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Biological Nitrogen Fixation in Upland and Marginal Areas of the U.K [and Discussion]

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Biological nitrogen fixation in upland and marginal areas of the U.K.

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The limitation of pasture, and hence livestock production, in the uplands of the United Kingdom by lack of available soil N is described. It is shown that fixation of 100–150 kg N ha^{-1} annually by white clover (*Trifolium repens*) is the key to sustained pasture improvement and to economically viable production systems so making agriculture less marginal in these areas. Some results of research on the nutrient, microbial and management requirements to establish and maintain upland pastures containing at least 25% clover dry matter (d.m.) in the total herbage d.m. production in spring are illustrated. Enhanced N_2 fixation by white clover in upland agriculture will depend on increases in efficiency due to selection of rhizobia and rigid matching of them with clover genotype and the environment, on extension of the season of fixation by choice of clover with low-temperature thresholds and by carefully controlled grazing of the swards, and on extension of the area of improved pasture. The potential for the latter alone is considerable since improvement of an additional 10% of the better upland soils by establishment of existing varieties of white clover and strains of *Rhizobium* would result in fixation of approximately 50 kt N annually, worth £20 M at today's fertilizer prices.

1. Introduction

The aim of this paper is to indicate the role and place of biological N_2 fixation in upland and marginal areas of the U.K. with major emphasis on recent work carried out at the Hill Farming Research Organisation (H.F.R.O.). Attention is directed solely at land that is marginal in the sense of agricultural production, and no attempt is made to discuss areas that might be described as marginal in the non-agricultural sense e.g. road verges, hedgerows, mine-spoil heaps and unutilized wet bogs.

Although the uplands constitute about one-third of the land area available for agriculture in the U.K. about 4 M ha of which are rough grazings (unimproved native pastures), they produce only 7% of the nation's gross agricultural product in mainly livestock enterprises (Cunningham 1980). Pasture growth, and hence animal production, is limited biologically by unfavourable climate, site, soil, vegetation and utilization system (Floate 1977; H.F.R.O. 1979). In particular, upland soils are acid and low in available nutrients (Floate 1977). Because of this and because of high rates of leaching, low temperatures and small numbers of decomposer organisms, organic matter (o.m.) accumulates either within the profile or on the soil surface, leading to peat production, the extent of which increases with altitude and with rainfall. The rates of o.m. decomposition and nutrient mineralization are slow, which leads to the paradoxical situation that, while the rooting zone of upland soils possesses high total amounts of N (10 t ha^{-1}) and phosphorus (2 t ha^{-1}), little is available for uptake by plants. Thus, lack of available N is a major limiting factor to pasture growth. For example, the average annual production of herbage dry matter for an *Agrostis–Festuca* sward growing on a brown earth soil (pH 4.8) at 200 m altitude in the east of Scotland is 2.5 t ha^{-1}, but with more N this can be doubled to 5 t ha^{-1}, i.e. to the average annual growth limit set by temperature (Newbould 1981).

A feature of much of the agriculture in the uplands, but especially hill sheep farming, is that the lack of N cannot be made up by annual additions of fertilizer N since the levels of production cannot sustain the annual cost. Application of 200 kg N ha^{-1} annually, plus maintenance fertilizer, to a grass sward producing 5 t d.m. costs £88 while a grass–white clover sward producing 4 t d.m. can be maintained for about £16 annually. Thus, attention focuses on the possibility of adding to the supply of available nitrogen from biological N_2 fixation, especially by white clover.

Table 1. The sources and range of biological N_2 fixation in (*a*) the rough grazings and (*b*) improved pastures of the uplands

source	annual fixation / kg N ha^{-1}	references
	(*a*) *rough grazings*	
free-living microorganisms		
Clostridium sp., *Azotobacter* sp.	1–13	Sprent (1979), Granhall (1981)
cyanobacteria (e.g. *Nostoc* sp.)	1–26	Lockyer & Cowling (1977)
lichens	1–26	Hitch & Stewart (1973)
non-leguminous plants and root associations		
Alnus glutinosa	15–28	Bond (1972), Akkermans & van Dijk (1976)
Myrica gale	30	Sprent *et al.* (1978)
Calluna vulgaris	trace	Bond & Wheeler (1980)
Erica cinerea	trace	Skeffington & Bradshaw (1980)
Agrostis tenuis – Festuca rubra	3	Skeffington & Bradshaw (1980)
Blanket bog (Moor House)	0.5–32	Martin & Holding (1978)
legumes		
Ulex europaeus	26	Skeffington & Bradshaw (1980)
Sarothamnus scoparius	30–145	Dancer *et al.* (1977), Sprent (1979)
Medicago lupulina, *Trifolium repens*, *Trifolium campestre*, *Lotus corniculatus*	10–30	Haystead (1981)
	(*b*) *Improved pastures*	
ryegrass – white clover		
Wales: mineral soil	90	Munro & Davies (1974)
peaty podzol	98	Munro & Davies (1974)
Scotland: brown earth	100	Haystead & Lowe (1977)
brown earth	125	Newbould & Haystead (1978)
deep peat	125	Newbould & Haystead (1978)
three soils	81	see table 2.
Lotus uliginosus	40–60	Wedderburn (1980)

2. Biological N_2 fixation

The main sources of biological N_2 fixation in the uplands and some estimates of the amounts of N fixed are shown in table 1.

(*a*) *Rough grazings*

The values are approximate only since not all are assessed in the uplands and most are determined from measures of acetylene reduction with the standard conversion factor (3:1). The uncertainties of this procedure have been well described by Masterson & Murphy (1976) and

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Haystead (1981). Moreover, the high values shown for non-leguminous fixation are for special cases with groves of trees and are not truly applicable to sparse, scrubby upland rough grazings. It is probably more realistic to estimate that free-living, associative and non-leguminous symbionts in U.K. rough grazings contribute not more than 5–10 kg N ha^{-1} annually by biological fixation. Wild white clover and medicks, which occur at low density in acid grassland when the pH of the soil is about 5.2, are estimated to fix no more than 30 kg N ha^{-1} annually.

Table 2. Estimated contribution of white clover to herbage production and the N economy of improved upland pastures in the U.K. and New Zealand

annual herbage production, N uptake and fixation/(kg ha^{-1})

soil (vegetation type)	indigenous† d.m.	N (%)	N uptake	ryegrass – white clover‡ d.m. grass	d.m. clover	% clover	N uptake	N fixation	fixation efficiency kg N t^{-1} clover d.m.
United Kingdom									
brown earth (acid grassland)	2500	2.0	50	3012	1066	26	97	47	44
wet peaty podzol (grass heath)	1500	1.75	26	2522	1633	39	118	92	56
deep peat (blanket bog)	1400	1.2	16.8	3076	1190	28	121	104	87
			mean...	**2870**	**1296**	**31**		**81**	**62**
New Zealand§									
nine sites			mean...	**8400**	**3130**	**27**		**185**	**63**

† Estimated average yields and N content (H.F.R.O. 1979).
‡ Measured total in 1977 for three cuts of swards in second harvest year of *Rhizobium* – white clover trials in west of Scotland (J. Frame, personal communication 1980; Newbould *et al.* 1981).
§ Hoglund *et al.* (1979).

(*b*) *Improved pastures*

There is little published information; the data of Munro & Davies (1974) come from assessments of N uptake for grass-only and grass–clover swards, and those of Newbould & Haystead (1978) are from integrations of acetylene reduction data taken at monthly intervals and using the standard conversion factor (see §3*a*(iv)); only the data of Haystead & Lowe (1977) are based on calibrations with ^{15}N uptake from small amounts of labelled fertilizer.

The figure of 81 kg N ha^{-1} annually was estimated for three swards established by the West of Scotland Agricultural College as part of the national series of *Rhizobium*–white clover trials (Newbould *et al.* 1981). The method of calculation of the data in table 2, which was to subtract N uptake (indigenous) from N uptake (ryegrass–white clover), takes no account of any increased mineralization of soil N that may follow the addition of lime and phosphate, of other inputs or losses of N, or of the proportion of fixed N in the roots or in the rhizosphere. Nevertheless, it provides an approximate basis for comparison with data recently collected in New Zealand (Hoglund *et al.* 1979). It also illustrates, from a comparison of the three upland soils, the important part that the supply of soil N (mineralization) may play in determining biological N_2 fixation by white clover.

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3. Nitrogen fixation and transfer by white clover

Work at H.F.R.O. has concentrated on the nutrient and microbial requirements to establish and maintain white clover in hill pastures, assessments of the amount of N fixed, and the effects of defoliation by grazing animals on transfer of the fixed N to companion grasses.

(a) *Establishment*

The requirements to establish white clover in improved hill pastures were broadly known in the early 1970s (N.S.C.A. 1972) but the existence of considerable variation in the amounts of lime and fertilizers prescribed by the different advisory services and in the need for inoculation with microorganisms (rhizobia and mycorrhiza) necessitated further quantification.

Table 3. Response in production (July to October) and in nutrient cycling of a grazed white clover – ryegrass sward established with 5 t $CaCO_3$ ha^{-1} on deep peat to top dressing with fertilizer (Floate *et al.* 1981 *a*)

fertilizer added (kg ha^{-1})		herbage production (kg d.m. ha^{-1})				return of N and K in urine in 2 weeks (kg ha^{-1})	
P	K	white clover	s.e. mean†	perennial ryegrass	s.e. mean†	N	K
0	0	50	2[a]	451	18[a]	3.2	2.2
0	100	54	5[a]	648	61[b]	—	—
80	100	349	21[b]	1242	73[c]	23.0	23.9

† Within each column a significant difference between means $P > 0.05$ is indicated by a different letter.

(i) *Nutrients*

It is now known that the pH of the soil must be increased above pH 5.2 before white clover will grow well and 5–7.5 t ha^{-1} of lime is necessary; 40–60 kg P ha^{-1} accompanied by 60–100 kg K ha^{-1} are also essential. Biological responses in production of white clover herbage are found to much higher quantities of P and K than those given above, but the use of higher levels is not economically justifiable (Rangeley 1980). In peat soils it was found that a balance in the amounts of P and K must be achieved (Floate *et al.* 1981 *a*). These workers demonstrated, contrary to the popular belief that potassium only becomes a limiting element when pastures are cut for conservation, that in grazed swards on deep peat soils much of the potassium returned in urine is apparently lost from the system and, if not replaced by fertilizer additions, the plants become K deficient.

Data from one of their experiments are shown in table 3. They illustrate not only the importance of nutrient balance but also the impact of top dressing on return of N and K to the grazed pasture. The large response of the perennial ryegrass to the combined application of P and K is mainly due to the extra N transferred from the clover to the grass through urine.

(ii) *Rhizobia*

It is well known that upland soils have either no indigenous rhizobia or that most of the few strains present are ineffective at fixing N_2 (Holding & King 1963). It might therefore be expected that there would be no difficulty in showing large responses to the inoculation of white clover seeds with effective strains. However, a recent national series of collaborative experiments (Newbould *et al.* 1981) has shown that, whereas responses to inoculation occurred on deep peat soils and on some wet peaty podzols there was little or no response on the more mineral hill soils (dry peaty podzols and brown earths (table 4)). The lack of response on the latter soil type is disappointing since this soil has the best potential to produce herbage dry matter. Moreover, it was shown by the use of genetically marked strains that the introduced rhizobia were able to form nodules on clover in these soils but that inoculation was without overall agronomic effect on the growth of white clover and its companion grass. The reason for this lack of response is still a matter of speculation. It may reflect extra mineralization of N once these soils have been limed, thus invoking the well known interaction between mineral N, nodulation and N_2 fixation (Cowling 1961; Dancer *et al.* 1977; Haystead & Marriott 1978).

TABLE 4. RESPONSE OF WHITE CLOVER SHOOT PRODUCTION IN YEAR OF SOWING TO INOCULATION WITH *RHIZOBIUM* (FROM NEWBOULD *ET AL.* 1981)

soil type	number of sites	herbage production/(kg d.m. ha^{-1}) no inoculation	inoculation	s.e.d.	significance
brown earth	1	77	94	14	n.s.
dry peaty podzol	1	126	129	26	n.s.
wet peaty podzol	2	65	93	20	n.s.
deep peat	2	61	120	28	inoculation**

(iii) *Mycorrhiza*

In recent years there has been recognition of the role in P uptake of mycorrhizal associations between plant roots and fungi. Work by Hall *et al.* (1977) and Powell (1979) in New Zealand, Hayman & Mosse (1979) in Wales, and Rangeley *et al.* (1981) in Scotland has shown that, in some circumstances, an increase in the proportion of white clover roots occupied by the fungus, or a change in the strain of fungus causing infection, can result in a larger plant, a higher content of P, more nodules and greater N_2 fixation. Results are unpredictable, as shown by the data in table 5. White clover growing in deep peat soil in the laboratory, but not in the field, responded to inoculation with *Glomus mosseae* L1. By contrast, while white clover in the brown earth soil showed no significant response in the laboratory there was a response in the field to *Glomus etunicatus*, but not until the first harvest year of the experiment. While there is some doubt as to the causal ties between the amount of mycorrhiza, the uptake of P, the growth of the plant and the production of nodules, it is clear that the number, size and effectiveness of the nodules are considerably increased.

Further work is required on methods of inoculation, the nature of the inoculant, and the mechanisms of the symbiosis, before predictable and agronomically significant benefits of mycorrhizal inoculation of white clover can be produced consistently under field conditions.

(iv) *Levels of nitrogen fixed by white clover*

Once established, it is important to assess how much N is fixed by white clover and how this varies through the season and is affected by utilization and by additions of fertilizer N.

Seasonal changes in N_2 fixation by white clover, assessed by acetylene reduction during 1976 (a very dry year), are shown in figure 1 and, despite all the uncertainties associated with the

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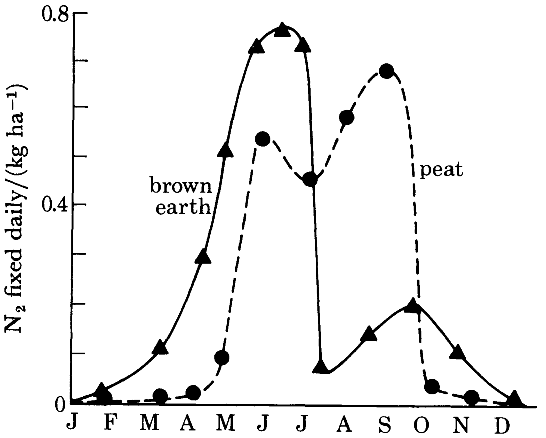

FIGURE 1. Changes throughout a growing season (1976) in fixation assessed by acetylene reduction by white clover growing in two types of upland soil (Newbould & Haystead 1978).

TABLE 5. RESPONSE OF WHITE CLOVER (CV. NEW ZEALAND GRASSLANDS HUIA) TO MYCORRHIZA IN LABORATORY AND FIELD (FROM RANGELEY *ET AL.* 1981)

soil	place units (fertilizer)	o.m.	+m.†	s.e.d.	significance
		herbage production			
deep peat	laboratory g per 3 pl. (20 kg P)	0.26	0.45	NA‡	m.*
	field kg ha^{-1} (20 kg P)	129	116	NA‡	n.s.
brown earth	laboratory g per 3 pl. (40 kg P)	0.24	0.43	0.24	n.s.
	field kg ha^{-1} (40 kg P)	841	1930	284	m.*
		infected root length (%)			
deep peat	laboratory	1	47	4.0	m.***
	field	37	52	6.3	m.*
brown earth	laboratory	35	42	5.3	n.s.
	field	25	49	10	m.*

† *Glomus mosseae* L1 for deep peat; *Glomus etunicatus* for brown earth.
‡ Data analysed by logarithmic transformation.

calibration factor, integration of the curves suggests that about 125 kg N were fixed per hectare of white clover pasture in each soil type in a year. The marked fall in N fixed in July on the brown earth site was closely linked with the onset of drought conditions and probably reflects stress due to that factor (Sprent 1979). If fixation had not been reduced by drought in July and August it is likely that about 150 kg N would have been fixed in this soil. Particular interest attaches to measurements made in February, March and November at the brown earth site. Significant quantities of acetylene were being reduced, implying that N_2 fixation was occurring, although there were no signs of herbage growth at these times. These observations suggest that

N_2 fixation can proceed supported only by stored carbohydrates, and attempts have been made to investigate this further (Haystead *et al.* 1980).

It is of considerable importance to determine the effect of fertilizer N on the growth of clover and nodules and the amount of N the latter are fixing. A small dressing of N is often used to enhance establishment of the companion grass. Haystead & Lowe (1977) examined this problem on a deep peat soil at Lephinmore, Argyll. Their data, for one year only, suggested that up to 90 kg N could be applied without detriment to the future growth and N_2 fixing ability

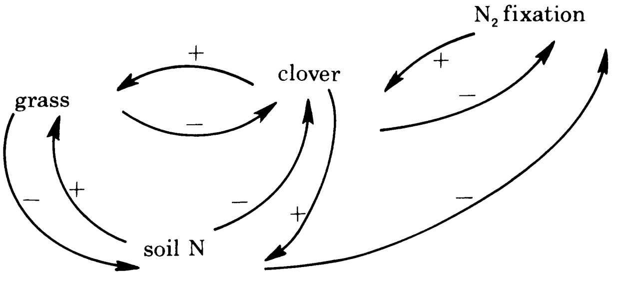

FIGURE 2. A casual loop diagram relating amount of grass, clover and soil N in a sward to N_2 fixation. If an increase in one component leads to an increase in another component they are connected by an arrow with a +; the converse is indicated with a –. (Adapted from Reiners (1981).)

of white clover. Other workers (Dancer *et al.* 1977) have suggested that with amounts of N fertilizer greater than 50 kg there are marked effects on nodulation. With established clover, Moustafa *et al.* (1969) found that more than 50 kg N reduced N_2 fixation to 20% of that recorded in the absence of added N.

Considerably more needs to be known about these interactions and there is a need to have more precise knowledge of the amount of mineral N in the soil solution resulting from mineralization, since this may account for some of the contrasted observations on the tolerance of white clover plants to combined N.

(*b*) *Management of swards with white clover*

The objectives to management of a white clover–grass sward are to have maximum impact on the grazing animals (Thomson 1979) while optimizing N_2 fixation and minimizing losses of N from the system.

The situation is complex (Snaydon & Baines 1981) because of the multiple and feedback interactions among soil N, grass growth, clover growth, direct and indirect effects of grazing, and weather, both in the present and previous seasons. The diagram shown in figure 2 illustrates but a few of the complex interactions in the system. There is insufficient information to model even the simplest situations, although progress is being made (Ennik 1981; Rhodes 1981). Moreover, most of the published work (Jackman 1971; Brougham *et al.* 1978; Vallis 1978) relates to rotationally grazed pastures and there is little precise information on how best to manage swards grazed continuously from April or May to July and from August or September to October, as prescribed in the U.K. hill two-pasture system designed to optimize the impact of improved pasture on livestock production (Eadie 1970). Before studying the grazed sward, attempts were made to assess aspects of the physiological response of clover growth and fixation to defoliation, the transfer of fixed N to companion grasses, and hence the effect on nutrient cycling and the need for maintenance fertilizers.

(i) *Physiological effects of defoliation of white clover*

King (1963) had earlier shown that heavy grazing of indigenous white clover populations resulted in small leaved, prostrate forms of white clover. Subsequently, King *et al.* (1978) found predominantly acropetal movement of assimilates in white clover, a view supported by Halliday & Pate (1976), with the consequence that defoliation reduces leaf and petiole size and harvestable yield per plant, but the effects on N_2 fixation were not ascertained. However, Haystead & Marriott (1978) found that removing all the fully expanded leaves from white clover had no effect on nodule numbers or on N_2-fixing activity during the phase of early season rapid growth; nor did they find any evidence of diurnal rhythms of N_2-fixing ability in grazed clover swards.

In a more detailed study, Haystead *et al.* (1979) found that there was a fairly constant relation between net photosynthesis, root respiration and acetylene reduction in mature stolonating white clover. Haystead *et al.* (1980) subsequently showed that 10% more of the C fixed each day is available for growth in plants supplied with combined N than those dependent solely on fixed N. Ryle *et al.* (1981) have confirmed this observation but suggested that the energy cost of fixation is 12% of the C fixed. Both groups of workers believe that the difference in C use between plants grown on combined and fixed N is shown in the root systems, with growth of the latter being greater in the plant supplied with combined N. This type of study, and particularly that on the effect of contrasted severities of defoliation, is being continued with simulated swards of white clover, and it is hoped eventually to extend the work to grazed swards.

(ii) *Nitrogen transfer, nutrient cycling and maintenance fertilizer*

The main route by which N fixed in white clover plants is transferred to companion grass is in the urine of animals which have grazed the sward (see table 3). Floate (1981) has recently reviewed this subject and has shown that there are direct effects of grazing, which include the consumption of herbage, the trampling of soil and spoilage of herbage, the excretion of dung and urine, and the removal of N by sale of animal products. Grazing also has indirect effects due to the modification of botanical composition and sward structure and the alteration in the proportion of N returned to the soil via plant and animal pathways, so affecting decomposition and mineralization rates of organic matter. Floate's evidence shows that passage through the rumen makes herbage N and P more available for subsequent plant uptake than herbage falling as litter on the soil. For upland pastures he has found that grazing control and more intensive stocking can, within 2 or 3 years, increase the size of the labile soil pools of these elements about tenfold (Floate *et al.* 1981*b*).

Haystead & Marriott (1979) and Haystead (1981), in a review of below-ground mechanisms, suggest that transfer to grass of N fixed by white clover takes place mainly between growing seasons. This may help to explain why good clover growth in one season is followed by good grass growth in the next season, irrespective of prevailing weather conditions. The chain of transfers followed by N released by exudation from clover roots or by decay of roots and nodules through bacteria, protozoa and mesofauna is a complex one, but the importance of below-ground 'grazing' and the changes in C:N ratio that occur and result in eventual release of mineral N to the soil solution for grass uptake are slowly being elucidated (Coleman *et al.* 1981). The use of ^{15}N techniques may lead to further advances in this area.

Despite the return of nutrients, especially N, P and K, in excreta to the improved areas of hill land, white clover can only be kept in these pastures if the soil pH is maintained above pH 5.2 and levels of nutrients such as P and K are not allowed to fall to a level that cannot sustain growth and fixation. Work to quantify the precise amounts needed for contrasted upland soils is in progress.

4. Potential for increases in N fixation in the uplands

(a) *Per unit area of improved pasture*

The data in table 2, though approximate, indicate that fixation efficiencies (kilograms N fixed per tonne clover shoot d.m.) for white clover growing in parts of upland U.K. and in New Zealand (Hoglund *et al.* 1979) may be similar. The figures given by Cowling (this symposium) for lowland U.K. pastures are also of the same order. This confirms that the amount of clover herbage and its photosynthetic performance are the main factors determining the amount of N fixed. It also suggests that the higher total amounts of N fixed each year in New Zealand and in lowland U.K. than in upland Britain are related more to the length of the growing season than to any other intrinsic difference in performance once the clover plants are established. The apparent universality of these N_2 fixation efficiencies might indicate that the easiest way to increase N_2 fixation is to increase the proportion of white clover and, ultimately, to use pure swards. However, this is not satisfactory for a number of reasons: first, white clover does not produce sufficient total dry matter by itself; secondly, it is difficult to maintain a pure white clover stand since it is easy for graminaceous and dicotyledonous weeds to gain access; thirdly, farmers are concerned that bloat and fertility problems might occur in their livestock. Another reason for growing grass with the clover in addition to the need for bulk herbage dry matter is to absorb any mineralized or transferred N as soon as possible and to prevent its interfering with the N_2 fixation process. This rapid removal of soil N has the added advantage that less N is available for leaching, and Low (1973) has shown that less N is lost from grass–clover than from clover-only swards.

The three main ways to improve the amount of N fixed per unit area are to devise grazing strategies to ensure the maintenance of an adequate leaf area index for clover, to extend the growing season by selection of suitable clover and rhizobia, and to find ways to limit the amount of N in the soils.

(b) *In upland U.K.*

Given that the national objective is more meat production from the upland areas of the United Kingdom with minimum inputs of money and energy, this can be achieved by extending the amount of rough pasture that is improved to ryegrass–white clover. To extend the establishment of white clover pastures fixing about 100 kg N ha^{-1} annually to 10% of Scotland's hill land and to 30–40% of Wales's hill land, targets specified by Cunningham (1980) and Munro (1973) respectively would mean the improvement of a further 0.5 Mha, with a total fixation of about 50 Mt of N per year, worth £20 M at today's price of N fertilizer (£0.40 kg^{-1}). Enhancement of N_2 fixation in the uplands by this means depends more on socio-economic and political decisions than on technological advances.

The attainment of increases in N_2 fixation in upland swards by any of the methods described (increase in unit efficiency, extension of season, extension of area) may eventually be limited by lack of phosphorus if its price continues to rise. P as triple superphosphate now costs £0.78

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kg^{-1}, almost double the cost of N. There are already signs that even lowland farmers are not maintaining the pH of their improved pastures, and a decline in the amount of P added, both to establish and maintain improved hill pastures, would have a serious effect on the growth and performance of white clover. Thus it is possible that a more apt practical measure of fixation efficiency for white clover than one based on energy use or d.m. might be kilograms N fixed per kilogram P added. On this basis, it would appear that perennial ryegrass – white clover pastures in upland U.K. established with 60 kg P and maintained with a further 20 kg P each year, averaged over 10 years and fixing 100 kg N ha^{-1} annually, has an efficiency of about 4 kg N fixed per kilogram P applied. This compares directly with results from annual legume pastures in dry land Australia, where 3–4 kg N are fixed per kilogram P added as superphosphate (E. A. Carter, personal communication 1981). Because P affects fixation directly and through its effect on the size of the clover plant, it may be that alternative strategies will be needed to ensure that symbiotic fixation in upland and marginal situations receives adequate P. The use of mycorrhizal fungi to optimize collection of soil P by legumes thus becomes of considerable potential importance.

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Discussion

A. J. Holding (*Department of Agricultural and Food Bacteriology, The Queen's University of Belfast, U.K.*). In the four preceding papers, we have heard about the exciting advances in the genetics of N_2 fixation (Professor Postgate) and the potential of *Vicia faba* (900 kg ha^{-1} annually), lowland white clover–grass swards (200 kg) and upland clover–grass swards (150 kg) to fix N_2, by Dr Sprent, Mr Cowling and Dr Newbould respectively. These rates of fixation are rarely achieved in the practical farming situation and it seems important to discuss the ways of increasing N_2 fixation in British agriculture.

Concerning genetics, the genetic screening of rhizobia for symbiotic properties might provide more precise criteria for the selection of inoculant rhizobium strains. However, not only N_2-fixing potential but competitive ability and persistence in soil and the rhizosphere will require to be considered. Other ways in which basic research knowledge might improve field fixation rates are eagerly awaited.

Some grain legumes, for example *Vicia faba*, appear to be capable of fixing more N_2 than other crops. The sensitivity of existing varieties of *Vicia* to nutritional and climatic stresses and to disease markedly reduces the fixation rate and 140 kg ha^{-1} is quoted as an average figure. It seems important that research priority should be given to overcoming some of these factors, together with acquiring data on the economic value of grain legumes compared with other protein sources in feed concentrates.

The complexity of grazing systems has been emphasized by Mr Cowling. Recent data suggesting that the average yearly rate of N_2 fixation in clover–grass swards is 11 kg ha^{-1} is alarming, when the potential is nearer 200 kg ha^{-1}. Greater emphasis on the management of clover in mixed swards is justified, particularly in situations where an input of N of 200 kg ha^{-1} would provide an adequate herbage yield for grazing. It should also be recognized that the palatability and nutritional value of clover can provide up to 25% greater live weight gain than stock fed on grass alone.

More attention should be given to the use of other legume crops, for example red clover and lucerne, in lowland grazing situations.

Approximately one-third of the total agricultural land in the British Isles is in upland areas. The low N_2 fixation rates in reseeded pastures are frequently attributed to the short plant growing season. However, the potential for increasing the productivity of these areas must be large, and inadequate emphasis seems to have been given to breeding clovers and other legumes adapted to the climatic and soil environments found in the uplands. Agronomic practices that lead to better establishment and persistence of clover should be further developed. In the upland situation, as on lower ground, plant factors generally appear to be limiting production. Continuing *Rhizobium* research should ensure that effective populations can be maintained.

It is in the interest of British agriculture that much higher N_2 fixation rates by legumes should be achieved wherever possible.

J. V. Lake (*Agricultural Research Council Letcombe Laboratory, Wantage, U.K.*). Mr Cowling mentioned that irrigation arrests the decline generally noted in experiments with white clover and Dr Newbould said that 'good clover' and 'good grass' years could be identified. Are 'good clover' years synchronized for all fields in a region, i.e. triggered by a weather-dependent root environment factor such as water, or can a year be 'good' for grass and for clover in adjoining fields, implicating management rather than weather as the dominant influence?

P. Newbould. My observations made mainly in the East of Scotland suggest that 'good clover' years tend to be synchronized in a region, with the implication that environment, and especially moisture supply, is probably a prime determinant of this. Cowling's work (this symposium) has clearly shown the responsiveness of white clover to irrigation and conversely its sensitivity to drought and disease, and I believe that a 'good clover' year tends to be a wet one. However, sufficient variation in clover content in any year occurs between neighbouring fields on the same farm, and on adjacent farms, to illustrate the complexity of the interactions between environment, disease, N supply and management factors, some of which I briefly described in my paper. The recent observation by Haystead *et al.* (1980) and Ryle *et al.* (1981), that clover plants effectively fixing atmospheric N and hence equivalent to large dominant plants in a 'good year' may have a smaller root:shoot ratio than plants using mineral N, suggests that well established clover plants in one season may be more liable to suffer from stress in the next season, particularly if it follows a cold winter or a cool dry spring. Loss of plants, or diminution of vigour from such stresses, coupled with the availability of an abundant supply of mineral N released from decomposing clover roots and nodules to support highly competitive companion grass plants with deeper root systems and with greater cold tolerance than clover, combine to provide some explanation of why 'good grass' years alternate with 'good clover' years. It is clear that 'good clover' years will never occur if insufficient clover plants are established in the year of sowing, and Professor Holding is quite right to emphasize this point at the start of the discussion. Good management (i.e. preparation of a firm yet fine seedbed with adequate nutrients and suitable pH, timeliness and intensity of first grazing, and judicious use of mineral N) is the dominant influence at this stage in the life of the pasture. Thus it is apparent that further observational and modelling work is required to enhance the predictability of clover establishment and to elucidate the complex web of factors that interact to influence grass–clover balance in grazed swards.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES