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Phosphorus in grasslands: its understanding, control and use

A F HARRISON[1] and K TAYLOR[2]
[1]*Institute of Terrestrial Ecology, Merlewood Research Station, Grange-over-Sands, Cumbria, England*
[2]*Department of Biology, University College London, Gower Street, London*

1 Introduction

Hill and upland sheep-grazed grasslands are frequently deficient in phosphorus (P) and to a variable extent, and this deficiency, together with the effects of poor climate, restricts sward productivity (Reith 1973; Newbould 1974; Newbould & Floate 1979). The maintenance or improvement of the productivity of grasslands depends on sustained or improved soil fertility, whilst the conservation of the varied and often special floristic composition of grasslands may depend on a relatively low or delicately balanced level of fertility. Clearly, therefore, if we are to manage hill and upland grasslands to maximize farm outputs and financial returns, yet also conserve their wildlife value, we need to understand the processes involved in the phosphorus cycle of these ecosystems and how to manipulate them to our advantage.

2 Soil phosphorus

The first question which needs answering is 'Why are hill and upland grassland soils P deficient, when they contain 500-3000 kg P ha^{-1} in the top 0.5 m of the soil profile?' (Floate 1962; Newbould & Floate 1979; Perkins 1978). The basic reason is that the vast majority of the phosphorus in the acid hill soils is 'unavailable' to plants, being bound in relatively stable organic matter or complexed in insoluble compounds with iron and aluminium. The organic form of phosphorus is often 65–80% of the total amount in the top 0.5 m of soil, and may approach 95% of that in the surface soil layers. Generally, the amount and proportion of phosphorus in the organic form increase with the altitude and rainfall of the site, the organic matter content of the soil and the thickness of the mat layer on the soil surface (Floate 1962; Harrison 1985, 1987). However, the plant production potential, shown using the common bent-grass (*Agrostis capillaris*) and white clover (*Trifolium repens*) as test plants (Harrison & Hornung 1983), is highly significantly negatively related to the proportion of the soil phosphorus in the organic form (Harrison 1985). There is a tendency for hill soils to accumulate organic matter because of its slow decomposition, both in the mineral (Clement & Williams 1964) and surface mat layers (Floate 1970a; Shiel & Rimmer 1984), particularly in areas with low grazing pressure (Gillingham 1980). Acidification of the soil through leaching of soil bases (Newbould & Floate 1979) and the addition of nitrogenous fertilizer (Shiel & Rimmer 1984) promotes the accumulation of organic phosphorus in the soil (Floate 1962, 1973; Walker 1962). Fertilizer phosphorus may end up in either or both of the surface mat and soil humus (Blair *et al.* 1976; Parfitt 1980). Accumulation of phosphorus in the organic form exacerbates the problems of P deficiency, by reducing the amount of phosphorus available in the soil (Jackman 1964a, b; White *et al.* 1976).

3 Phosphorus cycling

The phosphorus available to plants (2–10 kg P ha^{-1} Newbould & Floate 1979) is usually a very small proportion of the total present in the soil. Generally, as the available phosphorus is taken up from the soil by the roots of the grass sward, it is replenished through the processes of organic matter decomposition and organic phosphorus mineralization by the soil micro-organisms and fauna, and by leaching of the surface mat by rain. The availability of phosphorus is, indeed, largely controlled by the mineralization processes. These are dynamic processes changing in rates with the seasonal, climatic and soil conditions, and play a vital role in the maintenance of the phosphorus cycle, and hence the fertility of the soil.

A typical phosphorus cycle of an upland grassland is presented in Figure 1, which is that for a phosphorus-deficient bent-grass/fescue (*Agrostis/ Festuca*) sward at Llyn Llydaw, Snowdonia, north Wales (Perkins 1978). The site is at 500 m elevation, has an annual rainfall of 380 cm, a mean annual temperature of 7.2°C and is grazed by sheep (12.5 animals ha^{-1}) from April to October.

In this grassland ecosystem, only a small proportion (0.5%) of the total phosphorus capital is in the living biomass and about half is below ground. The living vegetation contains about 7.7 kg P ha^{-1} and an estimated 4 kg P ha^{-1} is in soil fauna and micro-organisms, the latter being more than in the sheep. A further 5.7 kg P ha^{-1} occurs in standing dead grass and litter mat on the soil surface. The annual plant uptake of phosphorus (16 kg P ha^{-1} yr^{-1}) is higher than the total amount returned to the soil in plant litter, by root death and in sheep faeces (14 kg P ha^{-1} yr^{-1}), because an estimated 1.2 kg P ha^{-1} yr^{-1} is lost from the site in faeces excreted by sheep on to lower ground when they camp at night. Transfer of phosphorus by sheep from one area to another has been recorded elsewhere (Gillingham & During 1973), and 0.8 kg P ha^{-1} yr^{-1} is removed in sheep products. Cycling phosphorus may also be reduced through some accumulation of soil organic matter, but the loss has not been estimated for this site. The available phosphorus in the soil is, however, largely replenished by decomposition

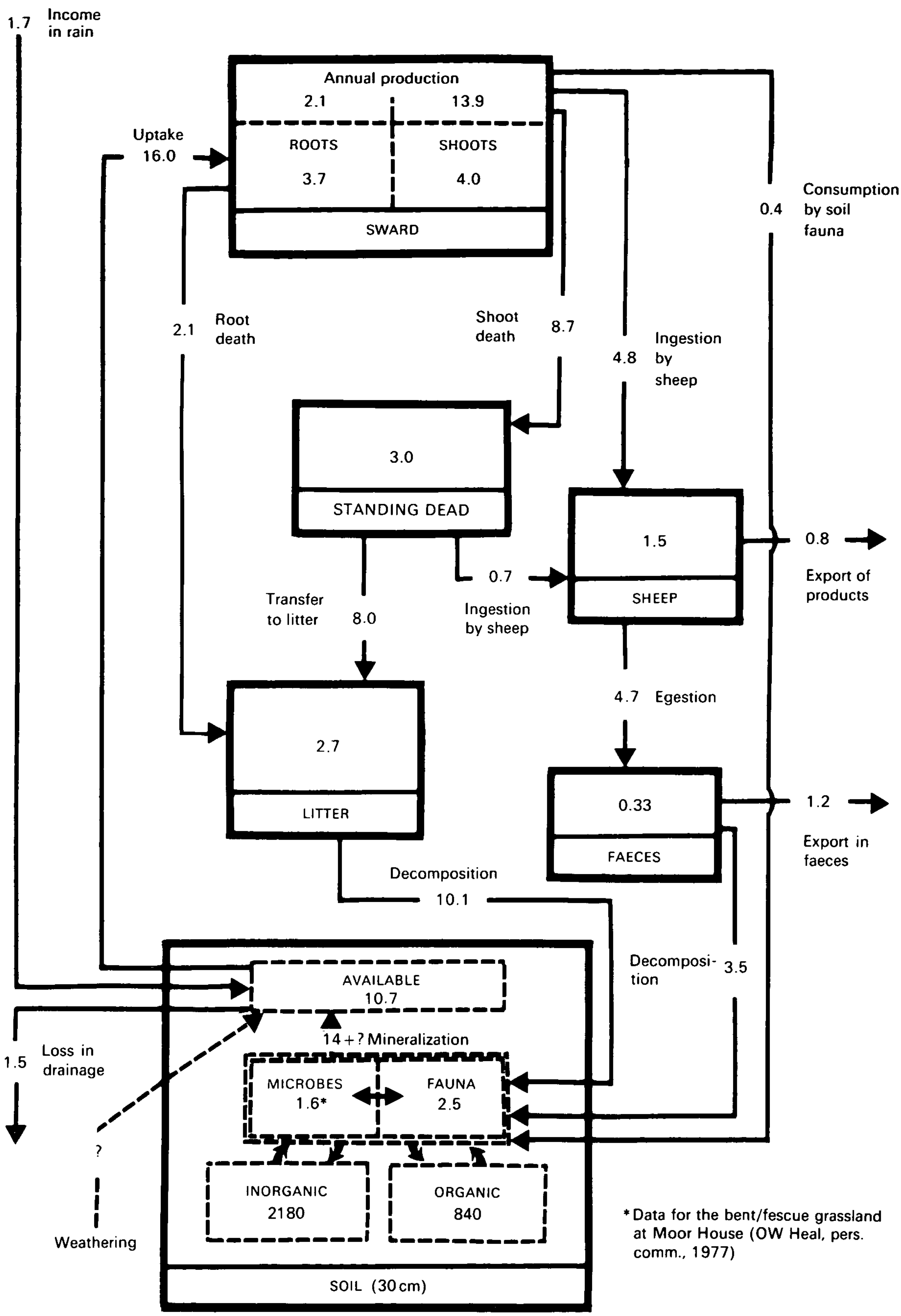

Figure 1. Phosphorus cycle of a bent/fescue grassland (Llyn Llydaw, Snowdonia, north Wales), based on Perkins (1978): contents in kg P ha^{-1} and transfers in kg P ha^{-1} yr^{-1} (source: Harrison 1985)

of the organic matter returned to the soil and the consequent release of the phosphorus contained to the available supply.

The processes of organic matter decomposition and release of the phosphorus for recycling are dynamic, and the rates are constantly changing. Temperature and moisture conditions in the soil are important factors governing the release of phosphorus from organic matter in hill grasslands (Floate 1970b, c, d), so there is a marked seasonal variation in the availability of phosphorus in the soil (Gupta & Rorison 1975). Changes in grazing pressure by seasonal grazing management may alter the amounts of phosphorus returned in urine and faeces, and hence amplify the natural seasonal pattern of available phosphorus. Phosphorus availability also varies in different layers of the soil, probably being greatest at the soil surface (Gupta & Rorison 1975).

The uptake of phosphorus by the grass sward varies with its seasonal growth pattern and is also affected by temperature and moisture conditions. In low-phosphorus soils, P taken up by some plants in one period of the year may be temporarily stored to support growth in other periods when conditions are unfavourable for uptake or when the soil is depleted (Grime 1979). In addition, the patterns of phosphorus uptake by the sward may be influenced by rooting depths of the different plant species present (Goodman & Collison 1982). The vesicular/arbuscular mycorrhizal development on the root systems of the sward species stimulates phosphorus uptake by plants by increasing the effective root system surface area and soil volume for phosphorus absorption (Sanders & Tinker 1971; Sparling & Tinker 1978; Fitter 1986). Whilst mycorrhizal infection may improve total sward production, selective mycorrhizal development may be an important competitive factor in the survival of particular plant species in a complex P-deficient sward (Read *et al.* 1976).

4 Grassland improvement

Several management practices can be employed to improve the rate of phosphorus cycling and thus the productivity of hill grasslands: (i) fertilizing; (ii) liming; (iii) increasing stocking rate; (iv) ploughing and reseeding; (v) introduction of earthworms; and (vi) inoculation with mycorrhizas.

The main way to improve the phosphorus status of hill and upland grassland soils, particularly when there is a net outflow of the element (see Figure 1), is to apply phosphorus either as slurry or as fertilizer. Slurry applications may not be as effective as fertilizer per unit phosphorus applied, as much of the phosphorus contained is in slowly mineralizing organic forms, but it has a cost advantage where its application is practical. There may be some disadvantages, however, as it may induce unfavourable soil conditions for micro-organisms and fauna (McAllister 1977). Fertilizer applications of 25-75 kg P ha^{-1} are often recommended (Newbould 1974; Newbould & Floate 1979) at various intervals of 2-8 years, depending on soil and pasture conditions.

Liming soils to increase soil pH (Pearson & Hoveland 1974) brings about an increase in microbiological activity (Jackman 1960; Macdonald 1979) which, in turn, stimulates the decomposition of soil organic matter (Jackman 1960; Broadbent 1962). Increasing soil pH through liming also increases the solubility of iron and aluminium complexes with organic and inorganic phosphorus (Jackman & Black 1951; Hsu & Jackson 1960) and increases the rate of mineralization of organic phosphorus in soils (Thompson *et al.* 1954). Together, these increases improve the rate of cycling of phosphorus and increase grassland productivity (Floate 1962; Floate *et al.* 1973).

Under increased grazing pressure generated by raising the stocking rate, there is an increase in the degree of pasture utilization. This results in a lowering of the rate of return of dead plant material to the soil, and thus a reduction in the thickness of the surface mat of organic matter and a decrease in the carbon/organic phosphorus of the soil profile (Floate 1970a, b). In addition, there are the increased returns of phosphorus to the soil in urine and faeces, the phosphorus in the latter being potentially more available than that in decaying plant material (Floate 1970a). Both processes improve phosphorus cycling, enhance sward productivity (Rawes & Welch 1969; Floate 1970a, 1973) and improve properties of these hill soils (Floate 1962, 1970a; Walker 1962). However, increased grazing pressure may result in an accumulation of organic phosphorus in the soil, possibly through increased faecal returns (McLachlan 1968; Floate 1973), so, in the longer term, fertilizer phosphorus applications are also necessary.

Ploughing of upland grassland soils often results in an increase in the rate of decomposition of accumulated organic matter, as soil disturbance improves aeration, stimulates microbial activity and makes the organic matter more accessible for decomposition (Rovira & Greacen 1957; Maltby 1979, 1984). Phosphorus locked up in the organic matter may, therefore, be mobilized for potential plant uptake (Thompson *et al.* 1954; Jackman 1964b). However, the mobilized phosphorus may be directly fixed by iron and aluminium to become unavailable to plants, particularly if the ploughing should expose iron-rich layers – many hill grassland soils have a high capacity to fix phosphate and render it unavailable to plants. Thus, ploughing may not have the desired effect on all soils, of actually increasing the amount of phosphorus cycling. For reseeding with an improved grass species and clover, it may be necessary therefore to apply lime and fertilizer (Munro *et al.* 1979; Newbould & Floate 1979).

The introduction of earthworms into grasslands has been shown to enhance the grassland productivity (Stockdill 1966, 1982; Hoogerkamp *et al.* 1983). In acid upland grasslands, it may be necessary to apply some lime to adjust soil pH, before attempting to introduce earthworms of the right species (Syers & Springett 1984). Earthworms improve soil aeration, microbial activity and soil organic matter decomposition, and hence should stimulate phosphorus cycling. It is not known, however, if there have been any experimental attempts to introduce earthworms and assess their effects on grassland production in upland Britain.

As there are proven benefits of mycorrhizal infection of root systems on the phosphorus uptake by plants, attempts could be made to enhance the degree of plant infection by artificial inoculation. Attempts to inoculate plants in acidic hill soils with mycorrhizas may also necessitate prior liming to modify soil pH, as mycorrhizas most successfully develop at about pH 6.0 (Graw 1979; Newbould & Rangeley 1984). Some trials in mid-Wales have shown that grass plants may benefit from inoculation with appropriate mycorrhizal fungi (Hayman 1977). Though liming may increase the degree of mycorrhizal infection in plants, the productivity of the plants may not be improved (Newbould & Rangeley 1984).

5 Floristic composition

An inevitable problem with the above soil/site management practices is that the floristic composition of the swards will be changed. These changes frequently reduce, sometimes markedly, the conservation value of the upland grasslands. Some of the floristic changes may be directly attributable to the altered levels of phosphorus availability. Many of the species present in upland grasslands survive when the availability of phosphorus in the soil is low, and some species can react vigorously to increases in phosphorus supply (Bradshaw *et al.* 1960; Clarkson 1967; Rorison 1968; Jeffrey & Pigott 1973; Atkinson 1983). So, fertilizing grassland swards with phosphate causes major changes in the species composition (Milton 1940; Sears 1953; Jeffrey & Pigott 1973; Pigott 1982), and may result in a considerable reduction in the number present (Jeffrey & Pigott 1973).

Many changes in species composition of grasslands are also caused by liming (Milton 1940; Sears 1953; Pigott 1982), some of which may be indirectly induced by changes in phosphate availability. However, changes in calcium availability resulting from liming can have direct and marked influences on the growth and survival of many acidophilous plants. Varying the grazing pressure by changing the stocking rate can also result in changes in the floristic composition of swards. Some species, perhaps relatively rare ones, may flourish under heavy grazing pressure, whilst others become more abundant when sheep grazing is removed (Welch & Rawes 1964; Rawes 1981). In some sites, removal of sheep grazing causes a reduction in the number of plant species in the sward (Watt 1957; Welch & Rawes 1964), and some changes in the flora may still be occurring 24 years after grazing removal (Rawes 1981). Though some of the changes in species might be brought about by changes in availability of soil phosphate through recycling in urine and faeces, induced by grazing pressures, major direct effects result from the grazing itself and trampling by the sheep and, after grazing is removed, from competition for light as the sward grows denser.

From the available data, it is clear that altering the phosphate status of upland grasslands, by whatever management practice, will induce many changes in the species of plants present in a sward. It is important to realize, however, that the effects of the management procedures designed to 'improve grasslands' are only of a temporary nature. Without renewal of fertilizer applications or continuity of management, the grasslands are prone to revert to the previous acidifying, low microbial activity, organic matter-accumulating state of lower fertility (Jackman 1964a, b; Floate 1977; Maltby 1979). The timescale for the natural reconstitution of the poorer nutrient status, acid soil conditions which favour many of the plant species of conservation interest, from limed, highly fertilized and perhaps reseeded pasture, is as yet unknown.

6 Management of soil phosphorus status

Clearly, as indicated in the introduction to this paper, we need to understand the patterns and processes of phosphorus cycling in upland grasslands, if we are to manage efficiently the productivity and the floristic composition of grassland swards.

One of the very basic necessities for efficient management of upland and hill grasslands for optimum productivity and floristic composition is to determine the soil phosphorus status by sensitive, reliable and practical methods. However, assessment of phosphorus 'availability' in hill and upland soils by current routine soil analysis is in most cases unsatisfactory (Floate & Pimplaskar 1976; Pimplaskar et al. 1982), due largely to the complex nature of the soil phosphorus chemistry and the dynamics of the phosphorus cycle influenced by the grazing sheep, as discussed earlier.

A new approach (Harrison & Helliwell 1979) for assessing the phosphorus status of soils has recently been applied to grasslands and is showing considerable promise. The bioassay is based on the physiological responses of plant root systems rather than soil analysis. The root response is determined as the rate at which ^{32}P-labelled phosphorus is metabolically absorbed from a standardized solution in the laboratory. The uptake rate by roots is related negatively and exponentially to the supply of phosphorus in the rooting medium (Harrison *et al.* 1985, 1986). Preliminary studies, relying on the responses of sheep's fescue (*Festuca ovina*), a most common species in upland and hill swards, have shown that the bioassay can be used to predict fertilizer responses and total sward productivity in upland grasslands (Harrison *et al.* 1986). As this method is particularly sensitive, and its sensitivity increases with decreasing soil fertility (Harrison & Helliwell 1979), it could provide a useful means of determining the phosphorus status of hill and upland grasslands, particularly if there are specific conservation aspects of floristic composition which have to be taken into account. The bioassay has the potential to be used both as a research tool in complex biological studies and in the practical routine manner for assessing fertilizer requirements.

7 References

Atkinson, C.J. 1983. Phosphorus acquisition in four co-existing species from montane grassland. *New Phytol.*, **95**, 427-437.

Blair, G.J., Till, A.R. & Smith, R.C.G. 1976. The phosphorus cycle - what are the sensitive areas? *Rev. Rural Sci.*, **3**, 9-19.

Bradshaw, A.D., Chadwick, M.J., Jowett, D., Lodge, R.W. & Snaydon, R.W. 1960. Experimental investigations into the mineral nutrition of several grass species. III. Phosphate level. *J. Ecol.*, **48**, 631-637.

Broadbent, F.E. 1962. Biological and chemical aspects of mineralisation. *Trans. Comm. IV and V, Int. Soil Sci. Soc. New Zealand*, 220-229.

Clarkson, D.T. 1967. Phosphorus supply and growth rate in species of *Agrostis* L. *J. Ecol.*, **55**, 111-118.

Clement, C.R. & Williams, T.E. 1964. Leys and soil organic matter. I. The accumulationm of organic carbon in soils under different leys. *J. agric. Sci. Camb.*, **63**, 377-383.

Fitter, A.H. 1986. Effect of benomyl on leaf phosphorus concentration in alpine grasslands: a test of mycorrhizal benefit. *New Phytol.*, **103**, 767-776.

Floate, M.J.S. 1962. *Pedogenetic relationships concerning forms of soil phosphorus and soil organic matter.* PhD thesis, University of Durham.

Floate, M.J.S. 1970a. Plant nutrient cycling in hill land. *Rep. Hill Fmg Res. Org., 5th*, 15-34.

Floate, M.J.S. 1970b. Mineralisation of nitrogen and phosphorus from organic materials of plant and animal origin and its significance in the nutrient cycle in grazed upland and hill soils. *J. Br. Grassld Soc.*, **25**, 295-302.

Floate, M.J.S. 1970c. Decomposition of organic materials from hill soils and pastures. III. Effects of temperature on the mineralisation of carbon, nitrogen and phosphorus from plant materials and sheep faeces. *Soil Biol. Biochem.*, **2**, 187-196.

Floate, M.J.S. 1970d. Decomposition of organic materials from hill soils and pastures. IV. Effects of moisture content on the mineralisation of carbon, nitrogen and phosphorus from plant materials and sheep faeces. *Soil Biol. Biochem.*, **2**, 275-283.

Floate, M.J.S. 1973. Soils associated with grass and heather moorland and some long-term changes related to grazing influences. *J. Sci. fd Agric.*, **24**, 1149.

Floate, M.J.S. 1977. British hill soil problems. *Soil Sci.*, **123**, 325-331.

Floate, M.J.S. & Pimplaskar, M.S. 1976. Some anomalous results for 'available P' in hill soils and experimental attempts towards their resolution. *J. Sci. fd Agric.*, **27**, 591.

Floate, M.J.S., Eadie, J., Black, J.S. & Nicholson, I.A. 1973. The improvement of *Nardus* dominant hill pasture by grazing control and fertilizer treatment and its economic assessment. In: *Hill pasture improvement and its economic utilisation. Colloq. Proc.*, no.3, 33-46. Potassium Institute Ltd.

Gillingham, A.G. 1980. Phosphorus uptake and return in grazed steep hill pastures. I. Pasture production and dung and litter accumulation. *N.Z. J. agric. Res.*, **23**, 313-321.

Gillingham, A.G. & During, C. 1973. Pasture production and transfer of fertility within a long-established hill pasture. *N.Z. J. exp. Agric.*, **1**, 227-232.

Goodman, P.J. & Collison, M. 1982. Varietal differences in uptake of ^{32}P-labelled phosphate in clover plus ryegrass swards and monocultures. *Ann. appl. Biol.*, **100**, 559-565.

Graw, D. 1979. The influence of soil pH on the efficiency of vesicular arbuscular mycorrhiza. *New Phytol.*, **82**, 687-695.

Grime, J.P. 1979. *Plant strategies and vegetation processes.* Chichester: Wiley.

Gupta, P.L. & Rorison, I.H. 1975. Seasonal differences in the availability of nutrients down a podzolic profile. *J. Ecol.*, **75**, 521-534.

Harrison, A.F. 1985. Effects of environment and management on phosphorus cycling in terrestrial ecosystems. *J. environ. Manage.*, **20**, 163-179.

Harrison, A.F. 1987. *Soil organic phosphorus: a world literature review.* Wallingford: Commonwealth Agricultural Bureaux International.

Harrison, A.F. & Helliwell, D.R. 1979. A bioassay for comparing phosphorus availability in soils. *J. Ecol.*, **16**, 497-505.

Harrison, A.F. & Hornung, M. 1983. Variation in fertility of UK soils. *Annu. Rep. Inst. terr. Ecol. 1982*, 98-99.

Harrison, A.F., Dighton, J., Hatton, J.C. & Smith, M.R. 1985. A phosphorus-deficiency bioassay for trees and grasses growing in low nutrient status soils. In: *Proc. int. Colloq. for the Optimization of Plant Nutrition, Montpellier, September 1984*, edited by P. Martin-Prevel, 957-963. Montpellier: AIONP/GERDAT.

Harrison, A.F., Hatton, J.C. & Taylor, K. 1986. Application of a root bioassay for determination of P-deficiency in high-altitude grasslands. *J. Sci. fd Agric.*, **37**, 10-11.

Hayman, D.S. 1977. Mycorrhizal effects on white clover in relation to hill land improvement. *ARC Res. Rev.*, **3**, 82-85.

Hoogerkamp, M., Rogaar, H. & Eijsackers, H.J.P. 1983. Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. In: *Earthworm ecology: from Darwin to vermiculture*, edited by J.E. Satchell, 85-105. London: Chapman & Hall.

Hsu, P.H. & Jackson, M.L. 1960. Inorganic phosphate transformations by chemical weathering in soils as influenced by pH. *Soil Sci.*, **90**, 16-24.

Jackman, R.H. 1960. Organic matter stability and nutrient availability in Taupo pumice. *N.Z. J. agric. Res.*, **3**, 6-23.

Jackman, R.H. 1964a. Accumulation of organic matter in some New Zealand soils under permanent pasture. I. Patterns of change of organic carbon, nitrogen, sulphur and phosphorus. *N.Z. J. agric. Res.*, **7**, 445-471.

Jackman, R.H. 1964b. Accumulation of organic matter in some New Zealand soils under permanent pasture. II. Rates of mineralisation of organic matter and the supply of available nutrients. *N.Z. J. agric. Res.*, **7**, 472-479.

Jackman, R.H. & Black, C.A. 1951. Solubility of iron, aluminium, calcium, and magnesium inositol phosphates at different pH values. *Soil Sci.*, **72**, 179-186.

Jeffrey, D.W. & Pigott, C.D. 1973. The response of grasslands on sugar-limestone in Teesdale to application of phosphorus and nitrogen. *J. Ecol.*, **61**, 85-92.

Macdonald, R.M. 1979. Liming and the growth of a mixed population of soil bacteria. *Soil Biol. Biochem.*, **11**, 633-636.

Maltby, E. 1979. Changes in soil properties and vegetation resulting from reclamation on Exmoor. *Rep. Welsh Soils Discuss. Grp*, no. 20, 83-118.

Maltby, E. 1984. Response of soil microflora to moorland reclamation for improved agriculture. *Pl. Soil*, **76**, 183-193.

McAllister, J.S.V. 1977. Spreading slurry on land. *Soil Sci.*, **123**, 338-343.

McLachlan, K.D. 1968. Stocking rate and the super phosphate requirements of sown pasture on an acid soil. *Aust. J. exp. Agric. Anim. Husb.*, **8**, 33-39.

Milton, W.E.J. 1940. The effect of manuring, grazing and cutting on the yield, botanical and chemical composition of natural hill pastures. *J. Ecol.*, **28**, 326-356.

Munro, J.M.M., Davies, D.A., Morgan, T.E.H. & Young, N.R. 1979. Pasture plant breeding and hill land improvement. *Rep. Welsh Soils Discuss. Grp*, no. 20, 49-79

Newbould, P. 1974. The improvement of hill pastures for agriculture. *J. Br. Grassld Soc.*, **29**, 241-247.

Newbould, P. & Floate, M.J.S. 1979. Problems of hill and upland soils. *Rep. Welsh Soils Discuss. Grp*, no. 20, 1-31.

Newbould, P. & Rangeley, A. 1984. Effect of lime, phosphorus and mycorrhizal fungi on growth, nodulation and nitrogen fixation by white clover (*Trifolium repens*) grown in UK hill soils. *Pl. Soil*, **76**, 105-114.

Parfitt, R.L. 1980. A note on the losses from a phosphate cycle under grazed pasture. *N.Z. J. exp. Agric.*, **8**, 215-217.

Pearson, R.W. & Hoveland, C.S. 1974. Lime needs of forage crops. In: *Forage fertilisation*, edited by D.A. Mays, 301-322. Madison, Wi: American Society of Agronomists, Crop Science Society of America and Soil Science Society of America.

Perkins, D.F. 1978. The distribution and transfer of energy and nutrients in the *Agrostis-Festuca* grassland ecosystem. In: *Production ecology of British moors and montane grasslands*, edited by O.W. Heal & D.F. Perkins, 375-395. Berlin: Springer.

Pigott, C.D. 1982. The experimental study of vegetation. *New Phytol.*, **90**, 389-404.

Pimplaskar, M.S., Floate, M.J.S. & Newbould, P. 1982. The suitability of different methods for assessing phosphorus status of hill soils. *J. Sci. fd Agric.*, **33**, 957-963.

Rawes, M. 1981. Further results of excluding sheep from high-level grasslands in the north Pennines. *J. Ecol.*, **69**, 651-669.

Rawes, M. & Welch, D. 1969. Upland productivity of vegetation and sheep at Moor House National Nature Reserve, Westmorland, England. *Oikos (suppl.)*, **11**, 7-72.

Read, D.J., Koucheki, H.K. & Hodgson, J. 1976. Vesicular arbuscular mycorrhiza in natural vegetation systems. 1. The occurrence of infection. *New Phytol.*, **77**, 641-653.

Reith, J.W.S. 1973. Soil conditions and nutrient supplies in hill land. In: *Hill pasture improvement and its economic utilisation. Colloq. Proc.*, no. 3, 5-17. Potassium Institute Ltd.

Rorison, I.H. 1968. The response to phosphorus of some ecologically distinct plant species. 1. Growth rates and phosphorus absorption. *New Phytol.*, **67**, 913-923.

Rovira, A.D. & Greacen, E.L. 1957. The effect of aggregate disruption on the activity of micro organisms in the soil. *Aust. J. agric. Sci.*, **8**, 659-673.

Sanders, F.E. & Tinker, P.B. 1971. Mechanism of absorption of phosphate from soil by *Endogone* mycorrhizas. *Nature, Lond.*, **233**, 278-279.

Sears, P.D. 1953. Pasture growth and soil fertility. 1. The influence of red and white clovers, superphosphate, lime, and sheep grazing, on pasture yields and botanical composition. *N.Z. J. Sci. Technol.*, **35**, (Suppl. 1), 1-29.

Shiel, R.S. & Rimmer, D.L. 1984. Changes in soil structure and biological activity on some meadow hay plots at Cockle Park, Northumberland. *Pl. Soil*, **76**, 349-356.

Sparling, G.P. & Tinker, P.B. 1978. Mycorrhizal infection in Pennine grassland. II. Effects of mycorrhizal infection on the growth of some upland grasses on γ-irradiated soils. *J. appl. Ecol.*, **15**, 951-958.

Stockdill, S.M.J. 1966. The effect of earthworms on pastures. *Proc. N.Z. ecol. Soc.*, no. 13, 68-75.

Stockdill, S.M.J. 1982. Effects of introduced earthworms on the productivity of New Zealand pastures. *Pedobiologia*, **24**, 29-35.

Syers, J.K. & Springett, J.A. 1984. Earthworms and soil fertility. *Pl. Soil*, **76**, 93-104.

Thompson, L.M., Black, C.A.& Zoellner, J.A. 1954. Occurrence and mineralisation of organic phosphorus in soils, with particular reference to associations with nitrogen, carbon and pH. *Soil Sci.*, **77**, 185-196.

Walker, T.W. 1962. Problems of soil fertility in a grass-animal regime. *Int. Soil Conf. N.Z., 1962*, 704-714.

Watt, A.S. 1957. The effect of excluding rabbits from grassland B (Mesobrometum) in Breckland. *J. Ecol.*, **45**, 861-878.

Welch, D. & Rawes, M. 1964. The early effects of excluding sheep from high-level grasslands in the north Pennines. *J. Ecol.*, **1**, 281-300.

White, E.M., Krueger, C.R. & Moore, R.A. 1976. Changes in total N, organic matter, available P and bulk densities of a cultivated soil 8 years after tame pastures were established. *Agronomy*, **68**, 581-583.