefore some intermediate proportion, and we suggest the optimum will be a trade-off between the benefits that clover is expected to bring to a mixture, two of which are best realised when the clover content is high (i.e. greater nutritive value compared to grass, and N inputs and yield), and one of which is best realised when the clover content is low (i.e. low losses of N to the environment). The issue therefore is, how much can clover content in a pasture be increased to capture the benefits of nutritional value, N fixation and yield without compromising the environmental integrity of the grass/ *clover* system?

Another expectation is that an optimal grass/clover balance can be sustained over time, leading to predictable outputs of animal product and N from the system. In all of this, we need to ensure that our expectations of clover performance in mixtures are realistic. It is appropriate, therefore, to identify factors that limit our ability to harness the advantages of white clover to the maximum, within the context of our *expectations* of clover performance.

Limitations to capturing the benefits of clover

1. *Nutritional value*

It is widely accepted that clover is superior to grass, particularly to unfertilised (N) grass, as an animal feed. But it is important to identify factors that limit the realisation of that superiority. Much of the information on the nutritional value of clover comes from *indoor* feeding trials, and smaller benefits are seen in those remarkably few studies in *outdoor* grazing conditions in which the components of intake and grazing behaviour on pure legume versus pure grass monoculture diets have been measured. In comparing clover and grass, it is essential to compare 'like with like', and to distinguish between the benefits per unit of food eaten, i.e. the *efficiency* of digestion, and differences in the *amount* of grass and clover eaten, as these will be subject to different constraints in the field.

(i) *Efficiency of digestion*

Some of the most revealing information comes from studies where equal quantities of clover or N-fertilised grass with similar digestibilities have been fed to animals and fluxes of N within the digestive tract have been measured. These show a relatively small, c. 15%, advantage to clover in the quantity of (plant plus microbial) protein available for digestion in the small intestine. Data from experiments with sheep (Table 2) show that this difference is due to lower losses of N in the rumen and hence greater efficiency of digestion of protein in animals eating pure clover. However, other data, this time from studies with cattle, show that the efficiency of digestion of protein can be *lower* for animals eating pure clover compared to grass (Ulyatt et al. 1988), even though the *amount* of protein reaching the small intestine was again about 15% greater on the all-clover diet. In this case the difference in efficiency is explained by higher crude protein content of clover (up to 27% of plant dry matter) compared to grass (about 21%), and associated differences in the amount of protein degraded to ammonia in the rumen and subsequently converted to urea. Protein wastage in the rumen can be considerable when the intake of crude protein is high, and pure clover diets are more likely to lead to high protein intake than pure grass diets because of the high N content of clover leaves (see later).

(ii) *Amount eaten*

In indoor studies, animals are seen to have greater instantaneous intake rates (ir) of clover than of grass and this is associated with faster breakdown, digestion and passage of clover in the digestive

Table 2: Efficiency of digestion of pure ryegrass or pure white clover diets by sheep in indoor feeding experiments, where total intake of the two diets is the same and digestibility and crude protein levels are similar.

		Perennial ryegrass	White clover
Organic matter intake	g/day	800	800
OM digestibility	%	80.4	81.6
Nitrogen intake	g/day	37.8	35.2
Protein-N entering }	g/day	15.1	17.4
small intestine }	% of N intake	40.0	49.4

From Ulyatt (1981)

Table 3: Time spend grazing, intake rate, and total daily intake of sheep grazing perennial ryegrass or white clover monocultures held at constant 6 cm sward surface height.

	--- Dry ewes ---		-- Lactating ewes --	
	Grass	Clover	Grass	Clover
% time spent grazing	47.5	30.6	42.3	39.1
Intake rate (g DM/min)	2.8	3.7	4.0	5.3
Intake (kg DM/day)	1.9	1.6	2.5	2.9

From Penning et al. (1995c)

system compared to grass. In *outdoor* studies, intake rates from clover monocultures are again seen to be some 1.5 to 2 times those of fertilised grass (Penning et al. 1995c). However, outdoors, high intake rates are not synonymous with high total daily intake. Animals grazing clover have been seen to take more, but shorter meals (Penning et al. 1991). Total grazing time (gt) on clover is consistently less than on grass (Table 3) and so, in non-lactating animals in summer and autumn, total daily intakes (ir × gt) from clover are not consistently greater (in some cases actually less) than from pure grass (Penning et al. 1991; Penning et al. 1996).

The explanation for this is that animals may control their intake to maximise long-term 'fitness' (Newman et al. 1995) rather than to maximise their daily intake. This concept is well established in behavioural ecology (McNamara & Houston 1986; Mangel & Clark 1988), but has not been widely applied to agricultural systems. Hence , when time is not limiting, daily intakes of grass and clover are similar as in both cases animals may meet their nutrient requirements by adjusting time spent grazing. It may only be in situations where the available grazing time potentially restricts their capacity to achieve their required daily intake that animals benefit by eating clover, in that a given intake can be achieved in less time. This was seen in

the above study in spring, notably when heavily lactating ewes and twin lambs grazed short (<3 cm) swards (Penning et al. 1995c).

There are two further limitations to realising the nutritional benefits of clover compared to grass in practice. First, in mixed grass/clover swards, the nutritional benefits of clover are limited by the typically low clover content (<20%) of the sward. Animals may graze selectively for clover, but this only serves to keep clover contents low in both the sward and, ultimately, in the diet. Moreover, the energy costs associated with attempting to select a high clover diet may themselves restrict daily intake and its net value (Thornley et al. 1994; Parsons et al. 1994a). Second, even when clover constitutes a large proportion of the pasture, and is readily accessible, animals 'dilute' the proposed benefits of clover by also eating substantial quantities of grass. Sheep, cattle and goats offered a free choice between large adjacent monocultures of grass and of clover select a mixed diet (of some 70% clover in the case of sheep), even though a monospecific diet of clover is readily available at no additional foraging cost and would, by conventional wisdom, maximise the daily intake of nutrients (Newman et al. 1992; Penning et al. 1995a, b; Parsons et al. 1994b; Cosgrove et al. 1996; and see also Illius et al. 1992). This appears to contradict basic foraging theory, but there is increasing evidence that there is a nutritional basis for this desire for a mixed diet, for example a mixed diet may help maintain optimal osmolality in the rumen (Cooper et al. 1995). Therefore, the criteria by which humans assess 'optimal' feeding (e.g. maximise intake/growth rate) are not the same criteria by which animals assess optimal feeding strategy ('fitness'). In mixed swards in particular, where animals have a free choice, we may expect serious limitations in our ability to impose our own notions of optimality over and above those of the animal.

2. *Contribution of clover to N input and yield*

The capacity for N fixation is an important attribute of white clover. It may therefore seem bizarre to consider the limitations associated with N fixation as a source of N for pasture growth, but there are some important consequences to consider. First, the metabolic costs of nitrogen fixation are greater than those of nitrate uptake. Ryle et al.(1979) showed that the respiratory costs of N fixation were equivalent to 11–13% of daily gross photosynthesis and that the growth of pure clover dependent totally on nitrogen fixation was only 60% that of pure clover fed ample mineral nitrogen fertiliser. This difference in productivity is partly explained also

by a reduced shoot:root ratio in N fixing legumes (Arnott 1984). Second, even though legumes may readily switch from N fixation to nitrate uptake as mineral N availability increases, clover retains some 15% of total uptake of N via N fixation, to its metabolic cost, even at high N availability (Davidson & Robson 1985; 1986a; 1986b).

However, as was the case with nutritional value, the major limitation to clover's contribution to N input and yield is its current typically low content in pastures (typically <20% of total DM). Not only is the overall proportion low, but clover is also distributed patchily. Clover content is also subject to long-term fluctuations at the whole-field scale (Steele & Shannon 1982; Rickard & McBride 1986), leading to what have become known as 'good clover years' and 'clover crashes'. This spatial and temporal uncertainty feeds the perception of inadequacy (in the clover germplasm) and risk (in farming practice) that has lead to the widespread and sometimes excessive use of mineral N fertiliser in intensive agriculture in the UK and Netherlands. The argument for using mineral N is gaining strength in New Zealand, and is hard to refute on the basis of research and practical experience with use of N fertiliser in intensive productive systems (Barr 1996; Clark & Harris 1996).

Clearly, then, there is great scope for increasing the clover content of pastures from the current low average levels of 10–20%. But we should be careful in our expectations of the increases in animal production that might result from raising clover content. A comparison in the UK of an optimally grazed grass/ clover mixture (circa 20% clover) with a clover monoculture, and a N-fertilised grass monoculture showed that animal production per ha from the mixture was 60–70% of that from the N-fertilised grass monoculture, and that even when the clover content of the pasture was maximal (i.e. a monoculture), yield increased to only 73% of that from N-fertilised grass (Orr et al. 1990; 1995). One major factor restricting animal yield from the clover monoculture, in the UK, was poor clover growth in Spring. New Zealand typically has milder winters and springs, but even with more favourable climatic conditions, white clover monoculture herbage yields in New Zealand are only about 75% of those from N-fertilised grass swards (Harris & Hoglund 1977). Optimistically, then, we can expect ryegrass/white clover mixtures with a high white clover content to approach the yields of pure grass swards supplied with adequate mineral N. There is a clear opportunity for research to develop the technologies that would enable these higher clover contents to be widely achieved.

3. Environmental impact

The above study also highlights that realising such an increase in performance in clover-based systems would be at an environmental cost. As can be seen in Figure 2, the swards of high (100%) clover content led to concentrations of nitrates in soil water (potential for leaching) that increased rapidly to >60 mg N/l, approaching (within 18 months of establishment) that seen below the heavily (indeed excessively) fertilised pure grass. Only unfertilised grass, and the grass/clover swards (with <20% clover) sustained low concentrations of N in soil water.

It is not the aim of this paper to argue the virtues of fertilised grass versus grass/clover, but to attempt an objective assessment of the prospects and limitations to modifying clover-based systems. Studies in the UK suggest that grass and grass/clover systems may have very similar potential environmental impacts when compared at the same level of animal output per ha (Schofield & Tyson 1992). Thus the environmental argument should not be used to advocate either system unconditionally. In conclusion, as is becoming increasingly accepted, the benign environmental image of grass/clover is not a feature of the clover itself, but of the two species growing together. Opportunities for improvement will not be realised without attempting to understand the very nature of how the two species live together at all (their co-existence) and what the consequences of this are.

4. Co-existence and self-regulation — its consequences and limitations

It is widely assumed that mixtures of grasses and legumes have a capacity to self-regulate the N-cycle and so achieve potentially better ratios of yield to N loss than fertilised grass. As pointed out by Scholfield et al. (1996) few studies have explored this hypothesis, even theoretically, as few models of soil/plant/animal interaction consider the mechanisms of N fixation and their spatial and temporal dynamics in grazed grass and legume communities. Self-regulation is understandably regarded as a beneficial opportunity, but it also potentially imposes some limitations to increasing clover presence in a mixture.

A recent model (Thornley et al. 1995; Schwinning & Parsons 1996a; 1996b) explores the basis of co-existence of grasses and legumes in grazed pastures and its implications. In the model, the capacity to co-exist is based on a competitive trade-off in which clover has the

Figure 2: Nitrate-nitrogen concentration of soil solution at 60 cm depth under an unfertilised grass monoculture (■—■), a grass monoculture receiving 420 kg N/ha/year (0- • -O), an unfertilised clover monoculture (●—●), and an unfertilised grass/clover mixture (◆—◆). From MacDuff et al. (1990).
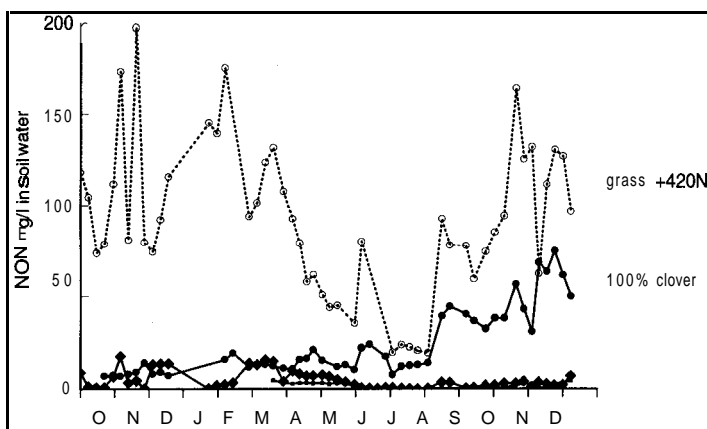
advantage at low mineral N by virtue of its capacity for N fixation, and grass has the advantage at high mineral N, by virtue of the reduced costs of N uptake compared to N fixation (see section 2, above) and greater competitive ability for C fixation. During periods of active clover growth, clover will enrich soil N and stimulate grass growth. During periods of grass dominance, however, grass will draw down soil mineral N. Thus the two species co-exist by generating between them a soil mineral N content that balances their competitive advantages. Analysis of this system shows that the interaction between the species is not one of 'competition' but 'exploitation' and this goes a long way to explaining the difficulties and limitations in manipulating grass/legume mixtures and their spatial and temporal unpredictability.

Firstly, because co-existence depends on the 'exploitation' of clover N fixation by grass (akin to a 'predator-prey' interaction), then attempts to increase the competitive ability of clover (the 'prey'), can actually lead to at least as much increase in grass (the 'predator'). In population theory this is known as the 'paradox of enrichment' (e.g. see Rosenzweig 1977). There may therefore be only limited prospects for increasing the percentage of clover in a mixture Secondly, the model also demonstrates that, as in classic predator/prey interactions, the grass/legume association may be prone to oscillate-giving long-term cycles of grass and legume dominance of some 3 to 5 years, as observed in practice If, as the model suggests, long-term cycles of legume content, and patchy distribution of clover, are intrinsic properties of grass/legume systems, it is not going to be straightforward to dampen the spatial or year to year

fluctuations in clover content either by using alternative cultivars or by management intervention. Thirdly, although the model does illustrate the capacity for self-regulation of the soil mineral N environment by grass/legume associations, it proposes that in all cases increases in yield brought about by increasing clover content are seen to be synonymous with increasing N loss.

Opportunities

Manipulating grass/legume associations to realise the genetic potential of clover clearly means manipulating the balance of a complex system that depends as much on the contribution of the companion grass as on the clover *per se*. This will be affected by the grazing preferences of animals, the cycling of nitrogen patchily across the pasture, and so on the impact of heterogeneous soil processes. If we are going to answer the fundamental question of what is the optimal clover content, and how are we going to achieve it, research must be organised toward a longer-term commitment to critical experiments and models of these complex soil/plant/animal interactions. For this to be successful, and so to identify the real opportunities, it will be essential to transcend 'divisions' in research and to positively encourage interdisciplinary teams. Fundamental and theoretical studies are particularly valuable to focus expensive practical experiments, notably in situations where the practical outcome of manipulating the system is counter-intuitive. 'Practical relevance' should be a way to judge the outcome of research, and not the method applied to achieve it.

1. Manipulating the preference of herbivores

Opportunities exist for modifying the legume content of pastures in the context of the preferences of herbivores. The first most important opportunity lies perhaps in recognising that despite the stated nutritional advantages of clover, the optimal clover content in the diet from the animals perspective may be just 60–70%. If this is widely the case, the clover content of swards may not need to be increased so much, in an effort to achieve maximum performance per animal, that the adverse environmental impact of the high legume sward is encountered. Second, the strong, albeit partial preference for a diet of even 60–70% clover shown by sheep (and similarly by cattle and goats) is widely and correctly assumed to limit the clover content of swards. It is intuitive that decreasing the preference of animals for clover will increase the proportion of clover in the sward. However, it is counter intuitive that animals that show a low preference for one species, by increasing the amount of that species in the sward, actually end up

eating a larger proportion of that species in their diet than animals that showed a strong preference for it in the first place (Parsons et al. 1991). This is referred to as the 'paradox of imprudence' (Slobodkin 1974). Thus, if it were possible to reduce the preference for clover, this could increase the total amount of vegetation grown, and its nutritive value.

Modifying the preference of animals may prove difficult. However, in a sense, this is what different grazing methods (e.g. rotational grazing, set stocking) achieve because the defoliation patterns associated with them mean the relative grazing pressure exerted on grass and legume can differ. Short-term 'windows' of opportunity for clover growth are therefore available under rotational management if environmental conditions allow clover to exploit them. However, strategic changes to grazing method cannot alter the long-term outcomes of grass/clover interactions determined by soil N availability.

A potentially more powerful way of equalising grazing pressure on clover and grass, and managing the effects of grass/clover competition, is to spatially separate the grass and clover within a field. Rather than trying to modify animal preferences, this approach could *use* their preferences to present area ratios of each component that better match the animal's perspective of what constitutes optimal grass/clover balance. These same animal preferences will then ensure that neither species is grazed to extinction. Spatial separation would neatly remove the complex competitive interaction between grass and clover altogether, and present appealing opportunities for targeting management inputs to the needs of individual pasture components without compromising the performance of associated species. On the downside, however, it would also remove some of the N self-regulation capacity of an intermingled mixture, and increase the potential for total N losses, particularly if a clover monoculture was grown alongside a fertilised grass monoculture (see Figure 2).

2. Modifying physiological and morphological attributes of clover

Here we draw heavily on our recent soil/plant/animal model (Schwinning & Parsons 1996a; 1996b) as it is one of few tools we have to consider the knock-on consequences of manipulating one aspect of this spatially and temporally complex system on the performance of the soil/plant/animal system as a whole. First, although the model proposes that to improve the competitive ability of clover, or its contribution to N inputs, can lead to as much increase in grass as in clover (and so little increase in clover %) it is essential to appreciate that virtually all these scenarios *do* increase the yield per ha and the nutritive value of the grass/clover

association (Table 4). It is a trivial but important point that the aim therefore is not necessarily to increase clover *percentage*, but its contribution to C and N flux. Failure to recognise this may mean we mistakenly reject scenarios that did not increase % clover *per se*.

Table 4: Predicted effects of manipulating physiological attributes of white clover on yield, clover content, grass/clover balance and N losses of a grass/clover pasture. 'Default' simulation is based on published data for competitive ability and N fixation attributes of existing white clover cultivars. Based on a model of grass/clover dynamics (Schwinning & Parsons 1996a; 1996b).

	Pasture yield (g C/m^2/d)	Clover %	Total biomass -- (g C/m^2) -- Clover	Grass	N losses (g N/m^2/d)
Default	0.96 (100)	51	132	126	0.223
Increasing competitive ability of clover	1.14 (118)	51	161	156	0.265
Increasing efficiency of N fixation	1.18 (122)	46	126	145	0.273
Decreasing retention of N fixation	1.03 (107)	64	154	85	0.238

Second, models such as this suggest specifically how clover's N inputs, via N fixation, might be manipulated to most advantage. The aim should not be simply to increase N fixation, but specifically to increase the metabolic *efficiency* of N fixation, that is the rate of N fixation per unit substrate C, or the N fixed per unit biomass. As mineral N rises, following an increase in clover presence, it is important that the relatively inefficient fixation of N does not compete for substrates with the more efficient uptake of mineral N in the legume. Consequently, the model also proposes that benefits arise by modifying the characteristics of N fixation in response to mineral N so that the specific rate of N fixation falls more rapidly as mineral N increases, and for less N fixation to remain engaged. This again may seem counter-intuitive but it is consistent with the ecological perspective that few if any legumes have evolved without the capacity to take up mineral N, as to fail to do this would be a major disadvantage. The model proposes that unless legumes switch faster or more extensively to mineral N uptake, their contribution to higher fertility, higher yielding associations will be limited. However it is equally important that, should mineral N fall subsequently, clover must be able to re-engage N fixation. We may yet find that this is precisely why clover has evolved a strategy to retain some N fixing capacity during periods of high mineral N availability, and we may yet therefore have to live with the consequent inefficiencies.

Thirdly, it is widely seen that the consistently high N content in the leaves of clover is a major benefit, in its nutrient value and in photosynthetic productivity. But there is some evidence this may also be regarded as a limitation to growth. *Non-legumes* growing in low N environments sacrifice high N contents in leaves, allowing N contents to fall. This permits the creation of a far greater leaf area (and so light capture) than would be the case if all plants, like legumes, restricted leaf growth to that which could be produced at high, 5% N content. There is clearly a complex trade-off between the benefits of greater leaf area at low N (and so low carboxylase content) and a low leaf area at a high N (carboxylase) content. The high N content seen in the leaves of legumes with active rhizobia in their nodules is generally seen as evidence of a supply of N sufficient to meet the requirements for maximal leaf growth in the legume. However, legumes with ineffective nodules have also been observed to have leaves with high N content, but with very low rates of leaf growth and low DM production (Mytton *pers. comm.*; Wilkins 1996). This suggests that the rhizobial symbiosis is controlling (forcing high) the N content of the leaves, without meeting the requirements for maximal leaf growth, and so restricting DM production. A major opportunity lies in using non-fixing legumes as a tool to understand what it is about the rhizobium/ legume association that constrains the plant to producing leaves at a high N content. Non-nodulated, non N-fixing legumes have been seen to have lower leaf N contents but greater DM production. The critical test is whether reducing N content of leaves consistently permits greater DM production. Moreover, our current mathematical models suggest that without some capacity for N fixation, or some other species specific advantage, it is questionable if clover could co-exist with grass.

But it has been more widely proposed that legumes with a higher C:N ratio (lower N content) may offer opportunities to increase legume dry matter production, as well as offering greater scope, in the increased and more flexible supply of Carbon, for self-regulation of the N cycle in pastures. Despite their consequent lower crude protein content, these may still offer nutritional advantages (lower fibre content, rapid breakdown and passage in rumen).

Finally, much attention has been focused on modifying the morphology of legumes. Current research emphasises the role of branching and the clonal structure of clover populations in pastures (Brock & Hay 1996), and the opportunities for using intraspecific variation in branching propensity and internode length as a way of breaking the negative association between leaf size and stolon population density and improving the persistence

of larger-leaved types under intensive grazing (Caradus & Chapman 1996). However, the role that branching plays in governing the amount and spatial distribution of clover in a mixed pasture is not fully understood. Theoretically, it has been shown that the existence of patches within a pasture is not in itself evidence that the clover content is limited by the capacity of clover to spread laterally (Schwinning & Parsons 1996b). Rather, the patchiness can be shown to be a spatial expression of the interaction between clover and grass via the N cycle. In the heterogeneous soil N environment that arises in a grazed pasture, clover distribution may be limited by the rate at which invadable (low N grass) sites become available (Schwinning & Parsons 1996b). The greater opportunity may therefore lie in maximising the capacity of clover to establish and consolidate its presence in these areas, and studies of clonal integration and the control of branching are very important in this context.

3. *Tactical use of N fertiliser*

Although all the physiological evidence suggests that nitrogen fertiliser stimulates grass growth more than it stimulates clover growth (and so decreases the *relative* contribution of clover) it is not uncommon, under-standably, for farmers to apply mineral nitrogen at times when clover is not contributing adequately to N inputs. In this way, the 'tactical' use of nitrogen could be seen as helping to sustain a clover-based grassland agriculture, but clearly it is important to minimise the extent to which the fertiliser input itself reduces the long-term contribution of clover, or at best simply substitutes for clover N fixation. Harris & Clark (1996) demonstrate how close-grazing managements can reduce competition between grass and the clover component, following nitrogen input, suggesting that some clover content, if not fixation, can be retained. Here we concentrate on other opportunities, and pitfalls, in tactical N use.

In practical terms, the impact of N fertiliser on the overall grass/legume balance can be minimised by restricting nitrogen input to a limited number of areas on the farm, stimulating growth from what may become predominantly all grass areas, in times of feed shortage (or in some regions specifically to create 'surplus' for grass conservation/silage) while sustaining elsewhere a predominantly unfertilised (N) grass/legume system. This *spatial* solution to the tactical use of N is arguably preferable to attempts at a tactical *timing* of N inputs. Clearly, even in all grass systems, applying N fertiliser when mineral N contents of the soil are relatively high, and so N is not the major limitation to growth, is a recipe for financial as well as environmental loss. In all-grass systems this means avoiding N inputs during dry periods or in late season as the potential for growth falls

relative to the potential for N loss by leaching and run-off. Techniques for the rapid field testing of soil mineral N availability offer the chance to make informed decisions about tactical N use (e.g. see Scholfield & Titchen 1995). But in grass/clover mixtures, there are more complications.

Our recent model (Schwinning & Parsons 1996a; 1996b) demonstrated how the grass/legume interaction may be prone to fluctuations in species composition particularly following urine N deposition. However, the model also reveals that the heterogeneity (patchiness) brought about by spatially random urine deposition keeps different areas in a field 'out of phase' with respect to local grass or legume dominance. So, despite local oscillations in N status and species content, the patchiness actually dampens the fluctuations in clover presence at the field scale. Patchiness may therefore be shown to be beneficial to increasing long-term stability, though other sources of disturbance to clover growth may still lead to long-term fluctuations in clover content at the field scale, as are observed in practice. The work highlights that because these fluctuations are in part an intrinsic property of the system, attempts to intervene in what appear to be 'bad' clover years may actually exacerbate the fluctuations in clover content – decreasing its long-term predictability. This would arise because tactical N inputs, for example, help reset all patches 'in phase' and so the patch scale fluctuations become apparent at the field scale. It follows that clover content may in some years be low, not because clover is inadequate, but because that time happens to be a period of relatively high N, grass dominance. Once again, simple, on farm monitoring of soil mineral N status offers the opportunity for an informed decision regarding tactical N use.

Conclusions

Mixtures of grass/clover will continue to offer a valuable, low-cost and productive alternative to fertilised grass. With prospective increases in clover content, it should be possible with a grass/clover association to narrow the gap in yield between the two systems. There is no room, however, for emotional views – neither the nutritional benefits nor the benign environmental image of grass/legume system should be overstated. And in many cases, and in many ways, the benefits arising from improving clover are actually achieved via their impact on the associated grass. In terms of environ-mental impact, as yet there is little reason to believe that either system is better or worse than the other at the same level of productivity (Scholefield & Tyson 1992). But, in clover based systems, there is reason to believe that by virtue of the exploitation of fixed N by

grass, the system offers more chance for a self-regulation of the N cycle. The fact that clover contents may not need to increase above 50–60% to meet nutritional requirements of animals, would be very important in offering the prospect of retaining a large quantity of grass to respond to, and so control, fluctuations in mineral N availability and so the consequent release of N to the environment.

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References

Arnott, R.A. 1984. An analysis of the uninterrupted growth of white clover swards receiving either biologically fixed nitrogen or nitrate solution. *Grass and Forage Science 39:* 305–310.

Barr, S.J. 1996. A farmer's experience with high N fertiliser inputs on grass/clover pastures. *Agronomy Society of New Zealand Special Publication No. 11/Grassland Research and Practice Series No. 6:* 103–106.

Bryant, A. 1993. Lifting our production targets. *Proceedings of the Ruakura Dairy Farmers Conference 45:* 6–11.

Brock, J.L.; Hay, M.J.M. 1996. A review of the role of grazing management on the growth and performance of white clover cultivars in lowland New Zealand pastures. *Agronomy Society of New Zealand Special Publication No. 11/Grassland Research and Practice Series No. 6:* 65–70.

Caradus, J.R. 1993. Progress in white clover agronomic performance through breeding. *Proceedings of the International Grasslands Congress 17:* 396–397.

Caradus, J.R.; Chapman, D.F. 1996. Selection for heritability of stolon characteristics in two cultivars of white clover. *Crop Science 36:* (in press).

Chapman, D.F.; Mackay, A.D.; Devantier, B.P.; Dymock, N. 1993. Impact of white clover cultivars on nitrogen fixation and livestock production in a New Zealand hill pasture. *Proceedings of the International Grassland Congress 17:* 420–421.

Clark, D.A.; Harris, S.L. 1996. White clover or nitrogen fertiliser for dairying. *Agronomy Society of New Zealand Special Publication No. 11/Grassland Research and Practice Series No. 6:* 107–114.

Cooper, S.D.B.; Kyriazakis, I.; Nolan, J.V. 1995. Diet selection of sheep: the role of the rumen environment in the selection of a diet from two feeds that differ in their energy density. *British Journal of Nutrition 74:* 39–54.

Cosgrove, G.P.; Anderson, C.B.; Fletcher, R.H. 1996. Do cattle exhibit a preference for white clover? *Agronomy Society of New Zealand Special Publication No. 11/Grassland Research and Practice Series No. 6:* 83–86.

Curll, M.L. 1982. The effects of grazing by set-stocked sheep on a perennial ryegrass/white clover pasture. *PhD thesis, University of Reading.*

Davidson, I.A.; Robson, M.J. 1985. Effects of nitrogen supply on the grass and clover components of simulated mixed swards grown under favourable environmental conditions. *Annals of Botany 55:* 697–703.

Davidson, I.A.; Robson, M.J. 1986a. Effects of temperature and nitrogen supply on the growth of perennial ryegrass and white clover. 1. Carbon and nitrogen economies of mixed swards at low temperature. *Annals of Botany 57:* 697–708.

Davidson, I.A.; Robson, M.J. 1986b. Effects of temperature and nitrogen supply on the growth of perennial ryegrass and white clover. Comparison of monocultures and mixed swards. *Annals of Botany 57:* 709–719.

Harris, S.L.; Clark, D.A.; Waugh, C.D.; Clarkson, F.H. 1996. Nitrogen fertiliser effects on white clover in dairy pastures. *Agronomy Society of New Zealand Special Publication No. 11/Grassland Research and Practice Series No. 6:* 119–124.

Harris, W.; Hoglund, J.H. 1977. Influences of seasonal growth periodicity and N-fixation on competitive combining ability of grasses and legumes. *Proceedings International Grassland Congress 13:* 239–243.

Illius, A.W.; Clark, D.A.; Hodgson, J. 1992. Discrimination and patch choice by sheep grazing grass-clover swards. *Journal of Animal Ecology 61:* 183–194.

MacDuff, J.H.; Jarvis, S.C.; Roberts, D.H. 1990. Nitrates*:* leaching from grazed grassland systems. pp. 405–410. *In:* Calvet, R. (ed.). *Nitrates, agriculture, eau.* INRA, Paris.

Mangel, M.; Clark, C.W. 1988. *Dynamic Modelling in Behavioural Ecology.* Princetown University Press, Princetown, NJ.

Martin, T.W. 1960. The role of white clover in grassland. *Herbage abstracts 30:* 159–164.

McNamara; Houston, A.I. 1986. The common currency for behavioural decisions. *American Naturalist 127:* 358–378.

Newman, J.A.; Parsons, A.J.; Harvey, A. 1992. Not all sheep prefer clover*:* diet selection revisited. *Journal of Agricultural Science 119:* 275–283.

Newman, J.A.; Parsons, A.J.; Thornley, J.H.M.; Penning, P.D.; Krebs, J.A. 1995. Optimal diet selection by a generalist grazing herbivore. *Functional Ecology 9:* 255–268.

Orr, R.J.; Parsons, A.J.; Penning, P.D.; Treacher, T.T. 1990. Sward composition, animal performance and the potential production of grass/white clover swards continuously stocked with sheep. *Grass and Forage Science 45:* 325–336.

Orr, R.J.; Penning, P.D.; Parsons, A.J.; Champion, R.A. 1995. Herbage intake and N excretion by sheep grazing monocultures or a mixture of grass and white clover. *Grass and Forage Science 50:* 31–40.

Penning, P.D.; Rook, A.J.; Orr, R.J. 1991. Patterns of ingestive behaviour of sheep continuously stocked on monocultures of ryegrass or white clover. *Applied Animal Behavioural Science 31:* 237–250.

Penning, P.D.; Parsons, A.J.; Orr, R.J.; Harvey, A.; Yarrow, N. 1995a. Dietary preferences of heifers for grass or clover, with and without romensin slow-release anti-bloat boluses. *Animal Science* (in press).

Penning, P.D.; Newman, J.A.; Parsons, A.J.; Harvey, A.; Orr, R.J. 1995b. The preference of adult sheep and goats grazing ryegrass and white clover. Proceedings of the 4th International Symposium on the Nutrition of Herbivores, Clermont-Ferrand. *Annales Zootech 44, Suppl. 113.*

Penning, P.D.; Parsons, A.J.; Orr, R.J.; Harvey, A.; Champion, R.A. 1995c. Intake and behaviour responses by sheep, in different physiological states, when grazing monocultures of grass or white clover. *Applied Animal Behaviour Science 45*: 63–78.

Parsons, A.J.; Harvey, A.; Johnson, I.R. 1991. Plant-animal interactions in a continuously grazed mixture. 2. The role of differences in the physiology of plant growth and of selective grazing on the performance and stability of species in a mixture. *Journal of Applied Ecology 28:* 635–658.

Parsons, A.J.; Thornley, J.H.M.; Newman, J.A.; Penning, P.D. 1994a. A mechanistic model of some physical determinants of intake rate and diet selection in a two species temperate grassland sward. *Functional Ecology 8:* 187–204.

Parsons, A.J.; Newman, J.A.; Penning, P.D.; Harvey, A.; Orr, R.J. 1994b. Diet preference of sheep: effects of recent diet, physiological state and species abundance. *Journal of Animal Ecology 63:* 465–478.

Rickard, D.S.; McBride, S.D. 1986. Irrigated and non-irrigated pasture production at Winchmore. *Technical Report 21. Winchmore Irrigation Research Station.*

Rosenzweig, M.L. 1977. Aspects of biological exploitation. *Quarterly Review of Biology 52:* 371–380.

Ryle, G.J.A.; Powell, C.E.; Gordon, A.J. 1979. The respiratory costs of nitrogen fixation in Soybean, Cowpea, and white clover. *Journal of Experimental Botany 30:* 145–153.

Scholfield, D.; Tyson, K.C. 1992. Comparing the levels of nitrate leaching from grass/clover and N fertilised grass swards grazed with beef cattle. *Proceedings of the European Grassland Federation. 14th General Meeting, Lahti, Finland 1992:* 530–533.

Scholfield, D.; Titchen, N.M. 1995. Development of a rapid field test for soil mineral nitrogen and its application to grazed grassland. *Soil Use and Management 11:* 33–43.

Scholfield, D.; Lockyer, D.R.; Ledgard, S.F. 1996. The simulation of N-fixation by white clover within a model describing N-flows in grazed grassland. Abstract, AFRC Modellers Group Workshop, 1995. *Journal of Agricultural Science* (in press).

Schwinning, S.; Parsons, A.J. 1996a. Analysis of the co-existence mechanisms for grasses and legumes in grazing systems. *Journal of Ecology* (in review).

Schwinning, S.; Parsons, A.J. 1996b. The population dynamics of stoloniferous N-fixing legumes in mixed pasture with grass: *Journal of Ecology* (in review).

Slobodkin, L.B. 1974. Prudent predation does not require group selection. *American Naturalist 108:* 665–678.

Steele, K.W.; Shannon, P. 1982. Concepts relating to the nitrogen economy of a Northland intensive beef farm. pp. 85–89. *In:* Gandar, P. (ed.). *Nitrogen Balances in NZ Ecosystems.* DSIR, NZ.

Thornley, J.H.M.; Parsons, A.J.; Newman, J.A.; Penning, P.D. 1994. A cost-benefit model of grazing intake and diet selection in a two-species temperate grassland sward. *Functional Ecology 8:* 5–16.

Thornley, J.H.M.; Bergelson, J.; Parsons, A.J. 1995. Complex dynamics in a carbon-nitrogen model of a grass-legume pasture. *Annals of Botany 75:* 79–94.

Ulyatt, M.J. 1981. The feeding value of herbage: Can it be improved? *New Zealand Journal of Agricultural Science 15:* 200–205.

Ulyatt, M.J.; Thomson, D.J.; Beever, D.E.; Evans, R.T.; Haines, M.J. 1988. The digestion of perennial ryegrass (*Lolium perenne* L. cv. Melle) and white clover (*Trifolium repens* L. cv. Blanca) by grazing cattle. *British Journal of Nutrition 60:* 137–149.

Wilkins, R.J. 1996. Improved technology for production efficiency and utilisation efficiency. *In:* Pollot, G.E. (ed.). *Grassland into the 21st Century. British Grassland Society Occasional Symposium No. 29:* 210–224.

Woodfield, D.R.; Caradus, J.R. 1994. Genetic improvement in white clover representing six decades of plant breeding. *Crop Science 34:* 1205–1213.

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