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Soil:plant relationships of species-rich *Molinia caerulea* dominated communities of the Culm Measures, North Devon, with special reference given to phosphorus cycling

by

M. Jane Goodwin

A thesis submitted to the University of Plymouth in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

Seale-Hayne Faculty of Agriculture, Food and Land Use

In collaboration with Institute of Grassland and Environmental Research

September 1995

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Abstract

Soil:plant relationships of species-rich *Molinia caerulea* dominated communities of the Culm Measures, North Devon, with special reference given to phosphorus cycling.

Margaret Jane Goodwin

A semi-natural community known locally as Culm grassland in Devon and N. E. Cornwall is under threat from agricultural improvement, abandonment and inappropriate management. In the last fifty years 87% of the original area has been lost. Further loss may be prevented by an examination of the factors that influence the plant community and how they may be manipulated by management. Thus the research described in this thesis addressed the soil conditions and the plant communities, with particular reference to phosphorus cycling.

In 1992 a preliminary characterisation of soil nutrient and water conditions, and species composition was conducted on a pristine Culm grassland, an improved grassland and a formerly abandoned Culm grassland. A significant elevation in soil extractable phosphorus was found in mid-April in response to fertiliser applications on the improved grassland. Similarities with previous research and an absence of a similar pattern in mineral nitrogen prompted a detailed investigation of phosphorus dynamics in 1993. A better indication of plant 'available' P was found by removing soil solution directly using novel methods of centrifuging and suction cups. Environmental conditions were highly influential. Low concentrations of P in suction cup solutions on Culm grassland indicated that Culm species may remove P at very low concentrations. An investigation of the above-ground biomass found that the uptake of P was highest in *M. caerulea*. *M. Caerulea* also influenced the return of P to the soil via organic matter through the production and subsequent breakdown of large quantities of litter. Additions of P to turfs caused a perturbation by enhancing the uptake of P by *M. caerulea* and increasing P fixation.

The data was employed to produce a schematic model of the Culm grassland which identified input and outputs, storage compartments and transfers within the P cycle. This contributed towards making management recommendations for a range of Culm grassland communities which may be maintained, improved or recreated.

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Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for an award at any other University.

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Revelant scientific seminars and conferences were attended at which work was presented.

Conferences attended with poster presentations

1) The joint British Grassland Society and British Ecological Society meeting of Grassland Conservation Management, University of Leeds, September, 1993
Soil nutrient availability of species rich and species poor Culm grassland

2) British Ecological Society Winter meeting, University of Stirling, January, 1994
Evaluation of methods employed to monitor soil phosphorus availability of a semi-natural grassland in North Devon.

3) British Ecological Society Winter meeting, University of Birmingham, December, 1994

CHAPTER ONE

INTRODUCTION

1.1 Introduction

The purpose of this research is to examine the environmental conditions; especially nutrient availability, which support a semi-natural grassland community in South West Britain. A key nutrient in such systems is phosphorus which is given special attention in this study. This semi-natural grassland is characterised by a significant presence of *Molinia caerulea* (Purple Moor Grass) together with varying amounts of rushes, sedges, ericaceous shrubs, herbs, bryophytes and other grasses. The species composition is highly variable and the grassland is species-rich in comparison to improved grassland nearby. The vegetation is composed of a wide range of communities including wet, acid grassland, wet heath, fen and mire and is referred to by its local name of Culm grassland in this study. This highly variable vegetation type owes its existence to particular environmental conditions and traditional agricultural practices. It is managed by cattle grazing in the summer and winter burning or topping. This is vital in preventing the domination of a few species especially *M. caerulea* and for the maintenance of species richness. Like most semi-natural communities it is under pressure from agricultural intensification particularly fertiliser applications. Recent studies (see Chapter Four) have indicated that phosphorus availability is a limiting factor in maintaining semi-natural communities and this is the justification for choosing phosphorus availability which will form a major part of this project. An emphasis is placed on the practical applications of the project which may enable conservation management to become more specific and the resulting changes more predictable.

In this introductory chapter the importance of Culm grassland in Britain and Europe and the limited information on environmental conditions, particularly soil conditions, is highlighted. To understand the soil:plant relationships of this semi-natural community a review of factors controlling and modifying nutrient availability and how this may effect species-composition is given. This is followed by discussion of possible methods of monitoring soil nutrient availability both in soil and plant material. Subsequently research objectives and aims are presented together with a structure of the thesis.

1.2. History of semi-natural grassland in Britain

In Britain all semi-natural grasslands are plagioclimax communities, as succession to the natural forest climax community is prevented by management imposed by humans. A diverse range of plant communities developed in Britain controlled by climate, underlying geology and soil conditions which were maintained by management. The vegetation of Britain is influenced by an Atlantic climate of cool, moist and windy conditions. Within Europe the Atlantic region reaches as far east as southern Sweden, west Poland and the western Alps (Polunin and Walters 1985).

The first recorded human impact on climax vegetation was in the clearance of well-drained sandstone and limestone terrain by Mesolithic people (Green, 1990). By 5000 years ago Neolithic arable and pastoral agriculture was indicated by the fluctuation of herbaceous and tree pollen levels (Ratcliffe, 1984). At the end of the Middle Ages agriculture had become the economic mainstay of Britain. Cereals prevailed in the lowlands, and permanent grassland in the west. The distinction between cereals and grassland became greater as crops were protected by fencing out animals which led to hedgerows becoming a feature of the landscape. Semi-natural grasslands were maintained with extensive grazing by cattle, sheep and horses. Rabbits also had a significant influence in some regions. Fire was also used to regenerate heather, and cutting of peat for fuel created heterogenous soil conditions.

These grassland communities are classified as neutral, acid, calcareous and wet grasslands and heathlands. Their distribution, species composition and current status is summarised in Table 1.1. It is evident from Table 1.1 that large losses of semi-natural vegetation has occurred, mostly following the Second World War (Baldock, 1990 and Fuller, 1987). Also much of the remaining grassland has reduced in wildlife conservation value. The Nature Conservancy Council estimate that no more than 20% of the total area of chalk grassland existing in 1939 survives today with its original floristic richness (Ratcliffe,1984). Also 40% of lowland heaths, 50% of lowland wetlands and 30% of upland moors were lost or significantly damaged over the same period.

Table 1.1 A summary of species-composition and current status of grasslands in Britain
(Ratcliffe 1984, Polunin and Walters 1985, Rieley and Page 1990, Baldock 1990, van Dijk unpub.)

Grassland Type	Description, Location (Britain and Europe) and Soil Conditions	Species Composition (main components)	Current Status
Neutral	Hay meadows and lowland pastures. Eurosiberian region and to the Mediterranean. Wide range of soil types, not on extremes of acidity. Class : Molinio-Arrhenatheretea, Orders : Molinietalia, Arrhenatheretalia	Meadow Foxtail, Red Fescue, Yorkshire Fog, Meadow Fescues, Common Knapweed, Common Sorrel, Red Clover, Tufted Vetch, occasional Bryophytes	Remainder of unimproved neutral grassland within total grassland : Hereford and Worcester - 5.7% Cumbria - 3.0 %
Acid	Rough grazing and moorland in Upland Britain. Throughout Europe towards Siberia. Shallow podzolised soils. Class : Nardo-Callunetea, Order : Nardetalia	Mat Grass, Bent grasses, Sheeps Fescue, Sweet Vernal-grass, Wavy Hair-grass.	150 000 ha of upland reclaimed from 1950-1980. Only 20 % of enclosed upland grassland does not receive nitrogenous fertilisers.
Calcareous	Species-rich vegetation on calcium carbonate rich soils. C. and W. Europe. Chalk of S. and S.E. England from Kent and Salisbury Plain to Yorkshire Wolds. Jurassic limestone escarpment from Cotswolds to Lincolnshire edge. Class : Festuco-Brometa, Order : Brometalia erecti	Upright brome, Tor-grass, Meadow Oat, Common Rockrose, Pyramid Orchid, Dwarf Thistle, Quaking Grass, Glaucous Sedge, Lesser Knapweed, Burnet Saxifrage, Ribwort Plantain.	In Dorset 71 % decline in area from 1934 - 1972 and in 1984 only 2.6 % remains. Only 53 % of total area of Chalk grassland is still of high nature conservation interest in Britain.
Wet	Wet grazing marshes and mires with valley mires, raised bogs and fens. Also wet heathland. In areas of high rainfall on acid, mineral deficient soils with poor drainage allowing peat to accumulate. Class : Parvocaricetea, Scheuchaerietea, Oxycocco-Sphagnetea	Communities highly variable in relation to water conditions. Common component of mosses particularly Sphagnum with Purple Moor-grass, Deer Grass, Cotton Grass, Heather.	60% of lowland raised mires lost or significantly damaged 1948-1978. East-Anglian Fenland decrease by 71 % 1037-1825. A third of area underlain by peat in Britain drained by 1980.
Dry Heathland	Oceanic distribution in Europe. East Anglia, south and west England, Pennines, eastern and northern Scotland. Wetter western districts replaced by peat-forming wet heaths or blanket mires. Acid podsolised soils on fast draining parent material. Class : Nardo-Callunetea, Order : Calluno-Genistion	Main component is Heather with Petty Whin, Western Gorse, Broom, Bilberry, Common Milkwort, Heath Grass, Wavy Hair Grass, Bristle Bent, and also some mosses	Six main heathland areas (Dorset, Hampshire, Surrey, Lizard Penninsular, Suffolk sandlings and Breckland) lost 40 % of their area from 1950-1984.

Agricultural improvement has been largely responsible for the loss of semi-natural grassland. Government grants have encouraged for example drainage of lowland flood plains, valley mires, raised bogs and wet grazing marshes (Peet, Glen-Lewin and Walker, 1983). As a result many fens have reduced in area or even dried out in response to a lowering of the water table (Ratcliffe, 1984). Ploughing and reseeding has had a major impact particularly on calcareous grassland as low yielding species have been replaced by arable crops and high yielding grasses such as *Lolium perenne*. Surviving unprotected chalk grassland is often restricted to inaccessible scarps and slopes. Improvement is usually associated with fertiliser and herbicide applications. This has played a key role in increased productivity and has affected acidic heathland, in particular (Ratcliffe, 1984). Also a lack of management has been detrimental to semi-natural grassland which allows the encroachment of scrub and reversion to rank grass. This is typical of small unploughed areas of chalk grassland which are not economically unviable. (Green, 1989).

Similar semi-natural vegetation may be found in Europeand and this has also declined mainly in response to agricultural intensification, although information is scant and highly variable (Van Dijk unpub.). The area of permanent meadow pasture in the EC has declined at an annual rate of 0.5% since 1973 (Baldock, 1990). Wetlands in France are being lost at a rate of 10 000 ha per annum and in Belgium up to 1200 ha per annum has been lost since 1960 (Baldock, 1990). The peatlands of Ireland remain one of the strongholds but are now under threat from drainage and fertiliser applications (Van Dijk unpub.). In the Netherlands only 9000 ha out of 250 000 ha of peatland remains undrained. Dry grassland on chalk soils in the Champagne region of France has declined by 99% in the last 30 years. The percentage of land area covered by heaths has declined in Belgium from 40 to 4% and in Denmark from 26% in 1850 to 2% in 1982 (Baldock, 1990). Future changes land management within the European community will be heavily influenced by European policies and CAP reform such as the introduction of agri-environment schemes and Environmentally Sensitive Areas.

1.3 Semi-natural grassland in South West England

A distinctive type of semi-natural grassland remains today in Devon and North West Cornwall called by the local name of Culm grassland. Vegetation with similar plant communities may be found in South-West Wales and South-West Scotland and are known as Rhos pastures or wet heathland (Evans 1989, Wolton 1991). The vegetation embraces a complex of wet, acid grassland, wet heath, fen and mire communities. It is characterised by the presence of *M. caerulea* which often contributes to 50% or more of the vegetation cover. Rushes, sedges, ericaceous shrubs, bryophytes, grasses and herbs such as *Cirsium dissectum*, *Lathyrus montanus*, *Dactylorhiza maculata* and *Succisa pratensis* are important components. Fauna such as Curlew, Lapwing, Harvest mice and the rare Marsh Fritillery butterfly (DWT, 1991) are supported by this vegetation.

Despite it being of national and international importance there is a poor understanding of this highly varied vegetation. Following work by researchers such as Tansley (1911) and Tutin, Heywood, Burges, Valentine, Walters and Webb (1964), the Braun-Blanquet classification system comes some way in defining Culm grassland vegetation as the Class *Molinio-Arrhenatheretea* and Order *Molinietalia* (Rieley and Page 1985, Ellenberg 1988) as shown in Table 1.2. The application of the National Vegetation Classification (NVC) has made further advances in classifying most of the main communities present as mires (Rodwell, 1991). As the boundaries of these communities often intergrade, partitions which are often artificial are difficult to define. However, Culm grassland is characterised by containing any two out of the five main communities in Table 1.3. Further details of these communities and how they may be altered by management are discussed by Devon Wildlife Trust (DWT) (1989) and Rodwell (1991). Also Culm grassland occupies an interesting position in the British grassland flora as it supports a mixture of Southern and Northern phytogeographical elements. A number geographical elements was proposed by Mathews (1937) and those most applicable have been described by Poreley (1991) and are listed in Table 1.4. Most species are found within the Oceanic West and Continental North elements together with other species which belong to the wide Eurasian or European elements.

Table 1.2 Phytosociological classification of Culm Grassland (Rieley and Page, 1985)

	Latin name	Vegetation and soils	Key species present
Class	*Molinio-Arrhenathereteea*	Hay meadows and permanent pastures	Meadow Foxtail, Red Fescue, Yorkshire Fog, Timothy
Order	*Molinietalia*	Damp grasslands with water level fluctuations	Tufted Hair-grass, Southern Marsh Orchid, Adder's Tongue Fern
Alliance	*Calthion palustris*	Soils with high organic matter content and high water table.	Marsh Marigold, Greater Bird's Foot Trefoil, Brown Sedge, Wood Club-rush
	Filipendulion	Humus-rich, damp soils subject to periodic flooding.	Square-stalked St. John's Wort, Marsh Woundwort, Great Willowherb, Reed Canary-grass
	Junco-Molinion	More acid soils forming boundary between terrestrial and peat forming associations.	Devil's Bit Scabious, Heath Grass, Purple Moor-grass, Grass of Parnassus
Associations	*Ericetalia tetralicis*	Wet-heath on shallow nutrient-poor ombrotrophic peats	Cross-leaved Heath, Heath Rush, bog mosses *Sphagnum compactum* and *S. tenellum*
		Hummock forming Sphagnum-dominated vegetation.	Cross-leaved Heath, Bilberry, *Sphagnum papillosum, S. subnitens, S. imbricatum*
	Parvocaricetea	Low sedge communities of transition mires and calcareous fens and flushes.	Marsh Cinquefoil, Marsh Stitchwort, Common Yellow Sedge, Pennywort, Marsh Lousewort, bryophytes; *Calliergon cordifolium, Riccardia pinguis*

Table 1.3 The main NVC communities of Culm grassland (Rodwell, 1991)

Community	**Supporting conditions**	**Species composition**
M16 Cross-leaved Heath - *Sphagnum compactum* , wet heath	Very variable, influenced by water-regime, soil nutrients, grazing and burning	Mixtures of Cross-leaved Heath, Heather and Purple-Moor Grass
M23 Marsh Bedstraw - Sharp-flowered Rush, rush pasture	Ill-drained pasture bordering rivers and streams or reverted pastures	Soft and Sharp-Flowered Rush, Yorkshire Fog, Marsh Bedstraw
M24 Purple-moor Grass-Meadow Thistle, fen meadow	Soils waterlogged in winter, often quite calcareous and base-rich	Purple-moor Grass, Sharp-Flowered Rush, Carnation Sedge, Meadow Thistle
M25 Purple-moor Grass-Heath Tormentil, mire	Moist well-aerated peats and peaty mineral soils	Purple-moor Grass, Sweet-Vernal Grass, Meadow Sweet, Heath Wood-rush
M27 Meadow sweet-Angelica tall herb, fen	Seasonal water fluctuations, grazing absent	Meadow Sweet, Angelica, Great willowherb, Ragged Robin

Table 1.4 Phytogeographical Elements of Culm grassland (Poreley, 1991)

Phytogeographical Element	Distribution	Characteristic Species
Oceanic West European	Holland, Belgium, France, Spain, Portugal	Bog or heath plants, Marsh Thistle, Wavy St John's Wort, Lesser Skullcap
Continental Northern	C. and N. Europe	Peat communities, Angelica, Common Sundew, Marsh Cinquefoil, Marsh Violet
Oceanic Southern	S. Europe including the Med. and W. Europe. S and SW. England	Bog Pimpernel
Oceanic Northern	NW. Europe	Bog Asphodel, Bog Myrtle
Continental Southern	S. and C. Europe, SE. England	Greater Birdsfoot Trefoil
Continental	C. Europe, SW. Britain	Sawwort

Culm grassland therefore has a strong western bias to its species composition relating to its oceanic climate especially to high rainfall. It is also known that Rhos pastures are present in North-West Brittany (Wolton 1991). The extent of similar communities in Europe is most likely to be on the far western areas of Denmark, Holland, Belgium, France, Spain and Portugal and these were defined by Polunin and Walters (1985) as Atlantic vegetation. European communities similar to the five main NVC communities of Culm grassland were found by consulting the Tablefit manual (Hill 1993) and the CORINE biotopes manual (1991) and are presented in Table 1.5. Details of European communities may be found in Ellenberg (1988).

Table 1.5 European vegetation comparable to Culm grassland (Hill, 1993)

CORINE biotopes	National Vegetation Classification
C31.1 Wet heaths	
C31.11 Northern wet heath	M16
C37 Humid grassland and tall herb	
C37.1 Meadow Sweet grassland	M27
C37.2 Eutrophic humid grassland	
C37.217 Soft Rush meadow	M23
C37.3 Oligotrophic humid grassland	
C37.312 Acid Purple-moor grassland	M24, M25

The underlying geology in addition to climate has a large influence on species composition of Culm grassland. Of primary importance are the Culm Measures, deposited during the Carboniferous Period in a deep water marine trough (Durrance and Laming, 1982). The outcrop is shown in Figure 1.1. Today only 2% of the land surface of the Culm Measures supports Culm grassland (DWT, 1989). The Upper Measures dominate the large central area of the Culm and are characterized by the presence of sandstones and shales. The lower Measures comprise of a series of dark shales with a local incidence of lavas, tuffs, limestones, cherts, and grits. The term 'Culm' may have derived from the old English word 'col' for coal, which has been exposed in a few locations.

Subsequent folding and faulting of these deposits has produced four main soil types (Dartington Institute, 1986) characterised by certain soil series as shown in Table 1.6

Table 1.6 The relative coverage of soil types on the Culm measures
(Dartington Institute, 1986)

	Soil type	Soil series and associations	Percentage (%)
1	Brown Gleyed brown	Neath, Dunsford Holsworthy	52
2	Surface / ground water gleys	Tedburn, Brickfield	29
3	Podzols	Loxhore	12
4	Pelosols	Hallsworth (Halstow)	7

Details of these complex series are discussed by Findlay, Colbourne, Cope, Harrod, Hogan and Staines (1984), and often have poor drainage and structure. Soil conditions associated with these properties are further exacerbated by a high, mean annual rainfall of 1150 mm for North Devon (Harrod, 1977) which results in soils which are nutrient-poor and difficult to manage.

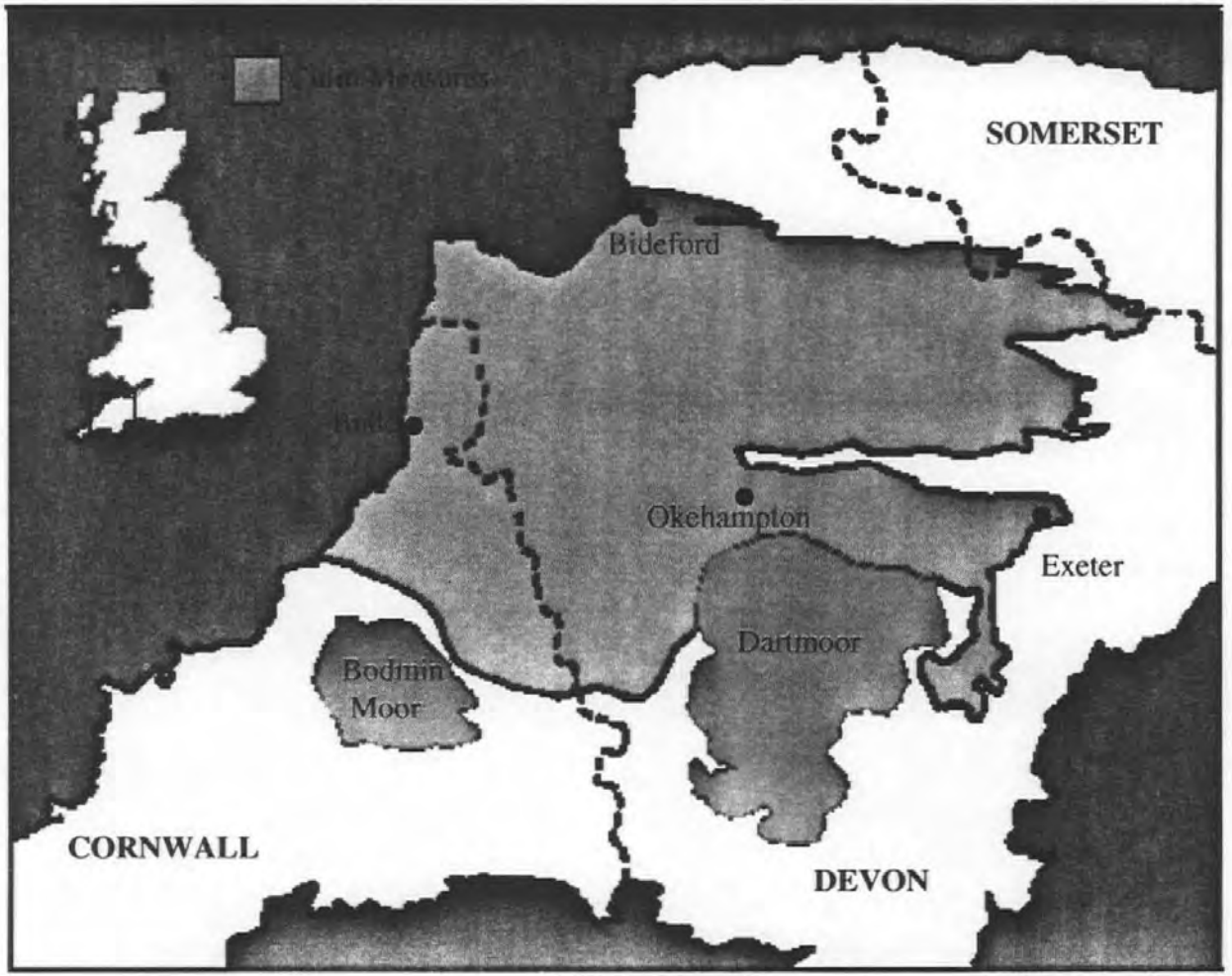


Figure 1.1 The Distribution Of Culm Measures In South-West England

Culm grassland communities have been influenced traditional methods of management which have continued for centuries as soil conditions make cultivation difficult. Since the Second World War developments in drainage and the increased use of artificial fertilizers has enabled this low productivity land to be converted into productive pastures. A dramatic decline in semi-natural Culm grassland area has resulted, with an estimated 92% loss since the beginning of this Century (DWT, 1989). The remaining area is highly fragmented as 3000 hectares in Devon are spread over 450 sites, with most of the larger areas designated as SSSIs. Agricultural improvement as recommended by ADAS (1978) including drainage (Armstrong and Garwood, 1991) is responsible for 87% of the loss. Abandonment with ensuing scrub invasion and inappropriate management accounts for the remaining 13%. The relative coverage of the different communities has also altered. The M24 community contributes to only 9.5 % of the remaining Culm grassland whereas M25, M23 and M16 contribute 31 %, 19 % and 15 % respectively. To rectify or slow down this loss, grants have been made available to Culm grassland owners through the Wildlife Enhancement Scheme (English Nature, 1991) and the Countryside Stewardship Scheme (Countryside Commission, 1992) which involves the formation of long term management plans.

1.4 Soil:plant relationships : a review

1.4.1 Introduction

In recent years countryside conservation has progressed from preservation and protection (Westhoff, 1983) to the concept that human intervention, in the form of management, is vital in creating and maintaining a variety of systems particularly semi-natural grassland (Evans, 1992). To understand how the application of management may effect a community it is important to have a knowledge of the relationship between the soil and vegetation of a particular system. The aim of this review is to explore how Culm grassland fits in with current information and theories of this relationship, and pinpoint areas where there is a paucity of information which may be supplemented by this study. The review concentrates on how soil conditions, particularly soil nutrient availabilit, may influence semi-natural plant communities in general, and more specifically Culm grassland where possible.

First, environmental factors most important in influencing nutrient availability of Culm soil are discussed. This discussion includes general chemical factors followed by a more detailed review of soil phosphorus availability which is of particular interest in this project. A discussion of the modification of nutrient availability directly and indirectly and how in theory it may effect the community composition is followed by a summary of strategies and vegetation processes required by plants to adapt to the Culm grassland environment. A final section covers the various methods currently employed to monitor nutrient availability including soil and plant analysis some of which were utilised in this study.

1.4.2 Factors controlling soil nutrient availability

Some plants have evolved and adapted to agriculturally unproductive soils of the Culm Measures which are often low in available nutrients. The nature of the soils formed are complex and are influenced to a large extent in Devon as elsewhere by climate and topography. Subsequent accumulation of organic matter from plant death and decay influences the cycling of nutrients in the system. These factors influence physical and chemical conditions which in turn effects the release of nutrients from the soil to the plant roots. Chemical and physical factors will be discussed separately, although in reality they have a combined influence (Brouwer, 1978). Of prime importance in this investigation is the effect of general chemical factors on soil nutrient availability. Studies by Lloyd and Pigott (1967) and Rorison (1971) and more recently Gough and Marrs (1990 a,b), Marrs, Gough and Griffiths (1991) and Pywell, Webb and Putwain (1994) have suggested that low availability of soil phosphorus plays an influential role in the maintenance of species-rich grassland. To investigate its influence on Culm grassland, this project concentrates on phosphorus availability which is reviewed in detail in the following sections.

a) Chemical factors

i) General

The dominant sources of available nutrients required by plants in semi-natural systems like Culm grassland are mineral weathering and organic matter mineralisation. The products of mineral weathering such as silicate clay minerals, calcite, apatite and gypsum are complex insoluble compounds and serve as reserves for nutrients. The clay or inorganic particles act as the solid phase release cationic nutrients such as K, Fe, Mn and Zn. Expanding lattice clay minerals such as Montmorillonite may be particularly influential as their 2:1 structure provides a larger area for cation exchange, as discussed by Mengel and Kirkby (1979) and Russell (1988). The breakdown of dead plant material and excrement forms an organic matter pool which is broken down by soil organisms releasing carbon, nitrogen, sulphur, phosphorus as well as minor elements. Organic matter provides the main soil reserve of nitrogen and also some phosphorus and sulphur. Reversible biological and chemical

processes enable nutrients to become soluble (non-labile to labile) and available for plant uptake. Soil pH has a significant effect on release of nutrients particularly phosphorus by the exchange of hydrogen ions for other cations on the soil colloids known as buffering (Rowell, 1994).

Nutrients in the ionic form are made available to plants via the soil solution. The latter is highly variable in quantity and chemical composition due to a number of factors such as plant uptake rate, temperature, water content and incomplete connection between soil pores which affect mineralisation rates and chemical equilibria. The quantity of nutrients within the soil solution is often far less than plant requirements over a growing season which is particularly true for phosphorus availability. For example, a cereal crop requires 20 kg P ha^{-1} while the soil solution contains only 0.5 - 1.0 kg P ha^{-1} at any one time (Brady, 1984). Soil solution may also contain different chemical species of a nutrient such as phosphorus which may be more or less available to the plant. Ron Vaz *et al.* (1993) have defined chemical species of phosphorus in soil solution as total dissolved P (TDP), dissolved reactive P (DRP), dissolved organic P (DOP) and dissolved condensed P (DCP). Further experiments found that these chemical species may alter in their relative contribution to total solution P in response to fertiliser applications (Shand, Macklon, Edwards and Smith, 1994). Nutrient availability not only depends upon nutrient concentration but also the ability of the soil to maintain nutrient concentration (Nye, 1968). The release of nutrients will depend on quantity (the labile pool of easily exchangeable nutrients) and intensity (soil solution concentration) factors (Fried and Shapiro, 1961; Holford and Mattingley, 1976; Russell, 1988; Raven and Hossner, 1994). This concept is commonly employed in soil phosphate studies where soils have different abilities to absorb phosphate.

Essential elements for plant growth such as nitrogen, phosphate, potassium, calcium, magnesium and sulphur must be present in a specific concentration range within the soil solution to allow sufficient uptake for optimal growth (Brady, 1984). Minor elements such as iron, chlorine, copper, manganese and zinc are also essential in small quantities. Table 1.7 shows a general summary of the elements essential for plant growth. This includes the relative quantities which may be extracted from the soil by laboratory methods and may be available for plant uptake. Overestimation by soil extractable values is indicated by the fact that much smaller amounts are utilised by plants. The elements form various structures and carry out various functions within the plant. Their deficiency may be very damaging to the plant's growth and reproduction.

Nutrient requirements of the Culm grassland community will vary according to species and also through time depending on growth stage and type of plant organs supplied. In general plants require high level of nutrients at the early growth stages and results in a high uptake rate. The rate of uptake reaches an equilibrium once the stems elongate and then slows during translocation of nutrients from the leaves and stems to the grains, during the ripening period (Mengel and Kirkby, 1979). Thus plant requirements may also influence the release of nutrients from the soil complex. Uptake of nutrients particularly phosphate is related to the mobility of ions and the proximity of root absorbing surfaces (Russell, 1988). A plant absorbs nutrients by disseminating a dense mass of roots between soil colloids. Nutrients move by mass flow to the roots along a concentration gradient and a nutrient depletion zone is formed following uptake. The size of the depletion zone will depend on the different rate of movement by the ions. Typically nitrate which diffuses more rapidly will have a much larger depletion zone than phosphate which moves at a slower rate. Roots themselves may also influence nutrient uptake by for example excreting organic and inorganic substances which may affect the availability of iron, copper and zinc.

Table 1.7 The major and some minor minerals used by plants (Moore and Chapman, 1986; Baron, 1979)

Element	Form adsorbed	Soil Extractable (mg kg^{-1})	Quantity utilized (% dry weight)	Principal Functions	Effect of Deficiency
Major Elements					
Phosphorus	$H_2PO_4^-$	2 - 20	0.4	Involved in energy transfer (ATP and ADP). Nucleic acids. Phosphorylation. Coenzymes	Small-sized plants; dull, dark green
Nitrogen	NO_3^- (NH_4^+)	0.5 - 10 (0.1 - 1)	3.5	Amino-acids, proteins, and nucleotides	Chlorosis
Potassium	K^+	50 - 200	3.4	Enzyme, amino-acid and protein synthesis.Stomatal opening\closing and osmotic relations. Cell membranes	Leaves have yellow edges; early death
Calcium	Ca^{2+}	100 - 2500	0.7	Calcium pectate of cell-walls. Development of stem and root apices. Enzyme activation.	Stunting of the root and stem
Magnesium	Mg^{2+}	20 - 50	Small quantity	Part of the chlorophyll molecule. Activator of some enzymes in phosphate metabolism.	Chlorosis
Sulphur	SO_4^{2-}	0.4 - 2	Small quantity	Proteins which contain thiol groups. Active groups in enzymes and coenzymes.	General chlorosis
Minor Elements					
Iron	Fe^{2+}	50 - 100	Small quantity	Chlorophyll synthesis. Cytochromes and some enzymes.	Chlorosis
Chlorine	Cl^-	0.04 - 0.4	0.8	Osmosis and anion/cation balance; probably essential in photosynthesis.	Effects slight
Copper	Cu^{2+}	20 - 300	Trace (<0.0001)	Activator group of polyphenol and ascorbic oxidase enzyme systems. Photosynthesis.	Dieback of shoots
Manganese	Mn^{2+}	4 - 400	Trace (<0.0001)	Activator of some enzymes. Photosynthesis.	Chlorosis
Zinc	Zn^{2+}	100 - 4000	Trace (<0.0001)	Activator of some enzymes. Photosynthesis.	Leaf malformation

ii) Soil phosphorus availability

As phosphorus availability is often a limiting factor in semi-natural grassland systems it is important to review why and how it could act as a limiting factor in Culm grassland. Phosphorus originates from the weathering of the mineral apatite contained within soil parent materials (Foth, 1990). Apatite weathers slowly and releases the ion $H_2PO_4^-$ in to soil solution. This orthophosphate ion may be immobilised in a number of ways such as by the uptake by plant roots and microorganisms and is converted to organic forms in plant tissue and microbial biomass. Phosphorus is a major macronutrient required by plants for growth and is involved in the transfer of energy and reproduction (Emsley, 1982). The fraction of P largely absorbed by plants are the primary and secondary orthophosphate ions $H_2PO_4^-$ and HPO_4^{2-} (Tisdale, 1989), which may be detected by the colorimetric method described in Chapter Two. Below a soil solution pH of 7.2 the main form of P found in soils is $H_2PO_4^-$ and this form was most likely to be predominant on both improved and Culm grassland soils. This is released again into soil solution via the breakdown of organic material during plant decomposition and mineralisation of organic matter. These processes of have been described in detail by Mengel and Kirkby (1979), Emsley (1982), Harrison (1987), and Russel (1988).

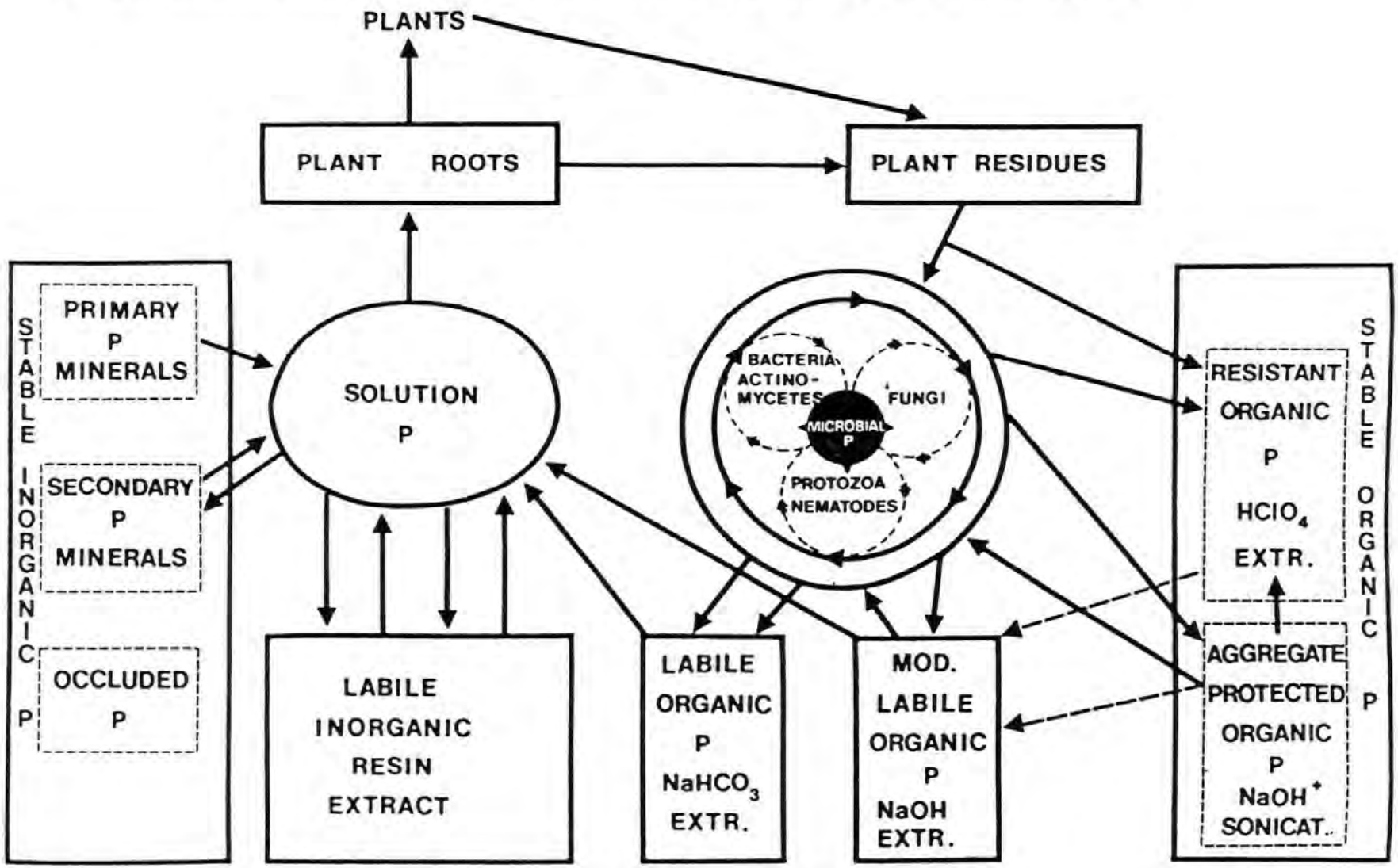
Available P has been defined as the fraction removed by plants from soil solution and is also influenced by processes of fixation and dissolution in the soil (Russel, 1988). As P is released in to soil solution it rapidly reacts with other ions forming calcium, iron and aluminium phosphate precipitates depending on pH and becomes adsorbed to clay minerals (Foth, 1990) as shown in Figure 1.2. The presence of the above impurities makes attempts to relate P to specific soil minerals difficult (Russell, 1988). These forms of P are unavailable for plant uptake which may classified as occluded or non-labile P and results in very low concentrations in soil solution. The application of artificial fertilisers, as would happen when Culm grasslands are improved, has been found to not substantially increase soil solution concentration. However a build up or residue of P in the upper soil horizon has been found (Russell, 1988) due to the occlusion or fixation of P. This is particularly true for clay soils, as in the case of Culm grassland soils, which provide a greater number of

bonding sites for P in comparison to sandy soils (Marrs, 1990). Little information is available on soil solutions of unimproved soils but they are thought to be lower than the range of 0.3 to 3 kg P ha^{-1} in agriculture soils quoted by Mengel and Kirkby (1979).

The slow release of fixed or occluded P from the mineral storage compartments in to soil solution (Figure 1.2), results in P often becoming a limiting factor of agricultural production and natural plant communities. Culm grassland, like many oligotrophic systems, is reliant on this slow release of P from the storage compartments. The concentration of P in solution is maintained by a dynamic equilibrium between the non-labile and labile (unavailable to available) forms of P and is of prime interest in this study. This ability of the soil to fix and release P and maintain the concentration of P in soil solution may be known as the phosphate buffer capacity (Mengel and Kirkby, 1979). A high buffering capacity indicates that the soil has a high fixation capacity for P and may maintain a constant concentrations of P in soil solution. To obtain a response substantial amounts of P would be required to increase P availability (Russell, 1988). The concentration in soil solution will also be influenced by the extent of P adsorption towards occlusion, rather than the total quantity absorbed (Elmsley, 1982). The quantity / intensity relationship described by Mengel and Kirkby (1979) attempts to explain the release of P.

On release from the soil complex the supply of P to plants is further limited by the insufficiency of mass flow and the reliance on diffusion of P through the soil solution to the root surface. Diffusion is affected by water content, tortuosity of the diffusion path, temperature and the P buffering capacity of the soil (Tisdale, 1985). It has important consequences on the availability of P to plants, as depletion of P around the root forms much larger zones which may be 100 times greater for phosphate than for nitrate (Mengel and Kirkby, 1989). Unlike P, nitrate is a mobile nutrient, relatively unreactive in soil solution, rapidly removed by plants or leached and is not fixed by the soil. Taking into account the limiting characteristics of P within the soil complex it is likely to a key factor in Culm grassland soils and forms a major part of the research.

Figure 1.2 **Schematic diagram of the measurable components of the P cycle (From Harrison, 1987)**



Of particular interest in this project is the release of P from the soil complex and its effect on the amount that may be removed by plants. The possible change in availability of P after fertilisation is of prime interest as this will effect species composition and conservation value. Thus P supply in Culm grassland soils will depend on the release and fixation of P to and from the soil solution which will also be influenced by plant demand. The first process is reversible whereas the second is irreversible. The dominance of the two processes on P concentration in soil solution was investigated by Fried, Hagen, Saiz del Rio and Leggett (1957). From their results they concluded that plant uptake was much slower than dissolution of P from the solid phase and in turn the solution concentration governed plant uptake. But the converse may be found as plant demands will deplete P from the soil solution around the root surface which induces a diffusion gradient. As the investigation of soil P in this study was undertaken independent of any study of direct P uptake by plants the influence of plants could only be assessed indirectly. It was proposed that soil solution concentration will indicate the actual P concentration which Culm grassland plants remove. This relationship may change over the growing season as plant demand changes. Although it was realised that soil P dynamics are highly complex it was important to obtain an insight in to P in soil solution as this has a great influence on the vegetation.

b) Physical factors

Physical conditions of the soil such as texture and structure have an indirect influence on nutrient availability. Texture and structure in turn is controlled by the proportion of sand, clay and silts within the soil. As the parent material is composed of mainly clay shales, Culm grassland soils are fine textured which tend to be silty-clay loams with a high proportion (38%) of clay present (Harrod, 1981). The ability of clay to swell and contract is often influenced by the amount of clay minerals with an expandable 2:1 structure such as montmorillonite (Russell, 1988). Clay soils also have a high water holding capacity which limits drainage. This results in anaerobic conditions which may prevent or slow down chemical processes involved in the release nutrients available for plant uptake. The presence of a high proportion of silt sized particles (50%) (Harrod,1981) which are composed of unstable minerals (Pitty, 1978) may weaken the aggregates. As a result the Culm soil

structure is often unstable and prone to compaction and poaching (ADAS,1978).

The physical nature of the soils particularly soil water regime and hydrology is influenced further by relief and slope which is characteristically undulating on the Culm Measures. The brown soils on the slopes are drier as they are relatively well-drained and permeable. The flatter areas are more prone to surface waterlogging while the foot slopes are affected by ground water fluctuations. The soils are found in these latter locations are characterised by the development of a gleyed horizon. The process of gleying is a key factor in horizon differentiation in Culm soils which involves the reduction, mobilisation and removal or redeposition of iron compounds. Periodic waterlogging allows re-oxidation produces soils with grey, yellowish and ochrenous colours and persistently waterlogged soils are wholly grey or bluish grey (Findlay *et al*, 1984). Periodic waterlogging provides reducing conditions which may slow down or prevent chemical reactions (Russell, 1988).

Soil structure alters naturally with depth and horizon differentiation and may have an indirect influence on nutrient availability as it controls heat transfer, aeration, bulk density, porosity and most importantly soil water availability. As plants remove nutrients dissolved in soil solution, soil water conditions will have an influence on nutrient availability. Due to their fine texture and high number of fines pores, Culm soils have a high water storage potential. As a result there is limited downwards movement of water or drainage through the soil profile which reduces the loss of nutrients through leaching. Slow movement of water may also cause drought during the summer months as water rising by capillary action, although present in clay soils, (Reid and Parkinson, 1987) may be insufficient in replacing losses by evapotranspiration. Drought on Culm grassland soil is unlikely as normal climatic conditions do not allow extensive drying out. The extent to which water is held within the soil pores is indicated by the suction or energy required to removed the water and will influence its availability to Culm grassland plants. Suctions necessary to remove water from Culm grassland soils will depend on the soil moisture characteristic curve (Reeve and Carter, 1991). As most plants can not remove water held at suctions greater than 1.5 MPa, about 30% of water is unavailable in clay soils, such as Culm soils (Mengel and Kirkby,

1979). Therefore, taking in to account climatic conditions, soil water availability is not a limiting factor on Culm grassland. The measurement of water conditions is part of the background information, to the main study of soil nutrient conditions especially phosphorus availability.

Semi-natural grasslands are susceptible to changes in water conditions particularly alterations in groundwater supply (Van Strien and Melman, 1987). Effects may be direct such as a reduction in available water or indirectly by changing nutrient availability over a relatively short period of time. Van der Woude, Pegtel and Bakker (1994) reported that the drainage of a community similar to Culm grassland in the Netherlands changed the availability of nutrients. This resulted in the community being limited by soil phosphate availability instead of the original nitrate limitation (Grootjans, Schipper and Van Der Windt, 1986). Grootjans *et al.* (1986) also investigated the relationship between fen meadow species composition and calcium content of groundwater. They found that characteristic species were restricted to areas of high water tables and had little relation to calcium content. A similar situation was encountered by Loach (1966) as the effects of low nutrient concentration in a *Cirsio-Molinietum*, were exacerbated by a consistently high water table which restricted rooting depth and ability of roots to remove nutrients. *M. caerulea* favoured high fluctuations of the water table which allows good aeration of the soil (Sheikh 1969, Proffitt 1985). Changes in plant community production and nutrient accumulation in response to groundwater levels, was investigated by Berendse, Oomes, Altena and Visser (1994). They found that raised groundwater levels reduced annual nitrogen mineralization which led to a 20% increase in the accumulation of nitrogen in the above-ground biomass.

1.4.3 Modification of soil nutrient availability

a) Increase in nutrient availability

Nutrient availability may be increased directly by the application of artificial fertilisers or manure and indirectly by atmospheric deposition and succession. Previous work on semi-natural communities has shown that increases have detrimental effects and are likely to be detrimental to Culm grassland communities. For example the effects of fertilisers on grassland were studied in the Park Grass experiment set up in 1856 at Rothamsted, England. A pasture divided into 20 plots received different combinations of fertilizers and resulted in a single species dominating 90-99% of the total plant biomass by 1959 (Thurston, 1969). A shorter term experiment by Elberse, Van Den Bergh and Dirven (1983) compared two unfertilized plots with two plots receiving NPK fertilizer in the Netherlands. Together with a 75% loss in species number, species composition had altered with the loss of *Festuca rubra* after 10 years and the establishment of *Arrhenatherum elatius* (L.) which was absent at the start of the experiment. Effects of nitrogen additions on vegetation of Somerset peat moor was investigated by Mountford, Lakhani and Kirkham (1993). In a relatively short time from 1986 - 1991 nitrogen additions were found to encourage grasses, and produced a rapid decline in species diversity, including a decrease in all *Carex* and *Juncus* species.

In some regions nutrient inputs to semi-natural vegetation has increased via atmospheric deposition. An increased concentration of nitrogen and sulphur inputs is thought to have played a role, in the replacement of *Erica tetralix* dominated heathland by *M. caerulea* in the Netherlands (Berendse, Bobbink, and Rouwenhorst, 1989). This has resulted in a decline in the associated rare plant species. *M. caerulea* was found to have a greater capacity for obtaining and storing nutrients at higher levels of fertility (Berendse, Oudhof and Bol, 1987). In Britain, atmospheric nitrogen inputs are thought to be partly responsible for the deterioration of *Calluna vulgaris* and the increase in grass cover in three East Anglian heathlands (Woodin and Farmer, 1993).

Changes in soil conditions have been found during succession (Miles, 1985). For example as *C. vulgaris* heathland develops into *Betula* woodland, soil conditions develop from a podzol to a brown-earth soil (Marrs, 1990). Studies by Wells, Sheal, Ball and Ward (1976) found an increase in supply of inorganic nitrogen in early succession from arable to grass. However, the evidence is not always so clear; Gough and Marrs (1990) found increases in nutrients whereas Berendse (1990) found decreases in nutrients as succession progressed. Therefore changes in nutrient may depend upon previous management and the soil type.

b) Manipulation of nutrient availability by management

To date there has been little study of the effects of management on the soil:plant relationships, particularly on Culm grassland. Most field experiments have monitored the effects on plant communities with very little information on the changes in soil nutrient availability. The application of management is important in the manipulation of nutrient availability to prevent a build up of nutrients within the key storage pools of the system. Most management strategies involve primarily the removal of plant material, methods of which have been reviewed by Marrs (1990), Bakker (1989) and Harrison (1985).

Management mainly involves the removal of plant material by grazing or cutting. Grazing was incorporated in the Llyn Llydaw study of an *Agrostis-Festuca* grassland. Sheep grazing removed a very small net amount of phosphorus but there was no net removal of nitrogen, calcium and magnesium (Marrs, 1979). Other than removing some nutrients, grazing has an impact on the transfer between vegetation and nutrient pools. At the Llyn Llydaw site, grazing reduced the accumulation in the litter pool, by permanently removing vegetation. In contrast grazing could increase nutrient cycling and biomass production and in turn cause a reduction in species richness (Marrs, 1985). Different systems of grazing management such as removing animals from the pastures at night could limit the return of excrement, which contains up to 90% of the nutrients consumed (Bradshaw 1980, Perkins 1978).

Intensive cropping was employed to reduce soil fertility in the Exhaustion Land Experiment reported by Johnston and Poulton (1976) and described concisely by Marrs (1990). It took 71 years of continuous cereal cropping to deplete available phosphorus which declined linearly with time. Cereal crops were also used at Ropers Heath in Suffolk to reduce fertility and aid restoration of the original heathland (Marrs, 1985). It was found that if all above-ground material was harvested a net removal of N, P, and K took place over two years. In this experiment the cessation of fertiliser application may have caused a reduction in available P, by causing it to incorporate into the organic matter. However, there is little information on this fixation and its subsequent long term release (Gough and Marrs, 1990).

Cropping involving the removal of grass to make hay or silage (or zero-grazing) is often compared to the effects of grazing. The influence of different cutting regimes were investigated by Bakker (1989) in a nature reserve in Holland. More nutrients were removed by a twice cut regime than a single cut regime but a poor relationship was found between soil nutrient removal and yield of standing crop. In fact the removal of nutrients was very low in comparison with the size of the soil nutrient pool and was a very slow process (Bakker, 1989). Rizand, Marrs, Gough and Wells (1989) suggest that the removal of grass clippings is more effective in maintaining a low phosphorus status.

Nutrient availability is also influenced by non-agricultural strategies such as burning, described by Gimmingham and Smidt (1983) in the management of heathland. It provides an efficient removal of above-ground biomass and produces regeneration gaps. Chapman (1967) showed that burning lowland heath removed 95% of nitrogen, 21% of phosphorus and 21% of potassium as smoke. The remaining nutrients are either left as ash, leached, fixed or removed by plant uptake. A more drastic method of removing nutrients is by topsoil removal (Marrs,1990) from which heathlands benefitted in the past, by peat cutting for fuel. Topsoil removal is ideal if the objective is to reduce nutrient availability immediately but it removes most of the seed bank which is vital for species regeneration.

c) Relationship between nutrient availability and species composition

i) Strategies employed to adapt to nutrient-poor environments

In order for plants to survive on Culm grassland strategies are required to combat the destruction of plant biomass by trampling and grazing (disturbance) and shortages of mineral nutrients (stress) or nutrient limitation (Chapin, Vitousek and Van Cleve, 1986). Of the three distinct types of strategies which are usually found in combination, (competitors, ruderal and stress-tolerators) theorised by Grime (1979), stress toleration is the most likely successful strategy employed on Culm grassland. Stress-tolerators such as *Erica tetralix* (cross-leaved heath) cope with high stress and low disturbance (Berendse and Elberse, 1989) and have efficient systems of nutrient acquisition. They are able to absorb low concentrations of nutrients and do not increase absorption capacity (Chapin, 1980). This strategy is typical of the grass species *Cynosurus cristatus* which did not respond to increased availability of phosphate (Bradshaw, Chadwick, Jowett, Lodge and Snaydon, 1960). This inability to increase nutrient uptake may result in competitive exclusion.

Plants may also respond phenotypically to nutrient stress by increasing the root:shoot ratio. Berendse and Elberse (1989) found that the root:shoot ratio increased with declining nutrient concentration. However, Chapin (1980) reported no change in Australian heath plants which were adapted to low phosphate conditions. These disparate results may be caused mycorrhizal interactions between plant roots and soil fungi as described by Harley and Harley (1987) which are most developed in unproductive habitats (Chapin, 1980). Infections of mycorrhizae have been found to increase the root surface area and in theory increase nutrient acquisition 10 to 100 fold. The hyphae extend beyond the root depletion zone and translocate nutrients to the host thereby increasing the amount of nutrients available to the plant (Harley and Smith, 1983). Infections are often associated with the uptake of phosphate, a common limiting factor in unproductive environments and may allow the plant to utilise different forms of phosphorus (Woldendorp, 1978). However, the presence of infection of Culm grassland species is currently unknown. There is a possibility of associations with some species of a *Molinietum caeruleae* association Mejstrik (1972).

The fluctuation in the availability of nutrients throughout a growing season may be more pronounced in nutrient-poor environments. Plants adapt by having a low relative growth rate (Chapin, 1980) which allows nutrients to be obtained over a long period of time (Grime, 1979). Also some species such as *Festuca ovina* and *Nardus stricta* are able to remove nutrients in excess of their utilisation. *Agrostis setacea* (*curtisii*) shows a progressive accumulation of phosphate within its tissues known as luxury consumption (Chapin, 1980) which has also been found to occur in *M. caerulea* (Berendse, Beltman and Bobbink, 1987) (see Chapter five). As most species of Culm grassland are perennials, nutrients are lost by the abscission of leaves and flowers, leaching of leaves, root death and removal by grazers (Berendse and Elberse, 1989). To reduce nutrient loss *M. caerulea* dies-off above ground in the autumn and nutrients are withdrawn into storage organs below-ground, ready for remobilisation at the beginning of the growing season. In contrast *Erica tetralix* a woody evergreen, retains its nutrients within its stems and leaves in preparation for remobilisation to the growing regions of the plant.

ii) Influence of nutrient availability on species composition

A likely effect of modification in nutrients status, particularly an increase in soil nutrient availability, is a change in species composition. A theoretical relationship of this change has been explored by Grime (1979) and Al-Mufti, Sydes, Furness, Grime and Band (1977). They postulate that an increase in availability of nutrients will encourage growth of more competitive species and thus increase biomass production. The more competitive species become dominant by competitive exclusion (Grime, 1973) to the detriment of stress tolerators which do not have the ability to respond to increased nutrient availability (Vermeer and Berendse, 1983) and decline in species-richness may occur. In the model species density (species number per unit area) responds to a decline in stress or disturbance and an increase in nutrient availability, which in turn relates to an increase in standing crop and litter production (Marrs, 1990). Al-Mufti *et al*. (1977) postulate that the point of change in this relationship is within the range of 350 - 750 g m^{-2} of dry matter production. Below this threshold, stress/disturbance dominates and above this threshold a few species may dominate.

Management may be able to exploit the thresholds within the model (Marrs, 1990), which may be important for the conservation of Culm grassland. The model is supported by Vermeer and Berendse (1983) in their study of fen communities who found a significant positive correlation between biomass and species number. Moore and Keddy (1989) studied the relationship within a single vegetation type and disagreed with these results. They found that within a vegetation type, the relationship between biomass and species number did not exist and results were dependent on the scale of the investigation. Gough, Grace and Taylor (1994) concluded from their study of 36 marsh communities that community biomass has a limited capacity to predict species richness across a broad range of habitat conditions. Although the response of communities is not conclusive, the model remains useful as it recognises points at which nutrient availability shifts which may lead to changes in species composition.

1.4.4 Monitoring nutrient availability

As previously discussed, soil nutrient availability of Culm grassland is governed by a combination of physical and chemical factors. It is possible to measure the total nutrient concentration within a soil, but this will only give an indication of the potential supply of nutrients and no indication of the proportion of nutrients actually available for plant uptake at any point in time. As a general guide only 1-2% of the total nutrient content of soils is readily available for plant uptake (Brady, 1984). Thus an available nutrient may be considered as the nutrient fraction in the soil which is accessible to plant roots (Mengel and Kirkby, 1979). Nutrient availability will depend upon the chemical and physical characteristics of a nutrient and may be assessed by a number of methods using either soil or plant measurements, or both together. Such methods have been widely used in the context of agricultural production, but not in the investigation of natural plant communities. In agricultural situations the nutrient supply rate and nutrient limitation are closely linked (Binkley and Vitouesk, 1989). In natural ecosystems this relationship is further complicated by differences in species composition, plant life stage and water supply. A central part of this project was the measurement of available nutrients, particularly phosphorus and its

relationship with plant nutrient concentrations. Nutrient availability may be measured by a number of techniques; all are indirect assessments of nutrient concentrations at the rhizosphere but it is necessary to make some attempt to assess relative nutrient concentrations in relation to management. These techniques are reviewed in the following sections a number of which have been employed in the project.

a) Extraction from the soil

Available nutrient concentrations are usually estimated by replacement with an extractant. This method has been used extensively and is reviewed by Black, Evans, White, Ensminger and Clark (1965), Blakemore (1966), Hesse (1971) and Allen (1974). A variety of extractants are employed for different ions depending on solution chemistry and may also be used to sequentially remove different fractions of a nutrient (Magid 1993, Bieleski 1973). For example, solution concentration may depend on the pH of the soil; this is particularly relevant to the extraction of phosphorus as shown in Table 1.8. This method is relatively simple, inexpensive and has been widely employed in the investigation of agriculturally improved soils and is useful in indicating relative impacts of management .

Table 1.8 Variety of extractants employed to remove phosphorus
(Moore and Chapman, 1986)

Extractant	pH	Soil Type	Extractant soil ratio
Sodium bicarbonate	8.5	calcareous	20 : 1
Truogs reagent	3.0	acid and neutral	200 : 1
Acetic acid	3.0	acid and neutral	40 : 1

However, there are problems of using chemical extractants particularly in the investigation of concentrations removed by semi-natural plant communities as studied in this project. A major problem is overextraction, as some less available forms as well as loosely held or more available forms of nutrients are replaced by the extractant (Moore and Chapman, 1986). This is particularly true in the investigation of phosphorus availability as aluminium and calcium phosphates may be released during extraction which are less available or occluded forms of P and are not normally removed by plants. Over extraction may be overcome by direct extraction of soil solution in either the field or the laboratory, methods of

which were reviewed by Adams (1974). Summerfield (1974) found that mire water was highly variable in composition and information including depth of plant roots, distance from the plant and time of year was required for more meaningful results. This may be provided by the removal of soil solution by suction cups, thoroughly reviewed by Litaor (1988) and Grossmann and Udlift (1991). Although there are problems with this method, they are simple to install, allow repeated measurement, and cause negligible soil disturbance. The source of the nutrient within the soil is unclear as it is difficult to measure the volume of soil the sample was extracted and from which pores it was obtained (England, 1974). The release of water will depend on the water release characteristics of an individual soil which was investigated by Reeve and Carter (1991) by applying different suctions with a centrifuge. Zabowski and Ugolinia (1990) found that solution composition relates to the tension at which water is held in the soil. Other methods of solution removal include column displacement and lysimeters which collect free-draining soil as employed by Lorenz, Hamon, and McGrath (1994) and Zabowski and Ugolinia (1990) respectively. Both these studies compared these methods with centrifugation and found contradictory results. Zabowski and Ugolinia (1990) suggest that centrifuging was better for determining potential nutrient availability whereas Lorenz *et al.* (1994) suggest displacement reflected to a greater extent nutrient uptake by plant roots. These results suggest that solution properties are greatly influenced by methods of sampling. However, when comparing P concentration in soil solutions Adams, Burmester, Hue and Long (1980) found there was very little difference between the above methods as concentrations were very low.

Ion exchange resins have also been used to extract nutrients from the soil in both the field and laboratory. The resins have various ions saturating the exchange sites depending on the anion or cation of interest. In the case of nitrate uptake investigations, the exchange sites are saturated with NaCl, and then buried in the soil for given time. The accumulated nitrate is then recovered by washing with KCl (Binkley and Vitousek, 1989). They may be used either free in solution or in mesh bags. Sibbeson (1978) investigated the efficiency of different resins to extract soil phosphorus by correlation with uptake by *Lolium perenne*, and found that the bicarbonate form had the closest correlation.

The ability of the soil to fix nutrients, particularly phosphorus, may provide information on potential nutrient availability. Soils that strongly fix P generally have a lower P availability than soils that can maintain higher levels of P in solution (Binkley and Vitousek, 1989). This has been investigated by shaking soil with different concentrations and monitoring adsorption and release of a nutrient. From this information sorption isotherms as described by Russell (1984) and Raven and Hossner (1994) are produced. Much work has been carried out by Barrow and Shaw (1975 a, b, c) in investigating the effects of temperature, time of contact and time since sampling, on fixation capacity. He, Yuan, Zhu, and Zhang (1991) used a similar method and postulated fixation could readily account for P uptake by plants and values obtained were equivalent measurement of available P, by sodium bicarbonate extraction. Phosphorus adsorption maxima have been used to distinguish heathlands which were either dominated by *Calluna vulgaris*, *Ulex europeous* or *Betula pubescens* (Marrs, 1990). This may be used to indicate the differences between improved and unimproved Culm grassland soil fixation capacity.

b) Plant nutrient content

Plants nutrient content may also indicate nutrient availability and has certain advantages as it allows differences in nutrient requirements between plant species and genotypes to be taken into account (Pegtel, 1987 and Barraclough, 1993). A general relationship is discussed by Bates (1971) in which a nutrient found in high concentration in plant material has a higher availability in the soil. The relationship follows an asymptotic curve, where at a critical nutrient level in the plant, a small change in plant nutrient content may occur despite marked increases in nutrient availability (Mengel and Kirkby, 1984). Jefferies and Willis (1964) found a similar relationship in their studies of the calcicole-calcifuge habit. Methods of plant material analysis have been reviewed by Moore and Chapman (1984) and Chapin and Van Cleve (1989). Factors such the age of the plant, the supply of the plant with other nutrients and the type of plant organ or tissue must be taken in to account and may produce highly variable nutrient concentrations (Bakker, 1980). However, high variability may be necessary for species to coexist and reiterates the differences between wild plant communities and crop plants (Hayati and Proctor, 1990).

The problems of variability may be reduced by employing a phytometer or bioassay which measures the growth or nutrient uptake of a test plant (Marrs, 1990). These experiments have been applied to a variety of soils as cited by Pegtel (1987) and Harrison and Helliwell (1979). Under controlled conditions the test plant is subjected to different combinations of nutrients or a single nutrient. The growth response of *Carex echinata* to N, P and K additions was used to assess the fertility of peat soil in South West England (Hayati and Proctor, 1990). Wheeler *et al.* (1992) used test plants to assess the fertility of undrained rich-fen soils and concluded that phytometer species should have a high relative growth rate, grow continuously, and have readily germinating seeds. However, the soils used are often mixed and disturbed which may increase nutrient availability. Pegtel (1987) overcame this by using undisturbed turfs to simulate field conditions.

Isotope labelling has been employed in nutrient uptake studies combining soil and plant removal methods (Larsen, Gunary and Sutton, 1965; He, Yuan, Zhu and Zhang 1991). Soils may be labelled with isotopes of important nutrients such as ^{15}N and ^{32}P and then the uptake is monitored by the appearance of the isotope plant tissues. Nye and Tinker (1977), Chapin and Van Cleve (1989) and Gigon and Rorison (1971) have reviewed the methods and principles employed. In broad terms uptake of a label is greatest where the element is deficient and lowest where the element is in excess (Marrs, 1990). ^{32}P was used to investigate the interaction of plants, litter, peat and water in the P cycle of a fen peatland by Richardson and Marshall (1986). They found that sedge uptake was extremely low in comparison to microorganism uptake.

A review of soil:plant relationships identified aspects which are most relevant to Culm grassland. It showed the paucity of information relating to soil nutrient and physical conditions in semi-natural plant communities. Information of seasonal change in these conditions was also found to be limited. Methods used to monitor nutrient availability were discussed critically. A change in nutrient conditions especially following fertiliser applications and agriculturally improvement is likely to have a strong effect on the Culm grassland community. Also management methods most likely to maintain Culm grassland were reviewed and are an important part of this project. Of particular interest in this project is the availability of phosphorus which has been identified as a limiting factor by other workers. Also when taking into account its characteristics and availability within soils which have been reviewed in detail, phosphorus levels are most likely to be a key factors in determining semi-natural Culm grassland.

1.6 Research objectives

As noted in the preceding section, Culm grassland is a complex mosaic of plant types and forms different associations often depending on the underlying soil conditions and the level of management applied. Within Devon the work of the Devon Wildlife Trust (DWT) has helped in increasing the public awareness of this community. This has been carried out by conducting extensive plant surveys, designation of Sites of Special Scientific Interest (SSSIs), ownership and management of reserves, production of a Culm Connections newsletter to Culm grassland owners and formulation of management plans. In addition a number of experiments are in progress at the Institute of Grassland and Environmental Research (IGER), North Wyke, Okehampton (Tallowin, pers. comm.).

Although much of the Culm grassland resource has been recorded and surveyed, information relating to the edaphic conditions which support this community, particularly soil nutrient availability is limited. The main objective of the project was to gain a better understanding of the environmental conditions and how management may influence these factors. Soil conditions may be altered by management, such as agricultural improvement, abandonment and the application of inappropriate management. These changes will have important implications for the supported plant communities. Therefore, it was decided to compare pristine Culm grassland with a grassland of lower conservation value such as an improved grassland and poorly maintained Culm grassland. Variation between these plant communities was indicated by detailed monitoring of soil conditions particularly nutrient, species composition and production ecology on a limited number of sites as detailed in Chapter Two.

Comparisons took the form of seasonal measurements which showed how the Culm grassland system fluctuates throughout a period of growth. A special interest was taken in the cycling of phosphorus because P has been found to be a key limiting factor in other semi-natural environments by Lloyd and Pigott (1967) and Rorison (1971) and more recently Gough and Marrs (1990 a,b), Marrs, Gough and Griffiths (1991) and Pywell,

Webb and Putwain (1994). They have suggested that low availability of soil phosphorus plays an influential role in the maintenance of species-rich grassland. This is further emphasised by the review of soil phosphorus characteristics. It was also important to identify points or thresholds within the system where alterations could be to the detriment or benefit of the community. The artificial manipulation of supporting conditions was implemented to supplement field data. Information collected during the project described the relative changes and transfer between compartments within the system which could aid the application of management strategies in the future. To obtain these objectives the following aims evolved:-

1) To characterise soil conditions under species-rich semi-natural, and species-poor grassland on the Culm Measures of North Devon.
2) To establish the impact of past and present management on soil nutrient status and physical conditions.
3) To relate seasonal fluxes in phosphorus availability to plant uptake.
4) To pinpoint the thresholds of phosphorus levels in which species-rich *Molinietalia* will exist.
5) To formulate a simple model of the soil:vegetation system under species-rich grassland on the Culm to be employed as a management tool.

The first and second aims were investigated in the 1992 field season and results are reported in Chapter Three which provides a characterisation of the Culm grassland environment and baseline for further study. These results indicated that soil phosphorus availability was an important factor and was studied further in 1993. This included an investigation of the third aim which is reported in Chapter Four and Five and provides detailed information on Culm soil phosphorus availability and Culm grassland plant production. These two chapters also include information to satisfy the fourth aim which is investigated in a phosphorus addition experiment, reported in Chapter Six. Finally the information collected over the two field seasons is employed to suggest strategies for phosphorus management in the Culm grassland system.

1.7 Summary

This chapter has highlighted the loss of semi-natural communities in Britain particularly since the Second World War. The semi-natural grassland which is the subject of this project has been reduced in area and quality by agricultural improvement of heavy, clay soils of the Culm Measures. Replacement of traditional management strategies of summer grazing and autumn topping or burning by ploughing, drainage and reseeding has diminished this valuable resource. Changes in soil conditions have altered or reduced the species-richness of the plant communities which are dominated by the presence of *M. caerulea*. These communities are highly varied depending on the underlying soil conditions and the input of management. It was decided to concentrate on the influence of soil conditions particularly nutrient availability under Culm grassland in comparison to an improved grassland. The review of soil:plant relationships within natural, agriculturally unimproved communities highlighted the paucity of information relating to semi-natural grassland. The review concentrated on chemical and physical factors which are most likely to influence nutrient availability and would require monitoring. The importance of phosphorus availability, a common limiting factor in unproductive environments was emphasised. Possible methods of monitoring nutrient availability were discussed both within the soil and plant material. It was also important to understand how management may manipulate nutrient availability and how this may effect species composition of Culm grassland. In order to achieve the objectives of the project an experimental design was formulated and methods were chosen. These are described in the following chapter.

CHAPTER TWO

EXPERIMENTAL DESIGN AND METHODS

2.1 Introduction

A review of soil:plant relationships in Chapter One found that limited research had been carried out on Culm grassland, particularly relating soil conditions to plant community structure. Detailed studies of soil conditions under other semi-natural plant communities were also found to be limited in number. Therefore, it was necessary to conduct an initial survey during 1992 to outline the main characteristics of the Culm grassland environment in comparison to that of an improved grassland. Information collected to achieve the first two aims of the project is used to highlight possible limiting factors such as soil phosphorus availability, which were studied in more detail in 1993. This chapter describes the experimental design and strategy, and the methods employed in the project. The experimental design includes detailed criteria for site selection, description, plot layout and experimental strategy. A discussion of the experimental strategy and statistical analysis of data follows. Modifications to the experimental design were made in 1993; these are specified in relevant chapters. Standard methods employed to monitor soil conditions and vegetation in the project as a whole are described in Section 1.4. Further evaluation of methods and techniques was conducted in later phases of the project and are discussed in more detail in later chapters.

2.2 Experimental design

2.2.1 Site selection

Experimental sites were selected following consultation with the Culm grassland inventory at the Devon Wildlife Trust, Exeter, which indicated a wide range of possible experimental sites varying greatly in size. The sites were found to be highly fragmented, and spread widely across the county from Exeter to Bude (see Figure 1.1). Potential sites were

restricted to those greater than three hectares, to reduce edge effects, and in accessible locations to enable regular visits and repetitive sampling. Sites were also selected according to the type of management, the length of time management has been implemented (past or present), type of plant community, the extent of agricultural improvement and location.

The number of potential sites are further reduced when selecting in accordance with the management regime. Records indicated that most sites were grazed, burned or mowed with the remaining sites being invaded by scrub due to lack of management. It was not usual for burning and mowing to be used as primary management strategies. These methods were usually implemented to control dominant species such as *M. caerulea* in the autumn, or in the case of burning only every few years. Abandoned or neglected sites are were not included as the y were not being actively managed. As sites controlled by grazing management were most widespread it was decided to concentrate on this type of management.

Sites were then vetted, to supply information relating to present grazing management. A site rented by IGER, North Wyke, at Fernhills Moor was selected to provide this information which since clearance of scrub in summer 1991, had a management strategy of early, late, and continuous grazing. A continuous grazing plot was chosen as it is most comparable to past management strategies. Cutting was introduced on replicated plots from May until September in 1992. Cutting was included in the experimental design only on this site in order to supplement data obtained by IGER. It provides an easier estimation of the offtake of herbage in comparison to grazing. Thus a grazing plot and a cutting plot was selected for study on Fernhills Moor.

The vegetation community of Fernhills Moor can be broadly defined as a *Cirsio-Molinietum* (Rodwell, 1991) including a substantial area of M16 *Erica tetralix - Sphagnum compactum* wet heath community (DWT and NCC, 1989). It was decided to search for other sites with M16 as it is relatively frequent within the Culm grassland vegetation. Records at English Nature local office, Okehampton were consulted to find this community to provide information on past grazing management. Staddon Moor, an SSSI, situated 6.4 km from

North Wyke, satisfied the criteria. Staddon Moor has been managed by the owner for about 40 years with store cattle grazing and topping in the autumn. A substantial area of the M16 community is present together with other Culm grassland communities.

A site was also required to provide comparative information of nutrient conditions between a species-poor community or improved grassland. Ideally this would include a site which had formerly been Culm grassland and had undergone recent agricultural improvement. An improved grassland field which had been Culm grassland 20 years ago was selected adjacent to Staddon Moor, and is farmed by the same owner. Three fields were selected in close proximity in order to minimise variation between sites due to environmental factors. The sites are located on soils belonging to the Hallsworth series with ancillary subgroups of the Tedburn, Brickfield and Cegin (Soil Survey of England and Wales, 1983). The soils are characterised by clay loams with surface water gleys (Harrod, 1981).

2.2.2 Site description

a) Fernhills Moor (Culm Grassland)

The grazing and cutting plots (Plates One and Two) are located on a south facing slope at an altitude of 150-170 m above O.D. The field is 6.5 ha in area and was covered in birch scrub until IGER cleared a central area of about three hectares. The main area is an M16 community dominated by *M. caerulea* with *Erica tetralix, Calluna vulgaris, Cirsium dissectum, Succisa pratensis* and *Ulex gallii*. The field is bounded by thick hedges and mixed Birch and Oak woodland and a deep wooded stream to the south. As a result the southern area of the field is wetter than the northern end.

Description of the soil profile at Fernhills Moor given in Appendix Eight (Harrod, 1995) indicates the presence of a litter layer above an undisturbed well structured horizon. This merges in to lower horizons where signs of gleying is evident (see Chapter One) as shown in Plate Three. A comparison with the soil profile of an adjacent improved grassland on the Hallsworth series, indicated some differences as detailed in Appendix Nine (Harrod, 1995).

The litter layer was absent and the upper horizon had been disturbed by ploughing producing a subangular blocky structure. In this horizon the rooting was less coarse as shown in Plate Four and the boundary merged in to a much thicker and greyer Ap horizon. The lower Bg horizon has a very similar structure and mottling as the profile at Fernhills Moor.

b) Staddon Moor (Culm Grassland)

A grazing plot (Plate Five) was set up on this site which is a plateau on a gently north facing slope at an altitude of 190 m above O.D. The field is 4.2 ha in area and was designated an SSSI in 1991 with support from the Wildlife Enhancement Scheme. Three main vegetation communities are found within this field; M23, M24, and M16 which each cover 1.4 ha in area. This mosaic of communities is further enhanced by the remains of a shallow ridge and furrow system. Water conditions are also found to vary with wetter areas in the west and an input by ephemeral streams running from the road. Drier areas are found in the eastern half and also on a mound which was formerly woodland. The grazing plot used in this study was located within an area of M16 in the drier area away from the field margins. From field observations the soil profile was found to be very similar to that at Fernhills Moor, with the exception of a denser root mat in the litter layer.

c) Staddon Moor (Improved grassland)

A grazing plot (Plate Six) was also set up in an improved grassland field adjacent to the Culm grassland field. This slopes ($< 5^0$) in a similar manner to the Culm grassland field and covers approximately 3.5 ha in area. The plot was located in an area absent of rushes which were present in some areas of the field. This field had been originally Culm grassland but was agriculturally improved after the Second World War. Improvement included ploughing, reseeding and application of lime but no artificial drainage. From field observations the soil profile was very similar to the improved grassland field adjacent to Fernhills Moor and had an abundance of very fine fibrous roots.

The pasture was reseeded approximately 15 years ago and receives an application of 250 kg ha^{-1} of 20:10:10 in the spring. This rate of application is equivalent to 50 kg N ha^{-1}, 11 kg P ha^{-1}, 21 kg K ha^{-1}. Fertiliser was applied on 14 April, 1992 and 10 March, 1993. The field is grazed, between May and October by about 15 young bullocks at a stocking rate of 4.3 animals ha^{-1}, which may move freely into the Culm grassland field.

2.2.3 Plot Design

In designing plots for the minimal area approach was considered as discussed by Southwood (1978) and Krebs (1978). They defined the minimal area as the smallest area that provides enough environmental space for a particular community type to develop its true characteristics of species composition and structure (Moore and Chapman, 1986). As the vegetation of each chosen community on each site was homogenous and small in height it was decided that relatively small plots would be sufficient to represent variations over the whole area. As the plot design set up by IGER (Tallowin, 1991) on Fernhills Moor has been found to be a reliable approach it was used as a reference. Therefore the plots were located in areas which were typical of the chosen community and away from the field margins and the wetter areas to reduce variability of conditions within the plots. A grazing plot was delineated on the Staddon Moor, Staddon Improved and Fernhills Moor fields measuring 45 m by 30 m. Pegs were used as markers to enable cattle to move freely across the plot. The cutting plot on Fernhills Moor designed by IGER (Tallowin, 1991) measured 30 m by 15 m and was surrounded by a wire fence to prevent access by cattle. The names of the four plots are abbreviated in the following table and reference to these abbreviations is used in this thesis.

Table 2.1 Abbreviation of plot names

Site	Plot Name	Management	Grassland Type
Fernhills Moor	Fernhills grazing (FG)	grazing	Culm grassland
	Fernhills cutting (FC)	cutting	Culm grassland
Staddon Moor	Staddon grazing (SG)	grazing	Culm grassland
	Staddon improved (SI)	grazing	Improved grassland

Plate 1. The grazing plot on Fernhills Moor, FG (Culm grassland)

Plate 2. The cutting plot on Fernhills Moor, FC (Culm grassland)

Plate Three Soil pit exposing soil profile at Fernhills Moor

Plate Four

Soil pit exposing soil profile at an improved grassland site near Fernhills Moor

Plate Five **The grazing plot on Staddon Moor, SG (Culm grassland)**

Plate Six **The grazing plot on Staddon Improved, SI (Improved grassland)**

2.3. Experimental Strategy

2.3.1 General sampling strategy

As the purpose of the investigation was to characterise Culm and improved grassland under different management strategies during a growing season, a detailed investigation of the four plots was necessary. Any experiment must be designed to measure factors involved and also measure their reproducibility to ensure validity, precision and coverage (John and Quenouille, 1977). As the whole system cannot be studied a method of sampling is necessary. This ensures that a representative sample of the whole system is taken. A number of sampling strategies are employed in environmental science and are reviewed by Greig-Smith (1983) and Krebs (1989), the most efficient being stratified unaligned random sampling (Greig-Smith, 1983). Randomization ensures that any point within the plot has equal chance of being chosen but this may lead to some areas being under or over-sampled. The use of stratification with randomisation achieves a regular spread of samples, is likely to give a better estimate and also variation between stratum does not contribute to overall variance (Moore and Chapman, 1986). As a regular spread of sampling was required the plots were stratified in to 15 equal sized sections measuring 10 m by 7 m. Stratification discussed by Krebs (1989) was influenced by the homogeneity of the vegetation and produced sections that were not comparable in size to the scale of variability within each plot (Greig-Smith, 1983). Therefore the samples were allocated by stratified random sampling.

The number of samples to be taken will depend on the relationship between the mean value and the sample size. The point at which the mean value ceases to fluctuate within a predetermined range is the minimum number of samples required (Kershaw and Looney, 1985). In the case of soil nutrient conditions the potential for variability across the plot is high with much of the variation occurring within one metre (Rowell, 1994) and often the rule of 'more the better' is applied. A pilot investigation was necessary to obtain a minimum sample number which was carried out by Tallowin (1991) who found that 15 soil samples provided a reliable sample mean value. With reference to the above discussion in identifying the point of equivalence, 30 replicates were employed in vegetation sampling. A

larger number of samples were taken as vegetation has greater heterogeneity than soil and this number allows application of some statistical methods. Sampling points were located in each section by striding according to x and y coordinates obtained from random number tables.

2.3.2 Soil conditions

Soil conditions were monitored during 1992 between the following depths:- 0.00 - 0.05 m, 0.0-0.15 m, and 0.15 - 0.30 m. These sampling depths were chosen to correspond to variations in the main rooting zone above the clay parent material as shown in Plate Three and Four. In order to monitor seasonal variation, sampling was undertaken during the growing season on four occasions; mid-April, mid-June, mid-August, and mid-October. The sampling intervals also allowed adequate time to conduct analysis in the laboratory. All soil sampling was carried as above unless otherwise stated. Sampling strategy was modified in 1993 and this is discussed in more detail in Chapter Four.

a) Soil physical conditions

The review of literature in Chapter One highlighted the influence of soil physical conditions particularly soil water content and tension, and the movement of water through the soil profile directly and indirectly on nutrient availability. Soil water content was measured in both field seasons of 1992 and 1993 in the upper horizons, to provide information on unsaturated water conditions. This information was further supplemented by measurement of soil water tension, organic matter content and bulk density in the 1993 field season at a depth of 0.1m. To ascertain the influence of saturated water conditions and the changing height of the water table, depths of 0.5 m, 0.8 m and 1.2 m were investigated on the Fernhills Cutting and Grazing plots during both field seasons. Equipment employed to measure water conditions in the field was located in three positions within each plot, replicated three times and protected by grazing cages where appropriate.

b) Soil nutrient conditions

A review of soil:plant relationships in Chapter One discussed strategies employed by plants to survive in environments of high stress such as low nutrient availability. To investigate the influence of soil nutrients conditions on Culm and improved grassland communities, the general nutrient status was studied during 1992. A more detailed study of phosphorus availability followed in 1993; this is discussed in Chapter Four. The nutrient status was evaluated by measuring the plant available fraction, which is only a small proportion of the nutrient held either in true solution, or on the soil colloids (Moore and Chapman, 1986). Essential plant nutrients nitrate-nitrogen, ammonium-nitrogen, phosphate-phosphorus, potassium, calcium and magnesium were measured. Acidification and presence of hydrogen ions was investigated by measuring pH, which effects for example the exchange of calcium, magnesium, aluminium and the solubility of phosphate (Rowell, 1994). Standard methods of chemical extraction were employed in this project (ADAS, 1989) in conjunction with the analysis of soil solution removed directly in the field. The latter may provide a more accurate measurement of plant available nutrient content as chemical extraction often removes nutrients in excess of plant requirements (see section 1.5).

Soil samples were removed at the defined depths with a trowel and sealed in a plastic bag and transported back to the laboratory. Sub-samples were removed from the bags to determine gravimetric water content and extractable nitrate-nitrogen and ammonium-nitrogen. The remaining soil was air-dried at room temperature, ground and sieved to 2 mm in preparation for chemical extraction. All values were expressed on a dry-weight basis.

c) Statistical analysis

Soil data collected during the study was analysed statistically using the Minitab statistical computing package. In order to test the reliability of experimental data and its reproducibility a number of statistical methods may be used which are reviewed by Cochran (1977), Finney (1980), Kershaw and Looney (1985) and Krebs (1989). The representativeness of the sample mean to the population mean is indicated by their standard errors (John and Quenouille, 1977) which measures the variation of the mean. This may be

used to set limits within which the true values fall with a degree of confidence or otherwise known as confidence limits. Thus exploratory data analysis was conducted using the mean and standard error and these statistics are presented throughout the thesis where appropriate. Standard error bars may be absent from graphs where the values are too small to represent graphically. The presence of outliers which effects the representativeness of the mean were deleted from the data set if values were greater than two standard deviations from the mean, as recommended by Hesse (1971).

In order to compare means and the effects of different treatments such as management and sampling depth it is necessary to ensure that samples being compared are drawn from populations showing a normal distribution and in which variances are independent of the means (Moore and Chapman, 1986). To check normality a number of methods reviewed by Finney (1980) were consulted and initially a histogram of the data was plotted followed by examination of residuals produced by analysis of variance. Non-normal distributed data showing skewness and kurtosis was manipulated by a number of transformations as discussed by Moore and Chapman (1986). Square root transformation was found to be most appropriate. Although there are tests available for non-normally distributed or non-parametric data they are less powerful as they rely on ranking of data. In testing for significant differences between means and the probability of obtaining the difference by chance, a null and an alternative hypothesis were formulated. Of a number of tests available, a relatively simple Tukey test was employed to find a significant effect of the different treatments using confidence limits of 0.05 and 0.01. Other associations between data was also explored using correlation methods and simple regression analysis.

2.3.3 Plant Communities

a) Botanical surveys

Botanical surveys of each plot were carried out in 1992 to characterise the floristic content of the communities. The surveys were carried out at the end of May and also at the end of August to record species which appear later in the growing season. Methods employed in this survey follow recommendations by the NVC (Rodwell, 1987, 1991). The size of the quadrat is often considered by using the relationship between the area and species number which will rise steeply and level off at a point which indicates the minimum size (Kent and Coker, 1992). However, as this was not possible to attain before the study, the vegetation structure and homogeneity was of prime consideration. It was decided to employ a relatively small quadrat (Southwood, 1978) measuring 0.25 m by 0.25 as the vegetation is small and most species are relatively abundant. A square quadrat was employed, although circular or rectangular quadrats are suggested to reduce error due to edge effect, the difference is thought to be negligible (Moore and Chapman, 1986). As botanical surveys were not the central facet of the project, speed and ease of measurement were also important factors. Floristic composition of each quadrat was assessed by frequency and cover parameters. Frequency was recorded to indicate how often a species was encountered. Cover of each species was measured subjectively and indicates the spatial contribution of a particular species to the community as a whole.

b) Plant production

The production of the plant communities was monitored during 1993 to investigate the influence of vegetation on the cycling of phosphorus within the Culm grassland system. The response of plant production to management was measured by applying defoliation over different time periods. Plant material was removed from the Staddon Moor (SG) and Staddon Improved (SI) plots using a sampling strategy described in Chapter Five. Standard methods to measure dry matter production and phosphorus content of the plant material were employed and are expressed on a dry weight basis.

c) Statistical analysis

Data collected from the botanical surveys was entered in a matrix form listing the percentage cover of species in each quadrat. Average percentage cover and frequency of each species on each plot was calculated and were classified according to the Domin scale from 1 - 10 and frequency scale V - I discussed by Rodwell (1987). The species were ranked according to frequency and in the case of Culm grassland plots, ranking was referenced to the SG plot. The ranked data was then compared visually with NVC tables thought to be most similar in composition. Additionally the data was entered in to the TABLEFIT program (Hill, 1993). Further data analysis was considered. As exploratory data analysis adequately describes and characterises the plant communities which was the aim of the plant surveys, time-consuming analysis was not carried out. Plant production data was described and statistically analysed in the same manner as soil conditions data collected in Section 2.3.2.

2.4 Methods

2.4.1 Soil physical conditions

a) Soil water content

Relative changes of soil water content over time and depth was monitored by employing standard destructive and non-destructive methods. A destructive gravimetric method was supplemented by a non-destructive measurement using time domain reflectometry. The gravimetric method involves removing a known weight of soil and drying at 105 ^{0}C until a constant weight is achieved (Black *et al.* 1965). The difference between the wet and dry weight is expressed as a percentage dry weight. This method is simple, reliable and of low cost. However, absence of a repeated measurement at a same point, results in replicate samples being affected greatly by soil heterogeneity (Moore and Chapman, 1986).

Time domain reflectometry (TDR) allows repeated measurement at the same point and is non-destructive. This novel technique is applied to Culm soils for the first time. Errors associated with this method are reviewed by Topp (1980), Dasberg and Dalton (1985), Topp and Davis (1985), Whalley (1993) and White, Knight, Zegelin, Topp (1994). TDR measures the dielectric constant of the soil, which is the ability of the soil to transmit an electrical pulse in comparison to the ability to transmit the same pulse through a vacuum. As the dielectric of most soil material is between 3 and 5 it provides a sensitive measurement (Smith and Mullins, 1991). The dielectric constant is calculated by measuring the time taken for an electrical charge to pass through the soil down a probe. A probe was constructed of three steel welding rods measuring 2mm in diameter which were placed vertically 25 mm apart in the soil. The rods measured the following lengths: 0.05, 0.15 and 0.30 m in 1992 and 0.01m in 1993. An average measurement of water content of the depths 0.00-0.05, 0.05-0.15, 0.15-0.30 m was obtained by successive subtraction of the upper, middle and lower depths. A pulse was sent down the centre rod using a Tektronics 1502B cable tester, which returns via the two outside rods. A trace is produced displaying the time taken or apparent length for the pulse to leave and return. The dielectric constant was calculated by

squaring the apparent length divided by actual length.

In an extensive study Topp, Davis and Annan (1980) found that the relationship between the dielectric constant and water content is independent of soil type, soil density, salt content, and temperature. They found that their data fitted a calibration curve which was used in this study to calculate volumetric water content using the dielectric constant.

b) Soil matric potential

Information of soil water content is supplemented further in this study by measuring the soil matric potential or the suction required to remove water from the soil pores. This is important as similar amounts of water may be held in different sized pores within the soil and will be available to plants at different suctions. Soil matric potential was monitored using a quickdraw tensiometer which is a mobile, easy method which requires no adjustment and calibration. The quickdraw tensiometer consists of a porous ceramic cup, attached via a liquid filled column to a vacuum dial. When the cup is in contact with the soil a hydraulic connection between soil water, and water in the pores of the cup is made. Water moves in and out of the cup until the pressure inside the cup equals the tension of the water outside the cup. Equilibrium was found to take approximately 15 minutes to an accuracy of +\- 0.25 kPa. An investigative depth of 0.01m minimised soil disturbance, and trapped air which causes a breakdown in the hydraulic connection (Smith and Mullins, 1991).

c) Water table fluctuations

Piezometers have been widely used to provide access to lower soil depths in order to monitor changes in the saturated zone and allow removal of water from groundwater sources. They are employed in this study to monitor water table fluctuations, that is the boundary between unsaturated and saturated soil. Information of soil water movement throughout the soil profile will supplement information of water contents in the upper horizons and increase understanding of Culm soil hydrology. Piezometers were constructed of plastic tubing measuring 0.05 m in diameter with the lower end sealed and small holes drilled around the circumference to allow entry of water. Three different depths were

monitored namely 0.5, 0.8 and 1.2 m below ground level, as the deepest piezometer may have tapped a water source of a higher hydrostatic potential than that of the soil surrounding the upper part of the tube. In this case water rises higher in the tube, than the water table actually reaches in the soil (Moore and Chapman, 1986). The level of water within the tube was recorded using a specially constructed electrical depth gauge.

d) Bulk density

Bulk density can be used indirectly to assess differences in soil structure and porosity which is reviewed by Black *et al.* (1965) and Moore and Chapman (1986). It was employed in this study to supplement information of the soil hydrology and enable conversions of soil analysis values to field values (Rowell, 1994). Bulk density was determined to a depth of 0.10 m by taking five cores per plot of field moist soil of a known volume, air-drying to obtain a constant weight. The dry weight was then divided by the original soil volume and expressed on weight per volume basis.

e) Organic matter by loss-on-ignition

Organic matter is assessed in this study to gain an indication of the size of the organic pool and how the cycling of dead material through the Culm soil system may affect nutrient availability. Due to the large number of soil samples collected in the study it was decided to employ the loss-on-ignition method to assess the soil organic matter content. Other methods such as wet oxidation (ADAS, 1986) which give a more reliable estimate of organic matter but are more time consuming. Although errors in the form of loss of volatile inorganic components were noted (Moore and Chapman, 1986) investigation of relative differences between plots was of prime importance rather than high levels of accuracy. Soil removed to a depth of 0.01 m was air-dried, ground and sieved to 2 mm in diameter. A sub-sample of 5 g was removed from five samples per plot and placed in a crucible which was weighed and heated to 850 ^{0}C for 30 minutes. The weight loss was taken as percentage of the oven dry soil weight.

2.4.2 Soil nutrient conditions

a) Chemical extraction of nutrients

Nutrients were extracted by employing standard methods currently employed by ADAS in analysing soil for advisory work and are described more fully in Bulletin RB27 (ADAS, 1986). This enables comparisons with previous work and other agricultural soil to be made. Any deviations from these methods are detailed in this section. Results were expressed on a air-dried weight basis.

Phosphate - phosphorus (PO_4-P) was determined during 1992 and 1993 by extracting 5 g of air-dried soil with 100 ml of sodium bicarbonate (Olsens reagent) at pH 8.5 and shaken for 30 minutes. Although the pH of the extractant is not comparable to the more acid soil of this study, it was decided to use this standard method to aid comparisons. The use of other more appropriate extractants as discussed in Chapter One was investigated during 1993 and reported in Chapter Four. The extract was filtered, neutralised using concentrated sulphuric acid and placed in a sonic bath to remove air bubbles. Phosphate was then determined using a Technicon Autoanalyser in the first field season and a Flow Injection Analyser in the second field season (Technicon Instruments Corporation, 1972 and Tecator Ltd, 1983). Problems of organic matter colouration of extracts were investigated in detail during 1993 and reported in Chapter Four. In the 1993 field season soils were analysed for total phosphorus content to obtain information on the storage component and the relative amounts of organic and inorganic phosphorus. Analysis was carried out by IGER, North Wyke following the methods by Murphy and Riley (1962) and Smith and Baine (1982).

Nitrate-nitrogen (NO_3-N) and ammonium-nitrogen (NH_4-N) were determined in 1992 to estimate the processes of nitrification and denitrification by extracting a solution from fresh soil within 12 hours of sampling to reduce microbial activity. Sub-samples of fresh soil weighing 10g was shaken with 50 ml of 2M potassium chloride solution for one hour. Although larger ratios of extractant to soil and longer shaking periods are suggested by workers as discussed in Chapter One, ratio of 5:1 was used as recommended by Rowell

(1994). This allows rapid analysis of samples within one day and reduces the amount of soil removed the field. The filtrate was analysed colorimetrically on the Technicon Autoanalyser following methods in the Technical Publication (1972). The results were converted to allow for dilution, water content and conversion to the individual forms of nitrogen.

Potassium, calcium and magnesium (K, Ca, Mg) were determined from the same extract by shaking 10 g of 2 mm air-dried, sieved soil with M 50 ml of ammonium-nitrate solution for 30 minutes. The filtrate was examined through an air-acetylene flame using a calibrated atomic absorption spectrophotometer. Potassium was determined directly from the filtrate by flame emission. Interference by other elements is thought to be negligible (Godden and Strobbe, 1981). Calcium and magnesium were determined by absorption. Lanthanum chloride was added to remove the interference of elements such as phosphate, aluminium and silicon.

pH was determined electrometrically with an accuracy of +\- 0.1 pH unit in 1992. A soil suspension was produced by stirring 10g of air-dry soil with 25 cm^3 of distilled water for 15 minutes (Rowell, 1994). The values were found to be highly variable which may be due to the movement of Ca^{2+} and Al^{3+} to displace H^+ in response soil dilution (Hesse 1971) when distilled water of about pH 5.6 is added to soil of a higher acidity. To standardize the method further a 0.01M $CaCl_2$ solution recommended by Skinner, Church and Kershaw (1992) which causes cation exchange and H^+ is displaced into solution. This suspension was found to reduce variation of the data and consistently lowered the values (which are presented in Chapter Three) by 0.5 units .

b) Extraction of soil solution

To combat over-estimation of nutrient availability by chemical extraction discussed in 1.4.2, soil solution was removed in the field using suction cups in 1992 and 1993, and centrifuging in the laboratory in 1993.

i) Suction cups

Suction cups installed in the field allow repeated measurement at the same point with a minimum of disturbance of soil when installed. The principles of operation are reviewed by Litaor (1988) and England (1974). In 1992 ceramic suction cups were constructed and placed vertically in the soil, consisting of a porous ceramic cup fixed to plastic tube and an inner polythene tube attached to a bung at the surface. Water moves into the cup when a suction is generated by a vacuum pump until the capillary pressure between the soil and cup reaches equilibrium (Grossman and Udlift, 1990). Water removed from the suction cups was analysed for NO_3-N, NH_4-N and PO_4-P on the autoanalyser which were found to be very low in concentration particularly for P which was below the level of detection of 0.5 mg l^{-1}.

In 1993 it was decided to continue monitoring P in soil solution and use different methods to improve detection. The adsorption of P by aluminium in the material of ceramic cups, a widely recognised phenomenon (Bottcher, Miller and Campbell, 1984) may have an influence on P concentrations. This was resolved by using an inert hydrophillic porous polymeric tube supplied by Van Walt Ltd. This specially constructed Rhizon Soil Moisture Sampler is 2.3 mm in diameter, 100 mm in length, and strengthened by an internal stainless steel wire. The suctions cups were placed at an angle to obtain an average over the whole depth of 0.1 m. A vacuum was produced by attaching an open 10 ml syringe to the suction cup. Solutions collected were then analysed on a Tecator Flow Injection Analyser employing a method which reduces the detection limit to 2 $\mu g l^{-1}$ for P (Perstorp Analytical Ltd, 1990). Limiting sample volumes to less than 10 ml, applying small suctions and frequent sampling may reduce changes in the sphere of influence of suctions applied and the effects on sample quality.

ii) Centrifuging

To reduce uncertainty of the sphere of influence of applied suction, soil solution was removed in the laboratory by centrifuging. The principles of this method are reviewed by Mubarak and Olsen (1976), Menzies and Bell (1988) and Reynolds (1984). A centrifuging system was set up following the design of Davies and Davies (1963) and Gillman (1976). This consisted of a pierced upper tube packed with soil which releases solution into a lower collecting cup. 60 g of fresh soil removed from 0.00-0.1 m depth was centrifuged at 1500 rpm for an hour and released 2 - 4 ml of solution. Experimentation found this to be the optimum time and speed to remove an adequate sample size. A critique of the technique is discussed in more detail in Chapter Four. The speed was low to prevent excessive compaction which may cause root collapse and leaching of ions to contaminate the solution removed (Ross and Bartlett, 1990). Centrifuging took place within 12 hours of sampling to reduce microbial action. Solutions collected were then analysed on a Tecator Flow Injection Analyser.

2.4.3 Plant communities

a) Botanical surveys

The frequency and cover of plants were recorded in botanical surveys during 1992. Identification was aided by advice from an experienced botanist and the use of keys such as Clapham, Tutin and Warburg (1962), Jermy, Chater and David (1982), Hubbard (1984), Fitter, Fitter and Farrer (1989), Fitter, Fitter and Blamey (1991) and Stace (1991).

b) Plant community production

Plant material removed during the field season of 1993 was analysed for total phosphorus content. The material was dried at 105 ^{0}C overnight, weighed, ground and stored. After consulting methods recommended, to remove organic material by ADAS (1986) and Moore and Chapman (1986), it was decided to follow a standard method by Astila, Agenian and Chau (1976) which is used by IGER, North Wyke. Solutions were analysed using a Flow Injection Analyser following methods recommended by Perstorp Analytical Ltd (1992) and results are expressed as dry weight of plant material.

2.5 Summary

Chapter Two has described the general experimental design and methods employed in the project as a whole which are summarised below. Further modifications are made in 1993 which are discussed in more detail in later relevant chapters. To achieve the aims and objectives of the project a stringent process of site selection was carried out. Detailed seasonal monitoring was made possible by selecting sites in close proximity which satisfied the criteria of the first and second aims. Two Culm grassland and one improved grassland sites were selected on which experimental plots were located. Four plots (Staddon improved, Staddon grazing, Fernhills grazing and Fernhills cutting) were compared by characterising the soil conditions and plant communities. An experimental strategy was formulated to ensure that experimental results are representative of the studied plots. Soil conditions were characterised by monitoring soil water and nutrient status using standard methods which are modified to investigate phosphorus availability in 1993. The plant community was characterised by recording floristic composition in 1992 which was supplemented by information of plant production in 1993 using standard methods.

1) Species-rich Culm grassland (SG) was compared to species-poor grassland (SI). Past management of Culm grassland (SG) was compared with introduced management (FG, FC).

2) Soil conditions were monitored on mid-April, mid-June, mid-August, and mid-October. The floristic composition was monitored at the end of May and August.

3) Unsaturated water conditions were monitored at depths 0.00-0.05, 0.05-0.15, 0.15-0.30 m using gravimetric and TDR methods. Saturated water conditions were monitored to depths of 0.5, 0.8 and 1.2 m using piezometers.

4) Information of soil matric potential, bulk density and organic matter content measured in 1993 supplements this information.

5) Soil nutrient conditions were monitored at depths 0.00-0.05, 0.05-0.15, 0.15-0.30 m using chemical extraction and direct removal of soil solution by suction cups. Modification of these methods were made in 1993 to also include centrifuging.

CHAPTER THREE

CHARACTERISATION OF THE CULM GRASSLAND ENVIRONMENT

3.1 Introduction

The review of literature in Chapter One showed that a variety of factors may influence soil nutrient availability of Culm grassland. As little previous research had been conducted, it was important to monitor a wide range of factors in the first instance. This has enabled factors of particular interest, such as phosphorus availability, to be focused on later in the project. Therefore, an initial survey of Culm grassland and improved grassland was undertaken during the first field season of the project (1992). The sampling strategy and methods described in Chapter Two were employed to monitor soil conditions and plant communities. The sampling dates for the whole project are detailed in Appendix One. This chapter reports these results by describing meteorological, soil physical and nutrient conditions and the species composition of the vegetation.

3.2 Meteorological conditions

Meteorological conditions during 1992 were found to be drier than the average conditions over a thirty year period from 1961-90 at North Wyke as shown in Appendix Two. The month preceeding sampling in April was extremely dry and very mild. Temperature and rainfall during April was similar to the thirty year period and was followed by a warm, dry May and June. The next two months were particularly wet and were followed by a dry September. These conditions were conducive to early plant growth and the possibility of checking of growth during the early summer months.

3.3 Soil physical conditions

Soil water conditions were monitored using gravimetric and novel time-domain reflectometry methods. Percentage water contents measured by TDR were found to be highly variable and did not correlate with gravimetric water contents, which were used to confirm TDR readings. Recent studies such as by Whalley (1993) and discussions by White *et al.* (1994) indicate that the calibration used by Topp *et al* . (1980) may not be independant of soil type. There were indications that a breakdown of this relationship occurred in peat and heavy clay soils. Individual calibration curves may be required for fine-textured soils as in the case of Culm soils. Therefore gravimetric water contents were chosen as being representative of unsaturated water conditions, rather than time-domain reflectometry, throughout this study.

Soil water contents of Culm grassland soils presented in Figure 3.1 were found to vary little throughout the field season of 1992 despite obvious variations in rainfall patterns. The water contents of the Culm grassland soil remained significantly different ($p<0.05$) from the improved grassland soils throughout the profile investigated. Although improvement did not include drainage the soil water conditions appeared to be more sensitive to variation in meteorological conditions than Culm grassland. Soil water contents were reduced by the dry February and March, and recovered to similar water contents of Culm grassland in mid-October. It may be postulated that recovery was prevented by high transpiration losses from early growing *Lolium perenne* and other species which have high nutrient demands (Holmes, 1989). This variation may be enhanced by a reduced water holding capacity of improved grassland soil which results from a higher bulk density and lower organic matter content presented in Table 3.1.

Figure 3.1 Variation of gravimetric water content (n=15), water table (n=3) with depth and season in relation to rainfall and temperature during 1992 (Standard error bars)

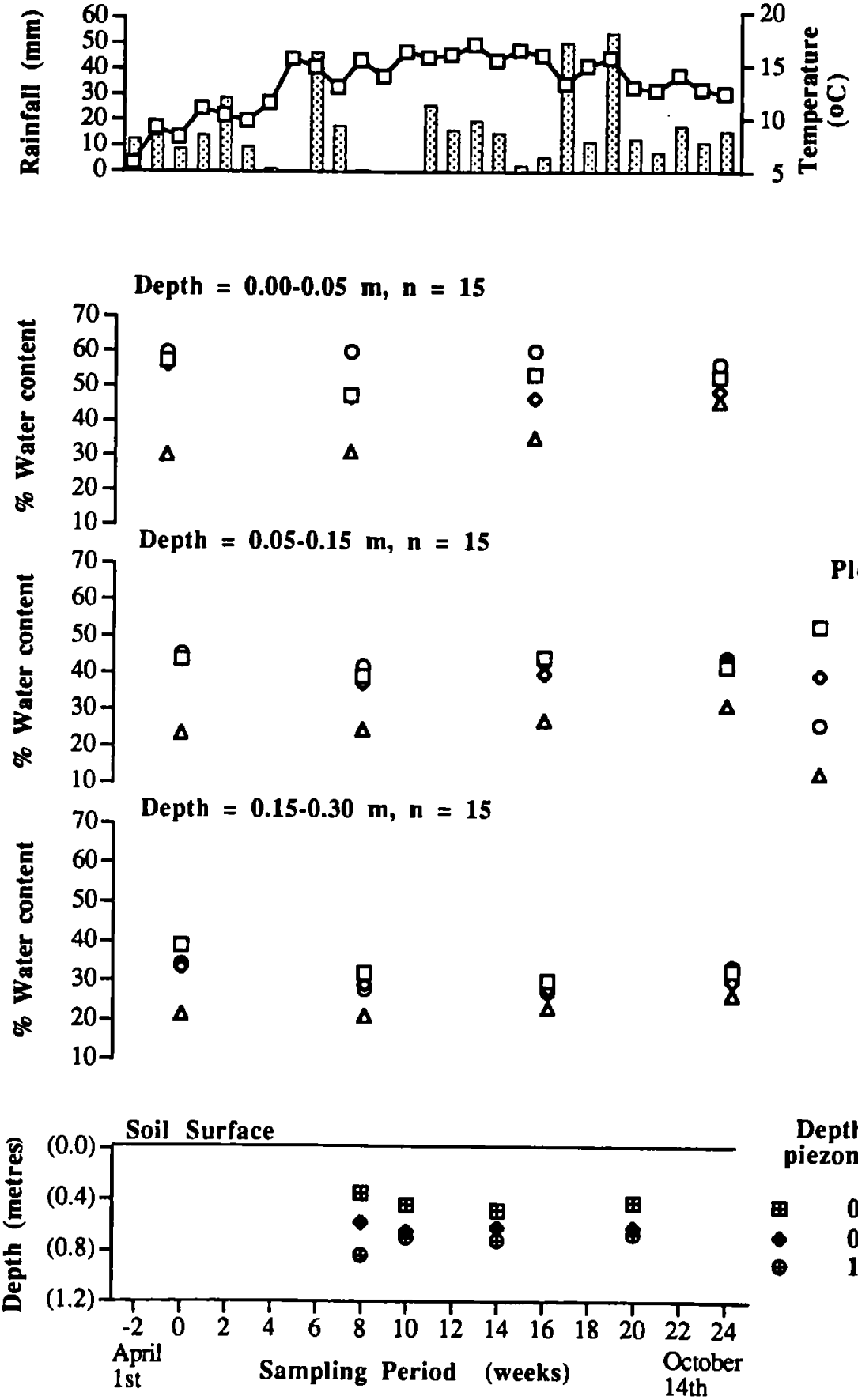


Table 3.1 Comparison of soil organic matter and bulk density of experimental plots

Plot Depth 0.00-0.01 m	Fernhills Grazing (FG)	Staddon Grazing (SG)	Staddon Improved (SI)
Bulk density (Mg m^{-3})	0.36	0.27	0.60
Organic matter (%)	20.90	28.20	15.20

Table 3.2 Variation of top soil pH (air dry soil), August 1992

Depth	Plot	Fernhills Grazing (FG)	Fernhills Cutting (FC)	Staddon Grazing (SG)	Staddon Improved (SI)
0.00-0.05 m	Mean (15)	4.23	4.33	3.71	5.59
	Standard error	0.05	0.05	0.05	0.07
0.05-0.15 m	Mean (15)	4.23	4.41	3.76	4.46
	Standard error	0.04	0.03	0.03	0.04
0.15-0.30 m	Mean (15)	4.19	4.41	3.94	4.44
	Standard error	0.04	0.03	0.02	0.04

Table 3.3 Comparison of Staddon Improved soil chemical conditions with other improved grasslands on the Culm measures

Site	pH	P	K	Mg
Staddon improved (mg kg^{-1})	5.2	10	250	87
ADAS index (depth 0.00-0.05 m, mean 1992)		1	3	2
South Nethercott Farm (mg kg^{-1})	5.7	14	250	104
ADAS index (depth 0.00-0.30 m, Dec. 91)		1	3	3
Rowden Moor - Tyson *et al.* (1992) (mg kg^{-1})	5.3	14	125	96
ADAS index		1	2	2

Variation of water contents with depth was most marked on Culm grassland plots. The uppermost depth (0.00-0.05m) was found to have a significantly higher water content ($p < 0.05$) than the soil below. An increase in bulk density with depth of soil contributed to this decline. Relative accumulation of water in the upper horizon could produce anaerobic conditions and a weak structure which may be susceptible to poaching and a reduce productivity. However, interpretation of the high percentage water contents must take into account the method employed. Water contents expressed as a percentage dry weight often indicate a higher value at a shallower depth, as a higher organic matter content has a lower specific gravity (Packham, Willis and Poel 1966). The variation of organic matter content was evident when comparing the three Culm grassland plots. Water contents at 0.00-0.05m were found to be significantly higher on SG ($p<0.05$) than FG and FC, as the soils of SG plot in Table 3.1 have a higher organic matter content.

The water table monitored using piezometers at Fernhills Moor remained below the soil surface throughout the sampling period from May to September, 1992, as shown in Figure 3.1. Equipment failure prevented monitoring before this period. It may be postulated that the water table usually remains at or near the soil surface from October until April. Variations in this pattern may be found in 1992, as February and March were much drier than average. The depth of water within the piezometer at 0.5 m was found to decline in response to a dry period during May and June. This contrasts with gravimetric water contents in soil to a depth of 0.30 m which may indicate that the water content between 0.00 and 0.03 m was maintained by water moving up the soil profile by capillary action (Reid and Parkinson, 1987).

Exploration of different depths indicated that water within the saturated zone behaved differently throughout the soil profile in response to horizon variation. Water remained within the piezometer measuring 0.5 m in length throughout the summer indicating that the water table did not fall below 0.5 m below the soil surface. Water within the deeper piezometers 0.8 and 1.2 m was found at a similar height and did not rise higher than 0.6 m below the soil surface. The presence of water moving laterally at a higher hydrostatic potential was not found. Therefore it may be concluded that the water table was perched above a zone which was continuous from 0.6 to 1.2 m below the soil surface. The height of the water table was very similar to a *Molinietum* studied by Sheikh and Rutter (1969). The water table did not rise above 0.3 m below the soil surface throughout the summer and was above 0.15 m in the winter period. The seasonal difference was much greater than valley-bog sites which varied by only 0.02 m between the two periods. The large variation in water table levels as suggested by piezometers on Fernhills Moor allowed aeration of the soil which encouraged the growth of *M. caerulea* (Loach, 1964).

Soil water conditions did not fluctuate to a great extent during 1992 despite variation in rainfall and temperature regimes. Although, this may be caused by the timing of sampling the results show that the hydrological system of Culm grassland soils was well balanced. Losses by evapotranspiration were balanced by capillary water moving vertically or laterally within the soil. This was aided by the water table remaining relatively high throughout the Summer. In contrast the soils of the improved grassland were influenced greatly by vegetation demands. The absence of a winter maximum and summer minimum of soil water conditions found in other agricultural situations (e.g. Reid and Parkinson, 1987) indicated poor drainage conditions and continued supply of water from below.

3.4 Soil nutrient conditions

3.4.1 pH

The pH of soils investigated did not vary with depth and were found to be comparable with acidic grassland defined by Duffey *et al.* (1974) as being between 3.5 and 6.0. As pH values did not change over the sampling period results of mid-August were presented in Table 3.2. The Culm grassland soil was more acidic than the improved grassland soil. The Fernhills plots were very similar and were significantly higher ($p<0.05$) than Staddon Grazing. Comparisons with other semi-natural communities in Table 3.4 show that values equate favourably with the *Agrostis setacea* acidic grassland, heathland and wet heathlands which were derived from similar soils and environmental conditions. To ascertain that SI was a typical improved grassland comparisons were made with two other pastures in Table 3.3 which had been Culm grassland. The pH of Staddon Improved was most similar to Rowden Moor at North Wyke and more acidic than South Nethercott. Values are slightly lower than the reccomendations of 5.5-6.0 by ADAS (1986) for grassland production. However, the highest proportion of improved grassland in the U.K. between 1983-88 (32%) was found to be in a similar pH range of 5.0 - 5.5 by Skinner, Church and Kershaw (1992) which indicated that SI was representative of improved grassland.

Table 3.4 Comparison of soil chemical conditions of Culm grassland with other semi-natural plant communities in Britain

	pH	P	K	Ca	Mg
				mg kg-1	
Community Type					
Culm grassland (Staddon Moor, average)	4.3	4.0	271.3	286	192.8
Acidic grassland (Duffey et al, 1974)					
a) Festuca-Agrostis Upland (Ben Wyvis, E. Ross)	5.2	1.3	112.0	395	n.i.
b) Agrostis setacea (Southwest England)	4.1 - 6.2	n.i.	n.i.	n.i.	n.i.
Heathland	4.8	8.2	18.5	449	38.0
Land reverting to heathland (Stoborough Heath, Dorset (Smith et al, 1991)	5.6	9.0	22.7	1535	20.8
Wet heathland (Rhos cilcenin, West Wales) (Evans, 1989)	4.7	5.0	26.8	13	14.6
Fen peat (Gordano Valley, N.Somerset) (Jefferies and Willis,1964)	3.6	n.i.	80.0	8980	275.0
Neutral grassland (Duffey et al, 1974)					
a) Neutral Molinia (Drostre Bank, Brecon)	6.1	27.0	240.0	7530	200.0
b) Flood meadows (Mickfield Sufford)	6.0	n.i.	93.0	4670	180.0
c) Water meadows (Langford, Dorset)	6.2	39.0	200.0	1530	160.0
Calcareous grassland (Rorison, 1971)	n.i.	1.6	108.0	9283	180.0
Chalk grassland (Hambledon Hill, Dorset) (Duffey et al, 1974)	7.6	7.0	150.0	11000	150.0
Sand Dune (Braunton Burrows) (Jefferies and Willis,1964)	7.9	n.i.	15.0	1252	240.0

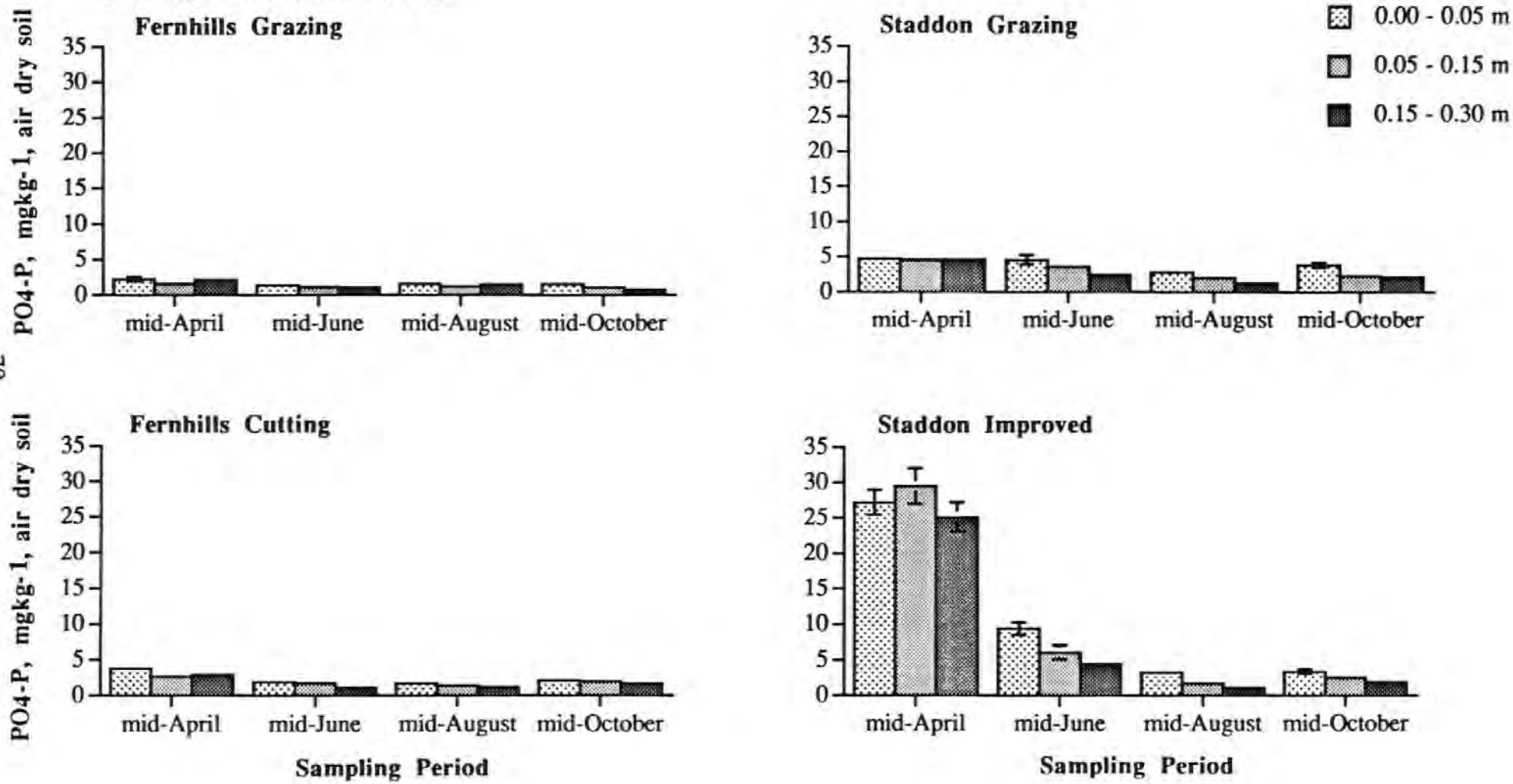
n.i. - no information

3.4.2 Phosphate-phosphorus (PO_4-P)

The phosphate status of Culm soils is of particular interest in this project as low concentrations may be more favourable to Culm grassland species (Gough and Marrs, 1990). The concentrations of phosphate-phosphorus (which will be referred to as P) presented in Figure 3.2. were comparable to those of the lowland wet heaths in Dyfed in Table 3.4. Levels under chalk grassland and Dorset heathland were slightly higher and those of calcareous grassland and neutral grassland were much lower. The soils were comparable to an ADAS index of 0 detailed in Appendix Three . The average P concentration for the sampling period on Staddon Improved was comparable to that of other improved grasslands in Table 3.3 which have an ADAS index of One.

The P concentrations on the Fernhills plots were not significantly different which indicated that recently introduced cutting and grazing regimes had limited impact on P. Therefore the longterm input of management was probably responsible for the significant difference ($p<0.05$) between Staddon Grazing and Fernhills plots. On SG the return and breakdown of organic matter from cattle excrement and disturbance by trampling over many decades has sustained nutrients turnover. The concentration of P in all the plots varied most ($p<0.05$) early in the growing season in mid-April with concentrations on SI approximately five times higher than Culm grassland. The application of fertiliser two weeks before sampling was responsible, and further stimulated plant demand which led to an increased rate of mineralisation. After mid-June the concentration of P on the plots was similar which suggested a slow down of mineralisation and plant uptake later. A decline was most prominent on SI which may be augmented by fixation to unavailable forms of P as indicated by reduction of the ADAS index from three to one. A similar variation was found on Staddon Grazing but to a lesser extent which may show that plant nutrient demands were lowered and not limited to a short period of time.

Figure 3.2
Seasonal variation of soil extractable phosphate-phosphorus in experimental plots during 1992 (n = 15, standard error bars)



3.4.3 Nitrate and ammonium nitrogen (NO_3-N, NH_4-N)

Values of nitrate and ammonium nitrogen are very variable in nature as processes within the nitrogen cycle are highly influenced by environmental conditions especially nitrification and denitrification. As a result, patterns of soil extractable nitrate and ammonium in Figures 3.3 and 3.4 were difficult to explain. Further variation was introduced by grazing and fertiliser applications (Mengel and Kirkby, 1979). For example, the NO_3-N concentrations in 0.00-0.05 and 0.15-0.30 m depths were not significantly different. Higher concentrations of NO_3-N were expected within the 0.00-0.05 m of soil, as the availability of nitrogen is raised by a higher organic matter content. Additionally, the Fernhills plots were found to be significantly different ($p<0.05$), except during mid-October, and FG significantly differed over time whereas FC did not.

Despite these anomalies, all four plots were found to have relatively low levels of nitrate-nitrogen in comparison to fertile soils which usually range from 28 - 280 mg kg^{-1} (Mengel and Kirkby, 1989). The concentration of NO_3-N on SI was significantly different ($p<0.05$) from the Fernhills plots and similar to SG which contrasts markedly with P conditions. This relationship may be attributed to long term management of SG which has encouraged continual organic matter breakdown and mineralisation of nitrogen. The significant increase in NO_3-N in mid-August and October could be related to a recovery of levels following a slow down in plant uptake towards the end of the growing season. The application of fertiliser had little impact on the improved plot unlike P concentrations. The NO_3-N applied was rapidly removed by the early growing grasses.

Ammonium-nitrogen was found to be higher than nitrate-nitrogen on all plots which is converse to the relationship postulated by Russell (1987). This may indicate the existence of denitrifying conditions bolstered by a relatively low pH and high soil water contents. The input of urine and dung was evident on FG as NH_4-N concentrations in mid-October at the 0.00-0.05 m depth were significantly higher than on FC ($p<0.05$).

Figure 3.3
Seasonal variation of soil extractable nitrate-nitrogen in experimental plots during 1992 (n = 15, standard error bars)

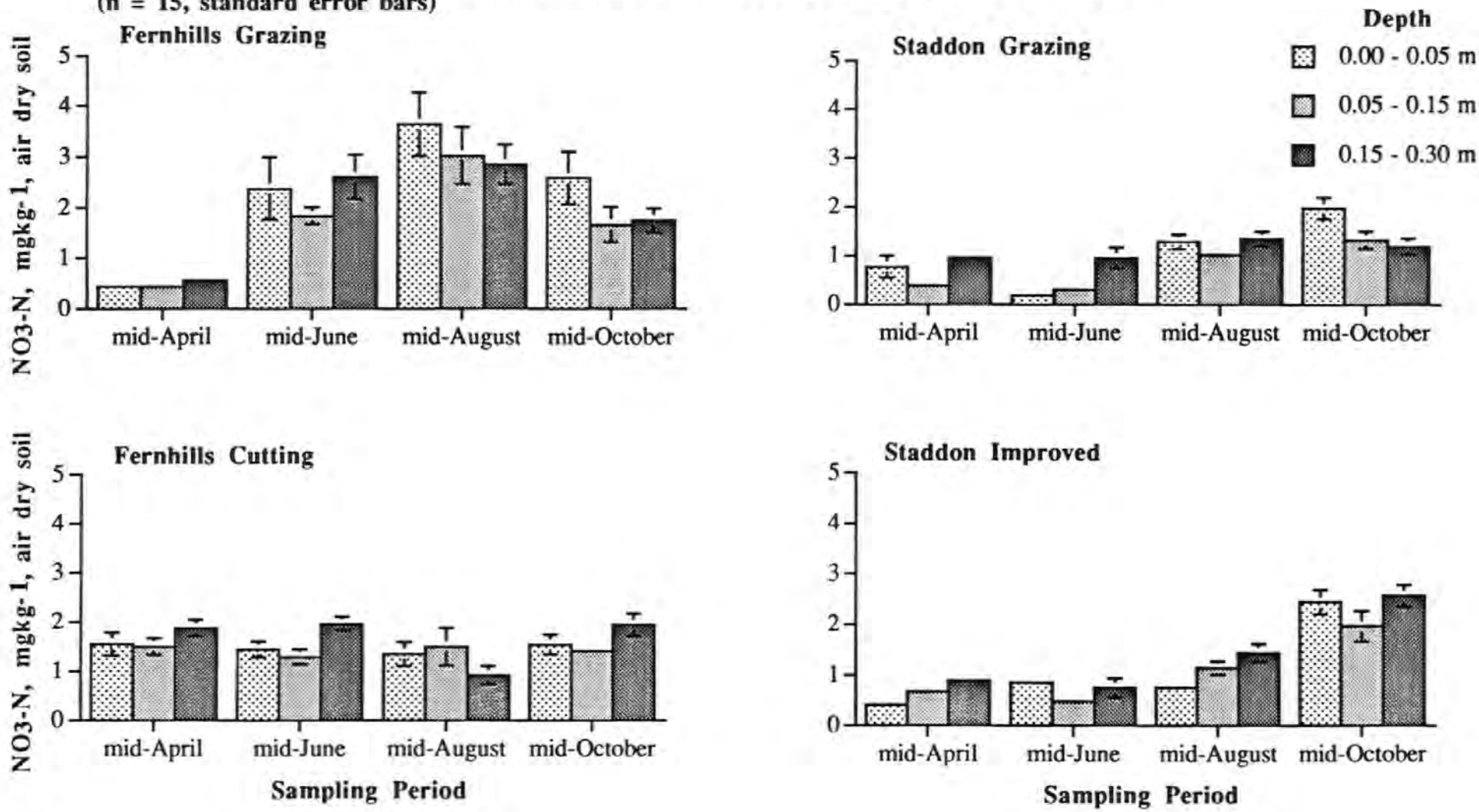
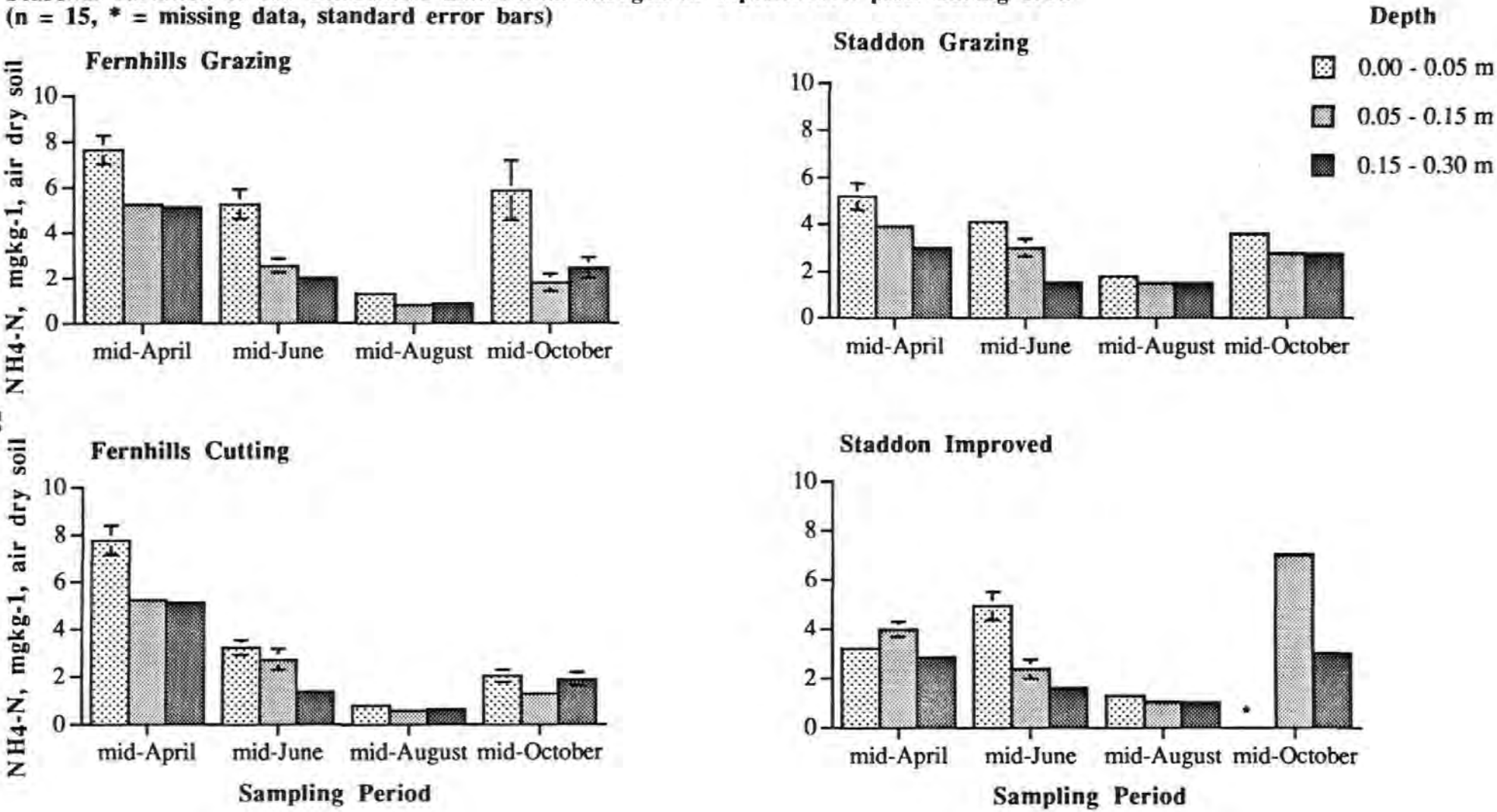


Figure 3.4
Seasonal variation of soil extractable ammonium-nitrogen in experimental plots during 1992
(n = 15, * = missing data, standard error bars)



3.4.4 Potassium

Potassium is an important nutrient as it enhances the synthesis and translocation of carbohydrates, encouraging cell wall thickness and stalk length. The concentrations of potassium on all the experimental plots in Figure 3.5 correspond to an ADAS index of three in Appendix Six. These concentrations were much higher than communities in Table 3.4 especially the wet heathland in West Wales. The clay-rich Culm soils weather rapidly and release potassium-bearing minerals such as feldspars and micas. Significantly ($p<0.05$) higher and variable concentrations of potassium were found in the 0.00-0.05 m depth. Fertiliser applications did not elevate the potassium concentrations on SI. The maintainance of concentrations suitable for agricultural production often require regular fertiliser applications because of a high fixation capacity. But concentrations remained above the ADAS (1986) recommended value of 121-240 mg kg^{-1} for grassland production.

3.4.5 Calcium and magnesium

As variation in extractable calcium and magnesium during the sampling period was limited only the concentrations for mid-June are presented in Figures 3.6 and 3.7 respectively. Concentrations of calcium on Culm grassland in Table 3.1 was most comparable to acidic grassland, higher than wet heathland and much lower than calcareous, chalk and neutral grassland. Significantly ($p<0.05$) higher concentrations of calcium on the Improved plot probably reflected past additions of lime. Magnesium was found to be lower than calcium on all plots except on Staddon Grazing and was analagous to wet heathland in West Wales in Table 3.1. Magnesium concentrations on the improved grassland were similar to the other improved pastures in Table 3.3 and related to an ADAS index of two (Appendix Three) which was reccommended by ADAS (1985) for optimum grassland production.

Figure 3.5
Seasonal variation of soil extractable potassium in experimental sites during 1992
(n = 15, * = missing data, standard error bars)

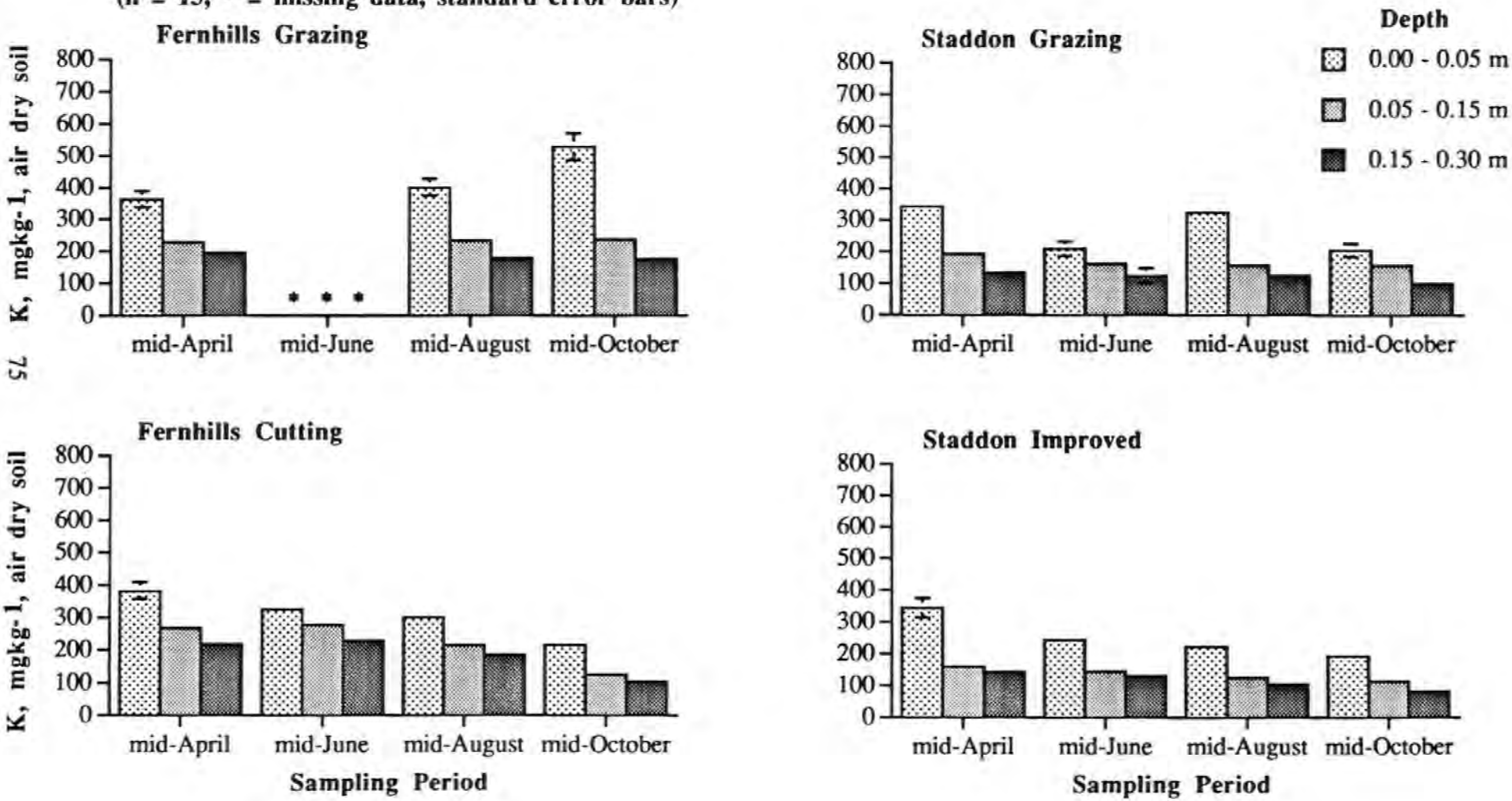


Figure 3.6
Variation of soil extractable calcium in mid-June, 1992
(n = 15, standard error bars)

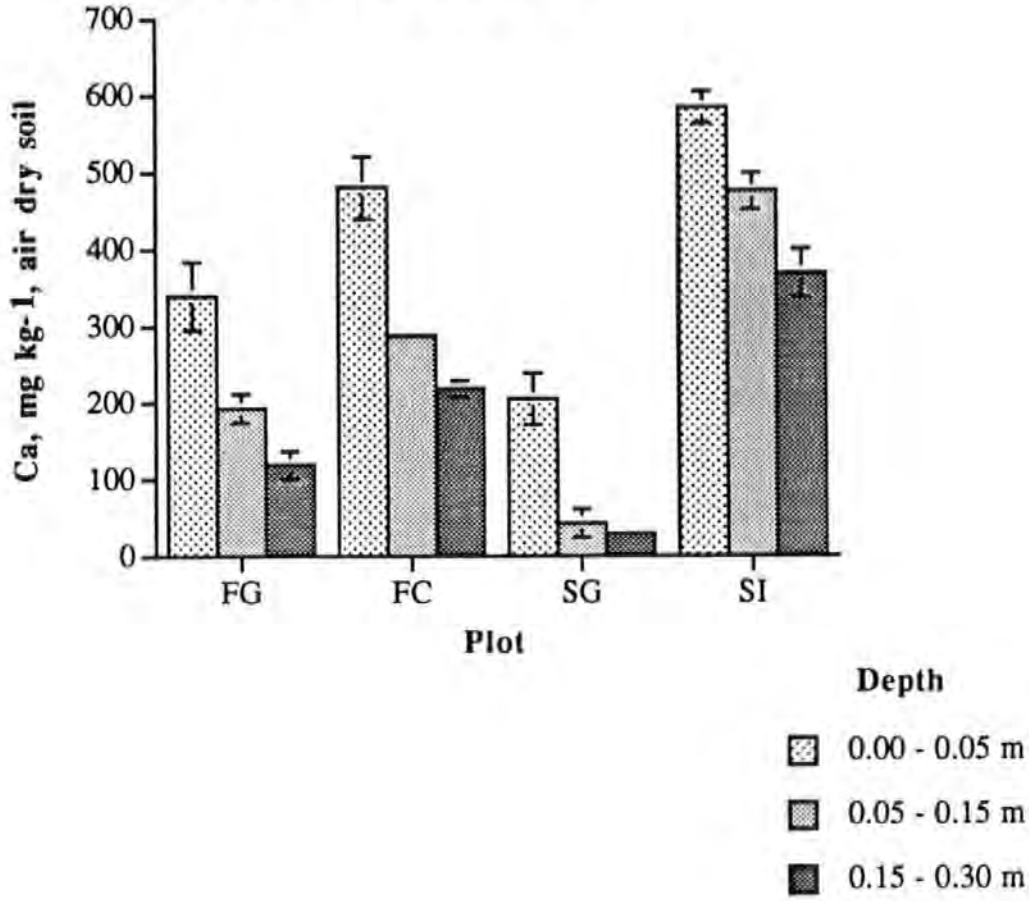
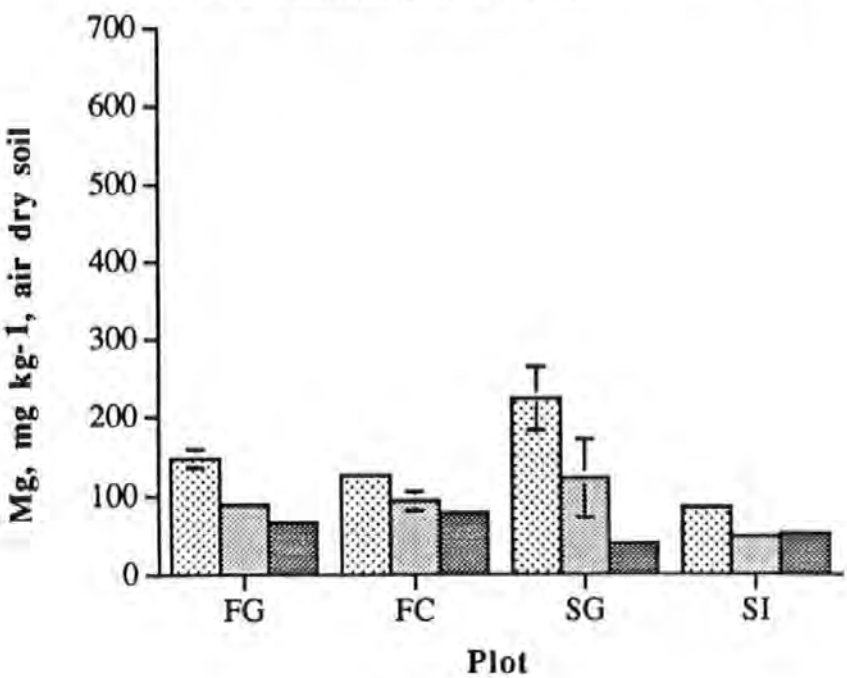


Figure 3.7
Variation of soil extractable magnesium in mid-June, 1992
(n = 15, standard error bar)



3.5 Plant Communities

3.5.1 Staddon Improved (SI)

Staddon Improved may be classified as a typical improved grassland in that it is a resown grassland of not less than five years in age (Holmes, 1989). Grasslands have been classified by Stapledon *et al.* (1945) and Hopkins (1985) with reference to botanical composition. This includes comparisons to percentage cover of *Lolium perenne*, *Agrostis stolonifera*, *Trifolium repens* and *Holcus lanatus*. The community on SI was composed of 15 different species presented in Table 3.5., was dominated by grasses and had a notable presence of flowers and soft rush. The percentage cover of these grasses were most comparable to a 30 years old pasture at North Wyke (Tallowin, Kirkham, Brookman and Patefield, 1990). The community was found to have close affinity, as demonstrated in Appendix Three, Four and Ten, with the NVC classifications of MG6 *Lolio-Cynosuretum cristati*, and MG10 *Holcus-Juncetum* (Rodwell, 1992). Comparisons with the two communities indicated that SI was within a continuum between the two communities.

Lolium perenne was not a significant component of the sward on SI, which tends to suggest that the pasture was old, despite the sward being reseeded between ten and twenty years ago. This may indicate that sward management is sub-optimal for *Lolium perenne* (Grime, Hodgson and Hunt, 1988), allowing a substantial presence of *Cynosurus cristatus* (Grime *et al.* 1988) and the invasion of non-sown species such as *Agrostis stolonifera* (Green, 1972). Conditions have encouraged the proliferation of *Holcus lanatus* together with *Juncus effusus* which probably reflects previous poaching. A potential for greater productivity exists as *Trifolium repens*, the most important pasture legume, (Grime *et al.*, 1988) is a constant component. A greater abundance of *Lolium perenne* which is highly palatable and tolerant to trampling, mowing and grazing would increase the productivity of the sward (Grime *et al.*, 1988). The botanical composition of SI has reverted from an original productive sward to one that was less productive and has a stable species composition in response to relatively low fertiliser inputs.

Table 3.5 Abundance and frequency of the flora on Staddon Improved

DATE	MAY		AUG	
FREQUENCY (F) ABUNDANCE (A)	**F**	**A**	**F**	**A**
SPECIES				
Holcus lanatus	V	7	V	7
Cynosurus cristatus	V	5	III	4
Trifolium repens	V	5	V	5
Anthoxanthum odoratum	V	5	I	4
Lolium perenne	III	1	V	5
Bare / litter	III	4	I	4
Bellis perennis	II	4	II	1
Juncus effusus	I	1	I	5
Festuca ovina	I	6	III	4
Taraxacum Sect.	I	4	I	4
Poa trivialis	I	1		
Ranunculus acris	I	2		
Agrostis stolonifera	I	4	V	5
Trifolium dubium	I	4	I	4
Quercus robur	I	1		
Cerastium fontanum	I	1	I	2
Leucobryum glaucum	I	4	I	2
Leucanthemum vulgare			I	3
Prunella vulgaris			I	1

3.5.2 Culm Grassland

The Culm grassland plots were more species-rich than the improved plot with 26, 18 and 14 species recorded for SG, FG and FC respectively. The Fernhills plots in Table 3.6 have significantly less species than Staddon Grazing. Percentage cover of *M. caerulea* was found to be greatest on the Fernhills plots as lack of management over a number of years has enabled this deciduous perennial to assert dominance and form tussocks (Berendse and Elberse, 1989). This has led to a higher litter cover and greater expanse of bare soil on Fernhills in comparison to Staddon Grazing. The much higher abundance of*M. caerulea* in relation to rushes indicated that the soils are not continually waterlogged as it has a low tolerance to waterlogging (Proffitt 1985, Grime *et al.*, 1988). On wetter areas *M. caerulea* gave way to rushes (Grime *et al.*, 1988), especially on Fernhills Grazing at the edge of the plot. Rushes were only recorded in three quadrats on Staddon Grazing. *Juncus effusus,* prevalent on acid soil, was more frequent than *Juncus conglomeratus* which favours base-rich soils and is less tolerant to ferrous iron toxicity (Grime *et al.*, 1988). Further evidence of non-permanent waterlogged conditions was indicated by the absence of *Sphagnum compactum* on all the plots. The bryophytes of the Culm grassland plots were of low cover particularly on Fernhills where the thick litter inhibits their development. The most abundant were *Leucobryum glaucum* and *Brachythecium rutabulum.*

The aesthetic qualities of the Culm grassland plots were enhanced by the presence of herbs, *Succisa pratensis*, *Potentilla erecta, Cirsium dissectum* and *Dactylorhiza maculata*, which are associated with infertile habitats (Grime *et al.*, 1988). *P. erecta* has an affinity for acidic soils (Grime *et al.*, 1988) and was found to be a constant component of Staddon Grazing but much reduced on Fernhills. *Dactylorhiza maculata* flowered the earliest in May followed by *C. dissectum* in early July, the latter was found to be in greater abundance on Fernhills. *S. pratensis* flowered in August and was found in greater abundance on Staddon Grazing. It is often restricted in cover as it regenerates almost entirely by seed which reduces its ability to recolonise new areas (Grime *et al.*, 1988).

Staddon Grazing was found to have the greatest number of sedge species. *Carex panicea* was the most frequent and abundant. It is a distinct glaucous perennial found in a wide-range of habitats particularly wetland (Jermy, Chater and David 1979). Most of the other sedges present were found to be closely associated with Culm soil conditions such as *Carex binervis*, which is closely associated with acid soils (Clapham, Tutin and Warburg, 1962) and *C. hostiana*, *C. nigra* and *C. pulicaris* which are indicative of moist soil conditions. However, in contrast *C.caryophyllea* was present but is associated with drier conditions (Jermy *et al.*, 1978).

A strong shrub element existed on the Culm grassland plots, particularly on Staddon Grazing. *Ulex gallii* was found to make a large contribution to the flora. Although less abundant on Fernhills, it was more advanced and reached up to one metre in height in this locality. The height was kept in check on SG by topping during the autumn. *C. vulgaris*, a characteristic component of heathland and moorland was most abundant on SG, where soil pH conditions were more suitable. This shrub, together with *U. gallii* has the ability to acidify the soil around its roots (Grime *et al.*, 1988).

The floristic composition of the Culm grassland plots were most comparable to the NVC classification of M24 *Cirsio-Molinietum caerulea* and the M16 *Ericetum tetralicis* in Appendices Four and Five, and also M25 *Molinia caerulea-Potentilla erecta* in Appendix Ten (Rodwell, 1992). There were close similarities with the *Juncus acutiflorus-Erica tetralix* M24c sub-community, but a close fit was not possible due to the absence of *Lotus uliginosus* and a large component of rushes. Although, *Lotus uliginosus* was absent from the plot on Staddon Grazing it was found in other areas of the field. The M16b *S. pratensis - C. panicea* sub-community was found to be a more suitable match, although *succisa pratensis* was only a small component. From this it may be concluded that the vegetation communities of the Fernhills plots were most comparable to M16b and the Staddon Grazing plot may be placed along a continuum between M16b and M24c.

Table 3.6 Abundance and frequency of the flora on the Culm grassland plots

PLOT	STADDON GRAZING				FERNHILLS GRAZING				FERNHILLS CUTTING			
DATE	MAY		AUG		MAY		AUG		MAY		AUG	
FREQUNCY (F)	F	A	F	A	F	A	F	A	F	A	F	A
ABUNDANCE (A)												
SPECIES												
Molinia caerulea	V	6	V	7	V	7	V	6	V	7	V	7
Festuca rubra	V	5	III	6	II	5	II	5	I	2	I	4
Carex panicea	V	5	III	5	I	1	I	2	I	1	I	1
Potentilla erecta	IV	6	III	4	I	2	II	1	II	1	III	5
Ulex gallii	IV	5	II	5	I	2	I	1	I	5	I	5
Calluna vulgaris	III	5	II	5	I	5	II	4	II	4	II	4
Anthoxanthum odoratum	III	4	II	4								
Erica tetralix	II	2	II	3	II	4	II	4	II	4	II	4
Dactylorhiza maculata	II	1			I	1			I	1		
Succisa pratensis	II	4	II	4	I	1	I	1	I	1	I	2
Nardus stricta	II	4	II	4								
Bare / litter	II	4	I	5	V	6	V	7	V	7	V	4
Leucobryum glaucum	II	4	I	4			I	5			I	4
Brachythecium rutabulum	II	4	I	4			I	4			I	2
Cirsium dissectum	I	5	I	5	II	4	III	4	III	3	III	5
Juncus effusus	I	4			II	4	I	4	II	4	I	4
Salix repens	I	4	II	4	II	1	II	4	I	2	I	3
Carex hostiana	I	4	I	3	I	1	I	2	I	5	I	2
Carex caryophyllea	I	1										
Carex demmisa	I	1										
Carex nigra	I	1										
Carex pulicaris	I	1							I	2		
Carex binervis	I	4	II	4								
Luzula multiflora	I	4									I	4
Holcus lanatus	I	1										
Pedicularis palustris	I	1										
Polygala vulgaris	I	1										
Scutellaria galericulata	I	1	I	2								
Polytrichium juniperum			I	4								
Thuidium tamariscum					I	4			II	4		
Juncus conglomeratus					I	4	II	4				
Lathyrus montanus					II	1	II	1	II	1	I	1
Betula pubescens					I	1	I	4	I	5	I	1
Carex flacca					I	1	I	2				
Serratula tinctoria					I	4	I	2				
Agrostis stolonifera			II	1								
Senecio aquaticus			I	2								
Cerastium fontanum							I	1				
Prunella vulgaris							I	1			I	1
Achillea ptarmica							I	1				
Quercus robur									I	1		

3.5 Summary

An initial survey during 1992 investigated the soil physical and nutrient conditions and floristic composition of Culm and improved grassland under different management regimes; these results are summarised below. The soil hydrology of Culm grassland was not effected to a great extent by fluctuations in climatic conditions indicating that the system was well balanced. In contrast the soil water contents on Staddon Improved was greatly influenced by both lower than average rainfall early in the year and evapotranspiration losses from the vegetation. Soil bulk density and organic matter content were also enhanced these contrasts. The pH of the soils were found to be slightly acidic. Acidity was most pronounced on the pristine Culm grassland plot (SG). Marked contrasts were found in the soil phosphorus status of the experimental plots. During mid-April the improved grassland soil had five times higher extractable P than the Culm grassland plots which remained relatively low throughout the sampling period. Similar contrasts were not found with the other nutrients investigated.

The plant communities of Culm and improved grassland were very different. Species composition of SI indicated that the site was not intensively managed and had become stable in response to low fertiliser inputs. However the site was found to be typical of other improved grasslands in the area. The Culm grassland that had been managed for many years was found to have a greater number of species than plots that had been unmanaged. *M. caerulea* was found to be greater component on these latter plots and was tussocky in nature. Shrubs had become larger in stature on Fernhills were kept in check by topping on SG. The small component of rushes and mosses and bryophytes indicate that soil conditions are not permanently waterlogged and are favourable to the abundance of *M. caerulea*.

From the results of this initial survey which are summarised below, it was decided to investigate soil P conditions in more detail in 1993. This is reported in Chapter Four. The botanical surveys indicated that *M. caerula* was an important component of the experimental plots. It was decided to monitor the production of the whole community in 1993 which is reported in Chapter Five, to ascertain how it influences other species and also cycling of nutrients within the Culm grassland system.

1) Soil water content did not vary during the sampling period from mid-April to mid-October, 1992. Water was ponded in the 0.00-0.05 m depth and downward movement of water was limited by the underlying clay parent material. The water table remained above a depth of 0.5 m from June until October 1992.

2) The soil pH of the Culm grassland plots was comparable to acidic grasslands particularly on Staddon Grazing which was significantly lower. A depressed pH value on the improved plot indicated that soil conditions were reverting.

3) Soil extractable phosphate-phosphorus was significantly higher on the improved grassland than Culm grassland. A similar pattern in nitrogen conditions was not evident. The soils are potassium rich with adequate supply of calcium and magnesium.

4) The concentration of nutrients in soil solution removed by ceramic suction cups were below the level of detection.

5) The Culm grassland plots were more species-rich than the improved grassland. The improved grassland was dominated by *Holcus lanatus* in conjunction with a small component of *Lolium perenne*. *M. caerulea* was found to dominate the Culm grassland plots particularly on those with recently introduced management. Continued long term management on Staddon Grazing has ensured a greater species-richness and topping has prevented shrubs proliferating.

CHAPTER FOUR

THE AVAILABILITY OF SOIL PHOSPHORUS IN THE CULM GRASSLAND SYSTEM

4.1 Introduction

Semi-natural plant species possess strategies to survive on low levels of available nutrients, particularly available P (Bradshaw, 1960). The survey of the plant communities in Chapter Three found that Culm grassland was characterised by plants possessing these strategies and tend to be perennials. The investigation of soil conditions suggested that phosphorus was an important limiting factor, as marked contrasts in P concentrations were found between Culm and improved grassland at the start of the growing season. Culm grassland therefore contrasted with improved grassland by being species-rich and having a low phosphorus availability. These findings concur with studies by Lloyd and Pigott (1967) and Rorison (1971) and more recently Gough and Marrs (1990 a,b), Marrs, Gough and Griffiths (1991) and Pywell, Webb and Putwain (1994) presented in Table 4.1, which suggested a link between species-richness and P availability. Extractable P concentrations were 5.8 times greater on the improved grassland than Staddon Grazing (Culm grassland) in mid-April and the annual average was 2.7 times greater. Similar contrasts in extractable nitrogen were not evident as also found by Marrs *et al.* (1989).

To investigate these contrasts in P status a detailed study of P availability of Culm and improved grassland was conducted during 1993. This study endeavoured to obtain a better indication of the range of P concentrations that were most suitable to Culm grassland species. There is evidence that P availability plays an influential role in the maintenance of species-rich grassland. A review of soil P availability in detail in Chapter One, Section 1.4.2 emphasises why P is often a limiting factor. Variation throughout the growing season was investigated by employing a soil extractable method and also novel methods of soil solution extraction.

Table 4.1 Comparison of Culm and improved grassland soil phosphorus availability with other contrasting vegetation types

Vegetation Type	Extractable P (mg kg^{-1})
Culm grassland (Staddon Grazing)	4.7
Improved grassland (Staddon Improved)	27.2
Present study: mid-April, clay soil, sodium bicarbonate	
Semi-natural grassland	9.0
Intensively managed agricultural grassland	68.0
Gough and Marrs (1990) clay soil, Truogs reagent	
Grass	8.2
Arable	62.0
Marrs et al. (1991) clay soil, sodium bicarbonate	
Arable field	19.6
Arable field abandoned in 1984	8.9
Grass meadow established before 1941	5.4
Gough and Marrs (1990) calcareous gley soil, Olsens	
Heathland (n = 3)	11.5
Abandoned pasture and arable (n = 4)	5.1
Currently farmed pasture (n = 3)	41.9
Pywell *et al.* (1994) humoferric podsols, acetic acid	

Table 4.2 Total phosphorus content of Culm and improved grassland soils

	Total phosphorus (mg kg^{-1})	
Plot	Mean (n = 5)	Standard error
Fernhills Grazing	363.0	26.9
Staddon Grazing	545.5	57.7
Staddon Improved	790.6	131.8

4.2 Experimental Design

4.2.1 Evaluation of Techniques

Three methods were employed to estimate the availability of P to plants in Culm soils. Firstly chemical extraction by sodium bicarbonate was carried out, as in the first field season. This extraction does not strictly indicate available P as it removes soil solution and loosely held P (labile) and will be referred to as extractable P. This was compared with the direct removal of soil solution by centrifuging in the laboratory and extraction of soil solution using non-P adsorbing suction cups placed in the field. These fractions will be referred to as solution P. In conjunction with these measurements soil water content and soil matric potential was monitored to ascertain the effect of water conditions on P. Monitoring of soil conditions continued throughout the 1993 growing season in conjunction with detailed plant community production measurements.

a) Sodium bicarbonate extraction

Sodium bicarbonate extraction is a tried and tested method which allows comparisons from year to year and also with agricultural soils. A number of factors should be considered despite the method being widely used for measuring 'available' P. Although it is thought to be insignificant in this study, air-drying of the soil has been found to affect concentrations of some fractions of P (Black *et al.*,1965). The use of chemicals to extract nutrients has been found to overestimate the fraction which is 'available' to plants and often the type of extractant is critical in controlling the fraction removed which was discussed in Section 2.3.1.

In acid and neutral soils, calcium phosphates (the most available forms of P in these soils) were probably more soluble in the presence of $NaHCO_3$. When sodium bicarbonate solution is added, ionic competition of HCO_3^-, CO_3^{2-}, OH^- ions for the P adsorbed on the surface of the soil particles occurs. Pioneering work by Olsen *et al.* (1954) indicated that the proportion of $NaHCO_3$ soluble P was closely correlated to the amount of P available

to plants. Further evaluation by Sibbeson (1983) in comparison with other soil P tests discussed in Section 2.3.1 ranked $NaHCO_3$ as intermediate in assessing P status.

However, as Culm grassland soils are acid-neutral it was decided to assess the influence of extractants by comparing sodium bicarbonate with acetic acid which may be more suitable for acid soils as a lower pH dissolves less organic matter (Moore and Chapman, 1986). A pilot study was undertaken in which soil was removed from the Staddon Grazing plot at a depth 0.00-0.05 m during mid-March, 1992. The experiment was conducted in a similar manner to sodium bicarbonate extraction employing ten replications and using 2.5 % acetic acid (Moore and Chapman, 1986). Concentrations of P were found to range from 2.55 to 4.19 mg kg^{-1} for sodium bicarbonate and 2.65 to 3.88 mg kg^{-1} for acetic acid. The values were not significantly different and it was concluded that the extractants removed similar amounts of soluble P and on this basis it was decided to continue with sodium bicarbonate extraction.

b) Centrifuging

Centrifuging has been employed to extract soil solution such as to remove displacement solutions (Adams,1974) and solutions resulting from adsorption experiments (Barrow, 1975a,b,c). Also centrifuging has been used to remove soil water at different tensions to investigate soil water characteristic curves (Smith and Mullins, 1989) as the centrifugal force and thus pressure applied may be manipulated accurately (Gillman, 1976). The source of soil water removed by this method may be more predictable than solutions removed by suctions cup (England 1974, Zabowski and Ugolini 1990).

The use of centrifuging in the investigation of concentration of nutrients in soil solutions in relation to plant uptake has been limited because, unlike sodium bicarbonate extraction, no standard method and equipment exists. When devising the experiment, factors such as amount and quality of soil solution released were taken in to account. It was essential for the method employed to provide an adequate sample of solution to analyse, which has not been altered by the process of extraction. Removal of water at high speeds will ensure

rapid removal of the solution but it has been found that high speeds may cause collapse of roots and leaching of ions (Ross and Bartlett 1990). Low speeds will require a longer spin time to attain soil solution which may allow processes such as microbial activity to alter the solution composition. Many studies combat the variation in water content of soil (particularly if they are dry) by drying and then rewetting to a known water content (Reynolds, 1984). This procedure was not applicable to this study as there was a likelihood that P levels would be altered. Interpretation of results would be aided by measuring water contents and as they remained fairly wet during 1992 they provided a natural advantage for the method.

Although a number of studies have found that the amount of water removed varies according to water content and speed of extraction (Gillman, 1976 and Shand *et al.*, 1994) there is no conclusive evidence that the phosphorus content varies. Time constraints of the study prevented a thorough investigation of these factors although they would require further study if the method was recommended. A pilot study of equipment and the optimum speed required to remove an adequate sample was undertaken. The method employed was able to remove approximately 4 to 10 mls of solution which was sufficient for analysis of P. The equipment used and the relatively small amount of soil centrifuged would not be sufficient for other analyses. Under these controlled conditions the tension at which the solution has been removed may be calculated.

c) Suction cup

The employment of suction cups to remove soil solution directly in the field and reduction in the possibility of contamination in the laboratory was discussed in Section 1.5.4. Whilst designing this experiment a number of factors were taken into account. Concentrations of phosphorus in solution removed by ceramic suction cups in Chapter Three were expected to be lower than soil extractable values, as suction cups remove solution directly from the soil and not from the soil colloids. As P levels removed by ceramic cups were below the level of detection of 0.5 mg l^{-1} which was discouraging but, it was important to continue monitoring soil solution from which plants obtain P.

It is well known that cup material has an influence on soil solution composition as a relatively large volume of water is resident within the cup and may react with the cup material. Reactions occur between Al_2O_3 in the cup material with P to form an insoluble compound of aluminium phosphates (Bottcher *et al.*, 1984, Zimmermann *et al.*,1978). The adsorption of P by different cup materials has been investigated by Bottcher *et al.* (1984). They found that ceramic material adsorbed and desorbed large amounts of P whereas porous teflon did not significantly adsorb P. Therefore it was decided to use a similar, inert porous material to prevent these interactions.

The availability of soil water and the ability of suction cups to remove water at different tensions was also taken into account when designing the experiment. Suction cups have been found to fail at low water contents or soil water tensions above 70-80 k Pa which are characteristic of agricultural soils during the summer. Centrifuging provided a useful alternative to extract soil solution during the summer. However, the likelihood of failure occurring was reduced as the Culm soils are continually moist (Figure 3.1). Unlike centrifuging, the tensions at which water was removed cannot be controlled in the field and the sphere of influence of the suction cup will alter according to soil water conditions. Thus, it was also vital to monitor variations in water content and matric potential in the field.

d) Analysis of soil solutions

Modifications were made to the analysis of soil solutions during 1993 as the level of detection of P was not below 0.5 mg l^{-1} in 1992. It was decided to employ a more sensitive method of analysis to allow detection at lower concentrations. A Tecator Flow Injection Analyser (FIA) was chosen to detect P colorimetrically to a detection limit of 2 $\mu g\ l^{-1}$ of phosphate-phosphorus, using stannous chloride as a colour agent (Perstorp Analytical Ltd, 1990). The solution to be analysed was injected directly in to the carrier stream preventing entry of air bubbles, which were found to affect the baseline reading on the Technicon Autoanalyser used in the first field season.

Before samples were analysed factors such as sample contamination and subsequent effects on analysis were reduced as far as possible. Small air bubbles were removed by placing samples and reagents in a sonic bath. Solutions removed by sodium bicarbonate extraction were particularly prone to organic matter coloration especially those from the Staddon Grazing plot. It was important to remove the coloration as it masks the indicator and impedes light transmission. Some coloration was removed by filtering which reduced the amount of suspended solids in the sample. Additions of charcoal were recommended by ADAS (1986) to remove this coloration but this enhanced P values inconsistently. The use of an anion absorption resin (Worsfold, 1993) widely employed to remove organic matter fractions, was also investigated but was unsuccessful in removing coloration. Therefore the solutions were analysed with some colour remaining which could not be removed by filtering. Although, the problem of the presence of coloration was not solved entirely, it was important to be aware of its effects and how variation between samples caused problems in standardising a suitable method.

4.2.2 Sampling regime

The sampling regime implemented in 1992 was modified to allow a detailed study of soil P conditions during 1993. Firstly, as the concentrations of extractable P did not differ significantly ($p<0.05$) between the grazing and cutting plots on Fernhills Moor it was decided to omit the cutting plot from the experimental design in 1993. Experiments conducted by Bakker (1989) and Rizand *et al.* (1989) suggested that mechanical removal and return of plant material was less likely to induce changes in nutrient conditions over a short time period than grazing. This is because grazing is less uniform and encourages the cycling of nutrients by increasing rates of mineralisation through dunging and trampling (Marrs, 1990).

Thus the three plots FG, SG and SI were studied in 1993 using the same number of replications (15) as in 1992. Soil was removed at a depth of 0.00-0.10 m to correlate with the main zone of rooting on Culm grassland and enabled an adequate sample size to be removed. Field equipment was placed in five positions on the three plots and replicated three times. Results of the first field season indicated that spring was a key time period of P availability on Culm grassland. To identify the period of peak mineralisation and major release of phosphate sampling was biased towards the spring season. To this end sampling was conducted at two-weekly intervals from mid-March to mid-June and then monthly until mid-September. Exact dates of sampling may be found in Appendix One and all sampling was carried as above unless otherwise stated.

Water content was monitored using the same methods employed in the first season to a depth of 0.01 m. The water table was also recorded on FG using piezometers as in 1992. The measurement of soil matric potential using a portable quickdraw tensiometer was included in 1993. This indicated the tenacity with which water was held in the soil matrix and is a major factor determining the availability of water to plants and in turn affects the availability of nutrients. Readings were taken at five points per plot.

4.3 Results and Discussion

4.3.1. Sodium bicarbonate extraction

During 1993 soil extractable P was found to be significantly higher ($p<0.05$) than P in soil solution by a factor of approximately one hundred. This indicated that the chemical extraction may overestimate P availability to plants and that the less occluded forms of P have been involved in ion exchange. The elevated level of P on the improved grassland was not evident during the second field season as shown in Figure 4.2. The concentrations of extractable P on SI in mid-April, mid-June, and mid-August were significantly different ($p<0.05$) from the first field season. This contrasted with Culm grassland plots as only mid-April was significantly different ($p<0.05$) from the first field season. During 1993 P concentrations on FG and SG significantly increased after mid-July in Figure 4.3, whereas SI decreased significantly ($p<0.01$).

Variation in soil extractable P from the first to the second field season was not expected. Possible causes included changes in management, weather conditions and sampling and analysis. A major reduction on the improved grassland may be explained by an earlier application of fertiliser on 10th March in comparison to an application on 14th April during the first field season. It is most likely that the applied P was removed rapidly by the nutrient demanding species. Although concentrations of P on SI were much lower than 1992, values remained significantly higher ($p< 0.05$) than Culm grassland until mid-September as shown in Figure 4.2. In contrast during 1992 the plots were not significantly different after mid-June. This may indicate that uptake of P is continuing over a longer period in the second field season on SI. Differences between seasons on both the Culm grassland plots, although small could be due to the impact of introduced management on FG and continued movement of cattle to and from SG and SI. This impact is unlikely to be responsible for significant changes in P values over such a short period.

Figure 4.1 Comparison of extractable phosphate-phosphorus in 1992 and 1993 (n =15, standard error bar)

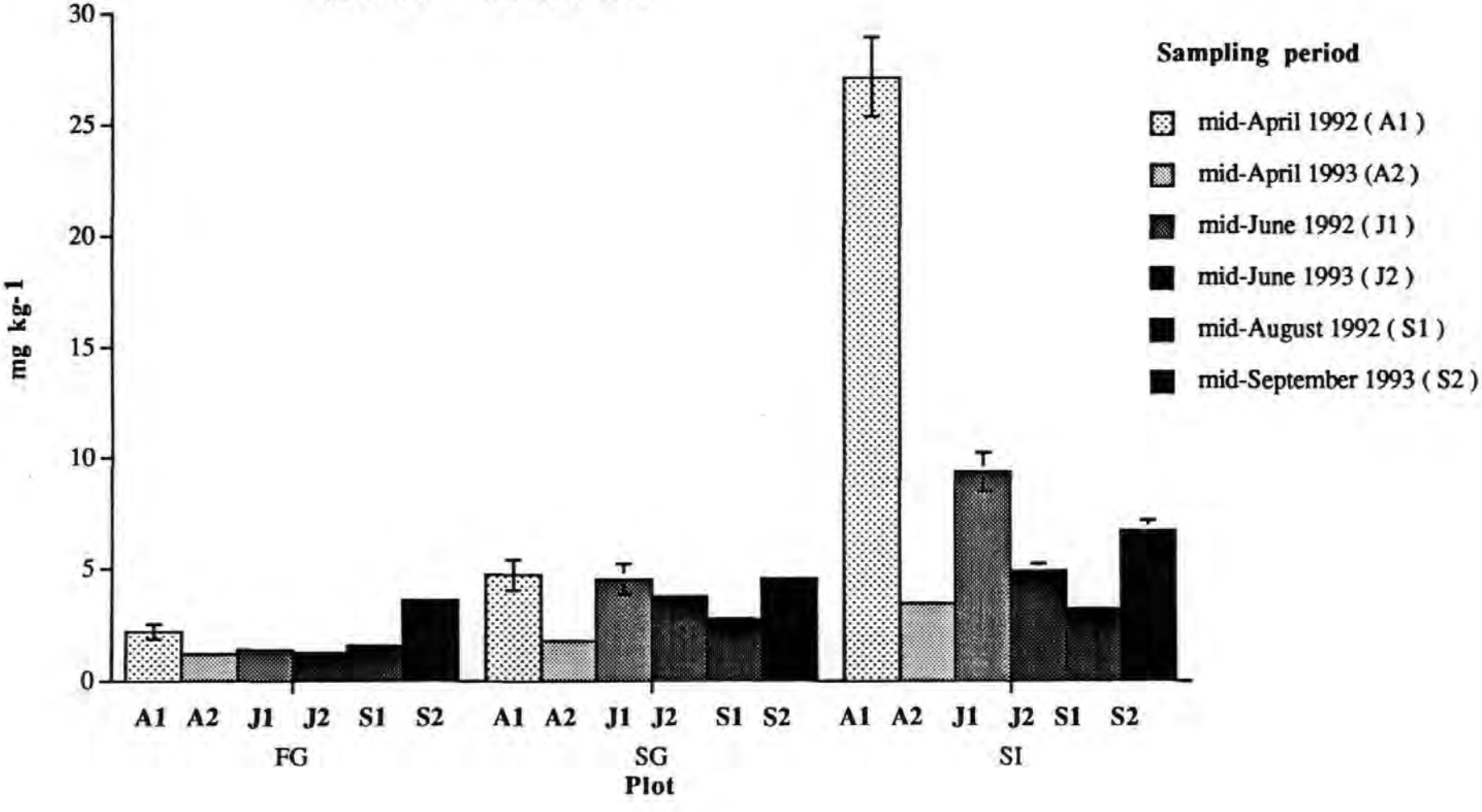
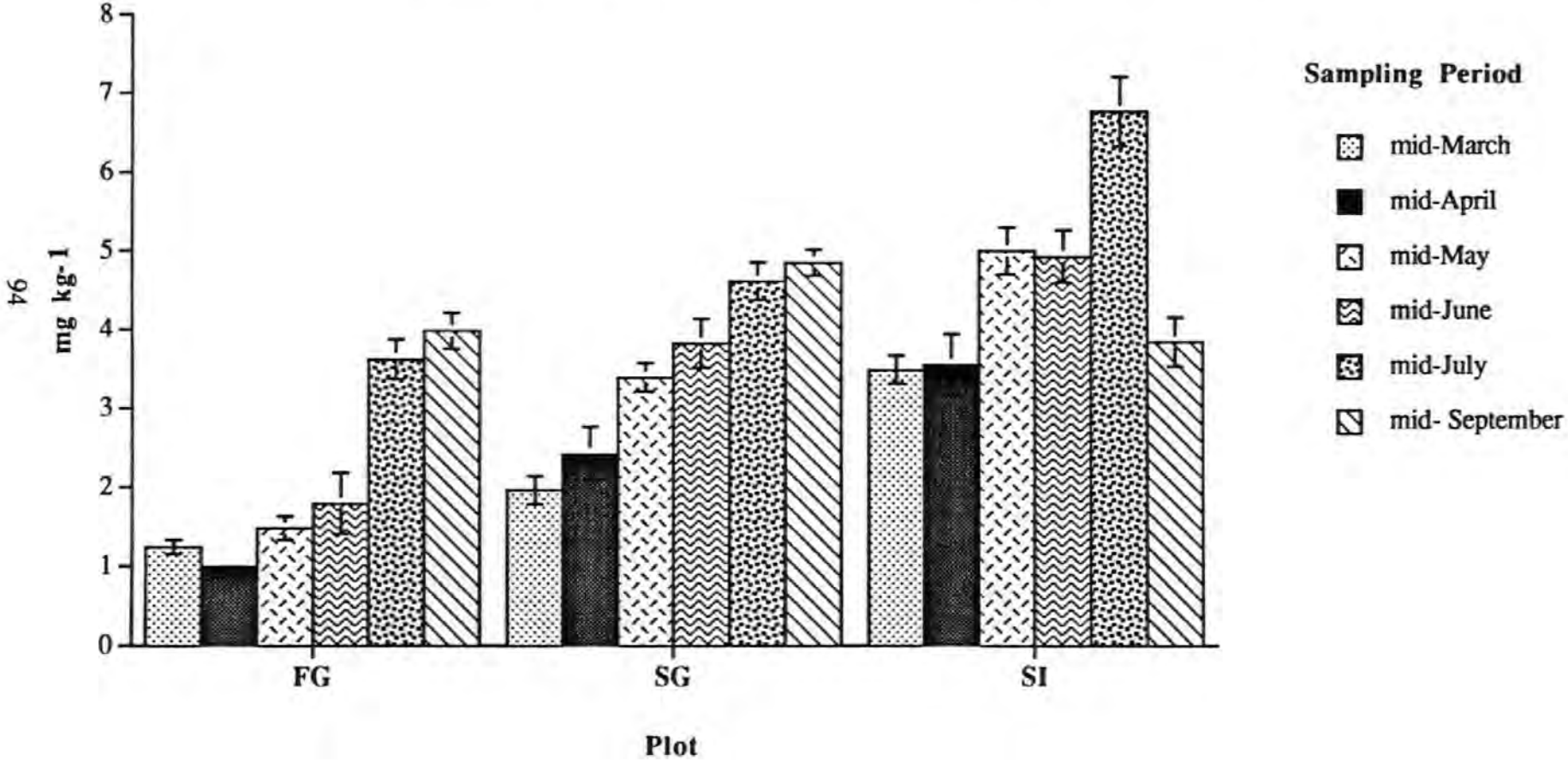


Figure 4.2 Seasonal variation of soil extractable phosphate-phosphorus during 1993 (n = 15, standard error bars)



The effects of changes in management may be enhanced by variations in the weather conditions from 1992 to 1993. Average temperatures during the first four months of 1993 were much warmer than 1992 and than the 30 year average at North Wyke. Average monthly rainfall during February and March was also much lower (see Appendix Two). These warm dry conditions stimulated soil chemical processes such as the breakdown of organic matter and particularly release of P from the microbial biomass component (Seeling and Zasoski, 1993). This was closely associated with early grass growth and subsequent higher demand for P particularly on SI. The following May, June and July were of average temperature and very wet probably reducing plant demand. This enabled a build up of extractable P towards the end of the sampling season, particularly on both of the Culm grassland plots. The increase of P on FG at the end of the sampling season was more abrupt than SG. This may be in response to vegetation differences as *M. caerulea* is more abundant on FG and may be responsible as it usually ceases uptake of nutrients before mid-August (Berendse *et al* 1989). Soil extractable P on SG was significantly greater than FG during mid-May and mid-June. The higher organic matter content on SG and its subsequent breakdown may be responsible for this variation.

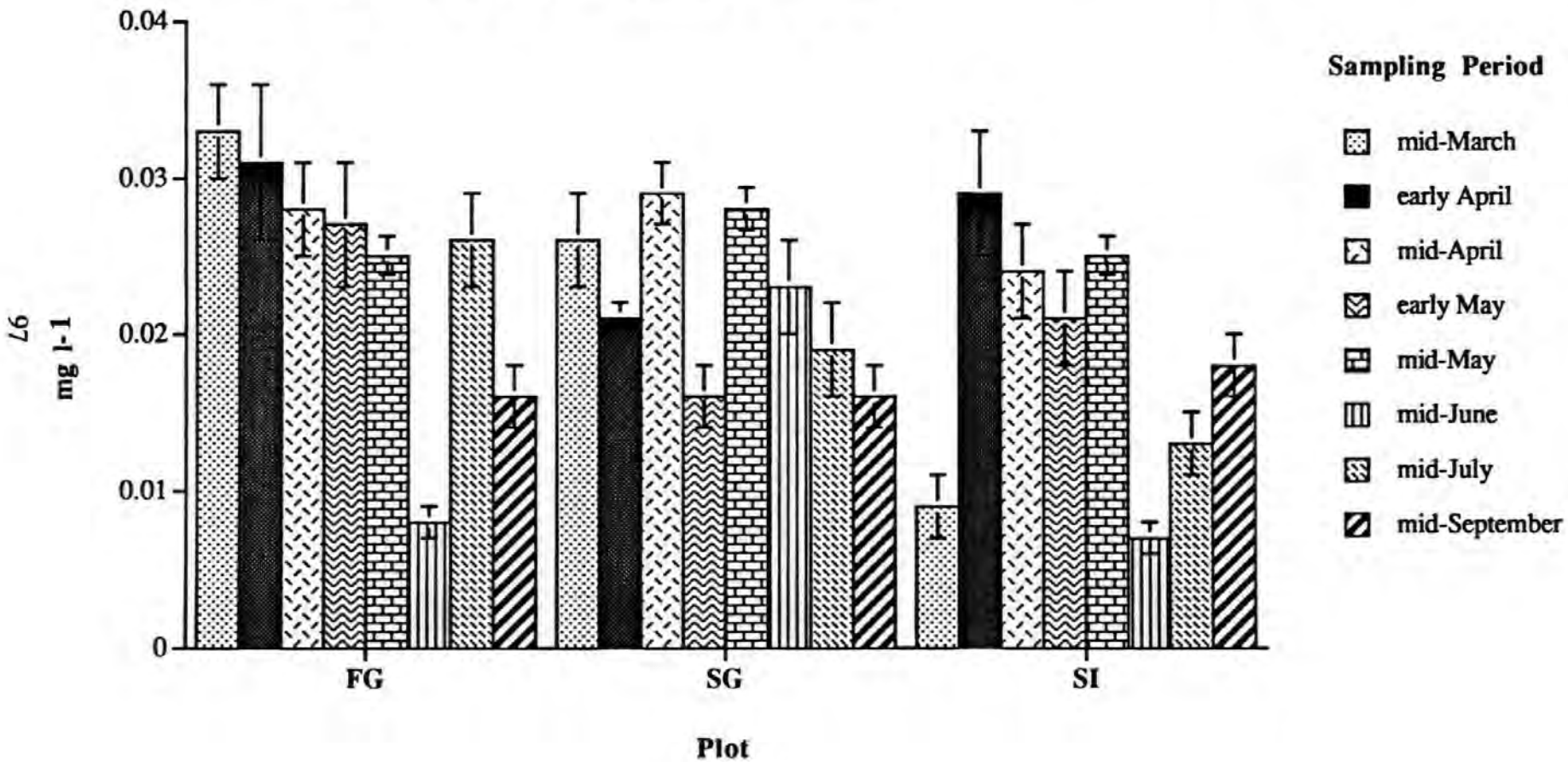
A change in analytical method may have had a limited influence on values during 1993. A more thorough attempt to remove contaminants in 1993 reduced the analytical error. The use of stannous chloride as a colour agent enabled P to be detected at much lower values which may highlight previously undetected variations. However, the weather conditions were most influential in producing variations from year to year. The variation of P concentrations from 1992 to 1993 indicated the importance of conducting experiments for more than one field season. Although P values on SI were lower in the second field season the impact of fertiliser application was still apparent as values remained greater than Culm grassland. The relative elevation of P on SI was confirmed by significantly ($p<0.05$) higher total soil phosphorus values than FG and SG in Table 4.3. A slight increase on the Culm grassland plots may be of concern in the future and may require further monitoring.

4.3.2 Centrifuging

Concentrations of P in soil solution removed by centrifuging were found to be significantly lower ($p< 0.05$) than values removed by sodium bicarbonate extraction. The distribution of the data was skewed and required square root transformation to conduct analysis of variance. Concentrations varied from 0.001 to 0.082 mg l^{-1} which was much lower than the range of 0.3 to 3 mg P l^{-1} in soil solution quoted by Russell (1988), although no information was provided by Russell (1988) on the method of extraction. Experiments employing centrifuging have produced similar results. Campbell, Kinniburgh and Beckett (1989) found a mean concentration of 0.011 mg l^{-1} P in clay soils of Oxfordshire.

Differences between the Improved grassland and Culm grassland as shown in Figure 4.4 were only significant in mid-March and mid-June. In mid-March concentrations on SI were lower than Culm grassland despite the application of fertiliser. In mid-June Staddon Grazing was significantly higher than the other plots. Therefore the impact of these different experimental treatments on solution P was only evident at the beginning and towards the end of the growing season. Additionally, some significant seasonal variations were found within plots during the sampling period apart from Staddon Grazing. In mid-June P values on FG were significantly ($p< 0.05$) lower than the other sampling dates. On Staddon Improved mid-March and mid-June were found to be significantly different ($p < 0.05$). Seasonal variation in soil solution P removed by centrifuging has been found by a number of workers. Campbell *et al.* (1989) found a cyclical variation of solution P; maximum concentration in later summer and early autumn, and a minimum in mid-winter. Shand *et al* (1994) found an annual maximum orthophosphate value of 0.075 mg l^{-1} in August 1989. Zabowski and Ugolini (1990) found P in centrifuged solutions to peak in summer and winter.

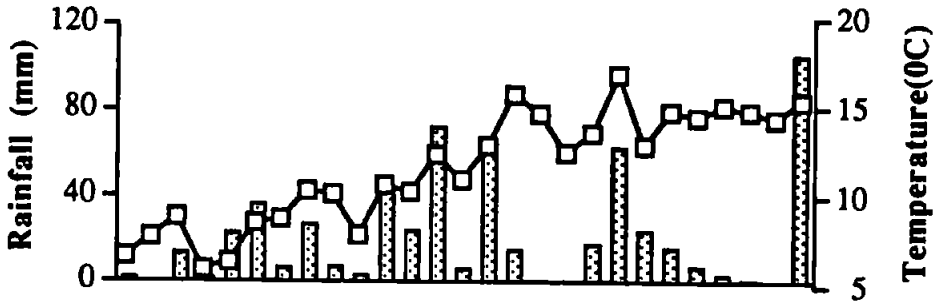
Figure 4.3 Seasonal variation of soil solution phosphate-phosphorus extracted by centrifuging (n = 15, standard error bars)



A similar seasonal variation was not evident in this investigation. This may be caused by a number of factors such as microbial activity and soil water conditions. For example large fluctuations in P levels as found by Falkengren-Gerup (1994), could mask overall seasonal change. Seeling and Zasoski (1994) suggested that microbial activity was largely responsible for fluctuations of P within a sterilisation experiment. Microbial activity reduces labile inorganic P by changing the amount of sorbed inorganic P and releasing organic P compounds into solution (Seeling and Zasoski, 1994).

Microbial activity and its effects on soil solution P concentration is in turn influenced by environmental factors particularly temperature and soil water conditions (Mengel and Kirkby 1979, Brookes, Powlson and Jenkinson 1982, Brookes, Powlson and Jenkinson 1985). The influence of gravimetric water content on the three plots studied was difficult to estimate as the values did not change significantly over the sampling period as shown in Figure 4.5. Soil water content particularly on Staddon Improved was expected to decline throughout the growing season when evapotranspiration exceeds rainfall input and followed by a recovery to field capacity levels during autumn rewetting (Reid and Parkinson, 1984). Clays soils such as Culm grassland soils have been regarded as having an uncertain and variable ability to dispose of rainfall (Reid and Parkinson, 1987). This is evident from the ponding in the upper layer of soil in 1992. A corresponding change on the Culm grassland plots would not have been expected as the soils were wetter and contained a greater amount of organic matter. Therefore a significant correlation between gravimetric water contents and P in centrifuged soil solutions was not found.

Figure 4.4
Variation of weekly mean rainfall and temperature and gravimetric water content (0.00-0.01m soil depth), 1993



Topsoil gravimetric water content (0.00-0.01m), 1993

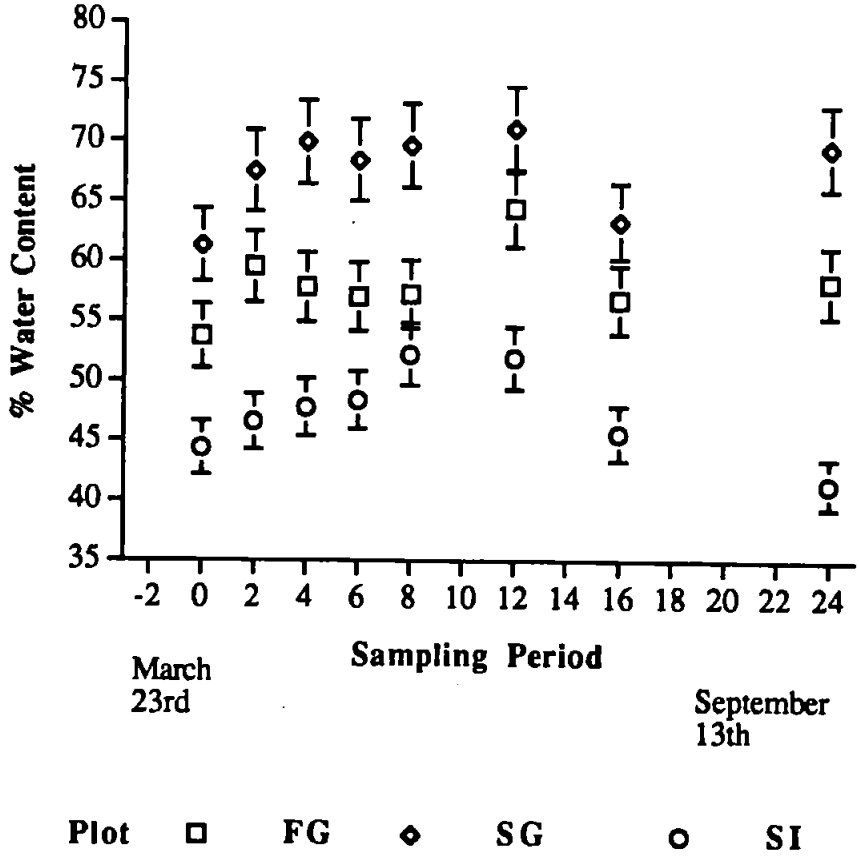
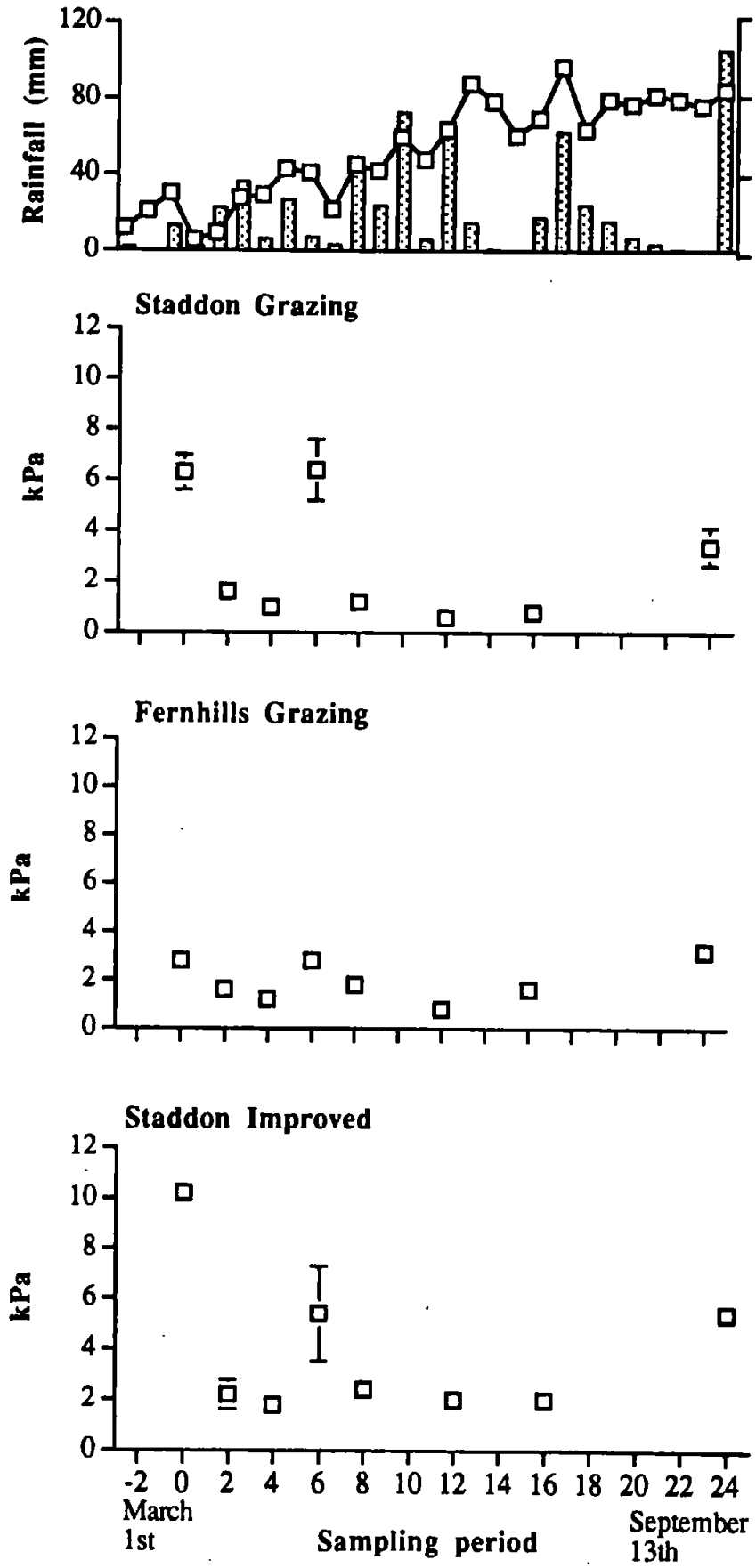


Figure 4.5
Variation of soil matric potential in comparison to meteorological conditions, 1993 (n=5, depth 0.00-0.01m, standard error bars)



A closer relationship was found between soil matric potential and the solution P concentrations indicating that solution concentration was not strictly a function of water quantity (Gahoonia *et al.*, 1994, Zabowski and Ugolini, 1990). Unlike gravimetric water content, the soil matric potential was found to vary during the field season. All plots in mid-March were significantly different ($p<0.05$) from each other and values on SG were lower than SI in mid-June as shown in Figure 4.6. The tenacity with which the water was held within the soil pores appeared to have a greater influence on P values. The measurement of soil matric potential provided a plant orientated measurement of soil water conditions. For most of the sampling season matric potential indicated that soil water conditions remained at field capacity and only exceeded 5 kPa on SI on two occasions. Thus any changes in plant demand and supply for P was masked by constant water conditions. Some variations would be expected as the solubility of soluble salts and cation exchange reactions are altered by some dilution (Walworth, 1992 and Ron Vaz, Edwards, Shand and Cresser, 1994). This was probably not evident as changes induced by plant uptake are counteracted by changing the diffusion gradient from the soil colloids to the plant root.

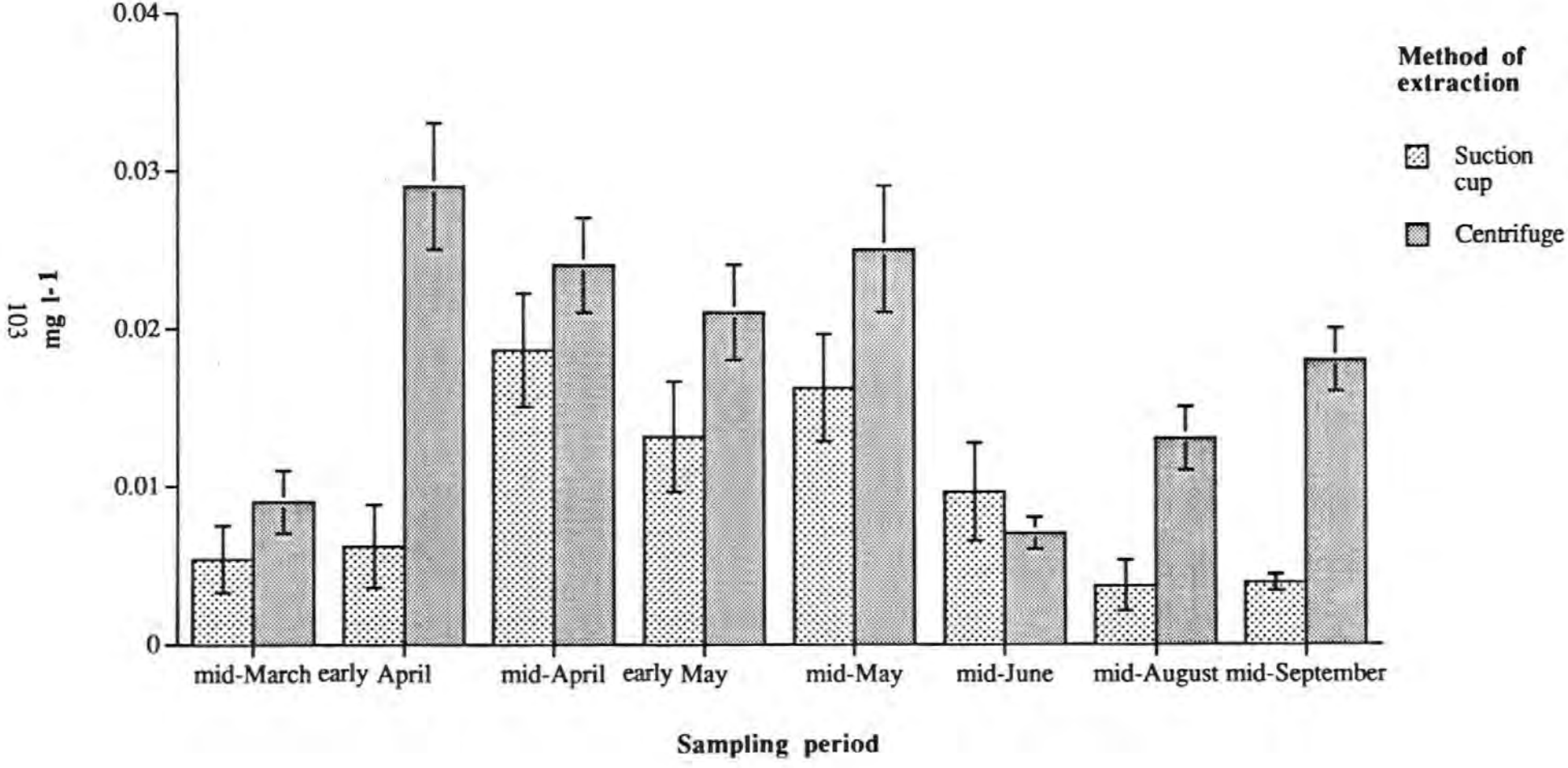
4.3.3 Suction Cup

Concentrations of solution P on SI removed by suction cups and centrifuging were presented in Figure 4.7. The Culm grassland plots were not presented as concentrations were found to be consistently below the level of detection of 0.002 mg l^{-1}. The results indicated that wild plants were able to remove P at very low concentrations despite Seeling and Zasowski (1994) quoting that 0.002 mg l^{-1} is the limit to plant P uptake. P was detected throughout the sampling season on SI. Concentrations were highly variable and a skewed distribution of data required square root transformation prior to statistical analysis. Although significant differences were only found between mid-April and mid-August, a trend of increasing concentration of P during the growing season was apparent. Values from mid-April to mid-June were not significantly different from P removed by centrifuging.

Significant positive correlations ($p<0.05$) were found between soil matric potential and suction cup values on mid-March, mid-April and early May. This indicated that as soil moisture tenacity increases the concentration of P increases. In this experiment suction cup values provided an improved indication of seasonal variation in P, especially in relation to plant demands. However comparisons of suction cup and centrifuged values were not ideal as the methods removed different fractions of soil water. The centrifuge method applied a pressure of 50 kPa which removed water from pore diameters of approximately > 15 μm, whereas suction cup applied a pressure of 10 kPa removed water from pores of >30 μm in diameter (Smith and Mullins, 1989). Thus water removed from large pores at low suctions may have different concentrations from that extracted from micropores at high suctions (England, 1974). Plants were more likely to take up water from the larger pores as lower suctions are required to remove the water from larger pores than smaller pores.

The results of this experiment suggest that centrifuging of Culm grassland soils removed more tightly bound water containing higher concentrations of P. Other studies have investigated the influence of tightly or loosely bound water by comparing lysimeter, centrifuging and suction cups methods. For example, Magid *et al.*, (1992) found that free-drainage lysimeters removed greater concentrations of P than teflon suction cells. They concluded that lysimeter solutions were not in equilibrium with the soil matrix as it is weakly bound to the soil colloids. As centrifuge solutions were in equilibrium they may provide an improved indication of P content, as the free-drainage component was largely absent from Culm grassland due to the nature of the soil with a high clay content. Another study by Falkengren-Gerup (1994) found concentrations in lysimeters comparable to those removed by centrifuging in this experiment. In contrast Zabowski and Ugolini (1990) found that concentrations in lysimeter solutions approached detection limits. Comparisons with other work must be approached with caution particularly if the soils have received high applications of nutrients. Additionally the fraction of water removed and the P content will be influenced by the moisture characteristic curve and the hysteresis effects caused by wetting and drying which is specific to a soil type.

Figure 4.6 Seasonal variation of phosphate-phosphorus removed by centrifuging and suction cup on improved grassland (n = 15, standard error bars)



4.4 Summary

The investigation of seasonal fluxes of soil P found that the concentration of P detected in soil solution was controlled by the method of extraction and was influenced by environmental factors particularly soil water conditions. The results of the investigation were summarised below and in Table 4.3. The use of sodium bicarbonate as an extractant indicated the gross differences between the 'availability' of P in the soils of improved and Culm grassland. Although the difference was less evident during the second field season of 1993 it was confirmed by the total soil P values. Removing soil solution directly attempted to more closely predict actual rhizosphere concentrations. Problems were encountered when values reached the limits of detection. The concentration in the soil solution was largely influenced by the suctions induced by extraction which showed some correlation with soil matric potential in the field. Centrifuging provided a useful back up to suction cups and further use was recommended particularly in situations in which suction cups are likely to fail during the summer.

1) Available P in soil solution was investigated using three methods; Sodium bicarbonate extraction, centrifuging and non-ceramic suction cups. Solutions were extracted at two-weekly intervals during the spring and at monthly intervals during the summer as plant uptake slowed down. Soil water conditions were monitored at the same intervals including gravimetric water content and soil matric potential.

2) The absence of elevated concentrations of soil extractable P on the improved plot in the second field season was attributed to alteration in environmental conditions. These conditions were also responsible for variation within season.

3) Concentration of P removed by centrifuging was 100 times lower than soil extractable values. Significant differences between Culm grassland and improved grassland were found in mid-March and mid-June. Concentrations were influenced by soil matric potential.

4) Concentration of P removed by suction cups was below the level of detection on Culm grassland. A trend of increasing suction cup P on SI occurred through the growing season.

Table 4.3 Extractable and soil solution phosphorus of Culm and Improved grassland soils, March-September 1993 (n = 15)

Sampling Period	PLOT								
	Fernhills Grazing			Staddon Moor			Staddon Improved		
		Sample Type			Sample Type			Sample Type	
	Sodium Bicarb	Centrifuge	Suction cup	Sodium Bicarb	Centrifuge	Suction cup	Sodium Bicarb	Centrifuge	Suction cup
	mg kg^{-1}	mg l^{-1}	mg l^{-1}	mg kg^{-1}	mg l^{-1}	mg l^{-1}	mg kg^{-1}	mg l^{-1}	mg l^{-1}
mid-Mar	1.20	0.033	< 0.002	1.70	0.026	< 0.002	3.35	0.009	0.005
April	*	0.031	< 0.002	*	0.021	< 0.002	*	0.029	0.006
mid-Apr	1.00	0.028	< 0.002	1.87	0.029	< 0.002	3.31	0.024	0.012
May	*	0.027	< 0.002	*	0.016	< 0.002	*	0.021	0.010
mid-May	1.48	0.025	< 0.002	3.25	0.028	< 0.002	4.73	0.025	0.016
mid-Jun	1.31	0.008	< 0.002	3.63	0.023	< 0.002	4.73	0.007	0.013
mid-Jul	3.62	0.026	< 0.002	4.42	0.019	< 0.002	6.49	0.027	0.002
mid-Sep	3.99	0.016	< 0.002	4.65	0.016	< 0.002	3.90	0.020	0.003

* not sampled

CHAPTER FIVE

VARIATION OF PLANT PRODUCTION WITH SEASON AND VEGETATION COMMUNITY

5.1 Introduction

Results of detailed soil analyses described in Chapter Four emphasised differences between the phosphorus status of the semi-natural and improved plant communities. This suggested that the availability of phosphorus was a limiting factor in the Culm grassland system in association with the type of management. However, it remained unclear at what level these limitations became effective in causing perturbations within the vegetation. Other limiting factors were known to be of importance in the Culm grassland system such as soil water conditions and pH (Chapter Three). The influence of other limiting factors such as light, temperature, competition, pollination, nutrient toxicity and pathogenicity (Etherington, 1978) were noted but measurement was beyond the scope of this study.

It was therefore decided to study the influence of the availability of phosphorus on the above-ground vegetation system of Culm and improved grassland. A detailed study intended to relate seasonal fluxes in nutrient availability to plant uptake and to pinpoint the thresholds of selected macronutrient levels below which species-rich *Molinietalia* will exist. Soil analysis provided an indication of nutrients available to a plant. However, soil analysis did not give an indication of the quantities of nutrients a plant actually requires and how they are utilized for growth. This information will aid the understanding of how different compartments of the system, that is soil and vegetation may be manipulated by management.

In order to collect information on how the Culm grassland community responds to phosphorus availability it was proposed to monitor vegetation growth. Plant growth can be limited by the availability of soil phosphorus. This was found to vary throughout the growing season and from year to year and involves assimilation of nutrients such as P, growth and reproduction which is manifested in the production of new plant structures. In

this study plant growth was referred to as the yield, that is the amount of material per unit area of whole community and also of individual species (Moore and Chapman,1986). This provided information on the relative influence by different species within Culm grassland on biomass production.

Plant material was removed at intervals during the growing season. Two strategies were implemented; either allowing the natural progression of growth (uninterupted growth) or to stagger growth (repeated defoliation) throughout the growing season. Uninterupted growth was monitored by removing material from previously unsampled vegetation at each sampling date. It was hypothesised that this allows the maximum standing crop to be obtained. Seasonal change in the plant community was indicated by changes in growth rate, amount of material produced and changes in the structure. The plant material was composed of the current seasons growth of new green shoots, and dead material or litter remaining from previous years. Also the relative decay of dead material had important consequences on the return of nutrients via the formation of organic matter. Repeated defoliation was monitored by removing material from the same place at each sampling date, thus allowing regrowth of vegetation between sampling. It was hypothesised that this promotes nutrient uptake and the young shoots of the regrowth material provide information on the current uptake of available phosphorus.

The nutrient content of plant material supplemented the above information as a nutrient may be expected to be greater where there is an increase in nutrient availability in the soil. It was likely that improved grassland would contain higher concentrations of phosphorus than Culm grassland plants. Interpretation was aided by accounting for the weight of the material as nutrient concentrations may be influenced by many factors (Chapman and van Cleve, 1989). It was recognised that plant uptake may show a poor correlation with soil P availability estimates. For example uptake may occur in excess of plant requirements and growth (Bates, 1971; Butler and Bailey, 1973). Despite these uncertainties a measure of the relative quantities of nutrients in compartments of the vegetation system was of importance to predict quantities removed by management.

5.2 Experimental design

An experimental design was formulated to remove plant material on the same SI and SG plots employed in the study of soil phosphorus dynamics. A comparison with the Fernhills grazing plot was omitted as the plant community there was found to be patchy caused by the tussocks of *M. caerulea*. Comparisons to soil available phosphorus was sought by sampling vegetation as close to the soil sampling dates as the practicalities of an intensive sampling regime would allow. It was realised that below-ground material such as roots may be influential in recycling of nutrients but sampling was impractical and only the above-ground standing crop was sampled.

5.2.1 Field procedure

a) Uninterupted growth on SG

Five subplots were marked with pegs within the original plot employed for soil sampling. The subplots were located within the areas of the plot in which exclusion cages were placed during the initial survey of soil conditions in 1992 (Chapter Three). Two extra areas were selected as shown in Figure 5.1 to increase the replication to five in order to reveal variability and obtain a true estimate of the mean which facilitated statistical comparisons. The subplots were protected from grazing cattle with electric fencing. Each subplot was divided as indicated in Figure 5.2, with field equipment placed in the centre of the subplot. The plant material was cut to ground level inside a quadrat measuring 0.25 m by 0.25 m. To obtain sufficient material for separation in to plant groups it was decided to remove material from two quadrats in each subplot. Therefore ten quadrats of material was removed on each sampling occasion. Each sampling date was allocated a number which was randomly placed on each subplot.

b) Repeated defoliation on SG and SI

A separate experiment was conducted by IGER, North Wyke in the areas measuring 1.0 by 0.5 m on the SG subplots as shown in Figure 5.2. This involved repeated removal of plant material at the same locations in a similar manner to grazing. The regrowth of material between sampling may indicate how the Culm grassland system reacts to management. This was compared to repeated defoliation on SI. The vegetation was cut at a height of 0.05 m above the soil at dates shown in Figure 5.2. All areas were cut at week 0 to produce a baseline at the start of the experiment. Insufficient growth at week 4 and 8 did not make a cut worthwhile until week 12 of the experiment. The areas were recut at varying time intervals from 4-12, 8-16, 0-12, 12-20, 0-20, 16-24, and 12-24 weeks to ascertain how the Culm grassland community responds at different times of the growing season.

A permanent quadrat measuring 0.25 by 0.25 m was placed within each of the five exclusion cages on SI as shown in Figure 5.1. Thus the quadrats were replicated five times. Plant material was cut to ground level and removed from each of the five quadrats at each sampling date, allowing regrowth to occur between sampling periods. Sampling was repeated on five occasions at each quadrat throughout the growing season. As shown in Figure 5.2 the dates corresponded to the seasonal growth experiment on the SG sub-plots.

5.2.2 Laboratory procedure

Plant material removed in the two experiments was transported to the laboratory and refrigerated. The vegetation from the seasonal variation experiment was separated into plant groups of grass, sedge, herb, rush, moss and litter to quantify their relative contributions to the total above-ground biomass. The material of the defoliation experiments was unsuited to separation due to its paucity on SG and absence of litter on SI. The fresh material from all three experiments was dried at 80 ^{0}C for 12-24 hours (Moore and Chapman, 1986) and then weighed. The dried vegetation or dry matter was then ground, stored and analysed later for total phosphorus content.

Figure 5.1
Location of subplots on Staddon Grazing and cages on Staddon Improved on plots employed in experiments during 1993

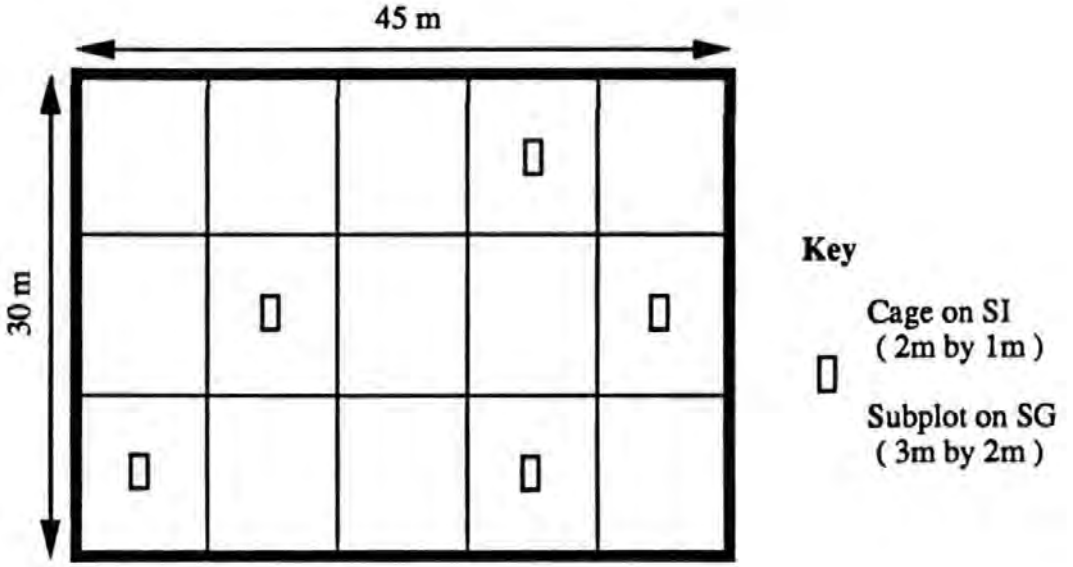
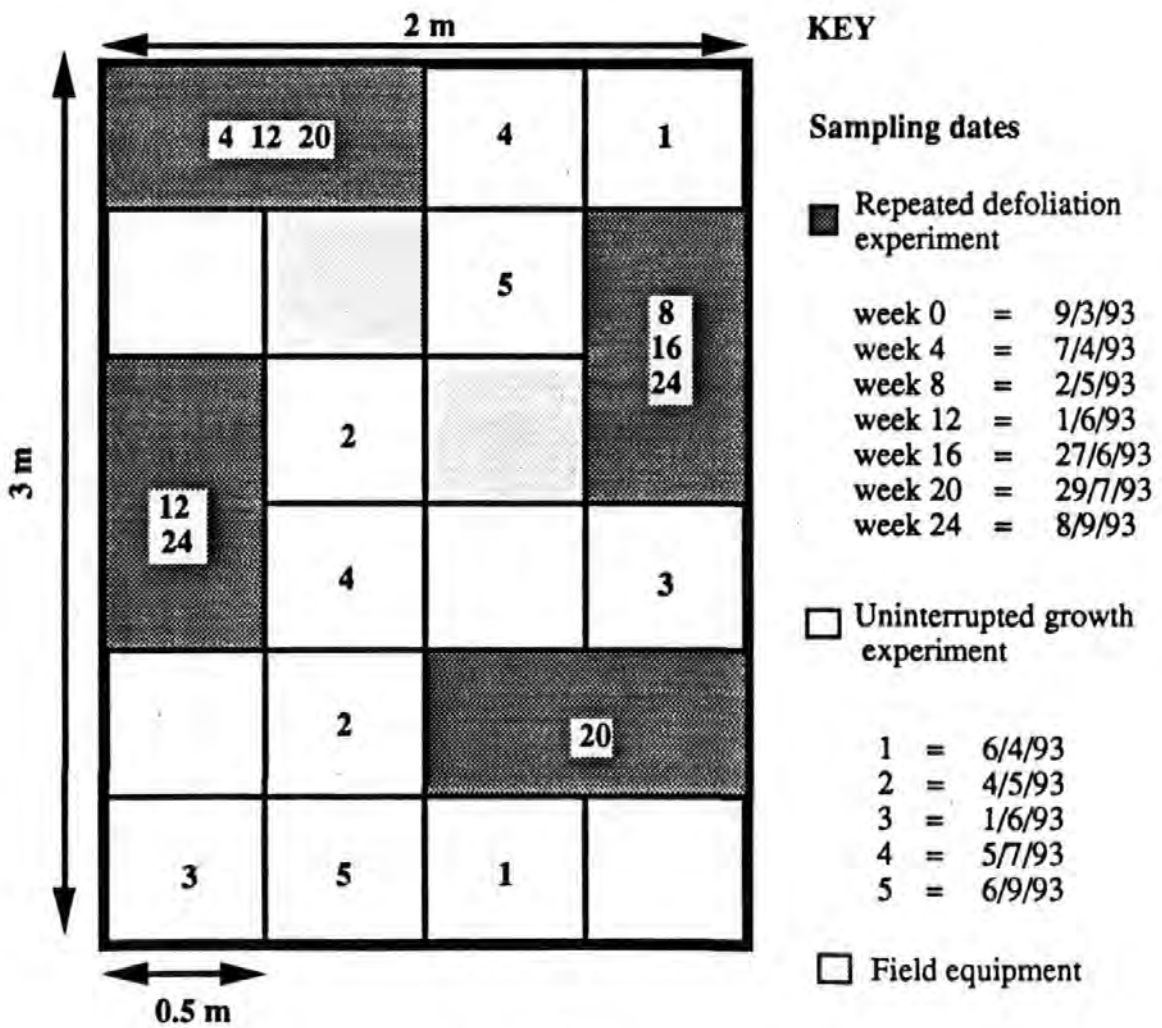


Figure 5.2
Design of sub-plots on Staddon Grazing incorporating uninterrupted growth and repeated defoliation experiments (n = 5)



5.3 Dry matter yield

5.3.1 Seasonal variation on Staddon Grazing (uninterrupted growth)

a) Standing crop

Peak standing crop on SG was found to occur in mid-July as shown in Figure 5.3 which was 6139.4 kg ha^{-1} for total biomass and 4508.8 kg ha^{-1} excluding litter. This amount of plant material was found to be in the same order of magnitude as other semi-natural grassland in Table 5.1. The yield was most similar to the *Molinietum* community sampled by Loach (1968). The total yield for mid-July was within the range quoted of 3500 - 7500 kg ha^{-1} by Al-Mufti *et al.* (1977) described in Chapter One in which a shift in species-richness occurs in response to changes in nutrient availability.

b) Live material

Considerable variation in the contribution of each plant group to dry matter yield was found on Culm grassland, as indicated in Figure 5.3 and Table 5.2. The total dry matter yield for each sampling date was dominated by grass and litter, with a smaller contribution made by sedges, mosses, shrub and herb groups as their percentage cover and frequency in Chapter Three were relatively low. The paucity of herb material and highly variable amounts of moss and shrub prevented investigation of significant differences over the growing season. The dry weights of sedge material did not change significantly throughout the growing season.

Grass production was dominated by *M. caerulea*. throughout the sampling season. Dry weights did not change during the first two months of sampling. Low weights of *M. caerulea* in mid-April were indicative of a deciduous perennial plant which dies off above ground during the winter. The greatest significant change occurred from mid-June to mid-July at the time when the stems elongates. The lack of dry weight accumulation from mid-July to mid-September corresponded to a decline in rate of growth in preparation for senescence. The pattern of *M. caerulea* yield accorded with results of Loach (1968). Milton (1947) found *M. caerulea* in upland Wales to peak in production in September at

335.5 kg ha^{-1} because of the limiting upland conditions. However, Berendse *et al.* (1987) in the Netherlands found it to reach a much higher production of 5860 kg ha^{-1} at a similar date probably reflecting higher soil nutrient availability.

c) Dead material

The litter was composed of small amounts of dead *C. vulgaris* stems, and mainly dead *M. caerulea* leaves together which was due to its growth habit in dying off above-ground by November (Loach, 1968). A similar strategy was found in *Brachypodium pinnatum*, a dominant species of chalk grassland (Bobbink, den Dubbelden, Willems, 1989). The litter fraction accumulated during the winter attaining a maximum of 854.4 kg ha^{-1} in mid-April. Over the growing season, litter correlated negatively with live *M. caerulea* ($p<0.01$). The yield of litter at the end of the winter may be indicated by the addition of the current season's green shoots which was 3343.8 kg ha^{-1} in mid-September. This was found to be most similar to the *Molinietum* from April to November 1961 studied by Loach (1968).

In Figure 5.3 the weight of litter declined significantly from April ($p<0.01$) until after June, indicating a rapid breakdown of litter from the previous season. From mid-April until mid-September 2353.8 kg ha^{-1} of material was decomposed which was almost two-thirds of the litter material. The rate of litter decomposition was found to form a negative exponential curve similar to a wet heathland in the Netherlands (Berendse *et al*, 1989). The breakdown of litter during one season will have a large influence on the cycling of nutrients during the next season. In the case of Culm grassland dominated by *M. caerulea*, litter accumulation will equal the litter from previous growing seasons and green material remaining at the end of the current growing season. This was found to be 3343.8 kg ha^{-1} in comparison to 3417.6 kg ha^{-1} of litter at the start of the growing season. It was noted that data was from two different seasons and factors controlling decomposition such as microbial activity may change. But a comparison suggested that litter was broken down and incorporated into the soil litter layer efficiently, which was indicated by relatively higher organic matter contents on Culm grassland (Chapter Three).

5.3.2. Effect of repeated defoliation

a) Staddon Grazing

Although no significant differences were found between the sampling dates, regrowth tended to decline after June. Regrowth of plant material attained a maximum rate between week 8 and 16 (2/5 - 27/6/93) as shown in Figure 5.4 and Table 5.3. Defoliation may have been effective in lengthening the growing season and encouraging regrowth even as the plant community prepared for senescence. The data was found to be highly variable which was largely caused by heterogeneity in vegetation cover.

b) Staddon Improved

The total material removed in Table 5.4 and Figure 5.4 during the sampling season on the Improved grassland was 7460.8 kg ha^{-1} which was low compared to ground level sampling on SG. Dry matter yield was constant during the months following initial removal of plant material in mid-April. A comparable situation was found by Tallowin *et al.* (1985) as pasture production did not change over a similar time period. Each value represents the vegetative growth of *H. lanatus* and the formation of new stems and leaves between sampling periods. A relative low yield may be caused by the high water contents as found in Chapter Four, the low application of 50 kg N ha^{-1} of fertiliser and the dominance of the grass *H. lanatus*. However, other improved grasslands on the same soil type were found to yield 7800 and 3288 kg ha^{-1} by Tyson *et al.* (1990) and Tallowin *et al.* (1990) respectively. These had received an application of 20 kg N ha^{-1} of fertiliser. Although comparisons were difficult to make due to the different sampling strategies the results may indicate that the Culm grassland was relatively productive which may be caused by the domination of *M. caerulea*.

Table 5.1

Comparison of Culm grassland (SG) peak plant dry matter production (excluding litter) with other similar vegetation communities

Vegetation community	Sampling Period	Dry matter yield (not including litter) kg ha^{-1}	P yield kg ha^{-1}
Culm grassland (SG) (present study)	mid-July	4509	1.5
Llety-Molinia (Milton, 1947)	July	1084	*
Molinietum (Molinia) (Loach, 1968)	August	5400	3.5
Molinietum (Bakker, 1989)	October	2100	4.0
Agrostis-Festuca (Perkins et al., 1978)	July	2200	4.0
Lolio-cynosuretum (Bakker, 1989)	June, July, Oct	2100	11.0
Mol.Arrhenatheretea (Bakker, 1989)	October	2040	4.0

* no information

Table 5.2 **Uninterrupted growth of above-ground plant biomass and contributing plant groups on SG** (kg ha^{-1}, Standard Error, n = 10)

	Sampling Date									
Plant group	**mid-April**	**S.E**	**mid-May**	**S.E**	**mid-June**	**S.E**	**mid-July**	**S.E.**	**mid-September**	**S.E.**
Litter	3417.6	259.4	2119.8	225.1	1652.8	250.2	1630.6	187.2	1063.8	159.1
Grass	216.3	30.9	620.2	57.1	1184.0	145.4	2074.2	179.2	2280.0	228.7
Sedge	284.0	60.3	247.2	39.9	238.4	38.8	309.6	76.9	455.1	65.8
Moss	1199.1	299.8	943.8	285.25	213.3	47.7	326.6	66.9	325.3	121.8
Shrub	441.6	*	408.0	*	328.0	*	1620.8	*	720.0	*
Herb	n.d	*	153.6	*	163.2	*	177.6	*	68.8	*
Total	5558.6		4492.6		3779.7		6139.4		4913	

* Incalculable

Figure 5.3
Dry weight of plant material removed by ground level sampling of uninterrupted growth on SG, 1993
(for sampling dates see Appendix One, n = 10)

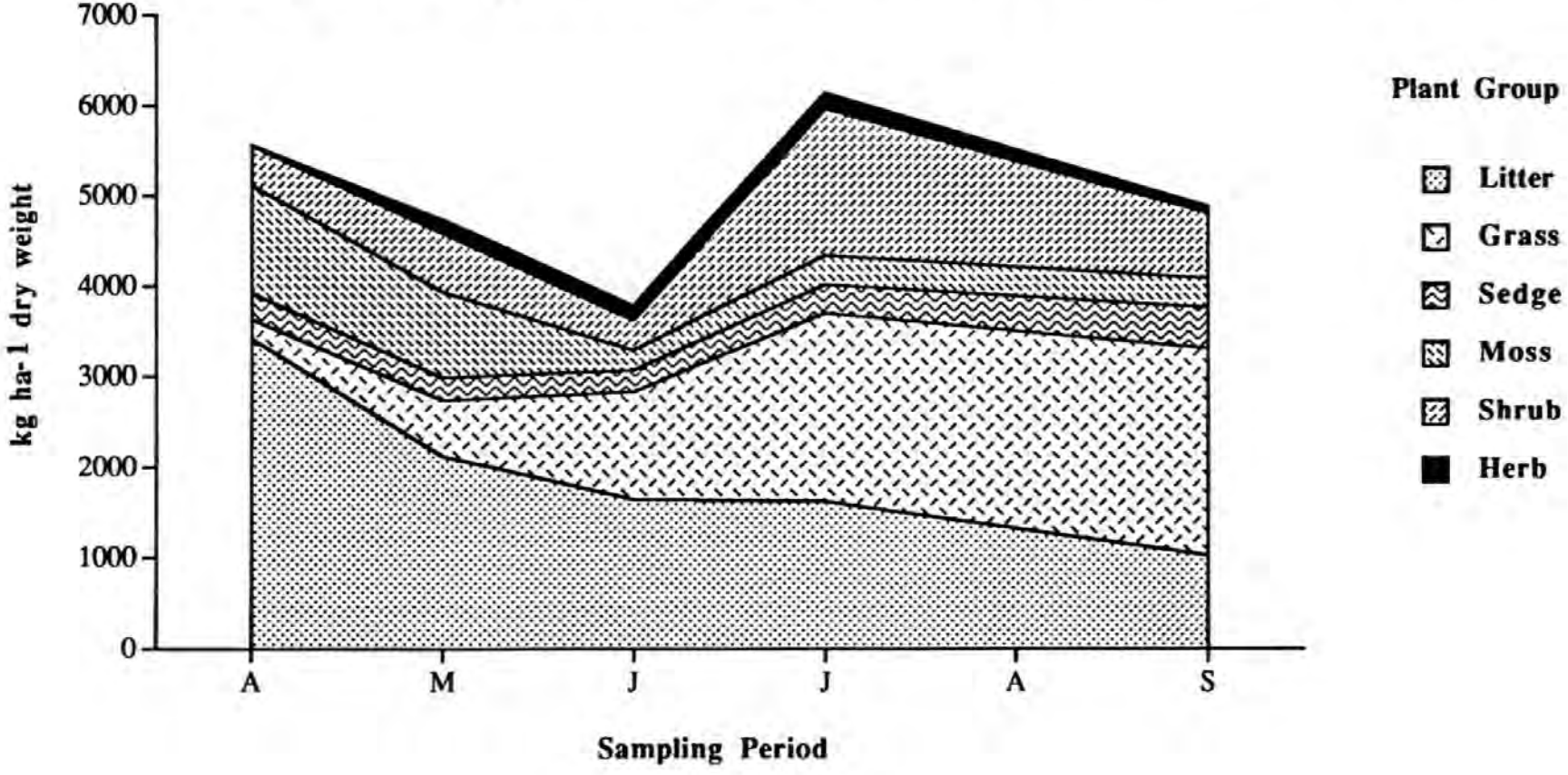


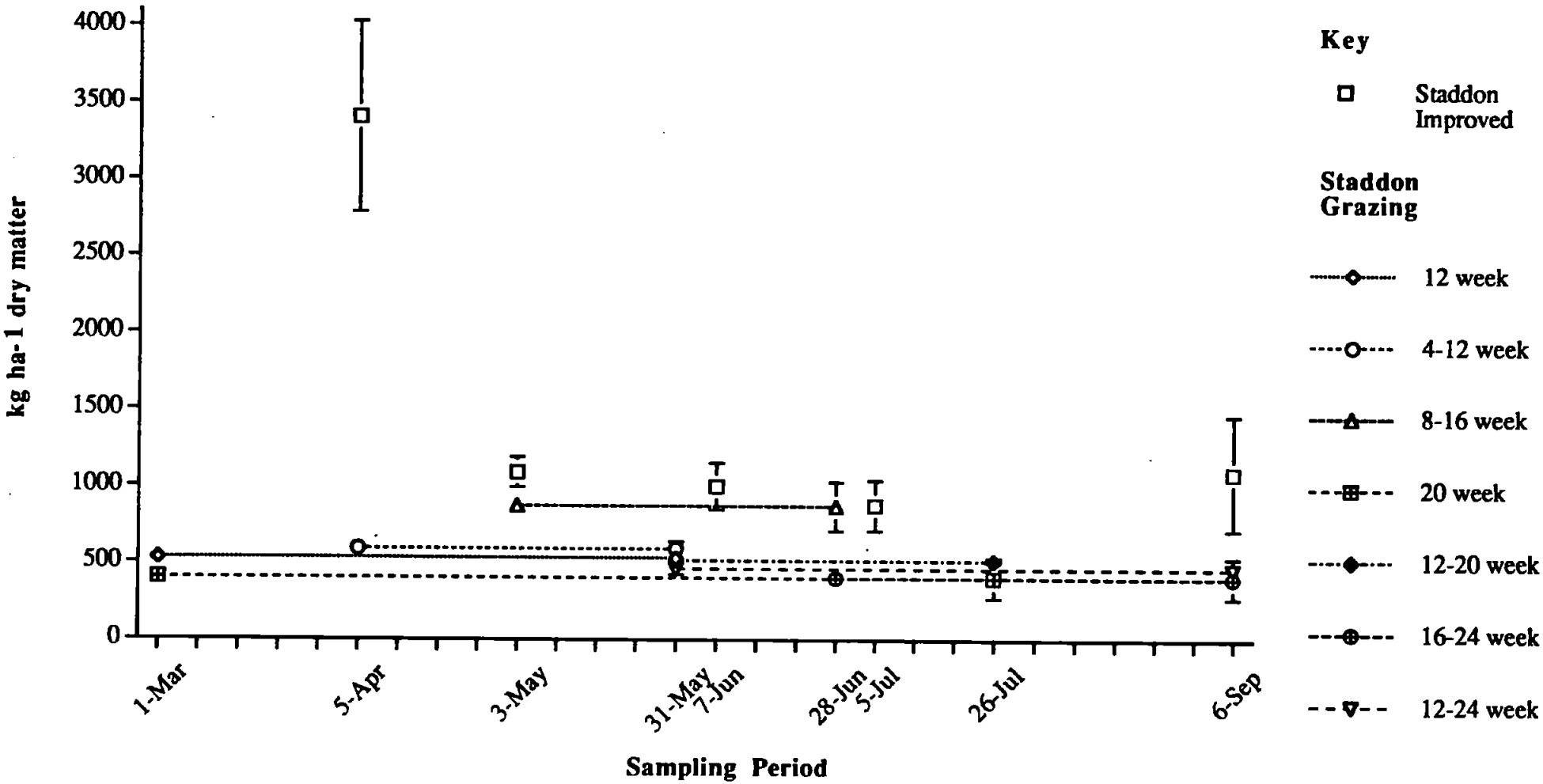
Table 5.3 Regrowth of dry matter after repeated defoliation on SG (n = 5)

Sampling dates	Sampling period	Dry matter (kg ha^{-1})	Standard error
1/3 - 1/6/93	0 - 12 weeks	530.4	106.0
7/4 - 1/6/93	4 - 12 weeks	590.8	71.6
2/5 - 27/6/93	8 - 16 weeks	869.6	161.4
1/3 - 29/9/93	0 - 20 weeks	403.4	131.4
1/6 - 29/7/93	12 - 20 weeks	512.8	75.7
27/6 - 8/9/93	16 - 24 weeks	403.2	131.4
1/6 - 8/9/93	12 - 24 weeks	461.2	59.4

Table 5.4 Regrowth of dry matter after repeated defoliation on SI (n=5)

Sampling dates	Sampling period	Dry matter (kg ha^{-1})	Standard error
6/4/93	0 weeks	3405.1	622.2
4/5/93	0 - 4 weeks	1089.9	97.6
1/6/93	4 - 8 weeks	998.4	151.7
5/7/93	8 - 12 weeks	876.2	165.2
6/9/93	12 - 16 weeks	1091.2	374.6
Total	0 - 16 weeks	7460.8	

Figure 5.4 The effect of repeated defoliation on dry matter growth on SG and SI, 1993 (n=5, standard error bars)



5.4 Phosphorus content in plant tissue

5.4.1 Seasonal variation of uninterrupted growth on Staddon Grazing

a) Standing crop

In Table 5.5 the total concentration of phosphorus within the dried plant material was found to peak in mid-June at 4.71 mg g^{-1}. This contrasted with peak dry matter yield in mid-July possibly indicating that plant growth lags behind nutrient uptake. A time-lag may be influenced by the different relative contributions of plant groups to the total uptake of phosphorus.

b) Live material

It was apparent that the herb and shrub component of Culm grassland had highly variable P contents as the plant structures have relatively long life spans in comparison to *M. caerulea* (Berendse *et al.*, 1989). Values were found to exceed the concentration in new shoots of *M. caerulea*. but the paucity of material prevented further data analysis. Fleming (1973) reported similar results in which herbs and legumes often exceeded concentrations in grasses. The concentration of P in sedges was relatively high and did not change significantly over growing season.

In Figure 5.5 *M. caerulea* was not the dominant contributor to the total P content in contrast to its dry matter production. The pattern of P content of plant material did not follow the yield of dry matter of *M. caerulea*. Concentration of P in *M. caerulea* only declined significantly ($p<0.05$) from mid-July to mid-September. Similarly, in Table 5.6 Loach (1968) found a pattern of decline from mid-July although dates do not correspond exactly with the present experiment. During this phase from mid-July to mid-September a 61% reduction occurred on SG. Berendse *et al.* (1989) found a decline in *M. caerulea* of 66.7% from early spring until the end of the growing season. A corresponding reduction in dry matter production was not found. It was noted by Chapin and van Cleve (1989) that this decline in P content was due to dilution caused by stem elongation as the formation of carbohydrates and proteins outstrips the rate of mineral uptake (Fleming, 1973). The

absence of this pattern may be caused by *M. caerulea* possessing different rates of vegetative growth, flowering, seed production and senescence, leading to different nutrient requirements in comparison to agriculturally productive grasses. This reinforced the need for sequential sampling over a growing season.

c) Dead material

The concentration of P in litter in Table 5.5 was much lower than the live material throughout the sampling period. A significant ($p<0.05$) increase from mid-April to May and June followed the pattern of green shoots of *M. caerulea* and a significant positive correlation ($p<0.05$) was found between the two plant groups. In contrast Berendse *et al.* (1989) found a reduction in litter P content during the first 4-6 months of the year Thus on SG there was a poor relationship between the dry weight and P content of litter. A relative increase may be attributed to the ingrowth of fungal hyphae during litter breakdown which proliferated and accumulated phosphorus (Berendse *et al.* 1989).

Between mid-July and mid-September the P content of the litter did not change significantly ($p<0.05$). However, the loss of P from the litter and senesced plant material may continue throughout the winter as indicated by a comparison of P present at the end and beginning of the sampling period. Assuming that all nutrients in green material in September becomes incorporated into litter, the litter will contain 0.36 mg P g^{-1} at the start of the growing season. As P in litter was 0.28 mg P g^{-1} in mid-April, a loss of 0.08 mg P g^{-1}. The P may have been either leached in to the decomposed litter layer or retranslocated to the below-ground storage organ. This redistribution has important implications for the cycling of nutrients within the Culm grassland system.

5.4.2 Effect of repeated defoliation

a) Staddon Grazing

The P content of the plant material varied considerably in Figure 5.6 and Table 5.7, in contrast to dry matter regrowth. Significantly ($p<0.05$) lower concentrations were measured after week 16. The concentration during week 8-16 was low in comparison to the peak amount of dry matter which was possibly due to a dilution effect. As values for regrowth of week 4-12 and 12 were not significantly different, a cut off point between week 12 and 16 during the month of June may be postulated. The results showed that maximum P accumulation may be induced early in the season from March until early June, which may be before cattle commence grazing.

b) Staddon Improved

Concentrations of P in Figure 5.6 were found to significantly increase until mid-June ($p<0.05$) and then significantly declined from mid-July to mid-September. The pattern of P uptake did not decline in response to rapid growth as discussed by Fleming (1973). It appeared that defoliation had impaired growth but not the ability to accumulate P and had induced luxury consumption (Russell, 1986). A similar situation was found by Garstang (1973), in that P content of plant material increased with successive cuts at four-weekly intervals from mid-May. The higher nutrient uptake of improved grasses was emphasised by the higher total P content of the regrowth material on SI in Table 5.8 in comparison to SG in Table 5.7. The concentration of P in the grasses were lower than 6.2 and 5.4 mg P g^{-1} quoted for *Holcus lanatus* and *Lolium perenne* by Wilman and Riley (1981). This provided further indication that conditions on a Staddon Improved were less than ideal for maximum production. Other low productive grasses were more comparable such as *Phleum pratense* (Timothy), *Dactylis glomerata* (Cocksfoot), *Festuca pratensis* (Meadow fescue) and *Festuca arundinacea* (Tall fescue) which have concentrations of 3.2, 3.0, 2.6, and 2.5 mg P g^{-1} respectively (Spedding and Diekmahns 1972).

Table 5.5 **Phosphorus content of above-ground plant biomass and contributing plant groups in uninterrupted growth on SG** (mg g^{-1}, Standard Error, n = 10)

	Sampling Date									
Plant group	**mid-April**	**S.E**	**mid-May**	**S.E**	**mid-June**	**S.E**	**mid-July**	**S.E.**	**mid-September**	**S.E.**
Litter	0.28	0.02	0.39	0.02	0.39	0.02	0.11	0.02	0.11	0.01
Grass	0.65	0.05	0.99	0.01	0.89	0.02	0.71	0.17	0.25	0.04
Sedge	0.74	0.07	0.64	0.03	0.57	0.07	0.62	0.16	0.55	0.13
Moss	0.42	0.02	0.49	0.03	0.27	0.01	0.52	0.04	0.19	0.01
Shrub	0.46	*	0.64	*	0.85	*	1.59	*	0.34	*
Herb	n.d	*	0.84	*	1.74	*	0.72	*	0.52	*
Total	2.55		3.99		4.71		4.27		1.96	

* incalculable n.d not detected

Figure 55
Total phosphorus in plant material removed by ground level sampling of uninterrupted growth on SG, 1993
(for sampling dates see Appendix One, n = 10)

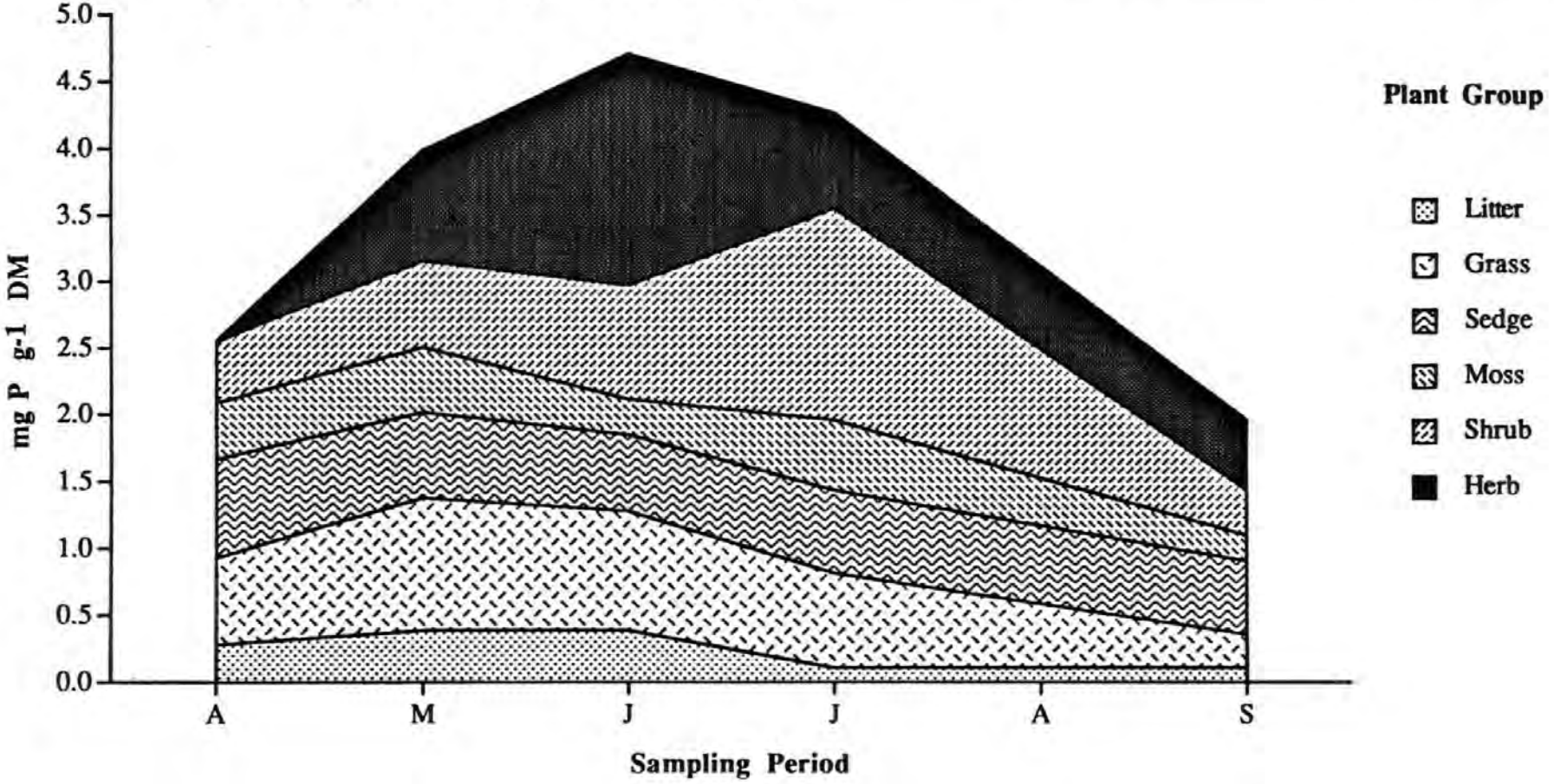


Table 5.6 Concentration of P in *M. caerulea* (mg P g^{-1} DM)

	Date			
Staddon Moor	3 May	19 July	13 September	
	0.99	0.71	0.25	
Loach (1968)	24 May	17 July	28 August	1 November
	5.04	6.40	3.35	3.31

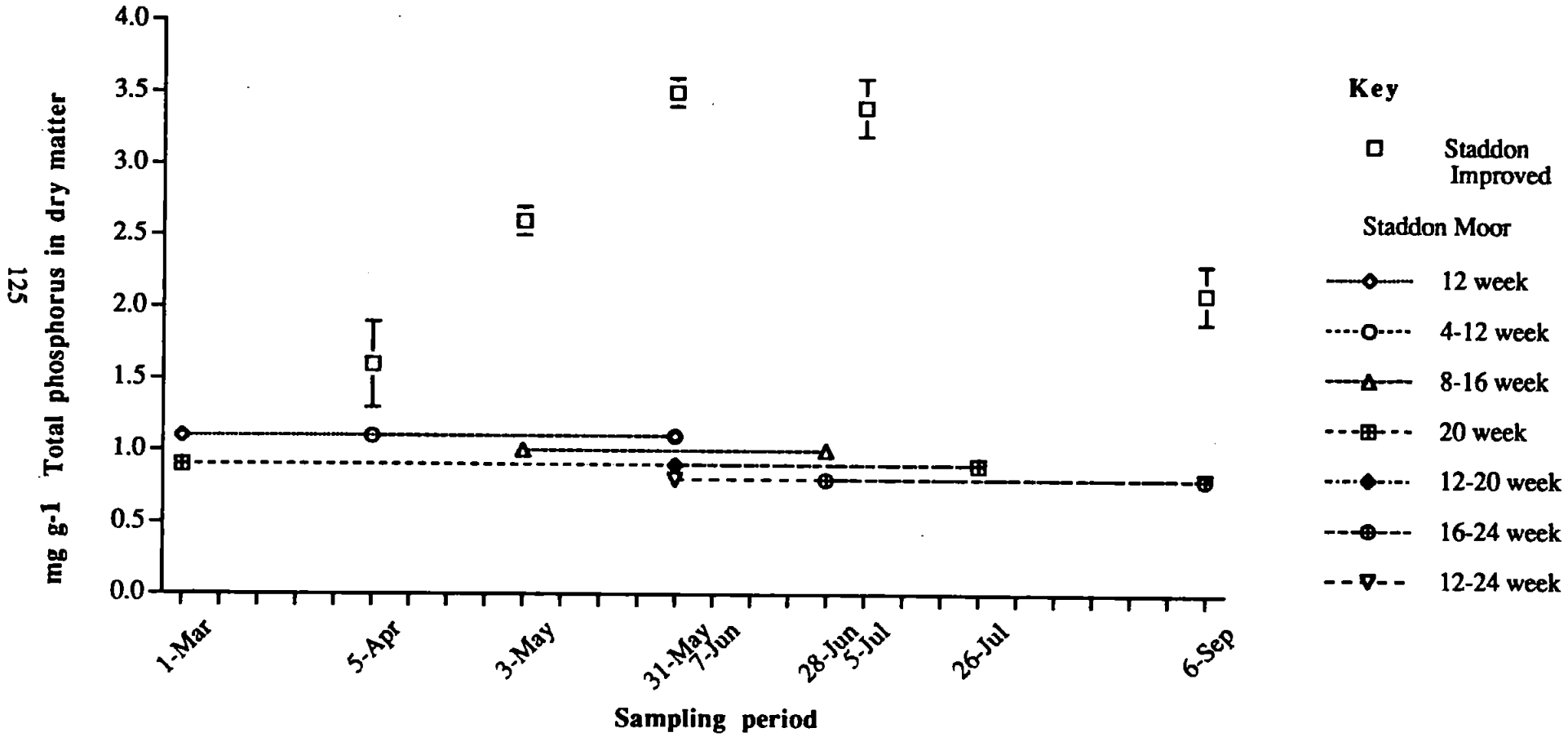
Table 5.7 Concentration of P in plant material after repeated defoliation on SG (n = 5)

Sampling dates	Sampling period	Total phosphorus mg g-1	Standard error
1/3 - 1/6/93	0 - 12 weeks	1.1	0.04
7/4 - 1/6/93	4 - 12 weeks	1.1	0.05
2/5 - 27/6/93	8 - 16 weeks	1.0	0.04
1/3 - 29/9/93	0 - 20 weeks	0.9	0.02
1/6 - 29/7/93	12 - 20 weeks	0.9	0.03
27/6 - 8/9/93	16 - 24 weeks	0.8	0.03
1/6 - 8/9/93	12 - 24 weeks	0.8	0.02

Table 5.8 Concentration of P in plant material after repeated defoliation on SI (n = 5)

Sampling dates	Sampling period	Total phosphorus mg g^{-1}	Standard error
6/4/93	0 weeks	1.6	0.3
4/5/93	0 - 4 weeks	2.6	0.1
1/6/93	4 - 8 weeks	3.5	0.1
5/7/93	8 - 12 weeks	3.4	0.2
6/9/93	12 - 16 weeks	2.1	0.2

Figure 5.6 The effect of repeated defoliation on the total phosphorus content of plant material on SG and SI, 1993 (n=5, standard error bars)



5.5 Total yield of phosphorus in dry matter

5.5.1 Seasonal variation of uninterupted growth on Staddon Grazing

a) Standing crop

In Table 5.9 and Figure 5.7 the total P concentration and dry matter production were multiplied to obtain the total yield of phosphorus. Due to paucity of data shrub, herb and moss could not be calculated. The yield of P peaked in mid-June at 1.97 kg P ha^{-1} but excluding litter produced during the previous season the peak yield of P was 1.46 kgP ha^{-1}. Values were found to be in the same order of magnitude as other semi-natural communities in Figure 5.1. The yield of P was most similar to the *Molinietum* studied by Loach (1968) which has a similar dry matter yield. Contrasts with other communities may be due to differences in soil type and management regimes (Bakker, 1989).

b) Live material

The yield of P in sedges was low and did not vary significantly over the growing season, as although the sedges had a relatively high P content they had a low dry matter production. The variation in total P content has been removed by taking into account dry matter production. A significant increase ($p<0.05$) in P yield of *M. caerulea* occurred from mid-April to mid-July. In Table 5.10 a similar increase of P in green shoots of *M. caerulea* was found by Loach (1968) and was followed by a decline at the end of the growing season. A decline of 0.05 kg P ha^{-1} was found on Culm grassland indicating that senescence was under way by mid-September which was not indicated by dry matter values.

c) Dead material

A decline of P yield in litter occurred after mid-July which followed the predicted pattern in which higher summer temperatures induce litter breakdown. The final yield of litter was lower than the yield in *M. caerulea* found by Loach (1968) on the 1st of November in Table 5.10. The constancy of litter production later in the season showed that although senescence was occurring and phosphorus in the leaves of *M. caerulea* was reduced, the leaves had not died at this point in time and were not contributing to the litter dry matter.

5.5.2 Effect of repeated defoliation

a) Staddon Moor

The yield of P in defoliated material on SG closely followed the pattern of dry matter production by peaking between 8-16 weeks as shown in Figure 5.8 and Table 5.11. This has accounted for an increase in growth rate which had been responsible for the decline in total P content. Again the period between 12-16 weeks was indicated as being a period of maximum uptake of P. Repeated periodic removal of plant material may induce greater uptake of P particularly at the early stages of the growing season.

b) Staddon Improved

In Figure 5.8 and Table 5.12 the yield of phosphorus was significantly different ($p<0.05$) in only mid-April and mid-September. During the intervening months the sampling strategy did not appear to effect P yield which remained substantially above values on SG, indicating that the improved grassland was able to respond to defoliation. A concentration of 2.5 mg P g^{-1} in young vegetative grass shoots was quoted by Garstang (1973) as being adequate for grass growth. This was exceeded during the months of May, June and July on Staddon Improved. Again defoliation appeared to encourage uptake of phosphorus for the growth of new plant structures. The increased uptake was not associated with an increase in dry matter production, indicating that more productive grasses were prone to luxury consumption.

Table 5.9 **Phosphorus production of plant biomass and contributing plant groups in uninterrupted growth on SG** (kg ha^{-1}, Standard Error, n = 10)

	Sampling Date									
Plant group	**mid-April**	**S.E**	**mid-May**	**S.E**	**mid-June**	**S.E**	**mid-July**	**S.E.**	**mid-September**	**S.E.**
Litter	0.97	0.10	0.85	0.10	0.67	0.66	0.17	0.02	0.12	0.02
Grass	0.14	0.03	0.61	0.06	1.08	0.15	1.20	0.30	0.57	0.11
Sedge	0.22	0.05	0.20	0.04	0.22	0.04	0.26	0.26	0.25	0.06
Total	1.33		1.66		1.97		1.63		0.94	

Figure 5.7 Total P yield of plant material of uninterrupted growth on SG, 1993 (n=5, standard error bars)

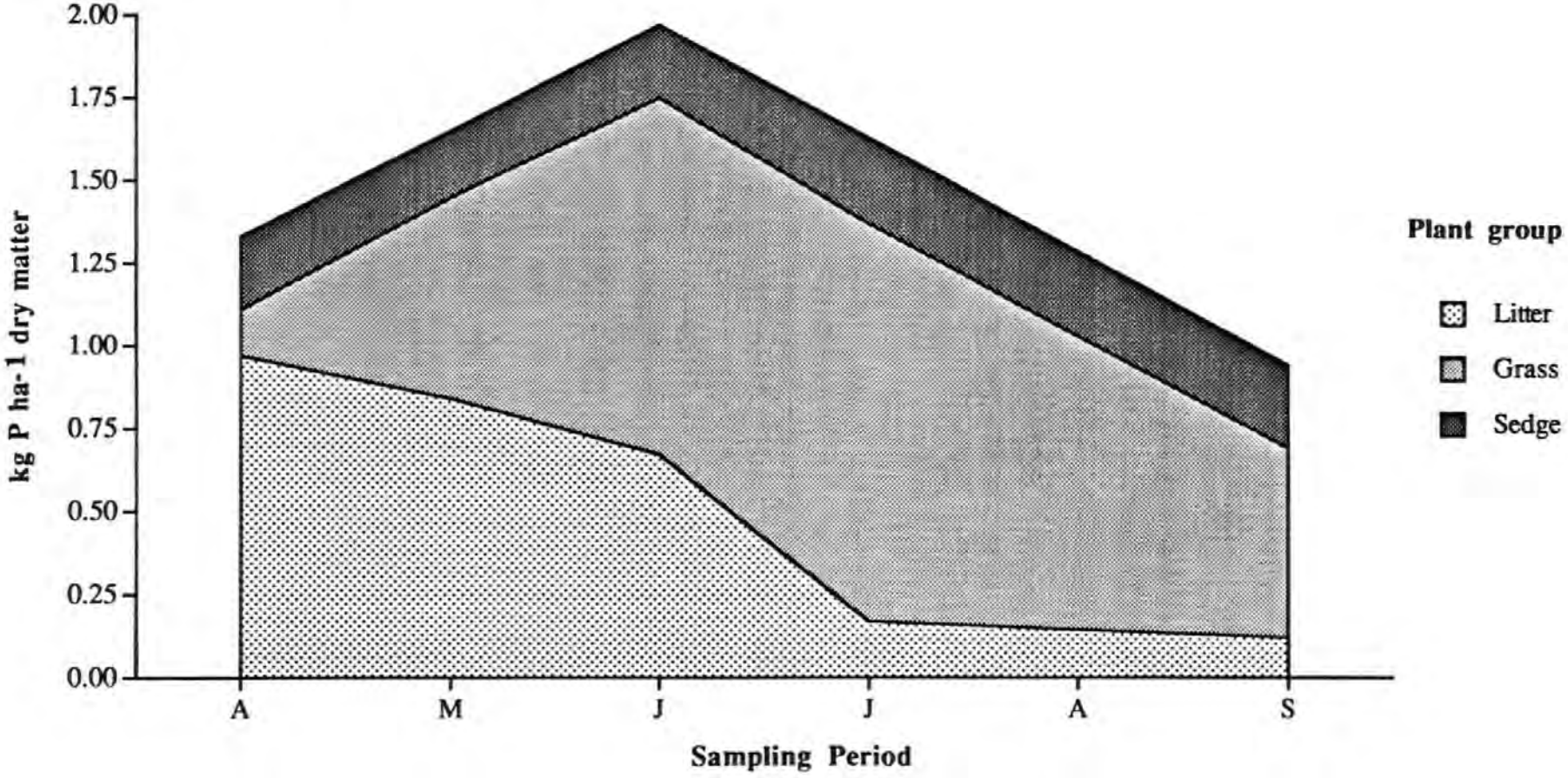


Table 5.10 The yield of P in *M. caerulea* (kg P ha^{-1})

	Date			
Loach (1968)	**24 May**	**17 July**	**28 August**	**1 November**
	1.80	**3.25**	**3.40**	**0.70**
Staddon Moor	**3 May**	**19 July**	**13 September**	
	0.61	1.20	0.57	

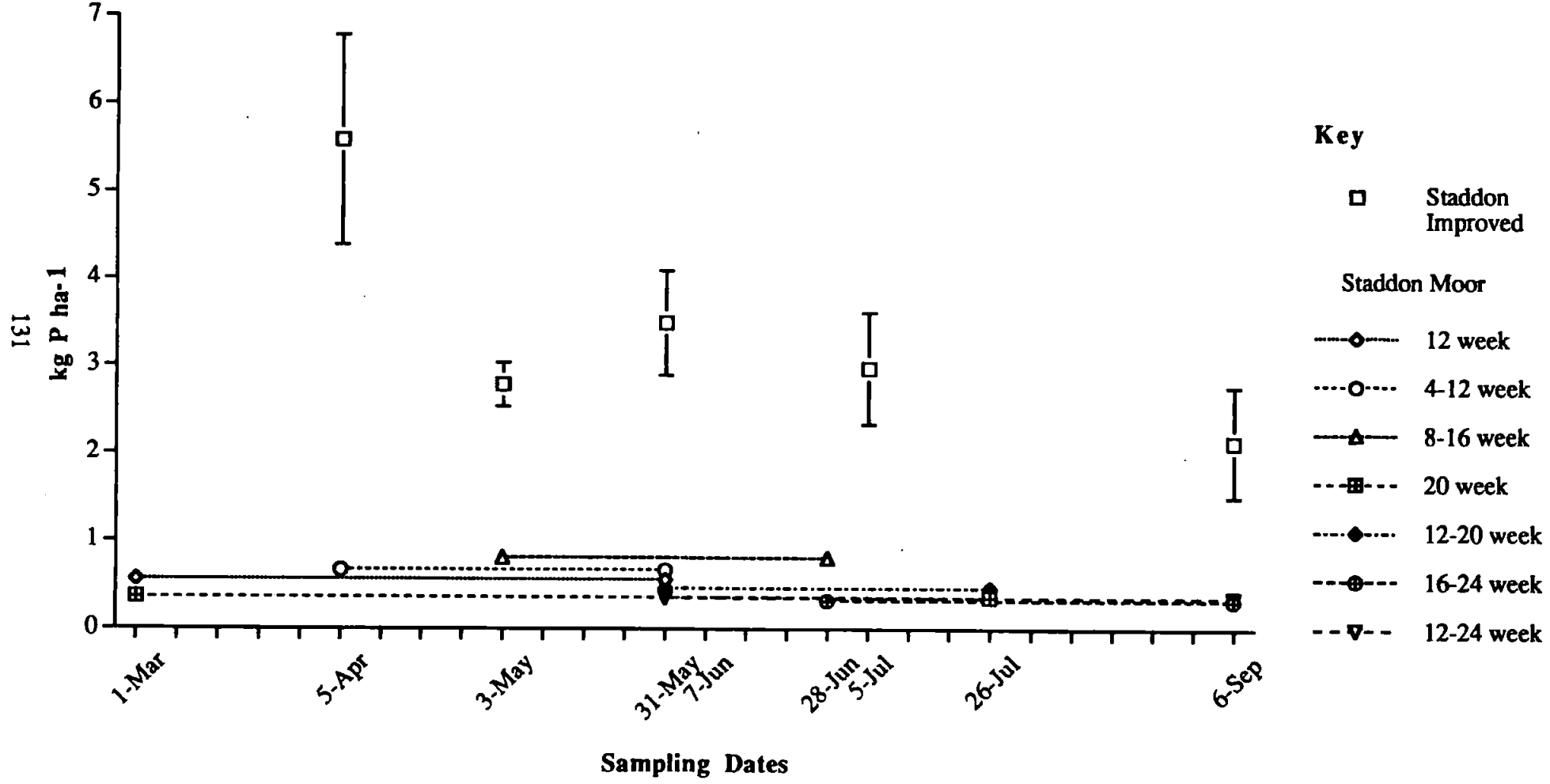
Table 5.11
The effect of repeated defoliation on the dry matter yield of P on SG (kg P ha^{-1})

Sampling dates	Sampling period	Total phosphorus in plant biomass	Standard error
1/3 - 1/6/93	0 - 12 weeks	0.56	0.10
7/4 - 1/6/93	4 - 12 weeks	0.67	0.07
2/5 - 27/6/93	8 - 16 weeks	0.81	0.12
1/3 - 29/9/93	0 - 20 weeks	0.36	0.12
1/6 - 29/7/93	12 - 20 weeks	0.46	0.07
27/6 - 8/9/93	16 - 24 weeks	0.32	0.10
1/6 - 8/9/93	12 - 24 weeks	0.35	0.05

Table 5.12
The effect of repeated defoliation on the dry matter yield of P on SI (kg P ha^{-1})

Sampling dates	Sampling period	Total phosphorus in plant biomass	Standard error
6/4/93	0 weeks	5.58	1.20
4/5/93	0 - 4 weeks	2.78	0.25
1/6/93	4 - 8 weeks	3.49	0.60
5/7/93	8 - 12 weeks	2.97	0.64
6/9/93	12 - 16 weeks	2.13	0.63

Figure 5.8 The effect of repeated defoliation on the yield of total phosphorus in plant material on SG and SI , 1993 (n =5, standard error bars)



5.6 Summary

It was interesting to find that the P content of the plant material did not follow the expected response curve of concentration of nutrients in the tissues against the growth of the plant described by Bates (1971) and Davidescu and Davidescu (1982). On SI a critical level was probably obtained, as no increase in dry weight occurred in response to an increase in nutrient content (Mengel and Kirkby, 1989), which explains absence of significant correlations. Additionally the pattern of *M. caerulea* on the Culm grassland was affected by many factors not measured in this experiment. For example, differences in age of tissues was very influential as tissues reduce in nutrient content with age (Mengel and Kirkby, 1989). The allocation of phosphorus to different *M. caerulea* plant parts was not taken into account unlike the investigation by Aerts and Berendse (1989). Other factors included the provision of other nutrients, and effect of moisture supply and temperature (Butler and Bailey 1973). Comparisons of P yield of *M. caerulea* with other components of the Culm grassland community could be attempted. Much work has been conducted in the Netherlands in the comparative allocation of nutrients to *M. caerulea* and the shrub, *E. tetralix*. (Berendse *et al.* 1987) and also green shoots of *C. vulgaris* of heathlands in Britain (Chapman, Hibble and Rafarel, 1975). However, comparisons with *M. caerulea* must take in to account the different growth habits and thus the distribution of growth of different parts of the plant (Chapman, 1975).

It was evident that *M. caerulea* was the key component of the Culm grassland system and controlled the cycling of P in the system through its deciduous perennial habit and production of litter. Seasonal production reached a maximum in mid-July which concurs with other workers. The defoliation experiment indicated that a higher production could be obtained if defoliation took place much earlier than when grazing normally starts in May. However, no significant correlations were found between the yield of P of *M. caerulea* and soil P concentrations particularly sodium bicarbonate extractable P. This poor relationship may indicate that sodium bicarbonate extractable P did not adequately predict plant available P for this system. Also soil measurements were taken at one point in time and plant nutrient

content was a result of accumulation over a period of time. In summary the following points may be made:-

1) Peak standing crop of Culm grassland was found in mid-July and *M. caerulea* was the dominant component. One third of the litter from the previous season was broken down from mid-April to mid-September

2) Defoliation on SG induced a growth response during June and July and on SI indicated low productivity.

3) Phosphorus content of Culm grassland vegetation peaked in mid-June correlating poorly with dry matter production. A 61% reduction in phosphorus content of *M. caerulea* occurred between mid-July and mid-September. Concentration of P in litter followed the same pattern as new *M. caerulea* shoots.

4) Higher concentrations of phosphorus was found in defoliated material before June.

5) The yield of P on Culm grassland excluding litter peaked in mid-July. The variation of phosphorus in plant tissue was compensated by taking into account dry matter production. Litter significantly declined after mid-June.

CHAPTER SIX

RESPONSE OF CULM GRASSLAND TO NUTRIENT ADDITIONS

6.1 Introduction

Investigation of the phosphorus dynamics of Culm grassland in Chapters Four and Five highlighted the need for a study of Culm grassland under controlled conditions. In particular highly variable field conditions were found to affect the concentrations of P within the soil solution. Controlling these environmental conditions particularly rainfall and temperature would enable a clearer indication of the processes occurring within the soil complex. Research workers have grown plants in pot experiments to assay different soil types. Problems have been caused by enhanced mineralisation induced by removal and mixing of the soil (Pegtel, 1986). Therefore it was decided to remove undisturbed soil in order to reproduce field conditions as closely as possible.

In Chapter Five *M. caerulea* was found to dominate the Culm grassland plant community and its response to controlled conditions was of most interest. To investigate further the thresholds of phosphorus availability at which this community existed, it was decided to induce a perturbation in the form of phosphate additions. This technique has been widely employed in other studies, such as Milton and Davis (1947), Willis (1963), Aerts and Caluwe (1989), Aerts and Berendse (1988), Bobbink (1991), French (1988) and Loach (1968). It was thought that *M. caerulea* would be most responsive to P additions via changes in soil P availability and was the focus of this experiment. In this chapter a preliminary study of the soil fixation capacity was undertaken followed by the setting up of the controlled turf experiment and additions of P. The response of the community was reported which has implications on the long term influence of nutrient additions.

6.2 Soil phosphorus fixation capacity

6.2.1 Background of experiment

A phosphate fixation or adsorption experiment was conducted to investigate the response of Culm soils to additions of phosphate. This information also indicated the P concentrations for application to the Culm grassland turfs. The ability of the soil to fix extra phosphate has a large influence on the P available for plant uptake. Net fixation of P may depend on the dynamic equilibrium between the processes at the surface of the soil colloids. These processes involve adsorption of P ions to the soil surface particles from the soil solution, subsequent build up and saturation of bonding sites and then desorption and release of P ions into soil solution (Russell, 1988). This technique has been used to provide some insight into the mechanisms and soil properties controlling P concentration in soil solution and thus plant uptake (Barrow and Shaw,1975 a,b,c). The extent of fixation was employed by Rizand *et al* (1989) to predict the effect of different grassland management strategies on P supply. Chapman, Rose and Basanta (1989) also investigated the adsorption by heathland soils in relation to successional change.

These adsorption \ desorption experiments have involved adding a P solution to soil which is then shaken for a period of time. The solution is then filtered and the P content analysed which indicates the amount lost from the soil solution and adsorbed to the soil particles. The soil is then shaken with distilled water to ascertain the amount of P desorbed from the soil surface. The time period for shaking is assessed on the point at which equilibrium is reached, that is the point at which adsorption and desorption occur at the same rate. However, the rate of desorption and adsorption may not follow the same curve due to hysteresis effects (Russell, 1988). In consultation with other similar experimental work it was decided to conduct a simple adsorption experiment with the knowledge that the processes involved are complex.

6.2.2 Experimental procedure

Soil was removed from Staddon Grazing and Staddon Improved to a depth of 0.1 m and field moist samples weighing 10 g were placed in conical flasks. 50 ml of distilled water was added containing the following concentrations of KH_2PO_4 :- no soil (control), 0, 0.05, 0.5, 5, 50, 500 mg l^{-1}. To allow statistical analysis the experiment was replicated three times. The soil was then shaken very gently to prevent breakup of particles and artificial exposure of bonding sites (Barrow, 1975a). A shaking period of 24 hours was conducted to allow for an equilibrium to be obtained (Richardson and Marshall, 1986). The solution was filtered and stored to find how much P was removed from the solution. To ascertain desorption, the soil samples were shaken with 50 ml of distilled water for 24 hours and then the solution was filtered and stored. The solutions were then analysed for phosphate-phosphorus using a Flow Injection Analyser. The amount of P adsorbed by the soil was the difference between the starting concentration and the remaining equilibrium solution concentration. The amount of desorbed phosphate was the amount released into the distilled water. The difference between these two amounts indicated the net fixation capacity of the Culm soils.

6.2.2 Results and discussion

The results of the experiment presented in Table 6.1 showed that most of the phosphorus was removed and adsorbed within the soil complex. The extent of this adsorption was indicated by the very limited release of P into the distilled water. The soil has the ability to fix P efficiently, although there is some indication that at the higher concentration of 500 mg l^{-1} the fixation capacity was reduced. The fixation capacity of the Culm and improved soils were not significantly different indicating that improvement has not lowered the net fixation capacity of the soils despite these soils having a greater total P and extractable P content.

Table 6.1 The concentration and percentage of applied phosphorus adsorbed by Culm and Improved grassland soils (n = 5).

Concentration of P added	Site			
(mg l-1)	Staddon Grazing	%	Staddon Improved	%
0.05	0.04	78	0.05	100
0.50	0.47	94	0.49	98
5.00	4.96	99	4.91	98
50.00	47.30	94	36.48	73
500.00	433.70	87	434.60	87

Table 6.2 Concentrations and timing of additions of phosphate to Culm grassland turfs under controlled conditions

Application	Level	mg P l-1	kg P ha-1
One	0	0	0.000
(week 3, 1/9/93)	1	5	0.025
	2	50	0.250
	3	500	2.500
Two	0	0	0.000
(week 9, 8/10/93)	1	100	0.520
	2	1000	5.200
	3	10000	52.000
Total	0	0	0
App One + Two	1	105	0.545
	2	1050	5.450
	3	10500	54.500

Table 6.3 Summary of procedures carried out during phosphorus additions

Week	Procedure
0 (10.8.93)	Remove turfs from field, place in glasshouse under controlled conditions
1	Insert suction cups into each turf to an average depth of 0.10 m
2	Equilibriate suction cups, trim turfs to 0.05 m, dry and store material
3 (1.9.93)	Add **Application One** phosphate solutions to a depth of 0.1 m
4,5,6,7	Remove solutions from suction cups at end of each week
8	Trim turfs to 0.05 m, dry and store material
9 (8.10.93)	Add **Application Two** phosphate solutions to a depth of 0.1 m
10,11,12,13	Remove solutions from suction cups at end of each week
14	Trim turfs to 0.05 m, dry and store material, remove soil sample from each turf for sodium bicarbonate extraction

6.3 Experimental design of turf experiment

The experimental design and procedure of the controlled turf experiment involving two stages of P applications is described in the following section in weekly intervals and summarised in Table 6.3.

Week 0 Species-rich turfs were removed on 10/8/93 from an area nearby the experimental plot on Staddon Grazing. Potential turfs containing *Succisa pratensis, M. caerulea,* at least one sedge and a shrub were selected. The turfs were extracted using the following procedure. Drainage piping measuring 0.20 m in diameter and 0.20 m in length was inserted into the ground with no compression of the soil evident. The use of piping minimised disturbance which was found by Pegtel (1987) to increase the rate of mineralisation. A relatively large circumference was selected to reduce the influence of edge effects. The turfs were then dug out with a minimum of disturbance to the surrounding vegetation. Two layers of muslin were fastened to the lower end of the piping to prevent loss of soil and contamination in transit. The turfs were placed on trays of fine sand in the glasshouse as shown in Plate Five and were watered daily with a known amount of distilled water to maintain field moist conditions. Temperatures were maintained between 15-20 ^{0}C and a constant day length was maintained by artificial lighting in order to slow down the senescence of *M. caerulea* towards the end of the growing season. The turfs were then allowed to equilibrate for three weeks before P was applied.

Week 1 and 2 The sward of the turfs was trimmed to a height of 0.05 m to ensure that each turf started at the same base level of plant material and to encourage nutrient uptake. This material was dried, weighed and stored for later analysis of phosphorus content. An inert, non-ceramic suction cup, which was used in the field during 1993 was placed in each turf at a depth of 0.10 m and allowed to equilibrate for two weeks before samples were taken.

Week 3 A range of what was considered to be low amounts of P was applied initially to the Culm grassland turfs to avoid the risk of saturating the plant\soil system. This first stage of P application detailed in Table 6.2 (Application One) was added to five replicate turfs to examine variability of Culm grassland. A syringe was used to inject the solution to a depth of 0.10 m at ten equidistant points on each turf. After the P was applied the turfs were not watered for a day to prevent dilution of the phosphate.

Week 4, 5, 6, 7 Soil solution was removed from the suction cups at the end of each week.

Week 8 The sward was trimmed to 0.05 m and the material was dried, ground and stored for analysis of P content.

Week 9 Concentrations of P in soil solution removed by suction cups were highly variable. Most values were below the level of detection of 0.002 mg P l^{-1} with concentrations of 0.6, 0.3 and 0.1 mg P l^{-1} recorded from three different suction cups. There was no indication of change of P in solution over time and results suggested that the applied phosphate had been fixed by the soil. In the second stage of the experiment (Application Two) P was applied in less conservative concentrations as shown in Table 6.2. The recommended application to soils of an index of 0 (ADAS) for P is 25 kg P ha^{-1} (60 kg P_2O_5 ha^{-1}). To ensure a maximum response to P a maximum application of 52 kg P ha^{-1} was used.

Week 10,11,12,13 Solution was removed from suction cups at the end of each week.

Week 14 The sward was trimmed to 0.05 m and the material was dried, ground and stored for analysis of P content. A soil sample was removed and left to dry, in order to carry out extraction using sodium bicarbonate.

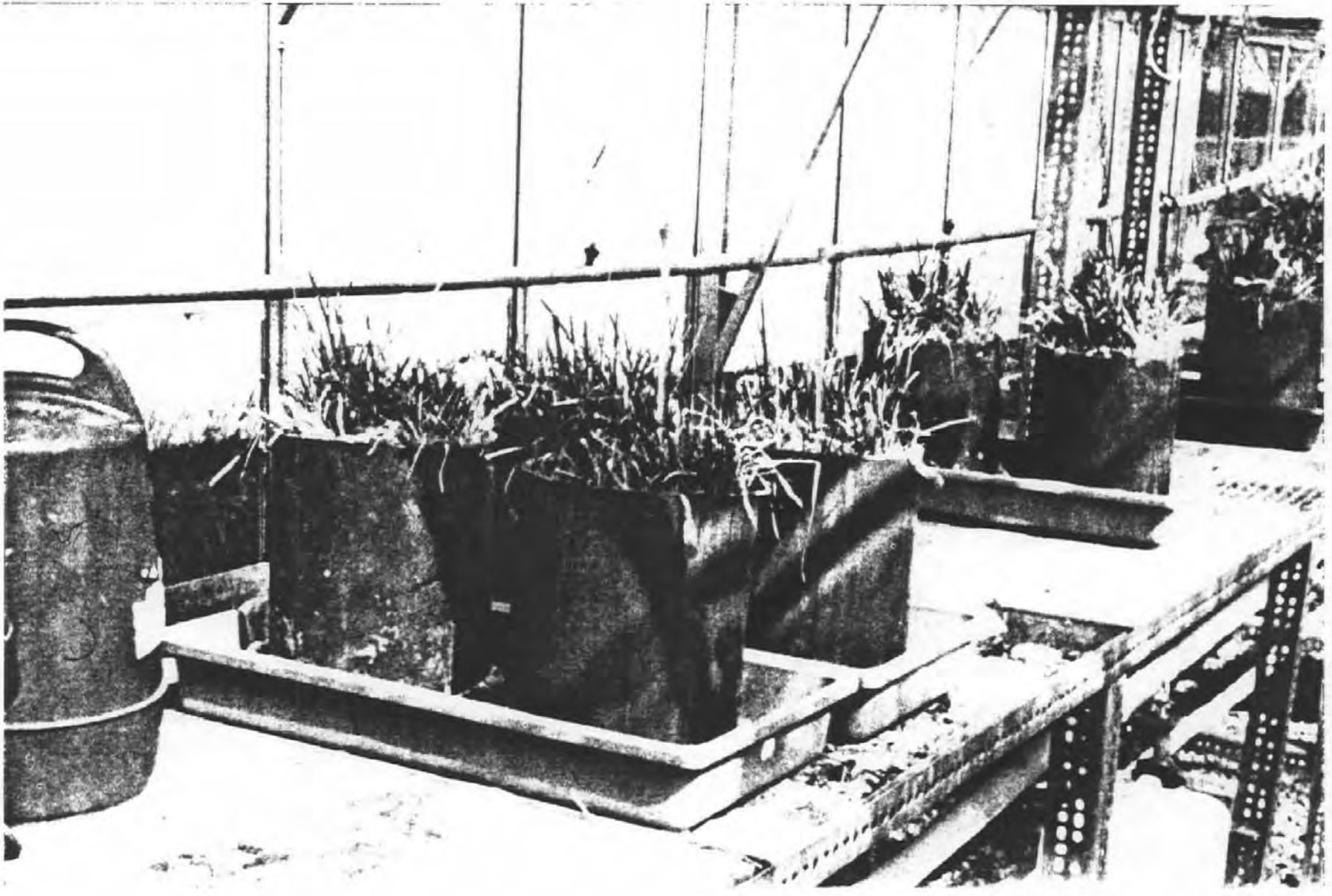


Plate Seven **The set up of Culm grassland turfs inside a glasshouse**

6.4 Results and discussion

6.4.1 Soil response to phosphorus additions

a) P in soil solution

Phosphorus concentrations in soil solution removed by suction cups were variable and no significant correlations with the level of phosphorus applied was found. During the first four weeks of the experiment most values were below the level of detection indicating that there was no direct P transfer from the syringe needle to the suction cup. This indicated that the system of phosphorus mineralisation, release into solution and subsequent uptake was highly tuned. A lack of response by solution P values further confirmed the application of conservative amounts in Stage one of the experiment.

The high variability of P in soil solution particularly during stage Two of the experiment confirmed field observation of variability. Most values were again below 0.002 mg P l^{-1} with elevations of 100 mg P l^{-1} in solutions from four suction cups after at the end of week 12 which received a total application of 10500 mg P l^{-1}. This variation could be due to experimental procedure as points of high concentration of P have been found after applications of fertilisers which remain in the soil for a substantial time (Russell, 1988). An elevation of values in response to this application of 52 kg P ha^{-1} may indicate adsorption and a delayed release into the soil solution. P applied in soil solution may have taken three weeks to reach the suction cups due to the slow nature of P diffusion. A reduction to below the level of detection in the 13 th week was possibly caused by plant uptake. However, these variations may in fact indicate the natural inherent variability of the soil P system on a micro-scale.

b) Air-dry soil extractable P

In contrast to soil solution results, a significant response ($p<0.05$) to P applications was found in sodium bicarbonate extractable P. The combined application of 54.5 kg P ha^{-1} at Level 3 caused a significant ($p<0.05$) increase in P to 6 of the ADAS index as shown in Figure 6.1. This indicated that P added had become loosely held on the anion exchange soil complex and not become fixed or occluded. A significant positive correlation between application rate and extractable P concentrations was further confirmed by regression analysis which found that phosphorus application was responsible for 90.3% of extractable P variation. The lower rates of P application did not have a significant ($p<0.05$) influence on extractable P concentrations in comparison to the control. This implied that the lower rates of application were fixed and a threshold exists as the fixation capacity declined with increased phosphorus application.

The mean extractable P concentration of the control turfs was 5.58 mg l^{-1} compared with a value of 4.42 mg l^{-1} obtained from undisturbed Culm grassland in the field in mid-July. The slight increase, although not significant ($p<0.05$) may be caused by mineralization induced by disturbance involving a combination of change in temperature regime and slight drying of the cores during equilibration. Subsequent effects on the experimental results was thought to be minimal as the turfs were treated in a similar manner and adequately replicated. The maximum P addition increased the amount of extractable P by 106.89 mg P kg^{-1}. In contrast by Ron Vaz *et all.* (1993) in their nutrient addition experiment produced a 40 mg P kg^{-1} increase. Warren and Johnston (1984) reported that additions of 5.51 kg P ha^{-1} produced an increase of 105 mg P kg^{-1} on an unlimed plot in the Park Grass experiment. Phosphorus was applied in lower concentrations over a 100 year period which allowed a build up of fertiliser residues. The large increase in phosphorus in response to P additions in this experiment has important consequences on build up of fixed P and the effect on the plant community.

6.4.2 Response of the vegetation to phosphorus applications

a) Dry matter production

Figure 6.2 showed that the addition of phosphorus and the increase of extractable P did not lead to an increase in dry matter yield. A significant growth response was not produced despite a substantial increase in extractable P at Level three. Other researchers have found an increase in dry matter in response to nutrient applications. Milton (1947) found that the addition of 8.22 kg P ha^{-1} to a *M. caerulea* sward increased dry matter production by a factor of 2.5, from 2.62 to 6.55 tonnes ha^{-1}. Additions of nutrients in the Park Grass experiment increased dry matter production of the first crop by a factor of 1.5 from 169 to 257 kg ha^{-1} (Warren and Johnston, 1984). Although much higher amounts of dry matter was recorded in the two above experiments in comparison to this turf experiment, the relative change from the control turfs was important.

A poor response of the plant community may be explained by species being genetically unable to respond to increased nutrient availability (Bradshaw *et al*. 1960). Experiments by Aerts and Caluwe (1989) and Aerts and Berendse (1988) showed a high increase in growth rate of *M. caerulea* seedlings in response to applications of P. *M. caerulea* seemed to have a high phenotypic plasticity and was found in both low and high nutrient heathland ecosystems (Aerts and Caluwe 1989). As *M. caerulea* dominated the turfs with cover values of over 90%, a similar response could be expected. Nitrogen supply may be acting as a limiting factor as suggested by Loach (1968) who found that the combined application of N and P stimulated a greater growth response. Applications of N itself produced an factor of 2 increase in dry matter production, whereas P produced a factor of 4, and N and P a factor of 11. A slight reduction, although not significant in the second stage may be influenced by the onset of senescence of *M. caerulea*.. The maintenance of summer temperatures (15-20 ^{0}C) and 16 hours of daylight had attempted to slow the process down. But it appeared that the removal of turfs had a great influence in this experiment particularly in the retranslocation of nutrients below ground. *M. caerulea* reach its maximum aboveground biomass at the end of the growing season in September which is followed by

retranslocation of nutrients from the dying leaves to a below-ground storage organ (Loach, 1968). But Loach (1968) found that the nutrient content of the storage organ did not increase greatly until November. Retranslocation of P below-ground may not be wholly responsible for a reduction in dry matter production in this experiment .

b) Phosphorus content of plant material

Further evidence of change in P availability was provided by the concentration of P within the plant material removed from the turfs as shown in Figure 6.3. A significant ($p<0.05$) increase in P was produced by the highest level of application and was significantly correlated with extractable P and level of P application. The results indicated that P was stored in *M. caerulea* tissues by the process of luxury consumption (Russell, 1988). In fact a *Molinietum* may take up 94% of its P requirements by July (Aerts and Caluwe, 1989) and later uptake of P did significantly effect growth of especially *M. caerulea*.. An increase in P concentration by a factor of four in this experiment was comparable to an increase of a factor of 2.9 in an experiment by Milton (1947). Concentration of P in *M. caerulea* remained relatively high at the end of the experiment confirming that it becomes less efficient at retranslocating nutrients nutrient availability increased (Aerts and Caluwe, 1989).

c) Phosphorus content of biomass removed from the turfs

Poor correspondence between total P content and dry matter production may be explained by the survival strategies of *M. caerulea*. By taking into account the total P content of all the material removed as in Chapter Five, a more accurate picture of plant response was identified as shown in Figure 6.4. The yield of P did not change significantly over time in response to P additions. Significant positive correlations was found between the yield of P and P application, extractable P and total P. The high plant P concentration was smoothed out by the much lower dry weights. This information further reinforced the above discussion in that the extra available P was not utilised by *M. caerulea*. for growth. It showed that the same dry matter production may be obtained by different treatments and the corresponding composition of the plant material may differ (Warren and Johnston, 1964).

Figure 6.1

The change of sodium bicarbonate extractable phosphorus in response to phosphorus additions to Culm grassland turfs(n=5, standard error bars)

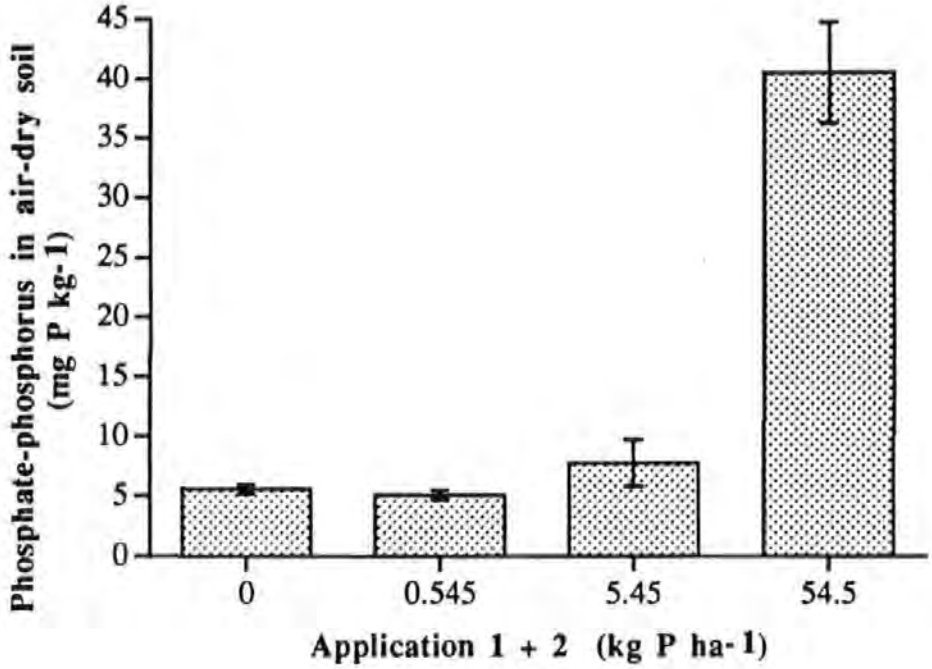


Figure 6.2

The change in dry matter production in response to phosphorus additions on Culm grassland turfs (n=5, standard error bars)

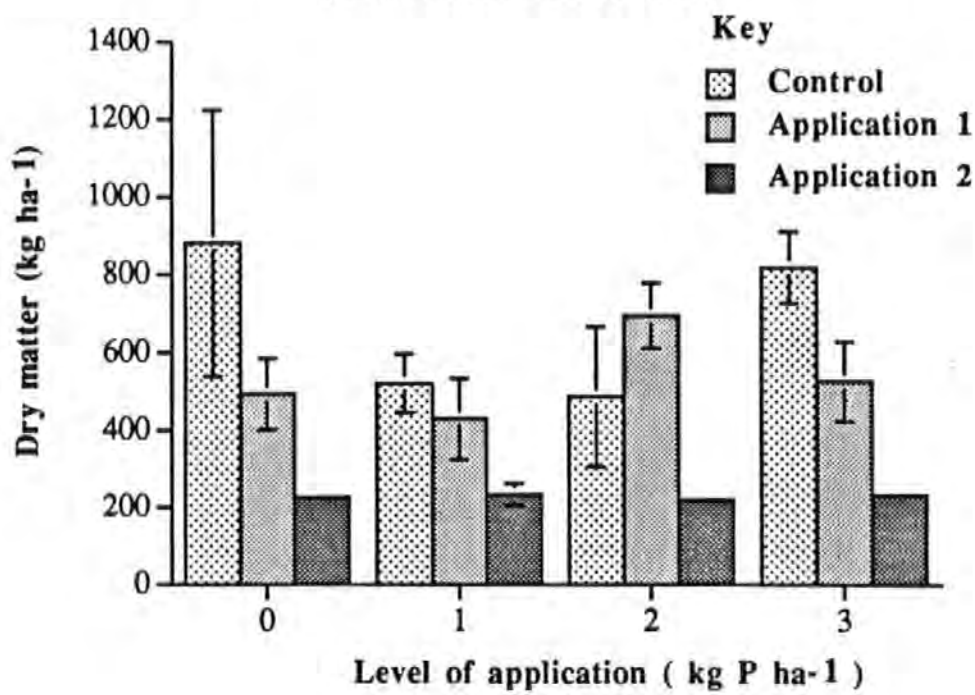


Figure 6.3

The total phosphorus content of plant material in response to phosphorus additions to Culm grassland (n=5, standard error bars)

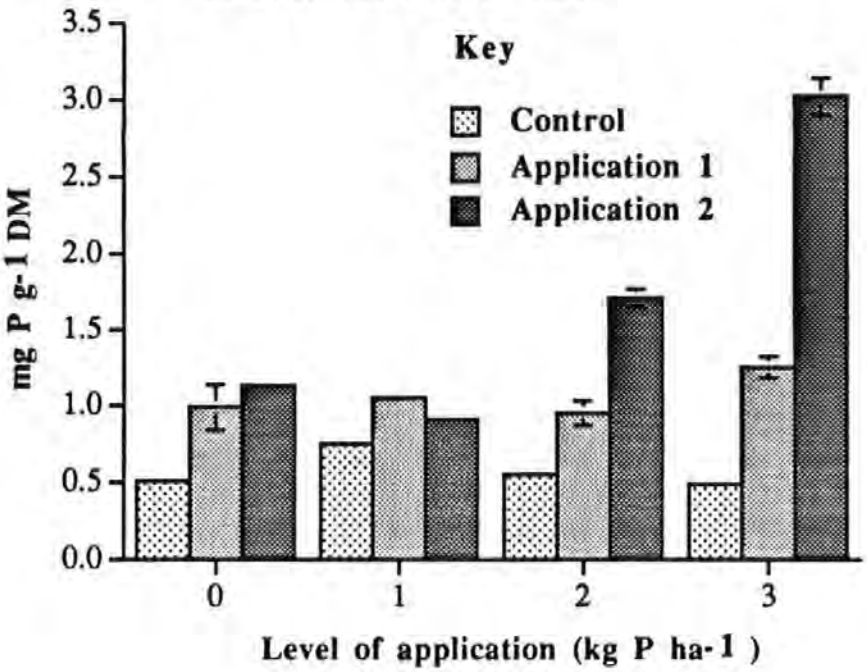
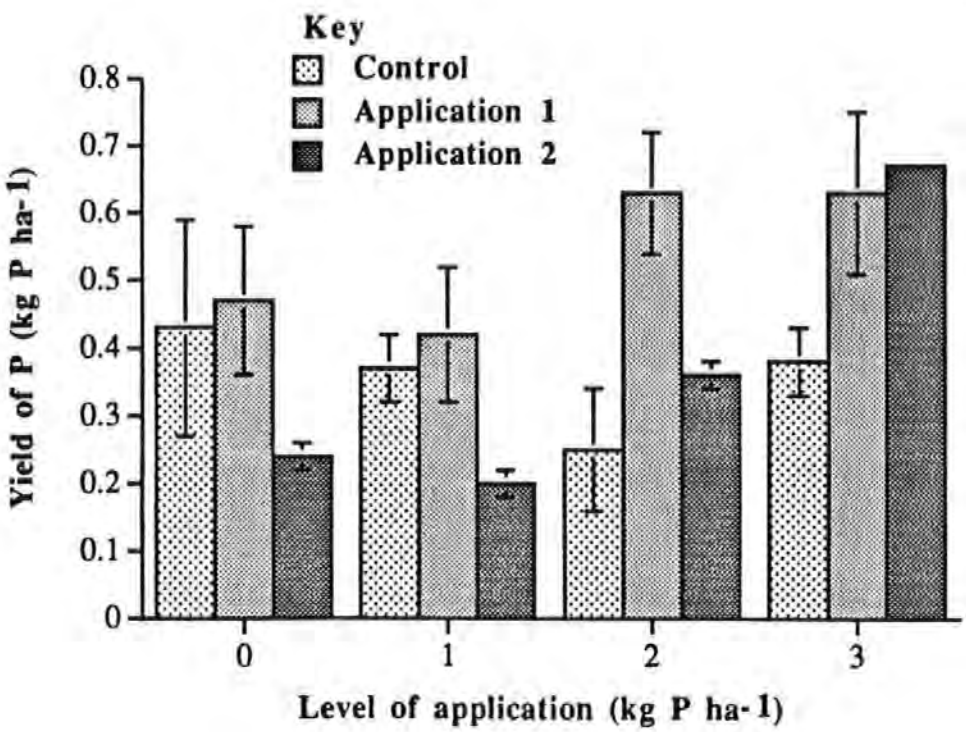


Figure 6.4

The yield of phosphorus of plant material in response to phosphorus additions on Culm grassland (n=5, standard error bars)



6.5 Summary

The results summarised in Table 6.4 show that the aim of producing a disturbance within the Culm grassland system was achieved. P was stored within the plant tissues instead of producing a growth response. This led to the conclusion that dry matter production was a poor indication of P availability in this experiment, which was probably due to conducting the experiment near the end of a growing season. If the turfs had been removed earlier in the growing season a greater growth response may have resulted. The soil had a high P fixation capacity and a change in extractable P values only occurred response to high P applications. This could have been remedied by applying P directly to roots free of soil as employed by Pegtel (1983). It was apparent that a threshold exists between the applications of 5.5 and 55 kg P ha^{-1} and their effect on the plant community. Levels of P within this margin may also be effective in causing perturbations in the culm grassland system.

Most nutrient addition experiments have monitored the changes in species composition of the plant community. It was difficult to predict the long term effect of P applications on the turf plant community. Berendse *et al.* (1992) compared dry matter production to Grimes' model (Grimes 1979) and found it reached the predicted threshold of 4-6 tonnes ha^{-1} after which a species decline would result, following the application of nutrients. This was not applicable as the dry matter production of the turfs was well below these figures. However, changes could involve the increased vigour of *M.caerulea* during following growing seasons on the turfs that received high concentrations of P. *M. caerulea* may out compete other species such as *Erica tetralix* (Aerts and Berendse, 1989; Aerts and Caluwe, 1989). *E. tetralix* in contrast to *M. caerulea* did not have a wide edaphic tolerance to respond to increases in nutrient availability. The information obtained in the experiment comes some way in describing the response of Culm grassland to disturbance and the cycling of P within the soil and plant system. This will be discussed in more detail in the following chapter together with suggestions of targeting management at certain points within the Culm grassland system.

Table 6.4 The response of extractable P, dry matter, Total P and P yield to nutrient additions on Culm grassland turfs

Week 14 of experiment	Total concentration of applied P - App 1 + 2 (kg P ha^{-1})			
Variable	**0.000**	**0.545**	**5.45**	**54.5**
Soil extractable P (mg kg^{-1})	5.6	5.1	7.8	40.4
Plant dry matter (kg ha^{-1})	226.7	234.7	220.0	233.3
Total plant P (mg g^{-1})	1.1	0.9	1.7	3.0
Total plant P yield (kg ha^{-1})	0.2	0.2	0.4	0.7

CHAPTER SEVEN

STRATEGIES FOR PHOSPHORUS MANAGEMENT IN THE CULM GRASSLAND SYSTEM

7.1 Introduction

The aim of this chapter is to bring together the findings of the four previous chapters and discuss the implications that these results have for the management of Culm grassland. The final aim of the project, that is 'to formulate a simple model of the soil:vegetation system under species-rich grassland on the Culm to be employed as a management tool, to aid future restoration,' will be discussed. The first part of this chapter discusses the key results relating to the Chapters Three, Four and Five of the project with results of the turf inserted in the appropriate section. The results are summarised in table form and as most of this data has been previously analysed in individual chapters referral to previous research will be limited.

A phosphorus cycle was formulated by discussing the data collected in the study and by taking a systems approach. The inputs, outputs and storage components are described together with the relative changes in the components during transfer. In order to facilitate comparisons some simplification of this complex system was necessary. It was realised that each component required study in more depth, particularly P mineralisation and the forms of P released. In this baseline study of Culm grassland it was decided to gain a broad picture of the system which could be refined at a later stage by further work. The cycling of P was compared to other systems previously studied together and suggestions were made on how the cycle may be manipulated. This information was finally integrated with possible management strategies to maintain or enhance floristic diversity on a range of Culm grassland sites.

7.2 A review of environmental conditions

7.2.1 Characterisation of the Culm grassland environment

An extensive study of soil conditions and plant communities of Culm grassland compared to an improved grassland was carried out in the first field season of 1992. The results highlighted the aspects which asserted a greater influence on the Culm grassland system than others. For example, a high variation in rainfall inputs resulted in small variations in water table fluctuations and soil water content over the growing season on Culm grassland. Vegetation of the improved grassland appeared to be the most marked contrast, although there were marked contrasts in the organic matter contents and bulk density of the soils. This led to the conclusion that water conditions alone were not the controlling factor within these chosen sites, although the dominance of *M. caerulea* and absence of *Sphagnum compactum* indicated a fluctuating water table (Rutter, 1985). The highly varied environmental conditions from year to year highlighted the importance of monitoring field conditions for more than one season.

A combined effect of water and nutrient conditions were likely to have the strongest influence. This was indicated by a lower pH on Culm grassland especially on SG than on SI. The pH of the Culm grassland was in accord with floristically similar wet heathlands in West Wales (Evans, 1989). The lower concentrations of calcium and magnesium was indicative of lower pH on the Culm grassland. The higher pH on improved grassland was attributed to the previous applications of lime. The influence of fertiliser applications on soil nutrients was most marked during the sampling period of mid-April. The significantly elevated the levels of extractable P on the improved grassland were shown in Table 7.1. Concentrations on the Culm grassland were significantly lower over the time period from mid-April to mid-June. A similar contrast was not found in the concentrations of mineral nitrogen. It was concluded that the low concentration of phosphate-phosphorus was one of the dominant factors in maintaining Culm grassland in common with other studies (Lloyd and Piggott, 1967; Rorison, 1971; Marrs *et al.*, 1989; Gough and Marrs, 1990) .

Past, low intensive management on SG appeared to have caused a build up of soil organic matter and a lower pH in comparison to FG. This was perhaps surprising since Fernhills Moor was unmanaged for many years. Scrub had encroached upon the Culm grassland which may be associated with nutrient enrichment following succession (Marrs, 1990). No evidence of nutrient accumulation may be due to the absence of disturbance. The vegetation community on FG was less species-rich and the strong presence of litter and bare ground was induced by the dominance of *M. caerulea.*

The impact of present or introduced grazing or cutting on the nutrient system of Fernhills Moor was not evident as it was introduced mid-way during the sampling season at the end of May. Therefore, there was no impact on P concentrations but grazing may have created greater variation in concentrations of mineral nitrogen. The absence of any impact by cutting on such a grassland has also been found by other workers such as Rizand *et al.* (1989). This led to the suspension of sampling on the cutting plot in the second field season. Some impact of management was evident in the breakdown of scrub debris and *M. caerulea* litter by trampling but did not appear to cause any change of species composition. The regrowth of scrub and *M. caerulea* tussocks were kept in check by the cattle grazing.

7.2.2. The availability of soil phosphorus in the Culm grassland system

Results from the preliminary characterisation study in 1992 indicated that the availability of phosphorus within the Culm grassland system was a key factor in maintaining this community. This was further reinforced with the knowledge of soil phosphorus dynamics (Emsley, 1982; Harrison 1987 and Tisdale 1989) and similarities found with other studies (Lloyd and Pigott, 1967; Rorison, 1971; Gough and Marrs 1990). It was also decided to investigate alternative methods of removing soil solution to obtain a better indication of concentrations plants actually remove from the soil (Moore and Chapman, 1986). A more detailed study of seasonal variation was undertaken by sampling from mid-March at two-weekly intervals and results summarised in Table 7.2.

The use of sodium bicarbonate to extract soil P was found to greatly over-estimate plant requirements, typically by three orders of magnitude. The use of sodium bicarbonate still showed the gross differences between the Improved and Culm grassland which was reinforced by the total P values. In the second field season these differences were less pronounced as the elevation at the beginning of the field season was absent. This may be due to an earlier application of fertiliser than compared to the first field season. An increase in P concentrations on SG could have been caused by varying environmental conditions which were warmer than the previous year. However, despite these variations from the first field season a general steady increase over the growing season was found on all the plots studied.

Soil solution was removed by centrifuging in the laboratory and inert non-ceramic suction cups in the field in 1993. These methods removed soil water directly to provide a closer idea of the concentration of P removed by plants. The P content of soil solution removed by centrifuging was highly variable and ranged from 0.009 to 0.029 mg l^{-1} on both Culm and improved grassland. A seasonal pattern of solution P found by other workers such as Campbell *et al.* (1989) was absent on SG. It was possible that any seasonal patterns were masked by the high variability in soil microbial activity and soil water conditions (Seeling and Zasowski, 1994). P within the soil solution removed by suction cup was only detected on the improved grassland. This indicated that centrifuging removed water from smaller pores containing higher concentration of P. A trend of increasing suction cup P was apparent and values were not significantly different from centrifuge values between mid-April and mid-June. Removal by suction cup was less variable and appeared to provide a better indication of P available to plants on the improved plot which was reinforced by Lorenz *et al.*, (1994). Very low concentrations on the Culm grassland plots indicated that the species are adapted to remove P at very low concentrations. A closer relationship was found between P concentrations of suction cups and matric potential as both these measurements are taken under field conditions.

The results of the controlled turf experiment further supplemented these findings. The lack of change in the concentration of P within the solution removed by suction cups indicated that the soil had a high fixation capacity. A second higher application of P produced highly variable concentrations on solution P indicating slow P diffusion through the soil. A significant increase in concentration of sodium bicarbonate extractable P was induced by the combined application of 54.5 kg P ha^{-1}. In fact a strong positive correlation was found between the level of application and 'available' P. The soil analyses thus indicated that a threshold exists in the fixation capacity between the applications of 5.45 and 54.5 kg P ha^{-1}.

7.2.3 Variation of plant production with season and vegetation community

Plant dry matter and nutrient yield was investigated by monitoring the natural growth cycle of the community on SG and the influence of defoliation, in comparison to SI. Peak biomass production was found to occur in mid-July with *M. caerulea* and its litter being the dominant component, as shown in Table 7.3. The productivity of Culm vegetation was found to be similar to other semi-natural grasslands. The breakdown of *M. caerulea* litter and the excess remaining at the end of the growing season appeared to be an important factor in the cycling of nutrients similar to findings by Loach (1968) and Bakker (1989). Defoliation was found to lengthen the growing season after mid-June.

The seasonal variation of total phosphorus content of the plant material had little relationship with dry matter yield. Concentrations were found to peak in mid-June, with *M. caerulea* no longer being the dominant component, due to high but variable concentrations accumulated in herbs and legumes. Litter was found to increase in P concentration while its mass declined during the growing season and was found to lose 1.42 mg P g^{-1} over the winter period. Defoliation had a highly variable effect on P concentrations and appeared to cause higher values from March to June than uncut grass during the same period. The more productive grasses on SI showed an ability to accumulate P within their tissues. Total P concentration was highly variable as environmental conditions and plant growth stages have a great influence on nutrient concentration.

Relationships became clearer when both dry matter and total P content were considered in unison. The variability of the data was reduced and peak phosphorus yield was found in mid-July. *M. caerulea* followed the expected pattern of an increase during the growing season followed by a decline at the onset of senescence. The dead material declined after mid-July and was added to during the autumn and winter. Regrowth following defoliation on Staddon Improved indicated that grasses on the improved plot were much more productive than Culm species.

The Culm grassland vegetation responded to nutrient inputs at the highest level of application. The threshold in fixation of P by the soil was not apparent in any change in dry matter production. Significant correlations were only found between total P, available P and the level of P application. In some way the growth was being limited by other factors, perhaps nitrogen limitation and the onset of senescence (Berendse *et al.*, 1987). A poor response was explained further by concentrations of P contained within the plant material. The highest level of application induced a significant increase in total P content. The results suggested that *M. caerulea* removed the majority of its nutrient requirements before the onset of senescence and any extra available nutrients was stored within the plant tissues. A significant amount of nutrient remained within the plant tissue as *M. caerulea* becomes less efficient at retranslocating nutrients as nutrient availability increases (Berendse *et al* 1987).

The results discussed above highlight the basic information needed to build up a systems approach to cycling of P within Culm grassland. Knowledge of the relative sizes of compartments within the soil and plant components and their variation throughout the growing season indicated the transfers of P within the system. The following sections will use the information from Staddon Grazing to produce a simple model of the P cycle in the form of a diagram which will be confined to Culm grassland.

Table 7.1 Summary of the environmental conditions of Culm and improved grassland plots in the 1992 field season

		PLOT		
	Culm	Culm	Culm	Improved
Variable	FG	FC	SG	SI
pH	4.2	4.3	3.7	4.6
Phosphate-P mid-April	2.2	3.8	4.7	27.2
Phosphate-P mid-June	1.4	2.0	4.6	9.4
Organic matter (%)	20.9	*	28.2	15.2
Number of species	18	14	26	15
% cover of Molinia	47.1	41.8	31.6	n.d.
% cover of bare/litter	36.8	39.4	9.6	n.d.

* not sampled n.d. not detected

Table 7.3 Seasonal variation of plant production on Culm grassland

Variable	Sampling period					
		A	M	J	J	S
Dry matter	live	2141.0	2372.8	2126.9	4508.8	3849.2
(kg ha^{-1})	dead	3417.6	2119.8	1652.8	1630.6	1063.8
	Molinia	216.3	620.2	1184.0	2074.2	2280.0
Total P	live	2.3	3.5	4.3	4.2	1.9
(mg P g^{-1})	dead	0.3	0.4	0.4	0.1	0.1
	Molinia	0.7	1.0	0.9	0.7	0.3
P yield	live	0.4	0.8	1.3	1.5	0.8
(kg P ha^{-1})	dead	0.9	0.9	0.7	0.2	0.1
	Molinia	0.1	0.6	1.1	1.2	0.6

Table 7.4 The response of Culm grassland turfs to P additions

Final trim (week 14)		Treatment (kgPha^{-1})		
Variable	0.000	0.545	5.450	54.500
Available P (mg kg^{-1})	5.6	5.1	7.8	40.4
Dry matter (kg ha^{-1})	226.7	234.7	220.0	233.3
Total P (mg P g^{-1})	1.1	0.9	1.7	3.0
Yield of P (kg P ha^{-1})	0.2	0.2	0.4	0.7

Table 7.2 Seasonal variation of soil P conditions on Culm and Improved grassland during the 1993 field season

Plot	Staddon Grazing							Staddon Improved					
	Sampling Period (mid-month)							Sampling Period (mid-month)					
Phosphate-phosphorus	M	A	M	J	J	S		M	A	M	J	J	S
Soil extractable (mg kg-1)	1.7	1.87	3.25	3.63	4.42	4.65		3.35	3.31	4.73	4.73	6.49	3.90
Centrifuge (mg l-1)	0.026	0.029	0.028	0.023	0.019	0.016		0.009	0.024	0.025	0.007	0.027	0.020
Suction cup (mg l-1)	*	*	*	*	*	*		0.005	0.012	0.016	0.013	0.002	0.003
Total (mg P kg-1)	545.5							790.6					

* not detected

7.3 Phosphorus cycling within the Culm grassland system

7.3.1 Inputs and outputs

In order to suggest possible strategies for P management in Culm grassland it was important to highlight the main features of the system and the points at which the system may be perturbed. The main compartments of SG are simplified in a schematic diagram in Figure 7.1 including the inputs, outputs and storage compartments with transfers of P indicated by arrows. Comparisons with cycling of P on Staddon Improved was made within the text where possible.

The inputs of P from external sources in to the system may include animal excrement and atmospheric deposition. Although these parameters were not measured in this study some can be estimated from previous work. Atmospheric deposition of less than 0.2 kg P ha^{-1} a^{-1} was quoted by Chapman and Webb (1978) as having little influence on soil nutrient content over the short term. Animal excrement may have some effect on nutrient cycling as 90% of nutrients removed by grazing animals are returned to the system via excrement to be broken down in to organic matter (Perkins, 1978). Actual amounts and quality may be influenced by the movement of grazing animals between the Improved and the Culm grassland field. Inputs on the SI was also supplemented by the application of fertilisers during spring, which has produced a marked contrast in total soil P value of 474.4 kg P ha^{-1} in comparison to 147.3 kg P ha^{-1} on SG. Additionally, typical agricultural soils contain 50% of organic and inorganic P (Rowell, 1994) whereas soil on SG was composed of 84% organic P and 16% inorganic P.

Outputs from the system may include leaching, drainage and removal of plant material by management. Movement of soil water down profile was limited as indicated by the 'ponding' of water in the upper layer of soil in the 1992 field season. Drainage, if present probably occurs at a slow rate due to the heavy texture and low porosity of the soil. Loss through this pathway may be limited due to the fact that most P is immobile and forms

insoluble complexes with iron and aluminium compounds at low pH and anaerobic conditions. In heathland systems the loss of P via this pathway was thought to be limited to 0.03 kg P ha^{-1} a^{-1} (Chapman, 1989). Plant removal by management has been found to be most influential in cycling of P within the vegetation systems (Marrs, 1990). Many studies have attempted to use management to control the cycling of nutrients within the soil:plant system by manipulating the different storage compartments and transfers between the compartments as discussed in Chapter One. Thus an understanding of these aspects within the Culm grassland system is important in formulating management strategies.

7.3.2 Storage Compartments

The main permanent storage compartments of phosphorus within Culm grassland were found to be at the adsorption complex of the soil matrix and the organic matter component. In simplified terms these are known as inorganic and organic P in Figure 7.1. Although it was recognised that below-ground roots were an important storage component, practicalities of the study did not allow their investigation. The relative quantities of these fractions contributing towards total P have an important influence on the release and uptake of P by plant roots. Inorganic P derived from weathering of soil minerals is adsorbed to the surface of clay minerals, hydrous oxides, carbonates and Fe and Al phosphates. P derived from organic matter breakdown found in complex forms (Russell, 1986) is associated with the uptake and death in the microbial biomass (Harrison, 1985). The ability of Culm grassland soils to store P was indicated by the elevated total P values found on the Staddon Improved site. The addition of phosphate to the Culm grassland turfs showed an ability to fix increased P on the adsorption complex until a saturation threshold was attained. This addition may have an indirect effect via the stimulation of organic matter mineralisation. The threshold may have been exceeded due to the influence of increased plant demands encouraging the breakdown of organic matter. This breakdown had released P into the soil solution and affected the equilibrium between free and adsorbed P ions (Gough and Marrs, 1990).

Release of P from the adsorption complex as shown in Figure 7.1. may be indicated by sodium bicarbonate extractable P values. Results in Chapter Four found a 100 fold reduction in P in comparison to total P storage compartment indicating that very small amounts were loosely held on the soil complex and within the soil solution. The release of extractable P was of similar magnitude on Staddon Improved showing that release does not always equate with total P content. This may be due to the lower organic matter and thus the mineralisation and immobilisation of organic P has an important influence on the processes occurring at the adsorption complex. The concentration of P within the soil solution is 100 fold lower than extractable P suggesting that a very steep concentration gradient exists between the soil adsorption sites and plant root cells. Release into soil solution was evidently influenced greatly by plant demand which was reiterated by higher suction cup soil solution values on the SI site. Amounts of P in soil solution were maintained in a state of dynamic equilibrium between plant demand and readsorption processes (Floate,1987). This was shown by the fact that concentrations of P in centrifuged solutions did not alter to a great extent over the season.

The low concentrations of P in soil solution on Culm grassland indicated that plants, particularly *M. caerulea* can remove P at very low concentrations. The accumulation of P within *M. caerulea* was the largest component of total green material. In the absence of defoliation maximum accumulation took place in mid-July with a increase from mid-April until this period. A slow down in P demand was shown by an increase in available P after mid-July and indicating that the release of P at the soil complex being more dominant than plant uptake at this point in time. It was evident that Culm plants had the ability to accumulate relatively large concentrations of P over time despite very low concentrations present in soil solution at any one time. However, previous research by Mejstrik (1972) and Harley and Harley (1987) suggested that uptake of nutrients may be enhanced by mycorrhizal interactions. This large variation between the concentration of plant and soil P showed that no simple relationship exists between species uptake and availability of nutrients (Hayati and Proctor, 1990). The removal of plant material from the system will remove P obtained from the soil and maintain the cycling and uptake of P.

M. caerulea also influenced the amount of nutrients returned to the soil via litter decomposition and therefore has a great effect on nutrient cycling through this pathway. The soil organic matter content was found to be elevated in comparison to FG and SI as decomposed litter material accumulated within the upper 0.10 m of the soil. Although litter remaining from the die-back of *M. caerulea* from the previous season was broken down in the following season, an excess remains which may impede P turnover as found by Dickinson (1989). Removal of *M. caerulea* during the growing season would have a great influence on the litter composition at the end of the Autumn. Grazing on SG has encouraged breakdown whereas on FG an absence of disturbance has decreased the rate of breakdown. As organic matter accumulates, up to 90% of P in the top soil may become organically bound (Harrison, 1985) which may in turn reduce the amount of labile and thus plant available P upon which Culm grassland species rely.

7.3.3 Transfers and manipulation by management

A discussion of the input, outputs and storage compartments of Culm grassland has shown that the yield of *M. caerulea*, the breakdown of its litter and subsequent accumulation of organic matter is a major component of the P cycle particularly as *M. caerulea* is self-perpetuating. The return or transfer of dead material has a large influence on the proportion of organic P making up the total soil P content. The inorganic component was less likely to have a direct effect on cycling of P on Culm grassland as the soil has a high fixation capacity and release from the adsorption sites is limited. P adsorption maxima have also been employed to classify heathland in relation to the presence of *C. vulgaris* (Chapman, Rose and Basanta, 1989). Relatively high adsorption maxima were related to the invasion of *Ulex europaeus* although *C. vulgaris* was able to still assert dominance in response to active management. Manipulation of these components has been attempted by many workers (Chapter One). However, these were mostly longterm as found by Rizand *et al.*, (1989) in their experiment of adsorption properties. They reported that it took 22 years to produce a slight increase in the availability of P in response to the return of clippings.

The most important periods of the P cycle on Culm grassland was found in mid-April, mid-July and mid-September and are shown in Figure 4.2, 4.3 and 4.4 respectively in units of kg P ha^{-1}. The values of soil P were calculated by allowing for volume of soil by taking into account bulk density and assuming 50% soil water content. An important period of release and uptake of P on SG was found between the sampling periods of mid-April and mid-July. The most variable components of the cycle were estimated as total plant P yield, litter and soil extractable P, which are primarily involved in the transfer of nutrients within the cycle. In mid-April this amounted to 2.95 kg P ha^{-1} which is 2% of the total soil P and in mid-July the transfer was 3.05 kg P ha^{-1} which is also 2% of the total soil P. These periods relate to the key soil P mineralisation period and the maximum biomass production of *M. caerulea*. An increase in extractable P was found to occur and at the same time an increase in live material particularly *M. caerulea* took place. This was balanced by a reduction in the litter component which may explain the similar percentage transfer of nutrients at the two sampling dates. Thus, P uptake by *M. caerulea* has the greatest impact on P availability within the soil from mid-April to mid-July. The uptake of P in all live material during this three month period amounts to a rate of 0.06 kg P ha^{-1} day^{-1} which is in the same order of magnitude to the uptake rate of 0.02 found by Oorschott (1994) on Culm grassland. Concentrations removed per day were 10 times greater than concentrations found in soil solution removed by centrifuging. Plant demand per day was reported to be much higher than concentration of P in solution (Mengel and Kirkby, 1986) and (Russell, 1988). The results suggested that in order to manipulate P cycling in the system the removal of above-ground material should occur during this period as indicated by the defoliation experiment carried out on SG. Successive removal may induce greater removal of P as growth response was encouraged. This will have maximum effect on both soil and plant components of Culm grassland during a period when maximum change occurs and when the community will be most vulnerable. It may also be of particular importance in maintaining long term species-richness and composition of a community.

The method used to remove the live material may include grazing, cutting or burning which are discussed in more detail in Section 7.4. Although there are differences in the effects of these methods, workers have found that attempts manipulate soil nutrient stores are very long term and benefits may not be evident for many years (Bakker, 1985). This may suggest that management may be ineffectual in the short term (Bakker, 1985) but removal will influence the amount of material remaining at the end of the growing season. The sampling period of mid-September on SG was found to be a key time for the senescence of *M. caerulea* and formation of litter. The transfer of P was found to be 2.37 kg P ha^{-1} or 1.6% of the total soil P in Figure 7.4 indicating a reduction in transfer and possibly addition to the storage compartments such as total P or the below-ground plant roots.

Management particularly on SG should also concentrate on the amount of material remaining at the end of the growing season and the excess remaining from the previous growing season. This may be most applicable to Culm grassland which has not been managed appropriately in the past and where a build up of litter has occurred. Transfer from live to dead *M. caerulea* should be manipulated to ensure a greater removal of live material during the growing season to reduce the amount left to die-off. Cutting of *M. caerulea* will have limited influence, unlike trampling during grazing, on the breakdown of litter from the previous season. Burning could be employed but may result in 80% of P returning to the soil in the form of ash (Chapman, 1967).

Figure 7.1

Schematic representation of the phosphorus cycle of the Culm grassland system

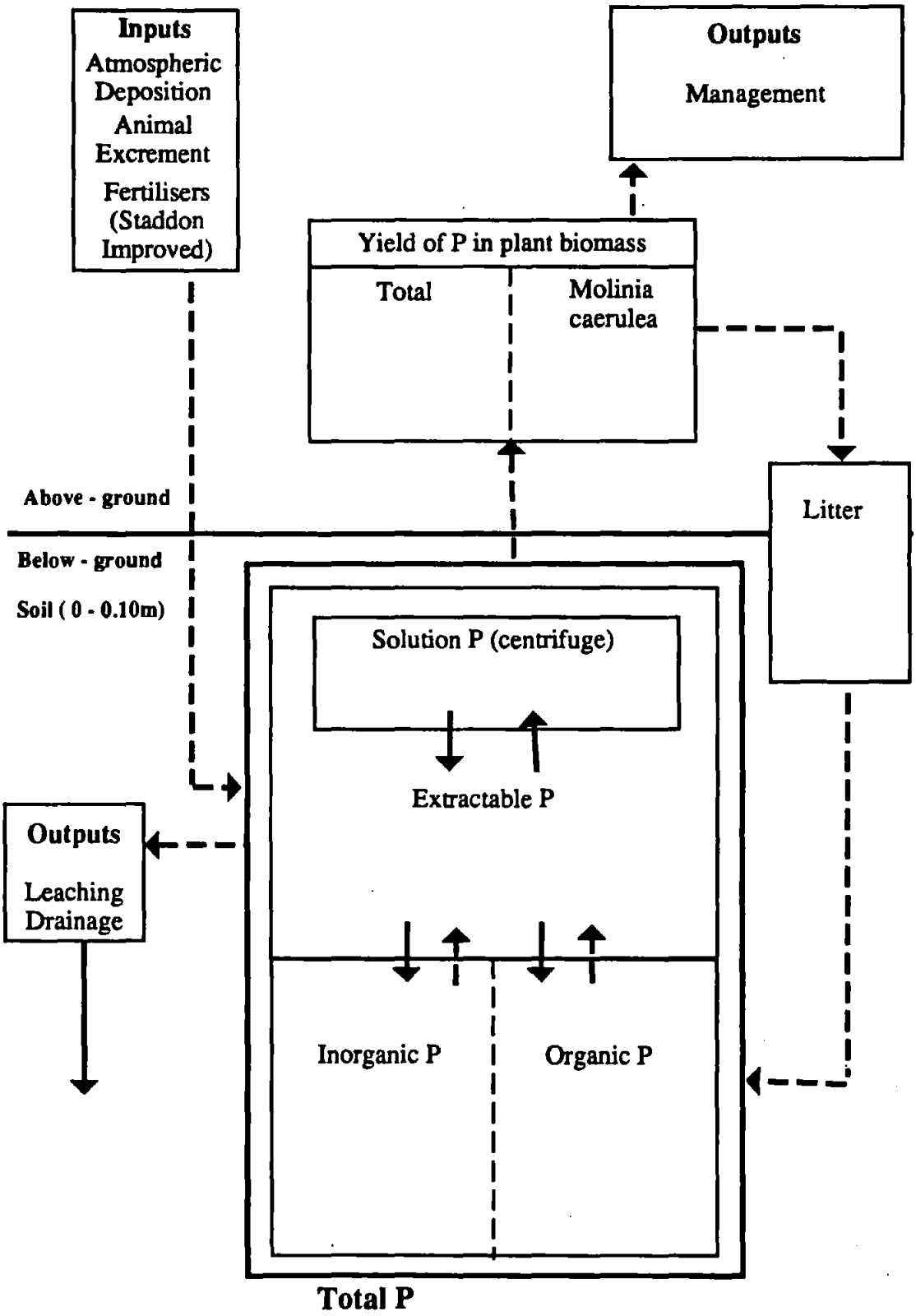


Figure 7.2

The relative quantities of P in the Culm grassland system at mid-April (all units in kg ha^{-1})

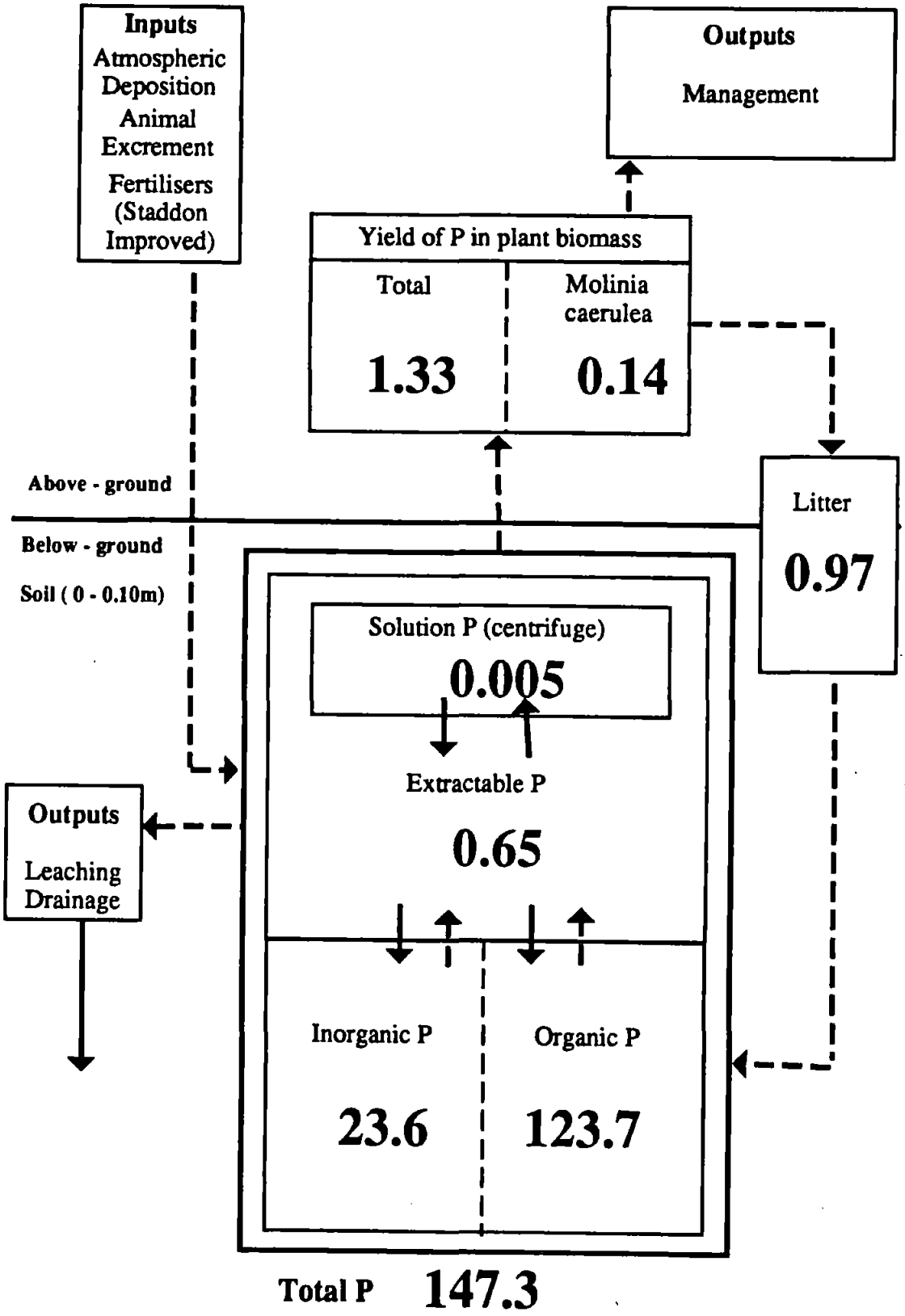


Figure 7.3

The relative quantities of P in the Culm grassland system at mid-July (all units in kg ha^{-1})

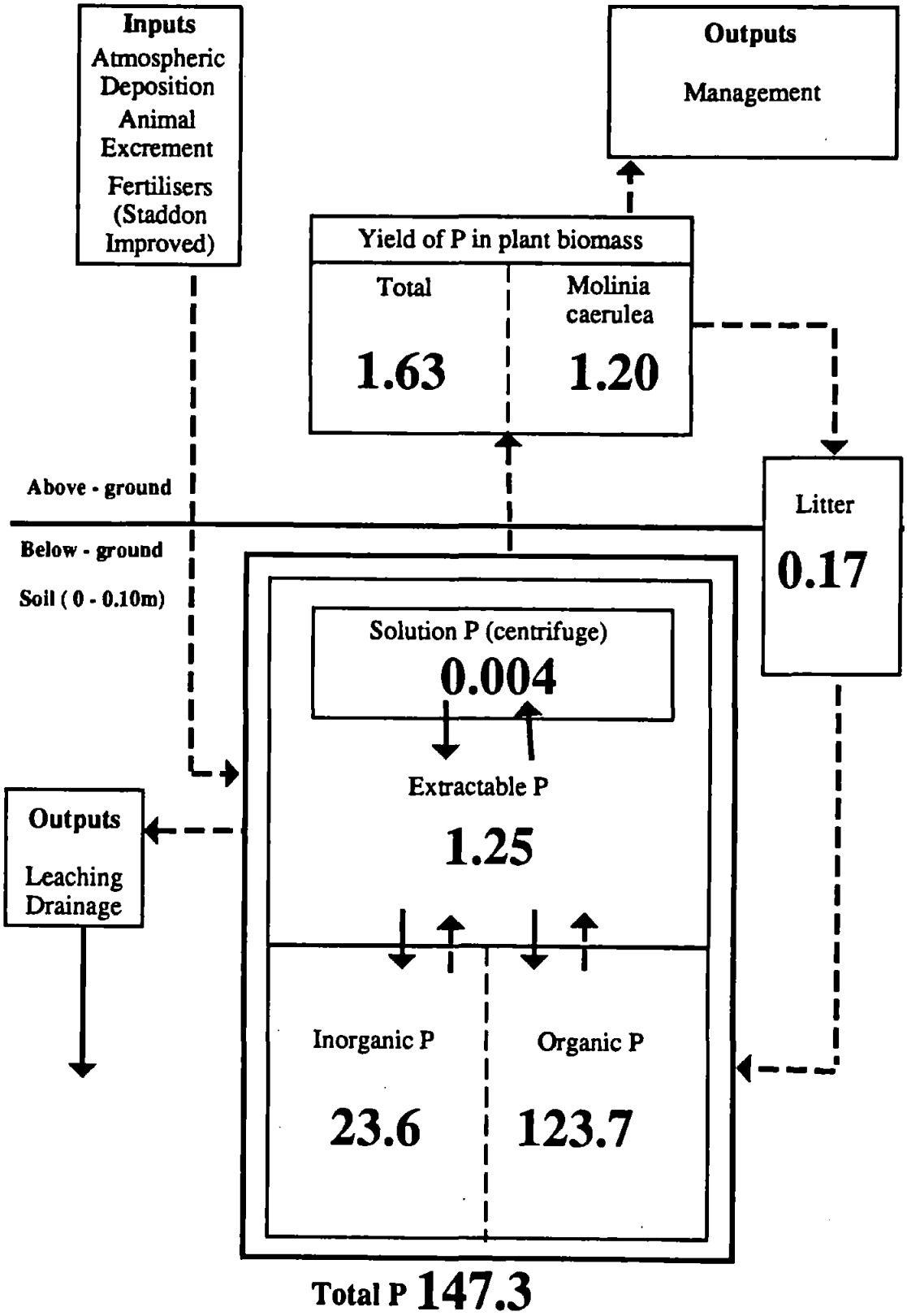
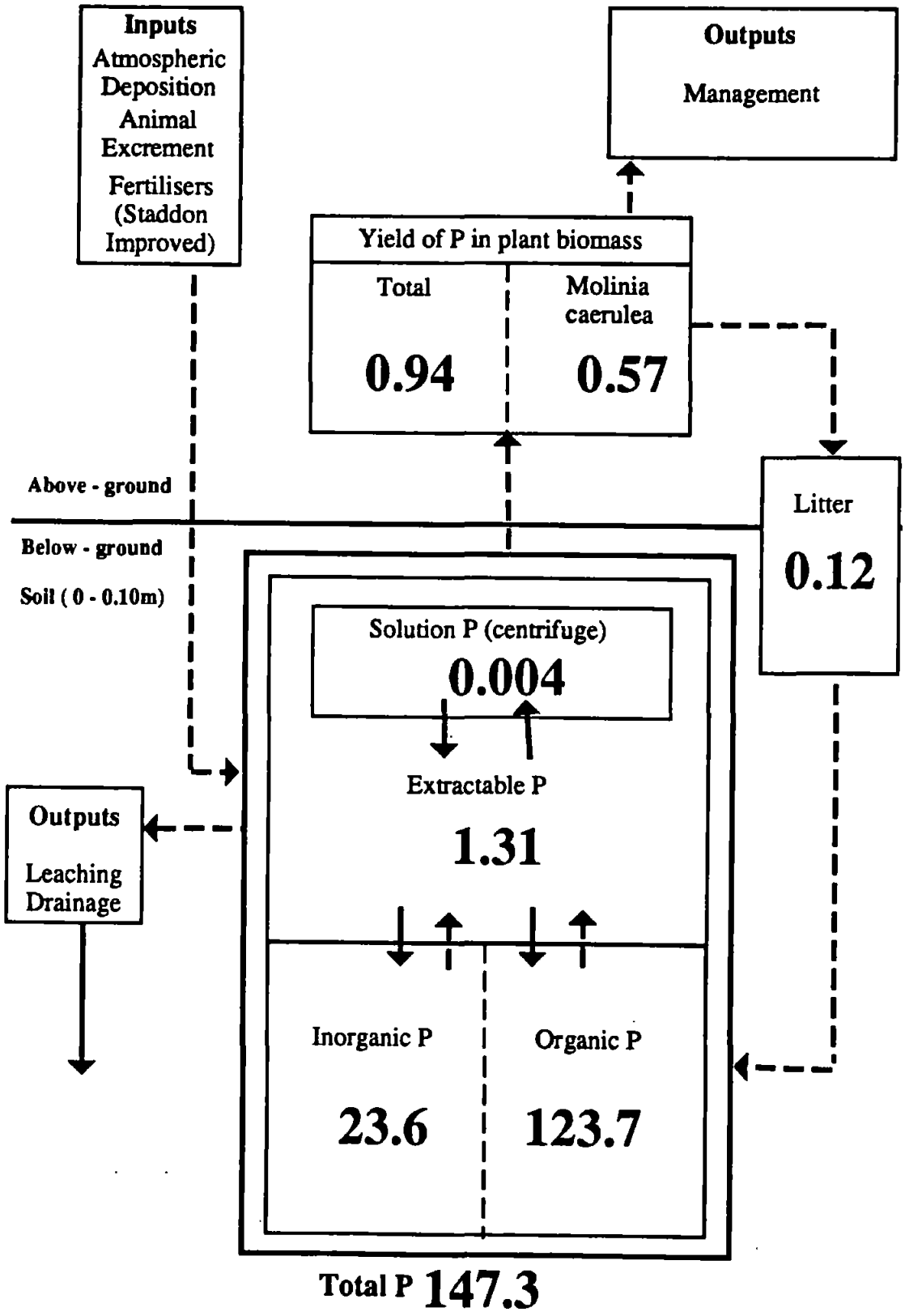


Figure 7.4

The relative quantities of P in the Culm grassland system at mid-September(all units in kg ha^{-1})



7.3.4 Comparisons of P cycling in other systems

To put the possible impact of management on the Culm grassland in context, comparisons with the cycling of P within other vegetation systems were made. A number of studies of phosphorus cycling has taken place within other plant communities. For example, the rate of accumulation and the breakdown of organic matter was important in forest, cereal, heathland and grassland systems (Harrison, 1985). In forest systems there is a very slow rate of P cycling as the breakdown of organic matter is inhibited by the presence of lignin and tannin. Cereal systems rely on the continual inputs of fertiliser to replace nutrients removed by heavy cropping and have a limited organic matter content as little material is returned to the soil. Much work has been carried out on heathland in Britain (Chapman, Rose and Clark, 1989), which is dominated by *C. vulgaris*. Comparisons are tenuous due to different plant survival strategies (Grime, 1989) and methods to reduce nutrient loss (Berendse *et al.*, 1987).

For comparisons with data produced in this study, a plant community dominated by grasses would be most appropriate. Grassland such as *Agrostis-Festuca* discussed by Perkins *et al.* (1978) has a much lower biomass production due to the upland environmental conditions. The most comparable community is one that is dominated by *M. caerulea* such as a *Molinietum* studied by Loach in Bramshill Forest, Crowthorne, Berkshire (1966, 1968 a, b). In one experiment Loach (1968a) found that the total P of the upper soil layer of a *Molinietum* dominated by *M. caerulea* to be 471 mg kg^{-1}, which is similar to values found on the SG plot. The range in P content in the plant material was very similar on the *Molinietum* from 1.8 to 3.4 kg P ha^{-1} and a similar excess of 0.7 kg P ha^{-1} within the plant litter was found (Loach, 1968). A more recent study by Oorschott (1994), at a Culm grassland site along the river Torridge in North-west Devon, found that the production of 3280 kg ha^{-1} in a *Cirsio-Molinietum* community was in the same order of magnitude as SG.

In the wet heathlands in the Netherlands the production of *M. caerulea* was much higher than Culm grassland as a result of increased nutrient availability from atmospheric sources (Berendse *et al.*, 1989). *M. caerulea* was found to be self-perpetuating as 70-90% of its nutrient supply originated from the decomposition of its litter and humus. Miles (1987) found that *M. caerulea* had a positive relationship with nutrient availability, and a positive feedback between plant and nutrient flux appeared to be in operation. The response of *M. caerulea* to P additions during the controlled turf experiment was similar to results of fertilisation experiments reported in the Netherlands (Berendse *et al.*, 1989) and by Oorschott and Kerkhof (in prep). Productivity was found to increase and was associated with a decrease in efficiency of nutrient retention. Comparisons with the above experiments are useful in giving an indication of the likely effects of nutrient enrichment on Culm grassland sites.

The previous section has suggested points and periods within the Culm grassland P cycle which may be targeted by management. The type of management employed and its timing and magnitude will depend on many factors such as the current species-composition of the plant community and resources. These factors will be discussed in the following section together with practical suggestions of how manipulate soil conditions of Culm grassland.

7.4 Development of management strategies to manipulate Culm grassland soil conditions

7.4.1 Introduction

Results of the study reinforced the concept that the manipulation of vegetation and soil conditions by management is vital for the continued existence of Culm grassland which make it a habitat of national importance. The implementation of management to a Culm grassland community will be influenced by a host of factors which are often site specific. However, there are broad strategies which are applicable to a range of sites relative to the prominent controlling environmental factors.

A site manager may be advised to undertake a survey of each site as undertaken by this study to collect information on past and current management, the present NVC communities and underlying soil nutrient and water conditions. Although it is common to conduct botanical surveys, a detailed survey of soil conditions is largely neglected, often as a result of time constraints. This study has indicated that cycling of nutrients has a large influence on botanical composition. Once the information has been collected management decisions will be influenced by capital costs of labour, equipment, and possible loss in income due a lower agriculture output.

The site manager must use these constraints in forming management objectives for nutrient manipulation which may be further influenced by individual views on the desired community and timescales over which this may be achieved. Management will be implemented to either maintain, improve or recreate Culm grassland communities and their associated soil conditions. The objectives will include not only species-richness but also the encouragement of certain species which have an important conservation value.

7.4.2 Maintenance of Culm grassland communities

The aim of management in this category is to prevent a degradation of the community by continuing the present strategy and avoiding damaging practices. Thus this will include the maintenance of nutrient levels and cycling of nutrients by preventing nutrient inputs or an accumulation. A permanent alteration and reduction of conservation value may be masked by natural fluctuations in floristic composition. Information of natural fluctuations may be gleaned from past records or most likely from the site manager or farmer. The response of the community to previous changes in management will have important implications. Culm sites of high conservation value remaining today may be roughly divided in to either valley or plateau often relating to differences in water conditions.

a) Plateau Sites

The plateau sites of Culm grassland are most vulnerable to change as they tend to be relatively drier and are waterlogged at infrequent intervals. Thus, the Culm plateau sites are restricted particularly to larger areas such as moors like Rackenford and Knowstone Moors which are managed by the Devon Wildlife Trust (DWT). The SG site may be threatened by factors such as agricultural runoff from surrounding improved grassland, ease of accessibility for improvement and isolation from other areas of Culm grassland.

The NVC communities M16 and M24 as found on Staddon Grazing are most abundant on plateau sites and are described in detail by DWT (1989) and Porley (1991). These communities are maintained by preventing any one species such as *M. caerulea* or shrubs from becoming dominant. The study on Staddon Grazing site indicated a build up of soil organic matter in comparison to Fernhills Grazing. This may be due to inadequate removal of *M. caerulea* leaving a substantial amount of litter. A build up may also result from the cattle freely moving from the improved field to the Culm field. The soil conditions may be effected by this particularly following the application of fertiliser. Ideally the two fields should be grazed separately and this may cause an increase in grazing pressure. A compromise may be reached in only allowing cattle to move from SI after June.

An important component of these drier communities are shrubs which require another method of control as they are not usually eaten by cattle. Their dominance may cause localised changes in the soil conditions such as *C. vulgaris* may decrease pH around the plant (Chapman, 1985) and *Ulex gallii*, a leguminous species, may encourage an increase in nitrate availability which in turn allow competitive species to dominate. The litter of shrubs may be a problem as it does not breakdown as fast as *M. caerulea* leaves and may produce a thick layer of dead material.

The main methods of control are burning or topping in the Autumn. On Staddon Grazing topping produced a short, uniform sward. Thus, topping should be done in strips with adjacent strips being topped in alternate years and thus producing different canopy heights to provide a diversity of cover. If a higher grazing pressure had been employed topping would be implemented infrequently every two to three years. A reliance of topping on SG has allowed litter to build which could be prevented by either raking it off which requires labour or by burning. Burning would be ideal but it requires careful planning and correct conditions to ensure other species are not damaged (Wolton, 1992). Therefore, to maintain communities on relatively drier Culm sites grazing with cattle should alone be sufficient if well managed to control *M. caerulea*. Burning should only be used in a situation where there has been an accumulation of litter.

Management may also be directed towards conserving certain species which are under threat or reduced in their frequency. Characteristic species of plateau sites are those which provide the aesthetic value such as *C. dissectum* and *D. maculata* which flower early in the growing season and provide food for insects. But as this coincides with the grazing period the flower heads are often destroyed which reduces seed production. The very action that maintains the soil conditions suitable for these plants may be threatening their continued reproduction. To minimise these effects it is advisable to protect areas from grazing where the cover substantial. A similar strategy may be applied during the Autumn topping or burning which removes the flower heads of *S. pratensis*. This species provides the main food source for the butterfly Marsh fritillary which is declining in abundance.

b) Valley Sites

Culm grassland is also found in valley sites which have owe their continued existence to their inaccessibility and low agricultural value. Negative management impacts may include direct drainage of the site or surrounding area and nutrients inputs from agricultural run-off. Many valley sites act as buffer zones between agricultural land and a watercourse such as Kismeldon near Holsworthy, North Devon. These sites tend to remain waterlogged for most of the year which support a flora adapted to acidic peat soils and low nutrient availability (Rodwell, 1989). Deoxygenated conditions require plants to be adapted to the ammonium form of nitrogen and relatively high concentrations of manganese and aluminium (Hayati and Proctor, 1989).

Continued maintenance of these communities relies upon the management of water conditions to prevent any drying out and allow fluctuations in water table level as drying out may increase the rate of mineralization (Oomes, 1988). Management may include rotational clearing of ditches in small stretches and removal the spoil away from the area as it may be nutrient enriched. Total blockage of drainage ditches would allow waterlogged conditions to prevail but would make further management difficult. The long term effects on species composition is difficult to predict as information on the water preferences of species is limited.

The communities found in these wetter areas are often highly complex and usually form small areas specific to the water conditions. Similar conditions are found along streams and water courses on plateau sites but are restricted and under threat. The communities are related to a range of water conditions. For example periodically waterlogged on the flood plain (S28), permanently waterlogged at the edge of streams (S3, M27, S27), and also stagnant water in pools (M29) and slowly moving in springs and flushes (M6) which are interspersed within the M23 rush pasture (DWT/NCC, 1990 and Porley, 1991). In general the communities are characterised by the presence of rush, mosses and liverwort species. In this category of Culm grassland sites, a very flexible but deliberate approach is required as these sites are often mismanaged or neglected as conditions are difficult.

A major increase in the abundance of rushes on Culm grassland is a symptom of inappropriate management such as heavy poaching by cattle. The rush may be detrimental as it shades and smothers the low growing species such as sedge and herbs. As rushes do not die-off they cannot be burnt and are best controlled by cutting and grazing. Cut material should be remove to prevent a blockage in the cycling of nutrients as cuttings breakdown slowly under these anaerobic conditions. Raking or the use of a flail mower to chop the material into small pieces would be ideal. In more accessible sites and where conditions are firm enough to avoid poaching grazing may be recommended. The rush pastures such as the sub-community M23a often contain more productive grasses such as *Holcus lanatus* and *Agrostis* spp (Porley, 1991). These will provide palatable forage over much of the Summer. Grazing pressure may be increased by up to 50% in comparison to *M. caerulea* dominated fields (Wolton, 1992).

Management may also be directed towards specific species such as *Filipendula ulmaria* (Meadow sweet) which is the dominant component of the M27 *Filipendula ulmaria* - *Angelica sylvestris* tall herb fen. This community is supported by very wet, fairly base-rich and moderately fertile soils (DWT/NCC, 1990). Its dominance is in fact due to the absence of grazing (Porley, 1991) which allows it to grow tall by smothering the lower growing species. Nutrient enrichment may be indicated by the abundance of grasses such as *M. caerulea*, *Holcus lanatus* and *Dactylis glomerata* in the lower tier of vegetation. The M27 community is thus relatively species-poor but has a significant conservation value as it is limited to specific environmental conditions and relies upon the continued absence of grazing. However some management may be required periodically such as light grazing for one growing season in three and the reduction of vegetation height by cutting.

7.4.3 Improvement of Culm grassland communities

A decline in conservation value of Culm grassland communities has resulted from neglect and application of inappropriate management. Neglect has resulted from lack of funds or the desire to either agriculturally improve the land or to maintain Culm grassland, or even the lack of knowledge that Culm grassland requires management to prevent succession towards a woodland community. Inappropriate management has often led to decline in species-richness as one or a few species have become dominant.

a) Absence of management

Culm grassland has become particularly vulnerable to the absence of management as fields are often inaccessible and are not conducive to modern agricultural production. In the absence of management the Culm may be invaded by scrub species such as *Rubus fruticosus* (Bramble), *Crataegus monogyna* (Hawthorn), *Betula pendula* (Birch), *Ulex gallii* (Gorse), *Calluna vulgaris* (Heather) and *Pteridium aquilinum* (Bracken). *M. caerulea* may become very high and rank, and produce high quantities of litter. The scrub moves in from the margins of the fields with which it forms a continuum and will eventually dominate the area. This was found on Fernhills Moor. The M16 *Erica tetralix* - *Sphagnum compactum* wet heath is most vulnerable to scrub invasion. The scrub may be removed by cutting, spot treatment with herbicides, and then burning the offcuts and litter, but it is important to leave scrub in areas to provide a mosaic of habitats.

Although some workers such as Marrs (1990) have suggested that succession towards a climax community is associated with soil nutrient enrichment, it was not apparent on FG. The likelihood of this occurring must be taken account when scrub is removed on sites. Disturbance during removal may cause an influx of ruderal species and increase the rate of organic matter breakdown which was restricted by the build up of litter at the soil surface. A certain amount of disturbance is required to encourage desired species such as *Cirsium dissectum* , which was found to increase in cover on Fernhills Grazing three years after scrub removal. Introduction of management after scrub removal is ideal to prevent scrub

returning and to break up of debris. Although no difference in the effects of cutting and grazing on soil P availability was found on FG, a grazing regime appeared to control the influx of unwanted species. Grazing will prevent *M. caerulea* and the rushes asserting dominance but may cause problems with the input of excrement. If the soils are nutrient enriched after scrub invasion it may be wise to utilise a cutting and removal regime to ensure that nutrients are not returned to the soil. In this situation burning of litter and scrub may not be advisable as much of the nutrients are returned to the soil via ash (Chapman, 1989).

b) Inappropriate management

Inappropriate management has resulted in either a reduction in conservation value or even the total loss of Culm grassland. As discussed in Section 7.4.2 *M. caerulea* and rushes are likely to become dominant may lead to an altering of nutrient cycling within the Culm grassland system. To ensure an impact on the soil nutrient system, management strategies must often be quite severe and drastic. Culm grassland is fairly robust and will recover from positive management strategies.

The lack of grazing of *M. caerulea* may allow it to form tussocks and accumulate large amounts of litter. The M25 *M. caerulea - Potentilla erecta* mire is a community characterised by *M. caerulea* tussocks. This species attains dominance in wet but well aerated soils with preference to fluctuating water table conditions (Loach, 1968). The dominance of *M. caerulea* may be an indication of nutrient enrichment as it can respond positively to an increase in soil nutrient availability (Chapter Six, Berendse *et al* 1989). Once these nutrient inputs have been identified, prevented or reduced, management must aim to reduce these effects on the plant community. Firstly the litter should be removed and burnt away from the site but this is not usually practical. The introduction of a higher stocking levels during following growing season will break up the tussocks and provide disturbance enabling other species to return. High levels of defoliation could also induce greater uptake and removal of nutrients as suggested by the experimental results in Chapter Five.

Rushes are the dominant component of the M23 community. If nutrient enrichment has occurred particularly from agricultural run-off near water courses conditions may be too wet to allow more productive grasses to attain a greater cover. These communities tend to be relatively low in species and are characteristic of land that was improved in the past. Dominance of *J. acutiflorus* (M23a) is a threat to the nationally scarce plants *Hypericium undulatum* (Wavy St John's wort) and *Carum verticillatum* (Whorled caraway). Management should involve opening up the canopy by cutting the rushes and removing the material and introduction of a grazing strategy to encourage *M. caerulea* and the sprawling herbs such as *Galium palustre* and *Lotus uliginosus*.

7.4.4 Recreation of Culm grassland

Recreation of Culm grassland requires a more drastic input of management to alter soil conditions, as the extent of improvement away from the original Culm grassland increases. Potential sites may range from reverted grassland, improved grassland, short-term grassland leys, and arable cropping. The success of any strategies applied will depend on the size of the field and whether it is surrounded by Culm grassland which would aid species recruitment. Being surrounded by other improved fields would decrease the likelihood of success due to threats of agricultural run-off and species isolation. Success would be enhanced by the field having been Culm grassland in the past. The length of time since agricultural improvement had occurred might be obtained from an examination of the seed bank. Sites most conducive to reconstruction will be those that were improved recently and surrounded or adjacent to Culm grassland.

As the severity of improvement away from Culm grassland increases, phosphorus stored within the soil complex is likely to increase. Results in Chapter Six showed that added phosphorus is adsorbed efficiently on to the soil matrix and release is very limited over a short period of time. Release may pose future problems if plant demands remain high after the cessation of fertiliser applications. The rates of release of total P from the soil complex are difficult to predict but even when cropping is maintained reduction in phosphorus levels

is very low (Poulton, 1966). Therefore reductions induced by management are likely to be very long term as the level of nutrient storage increases.

The most successful re-creation will take place on land of low agricultural potential which is already reverting. In Chapter Three the improved grassland field was found have reverted to a steady state. Water conditions may be most suitable for Culm species and low fertiliser applications were not sufficient to maintain grasses with high nutrient requirements. Thus alterations in management strategies will be minimal to include the cessation of fertiliser application during the spring in order to reduce the vigour of the competitive grasses. Staddon Grazing (Culm grassland) would further benefit as nutrient inputs via the grazing cattle from the improved field will be reduced. A grazing management strategy should be continued to provide disturbance to aid recolonisation of Culm species.

Before management is implemented on improved sites, it would be wise to carry out soil tests to ascertain the P status of the soils. These will tend to be higher on land that has been subjected to high applications of fertiliser which will be evident from total soil P values in the topsoil. Strategies should aim to strip soil P together and also restore water conditions. This could include blocking of drains and ditches and even the artificial damming of water as attempted by Oomes (1989) which was found to alter nutrient limitation. Altering the nutrient stores may be attempted by adding fertilisers and removing topsoil as discussed in Chapter One. However, these methods are expensive and have detrimental effects on the seed bank and species recolonisation. On the Culm Measures the most practical method would involve increasing plant nutrient uptake which was shown to be possible by defoliation in Chapter Five. Stripping of soil P by silaging or hay ensures that return of nutrients is limited and also allows an agricultural return on the land to be obtained. Grazing could follow cropping on grassland sites to provide disturbance. But the timescale over which alteration will appear will increase with the level of improvement. The recreation of Culm grassland from arable will be very long term involving reseeding of wild flower mixtures and insertion of pot plants.

CHAPTER EIGHT

CONCLUSIONS AND FURTHER WORK

The object of this research was to obtain a greater understanding of the Culm Grassland ecosystem, paying special attention to the relationship between soil conditions and plants. To accomplish these objectives a number of aims were formulated and listed in Section 1.4. This chapter will discuss these aims and the extent that these aims have been achieved during the research period. In view of these discussions suggestions of further work to supplement these aims are made. In conclusion the wider implication of the research results are discussed.

The following two aims were investigated during the first field season of 1992 :-

1) To characterize soil conditions under species-rich semi-natural, and species-poor grassland on the Culm Measures of North Devon.
2) To establish the impact of past and present management on soil nutrient status and physical conditions.

The first aim involved the comparison of Staddon Grazing and Staddon Improved plots and the second compared Staddon Grazing with the Fernhills Moor plots. Soil conditions were monitored by measuring soil nutrient availability and soil water conditions, throughout the growing season from mid-April to mid-October at two monthly intervals. The plant communities were also monitored at the end of May and end of August to ascertain species composition. There were marked differences between the Improved and Culm grassland plots, particularly in terms of soil pH and phosphorus content. The plant communities on Culm grassland were species-rich in comparison to the improved grassland, and Staddon Grazing was found to be in transition from an M16b to a M24c plant community. Past reversion of the community on Staddon Improved was indicated by the influx of non-sown species and the dominance of *Holcus lanatus* and the proliferation of rushes within the field. Past management on Staddon Grazing has kept *M. caerulea* and shrub species in

check in comparison to Fernhills Moor.

Although the information collected was restricted to one field season and one example of each management type, detailed study and optimal replication provided reliable background data on the character of Culm grassland. This enabled a detailed study of certain aspects to be carried out in the second field season and will also be useful for following researchers. Results collected in the first field season found that the availability of phosphorus was low in Culm grassland. This was proposed as being a limiting factor by other workers and was reinforced by the known dynamics of P within the soil. In mid-April the Improved plot was significantly higher than the Culm grassland plot in relation to phosphate - phosphorus.

Although, similar differences in mineral nitrogen was not found, other workers such as Oorschott (1994) suggest that plant production on organic soils such as on Staddon Grazing could be limited by both nitrogen and phosphorus limitation. Further study of this combined limitation would benefit the understanding of nutrient dynamics of Culm grassland. The type of limitation may also vary according to water conditions which did not vary a great deal between the sites studied. Investigation of valley sites may discover that this limitation changes as higher or more variable water contents alter nutrient availability, as found by other workers such as Vermeer (1986) and Verhoeven, Maltby, and Schmitz (1990).

An indepth study of the phosphorus limitation was carried out in the second field season in 1993 to satisfy the third, fourth and fifth aims of the project. This included the following aim:-

3) To relate seasonal fluxes phosphorus availability to plant uptake.

The extractable soil phosphorus values of the improved and Culm grassland were only significantly different at the mid-April and mid-June sampling dates. This prompted a modification of the experimental design in the second field season, to concentrate sampling at the beginning of the growing season. Seasonal fluxes of soil extractable phosphorus were monitored by three different methods. Extraction of P using the sodium bicarbonate method was most suitable in showing the gross differences between phosphorus concentrations on each plot. The direct removal of soil solution by centrifuging and suction cups gave variable results, particularly in centrifuged solutions which contained higher concentrations of P on Culm grassland. These methods of soil solution removal were found to be largely successful and further investigations are recommended. The use of centrifuging and suction cups in tandem provided interesting comparisons and provided a back up for equipment failure. The influence of these methods on nutrient concentration should be studied in detail. Further evaluation of these techniques on Culm grassland should investigate the influence of water content on the concentration of P contained within the soil solution.

To relate soil information to plant uptake, plant material was removed from the Improved and Staddon Grazing plots. *M. Caerulea* was found to dominate the plant community and reached a peak phosphorus off take in mid-July and produced a large amount of litter at the end of the growing season. Defoliation was found to extend the growing season and encourage the uptake of P from the soil. Litter breakdown during the growing season and the amount remaining after the senescence of *M. caerulea* has important consequences on the accumulation of organic matter and the continued dominance of *M. caerulea.*

However, strong evidence of P limitation was not apparent. Contrasts were found between the P content of improved grasses and *M. caerulea*, but no significant correlations were found between P contained in the plant material and the soil P content of Culm grassland. This was probably due to complex soil P dynamics which were investigated in a relatively

simple manner in this study. Further study of these dynamics would include the different forms of P, particularly organic and the effect of the soil microbial biomass on P release. Culm grassland species were found to be able to extract P at low concentrations, as indicated by the suction cup values which were often less than 0.002 mg P l^{-1}. *M. caerulea* is able to adapt to these conditions giving it an advantage in comparison to other Culm grassland species.

As P uptake was influenced by many factors not measured in this investigation a study of the association of vesicular arbuscular mycorrhizal infection with plant roots may further explain the dominance of *M. caerulea*. Also the use of a phytometer may accurately examine uptake directly from the soil because uptake of P by *M. caerulea* may be supplemented by a below-ground storage organ. Knowledge of initial nutrient content and accumulation over a known period of time provides a closer association between soil and plant P content. Isotopic labelling of soil with an isotope of P would supplement this information as the forms will not be altered during accumulation within the plant material.

A controlled turf experiment was conducted towards the end of the growing season in 1993 in order to satisfy the following aim:-

4) To pinpoint the thresholds of phosphorus levels in which species-rich *Molinietalia* will exist.

Culm grassland turfs were removed and set up in a glass house under controlled conditions. Increasing concentrations of phosphorus were added to the turfs to produce a disturbance and was monitored by methods employed in the second field season. At the highest level of application of 54.5 kg P ha^{-1} a significant increase in sodium bicarbonate extractable P and P content of plant material was found. Lower concentrations of added P were fixed in the soil which as suggested by insignificant changes in soil solution P values. A threshold between the values of 5.45 and 54.5 kg P ha^{-1} was found which may cause a shift in species dominance. Work may go further to pinpoint this threshold in P levels by removing turfs in

the spring particularly before the onset of senescence which had a great influence on the results. The addition of concentrations of P within these margins found by the turf experiment may identify more clearly shifts in soil P availability. Additionally a study of the impact of different nutrient combinations such as N, P and K may indicate changes or shifts in nutrient limitation.

Although there was little effect on plant dry matter yield at the end of the experiment *M. caerulea* may be able to increase in abundance through displaying a competitive advantage over other semi-natural species. The dominance of *M. caerulea* may be aided by release of fixed P from the adsorption complex over time. Thus further investigation of P adsorption and release dynamics in response to plant demand is vital. Nutrient additions may also effect the breakdown of organic matter which appears to have a key role in storage and release of P in Culm grassland. The rate of breakdown of litter and its incorporation in to the soil will further influence the quantity and also quality of the organic matter component. Further study could involve comparisons of litter breakdown in the presence or absence of management.

Information collected during the study was used to satisfy the final aim of the project :-

5) To formulate a simple model of the soil:vegetation system under species-rich grassland on the Culm to be employed as a management tool.

A simple model of the Culm grassland P cycle was compiled for the Staddon Grazing site. Relative sizes of storage compartments were highlighted, particulary the 100 fold decrease of P concentration from total to extractable P. Plant P uptake was found to be 10 times higher than the concentration of P in soil solution indicating that plants remove very low concentrations and that chemical equilibria are delicate and sensitive. The vegetation system influenced the soil conditions via plant litter breakdown and incorporation into organic matter. Areas of the cycle to be targeted by management were suggested and the removal of plant material was highlighted as having the greatest effect on cycling of P. The formulation

of a simple P cycle has come some way in describing the Culm grassland system particularly soil P availability.

The formation of organic matter and its mineralisation seems to be the most important factor effecting the availability of P in Culm grassland. Investigation in to the effect of different management strategies on organic matter is vital. This is most relevant in making recommendations to maintain the conservation value, as different nutrient limitations may be found in valley and plateau sites. Further work should thus include investigation of organic matter on a greater range of sites but in less detail. This should include sites which have been abandoned or inappropriately managed as nutrient enrichment and a build up of organic matter may have occurred which may require unique management strategies.

Comparisons of Culm grassland with an improved site has shown the different behaviour of P storage in soils with a lower organic matter content. The mechanisms of release may be different as a result and may rely on mainly release from the inorganic fraction. A study of a range of improved sites with different P status may provide more information and methods for restoration of Culm grassland conditions may be more specific. In fact restoration may have to take in to account the change in nutrient limitation from one that is dominated by phosphorus to one that involves many factors such as nitrogen, pH and water conditions.

Wider Implications of the Research

The characterisation of Culm grassland soil conditions and vegetation suggested that phosphorus was a limiting factor (see Chapter Three). The soil extractable P values were significantly lower on Culm Grassland (3.8 mg kg^{-1}) than improved grassland (27.2 mg kg^{-1}) particularly at the start of the growing season. Further study of soil P conditions found that P in soil solutions were also significantly lower on Culm grassland (< 0.002 mg l^{-1}) than improved grassland (0.016 mg l^{-1}). This indicated that release and plant uptake of P was much lower under an unimproved plant community. However, P is not necessarily the only limiting factor under Culm grassland. For example the additions of P to Culm grassland turfs did not significantly increase dry matter production even in response to a total application of 54.5 kg P ha^{-1}. In contrast a significant increase of phosphorus within the plant material from 1.1 to 3.0 mg g^{-1} suggested that other factors were involved in limiting nutrient uptake and assimilation. These limiting factors could include poor nitrogen supply which may have prevented the formation of plant structures in the above experiment. Also pH and the deficiency of minor nutrient elements may act as limiting factors. These limitations have been found in other communities such as chalk grassland, peat and heath systems (see Chapter One).

Results of the phosphorus addition experiment have important implications on the impact of agriculture improvement on the Culm grassland plant community. A significant increase was observed in soil extractable P from 5.6 to 40.4 mg kg^{-1} in response to a total application of 54.5 kg P ha^{-1}. This indicates that the soil has the ability to store P which may be utilised by plants in the future, particularly if a combined application of nitrogen and phosphorus fertilisers is made. This will enable some species to grow at faster rates and out-compete species which are adapted to stress toleration, as discussed in Chapter One.

Although P is not necessarily the only limiting factor of Culm grassland, the study of P cycling alone has identified key aspects of the Culm grassland system which are most influential in controlling species composition. For example, the transfer of P within the

system involving total plant P yield, litter and soil extractable P was very small in comparison to the soil total P content. In mid-April the proportion of P transferred, of the soil total P content was only 2% and in mid-September it was 1.6%. The amounts of P involved in inputs, outputs and storage are likely to be in the same order of magnitude on other Culm grassland sites, despite the variation in soil conditions and plant communities from site to site as discussed in Chapter One. The relative size of P transfers will be very similar to Staddon Grazing and thus will enable managment recommendations made in Chapter Seven, to be applied to range of Culm grassland sites in more scientific manner.

Management needs to be directed towards manipulating the transfer of P within the Culm grassland system. Other research work as discussed in Chapter One has found that it takes many years to directly reduce soil P values, so management should be directed towards the manipulation of plant material. Successive defoliation on Staddon Grazing induced a greater uptake of P early in the growing season, from March until early June. Uninterrupted growth of the plant community showed that *M. caerulea* was the dominant component, and should be removed in sufficient amount to reduce its vigour. The type of management most applicable to Culm grassland is cattle grazing due to the limitations of site accessibility and drainage conditions. Grazing not only removes plant material but also encourages litter breakdown by trampling, in a manner which leads to variation within the plant community. Thus grazing should start as early as possible in the year from April onwards to remove and encourage regrowth of new plant shoots. It should continue throughout the summer particularly throughout June, the period *M. caerulea* was found to reach a peak yield of P (1.46 kg P ha^{-1}). Also grazing should be of an intensity that removes enough material to ensure that an excess does not add to the litter store at the end of the growing season. If these principles are applied to most Culm grassland sites *M. caerulea* will not become dominant and the community is likely to be species-rich.

The principles of management discussed above may be applied to vegetation communities other than Culm grassland. Of most relevence are the Rhos pastures in South-West Wales, South-West Scotland and North-West Brittany and also comparable communities in the far western edges of Europe as discussed in Chapter One. These communties are most likely to be influenced by low nutrient availability as identified under Culm grassland. The research as a whole suggests that the return of nutrients via litter breakdown and organic matter formation, and its subsequent mineralisation is the key control of nutrient cycling in these types of communities. This is indicated by the high proportion of organic phosphorus (84%) in the total soil phosphorus content on Staddon Grazing. In fact these communities may rely on litter accumulation which impedes nutrient turnover and thus maintains low nutrient availability. However, this may cause problems as certain low growing species are shaded out. Also a build up of organic matter may act as a 'nutrient time bomb' causing problems in the future if the organic matter mineralisation rate increases. It is therefore of vital importance in communties which rely on low nutrient availability to maintain a slow turnover and cycling of nutrients by traditional, less intensive grazing management.

The implementation of these management recommendations will depend on agricultural economics, European policies and the availability of grants. The targeting of money towards taking land out of production in set-aside of arable crops highlights this problem. Money should instead be directed towards farmers to manage the countryside in a environmentally responsible manner. The targeting of funds to carry out management should be based upon the scientific manipulation of soils and plant communities rather than politics.

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Appendix One

Sampling dates of field seasons 1992 and 1993

Dates of soil sampling in 1992

Sample number	Date
1	20-Apr
2	17-Jun
3	12-Aug
4	14-Oct

Dates of soil sampling in 1993

Sample number	Date	Sample Type		
		Sodium bicarbonate Extraction	Centrifuging	Suction cup
1	23-Mar	*	*	*
2	4-Apr		*	*
3	19-Apr	*	*	*
4	3-May		*	*
5	17-May	*	*	*
6	14-Jun	*	*	*
7	19-Jul	*	*	*
8	13-Sep	*	*	*

Dates of vegetation sampling in 1993

Ground level		Defoliation	
Sample number	Date	Week	Date
1	6-Apr	0	6-Mar
2	4-May	4	7-Apr
3	1-Jun	8	2-May
4	5-Jul	12	1-Jun
5	6-Sep	16	27-Jun
		20	29-Jul
		24	8-Sep

Dates of controlled turf experiment (1993)

Treatments	Date
Cores removed	10-Aug
Application 1	1-Sep
Application 2	8-Oct

Appendix Two Meteorological means at IGER, North Wyke, Devon (Alt. 180m) for 1992, 1993 compared to 30 year standard period 1961-90

	Mean Temperature (Centigrade)			Total Rainfall (mm)		
MONTH	Standard Period 1961-90	1992	1993	Standard Period 1961-90	1992	1993
JAN	4.5	3.5	7.1	129.1	38.4	149.2
FEB	4.3	5.7	5.1	97.2	42.9	20.4
MAR	5.7	7.3	6.6	88.8	64.0	27.5
APR	7.7	8.1	9.1	62.1	73.1	87.5
MAY	10.5	12.9	10.6	61.1	57.3	142.8
JUN	13.5	14.9	14.5	59.8	23.4	83.9
JUL	15.3	16.1	14.7	52.9	74.1	118.0
AUG	15.2	14.9	14.3	67.8	126.7	18.6
SEPT	13.3	13.1	12.1	75.6	47.6	148.1
OCT	10.8	7.9	8.0	100.8	97.4	111.7
NOV	7.2	8.7	5.9	113.6	193.9	58.6
DEC	5.6	4.7	6.3	125.9	102.5	243.4
YEAR	9.5	9.8	9.5	1034.7	941.3	1209.7

Appendix Three

Classification of soil analysis results for samples analysed by standard procedures (MAFF, 1994).

Index	Phosphorus (mg l-1)	Potassium (mg l-1)	Magnesium (mg l-1)
0	0-9	0-60	0-25
1	10 15	61-120	26-50
2	16-25	121-240	51-100
3	26-45	241-400	101-175
4	46-70	401-600	176-250
5	71-100	601-900	251-350
6	101-140	901-1500	351-600
7	141-200	1501-2400	601-1000
8	201-280	2401-3600	1001-1500
9	over 280	over 3600	over 1500

Appendix Four. Comparison of the floristic composition SI with NVC MG6 (May,1992)

Floristic table MG6	a	b	c	6	STADDON IMPROVED
Lolium perenne	V (1-8)	V (2-7)	V (4-7)	V (1-8)	III (1)
Cynosurus ctristatus	V (2-8)	V (2-7)	IV (2-8)	V (2-8)	V (5)
Trifolium repens	V (2-9)	V (1-8)	V (2-4)	V (1-9)	V(5)
Holcus lanatus	IV (1-8)	V (2-6)	II (2-5)	IV (1-8)	V (7)
Cerastium fontanum	II (1-5)	V (1-5)	IV (1-3)	IV (1-5)	I (1)
Festuca rubra	II (1-9)	IV (2-8)	IV (4-6)	IV (1-9)	
Agrostis stolonifera	II(1-7)	I (2-9)	I (6)	I (1-9)	I (4)
Alopecurus pratensis	II(1-7)	I (3)	I (2-4)	I (1-7)	
Ranunculus repens	II(1-7)	I (1-4)		I (1-7)	
Cirsium vulgare	II (1-3)	I (1)		I (1-3)	
Agrostis geniculatus	I (1-6)	I (1)		I (1-6)	
Deschampsia cespitosa	I (1-5)			I (1-5)	
Iris pseudacorus	I (1-6)			I (1-6)	
Anthoxanthum odoratum	I (1-5)	V (1-7)		II (1-7)	V (5)
Ranunculus acris	III (1-4)	IV (1-5)	I (1-2)	III (1-5)	I (2)
Rumex acetosa	II (1-4)	III (1-4)	I (2-3)	II (1-4)	
Hypochoeris radicata	I (2-5)	II (2-4)	I (2)	I (2-5)	
Luzula campestris	I (1-3)	II (1-5)		I (1-5)	
Rhytidiadelphus squarrosus	I (3-4)	II (1-6)		I (1-6)	
Trisetun flavescens	I (1-6)	I (2-4)	V (2-4)	II (1-6)	
Phleum pratense bertolonii	I (1-5)	I (1-4)	V (2-5)	I (1-5)	
Pimpinella saxifraga		I (1-5)	II (2-5)	I (1-5)	
Agrostis capillaris	III (1-8)	V (2-8)	IV (4-8)	III (1-8)	
Plantago lanceolata	II (1-6)	III (1-5)	IV (3-4)	II (1-6)	
Dactylis glomerata	III (1-8)	III (1-4)	IV (2-7)	III (1-8)	
Poa pratensis	II (1-5)	III (1-5)	III (1-5)	III (1-5)	
Cirsium arvense	II (1-5)	II (1-5)	III (3-4)	III (1-5)	
Taraxacum officinale agg.	III (1-3)	II (1-3)	II (1-3)	II (1-3)	
Bellis perennis	II (1-6)	II (1-4)	II (2-4)	II (1-6)	II (4)
Achillea millefolium	II (1-5)	II (2-5)	II (4)	II (1-5)	
Brachythecium rutabulum	II (1-7)	II (1-5)	III (2-4)	II (1-7)	
Poa trivialis	II (1-7)	II (2-5)	II (2-5)	II (1-7)	I (1)
Leontodon autumnalis	I (1-4)	II (1-4)	II (1-3)	II (1-4)	
Trifolium pratense	II (1-5)	II (1-7)	I (2-4)	II (1-7)	
Bromus hordeaceus hordeaceus	I (1-6)	II (1-6)	I (2)	I (1-6)	
Festuca pratensis	I (1-3)	I (1-4)	I (4)	I (1-4)	
Lathyrus pratensis	I (2-5)	I (1-3)	I (2)	I (1-5)	
Trifolium dubium	I (2-8)	I (2-7)	I (2)	I (2-8)	I (4)
Veronica chamaedrys	I (1-2)	I (1-2)	I (1)	I (1-2)	
Pleum pratense pratense	I (1-4)	I (2-4)	I (4)	I (1-4)	
Medicago lupulina	I (1-5)	I (2-3)	I (3)	I (1-5)	
Potentilla reptans	I (2-5)	I (3-7)	I (3)	I (2-7)	
Festuca ovina	I (2)	I (3)	I (7)	I (2-7)	I (6)
Poa annua	I (1-5)	I (2-4)	I (2)	I (1-5)	
Prunella vulgaris	I (1-4)	I (2-5)	I (3)	I (1-5)	
Eurhynchium praelongum	I (1-7)	I (1-3)	I (1-4)	I (1-7)	
Cardamine pratensis	I (1-2)	I (1-2)		I (1-2)	
Arrhenatherum elatius	I (1-3)	I (1-2)		I (1-3)	
Centaurea nigra	I (1-4)	I (2-4)		I (1-4)	
Juncus effusus	I (4)	I (4)		I (4)	I (1)
Plantago major	I (1-4)	I (1)		I (1-4)	
Potentilla anserina	I (1-3)	I (1-3)		I 91-3)	
Rhinanthus minor	I (3-4)	I (3-5)		I (3-5)	
Rumex obtusifolius	I (1-2)	I (4)		I (1-4)	

a Typical sub-community
b Anthoxanthum odoratum sub-community
c Trisetum flavescens sub-community
6 Lolio-Cynosuretum cristati (total)

AppendixFive.Comparison of the floristic composition SI with NVC MG10 (May,1992)

Floristic table MG10	a	b	c	10	STADDON IMPROVED
Juncus effusus	V (2-8)	III (1-4)	IV (2-6)	V (1-8)	I (1)
Holcus lanatus	V (3-8)	IV (4-7)	IV (3-7)	V (3-8)	V (7)
Agrostis stolonifera	IV (3-9)	V (5-8)	IV (3-8)	IV (3-9)	I (4)
Ranunculus repens	III (3-7)	V (3-5)	IV (3-6)	IV (3-7)	
Phleum pratense pratense	I (2-5)			I (2-5)	
Angelica sylvestris	I (2-4)			I (2-4)	
Carex panicea	I (3-5)			I (3-5)	
Pulicaria dysenterica	I (2-5)			I (2-5)	
Prunella vulgaris	I (4)			I (4)	
Juncus articulatus	I (3)			I (3)	
Juncus inflexus		V (3-8)		II (3-8)	
Carex hirta	I (4)	III (3-4)		I (3-4)	
Iris pseudacorus			V (1-7)	II (1-7)	
Alopecurus pratensis			II (2-6)	I (2-6)	
Filipendula ulmaria	I (4)		II (2-4)	I (2-4)	
Phalaris arundinacea	I (5)		II (3-7)	I (3-7)	
Lotus uliginosus	I (5)	I (2)	II (3)	I (2-5)	
Glyceria fluitans	I (3)	I (3)	II (2-5)	I (2-5)	
Myosotis scorpioides	I (3)		II (2)	I (2-3)	
Urtica dioica		I (2)	II (2-3)	I (2-3)	
Lychnis flos-cuculi			I (3)	I (3)	
Poa trivialis	III (2-5)	IV (4-6)	IV (2-5)	III (2-6)	I (1)
Cardamine pratensis	II (1-4)	III (2-4)	II (1-3)	III (1-4)	
Ranunculus repens	III (2-5)	III (3-4)	II (2)	III (2-5)	
Trifolium repens	II (3-9)	III (2-3)	I (1)	II (1-9)	V (5)
Lolium perenne	II (2-4)	II (3-4)	II (3-4)	II (2-4)	III (1)
Rumex crispus	I (2-4)	III (3-4)	II (2-3)	II (2-4)	
Alopecurus geniculatus	I (1-4)	II (3-4)	II (1-3)	II (1-4)	
Rumex acetosa	II (2-4)	I (2)	II (3-4)	II (2-4)	
Festuca pratensis	I (2-3)	II (2-4)	II (4-5)	II (2-5)	
Rumex obtusifolius	I (3-4)	II (2-3)	I (2)	II (2-4)	
Plantago lanceolata	I (2-4)	I (6)	II (1-3)	II (1-6)	
Potentilla anserina	II (2-5)		II (1-3)	I I(1-5)	
Cerastium fontanum	II (3)	I (2)	I (3)	II (2-3)	I (1)
Cirsium arvense	I (1)	II (3-4)	I (2-4)	I (1-4)	
Festuca rubra	I (4-5)	II (3-5)		I (3-5)	
Rumex conglomeratus	I (2-3)	II (3-6)		I (2-6)	
Calliergon cuspidatum	I (5-6)	I (5)	I (3)	I (3-6)	
Equisetum arvense	I (1-2)	I (4)	I (1)	I (1-4)	
Dactylis glomerata	I (4-7)	I (5)	I (6)	I (4-7)	
Trifolium pratense	I (4)	I (4)	I (2)	I (2-4)	
Polygonum hydropiper	I (2)	I (4)	I (3)	I (2-4)	
Poa pratense	I (3-5)		I (1)	I (1-5)	
Anthoxanthum odoratum	I (3)		I (2)	I (2-3)	V (5)
Caltha palustris	I (2)		I (4)	I (2-4)	
Stella alsine	I (3)		I (3)	I (3)	
Oenanthe crocata	I (4)		I (3)	I (3-4)	
Eurhynchium praelongum	I (3)		I (3)	I (3)	
Cynosurus cristatus	I (1-6)	I (3-5)		I (1-6)	V (5)
Agrostis capillaris	I (5-9)	I (5-6)		I (5-9)	
Taraxacum officinale agg.	I (1-2)	I (4)		I (1-4)	I (4)
Plantago major	I (2)	I (1)		I (1-2)	
Cirsium palustre	I (3)	I (2)		I (2-3)	
Equisetum palustre	I (1)	I (4)		I (1-4)	
Mentha aquatica	I (2-3)	I (1)		I (1-3)	
Festulolium loliacaem	I (1)	I (3)		I (1-3)	
Vicia cracca		I (3)	I (3)	I (3)	
Senecio aquaticus		I (4)	I (3)	I (3-4)	

a Typical sub-community
b Juncus inflexus sub-community
c Iris pseudacorus sub-community
10 Holco-Juncetum effusi (total)

Appendix Six. Comparison of the floristic composition SG,FG,FC with NVC M24 (May,1992)

Floristic table M24	c	24	STADDON GRAZING	FERNHILLS GRAZING	FERNHILLS CUTTING
Molinia caerulea	V (4-8)	V (1-8)	V (6)	V (7)	V (7)
Potentilla erecta	V (2-4)	V (1-4)	IV (6)	I (2)	II (1)
Succisa pratensis	IV (2-5)	V (1-6)	II (4)	I (1)	I (1)
Cirsium dissectum	IV (1-6)	IV (1-6)	I (5)	II (4)	III (3)
Lotus uliginosus	IV (2-4)	IV (1-4)			
Carex panicea	III (1-4)	IV (1-5)	V (5)	I (1)	I (1)
Galium uliginosum		III (1-5)			
Valeriana dioca		III (1-3)			
Centaurea nigra	I (1-3)	III (1-4)			
Juncus subnodulosus		II (1-5)			
Equisetum palustre		II (1-3)			
Vicia cracca		II (1-4)			
Filipendula ulmaria		II (1-5)			
Linum catharticum		II (1-3)			
Gymnadenia conopsea		II (1-3)			
Eupatorium cannabium		II (1-3)			
Phragmites australis		II (1-8)			
Campylium stellatum	I (2)	I (1-2)			
Cladium mariscus		I (1-6)			
Lythrum salicaria		I (1-3)			
Dactylorhiza incarnata		I (1-3)			
Holcus lanatus	III (2-5)	III (1-5)	I (1)		
Anthoxanthum odoratum	III (3-6)	III (1-6)	II (4)		
Hydrocotyle vulgaris	II (1-2)	II (1-3)			
Carex pulicaris	II (1-3)	II (1-3)	I (1)		I (2)
Luzula multiflora	II (1-3)	II (1-3)	I (4)		
Ranunculus acris	III (2-4)	II (1-4)			
Pseudoscleropodium purum	II (2-6)	II (1-6)			
Festuca rubra	II (4-7)	II (1-7)	V (5)	II (5)	I (2)
Cardamine pratensis	II (1-2)	II (103)			
Briza media		II (1-4)			
Rumex acetosa	I (3)	II (1-3)			
Epipactis palustris		I (1-4)			
Potentilla reptans		I (1-3)			
Hypericum tetrapterum		I (1-3)			
Cirsium arvense		I (1-4)			
Carex nigra	I (1-4)	I (1-4)	I (1)		
Trifolium pratense	I (1)	I (1-3)			
Polygala vulgaris		I (1-4)	I (1)		
Leontodon taraxacoides		I (1-3)			
Juncus articulatus		I (1-4)			
Eriophorum angustifolium		I (1-2)			
Dactylorhiza fuchsii		I (1)			
Galium verum		I (1-3)			
Cerastium fontanum		I (1-3)		I (1)	
Potentilla anserina		I (1-3)			
Juncus acutiflorus	IV (2-7)	II (1-7			
Juncus conglomeratus	III (1-7)	II (1-7)		I (4)	
Erica tetralix	III (2-4)	II (1-4)	II (2)	II (4)	II (4)
Galium palustre	III (1-3)	II (1-3)			
Dactylorhiza maculata	III (2-3)	II (1-3)	II (1)	I (1)	I (1)
Calluna vulgaris	II (1-5)	I (1-5)	III (5)	I (5)	II (4)
Juncus effusus	II (3-5)	I (1-5)	I (4)	II (4)	II (4)
Serratula tinctoria	II (1-3)	I (1-3)		I (4)	
Narthecium ossifragum	II (2-4)	I (1-4)			
Aulacomnium palustre	II (3-4)	I (1-4)			
Ranunculus flammula	II (1-3)	I (1-3)			
Hypnum cupressiforme	II (3-4)	I (1-4)			
Achillea ptarmica	II (2-4)	I (1-4)			
Agrostis canina canina	II (3-6)	I (3-6)			
Scutellaria minor	II (1-2)	I (1-2)			
Viola palustris	II (3-4)	I (3-4)			
Sphagnum auriculatum	II (2-7)	I (2-7)			
Hypericum undulatum	II (2-3)	I (2-3)			
Salix repens	II (1-4)	I (1-4)	I (4)	II (1)	I (2)
Pediculrais sylvatica	II (1-3)	I (1-3)			
Senecio aquaticus	II (1-2)	I (1-2)			
Thuidium tamariscinum	II (3-5)	I (3-5)		I (4)	II (4)
Eurhynchium praelongum	II (1-4)	I (1-4)			

Appendix Six. Comparison of the floristic composition SG,FG,FC with NVC M24 (May,1992)
Floristic table M24

	c	24	STADDON GRAZING	FERNHILLS GRAZING	FERNHILLS CUTTING
Cirsium palustre	III (1-3)	III (1-5)			
Angelica sylvestris	III (1-5)	III (1-5)			
Calliergon cuspidatum	III (1-3)	III (1-3)			
Mentha aquatica	III (2-4)	III (1-4)			
Carex hostiana	II (1-6)	III (1-6)	I (4)	I (1)	I (5)
Agrostis stolonifera	II (1-4)	II (1-4)			
Brachythecium rutabulum	II (1-6)	II (1-6)	II (4)		
Prunella vulgaris	II (2-3)	II (1-3)			
Deschampsia cespitosa	I (2)	II (1-4)			
Schoenus nigricans	I (8)	II (1-8)			
Plantago lanceolata	II (1-4)	II (1-4)			
Lathyrus pratensis	II (1-2)	II (1-2)			
Pulicaria dysenterica	II (3-4)	II (1-4)			
Rubus fruticosus agg.	I (1-2)	I (1-3)			
Salix cinerea sapling	I (2)	I (1-3)			
Danthonia decumbens	I (1-5)	I (1-5)			
Anagallis tenella	I (1-3)	I (1-6)			
Sphagnum subnitens	I (4-7)	I (1-7)			
Lychnis flos-cuculi	I (3)	I (1-4)			
Drosera rotundifolia	I (3)	I (1-3)			
Alnus glutinosa sapling		I (1-2)			

c Juncus acutiflorus-Erica tetralix sub-community
24 Cirsio-Molinietum caerulea (total)

Appendix Seven. Comparison of floristic composition SG, FG, FC with NVC M16 (May,1992)

Floristic table	b	16	STADDON GRAZING	FERNHILLS GRAZING	FERNHILLS CUTTING
Erica tetralix	V (1-7)	V (1-9)	II (3)	II (4)	II (4)
Calluna vulgaris	V (3-7)	V (1-9)	III (5)	I (5)	II (4)
Molinia caerulea	V (2-8)	IV (2-9)	V (6)	V (7)	V (7)
Spagnum compactum	II (1-6)	IV (1-8)			
Potentilla erecta	V (1-4)	II (1-4)	IV (6)	I (2)	II (1)
Succisa pratensis	V (1-5)	I (1-5)	II (4)	I (1)	I (1)
Polygala serpyllifolia	III (1-4)	II (1-4)			
Carex panicea	III (2-5)	II (1-5)	V (5)	I (1)	I (1)
Sphagnum auriculatum	III (4-7)	I (1-7)			
Salix repens	III (1-5)	I (1-5)	I (4)	II (1)	I (2)
Danthonia decumbens	III (2-6)	I (2-6)			
Sphagnum papillosum	II (2-5)	I (1-5)			
Juncus acutiflorus	II (2-3)	I (1-4)			
Myrica gale	II (5-7)	I (3-7)			
Cirsium dissectum	II (3-5)	I (3-5)	I (5)	II (4)	II (3)
Ulex gallii	II (4-7)	I (3-7)	IV (5)	I (2)	I (5)
Serratula tinctoria	II (3-5)	I (3-5)		I (4)	
Ulex europaeus	II (2-4)	I (2-4)			
Agrostis curtisii	II (1-7)	I (1-7)			
Festuca rubra	II (3-4)	I (3-4)	V (5)	II (5)	I (2)
Juncus effusus	II (1-3)	I (1-3)	I (4)	II (4)	II (4)
Luzula multiflora	II (2-3)	I (2-3)	I (4)		
Kurzia pauciflora		I (1-4)			
Drosera intermedia		I (1-3)			
Rhynchospora alba		I (2-4)			
Drosera rotundifolia		I (1-4)			
Campylopus brevipilus		I (2-7)			
Lepidotis inundata		I (3)			
Eleocharis multicaulis		I (1-2)			
Cephalozia macrostachya		I (2-3)			
Pinguicula lusitanica		I (3)			
Hypnum jutlandicum	II (3-6)	II (1-9)			
Cladonia impexa		II (1-9)			
Juncus squarrosus		II (1-6)			
Dicranum scoparium	I (1)	II(1-5)			
Cladonia uncialis		II(1-5)			
Racomitrium lanuginosum		II (1-8)			
Diplophyllum albicans		I (1-4)			
Pohlia nutans	I (1-3)	I (1-6)			
Pleurozium schreberi	I (2)	I (1-6)			
Campylopus paradoxus		I (1-5)			
Cladonia arbuscula		I (1-9)			
Sphagnum capillifolium		I (1-8)			
Cladonia floerkeana		I (1-3)			
Cladonia squamosa		I (1-3)			
Mylia taylori		I (1-7)			
Pleurozia purpurea		I (1-6)			
Lophozia ventricosa		I (1-4)			
Kurzia trichoclados		I (1-4)			
Sphenolobus minutus		I (1-4)			
Huperzia selago		I (1-2)			
Sphagnum tenellum	II (3-5)	III (1-10)			
Scirpus cespitosus	I (3-4)	III (1-8)			
Narthecium ossifragum	I (3)	II (1-6)			
Eriophorum angustifolium		II (1-8)			
Odontoschisma sphagni		I (1-5)			
Pinus sylvestris seedling	I (3)	I (1-5)			
Cephalozia connivens	I (1)	I (1-3)			
Cephalozia bicuspidata	I (1-4)	I (1-4)			
Ulex minor	I (9)	I (1-9)			
Carex echinata	I (4)	I (1-6)			
Pedicularis sylvatica	I (2)	I (1-2)			
Dactylorhiza maculata	I (1)	I (1-3)	II (1)	I (1)	I (1)
Leucobryum glaucum	I (1)	I (1-7)	II (4)		
Sphagnum subnitens	I (3-8)	I (1-8)			
Nardus stricta	I (1-2)	I (1-4)	II (4)		
Gymnocolea inflata		I (1-7)			
Cladonia furcata		I (1-3)			
Sphagnum cuspidatum		I (1-6)			
Betula pubescens seedling	i (3-4)	I (1-4)		I (1)	I (5)
Cladonia verticillata		I (1-3)			
Sphagnum molle		I (1-5)			
Eriophorum vaginatum		I (1-7)			
Odontoschisma denudatum		I (1-3)			
Campylopus pyriformis		I (1)			
Aulacomnium palustre		I (1-6)			

b Succisa pratensis- Carex panicea sub- community
16 Ericetum tetralicis (total)

Appendix Eight.

Soil profile description of Culm grassland at Fernhills Moor (Harrod, 1995)

L	0 - 2 cm	Litter and root mat
A_{h1}	2 - 19 cm	Dark grey; clay loam with many fine dark red mottles along root lines; slightly stony; moist; strongly developed fine granular peds; very porous; > 5% very fine macropores and fissures; abundant fine woody roots; gradually smooth boundary to:
A_{h2}	19 - 24 cm	Greyish brown; clay loam to clay with common fine red mottles along root lines; slightly stony; moist; moderately fine subangular blocky structure; moderately porous; 5% very fine fissures and macropores; many fine woody and fibrous roots; clear, smooth boundary to:
B_g	24 - 40 cm	Light grey; clay with many fine and medium reddish yellow mottles in ped interiors and few very fine red mottles; slightly stony; moist; strongly developed medium prismatic structure; very slightly porous; very few fissures and macropores; common fine fibrous roots; many dead; mostly concentrated on ped faces.

Appendix Nine.

Soil profile description of improved grassland adjacent to Fernhills Moor (Harrod, 1995)

A_{h1} 0 - 12 cm Dark greyish brown; clay loam with many very fine reddish brown mottles; stoneless; moist; strongly developed fine subangular blocky structure; very porous; > 5% very fine macropores and fissures; abundant fine and very fine fibrous roots; merging boundary to:

A_p 12 - 29 cm Brown; clay loam with very many fine and very fine reddish brown mottles; slightly stony with small and medium sandstone fragments; moist; moderately developed fine subangular blocky structure; moderately porous; 5 % macropores and fissures; many very fine fibrous roots; common black manganiferous nodules; clear wavy boundary to:

B_g 29 - 48 cm Light grey; silty clay with many fine and medium reddish yellow mottles and common fine red mottles in ped interiors; slightly stony; moist strongly developed coarse prismatic structure; very slightly porous; few very fine fissures; few very fine fibrous roots, concentrated in fissures between peds; common black manganiferous nodules.

Appendix Ten.

The application of the floristic data of plant communities on SG, FG, FC and SI to TABLEFIT

SG

C37.312	M25b	59	73	62	94	45	Molinia-Pot erecta mire	Anthox odoratum
C37.312	M24c	54	46	79	77	63	Molinia-Cirs dissectum	Jun acf-Eri tet
C37.312	M24	53	45	74	78	62	Molinia-Cirs dissectum	
C31.11	M16b	53	63	63	61	58	Erica tetr-Spha comp	Suc pra-Car pan
C37.312	M25	49	77	49	82	38	Molinia-Pot erecta mire	

FG

C37.312	M25a	48	47	55	95	48	Molinia-Pot erecta mire	Erica tetralix
C37.312	M24c	45	28	92	67	70	Molinia-Cirs dissectum	Jun acf-Eri tet
C37.312	M25	41	44	53	81	41	Molinia-Pot erecta mire	
C31.11	M16b	38	39	72	47	64	Erica tetr-Spha comp	Suc pra-Car pan
C37.312	M25b	37	35	56	70	43	Molinia-Pot erecta mire	Anthox odoratum

FC

C37.312	M25a	51	53	60	96	47	Molinia-Pot erecta mire	Erica tetralix
C37.312	M25	43	51	59	80	37	Molinia-Pot erecta mire	
C37.312	M24c	42	32	99	66	55	Molinia-Cirs dissectum	Jun acf-Eri tet
C31.11	M16b	39	42	76	49	54	Erica tetr-Spha comp	Suc pra-Car pan
C37.312	M25b	35	38	58	70	36	Molinia-Pot erecta mire	Anthox odoratum

SI

C38.111	MG 6a	55	65	93	57	54	Lolium per-Cynos cris	Typical
C38.111	MG 6	49	60	91	51	53	Lolium per-Cynos cris	
C38.111	MG 6b	49	53	100	54	59	Lolium per-Cynos cris	Anthox odorat
C38.12	MG 8	46	42	98	58	64	Cynos cris-Caltha palu	
C35.12	U 4b	41	44	86	44	63	Fes ovi-Agr cap-Gal sax	Hol lan-Tri rep

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