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PRIMARY PRODUCTION, DECOMPOSITION AND NUTRIENT CYCLING IN A BRACKEN GRASSLAND ECOSYSTEM

by

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C O N T E N T S

PREFACE

Ling-zhi Chen, from the Institute of Botany, Academia Sinica, Peking, China, spent a year at Merlewood, under the sponsorship of the Chinese Government. The aim of her visit was to gain experience in research on productivity and nutrient cycling and in the statistical analysis and mathematical modelling. A research project on braken was designed to provide both practical and theoretical experience and the results of that one year study are presented here. However it should be emphasised that the main reason for selecting a site on Hampsfell near to Merlewood was one of convenience. The study has also been limited in replication simply because of the lack of time available and priority was given to providing experience in a wide range of techniques. Despite these limitations, and the lack of time to do further analysis, the study has provided results worthy of publication and Mrs. Chen is to be congratulated on the effort and enthusiasm which she has put into the work, and on the way she has overcome language difficulties in developing her technical understanding.

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1. INTRODUCTION

Bracken (*Pteridium aquilinum*) is one of the most widely distributed ferns in the world. It appears in much of the temperate zone except desert or dry steppe. In Asia the bracken occurs in the temperate and subtropic forest zones. It is regarded as an agricultural pest in many countries of Europe, North America, Australia and New Zealand.

The distribution of bracken in Britain is wide and its total area has been estimated at 2.76% of the land area. The area of bracken for England, Scotland and Wales were 0.3, 6.0, 5.8% of the land area respectively (Taylor 1978). The spread of bracken is remarkable. The area of bracken in Wales had almost doubled in about 30 years. In Scotland 200,000 ha of hill land are bracken infested (Williams 1980). In Cumbria, vegetation survey based on a land classification, has shown its main distribution in marginal uplands. In land class 4, which occurred at the lower altitudes, the coverage of bracken reached 19% with smaller amounts (11-12%) in land classes 11 and 12 which occupied the middle and low fell respectively. There were 6-8% coverage of bracken in land classes 1, 6 and 10 (Bunce & Smith 1978). The total area of bracken estimated from percentage of cover and total area of each class was about 5% of total area of Cumbria (Heal 1976).

In the past bracken supplied people with some products, fronds yielded potash for soap-making and bedding for stock. The young fronds were eaten by stock, but bracken reduces grass growth, making shepherding difficult. Bracken fronds can produce poisoning in cattle and horses, the trouble often appears suddenly, but it can cause serious losses through staggers in horses as a vitamin deficiency disease. In cattle the disease caused by bracken is much more common as an upset of the blood; sheep are seldom affected. Rhizomes seem to be less poisonous and pigs can consume them

(Braid 1960). Bracken can also cause problems in afforestation by substantially reducing the growth of young trees.

The spread of bracken and its relentless encroachment of grazing and arable land in the upland and highland areas of Britain has caused much concern. The ecology of bracken has been studied in detail (Watt 1940-1976). Investigation of eradication of bracken has been carried out and methods of bracken control described. Use of machines for cutting bracken is one of the approaches for eradicating bracken. The ideal for cutting is to weaken the plant to the maximum extent. Ploughing the land where the bracken grows is also effective, rhizomes being thrown up by the plough, dried and killed. But mechanical means of control have only limited application where the greater part of infested land is unsuitable for the use of machinery. Another way of exterminating bracken is by trampling by stock. This destroys the young shoots when they are just unfolding or still below the surface but the weight of cattle could cause considerable damage in soft ground (Berry 1917; Braid 1947; Conway 1959; Conway & Stephens 1954; McCreath & Forrest 1958; Milne Home 1926; Smith & Fenton 1944; Stephens 1953).

Bracken control by herbicides has been investigated since 1960. The herbicides now in use for bracken control fall into two groups; one of which is primarily foliage-absorbed eg asulam and glyphosphate. The other is active through the soil eg chlorthiamid dicamba, dichlobenil and picloran. . However soil applied with herbicides is unsuitable for use on agricultural land because of the persistence and effectiveness of the herbicides against legumes. Available herbicides might be foliage-applied. Treatment with asulam must be carried out after full frond expansion but before the start of die back and maximum translocation to the rhizomes. It is generally agreed that bracken will recolonize in the absence of after treatments. The control of bracken presents difficulties

when the cost of treatment is limited by economic considerations (Williams 1980).

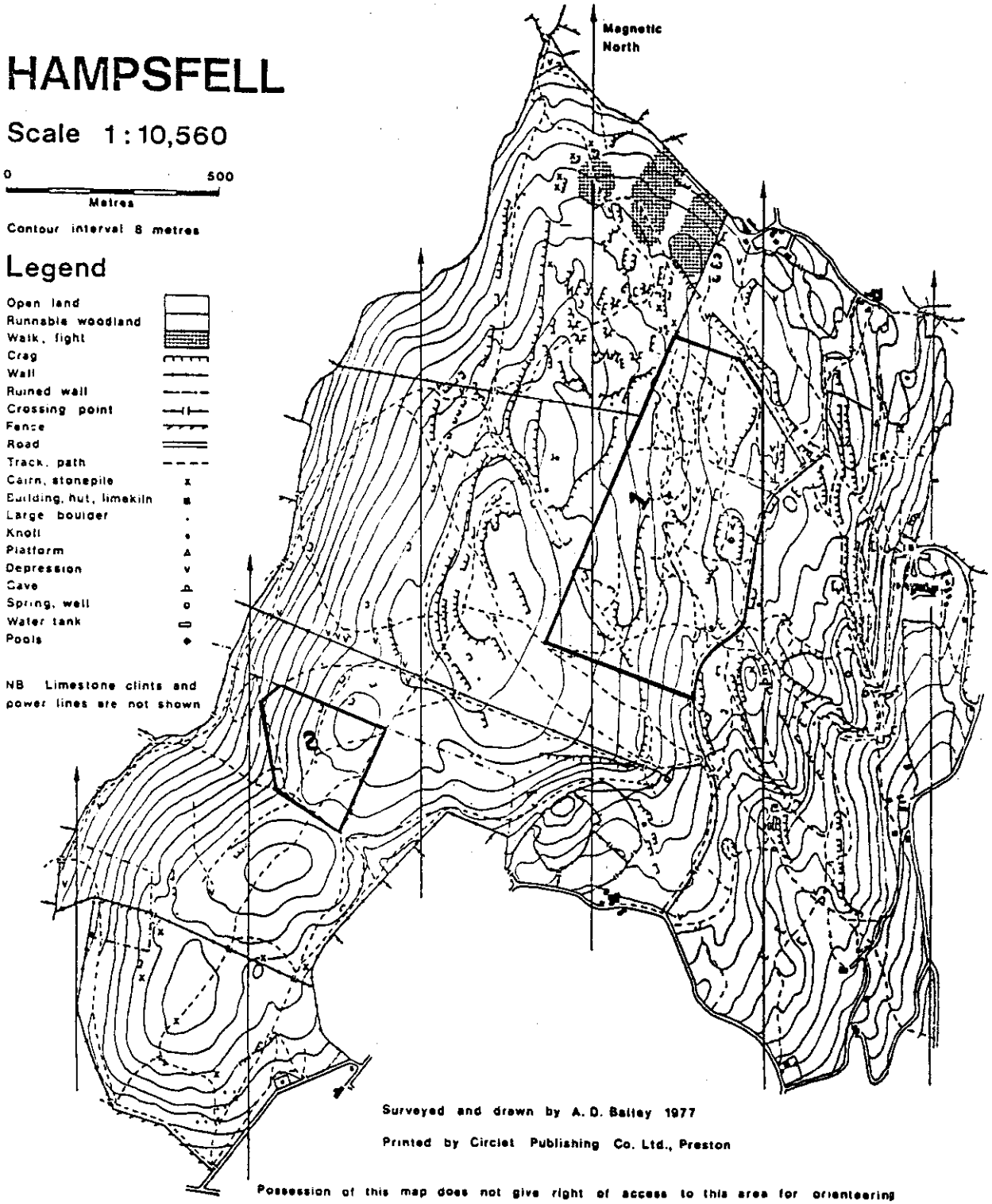
On the other hand, bracken, as one of the greatest potential energy crops is now under investigation. Annual production of bracken ranged from 2.4 to 60 t ha^{-1} with total standing crops from 15 to 153 t ha^{-1} (Callaghan *et al.* 1980), As world energy requirements are increasing, studies on the non-nuclear energy and on renewable sources derived from plants are becoming very important. Intensive studies on the bracken ecosystem will improve our understanding of energy resource from plants.

The aim of the present research was to determine net primary production, the main features of nutrient cycling and the rates of decomposition in the bracken grassland. The sites for intensive study were located on Hampsfell near Merlewood Research Station in Grange-over-Sands (1 and 2 on Map 1).

2 SITE DESCRIPTION

Hampsfell, situated at the south of the Lake District, is a limestone fell rising to a height of 238 m. The prominent scar of Hampsfell is chiefly an exposure of the Urswick limestone deposited in the lower carboniferous period. The limestones have usually been modified by weathering and erosion. The limestone surface consisted of grikes and clints. The grikes are the deep grooves which have been widened down vertical joint faces by weathering, clints are the resultant upstanding, flat to slightly round-topped blocks. Hampsfell has a relief character typical of carboniferous limestone with gently sloping terraces bounded by steeper but quite low scarp faces (Map 1). The limestone of Hampsfell is only thinly covered by soil at any point and there were many small and big exposures. The cover material is a brown, stony or silty loam which is seldom more than one metre thick except over deep infilled grikes (Ball, in prep.).

The principal soil on Hampsfell is a brown earth. Subordinate rendzinas occur locally on limestone outcrops. The dominant brown earth is usually 3-6 cm in depth with accumulations of bracken litter and a blackish brown humose surface horizon at depth 0-5 cm over a brown stony silty loam A horizon, passing into a yellow-brown to strong brown stony B horizon. Microrelief of the erosion surface of the limestone is one of the important factors contributing to the variability of the profile morphology in the brown earths on Hampsfell. The variable contribution of limestone to the soil stone content is partly a result of microrelief influence and the scarp-dip slope physiography of the limestone terraces, and apparently partly random. The nature and thickness of surface humic horizons are influenced by local variation in exposure and slope on the limestone



Map 1 The Study Area

terraces, and by the quality and type of litter able to accumulate (Ball, in prep.). The rendzina profiles consist of a shallow blackish brown humose loam mixed with large amounts of rock fragments. The mean depth of such soil to bedrock is typically around 10-15cm, but sometimes can reach 25-30 cm.

Hampsfell occupies a coastal position and its climate is oceanic. It has a growing season of 7-8 months from early April to the end of October. Annual mean screen temperatures are 9.5^{o}C. In the midsummer (July and August) the mean monthly temperature reached 15.6^{o}C. The mean temperature in February declined to 3.6^{o}C (temperature date sampled at Meathop, 3.2 Km from Hampsfell (White, in prep). Mean rainfall is very even throughout the year with a tendency for a minimum in February (7.5 cm) and a maximum in autumn (13.7 cm). The annual rainfall is about 120 cm. Normally no month has less than 5 cm rainfall with a consequent high humidity (data from Merlewood Research Station 1959-1979). The mean number of days when snow is lying is small, approximately 5.6 days at Merlewood, and the mean number of days with air frosts between May and October inclusive is zero. The windspeeds show maxima in March (3.6 m s^{-1}) and November (4.1 m s^{-1}). Annual mean windspeed is about 3.2 m s^{-1} (White, in prep.).

The vegetation type 26 of Cumbria is distributed widely in Hampsfell. The vegetation types 25 and 14 of Cumbria also occur on Hampsfell. The vegetation is composed of *Pteridium aquilinum* and grasses. The relatively pure bracken stands on deep soil had a coverage of 80-100% without other plants underneath the bracken. The sparse bracken stands were mixed with a large amount of grasses and herbs. The major species of grass were *Agrostis tenuis, Festuca ovina, Sieglingia decumbens, Sesleria caerulea, Anthoxanthum odoratum, Festuca rubra, Nardus stricta.* Herbs such as *Galium saxatile, Potentilla erecta, Trifolium repens, Campanula*

rotundifolia were frequent. Certain areas were occupied by grasses without bracken. A few trees such as *Quercus petraea, Fraxinus excelsior, Ilex aquifolium, Taxus bacata, Larix decidua, Acer psuedoplatanus* and *Corylus avellana* scattered on the rock.

3 PRIMARY PRODUCTION

The net production by an individual plant is the amount of organic matter which synthesizes and accumulates in tissue per unit time. It is the profit remaining from the photosynthesis of the plant, or its gross production minus its respiration. Some parts of the net production of the plant may be lost with the death and loss of tissues and in production measurement this loss must be taken into account. The sum of the net production by all individual plants in a unit area of the earth's surface is net primary production.

3.1 Method

There are several approaches to the measurement of primary production:
1) Harvest techniques are based on successive harvesting of plants from sample plots and determining their increment. In grassland studies, measuring the biomass of the plant community at the beginning of a study period and again at the end, allowing the calculation of increment by subtraction, has been used to determine net primary aerial production.
2) Net primary production can be measured by gaseous exchange techniques as well. Many methods of measuring net photosynthesis have been described, mainly based on carbon dioxide uptake including infra-red analysis of CO_2 content of air in plant communities or isolated plants or leaves
3) Radioactive tracer techniques have increased greatly in recent years. $C^{14}O_2$ has been used to study photosynthesis and the transport of carbohydrates within the plant (Milner & Hughes 1968; Whittaker & Marks 1975).

Annual below ground production in herbaceous perennials is difficult to evaluate as compared with the determination of above ground production, mainly owing to the difficulty in separating the current year growth of root or rhizome from the growth of preceding years. Annual below ground production is usually estimated by determining the annual biomass increment

of whole root systems. In the case of perennials, however, net increase in total root biomass during a one-year period may be very small since old rhizomes die as new rhizomes are formed. Instead of measuring annual change of total root biomass, the annual biomass increment of selected parts has been proposed to estimate annual root production in herbaceous perennials. This method is based on the separate determinations of 1) the biomass of a current year's mother rhizomes or tubers with attached roots and 2) that of daughter rhizomes or tubers with attached roots newly produced during the current growing season (Iwaki & Midorikawa 1968). Sampling of root sytems should be made at least twice a year, first immediately before shooting in spring and secondly at the end of the growing season.

In the present study harvesting techniques have been used with 10 quadrats, each 1 x 1 m^2 in size. The sampling units were randomly located within the bracken grassland using standard statistical methods. Measurement of above ground biomass by harvesting has been done each month during the growing seasons. At each sampling the number and weight of bracken fronds per unit area was determined and a sub-sample of frond was selected. The basal diameter of petiole, height and weight of individual fronds were measured. The aim of these measurements was to determine relationships to be used for rapid estimation of biomass.

Measurement of below ground biomass per unit area within soils with various depths, less than 30 cm was carried out by harvesting in November 1979 and February, March, May, July and September 1980. The production of the below ground part of bracken was estimated by annual biomass increment of the whole root system. Above ground and below ground parts of bracken were weighed respectively after being oven-dried at 80°C to constant weight.

3.2 The growth of bracken

Emergence of fronds was in April, temperature being one of limiting factors for bracken growth. Mortality of bracken is caused by spring frosts because of the susceptibility of young fronds. Severe winter frost may kill the shoots in the surface soil layer (Watt 1956). Bracken needs sufficient rainfall for its growth. It appears in the damp shady habitat but also in grassland and open hillsides where conditions are usually relatively dry. Thus it is a fern with the ability to withstand considerable degrees of water stress. The stomatal behaviour in bracken is different from some other ferns (Tinklin 1969), but it cannot grow in marshy or water-logged soil and it requires good soil drainage for active growth. Aeration deficiency may be one of the limiting factors for growth of bracken (Poel 1960, 1961). There was evidence that bracken disappeared in, and on the edge of, a pool on Hampsfell. As an original woodland plant bracken seems to be adaptable to a range of light intensities. In woodlands it was most prevalent in those areas where shade was least, with light intensity more than 30% of full intensity in the open (Burke 1953). Bracken grows robustly when the forest cover is removed especially in grassland. It seems to grow more vigorously on acid brown earth, brown podzolic and sometimes on podzolic soils with pH 3-5.5, but occasionally it appeared on the less acid soil pH 7-7.8.

On Hampsfell young shoots appeared above ground in the middle or the end of April and grew rapidly in the first two months (Fig. 3.1, Table 3.1). The maximum height of frond was reached in September, but by that time the weight of frond had dropped. The peak weight of fronds appeared in August. The diameters of petiole did not change significantly during the growing season.

Table 3.1 The height, petiole diameter and dry weight of individual bracken fronds during the growing season

Month	Height of frond (cm ± se)	Diameter of petiole (mm ± se)	Weight of frond (g ± se)	n
May	40.57 ± 2.32	7.25 ± 0.36	2.73 ± 0.29	81
June	79.69 ± 3.01	7.29 ± 0.18	14.55 ± 1.02	107
July	102.33 ± 9.12	7.86 ± 0.18	28.35 ± 1.49	95
August	121.28 ± 4.5	8.20 ± 0.22	29.91 ± 1.61	80
September	127.98 ± 4.9	8.05 ± 0.20	27.71 ± 1.33	88

The growth of fronds was markedly affected by the depth of soil on Hampsfell (Fig. 3.2). The bracken was mixed with grasses on shallow soil (10-20 cm depth), the cover of grasses being up to 60-70% under the bracken. Thus competition between bracken and grasses may occur. In the shallow soils the growth rates of fronds were only 0.75 cm d^{-1} in height and 0.12 g d^{-1} in weight. Those rates were lower than on soils deeper than 20 cm (1.66 cm d^{-1} in height and 0.52 g d^{-1} in weight). Growth rates declined during the season, although in the shallow soils the weight increment was greatest during June-July (Table 3.2).

Table 3.2 The growth rate in height and weight of bracken fronds

Date	Soil	Height (cm d^{-1})	Weight (g d^{-1})
20 May - 18 June	Deep	1.66	0.52
	Shallow	0.75	0.12
19 June - 29 July	Deep	0.93	0.39
	Shallow	0.39	0.24
30 July - 27 August	Deep	0.34	0.04
	Shallow	0.17	0.005
28 August - 30 Sept.	Deep	0.42	-0.06
	Shallow	-0.06	0.001

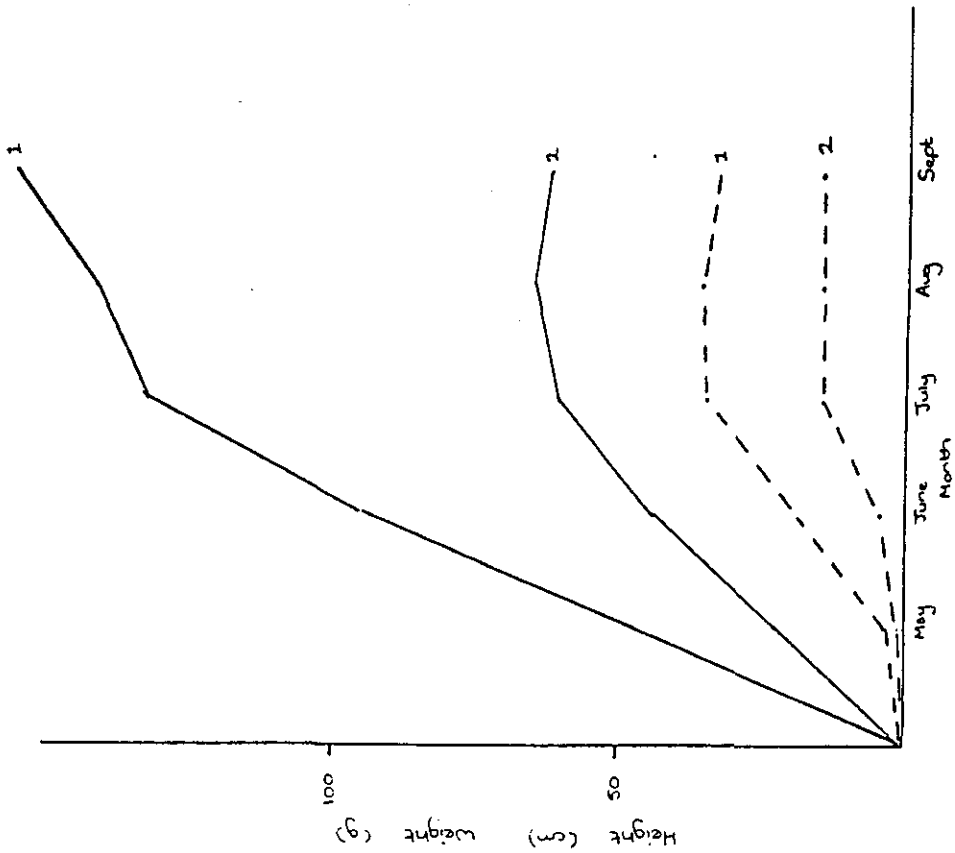


Fig. 3.1 The growth of bracken

Fig. 3.2. The growth of individual bracken in various habitats

3.3 The above ground biomass of bracken

The above ground biomass was harvested each month during the growing season and varied from month to month. The bracken aerial biomass per unit area was calculated from the weight of individual fronds and number of fronds per unit area. The average number of fronds per m^2 was 28-38 and had no marked seasonal change. The height per frond made a great contribution to the variation in biomass of bracken as did the depth of soil (Table 3.3). The linear regression analysis showed that the aerial biomass was significantly related to depth of soil and height of fronds, but not to number of fronds per m^2. Using two factors eg depth of soil and height of fronds the multiple correlation coefficient was high (Table 3.4). Combining three factors including number of fronds per m^2, the multiple correlation coefficient was slightly higher than that based on two factors. It means the soil depth and height of fronds were most important factors and height of fronds explains most of the variation because it reflects the importance of soil depth. The multiple regression equation varied from month to month.

Table 3.3 Linear regression between bracken aerial biomass g m^{-2} (y) and depth of soil cm (x_1); number of fronds per m^2 (x_2); Height of fronds cm (x_3)

Linear regression	r	n
$y = 72.20 + 12.22\ x_1$	0.406**	54
$y = 363.40 + 3.62\ x_2$	0.140	54
$y = -166.74 + 7.18\ x_3$	0.917**	54

** $P < 0.01$ *** $P < 0.001$

The peak biomass of bracken on Hampsfell averaged 794.2g m^{-2} in August and then declined (Fig. 3.3). The above ground biomass on deep soil might be 1-2.5 times higher than that on shallow soil. The maximum yield of bracken on deep soil reached 940 g m^{-2}, but only 430 g m^{-2} on shallow soil (Fig. 3.4).

Table 3.4 Multiple regression of bracken aerial biomass g m^{-2} (y) against soil depth cm (x_1), number of fronds per m^2 (x_2), and height of fronds cm (x_3) during the growing season

Date	Regression equation	R	n
Total	$y = -1.39x_1 + 7.36x_3 - 136.34$	0.918**	56
Total	$y = -1.33x_1 + 4.95x_2 + 7.43x_3 - 306.18$	0.938**	56
May	$y = 0.12x_1 + 1.12x_2 + 2.16x_3 - 65.36$	0.901**	15
June	$y = 0.57x_1 + 5.89x_2 + 6.57x_3 - 389.84$	0.936**	11
July	$y = 0.36x_1 + 5.14x_2 + 8.46x_3 - 390.49$	0.967**	10
August	$y = 4.17x_1 + 18.13x_2 + 7.22x_3 - 792.69$	0.954**	10
September	$y = 1.35x_1 + 4.12x_2 + 5.99x_3 - 286.09$	0.982**	10

** P = <0.01

The results for Hampsfell are similar to those published for other areas in Britain. Thus Callaghan *et al.* (in press) demonstrated that maximum yield of bracken above ground part at Chisworth in the Pennines and Lowick in the Lake District varied between 8.7 t ha^{-1} and 8.9 t ha^{-1} and senescent fronds yielded between 4.6 and 8.0 t ha^{-1}. The mature yield in Scotland varied from 2.43 to 31.6 t ha^{-1} at midsummer (Braid 1960), and in the Breckland in August the range observed by Watt (1964) was 4 - 1243 g m^{-2}. The mean bracken above ground production in UK has been estimated at 9.82 t ha^{-1} yr^{-1} (Callaghan *et al.* 1980).

3.4 The below ground biomass of bracken

The seasonal variation of bracken below ground biomass was not marked, but the results indicated decrease from November to February and an increase

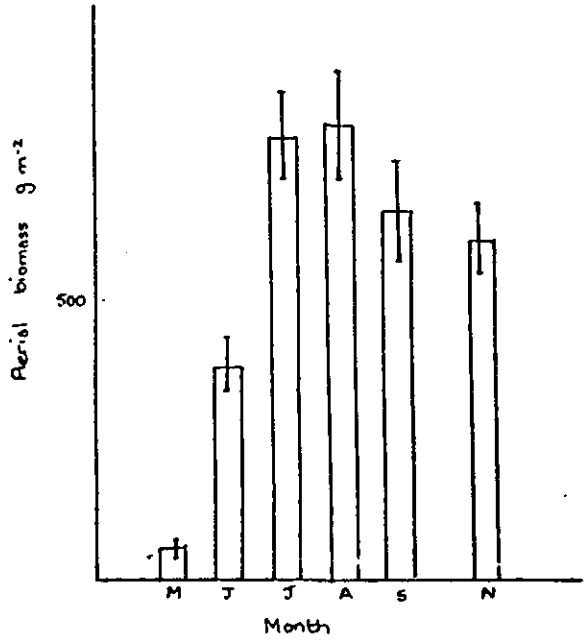


Fig 3.3 The aerial biomass of a bracken stand ($g\,m^{-2}$)

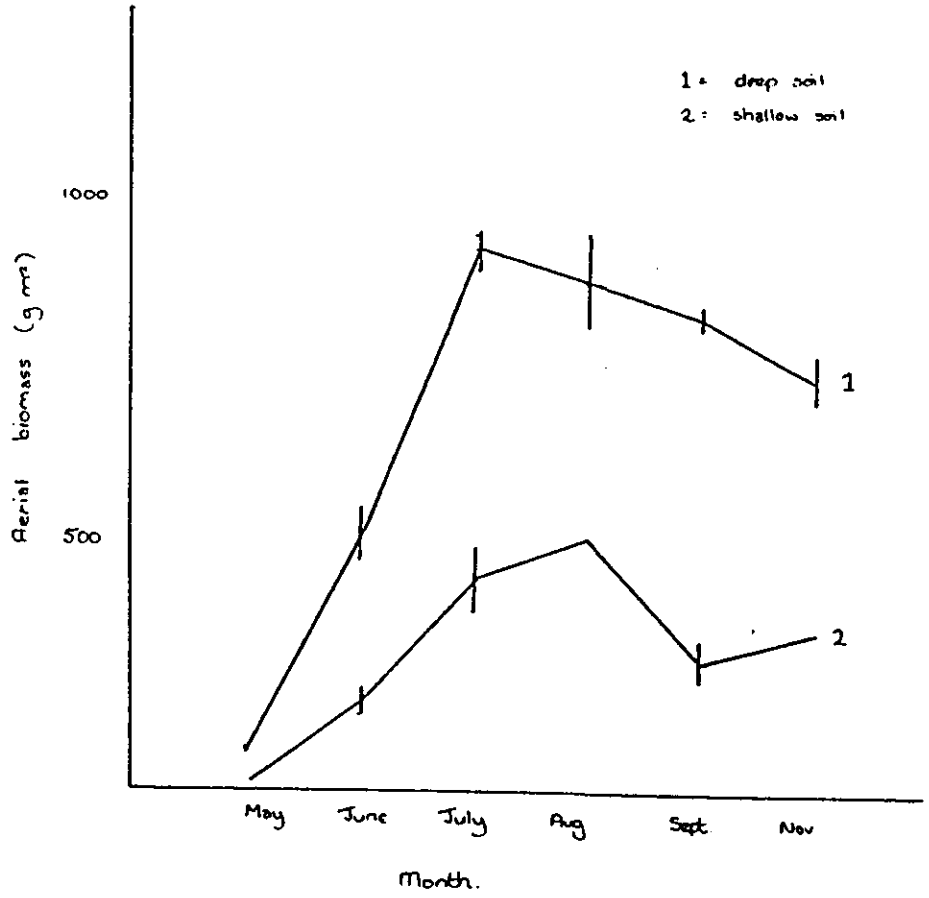


Fig 3.4 The variation of aerial biomass ($g\,m^{-2}$) on deep and shallow soil

during the growing season (Fig. 3.5). Below ground biomass in September was significantly higher than that in November 1979 and May 1980 (F ratio = 6.067, $P < 0.05$ and F ratio = 6.699 $P < 0.05$) (Table 3.5). During September the aerial biomass of bracken decreased suggesting translocation of material from aerial to below ground parts of the plant.

Table 3.5 Analysis of variance of below ground biomass during the growing season

Date	Source of variation	Sum of squares	Degrees of Freedom	Mean squares	F ratio
May 1980 July	Lot means	408935	1	408933	
	Individual	18275600	23	794591	0.515
May 1980 Sept.	Lot means	9391010	1	9391010	
	Individual	32289500	23	1403890	6.689*
July 1980 Sept.	Lot means	4900500	1	4900500	
	Individual	23361900	18	1297880	3.776
Nov. 1979 Sept.1980	Lot means	8570020	1	8570020	
	Individual	25427800	18	1412650	6.066*

* P = <0.05

Results in the present study showed the problems of interpretating of biomass data when a number of processes of growth, translocation and death can occur simultaneously, but other techniques can be used to isolate particular processes. For example, Whittle (1964a & b) used radioactive labelled carbon and showed that carbohydrates were imported from the rhizomes and from the lower pairs of pinnae as each pair of pinnae was unfolded. Import would last for a period time before export to the apical parts of frond began. Gradually only export took place both up the rachis to apical part of frond and down it to the rest of bracken. The velocity up the rachis was much less than the velocity down it. When the whole frond was unfolded, the export continued in the rachis only towards the rhizomes. Later spreading of labelled carbon was remarkably limited (Hamilton & Canny 1960). The diffusion constant in

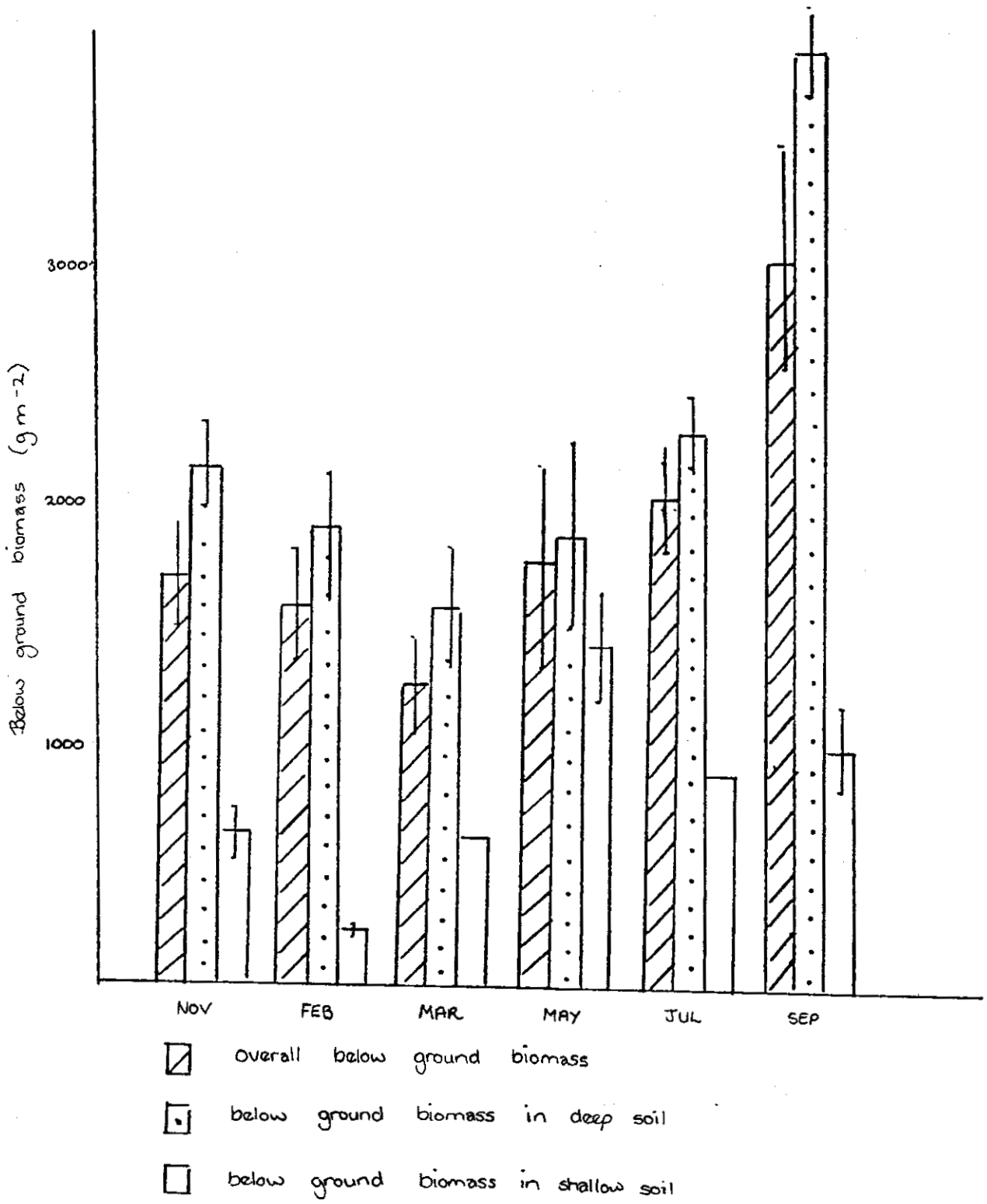


Fig 3.5 The below ground biomass of bracken stands ($g\ m^{-2}$)

bracken as in other plants, was dependent on temperature. The temperature optimum for the rate of mass transfer was between 25°C and 30°C. The translocation system would be capable of its maximum rate of mass transfer during the middle of sunny days when the temperature was high and the level of carbohydrate in a pinnae was also at a maximum (Whittle 1964a & b).

Returning to the present study, the below ground biomass was closely related to the soil depth and to above ground biomass. The major part of bracken roots and rhizomes was distributed in the soil surface layer of 0-15 cm and soil depth markedly affected the below ground biomass (Fig. 3.5). Multiple regression showed that below ground biomass was significantly correlated with soil depth, number of fronds per m^2, height of fronds and above ground biomass (Table 3.6). This type of model may be useful in predicting below ground biomass through measurements of above ground parts.

Table 3.6 Regression of below ground biomass of bracken in g m^{-2} (y) against soil depth cm (x_1), number of fronds m^{-2} (x_2), height of fronds cm (x_3) above ground biomass in g m^{-2} (x_4)

Date	Regression equation	R	n
May	$y = 0.51x_1 + 19.26x_2 + 52.14x_3 - 7.74x_4 - 437.95$	0.656	15
July	$y = 19.88x_1 + 16.38x_2 + 29.39x_3 - 1.89x_4 - 1108.98$	0.899**	10
September	$y = 11.17x_1 + 3.50x_2 + 10.95x_3 + 2.49x_4 - 515.83$	0.989**	10
Total	$y = 25.11x_1 + 16.77x_2 + 35.74x_3 - 3.17x_4 - 863.19$	0.849**	35
Total	$y = 26.77x_1 + 28.63x_3 - 2.17x_4 - 211.61$	0.822**	35

** P = <0.01

The below ground biomass on Hampsfell varied from a minimum on shallow soil of about 250 g m^{-2} to a maximum on deep soil of 3825 g m^{-2}. This compares with the dry weight of rhizomes in August averaged 1443 g^{-2} in a podsol and 1064 g m^{-2} from a brown earth in Breckland (Watt 1964). Braid (1960)

mentioned underground parts of bracken weighed from 12.15 - 121.5 t ha^{-1}.

3.5 The annual primary production

The net primary production of bracken grassland was estimated from above-ground and below ground biomass of bracken. The peak of bracken aerial biomass appeared in August but part of the matter was translocated to below ground part in autumn. The below ground biomass changed from February (t_1) to September (t_2). The annual production of below ground part was calculated by annual biomass increment ($B_2 - B_1$). The bracken losses by death and consumer organisms can be ignored in bracken stands. So net primary production can be calculated as NPP = annual increment of below ground biomass during $t_1 - t_2$ + Peak of above ground biomass - weight loss of above ground biomass in autumn.

The annual net primary production of bracken grassland on Hampsfell averaged 2009 g m^{-2} y^{-1} with maximum yield of 2667 g m^{-2} y^{-1} on deep soil and minimum yield of 1023 g m^{-2} y^{-1} on shallow soil. The net primary production of bracken stand in UK averaged 14 t ha^{-1} y^{-1} (Callaghan *et al.*, 1980).

4 DECOMPOSITION

The function of all ecosystems occurs within three major subsystems ie. plant subsystem; herbivore subsystem (including carnivore and various groups of heterophes); and the decomposition subsystem. The integrity of the ecosystem is maintained by the transfers of matter and energy between these three compartments. The plant subsystem is the basic producer of the system. Plants take up essential nutrients in ionic form from the soil and they return the nutrients to the soil as litter with compounds of high molecular weight. But the plant roots only can absorb the nutrients in "available" form of low molecular weight. Decomposition processes (catabolism) are therefore essential to the cycling of elements within an ecosystem. The litters are broken down by the decomposer community which mainly consists of fungi, bacteria and invertebrate animals. Thus decomposer organisms play a major part in nutrient replenishment of soil which is accomplished by the mineralisation of nutrient elements and by the formation of recalcitrant soil organic matter (Swift, Heal & Anderson 1979).

A variety of factors affect the decomposition processes: the chemical and physical quality of the plant debris and the environmental conditions into which the debris is deposited, especially temperature, moisture and the physical and chemical nature of soil.

An investigation of the decomposition of bracken petioles on six soil types of woodland was carried out by Frankland (1966). The results showed that decomposition of bracken petioles was a slow process. The weight loss of petioles in the first three years varied from 28.4-72.2%. Information on the decomposition of bracken pinnules has not been reported. The results of studies on the surface mycoflora of green bracken fronds were given by Godfrey (1974), conidia, microsclerotia and fungal hyphae were present on the frond surface.

The aim of the present studies was to determine the decomposition rate of bracken petioles and pinnules in the grassland and to determine the effect of different environmental factors (soil depth, microclimate) by measuring the rate of decomposition in different microhabitats.

4.1 Method

Studies on decomposition of bracken petioles and pinnules on Hampsfell were carried out from November 1979 to September 1980. Bracken which was recently dead was collected from a pure bracken stand on Hampsfell on 8th November 1979, air-dried, made up as weighed samples before replacing in the field. The petioles and pinnae of bracken were treated separately. The petioles were cut off 10 cm above soil level. Three segments, each 10 cm in length (approx. 1 g) were then cut from the base of each petiole. The diameters of petioles were 5-9 mm. After oven-drying at 40°C to constant weight the segments were mixed thoroughly, weighed and attached by nylon thread, 15 cm in length, to a numbered plastic label.

The pinnae were separated into small pinnules with a rachis (< 1 mm). If the rachis was greater than 2 mm diameter it was discarded. The pinnules were mixed thoroughly, enclosed in fine mesh (1 mm) terylene bags and oven-dried at 40°C to constant weight. The size of mesh bags was 9 x 9 cm^2. The bags and pinnules were weighed respectively. The pinnules in each bag were about 1.4 g. Each bag was attached by a 20 cm piece of nylon line to a numbered plastic label.

On 4 December 1979 the petioles and pinnules enclosed in the bag were placed on the litter layer of each site along a 10 metre transect with 20 cm between each sample. Four sites were used for studies of decomposition, three situated in the grassland on Hampsfell with various microhabitats eg. shallow soil with limestone outcrops, medium depth of soil on the

gentle slope and deep soil in the depression. The depths of soil in these three sites were 6.7 cm., 21.9 cm and 36.3cm. The fourth site, Eggerslack Woods, was located on the lower limestone slope. These woods were mainly of coppice origin. The average height of the trees is about 8 metres. *Quercus petraea, Acer pseudoplatanus, Betula pendula, Fraxinus excelsior* were present with *Quercus petraea* dominant and *Corylus avellana* forming an understorey. The ground flora was mainly composed of *Mercurialis perennis*. Bracken litters were placed where the canopy was more open and major species in the ground flora were *Pteridium aquilinum* and *Dryopteris filix-mas*. The shallow soil with limestone outcrops was a kind of rendzina. The soil group in other three sites was brown earth.

Samples were retrieved from the field after 20 and 40 weeks. The obvious extraneous material was removed from the samples, which were then weighed, oven-dried and re-weighed to provide an estimate of moisture content of litters. The weight loss of litters was obtained by comparison with the original weight of litters and the results were expressed as % weight loss.

Respiration is a measure of the loss of carbon dioxide by catabolic processes in the litter and was used to estimate the proportion of weight loss resulting from microbial respiration. Oxygen uptake by litters retrieved from the field sites was measured at 10^{o}C and field moisture in Gilson respirometers.

4.2 Weight loss of bracken litters

The total weight loss was used as the measurement of decomposition which comprised losses due to catabolism, leaching and removal or export following communition. The results showed that weight loss of bracken petioles and pinnules was about 20-22% after 40 weeks in field (Table 4.1).

Moisture content of the litter at the time of sampling provided some explanation of the variation in weight loss (Table 4.2). In the first four months (0-20 weeks) the loss rate of bracken petioles was higher than that of pinnules. There was significant difference in the rates of decomposition between petioles and pinnules (F ratio = 10.7, $P < 0.05$). During 20 to 40 weeks the loss rate from bracken petioles decreased but the loss rate of pinnules remained nearly constant from 0-40 weeks. There was no significant difference in the rate of decomposition between two parts of bracken after 40 weeks in field, although the decomposition rate of petioles was slightly higher. The decomposition rate of petioles on Hampsfell was greater than that in Roudsea Wood a few kilometers away (Frankland 1966), the average annual weight loss in petioles was 9.5 - 24.1% in various sites of Roudsea Wood, the annual weight loss in the first three years followed the same course.

Table 4.1 A summary of the mean (± se) weight loss (%), respiration ($\mu l O_2\ g^{-1}\ h^{-1}$ at $10^{\circ}C$) and moisture content (% dw) of bracken litters

Weeks in field	Weight loss %	Weight loss rate % d^{-1}	Respiration $\mu l O_2\ g^{-1}\ h^{-1}$ at $10^{\circ}C$	Moisture content % dw
Petioles				
20	14.4 ± 1.60	0.103	7.05 ± 0.40	272 ± 17.7
40	22.0 ± 1.55	0.079	21.38 ± 4.04	522 ± 26.5
Pinnules				
20	9.9 ± 0.48	0.071	13.11 ± 2.87	316 ± 21.2
40	20.9 ± 1.27	0.078	25.21 ± 4.99	556 ± 36.0

Table 4.2 Analysis of correlation between % weight loss (y) and % dw moisture content (x)

Weeks in field	Parts of bracken	Regression equation	r	n
20	petioles	y = 13.38 + 0.0036x	0.102	38
40	petioles	y = 11.18 + 0.021x	0.437**	35
20	pinnules	y = 8.77 + 0.0036x	0.252	39
40	pinnules	y = 12.87 + 0.014x	0.408**	39

** $P < 0.01$

The bracken litter showed a consistent weight loss over a number of weeks. The exponential regression of $\log_e$ weight remaining of bracken litter against time (t in year) indicated an annual decay rate of 0.321 g g^{-1} yr^{-1} for bracken petioles, 0.317 g g^{-1} yr^{-1} for pinnules (Table 4.3). Decay rate was derived as the regression coefficient of an exponential regression. Jones (1978) reported that the decay rates of *Calluna* shoots and *Eriophorum* leaves in blanket bog at Moor House were 0.1087 and 0.1854 g g^{-1} yr^{-1} for five years respectively.

Table 4.3 Decay rate derived from Log_e weight remaining of bracken litter against t in year

Part of bracken	Decay rate (g g^{-1} yr^{-1})	Log_e regression equation
petioles	0.321	y = 4.596 - 0.321 t
pinnules	0.317	y = 4.613 - 0.317 t

The decay rate of litter in a long period showed a lower rate than bracken litter on Hampsfell. But decomposition rate of *Rubus* and *Eriophorum* leaves in the first year on blanket bog was similar to bracken (Heal, Latter & Howson 1978). It is probable that the rate of decomposition decreases with time as the easily decomposed components are rapidly lost, leaving more resistant fractions with slow decay rates. The similarity of the early decay rates of bracken on Hampsfell and *Rubus* and *Eriophorum* at Moor House probably results from compensating effects of different factors; the soil and climate on Hampsfell will give faster rates than on the bog at Moor House, but the *Rubus* and *Eriophorum* probably have a higher intrinsic rate of decomposition because of their low lignin and high nutrient content relative to bracken.

There are a certain number of fungi appeared in the phloem and surface of petioles especially in the wet habitat on Hampsfell. A small amount of fungi appeared on the surface of pinnules. As Frankland (1976) reported, a different group of Fungi Imperfecti predominated after the first three months in petioles. By the end of the first year the phloem was no longer recognisable. Basidiomycetes were attacking the lignified cell walls and became dominant in the second year.

4.3 The respiration of bracken litters

The measure of respiration of litters provided the data of oxygen uptake or carbon dioxide output from the microflora and fauna in catabolic processes. The contribution of microbial respiration to weight loss was estimated from the measured oxygen uptake over the sampling period at field moisture levels.

The respiration rates of litters were significantly related to moisture contents of litters (Table 4.4, Figs. 4.1, 4.2). When the moisture contents of litters were less than 150-200%, the respiration rate was barely detectable, indicating that microbial activity was inhibited by moisture levels below about 150%.

Table 4.4 Analysis of relationship between respiration rate in $\mu l O_2\ g^{-1}$ at $10^{o}C$ (y) and % dw moisture content (x)

Weeks in field	Parts of bracken	Regression equation	r	n
20	petioles	y = 0.099x - 18.49	0.906***	19
40	petioles	y = 0.070x - 14.75	0.687**	17
20	pinnules	y = 0.075x - 11.67	0.944***	20
40	pinnules	y = 0.078x - 18.82	0.792***	20
20, 40	petioles	y = 0.068x - 12.00	0.801***	36
20, 40	pinnules	y = 0.070x - 12.16	0.838***	40

** P < 0.01 *** P < 0.001

The relationships between respiration rate and weight loss of litters was significant after 40 weeks in field (Table 4.5) and the respiration rate increased between 20 and 40 weeks (Table 4.1). The latter result contrasted with Heal *et al.* (1978), who showed that respiration declined with time during the early years of decomposition of some litters. However there was no significant decline of respiration in the slow decomposing litters on blanket bog at Moor House in the first year. Some of the variation can be explained by differences in moisture content between litter samples and in chemical composition of various litters.

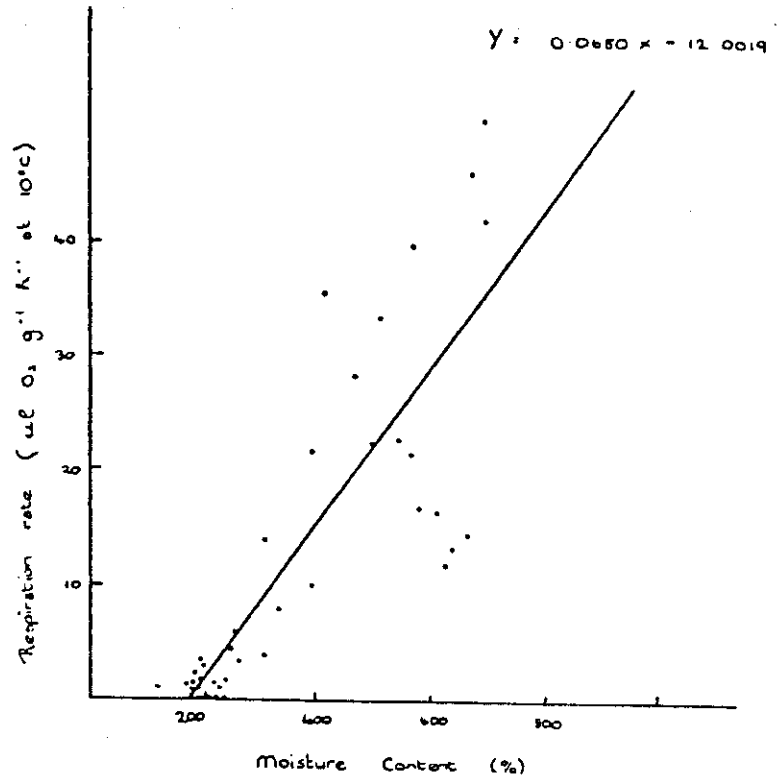


Fig 4.1 Linear regression between respiration rate in ul O_2 g^{-1} h^{-1} at 10°C and % dry weight moisture content of the petioles.

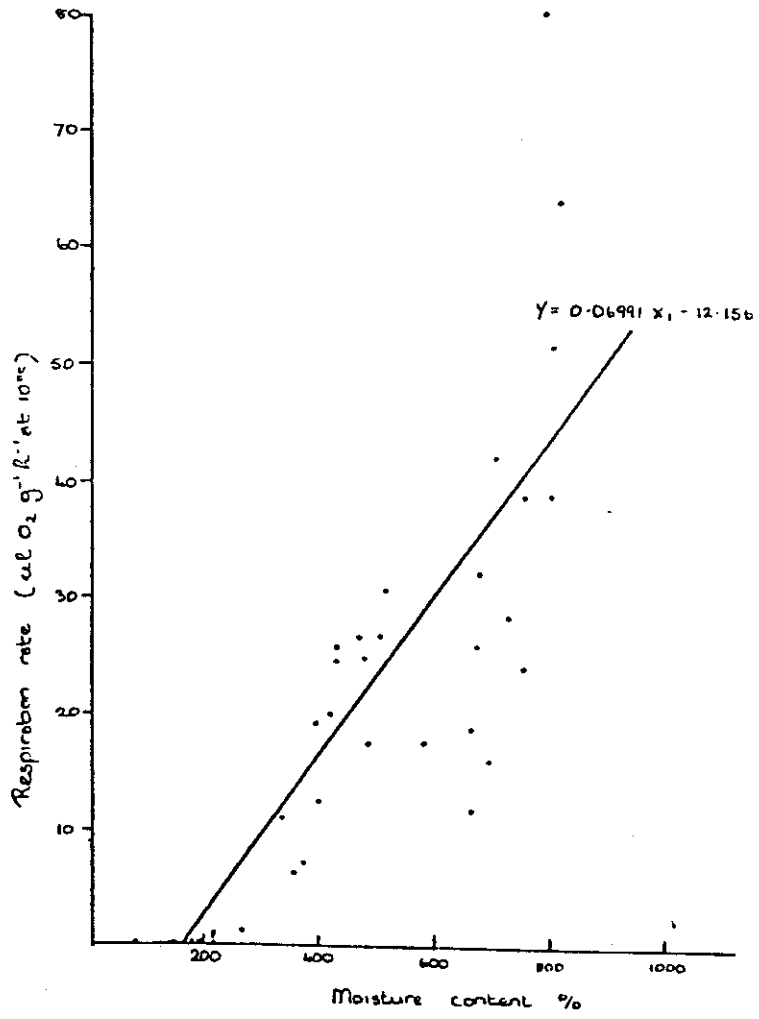


Fig 4.2 Linear regression between respiration rate (ul O_2 g^{-1} h^{-1} at 10°C) and percentage dry weight moisture content of pinnules.

Table 4.5 Analysis of correlation between respiration rate ($\mu l O_2\ g^{-1}\ h^{-1}$ at $10^{o}C$) (y) and % weight loss (x)

Weeks in field	Parts of bracken	Regression equation	r	n
20	petioles	y = 0.64x - 2.39	0.213	19
40	petioles	y = 1.54x - 10.12	0.569*	17
20	pinnules	y = 1.26x - 0.046	0.225	20
40	pinnules	y = 1.46x - 6.17	0.664**	20

* $P < 0.05$ ** $P < 0.01$

When weight loss and moisture content were combined the correlation with respiration rate was very high and explained 50-90% of deviation (Table 4.6). Regression surfaces showed the relationships between these three factors (Figs. 4.3, 4.4).

Table 4.6 Regression of respiration rate ($\mu l O_2\ g^{-1}\ h^{-1}$ at $10^{o}C$) against % weight loss (x_1) and % dw moisture content (x_2)

Weeks in field	Parts of bracken	Regression equation	R	n
20	petioles	$y = 0.45x_1 + 0.097x_2 - 24.81$	0.918***	19
40	petioles	$y = 0.60x_1 + 0.056x_2 - 19.52$	0.707**	17
20	pinnules	$y = -0.16x_1 + 0.076x_2 - 10.18$	0.944***	20
40	pinnules	$y = 0.89x_1 + 0.061x_2 - 28.40$	0.872***	20

** $P < 0.01$ *** $P < 0.001$

The relationship of respiration to temperature was not examined experimentally. However various studies on respiration of decomposing litters (eg Howard & Howard 1979; Bunnell *et al.* 1977; Flanagan & Veum 1974) have shown the positive relationships between respiration and

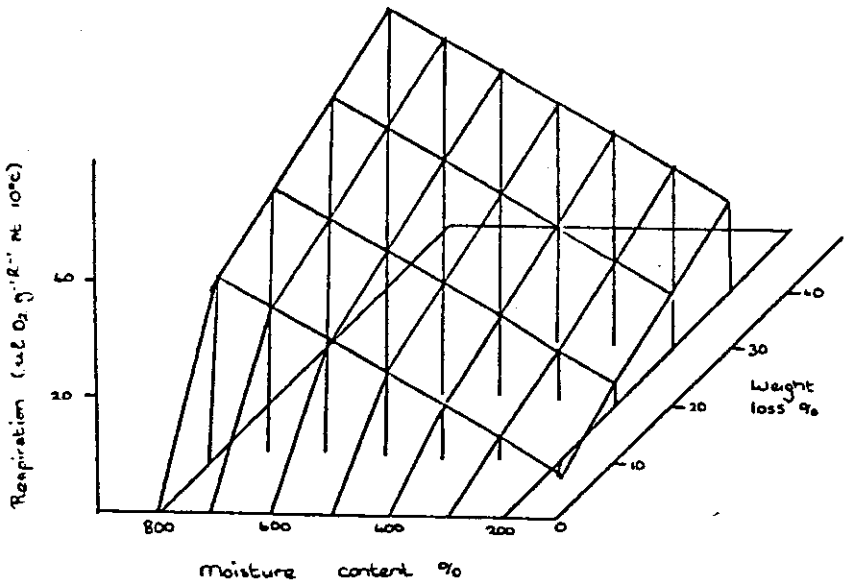


Fig 4.3 Multiple regression model of respiration rate in petiole litter after 40 weeks in the field.

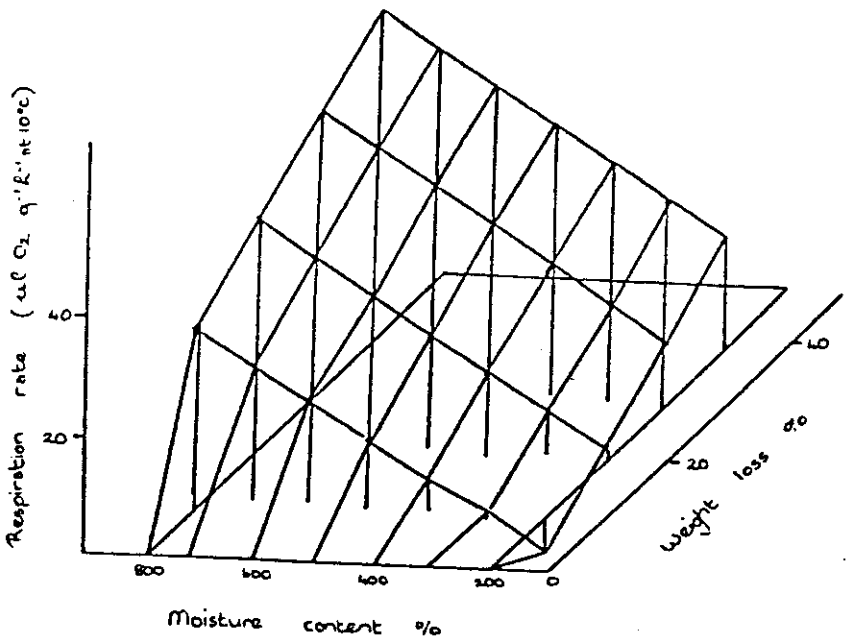


Fig 4.4 Respiration rate in pinnule litters as a function of moisture % and % weight loss after 40 weeks in the field

temperature. As an indication of the probable effect of temperature and moisture on respiration of bracken litters, response to temperature was assumed to have a Q_{10} of 2.0 ie respiration doubles with every 10°C rise in temperature. Figs. 4.5, 4.6 indicate the likely relationship between respiration rates of bracken litters, temperature and moisture content of litters.

As a first approximate estimate of the annual C loss in microbial respiration, the weight loss was calculated from the measured oxygen uptake at 10°C over the sampling period and corrected for field temperature assuming a Q_{10} of 2.0, and using monthly mean air temperatures. Moisture content of litter appeared unusually low in April and May 1980 in field samples (Table 4.1, 20 weeks) corresponding with very low rainfall in that period. Total annual O_2 consumption predicted from respiration was 0.2035 l O_2 g^{-1} for petioles and 0.2358 l O_2 g^{-1} for pinnules. The corresponding weight loss of petioles predicted from respiration in one year was 21.0%. Due to high moisture content and respiration rate, a weight loss of 24.4% was predicted in pinnules (Table 4.7). The results indicated that 73-88% of the observed weight loss could be attributed to microbial respiration. The data obtained in Moor House indicated the similar result, the weight loss of four litters predicted from respiration was 74-136% of the observed weight loss using a Q_{10} of 2.0 (Heal, Latter & Howson 1978).

Table 4.7 Weight loss of litters predicted from respiration rate compared with observed weight loss in a year

Litter	Weight loss % predicated from respiration	Observed* weight loss %
petioles	21.04	28.65
pinnules	24.38	27.42

* data were extrapolated from 40 weeks to 52 weeks

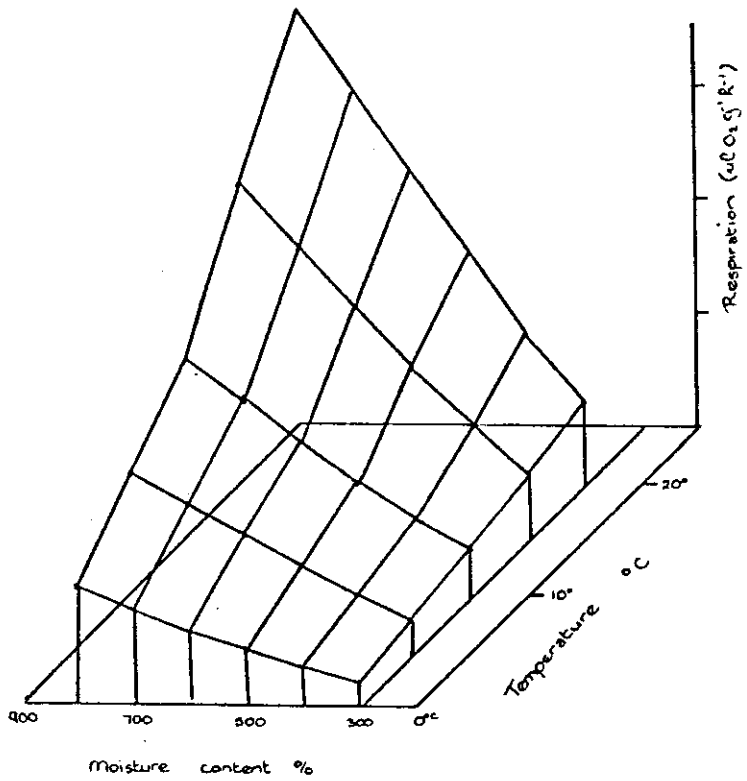


Fig 4.5 Pattern of microbial respiration in petiole litter
The respiration rate in petiole litters are influenced by temperature and moisture in 40 weeks time

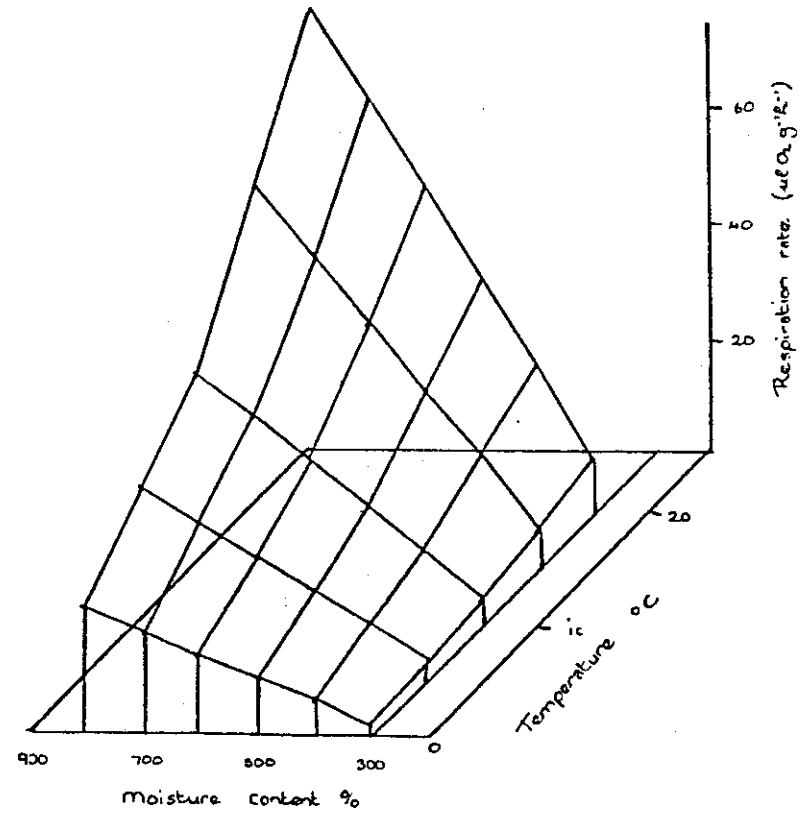


Fig 4.6 Pattern of microbial respiration in pinnule litters The respiration rate in pinnule litters is influenced by temperature and moisture in 40 weeks time

4.4 The change of chemical composition during decomposition

The bracken litters were collected in November 1979. The initial chemical constituents in bracken pinnules and petioles showed some differences, the pinnules were rich in nitrogen, soluble tannin, crude fat and, surprisingly, lignin as compared with petioles while the petiole litters contained relatively high concentrations of readily soluble potassium and holocellulose. (Table 4.8)

Of the initial concentration, losses from petioles in the first four months of decomposition were potassium 97%, soluble tannin 77%, ash 63%, soluble carbohydrate 39% and holocellulose 5% (Table 4.8). During that time 20-90% of initial amounts of above mentioned five major components were lost from petioles and the total loss reached 24.2 g per 100 g of initial petiole litters, the most important contribution being loss of holocellulose. In the meantime the amount of lignin in petiole litters increased 7.5 g per 100 g of initial litter. This increase is probably an artefact of the analysis, but the net amount lost by estimation of chemical composition in petioles was 16.7% (Table 4.9).

The losses of the initial concentration from pinnules were soluble tannin 60%, potassium 50%, soluble carbohydrate 32% and holocellulose 23% in the first four months of decomposition. 30-95% of the initial amount of these four components was lost from pinnule litters, their total contribution to loss (including ash loss) was 21.8 g per 100 g initial litters (Table 4.10). The holocellulose, soluble tannin and carbohydrate made large contributions to weight loss of pinnules. In the meanwhile the amount of lignin and nitrogen increased by 12.1 g 100 g initial litters. Thus the net amount lost, based on changes in the chemical composition in pinnules, was 9.7%.

TABLE 4.8 The change of chemical composition (% dw) in bracken litter with time

Time (weeks)	Parts of bracken	Ash	Na	K	Ca	Mg	Fe	Mn	P	N	Soluble carbo-hydrate	Holo-cellulose	Crude Fat	Soluble Tannin	Lignin (by difference)
0	petioles	5.7	0.070	2.2	0.14	0.073	0.004	0.015	0.020	0.2	2.8	81.0	0.55	1.5	8.45
20	petioles	2.1 ±0.05	0.011 ±0.002	0.064 ±0.01	0.20 ±0.01	0.077 ±0.003	0.01 ±0.003	0.016 ±0.004	0.021 ±0.0004	0.30 ±0.0008	1.68 ±0.10	76.5 ±0.25	0.72 ±0.38	0.34 ±0.031	18.66
40	petioles	2.35 ±0.13	0.007 ±0.0009	0.051 ±0.008	0.21 ±0.014	0.063 ±0.006	-	0.019 ±0.003	0.028 ±0.003	0.34 ±0.03	1.35 ±0.08	71.5 ±0.25	0.44 ±0.10	0.33 ±0.024	24.03
0	pinnules	3.6	0.078	0.16	0.50	0.19	0.026	0.025	0.093	1.31	4.0	48.0	1.70	6.5	36.2
20	pinnules	3.75 ±0.12	0.010 ±0.001	0.080 ±0.003	0.54 ±0.013	0.14 ±0.019	0.029 ±0.004	0.023	0.102 ±0.002	1.49 ±0.02	2.83 ±0.10	37.3 ±0.41	1.5 ±0.06	1.98 ±0.022	52.64
40	pinnules	3.95 ±0.13	0.013 ±0.001	0.091 ±0.017	0.60 ±0.063	0.11 ±0.021	-	0.029 ±0.005	0.081	1.53 ±0.048	2.73 ±0.14	21.65 ± 3.76	0.72 ±0.17	1.40 ±0.08	69.55

Table 4.9 The change of chemical composition amounts in petiole litter.

Time (weeks)	Weight loss (%)	Weight remaining (%)	Concentration (%)	Amount (g) remaining per 100g of initial litter	Amount remaining as % of initial amount	Amount (loss (-) or gain (+)) (g) per 100g of initial litter
Holocellulose						
0	0	100	81	81.0	100	
20	14.4	85.6	76.5	65.5	80.9	-15.5
40	22.0	78.0	71.5	55.8	68.9	-25.2
Soluble carbohydrate						
0	0	100	2,8	2.8	100	
20	14.4	85.6	1.68	1.4	50	-1.4
40	22.0	78.0	1.35	1.1	37.6	-1.7
Soluble tannin						
0	0	100	1.5	1.5	100	
20	14.4	85.6	0.34	0.3	20	-1.2
40	22.0	78.0	0.33	0.26	17.3	-1.24
Ash						
0	0	100	5.7	5.7	100	
20	14.4	85.6	2.1	1.8	31.6	-3.9
40	22.0	78.0	2.4	1.9	30	-3.8
Potassium						
0	0	100	2.2	2.2	100	
20	14.4	85.6	0.064	0.055	2.5	-2.15
40	22.0	78.0	0.051	0.040	1.8	-2.16
Nitrogen						
0	0	100	0.20	0.20	100	
20	14.4	85.6	0.30	0.26	130	+0.06
40	22.0	78.0	0.34	0.27	135	+0.07
Phosphorus						
0	0	100	0.02	0.02	100	
20	14.4	85.6	0.021	0.018	90	-0.002
40	22.0	78.0	0.028	0.022	110	+0.002
Lignin (estimated by difference)						
0	0	100	8.45	8.5	100	
20	14.4	85.6	18.7	16	189	+7.5
40	22.0	78.0	24	18.7	220	+10.2
Net loss from chemical composition						
20	14.4					16.7
40	22.0					23.7

Table 4.10 The change of chemical composition amounts in pinnule litter

Time (weeks)	Weight loss (%)	Weight remaining (%)	Concentration (%)	Amount (g) remaining per 100g of initial litter	Amount remaining as % of initial amount	Amount (loss (-) or gain (+)) (g) per 100g of initial litter
Holocellulose						
0	0	100	48	48	100	
20	9.9	91.1	37.3	34	70.8	-14
40	20.9	79.1	21.65	17	35.4	-31
Soluble carbohydrate						
0	0	100	4.0	4.0	100	
20	9.9	91.1	2.83	2.6	65	-1.4
40	20.9	79.1	2.73	2.2	55	-1.8
Soluble tannin						
0	0	100	6.5	6.5	100	
20	9.9	91.1	1.98	1.8	27.7	-4.7
40	20.9	79.1	1.4	1.1	16.9	-5.4
Ash						
0	0	100	3.6	3.6	100	
20	9.9	91.1	3.75	3.4	94.4	-0.2
40	20.9	79.1	3.95	3.1	86.1	-0.5
Potassium						
0	0	100	0.16	1.6	100	
20	9.9	91.1	0.08	0.073	4.6	-1.5
40	20.9	79.1	0.09	0.071	4.4	-1.5
Nitrogen						
0	0	100	1.31	1.3	100	
20	9.9	91.1	1.49	1.4	108	+0.1
40	20.9	79.1	1.53	1.2	92	-0.1
Phosphorus						
0	0	100	0.093	0.093	100	
20	9.9	91.1	0.102	0.093	100	
40	20.9	79.1	0.081	0.064	69	-0.029
Lignin (estimated by difference)						
0	0	100	36.2	36	100	
20	9.9	91.1	52.64	48	133	+12
40	20.9	79.1	69.55	55	153	+19
Net loss from chemical composition						
20	9.9					9.7
40	20.9					21.3

In the subsequent four months the rate of chemical changes in both petioles and pinnules slowed down. The concentration of lignin, nitrogen, phosphorus and calcium had increased and organic constituents except lignin, sodium, magnesium decreased. The increased concentration of nitrogen and phosphorus probably results from loss of carbon from litter during decomposition but some fixation of gaseous nitrogen could occur. The net total loss, from chemical components, was estimated to be 23.7% for petioles and 21.3% for pinnules, as compared with 22% of weight loss in petioles and 20.9% of weight loss in pinnules. The close similarity between results from chemical change and weight loss is partly forced by the lignin concentration being estimated by difference rather than by direct analysis ie lignin is taken as the difference between the sum of all measured components and the actual weight. However the results indicate that decomposition of holocellulose is the main process contributing to weight loss.

4.5 The microhabitat variation within sites

The litter microenvironments vary from place to place on Hampsfell and the production of bracken was modified by the depth of soil and by human management. Similarly the bracken litters also showed a variation in rate of decomposition in the various microhabitats (Table 4.11).

The decomposition rate of litters on shallow soil with limestone outcrops was slower than on the deeper soils at other places. The bracken growth on the limestone outcrops was sparse and mixed with a great number of low grass, where bracken is harvested in autumn. The litters were thus exposed to increased radiation and wind. The moisture content of the litter, used as an index of the relative wetness of the micro-habitats, was significantly lower on the outcrops than at other sites.

The relationship of weight loss and respiration to moisture (Table 4.2, Figs. 4.1, 4.2) indicate that the difference in moisture content of litters on shallow and deep soils could account for the observed difference in weight loss. On the other two sites in grassland dense bracken covered the ground, large amounts of litter were accumulated on the soil surface and the moisture contents of litters were high. The weight loss rates of bracken litters on the medium and deep soils were similar to each other (Table 4.12). Analysis of variance of weight loss in petioles in the three grassland sites gave an F ratio = 8.3145, $P < 0.05$, between shallow soil and medium depth of soil and F ratio = 10.930, $P < 0.01$ between shallow soil and deep soil. The decomposition rate of petioles in the woodland was similar to that in the sites with medium and deep soils in grassland. There was a significant difference in the weight loss of bracken petioles between the sites of shallow soil in grassland and deep soil in woodland (F ratio = 17.480, $P < 0.01$). An unexpected and unexplained result is that the decomposition of pinnules in woodland was similar to that on the grassland site with shallow soil, although the moisture content was much higher in the woodland.

4.6 Accumulation of litter

An independent estimate of the rate of disappearance of litters (K_L) can be obtained from the total annual input of litters (L) and the total amount of litters accumulated on the soil surface (X_L). Considering the detritus entering the decomposition subsystem in the nearly pure stand of bracken on Hampsfell, the annual input of bracken litter was about 720 g m^{-2}. The total amount of bracken litter accumulated on soil surface reached 2600-3500 g m^{-2} with some variation from place to place and from time to time (Perkins *et al.* 1978). The appropriate ratio was $K_L = L/X_L$, $K_L = 0.26$. The time taken for 95% of litter standing crop to decompose is $3/K_L$ and is estimated at 10-13 years (Table 4.13). The decay constant $K_L = 0.26$ described the decomposition of

Table 4.11 Weight loss of bracken litter in different grassland and woodland microhabitats

Location	Depth of soil (cm)	Weeks in field	Parts of bracken	Weight loss (%)	Moisture content (% dw)	n
Shallow soil with limestone outcrop in grassland	6.7 ± 1.58	20	petioles	11.61 ± 1.11	171.77 ± 4.64	9
	"	20	pinnules	9.3 ± 0.8	142.62 ± 11.31	9
	"	40	petioles	14.84 ± 1.28	280.41 ± 27.96	8
	"	40	pinnules	18.44 ± 0.55	254.29 ± 38.88	10
Medium soil on gentle slope in grassland	22.5 ± 1.99	20	petioles	14.24 ± 1.44	330.9 ± 26.76	9
	"	20	pinnules	9.5 ± 2.1	369.96 ± 40.22	10
	"	40	petioles	25.83 ± 3.33	520.06 ± 35.22	8
	"	40	pinnules	23.71 ± 3.57	581.42 ± 53.10	10
Deep soil in depression of grassland	36.3 ± 5.79	20	petioles	13.65 ± 0.82	335.39 ± 37.85	10
	"	20	pinnules	9.4 ± 0.9	390.98 ± 29.10	10
	"	40	petioles	21.89 ± 1.48	623.12 ± 19.65	10
	"	40	pinnules	23.88 ± 2.55	702.42 ± 47.12	10
Deep soil in woodland	48.0 ± 7.96	20	petioles	17.67 ± 0.74	246.1 ± 28.48	10
	"	20	pinnules	11.32 ± 2.3	343.5 ± 24.84	10
	"	40	petioles	25.23 ± 1.89	626.93 ± 16.97	9
	"	40	pinnules	17.08 ± 1.33	698.59 ± 8.34	9

Table 4.12 The rate of weight loss of bracken litter in different grassland and woodland microhabitats

Location	Time	Loss rate of petioles % d^{-1}	Loss rate of pinnules % d^{-1}
Shallow soil with limestone outcrop in grassland	December-April	0.083	0.066
	April-September	0.023	0.065
	Overall	0.053	0.066
Medium soil on gentle slope in grassland	December-April	0.102	0.068
	April-September	0.068	0.102
	Overall	0.092	0.085
Deep soil in depression in grassland	December-April	0.098	0.067
	April-September	0.067	0.103
	Overall	0.078	0.085
Deep soil in woodland	December-April	0.126	0.081
	April-September	0.054	0.041
	Overall	0.090	0.061

only the above ground components of the total organic matter in the system and is related only to the earlier stages of decomposition. However, the present decay constant can be regarded as an indication of broad magnitude of organic turnover in a relatively pure stand of bracken.

Swift *et al.* (1979) summarized the constant fraction loss rate K_L in six ecosystems types. The K_L value of bracken on Hampsfell is similar to that in boreal forest (0.21) but is lower than K_L in temperate deciduous forest (0.77) and grassland (1.5) although the input of litter is similar. The rate of disappearance of bracken litter therefore apprears to be a slower process than decomposition of grasses in grassland.

4.7 Rates of decomposition of bracken litter

Three independent approaches have been used to estimate the decomposition rate of bracken litter. Despite differences in techniques, these estimates are all of the same order of magnitude. 1) The weight loss of litter components was 20-22% after 40 weeks in field from which was derived the annual decay rate of 0.317 - 0.321 g g^{-1} yr^{-1} using an exponential regression of $\log_e$ weight remaining of litter against time. 2) The predicted value of total annual O_2 consumption by respiration in litter components showed that 21.04 - 24.38% weight loss were resulted from microbial respiration. 3) The constant fraction loss rate of total surface bracken litter, estimated from input and accumulated standing crop, was 0.26.

Table 4.13 Production and decomposition in a nearly pure stand of bracken on Hampsfell.

Net aerial primary production (g m^{-2})		940 ± 87.9
Litter input (g m^{-2} yr^{-1})		719 ± 55.2
Litter standing crops (g m^{-2})	April	3265 ± 310.4
	July	2625 ± 184.4
	September	2610 ± 412.3
Constant fraction loss rate (K_L)		0.26 (0.22-0.28)
95% turnover time ($3/K_L$ years)		10 - 13

5 NUTRIENT CYCLING IN BRACKEN GRASSLAND

In the moist mild climate of Hampsfell temperature and rainfall provide essential growth conditions for bracken, while the nutrient availability in soil strongly affects the productivity of bracken. The nutrient cycle within an ecosystem consists of the uptake of nutrients in inorganic form by plants from the soil and atmosphere. Through photosynthesis these inorganic elements are incorporated into more complex organic compounds within the plants; some nutrients are retained as current production, but a proportion is returned to the soil by the leaching of rainfall, or as litter fall and through the later death of plants. After re-mineralizing, the nutrients in dead organic material are again available for uptake by the vegetation. Additionally there are subsidiary cycles via secondary procedures but these are not considered in the present paper.

The depth and fertility of soil on Hampsfell influenced the production of bracken. The bracken absorbed available nutrients from the soil and reached the maximum biomass in the mid-summer. Before death some nutrients were translocated into below ground parts of bracken. Bracken died in the late autumn, some of the standing dead was harvested and eventually the remainder fell to the ground as surface litter. The surface litter is probably the major input of nutrients to soil although the decomposition rate of bracken was slow. An important approach was to determine and evaluate the cycle of plant nutrients together with the losses and gains for the whole ecosystem. The plant samples for chemical analysis were collected four times a year (February, May, July and November).

5.1 The nutrient budget in the soil of Hampsfell

A soil survey in Hampsfell was undertaken in April 1980. Fifteen profiles were described, 47 samples including various depths of soil profiles were obtained and eleven chemical variables were assessed for each sample.

Table 5.1 summarises the soil variables for Hampsfell. The soil which is a shallow rendzina, was rich in calcium, which showed large variation in the different profiles. The quantities of nutrients decreased from surface layer to deeper for each profile.

The variation between samples and depths is considerable and, to determine the main patterns of variation and interrelationship between the chemical variables, a series of statistical analyses were used; first a correlation matrix, then principal components analysis and finally cluster analysis.

The correlation matrix (Table 5.2) showed a strong positive correlation of acidity with calcium; loss on ignition was positively related to N, P, K, Mg and Na; extractable K, Na, Mg, Mn and total N were significantly related to most other variables; only Fe showed little correlation with other elements. Thus there is a strong, usually positive, relationship between most of the chemical variables. To determine the general pattern of relationships and to see whether or not there is a single common gradient the correlation matrix was used to derive eigenvalues and eigenvectors (Table 5.3, 5.4). A high proportion (51%) of the total variation was expressed by the first component which was dominated by loss on ignition and the variables identified above (N, P, K, Mg, Na). This component reflects the soil organic matter content and plant nutrients. The second component contributes an additional 24% and reflects the calcium content and pH. The third and subsequent components are much less important than the first two.

The cluster analysis (Fig. 5.1) did not show very distinct clustering of the sample but some groupings can be identified, particularly the separation of the superficial samples within which there is a group containing high Ca concentration. A group of Ca-rich samples is identified from a variety of depths. The remaining majority of samples is mainly from deeper horizons and shows little clustering.

Table 5.1 Summary of soil variables on Hampsfell

Variables			Mean	S.D.	C.V.%
1.	pH		5.05	1.05	20.7
2.	LOI (Loss on ignition) %		18.4	13.9	75.7
3.	Extractable Na	mg 100 g^{-1}	6.27	5.02	80.0
4.	Extractable K	mg 100 g^{-1}	15.76	15.81	100.3
5.	Extractable Ca	mg 100 g^{-1}	290.1	558.5	192.5
6.	Extractable Mg	mg 100 g^{-1}	9.71	9.17	94.5
7.	Extractable Fe	mg 100 g^{-1}	0.966	1.382	143.0
8.	Extractable Mn	mg 100 g^{-1}	8.48	9.24	109.0
9.	Extractable P	mg 100 g^{-1}	0.272	0.523	192.5
10.	Total P	% dry weight	0.050	0.022	44.0
11.	Total N	% dry weight	0.705	0.463	65.6

Table 5.2 Coefficients of the correlation between soil variables

	pH	LOI	extractable Na	K	Ca	Mg	Fe	Mn	P	Total P	Total N
pH	1										
LOI	0.166	1									
Na	-0.165	0.883***	1								
K	0.113	0.815***	0.685***	1							
Ca	0.857***	0.086	0.39**	0.116	1						
Mg	0.246	0.828***	0.86***	0.706***	0.433**	1					
Fe	-0.409**	0.266	0.076	0.349	-0.265	-0.008	1				
Mn	0.415**	0.273	0.404**	0.394**	0.48***	0.646***	-0.275	1			
P	-0.228	0.845***	0.776***	0.577***	-0.047	0.591***	0.05	0.101	1		
Total P	0.319*	0.388**	0.451**	0.532***	0.38**	0.568***	0.111	0.731***	0.22	1	
Total N	-0.042	0.933***	0.852***	0.813***	0.186	0.854***	0.268	0.396**	0.724***	0.558***	1

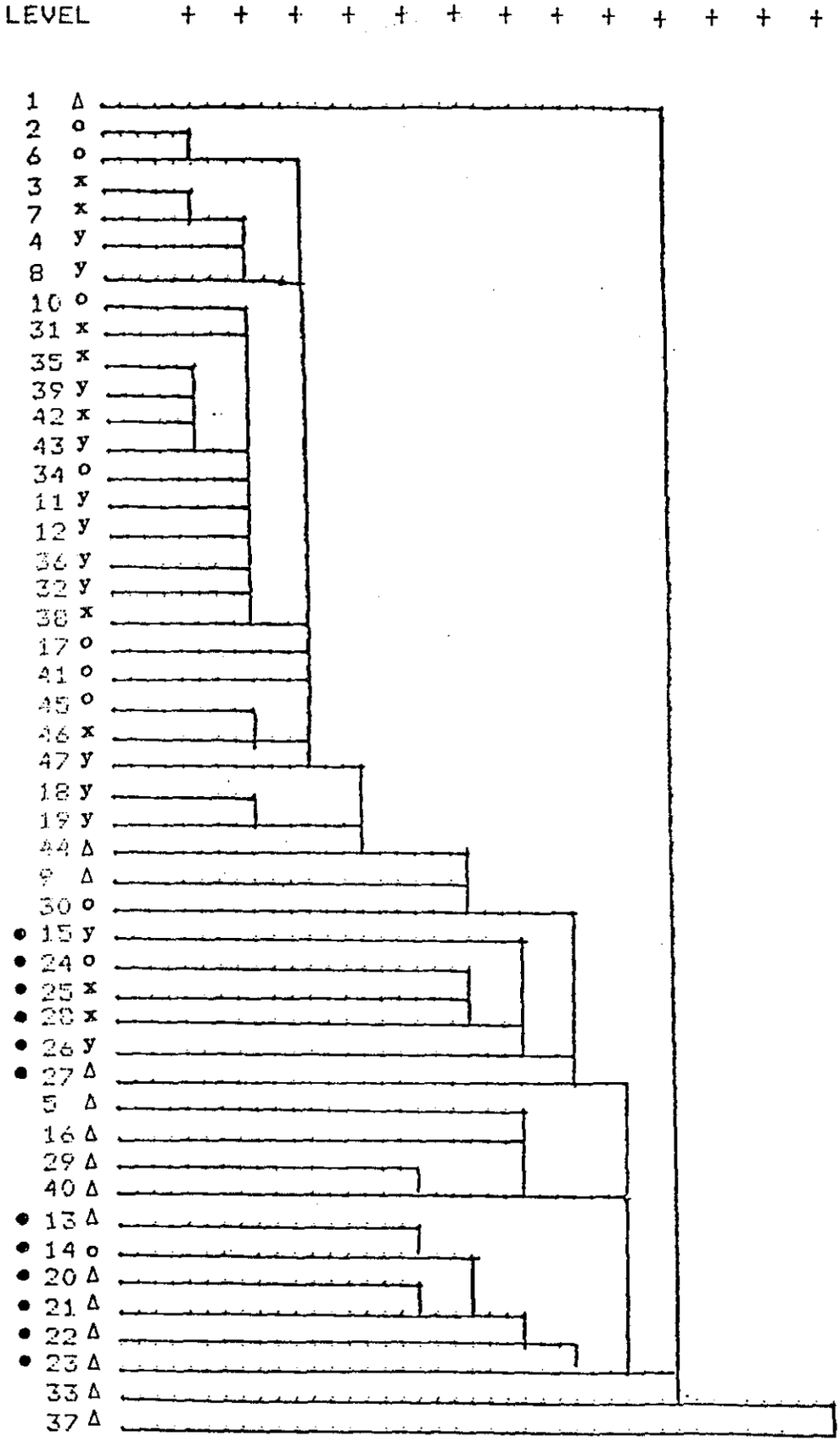
* P = <0.05
** P = <0.01
*** P = <0.001

Table 5.3 Eigenvalues of the first five components of soil variables in Hampsfell

Component	Eigenvalue	Proportion of variability	Cumulative proportion %
1	5.62	51.10	51.10
2	2.64	24.02	75.10
3	1.06	9.63	84.75
4	0.77	7.00	91.75
5	0.31	2.83	94.58

Table 5.4 Eigenvectors of the first five components of soil variables in Hampsfell

Variables		Coefficient for component				
		I	II	III	IV	V
pH	X_1	0.1472	[illegible]	-0.0993	-0.6823	0.2301
LOI	X_2	[illegible]	-0.3866	-0.2256	-0.1224	-0.1280
Extractable Na	X_3	[illegible]	-0.0232	-0.3869	-0.3556	0.1360
Extractable K	X_4	[illegible]	-0.2700	0.3586	-0.0194	-0.5963
Extractable Ca	X_5	0.3896	[illegible]	-0.0820	[illegible]	-0.1043
Extractable Mg	X_6	[illegible]	0.1632	-0.1278	0.0758	-0.5547
Extractable Fe	X_7	0.1489	-0.6450	[illegible]	[illegible]	0.0636
Extractable Mn	X_8	0.6170	0.6322	0.3790	[illegible]	-0.3756
Extractable P	X_9	[illegible]	-0.4411	-0.6912	0.1270	[illegible]
Total P	X_{10}	0.7034	0.3714	[illegible]	0.4852	[illegible]
Total N	X_{11}	[illegible]	-0.2270	0.0343	-0.0843	0.0182



The layers of soil (cm) Δ >0 x 10-20 • Ca content >2 mg/g
o <10 y 20-30

Fig. 5.1 Dendrogram for cluster analysis of soils in Hampsfell

From the data on concentration, and known depths and densities of the horizons the total amount of nutrients per unit area was calculated (Table 5.5).

5.2 The nutrients in bracken

The chemical composition of bracken has been reported in a series of papers (Hendrick 1918, 1921; Ferguson 1944; Hunter 1944, 1953) which showed that the nutrient content varied from different parts of bracken and from time to time. The nitrogen and potassium are principal elements in above ground parts of bracken. The major nutrient elements, such as nitrogen, phosphorus and potassium, in fronds changed considerably during the growing season, concentrations were highest in May and lowest in November, but relatively little variation occurred in rhizomes. In mid-summer the fronds had grown robustly and the large amounts of nutrients probably had been exported from the root system (including rhizomes and roots) with a decrease in the nutrient contents in the root system. The relatively large mass of the rhizome means that a small change in concentration of rhizomes could account for a large change in concentration of above ground parts. When the bracken fronds turned brown the nutrients in fronds significantly declined through translocation to the root system where concentration rose (Table 5.6) and also through leaching.

In general the concentration of elements was similar in pinnules and petioles except that P and N were about double in pinnules probably reflecting their higher protein content. The greater intercorrelation in pinnules and petioles than in rhizomes probably reflected greater seasonal variation (Tables 5.7-5.9). In pinnules and petioles, and to a lesser extent in rhizomes, N and P were strongly correlated with other elements, the correlation with Ca, Na, Mn being negative reflecting the opposite seasonal trends identified from Tables 5.7,5.8. In the pinnules and petioles Na, K, Ca and Mg were significantly intercorrelated. The concentrations of Na,

Fe and Ca were remarkably higher, by up to 10x, in rhizomes than in fronds. In contrast N, P, K were higher in pinnules and petioles than in rhizomes in the early part of the year but the relative position was reversed in autumn.

5.3 Nutrient cycling in bracken

The distribution and circulation of nutrients in bracken grassland is closely related to the dry matter of bracken. Therefore the dry matter cycle is described first.

The biomass of live fronds in July was 770 g m^{-2} assumed to be the maximum biomass, of which 587 g m^{-2} died. Therefore 183 g m^{-2} was translocated from above to below ground parts before death. The live root system increased from a winter minimum of 1564 g m^{-2} to an autumn maximum of 2986 g m^{-2}. Assuming a steady state, 1564 g m^{-2} will be present at the end of the winter, therefore 1422 g m^{-2} is lost over winter presumably in respiration and death. Dead rhizomes decreased from 282 to 121 g m^{-2}, a loss of 161 g m^{-2}, assumed to be through decomposition ie microbial respiration which on a steady state assumption would be replaced by death of live rhizomes. The difference of 1261 g m^{2} is presumably lost in root respiration over winter. Some material from the root system will be used for above ground growth in spring but this will occur after the winter minimum of 1564 g m^{-2}. The over-winter respiration by rhizome is a contribution to gross primary production but not to net primary production (Fig. 5.2). The results represent a first approximate of the transfer rates and cycling of the dry matter.

The best estimate of net primary production assumes no change in standing crop from one year to the next. On this assumption NPP of 748 g m^{-2} was obtained from estimated losses to dead material ie 587 g m^{-2} to standing dead plus 161 g m^{-2} to dead rhizomes. No estimate of loss by root, as opposed to rhizome, death was available.

Table 5.5 The total amount of nutrients in soil g m^{-2}) at an average depth of 25 cm

Dry weight of soil	Extractable (g m^{-2})						Total P	Total N
	Na	K	Ca	Mg	Fe	Mn		
159275	9.99	25.1	462.0	15.46	1.54	13.51	79.64	1124.0

An alternative estimate of net primary production assumes that the below ground increment from winter to autumn represents growth of the population ie the biomass is expanding within the site or may be expanding outwards with translocation. Given the assumption of growth the estimate of NPP was 2170 g m^{-2} yr^{-1} ie 587 to standing dead plus 161 to dead rhizomes, plus 1422 increment in root system. This is slightly higher than the earlier estimate in NPP by accounting for dead rhizomes.

Efficiency of bracken is indicated by the turnover, $\frac{\text{NPP}}{\text{standing crop}}$. The standing crop varied over the year from a minimum of 1564 g m^{-2} in winter to 2766 g m^{-2} in summer, giving a mean value of 2165 g m^{-2}. Efficiency is therefore 0.345, assuming NPP of 748 g m^{-2} or 1.00, assuming NPP of 2170 g m^{-2}. The lower estimate of turnover is similar to that of *Calluna* at Moor House, while the higher estimate is similar to *Eriophorum* at Moor House and to the *Festuca-Agrostis* grassland in Snowdonia (Smith & Forrest, 1978; Perkins *et al.* 1978).

The nitrogen content of the live standing crop increased from 14.8 g m^{-2} in winter to 27.1 g m^{-2} in autumn, an increment of 12.3 g m^{-2} yr^{-1}. An estimated 4.1 g m^{-2} was lost to standing dead in autumn. The loss to dead rhizomes was estimated as 0.97 g m^{-2} yr^{-1}. The annual uptake by the population on Hampsfell was therefore 16.4 g N m^{-2}. Leaching from the canopy is probably negligible (Carlisle *et al.*1967, Brown 1974). The

observed increment in standing crop (12.3 g N m^{-2}) may be lost over winter if steady state is assumed and the autumn standing crop returns to the level of the winter, or it may be retained if the population is growing (Fig. 5.3).

The annual cycle of nitrogen started with a below ground standing crop of 14.8 g N m^{-2}. By spring the increase in above ground part (1.5) and the increment to below ground standing crop of 3.6 g m^{-2} indicated an uptake of 5.1 g m^{-2} between February and May. During summer the further above ground increment was contributed from translocation from the root system, which although showing a decrease in standing crop, amounted to about 5.4 g m^{-2} from May to July. In autumn the senescence of live fronds resulted in a loss of 4.1 g m^{-2} to standing dead and resorbtion of 7.7 g m^{-2} which contributed to the below ground increment, the latter however still required an uptake of 5.9 g m^{-2} between July and November to balance. From the autumn below ground standing crop, 0.97 g m^{-2} is lost to dead rhizomes, and 12.3 g m^{-2} is either lost by leaching over winter or contributes to an incrementing standing crop. Efficiency of utilization of nitrogen in bracken (uptake: mean standing crop) was 0.82. The efficiency of nitrogen uptake from soil was 0.015.

An increment of 1.82 g m^{-2} of phosphorus content in live standing crop appeared during the growing season. An estimated 0.29 g P m^{-2} is lost to standing dead in autumn. The annual uptake by bracken on Hampsfell reached 2.12 P m^{-2}. Leaching caused a loss of 0.009 g m^{-2} P per year (Fig. 5.4). The phosphorus in standing crop averaged 2.05 g m^{-2}. The turnover rate of phosphorus in bracken stands was 1.03. The total phosphorus in soil was 80 g m^{-2} but extractable phosphorus in soil was extremely low (0.43 g m^{-2}). Efficiency of total phosphorus uptake from soil was 0.03, but uptake was 5x the amount of extractable phosphorus.

The potassium flow in bracken grassland showed a slightly different pattern from other elements, leaching caused a higher loss of 0.94 g m^{-2} yr^{-1}. An increment of 8.6 g m^{-2} of potassium content in standing crop was obtained from February to November. In midsummer a large amount of potassium was taken up from soil, but no more uptake was required in autumn (Fig. 5.5). The annual uptake of potassium by bracken reached 14.9 g m^{-2} giving a turnover rate of 0.59. The efficiency turnover of extractable potassium absorbed from soil was 0.59.

Bracken absorbed 12.8 g m^{-2} of calcium from soil during growing season compared to the amount in standing crops of 7.5 g m^{-2} (Fig. 5.6). The turnover rate (1.71) of calcium was higher than other elements. The efficiency of extractable calcium from soil was 0.028.

Table 5.6 The concentrations of nutrients (mean% ± se) in bracken with time

Date	Part of bracken	Na	K	Ca	Mg	Fe	Mn	P	N
May	Pinnules	0.026 ±0.001	3.13 ±0.060	0.14 ±0.007	0.30 ±0.004	0.025 ±0.006	0.017 ±0.001	0.69 ±0.039	4.64 ±0.099
July	Pinnules	0.073 ±0.013	2.21 ±0.16	0.45 ±0.050	0.20 ±0.005	0.009 ±0.002	0.037 ±0.005	0.19 ±0.018	1.96 ±0.081
November	Pinnules with a few petioles	0.030 ±0.003	0.14 ±0.024	0.36 ±0.025	0.11 ±0.009	0.039 ±0.013	0.028 ±0.005	0.078 ±0.011	1.09 ±0.074
May	Petioles	0.028 ±0.001	3.40 ±0.011	0.094 ±0.011	0.15 ±0.007	0.007 ±0.0007	0.0068 ±0.0005	0.28 ±0.021	2.22 ±0.095
July	Petioles	0.092 ±0.017	1.99 ±0.17	0.13 ±0.009	0.064 ±0.002	0.0018 ±0.0004	0.011 ±0.001	0.069 ±0.009	0.58 ±0.037
November	Petioles	0.058 ±0.005	0.43 ±0.096	0.37 ±0.078	0.12 ±0.019	0.014 ±0.0004	0.021 ±0.002	0.035 ±0.003	0.51 ±0.049
February	Rhizomes and roots	0.25 ±0.026	1.09 ±0.099	0.30 ±0.093	0.18 ±0.011	0.13 ±0.011	0.023 ±0.004	0.092 ±0.014	0.95 ±0.11
May	Rhizomes and roots	0.28 ±0.034	0.96 ±0.079	0.37 ±0.10	0.22 ±0.011	0.21 ±0.021	0.020 ±0.002	0.095 ±0.003	1.06 ±0.12
July	Rhizomes and roots	0.30 ±0.032	0.78 ±0.12	0.38 ±0.16	0.22 ±0.018	0.21 ±0.028	0.017 ±0.002	0.074 ±0.015	0.68 ±0.094
November	Rhizomes and roots	0.21 ±0.029	0.86 ±0.078	0.52 ±0.23	0.18 ±0.012	0.15 ±0.014	0.015 ±0.001	0.11 ±0.020	0.91 ±0.11
February	Dead rhizomes	0.079 ±0.007	0.42 ±0.055	0.17 ±0.056	0.15 ±0.016	0.23 ±0.022	0.024 ±0.003	0.048 ±0.006	0.57 ±0.043
May	Dead rhizomes	0.059 ±0.008	0.27 ±0.028	0.43 ±0.19	0.10 ±0.003	0.33 ±0.020	0.022 ±0.004	0.043 ±0.003	0.62 ±0.047

Table 5.7 Coefficients of the correlations between nutrients in the pinnules

	Ash	Na	K	Ca	Mg	Fe	Mn	P	N
Ash	1								
Na	-0.674**	1							
K	0.938***	-0.748***	1						
Ca	-0.64**	0.841***	-0.671**	1					
Mg	0.769***	-0.501*	0.757***	-0.737***	1				
Fe	0.326	-0.252	0.375	-0.319	0.574*	1			
Mn	-0.352	0.065	-0.283	0.493*	-0.734***	-0.293	1		
P	0.722***	-0.671**	0.782***	-0.823***	0.93***	0.603**	-0.519*	1	
N	0.822***	-0.682**	0.848***	-0.83***	0.965***	0.536*	-0.605**	0.968***	1

* P = <0.05
** P = <0.01
*** P = <0.001

Table 5.8 Coefficients of the correlations between nutrients in the petioles

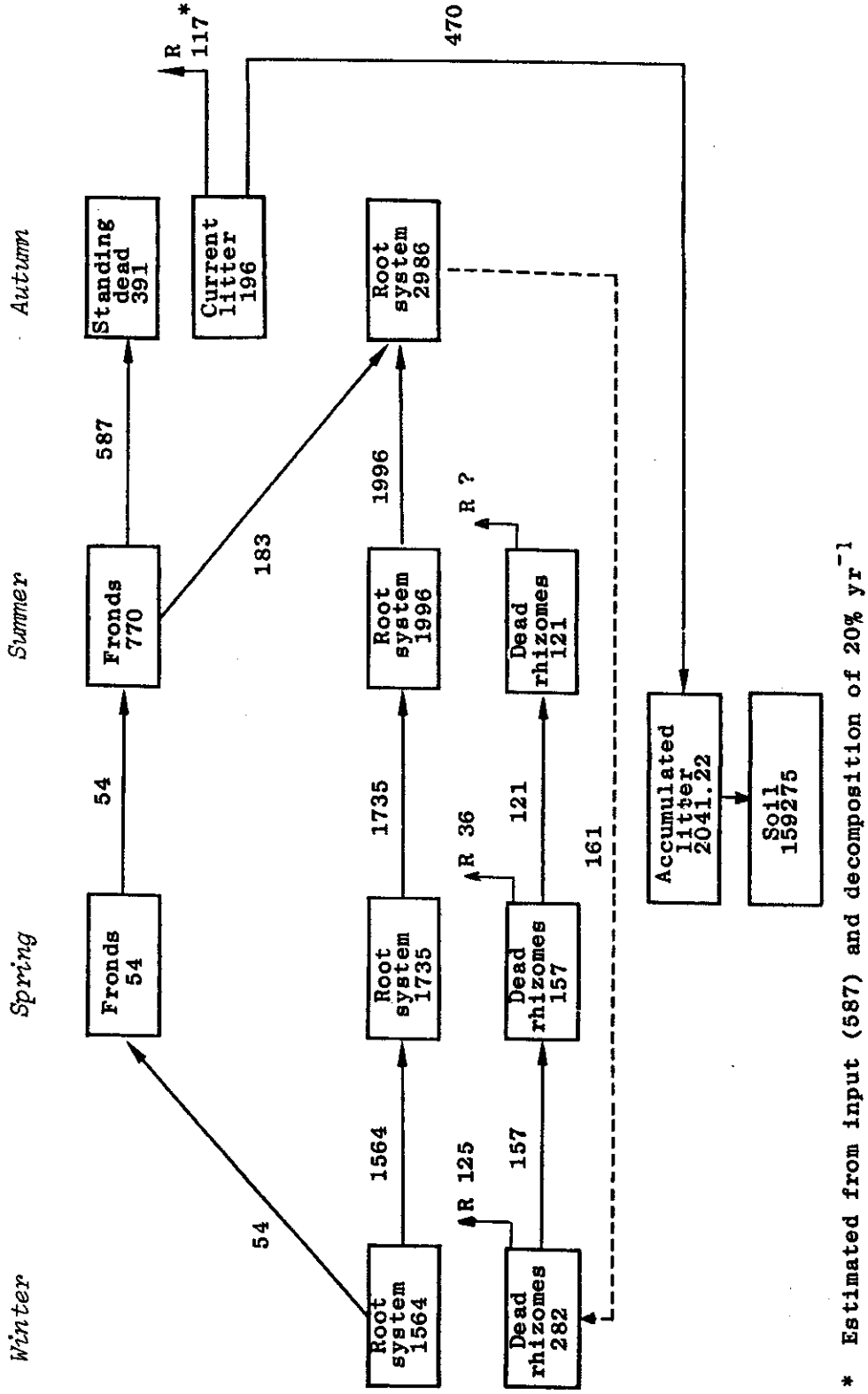
	Ash	Na	K	Ca	Mg	Fe	Mn	P	N
Ash	1								
Na	-0.718***	1							
K	0.972***	-0.807***	1						
Ca	-0.451	0.689**	-0.569*	1					
Mg	0.931***	-0.584**	0.874***	-0.399	1				
Fe	0.806***	-0.573*	0.76***	-0.421	0.826***	1			
Mn	-0.175	0.127	-0.136	0.264	-0.413	-0.312	1		
P	0.899***	-0.713***	0.887***	-0.62**	0.94***	0.827***	-0.369	1	
N	0.925***	-0.646**	0.873***	-0.418	0.974***	0.821***	-0.475*	0.919***	1

* P = <0.05
** P = <0.01
*** P = <0.001

Table 5.9 Coefficient of the correlations between nutrients in the rhizomes

	Ash	Na	K	Ca	Mg	Fe	Mn	P	N
Ash	1								
Na	-0.074	1							
K	0.195	0.122	1						
Ca	0.032	-0.313	-0.233	1					
Mg	0.276	-0.329	-0.406	0.543***	1				
Fe	0.8***	-0.247	-0.076	-0.103	0.408	1			
Mn	0.386	-0.037	-0.168	0.396	0.305	0.351	1		
P	0.127	0.066	0.515*	-0.423*	-0.57**	-0.066	-0.054	1	
N	0.079	-0.547***	0.053	0.616**	0.555**	0.107	0.25	-0.321	1

* P = <0.05
** P = <0.01
*** P = <0.001



* Estimated from input (587) and decomposition of 20% yr^{-1}

Fig. 5.2 The dry matter flow in bracken stands (g m^{-2})

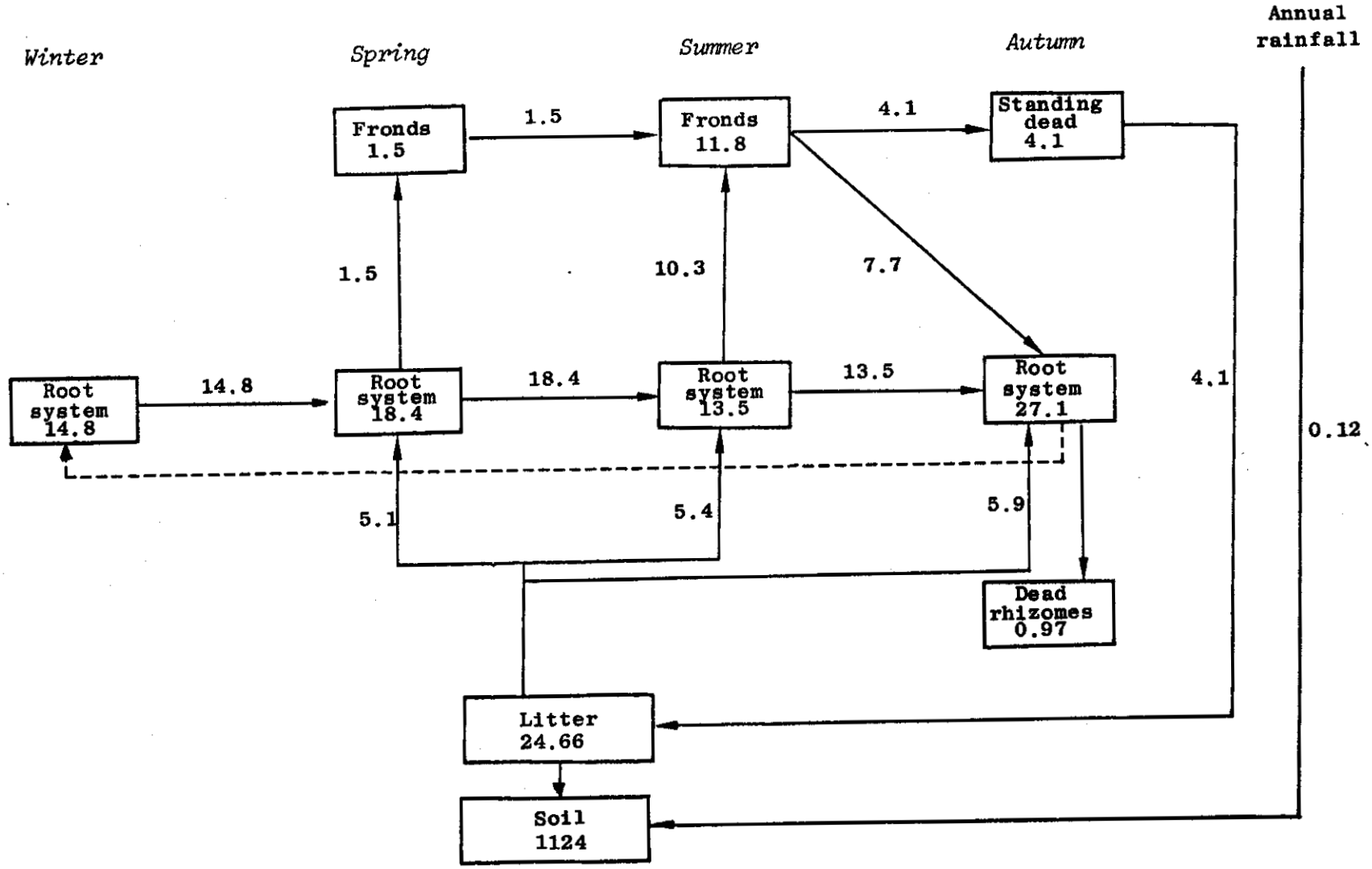


Fig. 5.3 Nitrogen flow in bracken stands (g m^{-2})

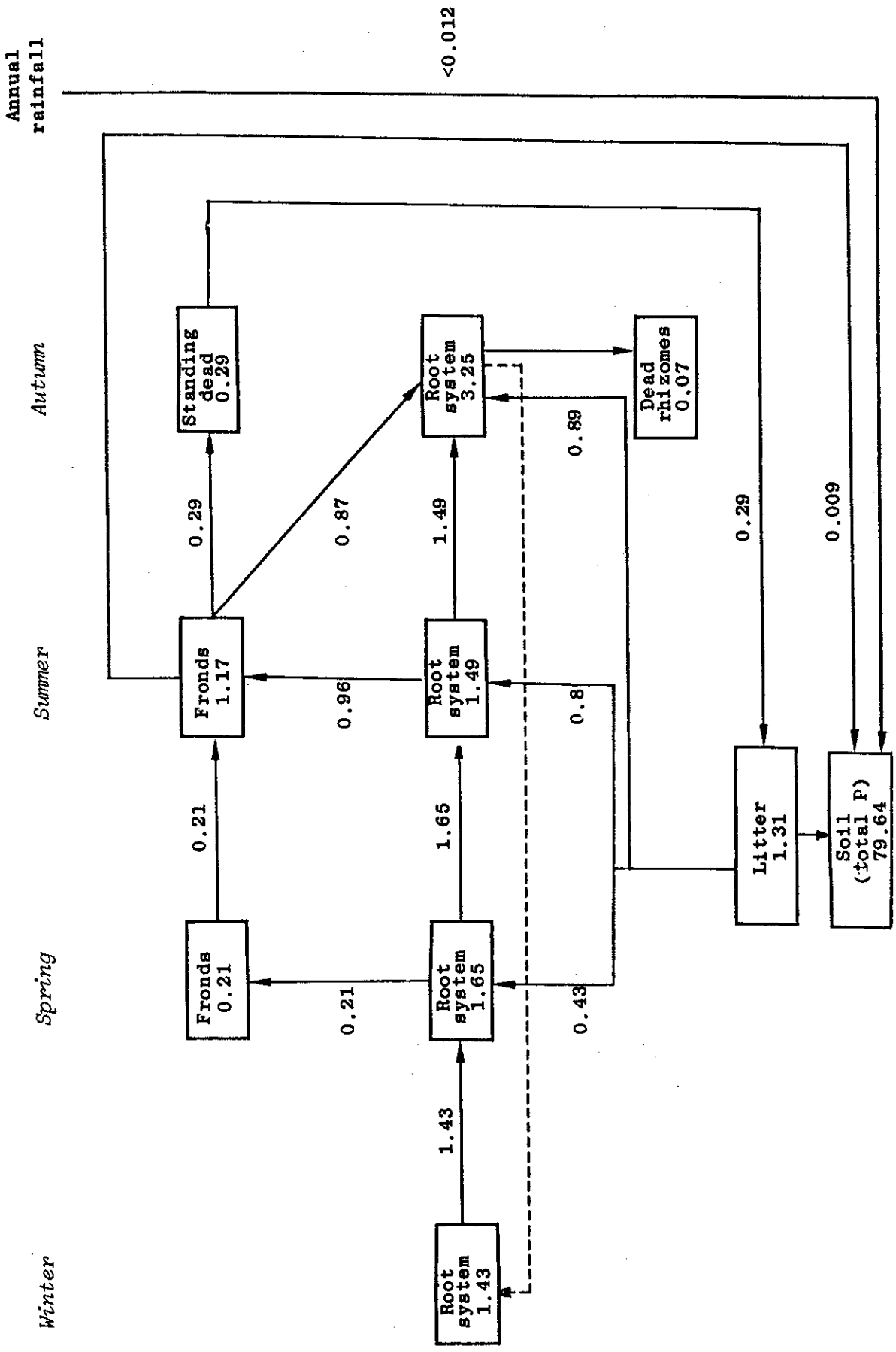


Fig. 5.4 Phosphorus flow in bracken stands (g m^{-2})

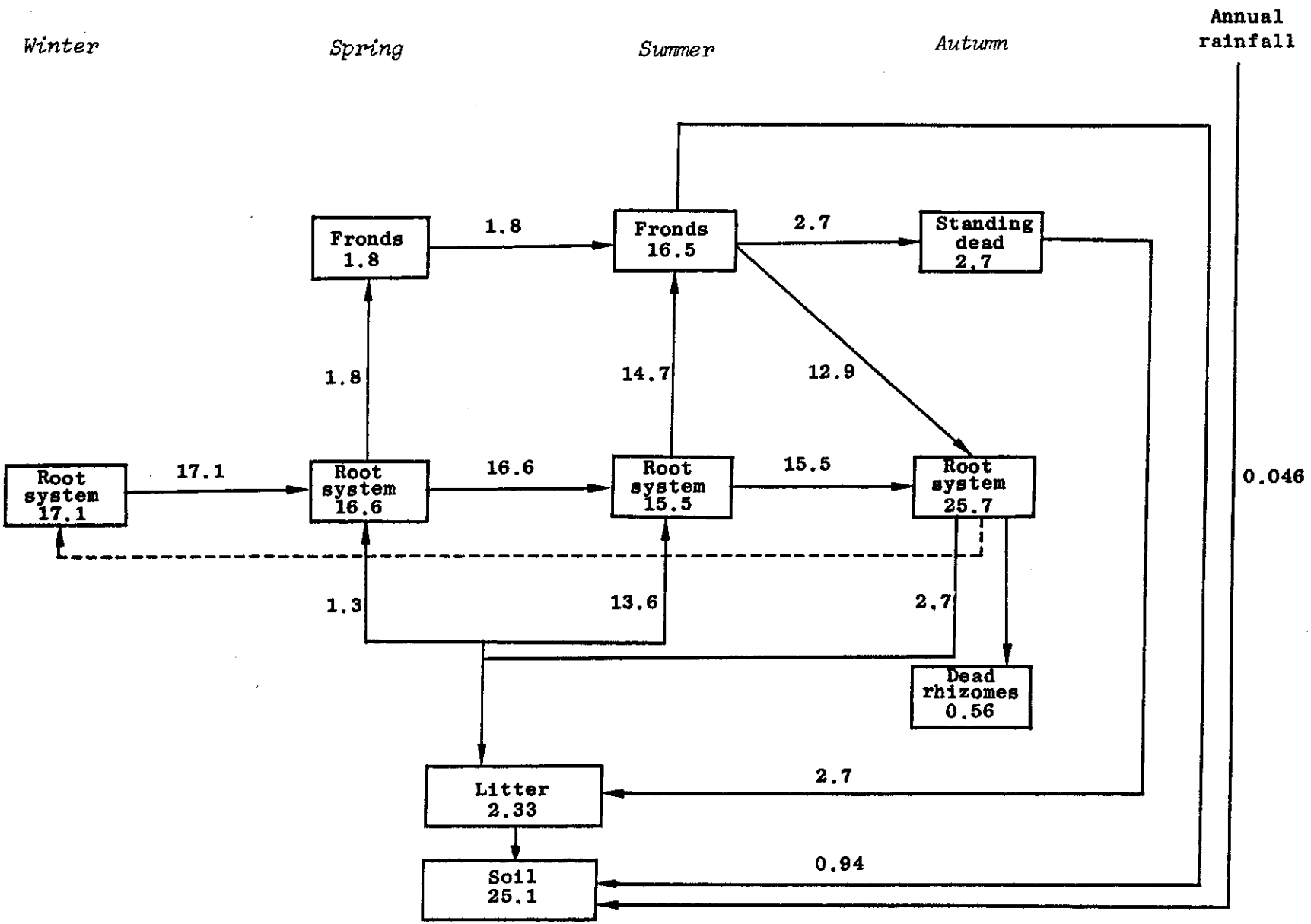


Fig. 5.5 Potassium flow in bracken stands (g m^{-2})

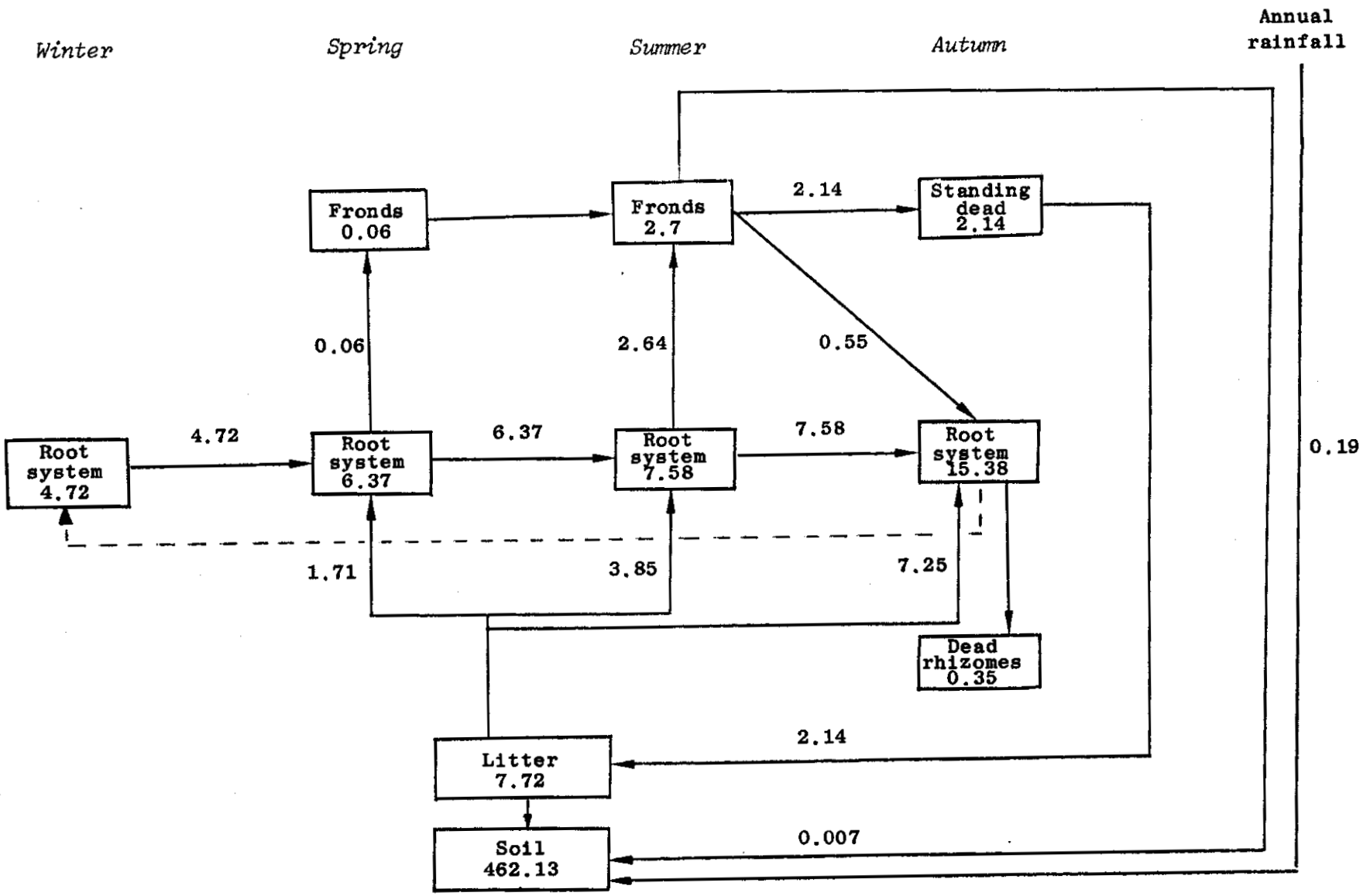


Fig. 5.6 Calcium flow in bracken stands (g m^{-2})

6 SUMMARY

The maximum aerial biomass of bracken on Hampsfell averaged 794 g m^{-2} in August, the seasonal variation of below ground biomass was not marked. The soil depth was one of the most important factors affecting the biomass of bracken. The annual primary production of bracken grassland averaged 2667 g m^{-2} yr^{-1} on deep soil and minimum yield of 1023 g m^{-2} yr^{-1} on shallow soil.

The annual decay rate of bracken litters measured in litter bags was 0.317-0.321 g g^{-1} yr^{-1}. The weight loss predicted from repiration indicated 73-88% of observed weight loss could be attributed to microbial respiration. Based on changes in chemical composition the fraction lost after 40 weeks in field was 0.24. The time taken for 95% litter standing crop to decompose is estimated at 10-13 years, calculated from an estimate of the constant fraction loss rate of 0.26 based on input of litter: litter standing crop. Thus four separate estimates of the annual loss rate range from 0.21 to 0.32.

The nutrient flow in bracken stands during year showed an increment of nutrients in standing crop from winter to autumn, reabsorbing the nutrients from soil to balance. In autumn the senescence of live fronds results in a loss to standing dead and some below ground standing crop is lost to dead rhizomes. Annual uptakes were estimated to be 16.4 g m^{-2} nitrogen, 2.1 g m^{-2} phosphorus, 14.9 g m^{-2} potassium and 12.8 g m^{-2} calcium. The turnover of elements by the bracken, in relation to mean standing crop, ranged from 0.59 for potassium to 1.71 for calcium. Compared with the standing crop in the soil, uptake ranged from 0.015 for nitrogen to 0.59 for potassium. Although the uptake of phosphorus was only 0.03 of the total soil phosphorus, it was 5.0 of the extractable fraction.

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