STUDIES ON PRIMARY PRODUCTION, NUTRIENTS AND DECOMPOSITION IN A MOWN GRASSLAND ECOSYSTEM

by

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ABSTRACT

The effects of mowing intensity and cessation of mowing on ecosystem structure and function in a semi-permanent grassland are studied, with particular application to amenity grasslands. Intensive mowing leads to increased investment in below-ground plant components in the second year after commencement of mowing. Large production following cessation of mowing leads to large surface accumulations of litter which limit grasses but favour the proliferation of forbs. Litter decomposition rates are strongly influenced by a combination of repeated wetting and drying and faunal activity.

Seasonal biomass dynamics of vegetation components are examined. Fluctuations of *N*, *P*, *K*, *Ca*, *Mg*, *Na*, *Mn* and *Zn* concentrations vary between plant components and according to mowing regime and are related to dry matter fluctuations. Nutrients are poorly conserved by grass communities and less than 5% of total ecosystem nutrients are contained within the vegetation, and less than 1% per annum are removed by mowing.

Below-ground components are studied in detail, as roots, rhizomes and a detached root fraction. The root system is categorized and its turnover and contribution to the detritus is considered. Earthworm studies indicate that populations are not enhanced by surface litter accumulations, although their activities can decrease root production without impeding aerial production and affect breakdown of below-ground components.

KEYWORDS : Amenity Grasslands, Mowing, Roots, Nutrients, Litter, Earthworms.

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PLATES 1 & 2 : Botanic Garden site, showing strip-mowing regime (SG, MG and LG). The flattest section of the site, nearest to the glass-houses, was used for the main sampling programme.

PLATES 3 & 4 : Adjoining paddock site (PAD) (above). Surface accumulations of litter lead to the development of tussock vegetation (below).

PLATE 5 : Adjoining paddock (PAD) in June 1979, showing large above-ground proliferation of tall grasses (particularly *Alopecurus pratensis*) and forbs (particularly *Rumex acetosa*).

PLATE 6 : 7 mm mesh litter bags (15 cm x 15 cm) positioned above the vegetation (air zone). Bags were positioned at different levels in the vegetation.

DEFINITIONS OF TERMS

Ash-free dry weight	Oven-dry weight excluding the residue left after combustion of the oven-dry sample at 500°C.
Biomass	Total dry weight or ash-free dry weight of a living plant component at a given time.
Standing crop	Total dry weight or ash-free dry weight of a given living and/or dead plant component at given time.
Nutrient pool	The amount of a given nutrient, expressed as $g.m.^{-2}$, of a given plant components or of soil. Soil pools are calculated to 10 cm. depth.
Capital	Mean biomass on an annual basis.
Turnover	The ratio of nett primary production to mean biomass (*P/B*).

Plant Components

Grass(es)	Above-ground living portions of grasses including leaf sheaths, blades, stolons and flowering parts.
Litter	Dead plant remains attached to or detached from the living plant.
Roots	All visible below-ground parts of plants separated after washing, but before flotation, and excluding rhizomes.
Rhizomes	Underground stems separated after washing including a small proportion of stem bases.
Detached roots	The fraction of plant material which can be separated by flotation after all visible roots and rhizomes have been removed.
Root system	Taken to include roots, rhizomes and detached roots.

CHAPTER 1

INTRODUCTION

Grasslands form a dominant feature of the British landscape, representing a plagioclimax vegetation dependent upon grazing or mowing for their continued existence. Species structure, management and utilization vary considerably, together with substratum, topography and climate. Temporary and permanent grasslands account for 62% of the agricultural acreage in England and Wales, and receive 32% of the fertilizers applied to land (Coppock, 1976). They are often characterized by pure swards or low diversity mixed swards, but include large areas of upland pasture. Permanent pasture and rough grazing cover well over half of the total land surface in Britain (Duffey *et al.*, 1974).

The remaining grassland areas of recreational, functional and aesthetic value, and of which agricultural productivity is not the primary aim, have been classified as amenity grasslands (NERC., 1977). They have been identified as a major natural resource with considerable potential for exploitation (Rorison and Hunt, 1980). Amenity grasslands are widely scattered over 4% of the British Isles, mainly in lowland regions, and range from intensively managed areas, such as sports turves, to road verges and semi-natural grasslands in country parks and nature reserves (Rorison, 1980). Extensively managed areas account for 75% of amenity grasslands, many of which were created and once maintained as part of the agricultural economy (Green, 1980).

Spedding (1971) described the ecology of agricultural grasslands and Duffey *et al.* (1974) discussed the history, classification, biological characteristics and management of semi-natural grasslands in the lowland areas of England. Hutchinson and King (1980) considered management

impacts on the structure and function of sown grasslands, and Harper (1971), Morris (1971), Rorison (1971) and Duffey *et al.* (1974) investigated the management of grasslands for conservation.

1.1 Above-Ground Studies

A review and assessment of the various techniques of estimating primary production from harvest data were presented by Kelly *et al.* (1974) and Singh *et al.* (1975) and methodology has been described by Milner and Hughes (1970). Singh *et al.* (1980) discussed productivity processes in detail. In Britain, primary production studies have been carried out in Pennine grasslands (Welches and Rawes, 1965), Sussex lowland grasslands (Williamson, 1976) and Snowdonia montane grasslands (Perkins *et al.*, 1978).

There is much published information concerning the agricultural aspects of herbivore-pasture interaction (*e.g. see* HFRO., 1979) including the effects of defoliation (clipping) on subsequent regrowth (Bokhari, 1977; Detling *et al.*, 1979) and the effects of grazing on grassland productivity (Sims and Singh, 1971; Vickery, 1972; Caldwell, 1975). Harper (1977) discussed predator-plant interactions and reviewed the effects of grazing animals.

Forbes *et al.* (1977) endeavoured to identify factors limiting output from permanent agricultural pastures, in an attempt to establish priorities for research and development.

1.2 Below-Ground Studies

The importance of below-ground components of grasses as structural, storage and physiologically active organs has been realized (Troughton, 1957; Weaver, 1968; Whittington, 1969; Carson, 1974; Torrey and Clarkson,

1974; Russell, 1977), but for the most part root production has hardly been seriously attempted in ecosystem studies, due to difficulties surrounding its study. Methods of studying root systems are reviewed by Ghilarov *et al.* (1968), Milner and Hughes (1970), Schuurman and Goedewaagen (1971) and Böhm (1979).

The dynamics of root biomass have been studied in various natural grassland ecosystems (Coupland and Johnson, 1965; Dahlman and Kucera, 1965; Bartos, 1971; Ares and Singh, 1974; Kotanska, 1976), in an old field ecosystem (Kelly, 1975) and in a Swedish hay meadow (Nilson, 1970). There have been a few studies in British grasslands (Troughton, 1957; Garwood, 1967; Perkins *et al.*, 1978), but none directly related to amenity grasslands. Perkins *et al.* (1978) recorded minimum root biomass during winter and spring, with maximum during summer in a Snowdonia montane grassland. Troughton (1957) stated that most root growth takes place during spring, with maximum growth reached before that of the herbage, and ceasing altogether by the time of flowering, with further growth in autumn. This seasonal cycle may be altered by severe defoliation, and old roots start to decay about the time of flowering.

Temperate zone grasslands are characterized by a shallow but large root biomass, often exceeding above-ground biomass (Coupland, 1979; Swift *et al.*, 1979). 20-30% of below-ground standing crop may be detrital roots (Clark, as cited by Coleman, 1976) and a considerable deposition of organic debris in soil during growth has been reported (Shamoot *et al.*, 1968; Sauerbeck and Johnen, 1976, 1977). Chapman (1976) considered that studies of relative productivity or nutrient budgets that are based solely on above-ground data are so incomplete that their conclusions are of doubtful validity.

1.3 Decomposition Studies

The integrity of terrestrial ecosystems is maintained by transfers of matter and energy between plant, herbivore and decomposer subsystems (Odum, 1971). In intensively grazed grasslands, herbivores rarely consume more than 25% of nett primary production, although more than half of above-ground production may be removed (Wiegert *et al.*, 1970; Swift *et al.*, 1979). Thus, there is a preponderance of energy flow along decomposer pathways, although energy flow studies have been characterized by emphasis on grazing pathways (Coleman *et al.*, 1976).

The majority of organic matter input into the soil is through root biomass (Schlesinger, 1977; Singh and Gupta, 1977), and the large below-ground component of nett primary production emphasizes the importance of below-ground decomposition studies. A few studies of root decomposition have been carried out (Stenina, 1964; Malone and Reichle, 1973; Wildung *et al.*, 1975; Herman *et al.*, 1977) and Waid (1974) reviewed root decomposition processes. The assessment of underground production, activity and loss rates emerged as a major focal point of research in the post-IBP era (see below) (Coleman, 1976), and Olson (1964) considered this to be one of the most challenging ecological problems in the next half century.

1.4 Nutrient Studies

Seasonal changes in nutrient concentrations result from the movement of nutrients during growth and senescence, although individual elements differ in their mobilities (Pritchard *et al.*, 1964; Allen *et al.*, 1974). Some are retained or translocated, whilst others are rapidly leached from plant tissues (Tukey, 1970; Clement *et al.*, 1972; Taylor, 1979). Koelling and Kucera (1965) found that considerable leaching takes place

from plant materials before deposition in the litter. Amounts of nutrients entering and leaving vegetation are particularly large in grasslands, compared to other ecosystems, because a large proportion of vegetation dies at the end of each growing season (Allen *et al.*, 1974; Jones and Woodmansee, 1979).

Nutrient cycling studies in grassland have been presented by Rodin and Bazilevich (1967), Floate (1970*a-d*), Butler and Bailey (1973), Frissel (1977) and Clark *et al.* (1980). Nitrogen has received particular attention (Delwiche, 1970), and nitrogen budgets (Bokhari and Singh, 1975; Woodmansee *et al.*, 1978) and simulation models (Reuss and Innis, 1977) have been formulated. Jones and Woodmansee (1979) discussed factors controlling the cycling of nitrogen, phosphorus and sulphur in annual grassland ecosystems and Perkins *et al.* (1978) investigated the dynamics of some major mineral nutrients in montane grasslands of Snowdonia.

1.5 Ecosystem Studies

Studies on the ecosystem scale were carried out under the aegis of the International Biological Programme (IBP) Grassland Biome studies, whose objectives were to obtain an integrated study of the basic processes of productivity, energetics and nutrient cycling in grassland, with particular emphasis on natural grasslands (Coupland, 1979). In Britain these studies were restricted to high moorland and montane grasslands, but provided a broad description of ecosystem structure and function (Heal and Perkins, 1978). In the United States a pioneering ecological modelling effort was attempted, to simulate biomass dynamics and responses to grazing, irrigation and fertilization (Innis, 1978; Breymeyer and Van Dyne, 1980). The studies changed the emphasis of many aspects of ecology from qualitative to quantitative phases (Van Dyne, 1978) and

provided models with some predictive capabilities to aid management decisions (Woodmansee, 1978). Other systems models of grasslands have also been published in recent years (Gilmanov, 1977; Parton *et al.*, 1978) and Seligman and Arnold (1980) examined simulation models of intensively managed grazing systems.

In a discussion of the US/IBP decomposition sub-model, Hunt (1977) acknowledged that there may be a problem of formulating a model too far ahead of its data base, but considered the model had not yet reached that stage of development. These programmes have involved large inter-disciplinary research efforts.

1.6 The Study in Perspective

Duffey *et al.* (1974) pointed out that most scientific studies on grasslands have been concerned with artificial swards, with most emphasis on yield and nutritive studies rather than on ecosystem dynamics. They discussed the wide difference of objectives between agriculturalists and wildlife conservationists. Snaydon (1980) accused ecologists and agronomists of separately providing a wealth of information, whilst each group has tended to disregard the work of the other. He asserted that generally ecologists disregard managed ecosystems, and agronomists often consider ecological principles invalid. Amenity grasslands, to a large extent, have been ignored by both. Forbes *et al.* (1977) noted that, with a few exceptions, no major research effort was being made to investigate the special problems of permanent grassland.

Malone (1970) considered that knowledge of the ecological consequences of vegetation management is becoming increasingly important, and that little attention has been given to the influence of cover manipulation on the fundamental processes of ecosystems. Harper (1971) suggested that the most sensitive management is likely to be achieved by an

understanding and manipulation of natural regulation, in order that ecology can become a predictive science. Bradshaw (1980) and Rorison (1980) stressed the lack of nutrient cycling data concerned with amenity grasslands, and considered that the ecosystem approach is most appropriate to research investigations. Grime (1980) stated that research objectives for amenity grasslands should be aimed towards understanding the major ecological processes and their implications for management.

1.7 Objectives

The research programme was planned as an individual study on the ecosystem scale based on limited resources, but which would help to bridge the gulf between ecological and agricultural studies by providing information concerning the natural regulation of grassland ecosystems. A comprehensive ecosystem study was clearly inappropriate, and the principal objectives were to investigate specific areas of grassland ecology which have been considered to be of particular ecological significance but which are poorly described in the literature or otherwise inapplicable to amenity grasslands.

Particular emphasis was directed towards study of the turnover of below-ground components of the vegetation in favour of detailed above-ground productivity studies for which accurate annual productivity estimates were not sought. A large part of the programme was devoted to attempts to elucidate methods which may help to overcome the numerous problems of root system investigations. The probable influence of cover manipulation on below-ground processes is particularly relevant in a management context and was incorporated into the study.

The more important functional significance of the decomposer sub-system, compared to the herbivore sub-system, led to the main emphasis

of the research on the former and particularly to measurements of organic matter input into the soil and breakdown rates. Extensive management of grasslands often leads to large surface accumulations of litter, the breakdown of which is poorly described and therefore was studied in detail. The effects of these surface litter accumulations were compared to a situation of two frequencies of mowing and removal of cuttings. Also the effects of large scale removal of biomass, as cuttings, were investigated.

In view of the significance of nutrients in the dynamic processes of ecosystems and their relevance to management practices, nutrient status and fluxes were investigated, particularly with respect to the implications of mowing or cessation of mowing. Fertilizers were not incorporated into the study.

Annual estimates of productivity and nutrient requirements are most easily obtained in steady-state ecosystems, but it was hoped that manipulation by mowing may provide a better insight into the dynamics of amenity grasslands and lowland pasture.

CHAPTER 2

SITES & METHODS

An area of semi-natural (*or* semi-permanent) grassland was selected as representative of a typical amenity grassland under conditions of extensive management, with no recent history of re-seeding or fertilization. At the onset of the research project in early 1977 the initial aims were to select management criteria broadly based on those of traditional hay meadow or rough pasture (Duffey *et al.*, 1974), typified by grassland management on many nature reserves and much marginal land. However, in 1978 the study was extended to incorporate a wider range of management practices and land usage encountered in amenity grasslands by introducing conditions of more intensive mowing and also sites removed from mowing or grazing pressures.

Ideally these sites would have been established prior to the study, but for statistical validity of comparison a satisfactory experimental design could not easily be achieved from sites of differing locations. The experimental area described below was considered to be the most appropriate basis for experimentation. Limitations of this experimental design are those of the time taken for establishment of stable conditions following the alteration of management regime, which was restricted to less than two complete growing seasons. Longer term effects of these management practices cannot be inferred with certainty from the present study.

2.1 Sites

2.1.1 Background

The principal study area is located inside the University of Keele botanic gardens (*O.S. 118/812449*), 183 metres above sea level and overlying upper carboniferous sandstone (Keele beds), with soil classified as a sandy loam at pH 5 to 5.2. Physical and chemical properties of the soil are tabulated in APP. 1.

The area of grassland was probably last ploughed in approximately 1745, with evidence of a ridge and furrow system remaining, and was enclosed as a paddock between 1880-90 (K. Goodway, *pers.comm.*). The field remained as pasture until 1966 when the site was adopted by the Biology Department and managed, for the most part, by regular mowing and removal of cuttings to maintain lawn conditions.

Additionally, an adjoining paddock was included in the study. Historically similar to the previous site, this field was not adopted by the Biology Department in 1966, and grazing was continued until 1976.

2.1.2 Experimental design

The research project was initiated in early 1977, and during that year the central section ofthe Botanic Garden site, approximately 40 m x 25 m allowing a minimum 10 m border, was mown twice and cuttings were removed. In May 1978 the study area was divided into 15 strips, representing 5 replicates of 3 mowing treatments which provided a compromise between validity of experimental design and ease of management. Each strip was 1.6 m wide, with the central metre used for experimental work, and further sub-divided into two 0.5 m wide strips, allowing ten

replicates of each mowing treatment (*see* FIG. 1). The flattest section of the site was used for the main part of the study.

In the adjoining paddock, a 15 m x 15 m area was fenced off to exclude rabbits, and the central 10 m x 10 m used as the experimental site. The site was divided into seven 1 m wide strips, 10 m in length, with 0.5 m wide pathways between each strip. Each strip was sub-divided into two 0.5 m wide lengths (*see* FIG. 2).

Sampling procedures at both sites are described below.

2.1.3 Mowing treatments

The mowing treatments at each site are shown in TABLE 1.

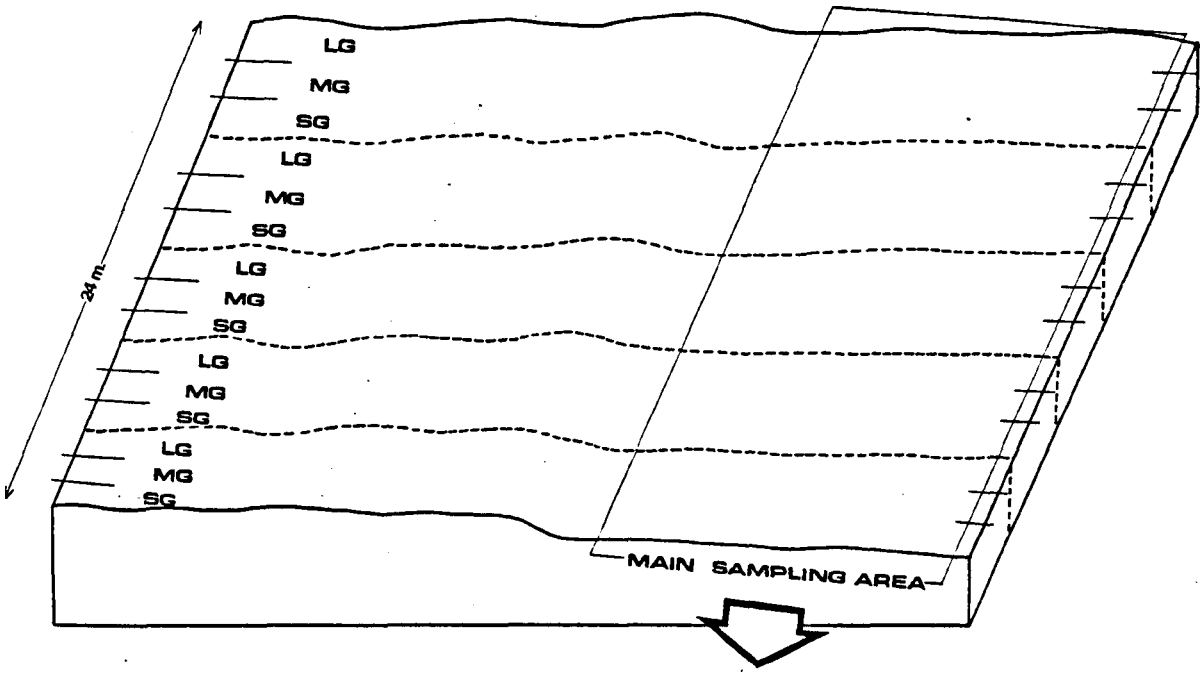
SITE	ABBREVIATION	MOWING TREATMENT
BOTANIC GARDENS	LG	Unmown from beginning of 1978.
	MG	Mown once per year in 1978 and 1979 Cuttings removed.
	SG	Mown regularly (approx. x 6 per year) in 1978 and 1979, to maintain short grass conditions. Cuttings removed
ADJOINING PADDOCK	PAD	Mown once in early 1977. Then unmown

TABLE 1 : Mowing treatments

2.2 Methods

2.2.1 Sampling Programme

Sampling procedures at both sites are outlined in FIGS 1 and 2. Strips in each zone (A, B, C) at the Botanic Garden site, and sampling quadrats in PAD, were randomly selected using random number tables. At the Botanic Garden site samples were grouped into 3 rows of 4 quadrats, to allow easy and rapid location of sampling points. Placement of quadrats in equivalent positions along rows of each treatment was an attempt to help to account for the high variability of below-ground



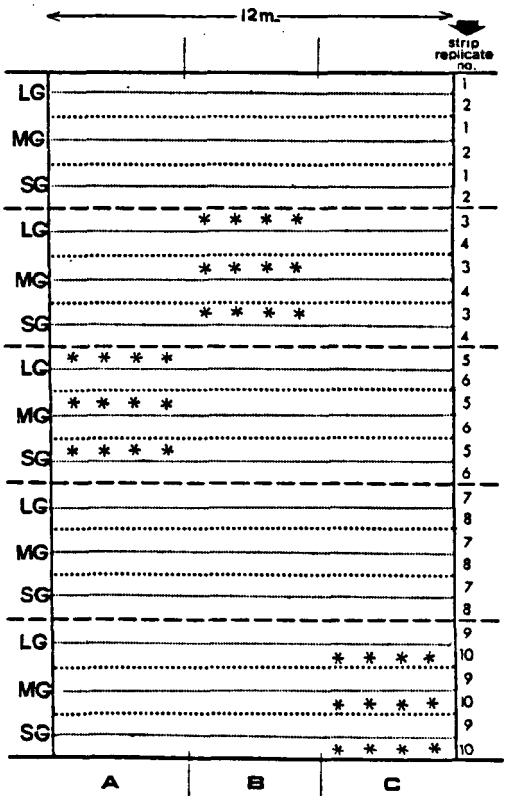


FIG 1 : Botanic Gardens site. Surface contours (above) and strip-mowing regime and main sampling programme (below). Four quadrats were positioned in randomly pre-selected strips in each zone (A,B,C) of each mowing treatment. For example, asterisks indicate positions of quadrats on one sampling occasion (see text).

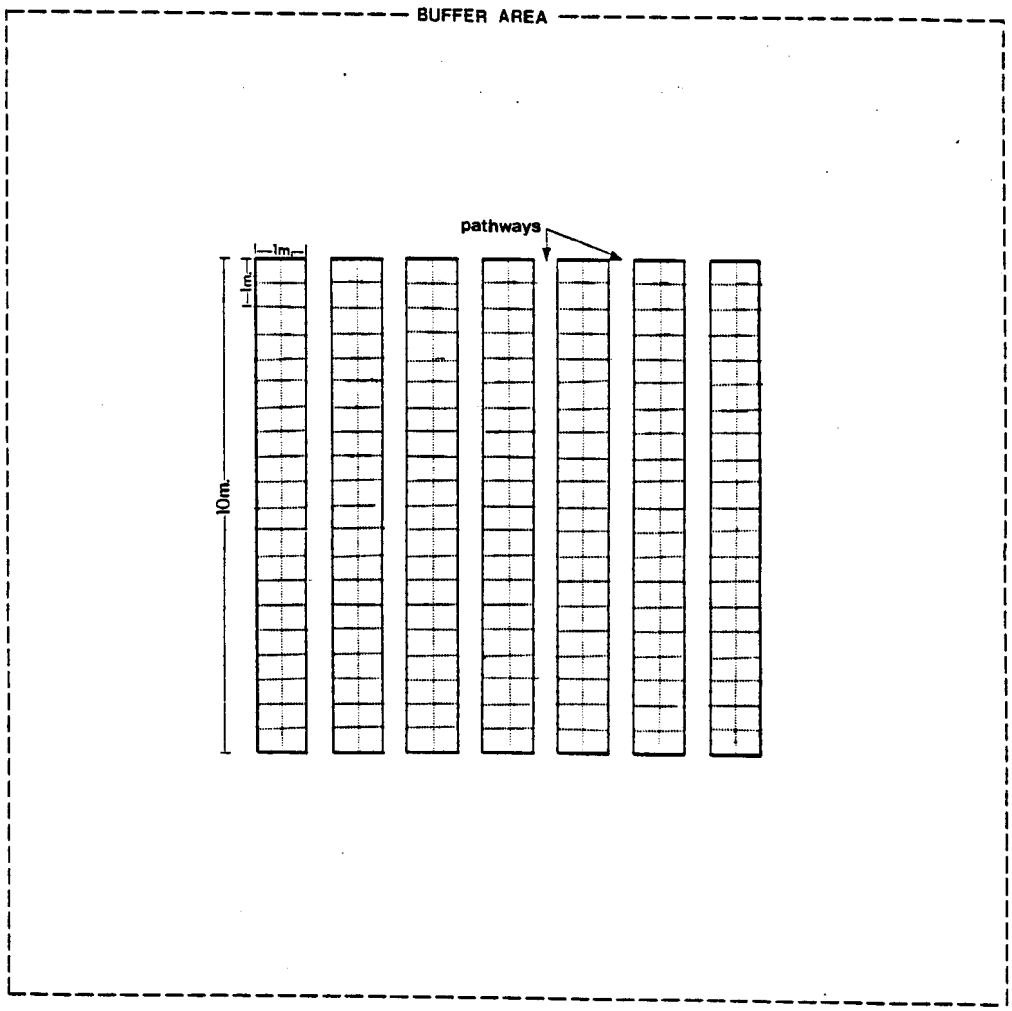


FIG 2 : Site layout in adjoining paddock (PAD). 0·25 m.^{2} quadrats were selected randomly in all experiments.

components by allowing for tests of paired comparisons. However, these techniques provided no advantages over comparisons of means (*also see* 7.3).

The large amounts of replication restricted sampling frequency to six weeks or more. Samples were collected less often in winter.

2.2.2 Above-ground standing crop

At each sampling date, above ground standing crop was cut to ground level inside 0.25 m x 0.25 m quadrats. Twelve replicates were taken in LG and PAD, and six in MG and SG which were sampled less frequently. As above-ground biomass became larger in LG and PAD, quadrat size was increased to 0.25 m^2 with six replicates.

Samples were sorted, often by sub-sampling, into individual species and litter components. They were then dried overnight at 105°C, weighed, finely ground and stored in sealed jars prior to chemical analysis.

2.2.3 Below-ground standing crop

Soil cores of 6.7 cm diameter were taken to approximately 15 cm depth, using a soil corer (APP. 2), then cut into 5 cm depth increments and stored at -18°C prior to washing.

A) Root Separation

Cores were thawed in water and washed over 250 µm brass sieves. The sandy loam separated easily from the root systems, aided by the freezing and thawing, and use of a dispersant (Schuurman and Goedewaagen, 1971) provided no advantages. All visible plant material was removed, re-washed and separated as accurately as possible into *root* and *rhizome* fractions. Any lignified (*forb*) roots were also separated.

The soil remaining in the sieves was transferred to a root washing apparatus (FIG. 3). The apparatus is similar to that used for extracting roots by Cahoon and Morton (1961) and Kummerow *et al* (1978). Considerable amounts of fibrous root material collected in the sieves

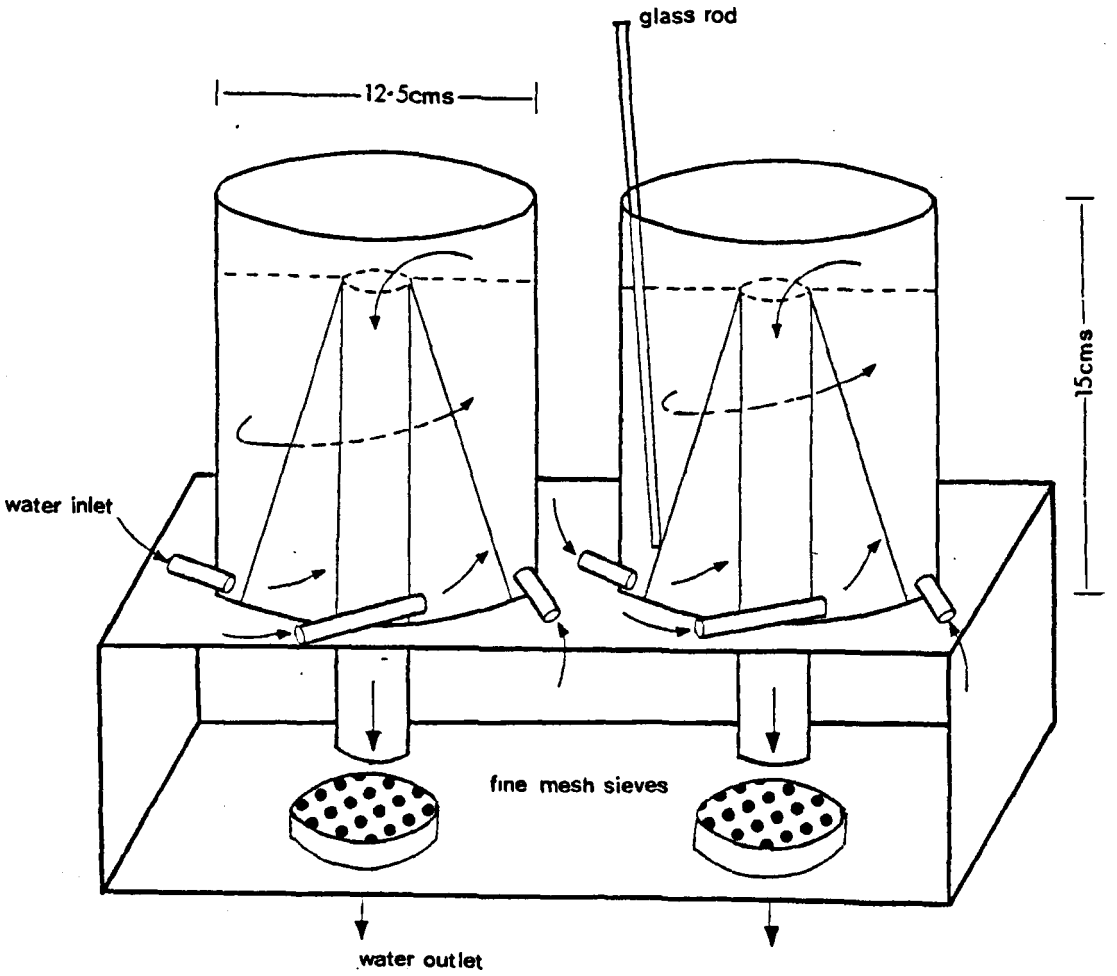


FIG 3 : Flotation apparatus for separation of detached roots from soil. The flotation vessels are made of brass, and separation is assisted by occasional stirring. Detached roots collect in fine mesh sieves (tea strainers).

of the apparatus and washing was continued until no more was removed. Microscopic examination revealed this fraction to consist of varying amounts of small pieces of fine roots with attached root hairs and root tips, an abundance of decaying roots and small pieces of rhizomes. The fraction represented 16-41% ($\bar{x}$ = 28.4%) of the total dry weight of below-ground plant components, and is described separately as *detached roots*. They are considered in more detail in the following chapters.

All below-ground fractions were dried overnight at 105°C, weighed, finely ground and stored in sealed jars prior to chemical analysis. Duplicate sub-samples from each set of samples were ashed at 500°C, to obtain a correction for soil contamination.

B) Vertical Distribution

Most below-ground plant components are near to the surface of the soil. More than 80% of root biomass (FIG. 4) and the entire standing crop of rhizomes are in the surface 10 cms. Standing crop of detached roots below this depth is negligible.

All data concerning below-ground components are represented for the surface 10 cms.

C) Horizontal Distribution

Dry weight distribution of below-ground components is extremely variable in a horizontal plane. The number of replicates (N) required for varying degrees of precision (D) was calculated using the following formula, given by Milner and Hughes (1971):

$$N = \left(\frac{t.s}{D.\bar{x}} \right)^2$$

where

s = standard error of trial samples.

Values of N for soil cores taken in September in SG and LG are shown in

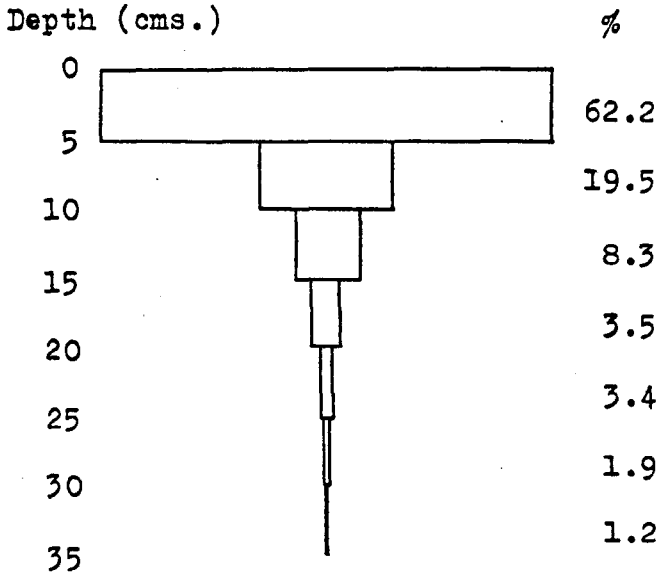


FIG 4 : Percentage of roots (dry weight) at varying depths.

TABLE 2. Clearly, obtaining precision within error limits much less than 5% would be impractical, and 12 replicates were selected as a suitable compromise and used throughout the main sampling programme. Canode *et al.* (1977) similarly found that a 5% error of the mean, with 12 cores, appeared most practicable in root production studies of *Poa pratensis*.

Frequency distributions and spatial distributions of below-ground components are discussed in more detail in APP. 3. Statistics are computed on dry weight data assuming a normal frequency distribution.

Methodology is described further under the relevant section headings. Statistical tests were computed mainly using the *BLIB.* statistical package on the *GEC 4080* at Keele Computer Centre. More detailed statistical analyses are described in the relevant sections.

REQUIRED ACCURACY (ERROR)	BELOW-GROUND COMPONENTS				ABOVE-GROUND COMPONENTS		
	Roots (0-10)	Rhizomes	Detached Roots	TOTAL	Grasses	Litter	TOTAL
(10%)	2.2, 1.5	4.2, 3.3	0.7, 1.4	2.5, 1.4	2.2, 2.3	5.5, 1.1	1.5, 0.6
(5%)	13.1, 9.2	25.1, 19.9	4.3, 8.2	14.7, 8.3	13.2, 13.7	33.0, 6.4	9.2, 3.8
(1%)	645, 452	1235, 980	211, 401	721, 407	649, 672	1623, 316	454, 188

TABLE 2 : Number of samples required for varying degrees of precision (from 6.7 cm diameter soil cores and 0.25 m x 0.25 m quadrats). Calculations represented are from September data. In each case the first figure refers to SG, and the second to LG.

CHAPTER 3

SEASONAL VARIATIONS IN STANDING CROP

The standing crop of above- and below-ground components of the vegetation were monitored during the study period from April 1977 until June 1979 by sampling throughout the year, but more regularly during the growing season. The aims of this part of the work were to examine the structural alterations within the ecosystem according to season and as affected by management regime. The intentions were to develop a monitoring programme against the framework of which additional experimentation could be developed. Thus, for example, periods of maximal changes within the vegetation could be identified which would indicate the optimal times of the year for study of the breakdown of above- and below-ground components. The distribution and investment of plant production in different components of the vegetation are essential to an understanding of the dynamics of the ecosystem.

Alterations of management regimes resulted in grassland ecosystems which were not in a steady state on an annual basis thus rendering productivity estimates less meaningful. Furthermore, accurate annual productivity estimates would entail more regular sampling in order that precise times and levels of peak biomass of different species could be measured together with some estimate of turnover (Singh *et al.*, 1975, 1980). For these reasons inferences concerning nett primary productivity are deferred in the present chapter, but are considered in more detail in Chapter 8 in comparison with other similar studies.

Methodology follows that described in the previous chapter. Results are considered in broad terms for both sites, followed by more detailed specification. Data are presented graphically in most instances, but where necessary are tabulated fully in the appendices together with appropriate tables or statistical analyses not included in the main text.

3.1 Standing Crop: Botanic Garden Site

Above and below-ground variation of standing crop from April 1977 to June 1979 is illustrated in FIG. 5, together with a summary of management variables (detailed in section 2.1.3).

During 1977, the entire site was mown twice; less frequently than in previous years. Peak above-ground standing crop between June and September was accompanied by a considerable depletion below ground.

During 1978, when the strip-mowing regime was introduced, peak below-ground standing crop was lower than in 1977 for LG and MG. No increase was evident in SG. Above-ground standing crop in MG was similar to the previous year.

Below-ground levels in LG continued to diminish during 1979, with above-ground standing crop remaining high over winter. Below-ground standing crop in MG remained at a similar level to the previous year, but in SG had increased significantly.

Thus a broad pattern emerges whereby increased above-ground standing crop, resulting from reduced mowing intensity is coupled with diminished below-ground reserves. Conversely, heavy mowing favours below-ground investment whereas medium mowing pressure produces

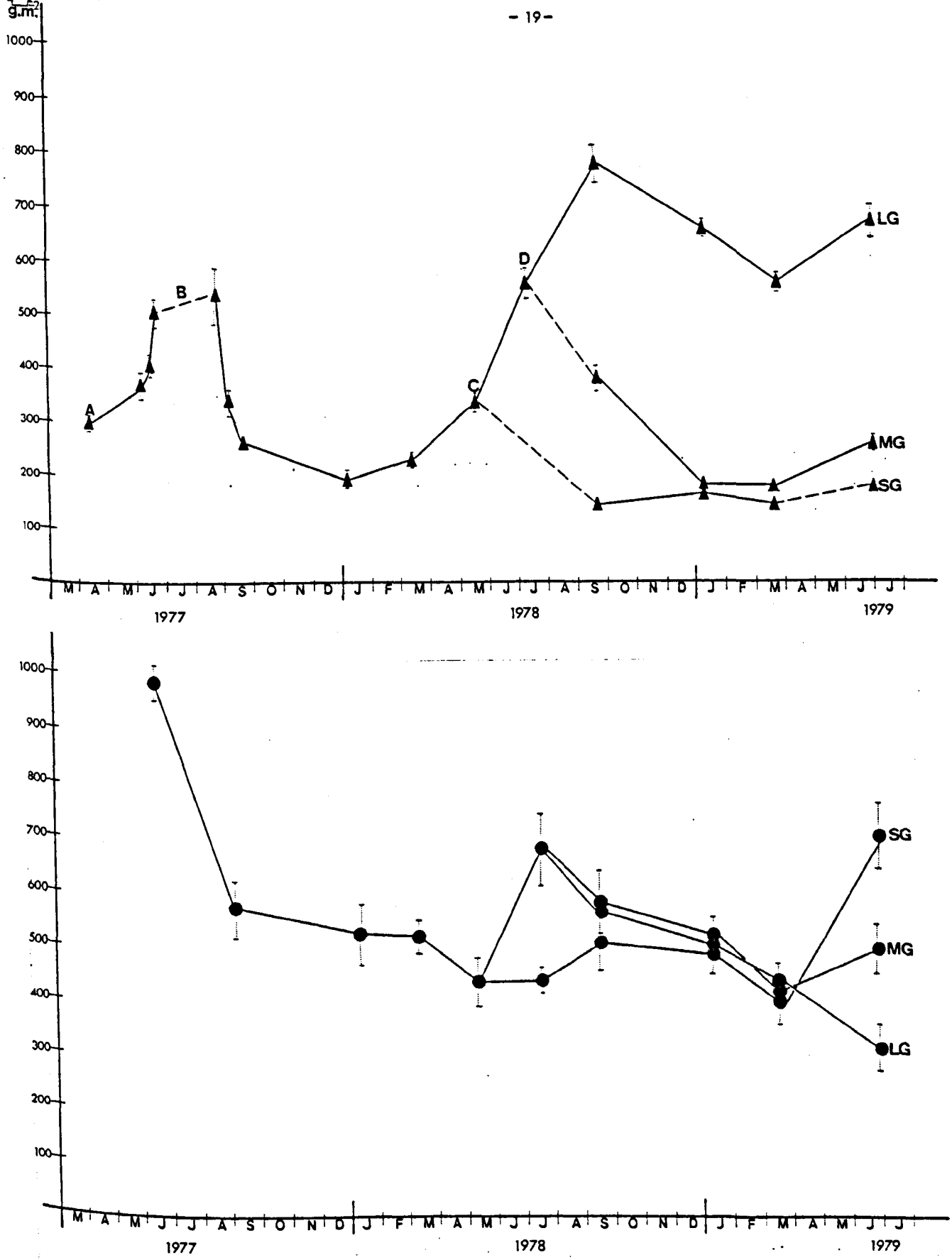


FIG 5 : Variation of above-ground standing crop (dry wt.) including litter (ABOVE), and below-ground standing crop (roots + rhizomes; ash-free dry wt.) (BELOW), for LG., MG. and SG.

Letters indicate treatment variables:
A =field heavily mown previous to this date.
B =field mown twice during 1977.
C =SG treatment started.
D =MG treatment started.
Hatched lines indicate mowing between sampling dates.

Values are means ± standard errors.

intermediate underground reserves. Recovery of below-ground reserves when heavy mowing is resumed (SG) does not take place in the first year.

3.2 Above-Ground Standing Crop in LG and PAD

Above-ground standing crop components in LG and PAD during 1978-9 are shown in TABLES 3 and 4 respectively. Total standing crop was initially higher in PAD owing to a large proportion of litter. Dominant grasses at both sites were *Agrostis tenuis* and *Holcus lanatus*, although the former is probably over-estimated due to certain vegetative resemblances with *Alopecurus pratensis* and *Anthoxanthum odoratum*. *Dactylis glomerata* and *Alopecurus pratensis* were common in PAD.

Forb biomass levels were low in LG, *Ranunculus repens* being the most abundant. In PAD, forb biomass was higher with an enormous production of *Rumex acetosa* during June 1979 (see PLATES).

These changes are illustrated in FIG. 6. A large above-ground biomass of grasses in LG during summer 1978 produced a large accumulation of litter that remained high until the next growing season when primary production was suppressed. In PAD, which had not been mown for almost an entire season prior to 1978, peak biomass was suppressed through 1978 as litter decomposed, resulting in a large production of forbs in 1979. *Rumex acetosa* appeared to be similarly abundant the following year.

3.3 Above-Ground Versus Below-Ground Standing Crop in LG and PAD

Data for above- and below-ground standing crop are shown on the same axis in FIG. 7, for LG and PAD, illustrating the preponderance of below-ground over above-ground standing crop throughout the year. Below-ground biomass reached a peak at the same time as above-ground biomass in 1978, but the following year seasonal increases were not evident during June. Highest biomass levels were reached around July 1978 in LG and September in PAD. Different species of grasses showed peak biomass levels at different sampling dates (TABLES 3 and 4).

	1978					1979		
	9 Jan	13 Mar	23 May	10 Jul	20 Sep	8 Jan	22 Mar	29 Jun
Agrostis tenuis[a]	-	-	122.4	207.8	253.4	71.5	12.4	173.2
Holcus lanatus	-	-	50.4	206.0	99.4	62.2	1.8	12.7
Festuca rubra *subsp.* rubra	-	-	11.2	13.3	4.7	4.5	1.5	2.3
Anthoxanthum odoratum	-	-	15.7	3.5	16.0			0.9
Lolium perenne	-	-	1.4	14.5	4.3			
Dactylis glomerata	-	-			0.4			
Other grasses[bcde]	-	-	4.5		1.3	0.2		
TOTAL GRASSES	-	51.3	205.5	445.2	379.3	138.4	15.6	189.0
Forbs[fgjk]	-	2.2	3.5	17.0	10.4	1.8	1.4	40.8
TOTAL LIVE BIOMASS	98.0	53.5	209.0	462.2	389.7	140.2	17.0	229.8
Litter	95.0	170.1	135.5	96.0	389.4	520.5	537.0	440.6
Forb litter						0.1	0.1	
Tree leaves						0.1	0.3	
TOTAL	193.0	230.2	333.9	558.2	779.3	661.5	554.7	670.5

TABLE 3 : Above-Ground Components of Standing Crop in LG during 1978-79. Data shown as dry weight ($g.m.^{-2}$). *a*, includes a small proportion of Agrostis stolonifera; *b*, Poa pratensis; *c*, Poa trivialis; *d*, Poa annua; *e*, Cynosurus cristatus; *f*, Rumex acetosa; *g*, Ranunculus repens; *h*, Heracleum sphondylium; *i*, Achillea millefolium; *j*, Taraxacum officinale; *k*, Cardamine pratensis.

	1978					1979		
	9 Jan	13 Mar	1 Jun	24 Jul	21 Sep	9 Jan	21 Mar	17 Jun
Agrostis tenuis[a]	-	-	25.0	121.5	56.0	16.5	2.5	5.9
Holcus lanatus	-	-	22.2	74.7	107.6	90.1	1.6	27.6
Festuca rubra *subsp.* rubra	-	-	23.3	20.1	32.9	14.1	0.8	25.1
Anthoxanthum odoratum	-	-	0.8	0.2	1.7	1.2		0.1
Lolium perenne	-	-	1.0	0.6				
Dactylis glomerata	-	-	7.6	21.1	21.9	0.1		29.3
Alopecurus pratensis	-	-						41.1
Other grasses[bc]	-	-	0.8					1.0
TOTAL GRASSES	-	28.4	80.7	237.7	219.8	122.1	4.9	130.0
Forbs[fhij]	-	2.2	10.8	25.2	54.5	16.2	9.7	317.5
TOTAL LIVE BIOMASS	76.0	30.6	91.5	262.9	274.3	138.3	14.5	447.6
Litter	399.5	330.9	409.9	246.6	258.6	296.1	260.8	124.2
Forb litter					28.9	0.4	3.3	12.8
Tree leaves		19.3	14.0		0.8	14.3	19.1	2.4
TOTAL	512.0	380.8	515.4	509.5	562.6	451.1	297.4	587.0

TABLE 4 : Above-Ground Components of Standing Crop in PAD during 1978-79. Data shown as dry weight ($g.m.^{-2}$). For legend see table 3.

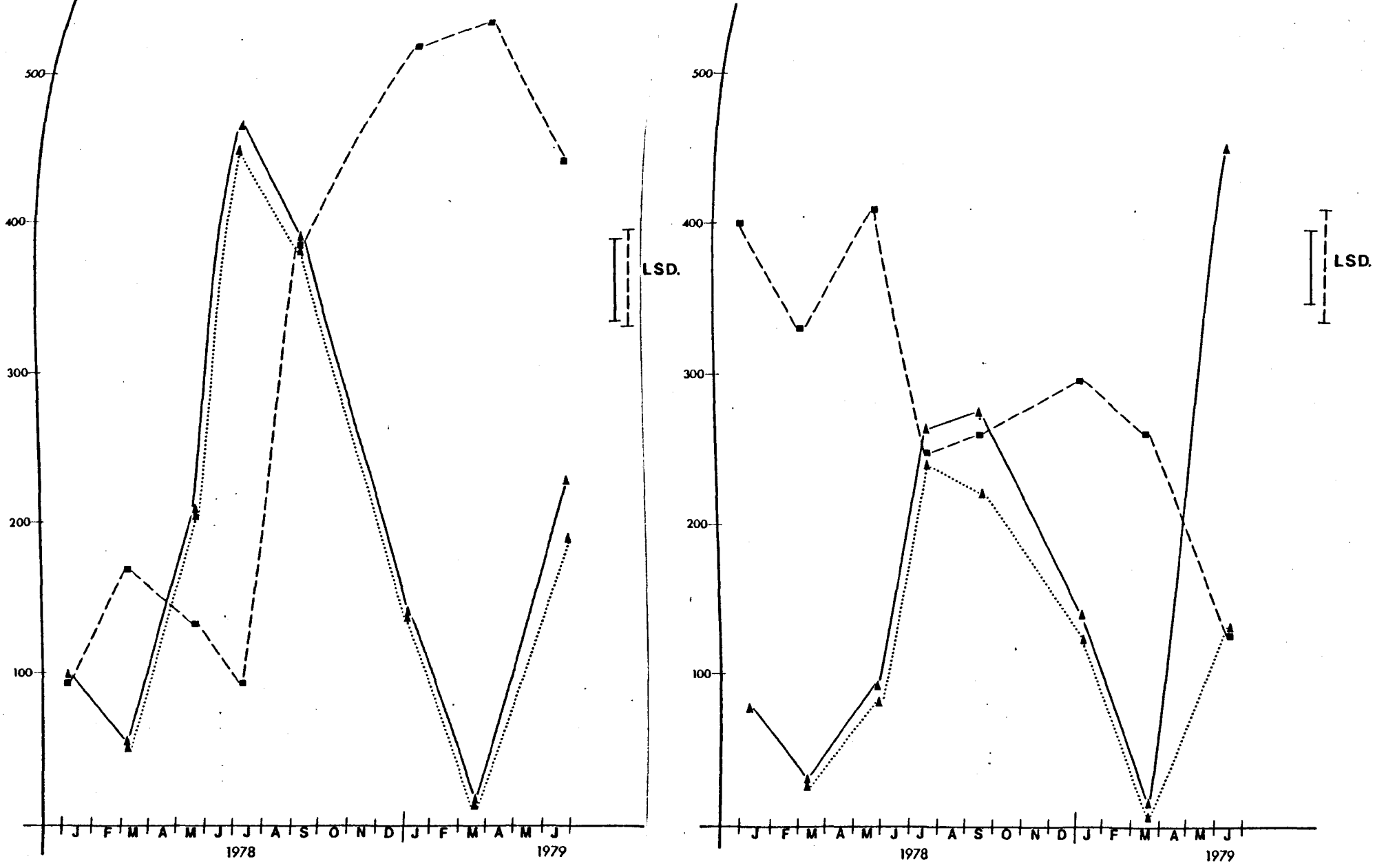


FIG 6 : Above-ground standing crop (dry wt.) in LG. and PAD. during 1978-79 for Forbs + Grasses (▲——▲), Grasses (▲·····▲), and Litter (exc. tree leaves) (■— — — —■).
Least significant differences are indicated.

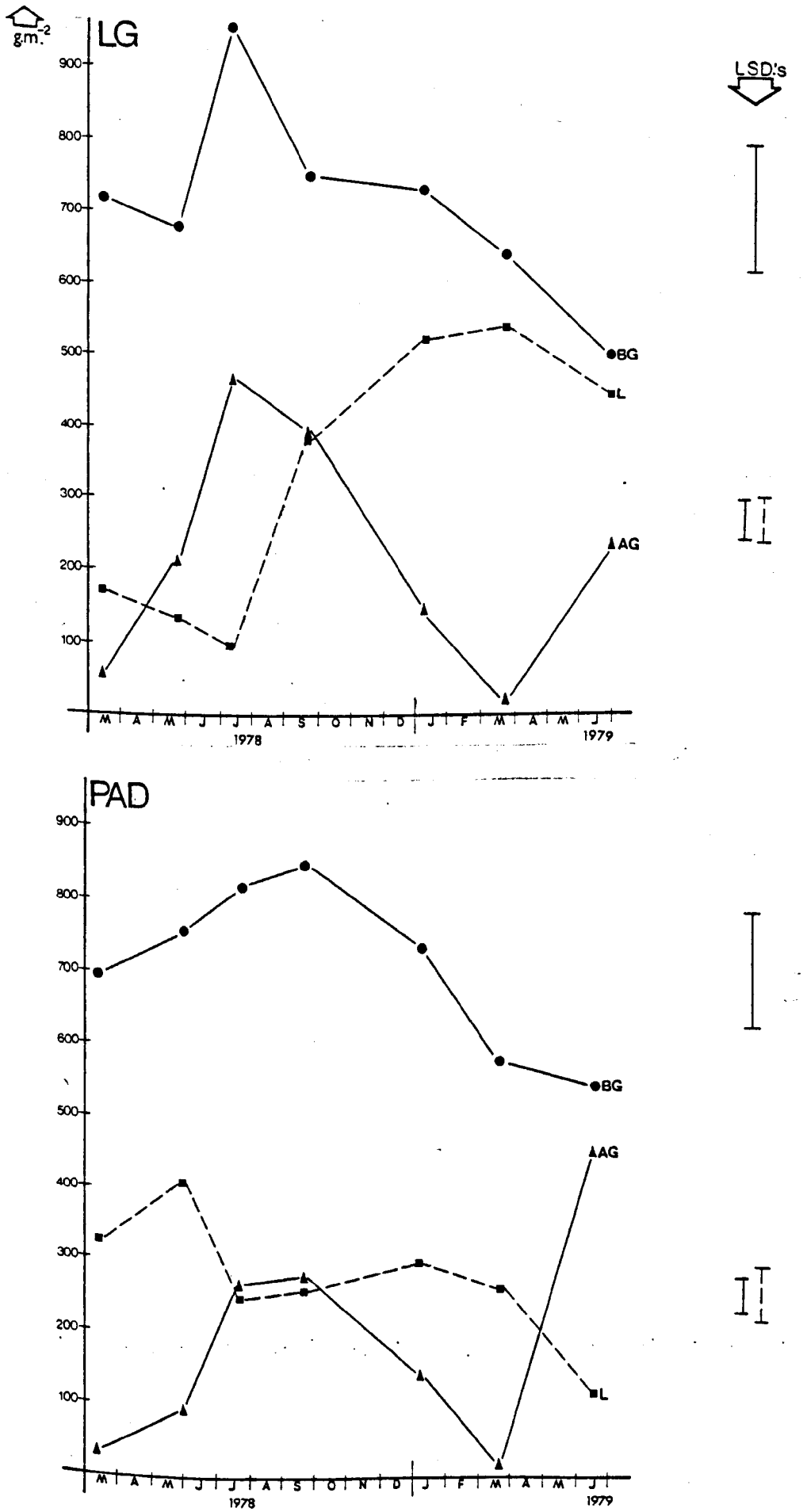


FIG 7 : Ash-free dry weight of TOTAL BELOW-GROUND ORGANS (●——●BG) and dry weight of above-ground GRASSES + FORBS (▲——▲AG) and LITTER (■——■L) in LG. and PAD. during 1978-79.

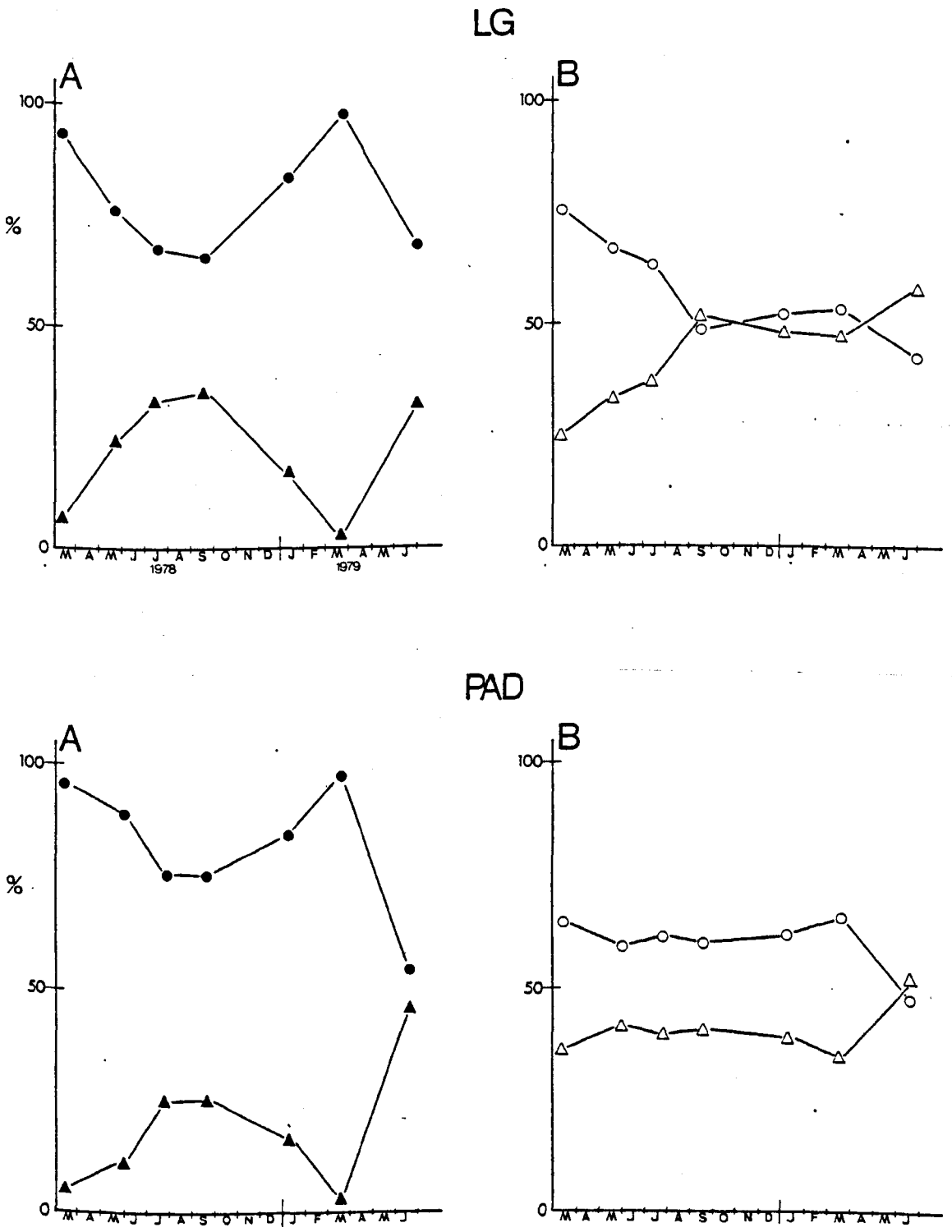


FIG 8 : Proportionate distribution of dry weight in LG (above) & PAD (below) between A) grasses (▲——▲) and total below-ground organs [a.f.d.w.] (●——●) as a % of total biomass, & B) grasses + litter (△——△) and total below-ground organs (○——○) as a % of total biomass + litter.

Seasonal variation in the proportionate distribution of biomass above- and below-ground is shown in FIG. 8, excluding (A) and including (B) litter. Proportionate contribution of below-ground dry weight was lowest during the growing season, and most significant during March when above-ground standing crop was minimal (A). Considering the inclusion of litter with above-ground biomass (B), dry weight was approximately equally distributed above- and below-ground during winter in LG. In PAD, roughly 40% of dry weight was consistently above-ground until June 1979.

A range of 54 to 98% of biomass was recorded below-ground (TABLE 5).

TREATMENT	RANGE	MEAN	DATA FROM *n* SAMPLING DATES
SG	82.5 - 92.4	88.1	*n* = 3
MG	73.1 - 93.0	82.9	*n* = 4
LG	65.7 - 97.4	78.9	*n* = 7
PAD	54.7 - 97.5	81.8	*n* = 7

TABLE 5 : Below-ground ash-free dry weight as a % of total biomass (excluding litter).

3.4 *Removal of Cuttings from SG and MG*

Cuttings removed from SG after mowing were collected and weighed from five out of the six mowings during 1979. 168.8 g.m.$^{-2}$ dry weight were removed, representing an annual removal of approximately 200 g.m.$^{-2}$ from SG.

Similarly, cuttings were removed and weighed from the single mowing of MG. 132.2 g.m.$^{-2}$ dry weight were removed, representing the annual loss from this treatment.

These losses in terms of nutrient removal are considered in Chapter 5.

3.5 Below-Ground Components

Heavy mowing in SG resulted in increased levels of roots, rhizomes and detached roots in June 1979 (FIG. 9). Recovery was delayed over the 1978 season, as previously described. Peak biomass of roots in 1978 was in September whereas late season growth produced the highest 1978 rhizome levels over winter. The seasonal pattern of detached roots was most similar to that of the roots.

In MG, with the same mowing regime from 1977 to 1979, seasonal pattern of roots followed that in SG but with a lower peak in June 1979. Standing crop in June was similar in both years. Detached roots diminished by about 50 $g.m.^{-2}$ over the sampling period. Rhizome biomass in 1979 did not increase to 1978 levels although a late spring in 1979 may have retarded the onset of growth. In overall terms, a slight downward trend was evident in MG.

In LG, roots and rhizomes decreased over the sampling period with peak biomass in early July 1978. Standing crop in late June 1979 was 46% and 61% lower than this respectively for roots and rhizomes. Highest peaks of detached roots were in July 1978, corresponding with root and rhizome peaks, and in January 1979.

In PAD, a similar decrease in root biomass and larger decrease in rhizomes was evident. Lignified (forb) roots have been added to the graphs for LG and PAD. Levels are quite low in LG but in PAD peak forb root biomass exceeds that of other components in September 1978. Root and detached root categories include an inseparable proportion of young forb roots, which may account for the maintenance of detached root standing crop through to 1979. A peak level is reached in January 1979, as in LG, and lowest standing crop in early June 1978 corresponds to the largest accumulation of litter (and restricted above-ground growth).

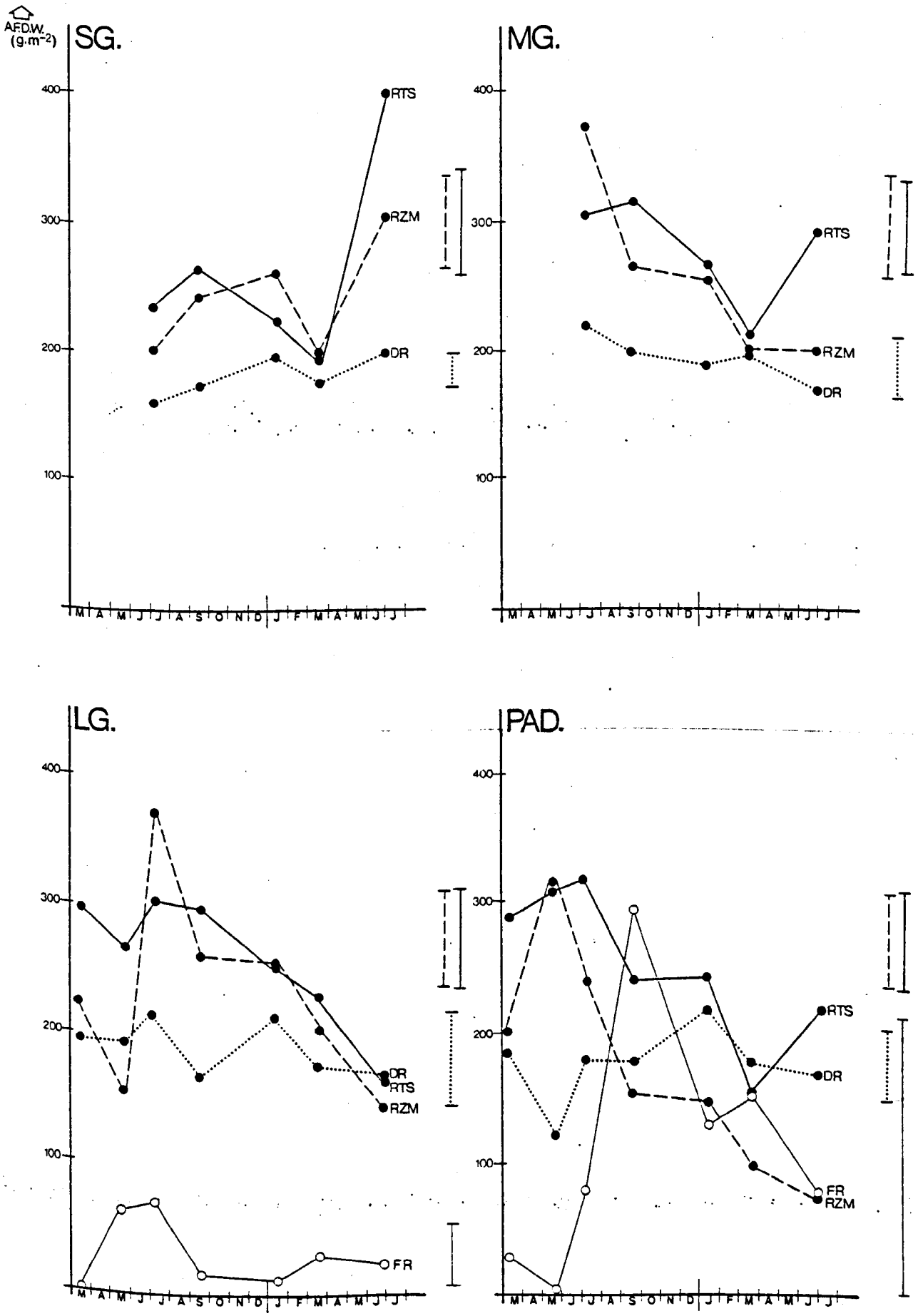


FIG 9 : Standing crop [ash-free dry weight] of BELOW-GROUND COMPONENTS during 1978-79. Roots (●——● RTS), rhizomes (●- - - -● RZM) & detached rts. (●·····●DR) are shown for each treatment, and lignified [forb] roots (○——○FR) for LG and PAD. Least significant differences are indicated.

Dry weight data for all components, above- and below-ground, were used in a multiple linear regression analysis* in an attempt to describe detached root fluctuations in terms of combinations of other dry weight variables within each treatment. However, statistically valid models could not be computed; values of r and *multiple* r were insignificant in all cases.

Instead, paired correlations between detached roots and roots, rhizomes and forb roots were calculated with data from original cores (12 per sampling date), rather than using mean values. Scatter diagrams are shown in FIG. 11 together with product-moment correlation coefficients and regression equations. In all treatments, detached root biomass is positively correlated with root biomass. In LG, roots, rhizomes and detached roots are all significantly ($p < 0.01$) correlated with each other.

3.6 Conclusions

The greater proportion of standing crop in semi-permanent grassland is held below-ground, providing a certain resilience to the cutting and/or grazing on which its continued existence depends (Spedding, 1971).

With less regular mowing, increased above-ground standing crop corresponds with reduced below-ground reserves which return to higher levels in the second year following the reintroduction of heavy mowing. If mowing is discontinued, the litter compartment increases enormously with approximately 40% of standing crop above-ground, resulting in reduced above-ground productivity the following season. Ensuing habitat conditions lead to plant-induced stress (Grime, 1978) and prevent continued community dominance by grasses. Chemical limitations are considered in Chapter 5. With mowing, 132 to 200 $g.m.^{-2}$ $annum.^{-1}$ dry weight was removed from the ecosystems.

Heavy mowing increased root and rhizome components. Roots

* SPSS Version 7 : Forward stepwise method (see App. 4).

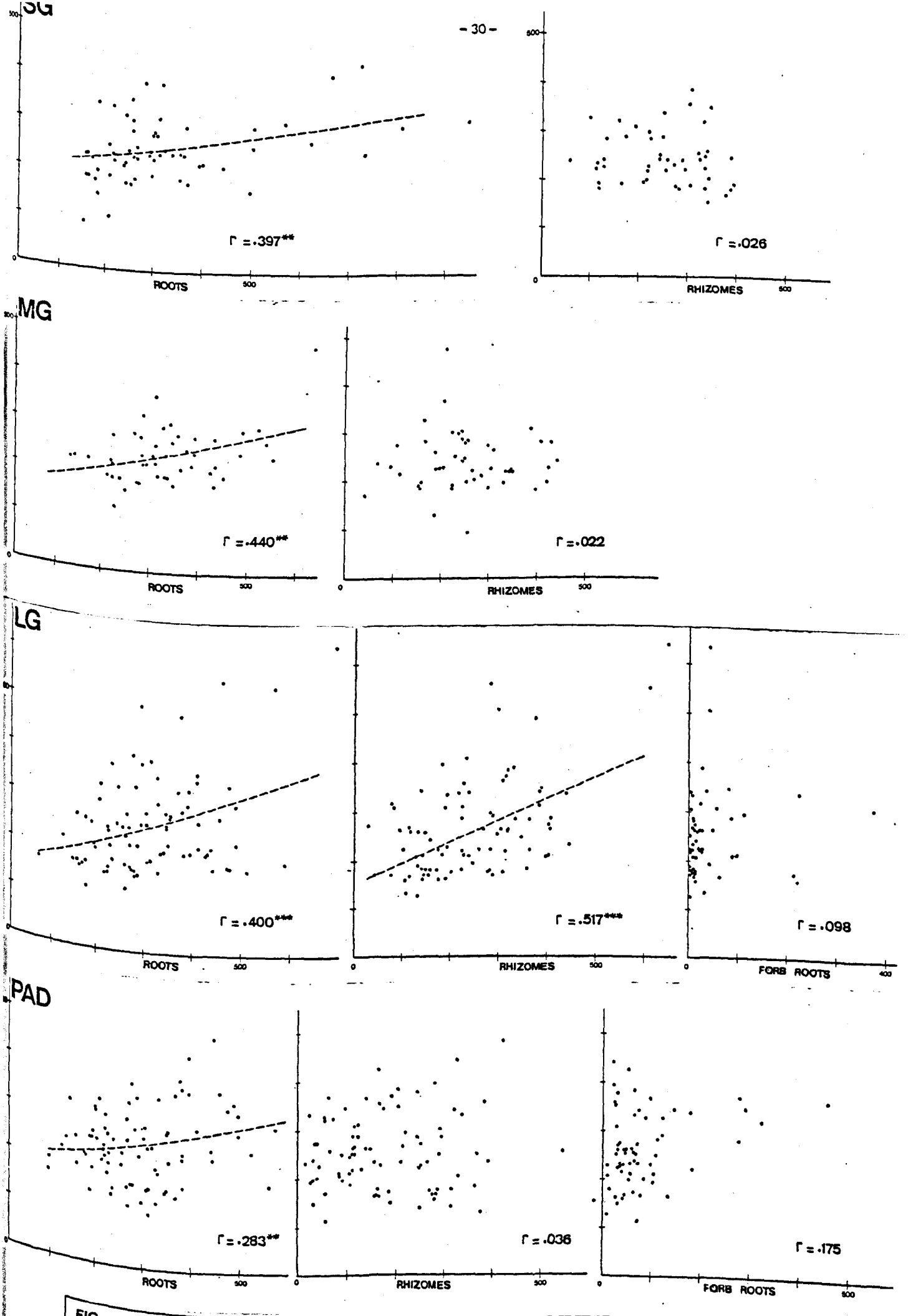


FIG. 11 : Scatter diagram plots of _DETACHED ROOTS versus other below-ground components. Each point represents dry wt. per core (expressed as $g.m.^{-2}$)

achieved highest biomass in June and rhizomes in late season, with highest detached root biomass also at those times. With reduced frequency of mowing, roots and rhizomes progressively diminished although detached root levels were slightly increased. Forb roots proliferated with increased above-ground forb production.

Fluctuations of detached root biomass were clearly influenced by root and rhizome biomass, but most closely associated with roots. This supports microscopical observations (Section 2.2.2). The detached root fraction is examined in more detail in the following chapters.

Thus a model experimental system was established, pertinent to the aims of the project.

CHAPTER 4

SEASONAL VARIATIONS OF NUTRIENT CONCENTRATIONS

There are very few grasslands in which soil nutrients are not limiting and the elucidation of nutrient cycles within ecosystems are a major goal of ecological research. An understanding of the nutritional equilibrium of the ecosystem is essential for effective management, particularly with respect to the manipulation of species composition and performance and the effective use of fertilizers (*see* Bradshaw, 1969, 1980). A comprehensive description of the circulation of nutrients is well beyond the bounds of the present study, but a study of variations of nutrient concentrations between plant components, seasonally and according to mowing regime may provide valuable information.

Plant materials collected during sampling were analysed for *N*, *P*, *K*, *Ca*, *Mg*, *Na*, *Mn* and *Zn*, which are listed roughly in order of the importance they have been afforded in the literature. The importance of nitrogen, phosphate and potassium as nutrients are well known, and the analyses were extended to examine whether significant alterations of other nutrients may also take place. Reduced concentrations of particular nutrients at certain periods may provide an indication of the times of limited supply from available soil pools.

4.1 Methods

Materials collected during sampling were sorted into component fractions, dried and weighed. Replicates were bulked, finely ground and stored in glass screw-top jars in preparation for chemical analysis on completion of field work. Methods follow those given by Allen *et al.* (1974), except where otherwise stated.

Duplicate subsamples (re-dried at 105°C) of 0.35 g were digested in a 1 ml perchloric/5 ml nitric/0.5 ml sulphuric acid mixture, then diluted to 50 ml prior to analysis. A separate digestion is described for the determination of nitrogen.

Glassware was cleaned in chromic acid, with an additional rinse in *HCl* prior to phosphorus determination. Double glass distilled water was used at all stages.

Nitrogen

Total nitrogen was determined using a semi-micro Kjeldahl method with Markham distillation apparatus followed by titration against *HCl* Prior digestion of sample (0.1 g) was in 3 ml sulphuric acid, heated with 2 g potassium sulphate-mercuric oxide catalyst. Accuracy of the apparatus was extremely high (within 1% error of the mean) and precision and replicability of samples were regularly checked.

Phosphorus

Phosphorus was determined as phosphate using the Molybdenum Blue method, with stannous chloride as the reducing agent. Adjustment of sample dilution to work within the ranges of the acid-stability plateau (Hess, 1971) was found to be particularly critical. Optical density was

measured with a *Bausch and Lomb Spectronic 20* spectrophotometer.

K, Ca, Mg, Na, Mn, Zn

These elements were determined using atomic absorption spectrophotometry (*EEL 240*) with an air/acetylene flame. Stability was high over the concentration ranges encountered, although it was necessary to integrate *Ca* readings. Lanthanum chloride was added as a releasing agent before determination of *Ca* and *Mg*.

In all cases, errors are within the expected ranges of accuracy given by Allen *et al.* (1974). Analyses were repeated for subsamples lying outside these limits. All data for nutrient concentrations of below-ground components have been corrected for soil contamination using the following formula:

$$\textit{Nutrient Concentration (\%)} = \frac{\text{corrected nutrient pool (B - C*)}}{\text{ash-free dry weight}} \times 100$$

(* see *Section 5.1*).

4.2 Results and Analysis

Seasonal concentrations of each nutrient are shown together with dry weight fluctuations in LG (FIG. 12) and PAD (FIG. 13). Considerable seasonal differences are evident between nutrients, compartments and treatments. In many instances nutrient concentrations are clearly related, positively or negatively, to standing crop in that or other compartments. Also, certain nutrients show markedly similar seasonal patterns.

Initially, cluster analysis techniques were implemented to investigate the feasibility of grouping data into a more manageable form. Essentially these are methods of classification which group variables (nutrients) that are highly correlated into clusters, and exclude from clusters those variables that are unlike (see APP. 4). Graphical illustrations of these analyses, using each of the 8 nutrients in 5 compartments (40

cases) on 6 sampling dates (variables), are shown for LG and PAD in FIGS. 14 and 15 respectively. Ten clusters have been selected as most appropriate.

Both analyses produce very similar cluster formations with virtually identical outliers. *N* and *Ca* are outliers for all components, with *P* and *K* in above-ground compartments (although litter *P* joins a large cluster). The two large clusters separate *Mg* (all components) and *P* (below-ground and litter) from *Na*, *K* (below-ground), *Mn* and *Zn* (all components). The latter cluster is distinguished by elements at very low concentrations.

The next stage of data analysis (with reference to FIGS. 12 and 13) was to examine the extent to which these seasonal patterns could be described in terms of dry weight fluctuations. Multiple linear regression analysis (APP. 4) was used to correlate each nutrient from each component (dependent variable) against grass, litter, root, rhizome and detached root dry weight parameters (independent variables). Results are summarized in TABLES 6 (LG) and 7 (PAD) with regression analyses and equations tabulated in detail in APPS. 5 and 6. In cases where satisfactory regression equations could not be computed, other nutrients were added to the list of independent variables in an attempt to obtain suitable regression equations (TABLE 8); detailed in APP. 7. Cause/effect relationships should not be inferred unless specifically stated.

To provide a perspective for the limited data available in MG and SG, nutrient concentrations from all four treatments (LG, MG, SG and PAD) have been shown on the same axes for grasses (FIG. 16), litter (FIG. 17), roots (FIG. 18), rhizomes (FIG. 19) and detached roots (FIG 20). One-way analysis of variance tests of difference were carried out on arcsin transformed data from each graph (APP. 8) and Spearman Correlation coefficients calculated between pairs of treatments (APP. 9).

A detailed account of these results (*sections 4.3 to 4.10*) is followed by the main conclusions (*section 4.11*).

4.3 Nitrogen (%)

In LG, peak biomass of grasses and rhizomes in July 1978 corresponded with lowest *N* concentrations in grasses, rhizomes and detached roots, but peak concentrations in roots (FIG. 12). Similarly in PAD, peak grass biomass corresponded with lowest grass but highest root concentrations (FIG. 13). Litter *N* concentrations in LG followed grass *N* concentrations with some time delay, but in PAD increased gradually through the sampling period.

Nitrogen concentrations in components were represented by 5 different outlying clusters in LG and PAD (FIGS. 14 and 15) suggesting individual seasonal patterns, each of which could be described in terms of dry weight parameters (TABLES 6 and 7) except litter concentrations in PAD. Peak standing crop of rhizomes in PAD was earlier than in LG (FIGS. 12 and 13) and a progressive decline through the sampling period was negatively correlated with root and rhizome *N* concentrations (TABLE 7).

Concentrations in grasses in MG and SG followed a broadly similar pattern to other treatments, although overwintering concentrations were higher than in LG and PAD (FIG. 16). Root and rhizome *N* concentrations were also similar to LG (FIGS. 18 and 19) but slightly lower, most notably in June 1979. Detached root concentrations (FIG. 20) were substantially higher in LG than in other treatments. Fluctuations of *N* concentrations are strongly correlated in MG and SG for all below-ground components (APP. 9).

4.4 Phosphorus (%)

Grass *P* concentrations in LG and PAD were lowest in June/July, and

below-ground *P* concentrations in LG were lowest in September (FIGS. 12 and 13).

Grass concentrations provided the only outlying cluster for this nutrient, and other components were grouped into cluster 5 (FIGS. 14 and 15).

In LG, only litter and rhizome *P* concentrations could be described by computed regression equations (TABLE 6), and in PAD only litter and grass *P* concentrations could be described (TABLE 7). LG grass, root and detached root *P* concentrations were inter-related: detached root *P* could be described by detached root *N* and *K* concentrations, and then used to predict root *P*, which could be used to predict grass *P* (TABLE 8). PAD root, rhizome and detached root *P* concentrations could be predicted in a similar way, after describing detached root *P* (TABLE 8). However, extrapolation of data in this manner may be unwise.

Phosphorus concentrations during winter in above-ground grasses and litter were lower in LG than in other treatments (FIGS. 16 and 17), whereas summer concentrations in detached roots were higher (FIG. 20). Inter-seasonal variations of root *P* concentration were more pronounced in LG and PAD than in other treatments (FIG. 18). Root and rhizome concentrations in MG and SG increased through the sampling period (FIGS. 18 and 19) although neither corresponded to below-ground dry weight parameters (*cf.* FIG. 9). Peak detached root concentrations in MG, SG and PAD were in March, and in LG in June (FIG. 20).

4.5 *Potassium (%)*

Grass *K* concentrations in LG were low during June 1978, but high in June 1979 (FIG. 12). Root and rhizome *K* concentrations in LG gradually increased through the sampling period, whereas root dry weight gradually declined. In PAD, seasonal fluctuations of *K* were notably different to LG in all compartments (FIG. 13), although in both treatments litter

concentrations were high in September. Below-ground concentrations were low in all cases, and may have been under-estimated through losses during washing (see *4.10*).

Grass and litter *K* concentrations formed outlying clusters in both LG and PAD (FIGS. 14 and 15). In LG, significant regression equations could be computed to describe *K* concentrations in all components, using dry weight parameters (TABLE 6). Grass *K* concentrations were negatively correlated with rhizome dry weight, and below-ground component concentrations were negatively correlated with below-ground dry weight parameters. In PAD, only rhizome and detached root concentrations could be described by dry weight parameters (TABLE 7). Rhizome *K* concentrations were negatively correlated with litter dry weight, and detached root *K* concentrations were negatively correlated with root dry weight.

Grass *K* concentrations in PAD were significantly higher than in other treatments (FIG. 16) and litter *K* concentrations were higher in PAD than in LG (FIG. 17). In roots and rhizomes seasonal fluctuations in *K* concentrations were similar in LG, MG and SG, although LG concentrations were significantly lower in all below-ground components (FIGS. 18-20).

4.6 Calcium (%)

Peak biomass of grasses and rhizomes in LG in July 1978 corresponded with high *Ca* concentrations in roots and litter (FIG. 12). Seasonal *Ca* concentrations in litter varied considerably in LG. Peak *Ca* concentrations in grasses was in autumn, and seasonal pattern followed standing crop with some time delay. Detached root *Ca* concentrations were lowest in May/June in both years. In PAD, seasonal *Ca* fluctuations were similar to LG in grasses and below-ground components (FIG. 13). Peak litter *Ca* concentrations preceded peak grass *Ca* concentrations in both treatments.

As with nitrogen, *Ca* concentrations in all components were outliers in the cluster analyses (FIGS. 14 and 15). In LG, regression equations

provided a satisfactory description of *Ca* fluctuations for all components in terms of dry weight, with grass and rhizome dry weight parameters particularly important (TABLE 6). In PAD, grass and rhizome *Ca* concentrations could not be described by dry weight parameters (TABLE 7), unless other nutrient concentrations were included with the independent variables (TABLE 8).

Calcium concentrations and seasonal fluctuations of *Ca* concentrations in grasses and litter were similar in all treatments, with a high coefficient of variation (FIGS. 16 and 17). Root and detached root *Ca* concentrations (FIGS. 18 and 20) were higher in LG than in MG and SG in which root *Ca* concentrations declined through the sampling period, whereas root *Ca* concentrations in PAD increased slightly. Detrital root *Ca* fluctuations were correlated in LG, MG and SG (APP. 9), and similar in PAD. Rhizome concentrations were similar in all treatments (FIG. 19).

4.7 Magnesium (%)

In LG, grass *Mg* concentrations reached highest levels during the growing season (FIG. 12) and in PAD peak grass *Mg* concentration as with *Ca*, was reached in September (FIG. 13). Rhizome *Mg* concentrations were highest during the growing season/in LG and PAD, although variations were not pronounced. The seasonal pattern of litter *Mg* concentrations followed grass *Mg* concentrations in both treatments, but in LG peak concentration was reached before that of grasses. Root and detached root concentrations in LG were lowest during the growing season. Detached root concentrations were higher than concentrations in the other below-ground components, in LG and PAD and increased through the sampling period in PAD.

Magnesium concentrations for all components were grouped into a large cluster with *P* concentrations, but excluding grass *P* (FIGS. 14 and 15). Regression equations provided a satisfactory fit with dry weight

parameters in most cases, except for grass *Mg* in PAD and rhizome *Mg* in both treatments (TABLES 6 and 7). Root *Mg* concentrations in LG and PAD were negatively correlated with rhizome dry weight. *Ca* and *Mg* concentrations in grasses in PAD are strongly correlated, and rhizome concentrations of both can be predicted from rhizome *P* concentrations (TABLE 8).

Seasonal patterns of grass *Mg* concentrations were similar in LG, MG and SG, but concentrations were much higher in the mown treatments (FIG. 16). Litter concentrations were also higher (FIG. 17). As with *K*, root and rhizome *Mg* concentrations were significantly lower in LG than in other treatments (FIGS. 18 and 19). Root *Mg* concentrations in MG and SG increased considerably in June, 1979. Detached root *Mg* fluctuations (FIG. 20) were most similar to root *Mg* fluctuations, in LG, MG and SG.

4.8 Sodium (%)

Grass and litter *Na* concentrations in LG followed variations in grass biomass (FIG. 12). Peak grass and litter concentrations of *Na* in PAD were in September, as with peak grass concentration of *Ca* and *Mg* (FIG. 13). As with *K*, low *Na* concentrations in below-ground components may have been under-estimated through losses during washing (see *4.10*).

Sodium concentrations were grouped into the two large clusters, although grass *Na* in LG lay just outside (FIGS. 14 and 15). *Na* concentrations could be described by dry weight parameters for all components, in LG and PAD, except for PAD grasses (TABLES 6 and 7). This could be described using grass *Ca* concentration together with rhizome dry weight (TABLE 8). In LG and PAD, root and detached root *Na* concentrations were negatively correlated with root or detached root dry weight.

Grass and litter concentrations of *Na* were higher in MG and SG than

in unmown treatments (FIGS. 16 and 17). Detached root *Na* concentrations were lower in MG and SG than in LG, but otherwise *Na* concentrations and seasonal fluctuations were similar in all below-ground components (FIGS. 18-20).

4.9 Manganese and Zinc (%)

Seasonal patterns of variation in LG and PAD were very variable and trends difficult to discern (FIGS. 12 and 13). Grass concentrations of *Mn* increased towards autumn in LG and PAD, and interestingly litter *Mn* concentrations were substantially higher than grass concentrations in both treatments. Similarly, *Mn* concentrations were higher in detached roots than in roots and rhizomes in both treatments. *Zn* concentrations in grasses were low during the 1978 growing season in both treatments, but increased in June 1979. Detached root concentrations of *Zn* were highest in September.

Mn and *Zn* component concentrations were mostly grouped within a single large cluster(6) although in a few instances *Mn* joined cluster 5 in LG (FIGS. 14 and 15). In LG, seasonal variations in concentrations are poorly described by computed regression equations (TABLE 6) unless other nutrients are introduced to the list of independent variables (TABLE 8). In PAD, dry weight parameters can be used to describe both nutrients in all components, except for *Mn* concentrations in grasses (TABLES 7 and 8).

Certain differences were evident between mown and unmown treatments (FIGS. 16-20). *Mn* concentrations in grasses, roots and rhizomes tended to be higher in mown treatments, and *Zn* concentrations in detached roots were higher in LG than other treatments.

4.10 Summation

Nutrient concentrations and their seasonal fluctuations are drawn

together, and the similarities and differences between components and treatments are discussed.

In LG, cessation of mowing led to large increases in biomass of grasses and below-ground components (particularly rhizomes) in the first season, after which the resultant accumulation of litter limited above- and below-ground production. Initial increases of grass biomass corresponded to lowest concentrations of *N* in grasses, rhizomes and detached roots and lowest *P* in grasses. Conversely, peak *Mg* and *Na* concentrations in grasses and rhizomes were reached with peak biomass. Rhizome biomass was negatively related to *K* concentrations in grasses whereas *Ca* and *Mn* grass and rhizome concentrations increased through the season to reach a peak in autumn.

Litter concentrations were correlated either to grass biomass (*Ca*, *Na*) or else followed grass concentrations with some time delay (*N*, *K*, *Mg*, *Na*). *P* concentrations were lowest over winter and negatively correlated with grass and litter standing crop, whereas *Zn* concentrations varied only marginally. *Ca* and *Mn* concentrations in litter were notably higher than in grasses.

Concentrations were generally lower in below-ground components than above-ground biomass, *Ca* and *Zn* providing the only exceptions. Extremely low below-ground concentrations of *K* and *Na* in all cases may have been under-estimated due to leaching during washing. These elements are rapidly leached from above-ground tissues (Tukey, 1970; Taylor, 1979), but removal of the major proportion of either is perhaps unlikely.

Root biomass reached a peak in June/July 1978, then declined through the sampling period. Peak root biomass corresponded to highest *N*, *Ca* and *Zn* concentrations in roots, and lowest *Mg*. *K* in roots and

rhizomes and *Na* in roots and detached roots increased through the sampling period, whereas *Zn* concentrations in rhizomes declined. *P* was lowest in September in all below-ground components.

Detached root concentrations of all nutrients except *Na* and *Zn* were higher than in other below-ground components. *Ca* in detached roots was lowest in May/June both years and *K* and *Mg* concentrations were negatively correlated with rhizome biomass.

An abstraction of the seasonal events most closely associated with these variations is given in TABLE 9; previous sections should be consulted for detailed information.

In PAD, the sampling programme began with a large accumulation of litter already evident. Primary production was limited during the first year. Rhizome biomass reached a peak in May/June then progressively declined, whereas detached root biomass was lowest in May/June with high levels over winter. Peak root biomass was in July.

N, *P*, *K* and *Zn* concentrations in grasses were lowest at the time of peak biomass, and *Ca*, *Mg*, *Na* and *Mn* concentrations were highest later, in September.

Litter concentrations of *N* and *P* increased gradually through the sampling period, and peak *Ca* and *Mn*% preceded peak grass concentrations. Other nutrients followed grass concentrations (*Ca*, *Na*) or grass biomass (*K*, *Zn*).

As with LG, concentrations in below-ground organs were lower than above-ground biomass except for *Ca* and *Zn*. A notable difference to LG is that most below-ground nutrients in PAD increased in concentration through the sampling period, although *N* and *Ca* fluctuations were very similar to LG.

Peak root biomass was correlated with lowest *Na* and *Mn* concentrations in roots while root *K* and *Mg* concentrations

were lowest in winter. Peak rhizome *Mg*, *Na*, *Mn* and *Zn* and lowest *N* concentrations corresponded to peaks in biomass, and peak detached root concentrations of *P*, *K*, *Mg* and *Na* corresponded to low root biomass. An abstraction of these results is given in TABLE 8.

MG and SG variations should primarily be compared to LG to obtain most valid inferences. Grass concentrations showed essentially similar fluctuations in LG, MG and SG, but concentrations were higher for *N*, *Ca*, *Mg*, *Na* and *Mn* in mown treatments (*P* concentrations over winter were also higher). *K* concentrations in grasses were notably different between treatments, especially in PAD which was consistently higher and led to higher litter concentrations in September. Litter concentrations were generally higher in mown treatments with SG levels higher than MG.

Below-ground concentrations of *N* and *Ca* were significantly lower in mown treatments, as were *Na* and *Zn* concentrations in roots and detached roots. Inter-seasonal variations in below-ground concentrations of *P* in MG and SG were less pronounced and concentrations increased through the sampling period whilst *Ca* concentrations declined. Below-ground fluctuations of *K* and *Mg* were similar to LG, but concentrations were much higher especially during the growing season. *Mn* concentrations in roots and rhizomes increased with mowing frequency.

Discontinued mowing resulted in reduced concentrations of *K* in all components. Higher concentrations in PAD suggests either a site difference or a return to higher levels at later successional stages.

Nutrient concentrations in above- and below-ground fractions of forbs are shown in APP. 10, and compared to concentrations in other components. They are considered in more detail in terms of nutrient pools in the following chapter.

4.11 Conclusions

1. Seasonal changes in nutrient concentrations between above- and below-ground components of the vegetation are varied, but often inter-related and correlated with fluctuations in biomass of one or more of these components.

2. Seasonal variations of *N* and *Ca* in all components and *P* and *K* in above-ground components demonstrate a marked degree of independence from each other, and from other component concentrations.

3. Increased biomass of above-ground grasses during the growing season is correlated with lowest *N* and *P* concentrations in grasses, but highest *Mg* and *Na* concentrations. *Ca* and *Mn* concentrations increase through the season to reach a peak in autumn, whereas *K* and *Zn* fluctuations are variable but tend to be lowest during the growing season.

4. Litter concentrations are primarily influenced by grass biomass and nutrient concentrations, although to a lesser extent for *N* and *P* (see Chapter 6). Concentrations in litter are higher in mown grasslands.

5. *Ca* and *Mn* concentrations are higher in litter than in grasses, and peak concentrations precede those of grasses.

6. Below-ground nutrients, with the exception of *Ca* and *Zn*, are in lesser concentrations than above-ground nutrients. *K* and *Na* concentrations are particularly low.

7. *N* and *Ca* concentrations are lowest in rhizomes and detached roots, and

highest in roots, during their peaks of biomass. Together with *Na* and *Zn* in roots and rhizomes, they are less concentrated in mown grassland.

8. Inter-seasonal variations of below-ground *P* concentrations are less pronounced in mown treatments, whereas *K*, *Mg* and *Mn* concentrations increased with mowing frequency.

9. Detached root concentrations, in all except *Na* and *Zn*, are higher than for other below-ground components. Seasonal patterns are distinctive although often negatively correlated with root or rhizome biomass.

10. Regression equations can be used to describe most component concentrations in terms of dry weight parameters. Otherwise, they can often be described in terms of other nutrient concentrations combined with dry weight parameters.

Dry weight and nutrient concentration data are combined in the following chapter to provide an examination of seasonal changes in compartmental pools. The conclusions of the present chapter are considered in a broader perspective in Chapter 8, and discussed in relation to available published information.

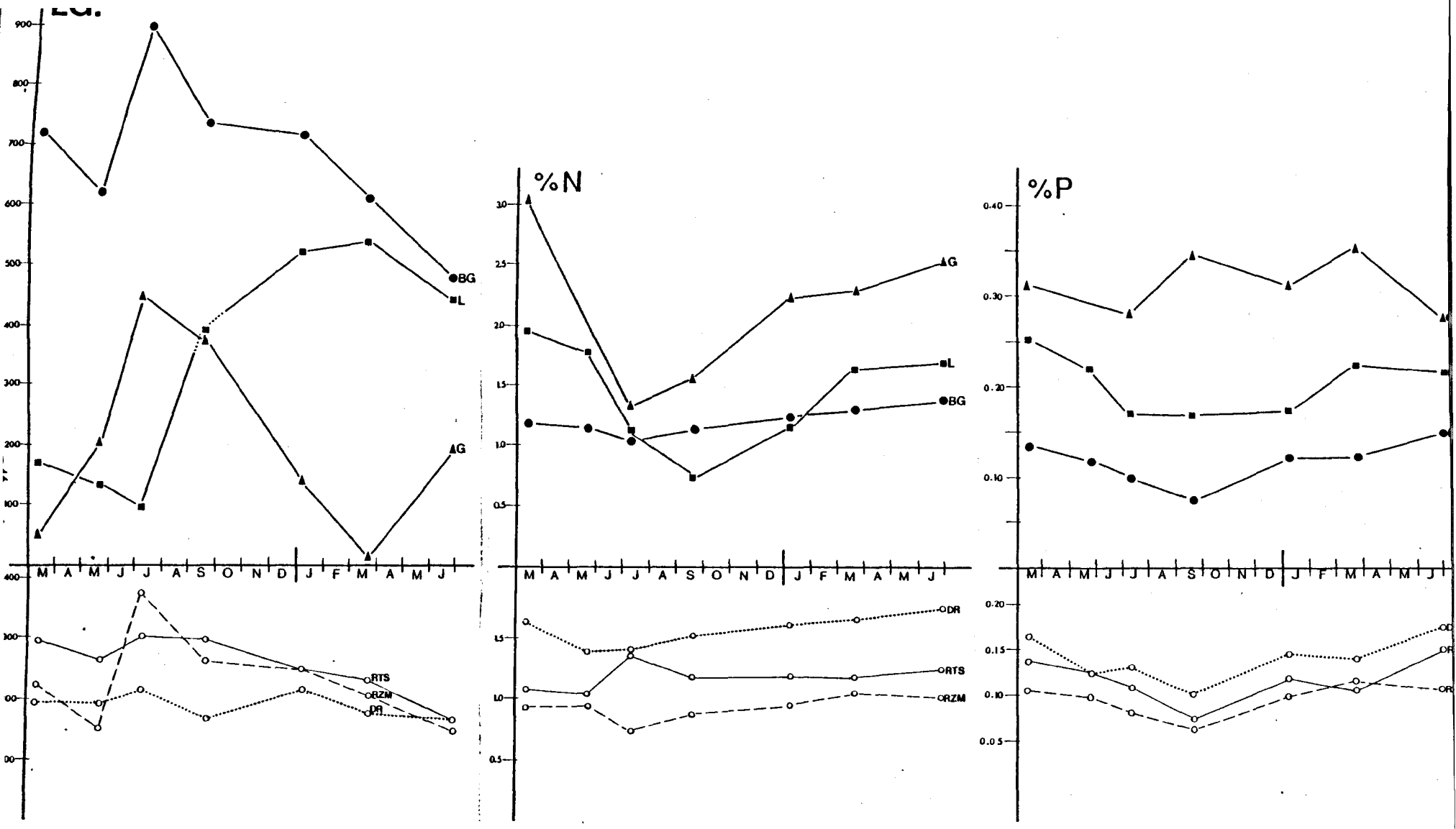


FIG 12 ; Variation of DRY WEIGHT with NUTRIENT CONCENTRATIONS (% dry wt.), in LG. treatment during 1978-79, for above-ground grasses [▲——▲G], litter [■——■L] and total below-ground organs [●——●BG] ; divided into root [○——○RTS], rhizome [○——○RZM] & *detached root [○·····○DR] fractions. See text.* *Continued overleaf..*

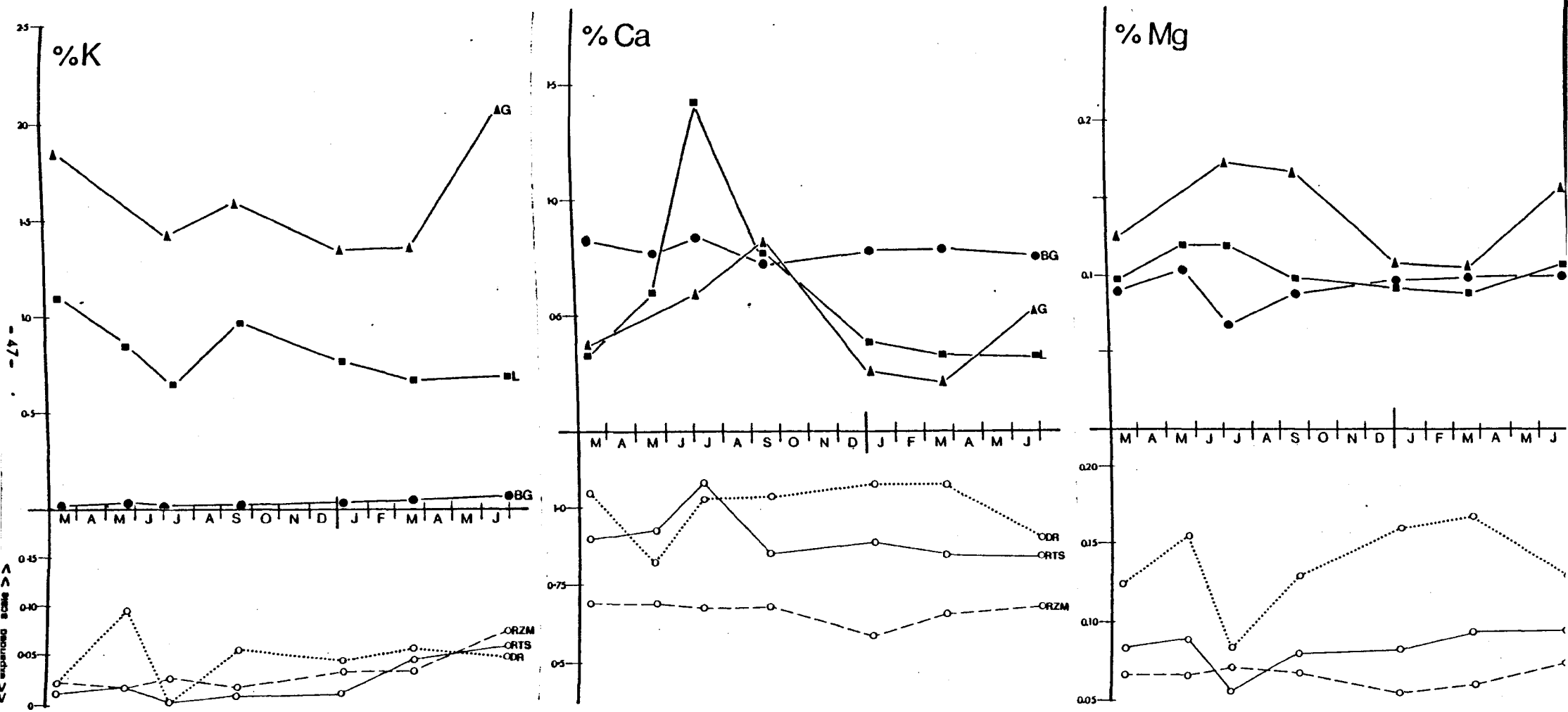


FIG 12 (contd.) : LG., 1978 – 79.
NUTRIENT CONCENTRATIONS (% dry wt.)

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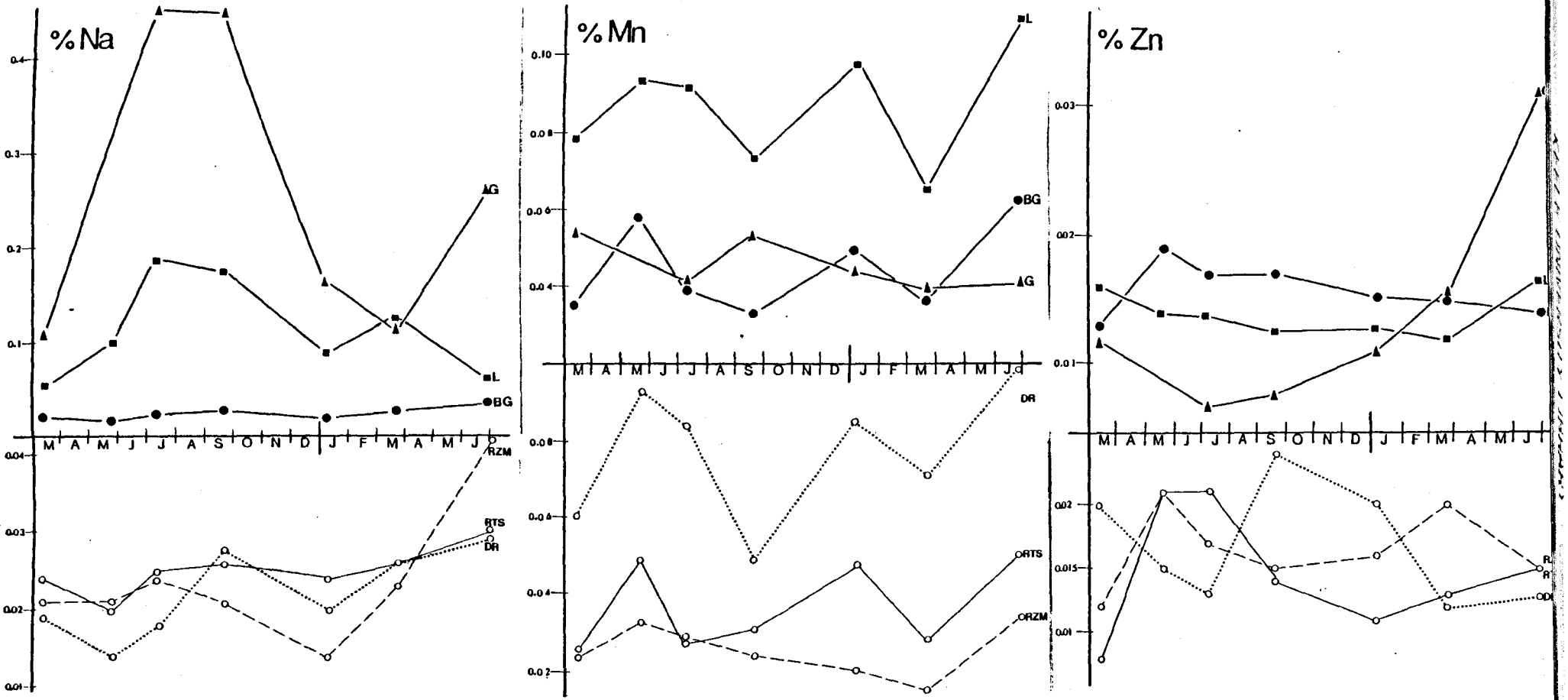

FIG 12 (contd.): LG., 1978-79.
NUTRIENT CONCENTRATIONS (%dry wt)

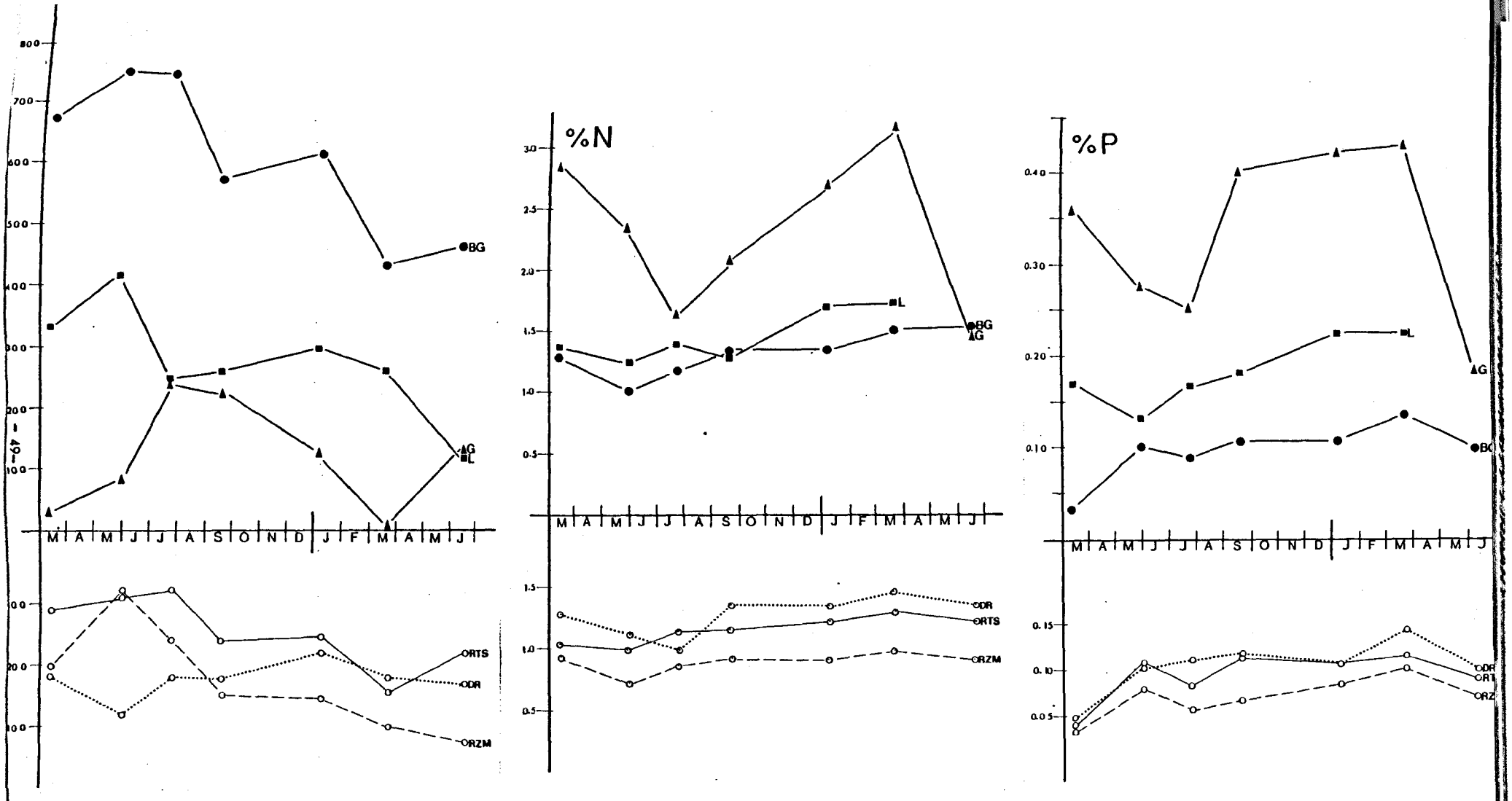

FIG 13 : Variation of DRY WEIGHT with NUTRIENT CONCENTRATIONS (%dry wt.), in PAD. treatment during 1978 – 79, for above – ground grasses (▲——▲G), litter (■——■L) and total below – ground organs (●——●BG); divided into root (○——○RTS), rhizome (○— —○RZM) & detached rt. (○·····○DR) fractions. See text.

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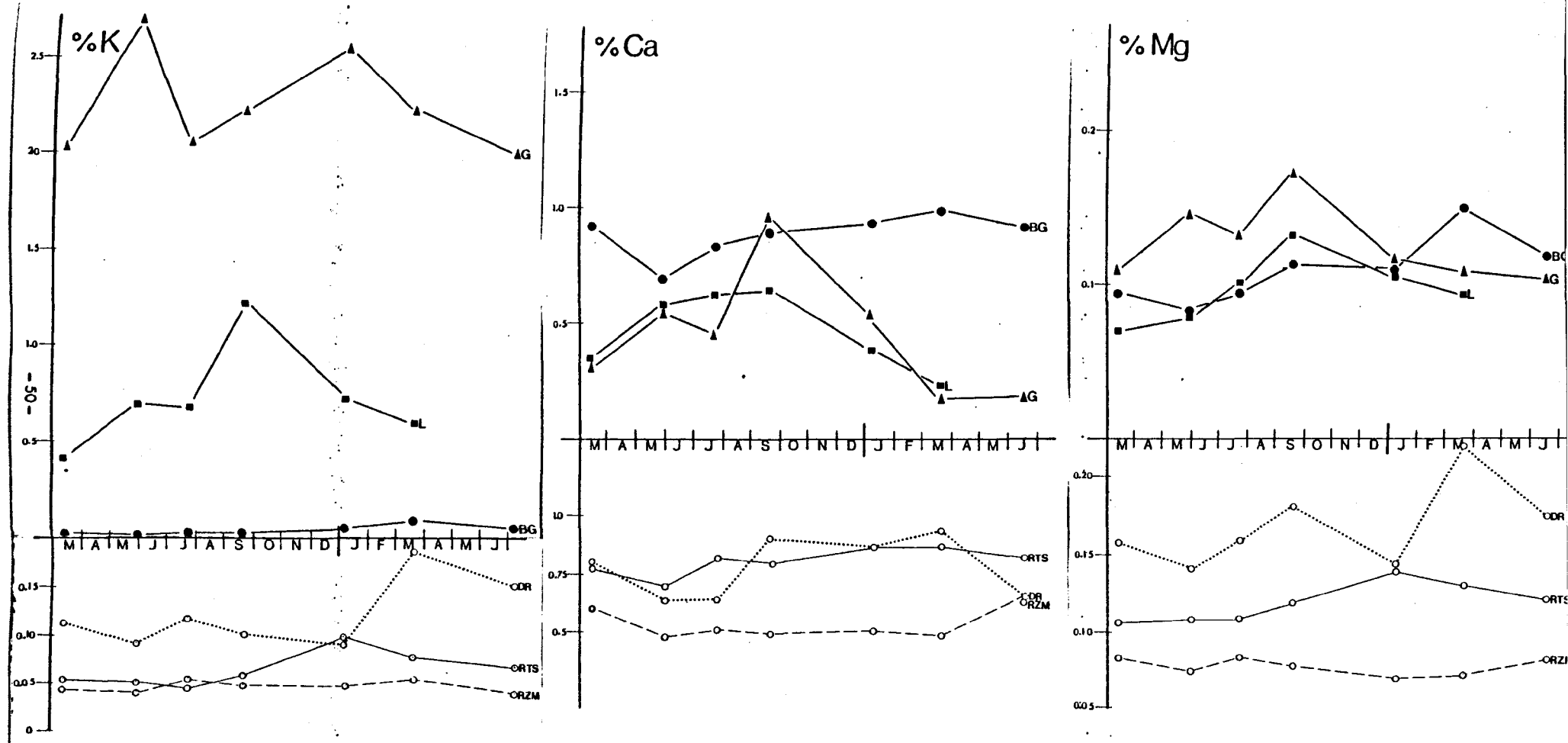

FIG 13 (contd.): PAD., 1978 – 79.
NUTRIENT CONCENTRATIONS (%dry wt.)

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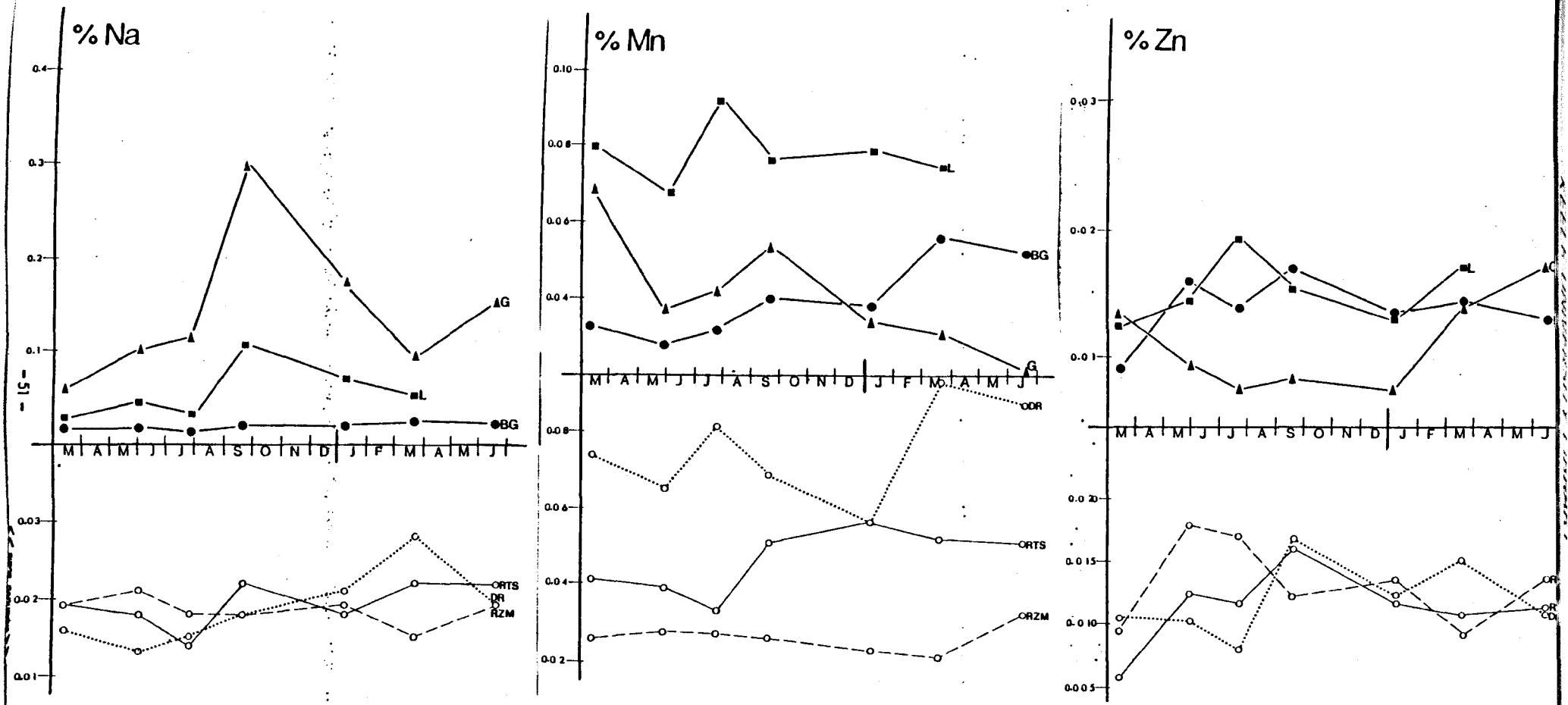

FIG 13 (contd.): PAD., 1978-79.
NUTRIENT CONCENTRATIONS (%dry wt.).

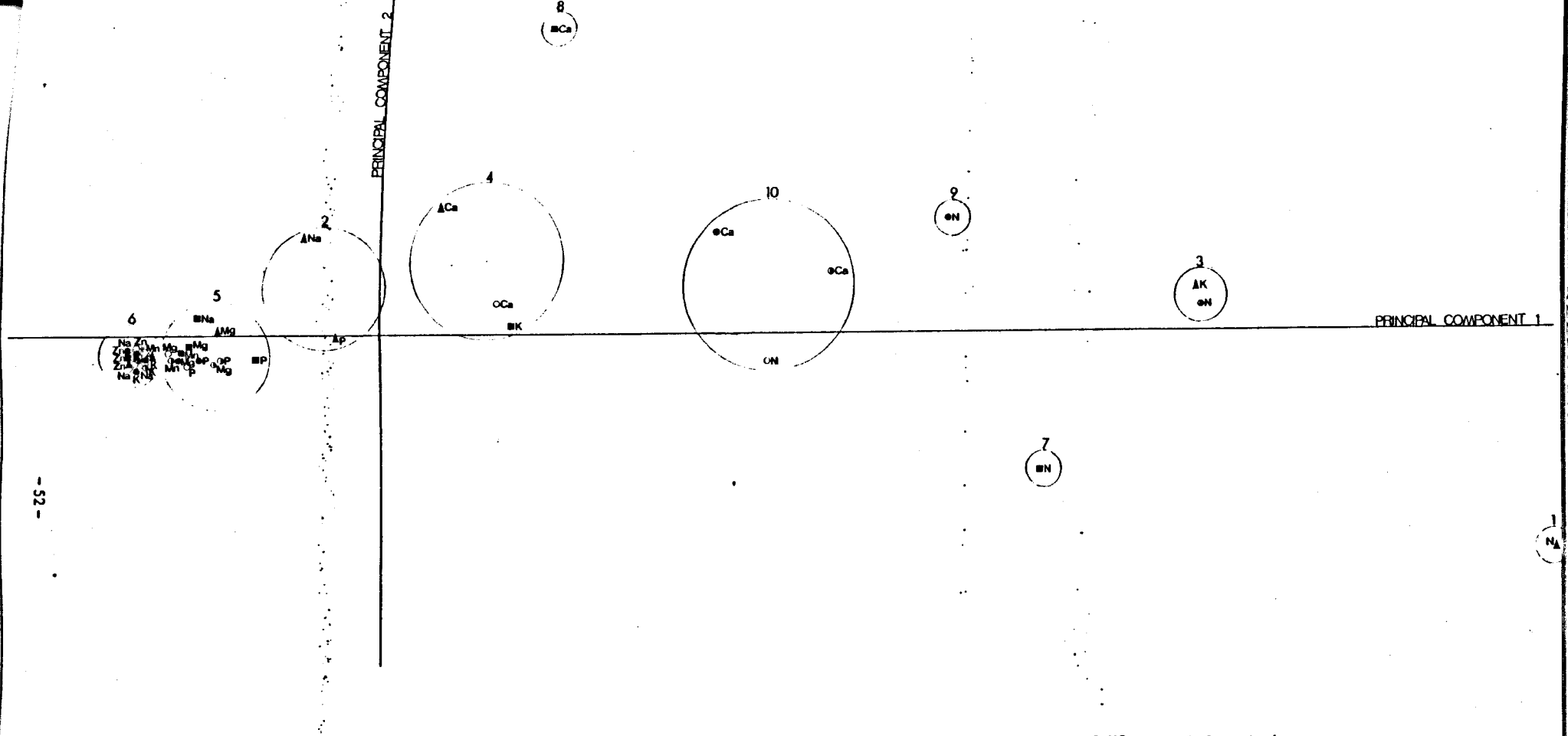

FIG 14 : Cluster analysis - LG.

Each point represents a case measured on each of six variables (sampling dates). Cases are nutrient concentrations (% dry weight) in Grasses (▲), Litter (■), Roots (●), Rhizomes (o), and Detached Rts(●).

Ten clusters, indicated by circles, have been selected. Cluster diagnostics are shown. See text.

SUMMARY OF CLUSTER DIAGNOSTICS (Wards method)

	NUMBER OF CLUSTER									
	1	2	3	4	5	6	7	8	9	10
F-RATIO (INTRA-CLUSTER VARIATION)	0.00	0.02	0.04	0.04	0.01	0.00	0.00	0.00	0.00	0.06
T-VALUE (INTER-CLUSTER VARIATION)	3.16	0.19	2.20	0.28	0.50	3.91	1.75	0.46	1.53	1.05

Small F-ratios indicate relatively low variation within the cluster. Large deviations from zero for the T-values indicate cluster values differ from the population mean. Each value is the mean for six variables.

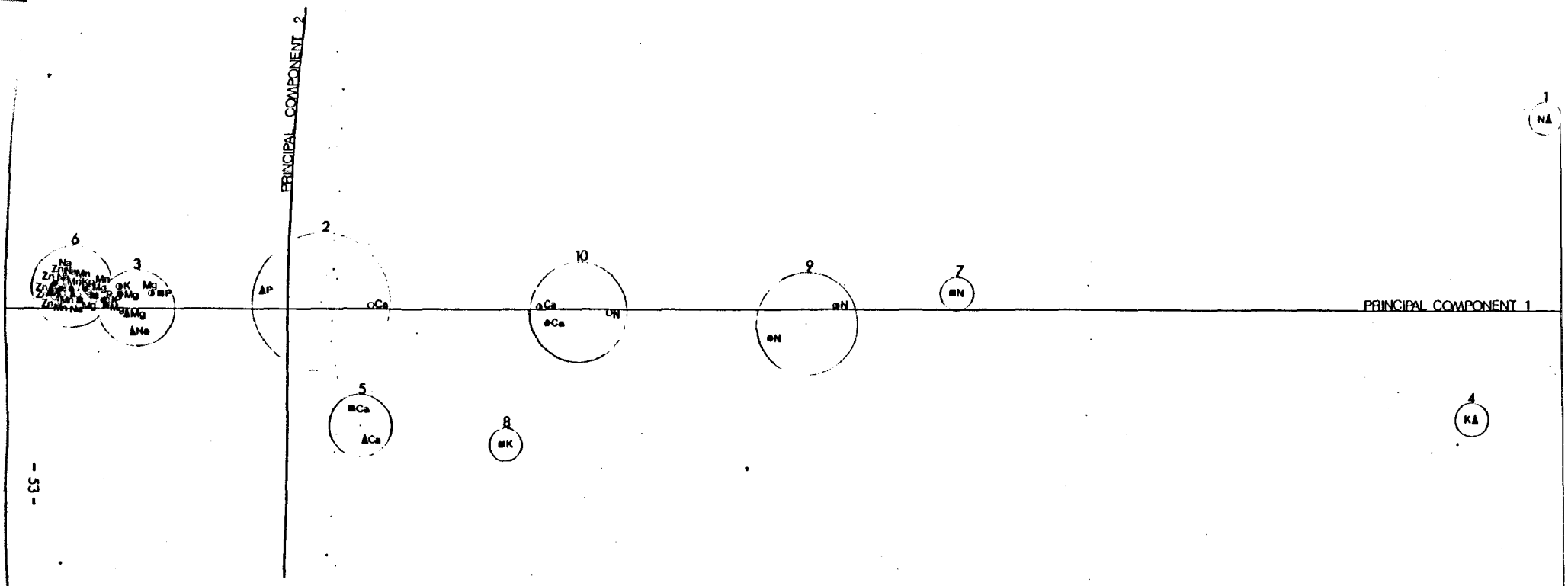

FIG 15 : Cluster analysis - PAD.

Each point represents a case measured on each of six variables (sampling dates). Cases are nutrient concentrations (% dry weight) in Grasses (▲), Litter (■), Roots (●), Rhizomes (o), and Detached Rts(●).

Ten clusters, indicated by circles, have been selected. Cluster diagnostics are shown. See text.

SUMMARY OF CLUSTER DIAGNOSTICS (Wards method)

	NUMBER OF CLUSTER									
	1	2	3	4	5	6	7	8	9	10
F-RATIO (INTRA-CLUSTER VARIATION)	0.00	0.03	0.00	0.00	0.02	0.00	0.00	0.00	0.02	0.01
T-VALUE (INTER-CLUSTER VARIATION)	3.40	0.08	0.44	3.19	0.23	0.59	1.78	0.58	1.38	0.75

Each value is the mean for six variables.

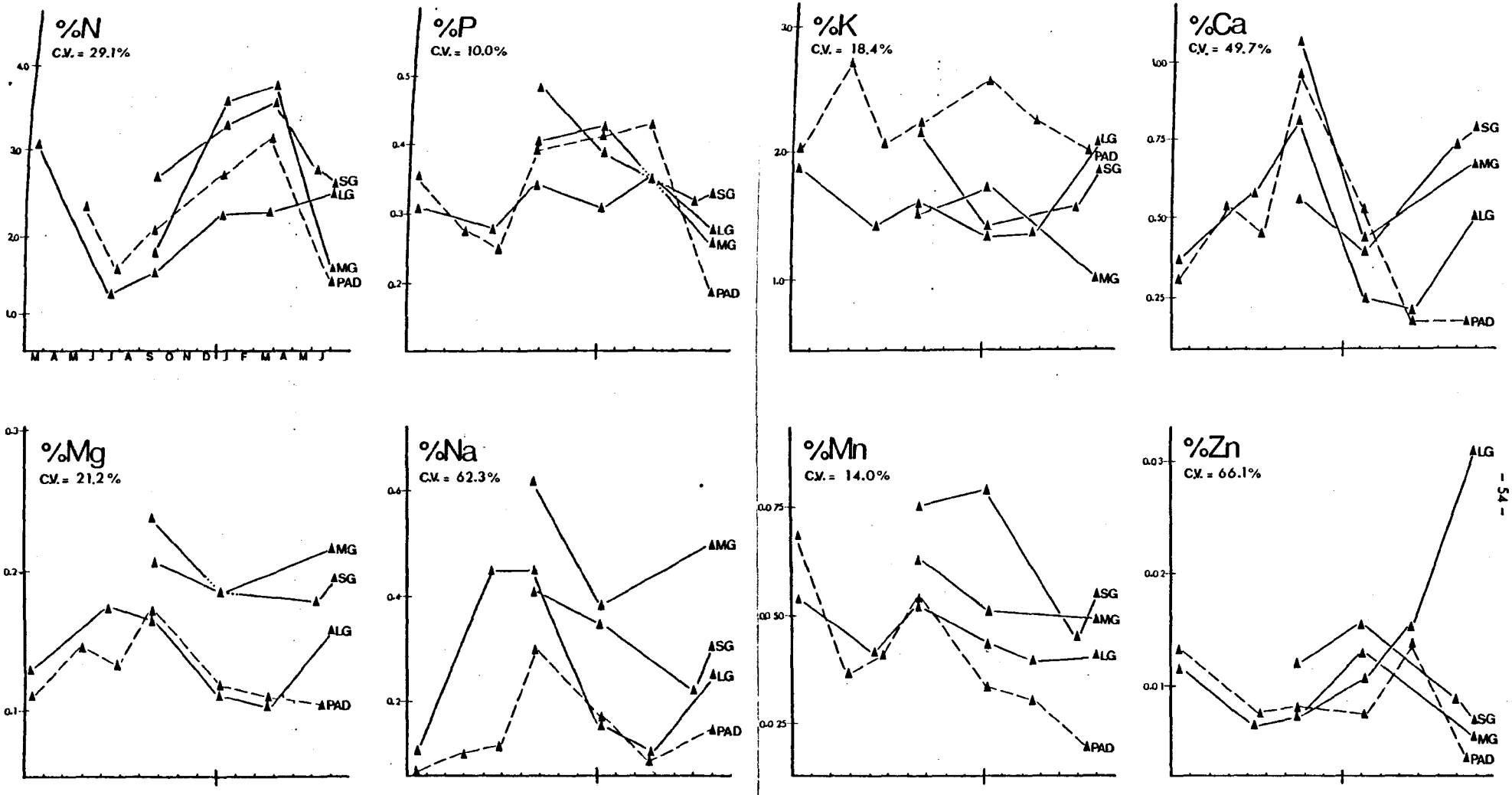

FIG 16 ; Percentage nutrients in above-ground GRASSES (dry wt. basis) from each cutting treatment during 1978 – 79. C.V. = coefficient of variation (for LG only).

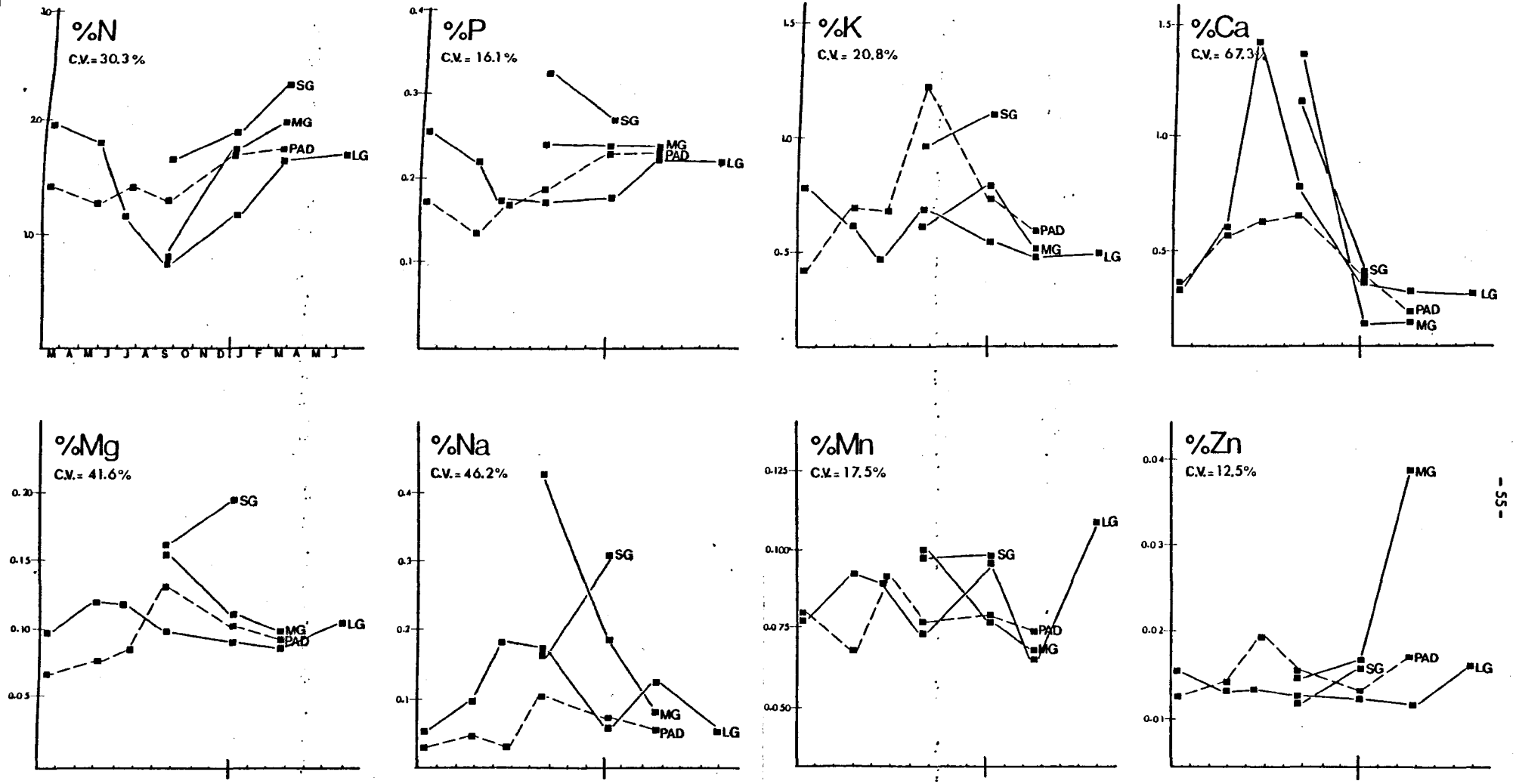

FIG 17 ; Percentage nutrients in LITTER (dry wt. basis) from each cutting treatment during 1978 – 79. C.V. = coefficient of variation (for LG only).

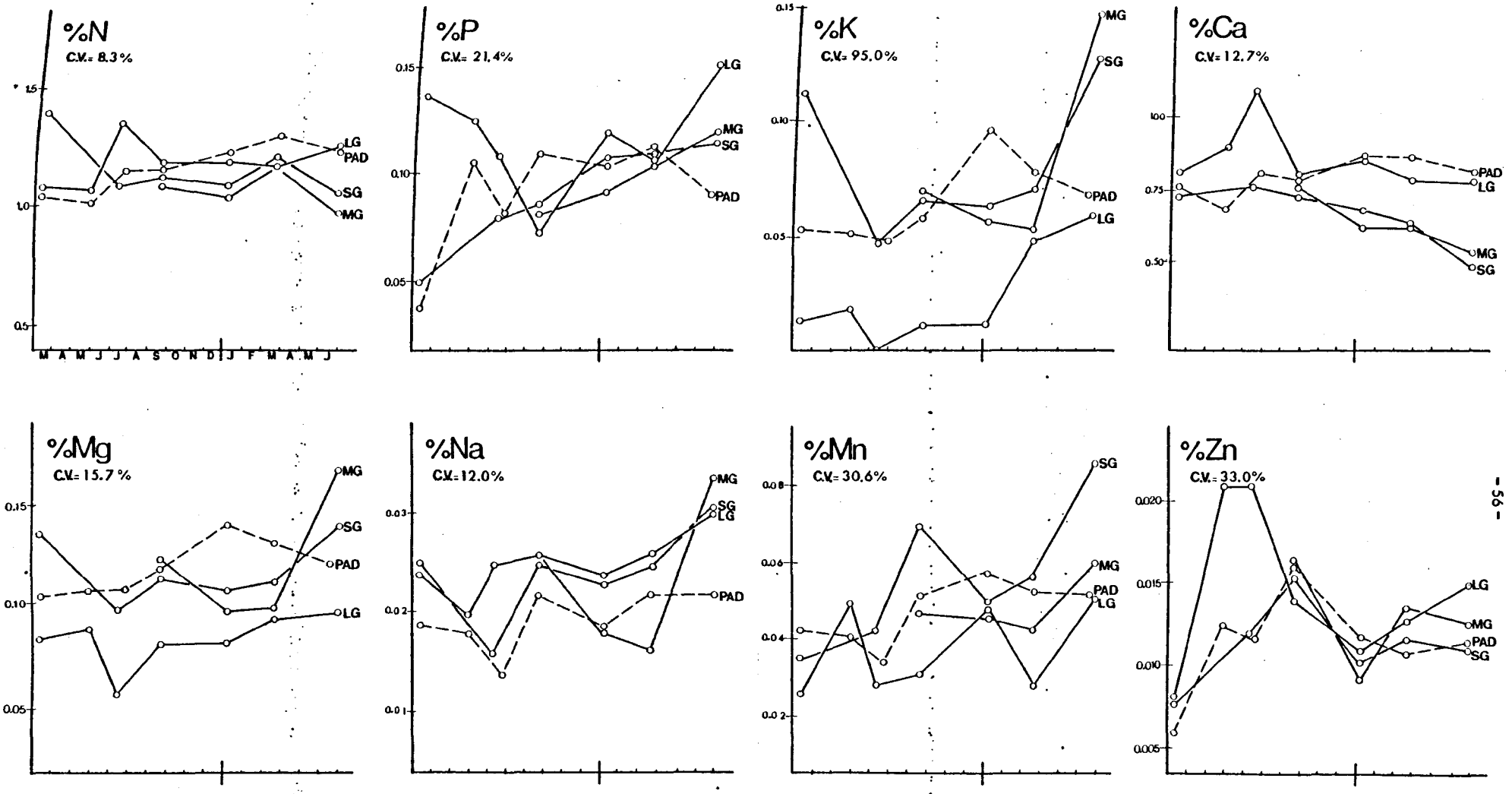

FIG 18 ; Percentage nutrients in ROOT fraction (dry wt. basis) from each cutting treatment during 1978 – 79. C.V. = coefficient of variation (for LG only).

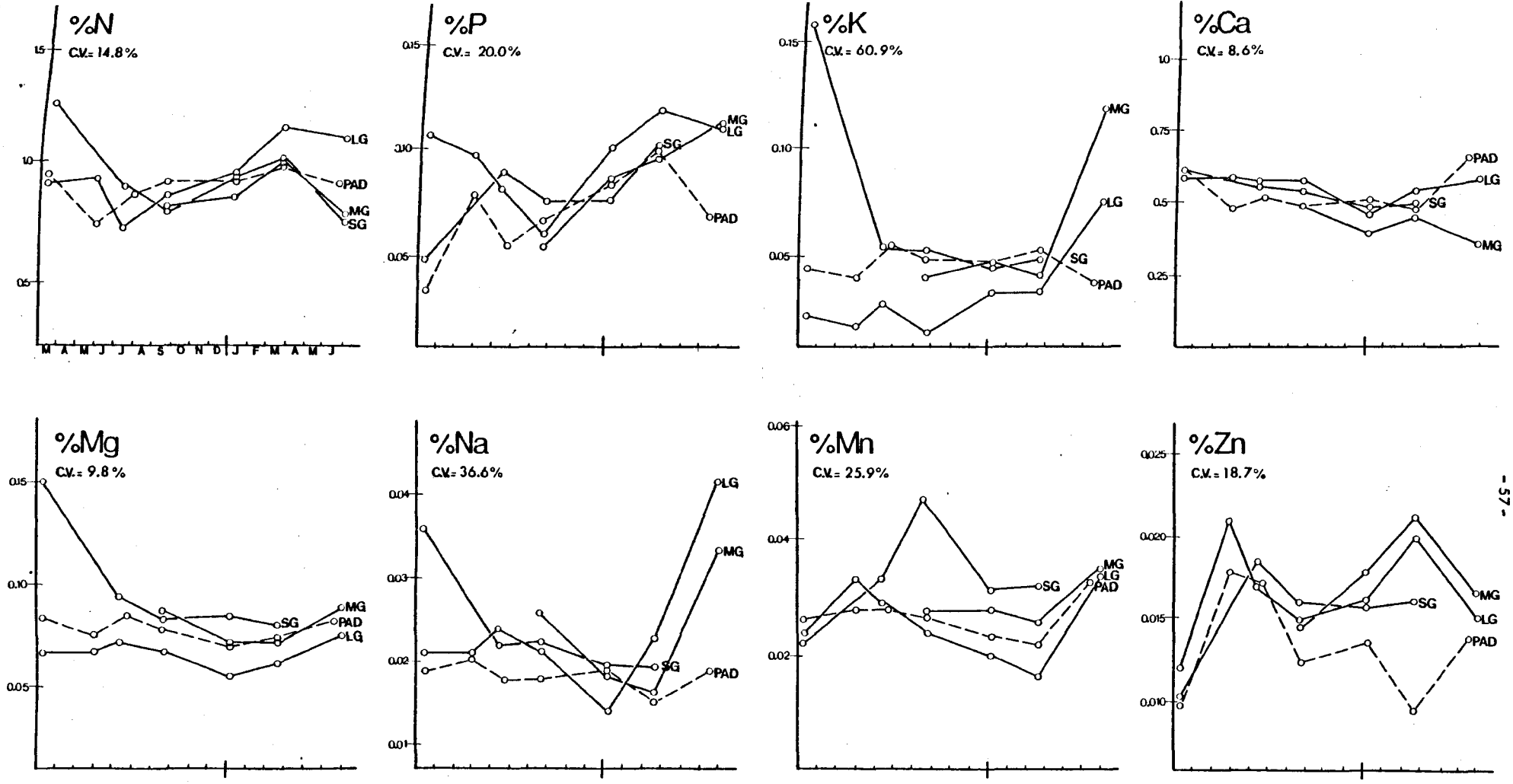

FIG 19 ; Percentage nutrients in RHIZOME fraction (dry wt. basis) from each cutting treatment during 1978 – 79. C.V. = coefficient of variation (LG only).

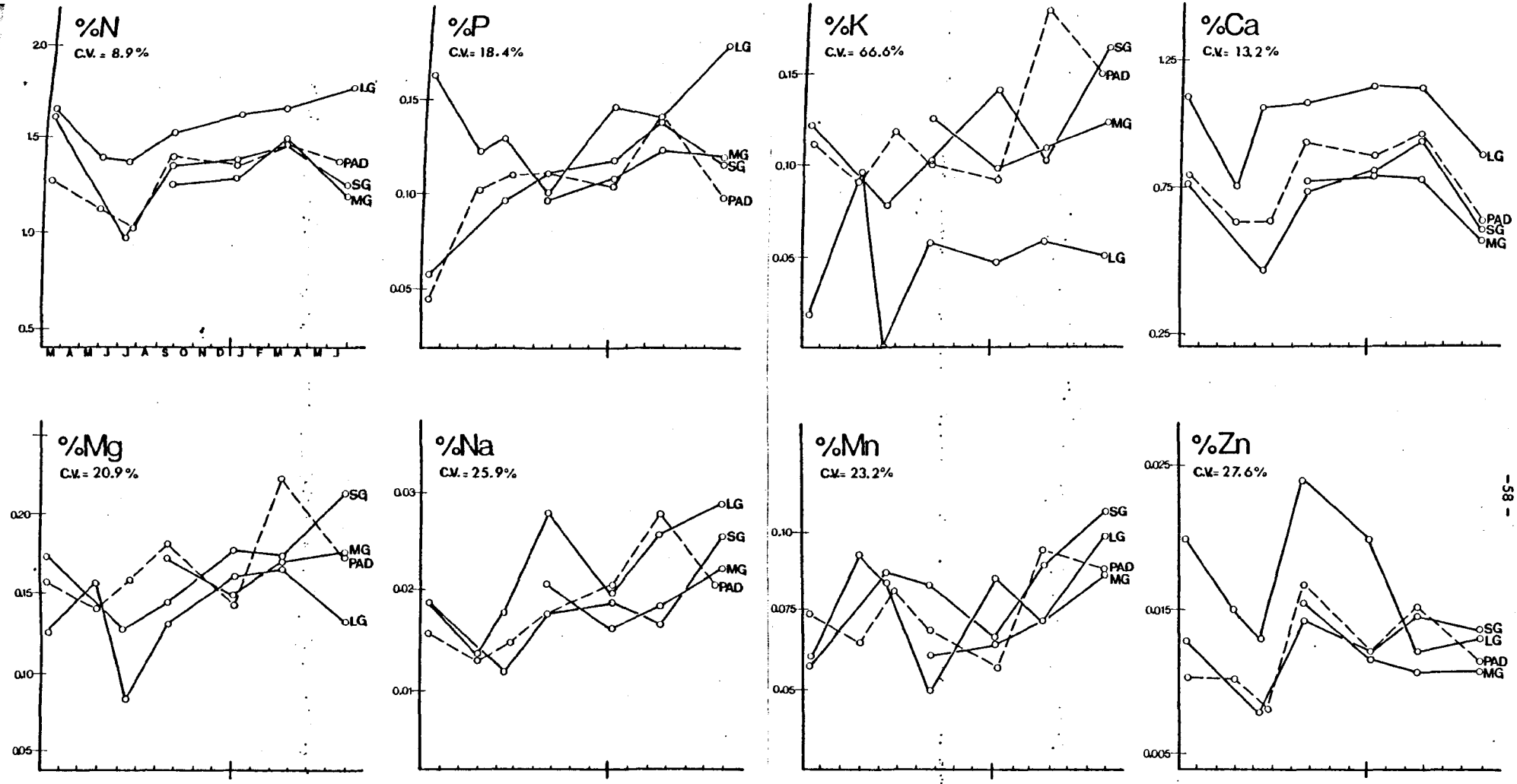

FIG 20 ; Percentage nutrients in DETACHED RT. fraction (dry wt. basis) from each cutting treatment during 1978 – 79. C.V. = coefficient of variation (LG only).

(LG)	GRASS CONCENTRATIONS	LITTER CONCENTRATIONS	ROOT CONCENTRATIONS	RHIZOME CONCENTRATIONS	DETACHED ROOT CONCENTRATIONS
%N	G(-)*	G(-), L(-), RTS(-)*	G, RTS(-), RZM*	RZM(-)*	RZM(-)***
%P		G(-), L(-), DR(-)*, RTS(-)**		G(-)*	
%K	RZM(-), L(-), G(-)*	RTS, RZM(-)*	RTS(-)**	RTS(-)**, L**	L**, DR(-)**
%Ca	G*	RZM*, G*	RZM*	L(-), DR(-)***	RTS, L, G(-), RZM*
%Mg	G*	G, L(-), RTS*, RZM**	RZM(-)***		L*, G(-)**, RTS(-)***
%Na	G***	RZM, DR*, L(-)**	RTS(-)*	RTS(-), L(-), DR(-), G*	DR(-)**
%Mn	RTS, RZM		RTS(-)		RTS(-), DR*
%Zn	RTS(-)**	L(-), RZM(-)*	G		

TABLE 6 : Multiple Regression Analysis (LG). Table shows order of independent variables (dry weights) brought into equations and levels of significance at each step (* 5%, ** 1%, *** 0.1%). Negative correlations are indicated and missing values mean no significance within 10%. Full results in Appendix 5.

(PAD)	GRASS CONCENTRATIONS	LITTER CONCENTRATIONS	ROOT CONCENTRATIONS	RHIZOME CONCNS.	DETACHED ROOT CONCENTRATIONS
%N	G(-)**, RZM(-)**		RZM(-)*	RZM(-)**	RTS(-)*
%P	RZM*(-), L**(-), G***(-)	RZM**(-)			
%K				L**(-)	RTS(-)
%Ca		G*, DR**(-)	RZM*(-)		RZM(-)**
%Mg		G, RTS*(-)	RZM(-)		RTS(-)*
%Na		RZM(-), G, L(-), DR**	RTS*(-)	L*	RTS**(-)
%Mn		L(-), RTS*	RZM(-)	RTS**	L(-), DR(-), G(-), RZM(-)*
%Zn	G(-)	L(-), DR(-)*	G, RTS(-), L(-)	RZM*	RTS(-)

TABLE 7 : Multiple Regression Analysis (PAD). Table shows order of independent variables (dry weights) brought into equations and levels of significance at each step (* 5%, ** 1%, *** 0.1%). Negative correlations are indicated and missing values mean no significance within 10%. Full results in Appendix 6.

LG

GRASS CONCENTRATIONS	LITTER CONCENTRATIONS	ROOT CONCENTRATIONS	RHIZOME CONCENTRATIONS	DETACHED ROOT CONCENTRATIONS
*P%=P%rts(-), G(-)***	*P%=N%l***	*P%=P%dr****	*Mg%=Mn%rzm**	*P%=N%dr, K%dr(-)**
	*Mn%=Mg%l, Na%l(-), Zn%l**	*P%=N%l, P%g(-)**	*Na%=K%rzm*, Mg%rzm***	*Ca%=RTS, Mg%dr**
		*Mn%=RTS(-), K%rts**	*Mn%=Mg%rzm**	

PAD

GRASS CONCENTRATIONS	LITTER CONCENTRATIONS	ROOT CONCENTRATIONS	RHIZOME CONCENTRATIONS	DETACHED ROOT CONCENTRATIONS
*K%=L, P%rts**	*N%=P%l**	*P%=P%dr**	*P%=P%rts**	*P%=N%rts, DR(-)**
*Ca%=Mg%g***	*K%=Mg%l*, L(-)***	*P%=Zn%rts*, G**	*P%=RTS(-), N%rzm(-)**	*K%=Mn%dr***
Ca%=Na%g, RZM***	*Na%=K%l*, Ca%l***	*K%=Mg%rts****	*Ca%=P%rzm(-)**	
*Mg%=Ca%g***		*K%=N%l**	*Mg%=P%rzm(-)**	
*Mg%=Na%g, DR(-)**		*Mg%=K%rts****		
Na%=Ca%g, RZM(-)***		*Mn%=Mg%rts**		
*Mn%=K%g(-), L, Na%g(-), DR**		*Zn%=P%rts**		

TABLE 8 : Additional Regression Analyses for LG (above) and PAD (below) in which nutrient concentrations are added to the independent variables (dry weights) in the equations. Negative correlations are indicated with levels of significance at each step (* 5%, ** 1%, *** 0.1%). Full results in Appendix 7.

(LG)		HIGHEST CONCENTRATIONS	LOWEST CONCENTRATIONS
N%	Grasses		peak grass biomass
	Roots	peak grass & root	biomass
	Rhizomes		peak grass biomass
	Detached roots		peak grass biomass
P%	Grass*		peak grass biomass
	Roots*		autumn
	Rhizomes		autumn
	Detached roots*		autumn
K%	Grass		peak rhizome biomass
	Roots	-increased through sampling period-	
	Rhizomes		
	Detached roots		peak rhizome biomass
Ca%	Grass	autumn	
	Roots	peak root biomass	
	Rhizomes	autumn	
	Detached roots	winter	

		HIGHEST CONCENTRATIONS	LOWEST CONCENTRATIONS
Mg%	Grass	peak grass biomass	
	Roots		peak root biomass
	Rhizomes*	peak grass biomass	
	Detached roots		peak rhizome biomass
Na%	Grass	summer/autumn	
	Roots	-increased through sampling period-	
	Rhizomes	peak grass biomass	
	Detached roots	-increased through sampling period-	
Mn%	Grass	autumn	
	Roots		peak root biomass
	Rhizomes*	autumn	
	Detached roots		autumn/winter
Zn%	Grass		
	Roots	peak root biomass	
	Rhizomes*	-decreased through sampling period-	
	Detached roots*		

Table 9 : Summary of main seasonal events associated with highest and lowest concentrations of each nutrient in components of standing crop in LG. Litter is omitted (see Chapter 6). Asterisks denote component concentration is poorly correlated with dry weight parameters.

(PAD)		HIGHEST CONCENTRATIONS	LOWEST CONCENTRATIONS			HIGHEST CONCENTRATIONS	LOWEST CONCENTRATIONS
N%	Grass		peak grass biomass	*Mg%*	Grass*	autumn	
	Roots	peak grass biomass			Roots		peak root biomass
	Rhizomes		peak rhizome biomass		Rhizomes*	peak grass biomass	
	Detached roots		peak grass biomass		Detached roots	low root biomass	
P%	Grass		peak grass biomass	*Na%*	Grass*	autumn	
	Roots*				Roots		peak root biomass
	Rhizomes*				Rhizomes	peak rhizome biomass	
	Detached roots*	spring			Detached roots		peak root biomass
K%	Grass*		peak grass biomass	*Mn%*	Grass*	autumn	
	Roots*				Roots		peak root biomass
	Rhizomes*	winter-low variation			Rhizomes	peak rhizome biomass	
	Detached roots	low root biomass	peak rhizome biomass		Detached roots		winter
Ca%	Grass*	autumn		*Zn%*	Grass		peak grass biomass
	Roots		early summer		Roots	autumn	
	Rhizomes*				Rhizomes	peak rhizome biomass	
	Detached roots	winter			Detached roots	autumn	

Table 10 : Summary of main seasonal events associated with highest and lowest concentrations of each nutrient in components of standing crop in PAD. Litter is omitted (see Chapter 6). Asterisks denote components concentration is poorly correlated with dry weight parameters.

CHAPTER 5

NUTRIENT POOLS

Data are combined from Chapters 3 and 4, which should be read in conjunction with the present chapter. The aims were to provide further study of the significance of nutrient changes by examining variations of the total standing crop of nutrients in each vegetation component (or *nutrient pool*) according to season and management regime. These are considered in perspective with total soil nutrients.

Further information may be provided in this way which could not be ascertained from nutrient concentration data. For example, large accumulations of litter in LG and PAD may limit the availability of certain nutrients which would not be indicated from nutrient concentration data. In the previous chapter it was noted that certain nutrients, for example *N* in grasses, were in minimum concentrations at times of peak biomass. The present chapter should indicate whether differing amounts of nutrients were involved, or whether large pools were bound in other components. Also the present chapter should provide information concerning the overall changes in all vegetation components combined, to indicate whether nett gains or losses to the soil take place, and furthermore the proportion of nutrients removed as cuttings.

Finally it may be possible to provide estimates of the annual requirements of each nutrient and help to provide an understanding of the nutrition of amenity grassland.

5.1 Methods

Soil samples for nutrient determinations were taken randomly from the treatment plots on two occasions; in November 1978 and April 1979. At least 15 samples were collected on each occasion, using a 2.5 cm auger to 10 cm depth. Samples were dried at 105°C and digested in a perchloric-nitric-sulphuric acid mixture prior to analysis. Allen *et al.* (1974) discuss the effectiveness of this digestion method, which may be unreliable for *Ca* and *Mg*. Analyses follow those described previously, except for *C* and *N* which were determined using a *Perkin-Elmer 240 CHN* microanalyser. No attempts were made to measure 'available' nutrients.

Soil nutrient concentrations are given in APP. 1. Pools of each nutrient in soil and vegetation components were calculated using the following formulae:

$$\text{SOIL NUTRIENT POOLS (A)} = \frac{\text{total soil nutrient (\%) x dry wt. soil (to 10 cm depth)}}{100}$$

$$\text{PLANT NUTRIENT POOLS (B)} = \frac{\text{dry wt. of component x nutrient concentration (\%)}}{100} - C$$

$$\text{CORRECTION FACTOR FOR BELOW-GROUND COMPONENTS (C)} = \frac{\text{total soil nutrient (\%) x ash wt. of sample}}{100}$$

5.2 Total Nutrients in LG

Total nutrients in each component of the vegetation in LG are shown in FIG. 21. Peak amounts of all nutrients in above-ground grasses, during the growing season, corresponded to largest amounts in rhizomes. Above-ground losses from grasses during winter resulted in large litter accumulations of *N*, *P*, *Mg* and *Mn* through the sampling period. *K*, *Ca* and *Na* reached highest levels in litter during autumn and winter, with large losses before the following growing season.

The amounts of nutrients below ground were consistently higher than in above-ground grasses for *N*, *Ca*, *Mn* and *Zn*. Above-ground reserves of *P* and *Mg* were higher during the growing season and *K* and *Na* were always in small amounts below ground. Nutrient reserves were of similar proportions in all below-ground components.

Root reserves of *N*, *Ca*, *Na* and *Zn* were highest during June/July 1978, followed by a progressive decline. Conversely, root *K*, *Mg* and *Mn* were lowest in June/July 1978. Root *P* was lowest in September, but levels were very variable.

Maximum reserves of *N*, *P*, *Ca*, *Mg*, *Mn* and *Zn* in detached roots were during winter. Detached root *K* and *Mg* were high in May/June, but low in June/July 1978.

Annual changes in the sizes of nutrient pools are shown in TABLE 11. Gains or losses of component pools are calculated by subtracting 1978 from 1979 values. Between March of these years, large increases in total plant component pools were caused by large accumulations of nutrients in litter. This represents nett uptake from the soil. Nett losses from vegetation components to the soil were evident between June 1978 and June 1979, corresponding to reduced production of grasses, roots and rhizomes. 11.7% increase of total vegetation *N* reflects

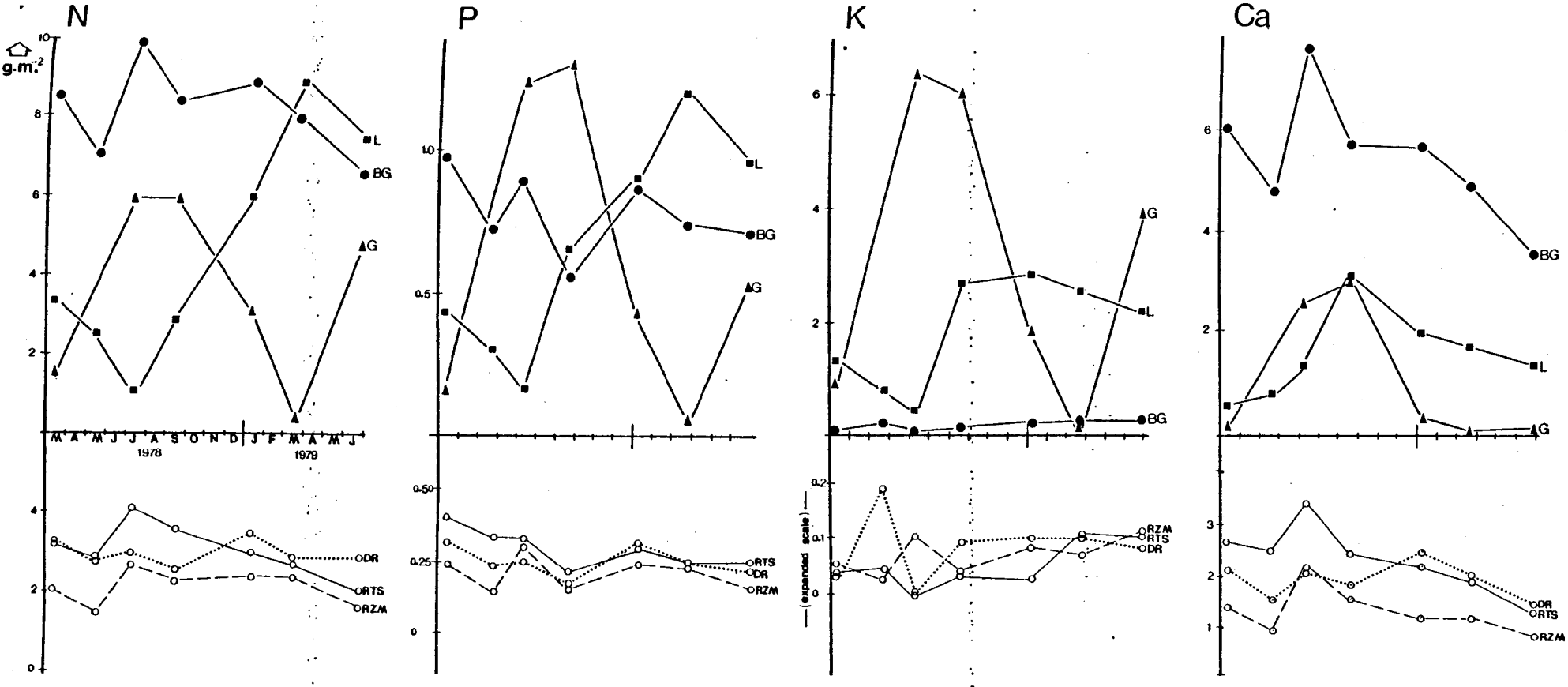

FIG 21 ; TOTAL NUTRIENTS in LG ($g.m^{-2}$) in above-ground grasses (▲——▲AG), litter (■——■L), and total below-ground organs (●——●BG) ; divided into roots (o——oRTS), rhizomes (o- - -oRZM) & detached rts. (o·····oDR) . Forb fractions are excluded .

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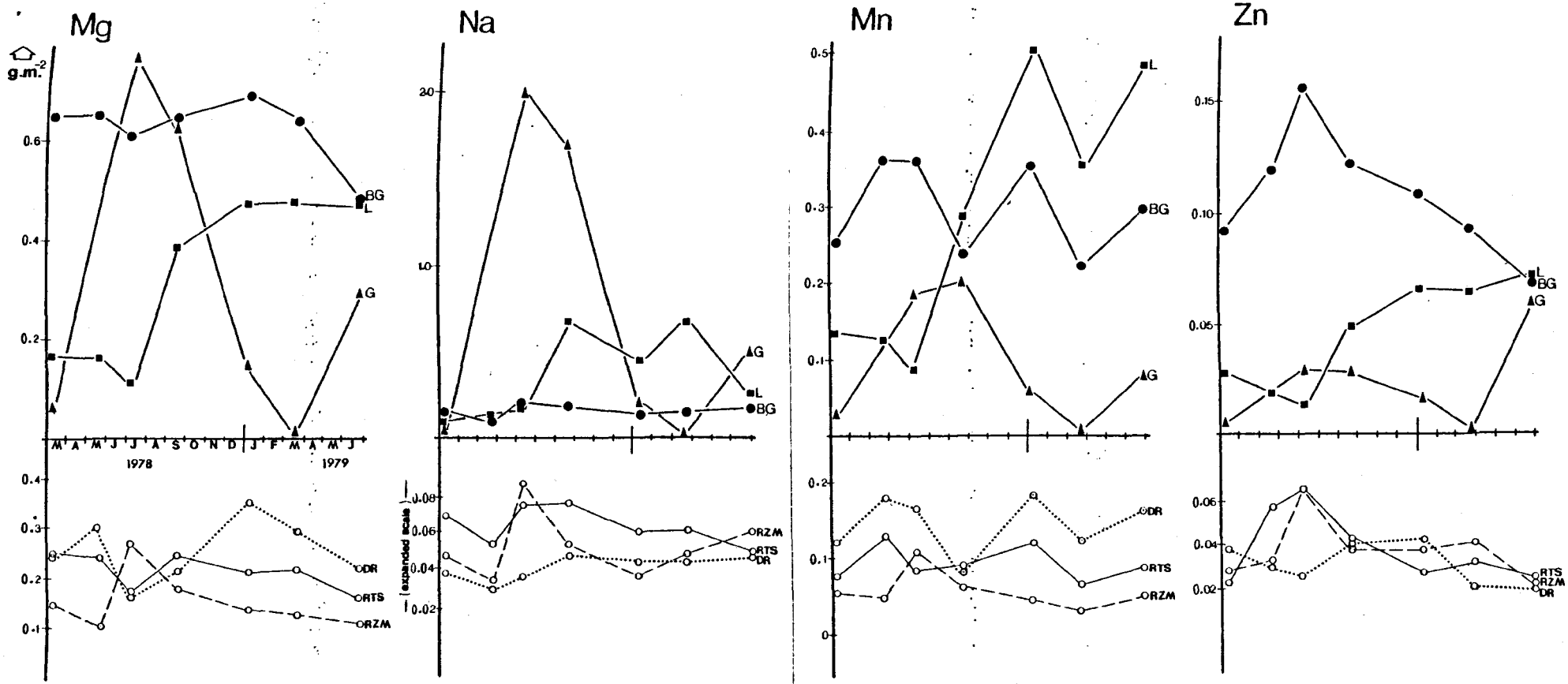

FIG 21 : (contd.) TOTAL NUTRIENTS in LG ($g.m^{-2}$) .

COMPONENT	*N*		*P*		*K*		*Ca*		*Mg*		*Na*		*Mn*		*Zn*	
	M-M	J-J	M-M	J-J	M-M	J-J	M-M	J-J	M-M	J-J	M-M	J-J	M-M	J-J	M-M	J-J
Grasses	-1.212	-1.143	-0.105	-0.719	-0.736	-2.425	-0.156	-1.627	-0.049	-0.473	-0.038	-1.511	-0.022	-0.109	-0.004	+0.030
Litter	+5.493	+6.396	+0.773	+0.792	+1.225	+1.735	+1.198	+0.044	+0.311	+0.357	+0.573	+0.086	+0.219	+0.393	+0.036	+0.058
Roots	-0.448	-2.065	-0.162	-0.083	+0.071	+0.099	-0.755	-2.083	-0.034	-0.016	-0.010	-0.027	-0.012	-0.001	+0.006	-0.041
Rhizomes	+0.291	-1.127	+0.002	-0.148	+0.016	+0.006	-0.218	-1.307	-0.022	-0.161	-0.001	-0.028	-0.022	-0.060	+0.013	-0.043
Detached Roots	-0.343	-0.084	-0.075	+0.042	+0.066	+0.083	-0.180	-0.603	+0.045	+0.053	+0.007	+0.013	+0.004	-0.002	-0.018	-0.005
TOTAL GAIN OR LOSS	+3.781	+1.977	+0.433	-0.116	+0.642	-0.502	-0.111	-5.576	+0.251	-0.240	+0.531	-1.467	+0.167	+0.221	+0.033	-0.001
% gain or loss	*+28.2%*	*+11.7%*	*+27.7%*	*-5.0%*	*+26.6%*	*-7.3%*	*-1.6%*	*-48.4%*	*+28.5%*	*-16.1%*	*+173.8%*	*-61.7%*	*+40.5%*	*+34.9%*	*+26.4%*	*-0.5%*

TABLE 11 : Annual changes of nutrient pools (g.m.$^{-2}$) in LG between 13 March 1978 to 22 March 1979 (M-M) and 10 July 1978 to 10 June 1979 (J-J).

larger accumulations in litter.

5.3 Total Nutrients in PAD

Total nutrients in each component of the vegetation in PAD are shown in FIG. 22. Peak amounts of nutrients in above-ground grasses were reached in September, except for *K* and *Zn* which were in largest amounts in July. Rhizome nutrients reached a peak early in the growing season, followed by a progressive decline. Substantial amounts of nutrients were bound in above- and below-ground forb fractions.

Litter nutrient dynamics were directly influenced by the current seasons biomass to a lesser extent than in LG. *N, P, K, Mg* and *Na* were lowest during the growing season, whereas *Ca, Mn* and *Zn* were highest in June 1978 followed by a decline.

Amounts of nutrients in above- and below-ground compartments were essentially the same as LG, excepting *Mg* which was lower in above-ground grasses in PAD. Root reserves of *N* and *Ca* reached peak levels in July, and *P* in June, followed by a decline until the next growing season. *K, Mg, Mn* and *Zn* tended to increase through 1978 with highest levels in winter. In detached roots, all nutrients were in largest amounts over winter, mostly with peak levels in June 1978, although *P* and *K* varied slightly.

Annual changes in the sizes of nutrient pools between March 1978 and March 1979 are shown in TABLE 12. Most nutrient pools decreased over the year (*cf.* TABLE 11), except for *P* which increased in all components except grasses. Otherwise, the main differences to LG were due to reduced litter pools. Changes in forb nutrient pools are not included, because annual data are not available, but standing crop in March 1979 is shown in the table. Forb biomass proliferated through the year, from low levels, and much of the nutrients lost from grass

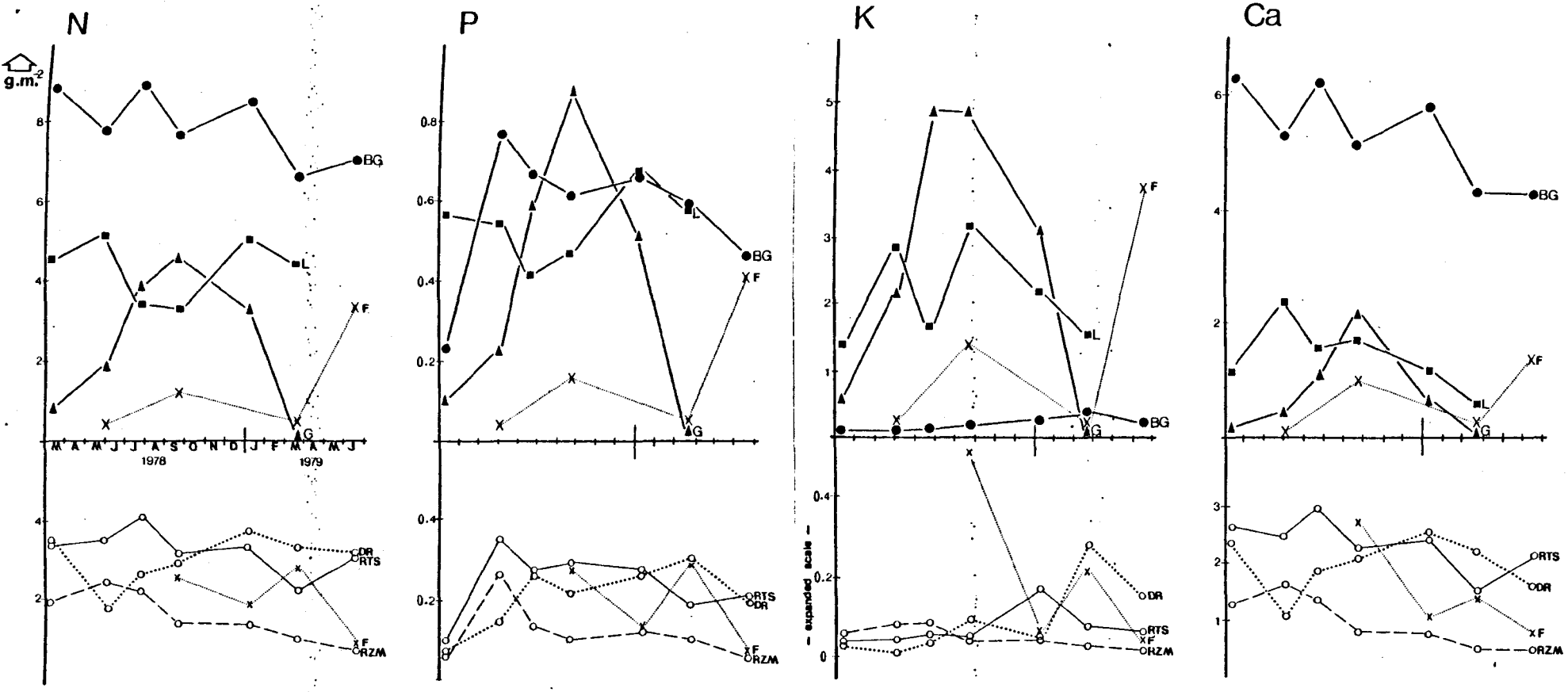

FIG 22 : TOTAL NUTRIENTS in PAD ($g.m^{-2}$) in above-ground grasses (▲——▲G), litter (■——■L) and total below-ground organs (●——●BG); divided into roots (o——oRTS), rhizomes (o- - - -oRZM) & detached rts (o·····oDR). Above- (X·····XF) and below- ground (x·····xF) forb fractions are also shown.

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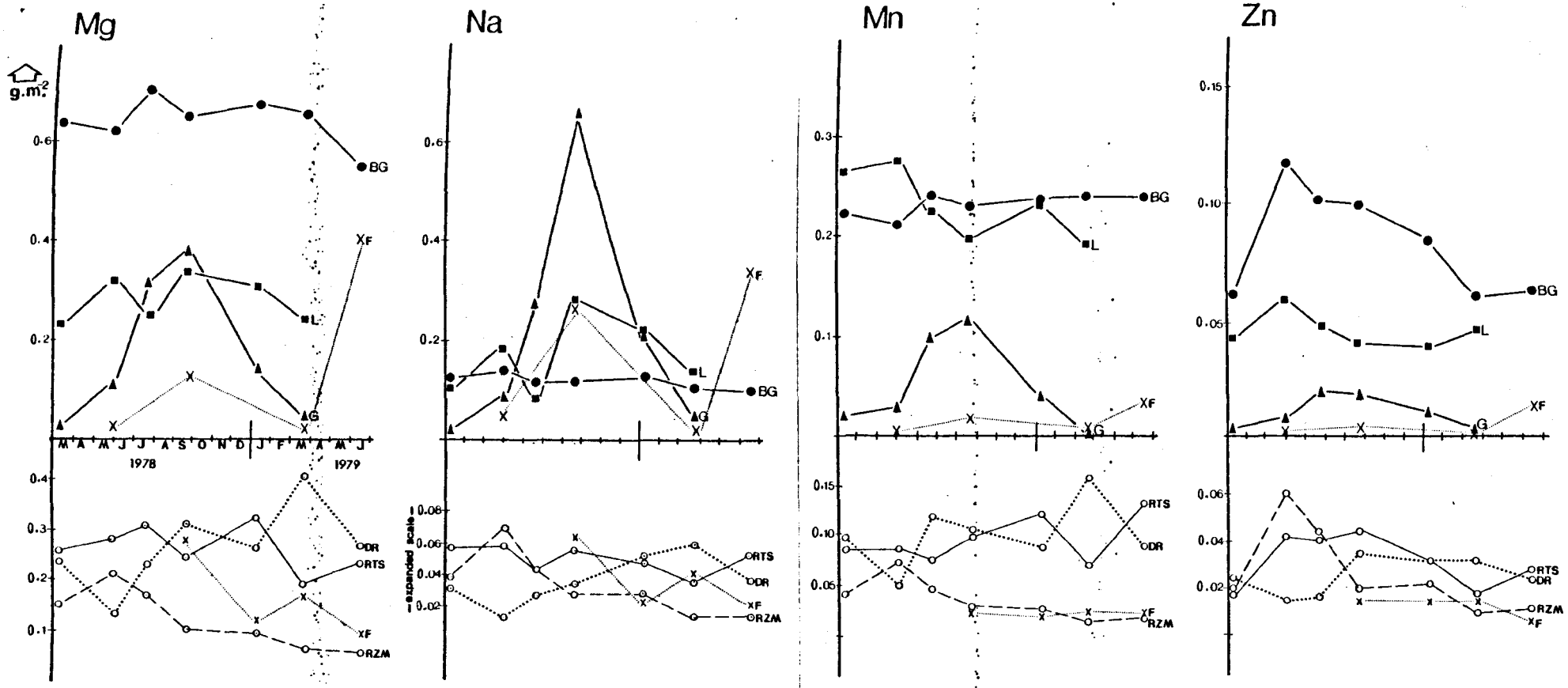


FIG 22 : (contd.) TOTAL NUTRIENTS in PAD ($g.m^{-2}$).

COMPONENT	*N*	*P*	*K*	*Ca*	*Mg*	*Na*	*Mn*	*Zn*
Grasses	- 0.651	- 0.081	- 0.470	- 0.080	-0.026	-0.012	- 0.018	-0.003
Litter	- 0.056	+ 0.020	- 0.152	- 0.545	+0.011	+0.04	- 0.071	+0.003
Roots	- 1.162	+ 0.087	+ 0.031	- 1.091	-0.070	-0.021	- 0.018	+0.001
Rhizomes	- 0.93	+ 0.036	- 0.024	- 0.760	-0.088	-0.023	- 0.027	-0.010
Detached Roots	- 0.11	+ 0.232	+ 0.257	- 0.119	+0.170	+0.027	+ 0.061	+0.008
TOTAL GAIN OR LOSS	- 2.909	+ 0.294	- 0.358	- 2.595	-0.003	+0.011	- 0.073	-0.001
% gain or loss	*-20.5%*	*+32.5%*	*-17.0%*	*-34.6%*	*-0.3%*	*+4.5%*	*-14.3%*	*-0.9%*
FORB STANDING CROP (March 1979)	3.294	0.342	0.495	1.432	0.193	0.060	0.027	0.015

TABLE 12 : Annual changes of nutrient pools ($g.m.^{-2}$) in PAD between 13 March 1978 and 21 March 1979, excluding forbs. Forb standing crop (above-ground + below-ground) in March 1979 is shown.

components must become bound in forb fractions.

5.4 *Effects of Mowing on Total Nutrients in Roots*

In roots (FIG. 23) total nutrients maintained broadly similar levels in all treatments although certain seasonal differences were apparent, particularly in July 1979. Contrary to LG and PAD, SG levels of *N*, *P* and *Ca* did not increase in May/June 1978 but together with MG levels they increased substantially in June 1979.

Seasonal pattern also differed between treatments for *K* and *Mg*. Reserves in LG were comparatively low in July 1978 but, together with PAD, increased over winter. Levels in MG were particularly high in June 1979, in both cases. *Na* levels were less variable in LG and PAD, and *Mn* and *Zn* in SG reached high levels in September.

5.5 *Effects of Mowing on Total Nutrients in Rhizomes*

In rhizomes (FIG. 24) total nutrients declined more rapidly through the sampling period in PAD than in LG. In most cases, as with roots, nutrient levels in SG did not increase during the 1978 growing season, but levels of all nutrients except *Ca* and *Mn* were higher in mown treatments in June 1979. *K* levels were notably high in SG in March 1978 and, as with roots, *Mn* reached highest levels in September 1978.

5.6 *Effects of Mowing on Total Nutrients in Detached Roots*

In detached roots (FIG. 25) all nutrients in SG, except *K* and *Mn*, were in lesser amounts than in LG during the 1978 growing season, but otherwise fluctuations were similar. Seasonal changes in *K*, *Mg* and *Mn* were extremely variable between treatments, and tangible differences are difficult to discern. *K* levels in all treatments were low during

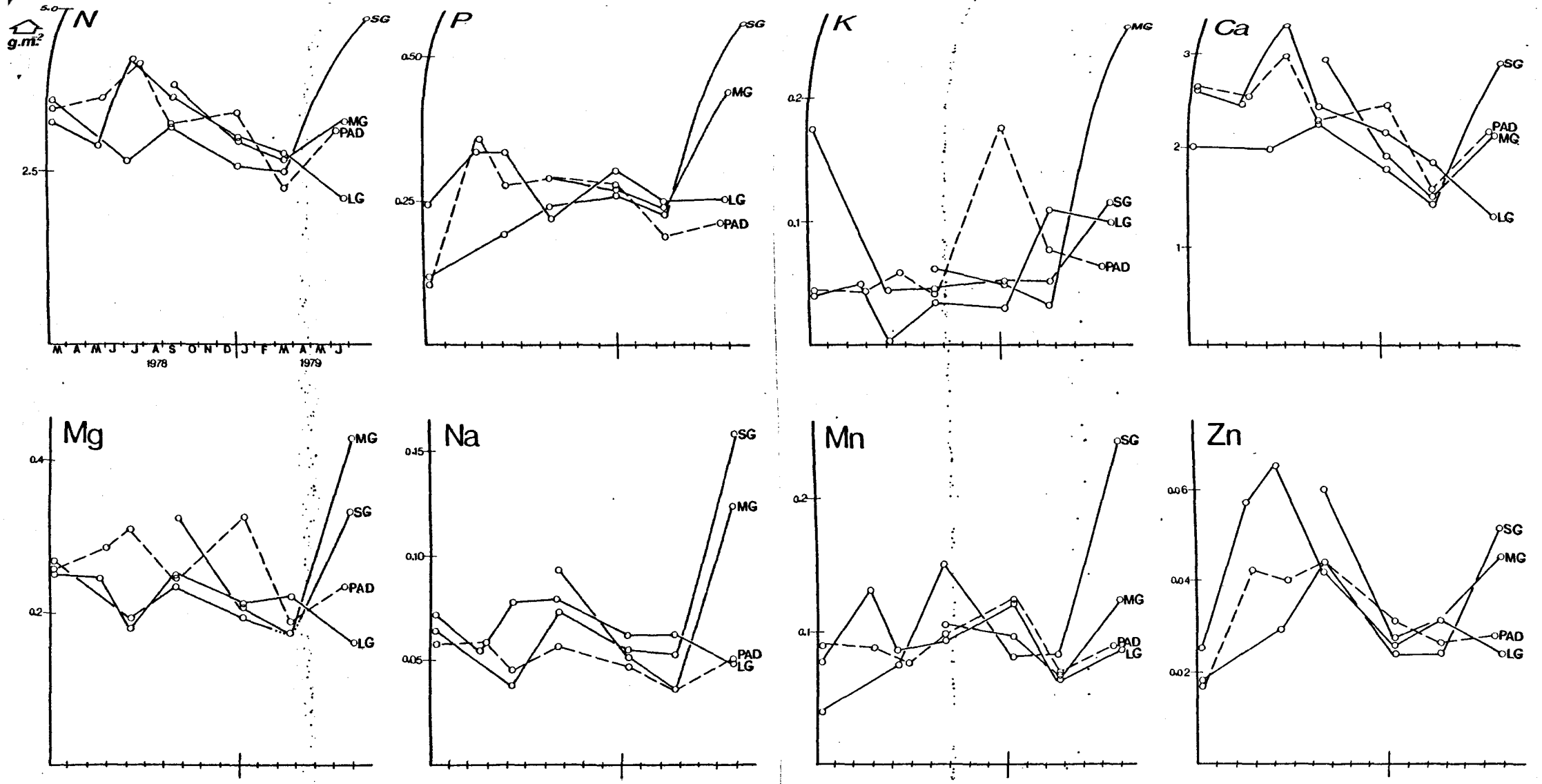


FIG 23 : TOTAL NUTRIENTS in ROOTS ($g.m^{-2}$) from each cutting treatment.

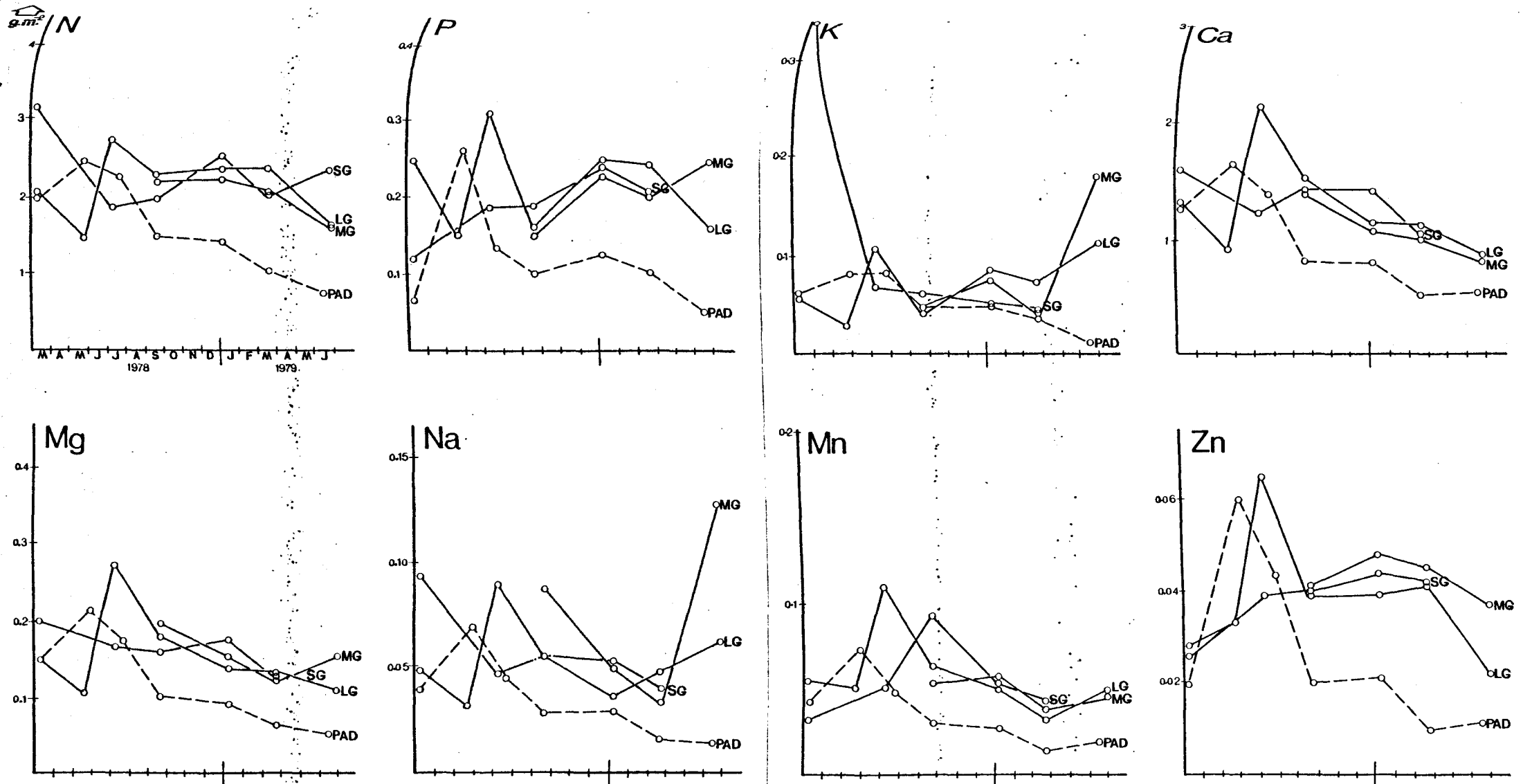


FIG 24 : TOTAL NUTRIENTS in RHIZOMES ($g.m^{-2}$) from each cutting treatment.

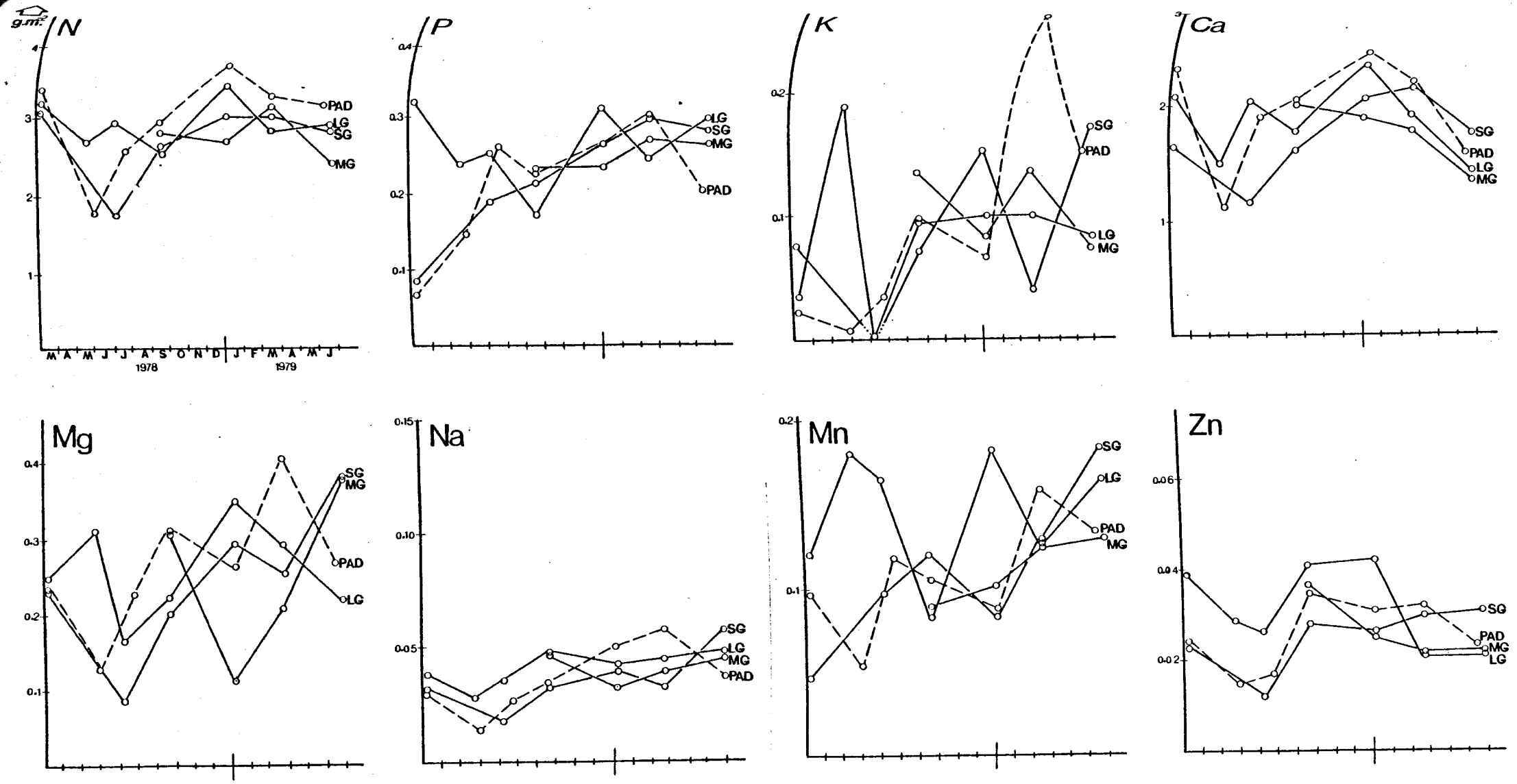


FIG 25 : TOTAL NUTRIENTS in DETACHED RTS($g.m^{-2}$) from each cutting treatment.

July 1978 with a winter increase, and June 1979 levels in SG were high whilst other treatments were low. Similarly *Mg* levels were high in SG and MG in June 1979, but over-wintering levels in MG were extremely low. Low winter levels of *Mn* in SG contrasted with high winter levels in LG.

5.7 *Distribution of Nutrient Pools*

Maximum and minimum proportions of nutrients in each vegetation component in LG are illustrated in FIG. 26, to provide a summary of variations described. Below-ground reserves of all nutrients, except *K* and *Na*, were always substantial and in overall terms roughly equally distributed between roots, rhizomes and detached roots. Levels in above-ground components were variable over a wide range, resulting in large scale cycling of nutrients between vegetation and soil. The illustrations should be compared with FIG. 21 for details of seasonal variations.

The proportions of total ecosystem nutrients in the vegetation are shown in TABLE 13. Less than 5% of total nutrients in the ecosystem enter the plant sub-system, in all cases except *Ca* and *Na*. Thus, most nutrients in this grassland ecosystem are either unavailable to the vegetation, or else unexploited.

5.8 *Nutrient Removal from Mown Treatments*

Dry matter removed after mowing was described in Chapter 3, and a consideration of the amounts of nutrients removed as cuttings is appropriate. Cuttings were chemically analysed from 4 of the 6 mowings in SG during 1979. The percentage of total vegetation and ecosystem nutrients removed are shown in TABLE 14. Percentages have been calculated from mean values.

Large proportions of vegetation nutrients are removed as cuttings.

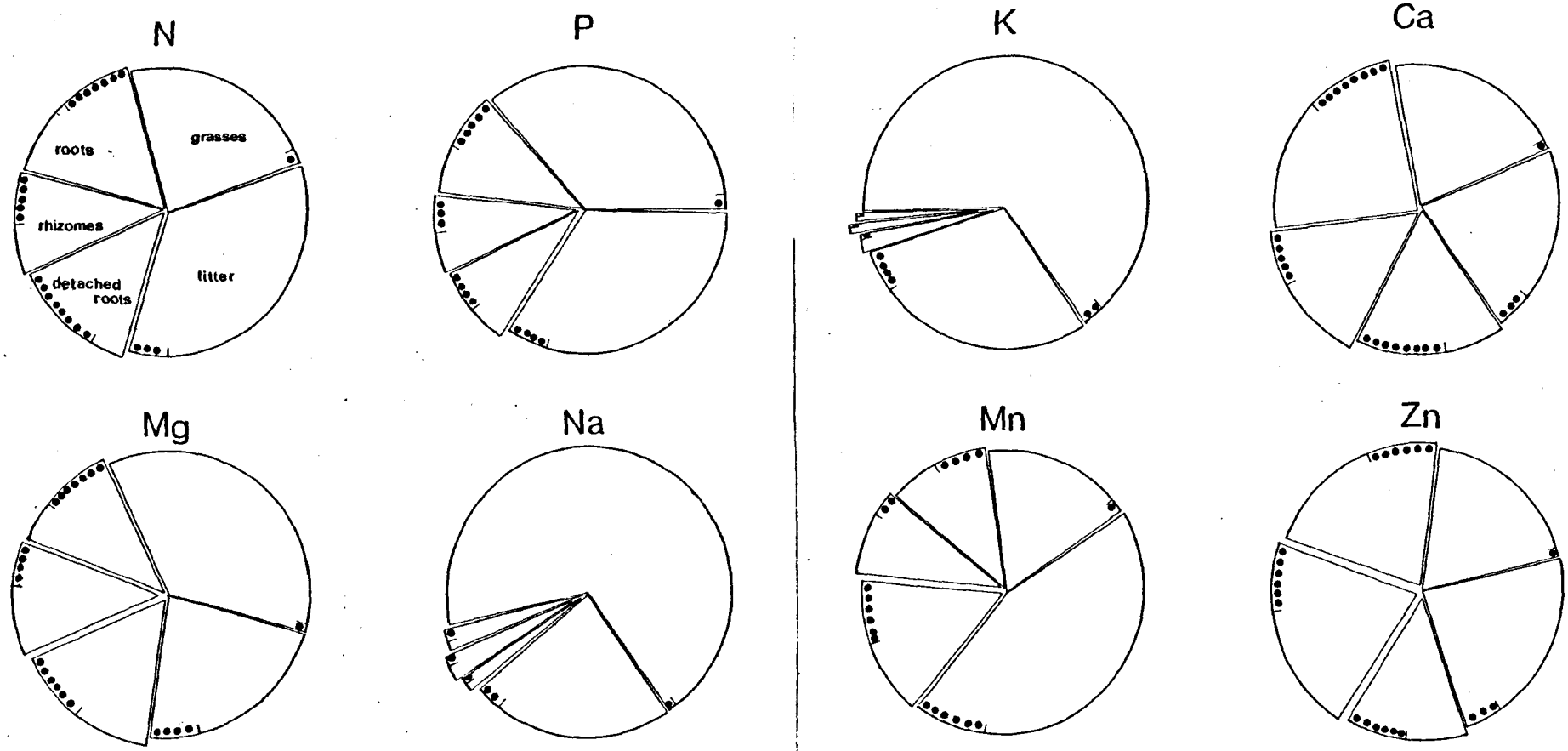


FIG 26 : Distribution of nutrients between components of vegetation in LG. Segments indicate maximum proportions in component, and dotted sub-divisions indicate minimum proportions. See text.

	N	*P*	*K*	*Ca*	*Mg*	*Na*	*Mn*	*Zn*
Maximum % in vegetation (date)	*4.45* (Jun.79)	*4.76* (Jul.78)	*3.17* (Sep.78)	*27.56* (Jul.78)	*0.76* (Sep.78)	*22.43* (Sep.78)	*1.08* (Jan.79)	*2.94* (Jul.78)
Minimum % in vegetation (date)	*3.22* (Mar.78)	*3.05* (Mar.78)	*0.89* (Mar.78)	*14.78* (Jun.79)	*0.40* (Mar.78)	*3.32* (Mar.78)	*0.49* (Mar.78)	*1.34* (Mar.78)

TABLE 13 : Maximum and minimum percentages of total ecosystem nutrients in vegetation (grasses + litter + roots + rhizomes + detached roots) in LG.

	N	*P*	*K*	*Ca*	*Mg*	*Na*	*Mn*	*Zn*
Total Nutrients Removed per Mowing ($g.m.^{-2}$)	0.768	0.104	0.521	0.284	0.064	0.095	0.023	0.002
% of Total Nutrients in Vegetation Removed per Mowing	*6.38*	*8.30*	*17.08*	*4.72*	*6.59*	*14.09*	*5.64*	*1.72*
% of Total Ecosystem Nutrients Removed per Mowing	*0.11*	*0.18*	*0.17*	*0.56*	*0.03*	*0.71*	*0.02*	*0.02*

TABLE 14 : Nutrients removed from SG as cuttings. Values are means of 4 mowings as a percentage of total vegetation and ecosystem nutrients (mean values).

On an annual basis (i.e.: six cuts per year), for example, approximately 38% and 50% of mean standing crop of *N* and *P* respectively are removed. *Na* and *K* removal are particularly large, with over 100% of mean standing crop of *K* removed per year.

However, extremely small proportions of total ecosystem nutrients are removed as cuttings; in most cases 1% or less per annum. Proportions of *Ca* removed are larger, but estimates should be treated with caution since extremely low concentrations in soil may have been under-estimated. Larger losses of *Na* are probably insubstantial, for an element so ubiquitous.

5.9 Conclusions

Nutrient investment in plant components differs according to management regime. In the first season following cessation of mowing a large nutrient investment in grasses, roots and rhizomes is followed by a decline, and accumulation of nutrients in litter. Increased biomass is suppressed after a further season of discontinued mowing and rhizome reserves decline, although forb fractions proliferate. Most litter nutrient pools are large in the first year following cessation of mowing but small during the second growing season, except for *Ca*, *Mn* and *Zn* which are retained in the litter. Large accumulations of nutrients in litter result in a nett increase in the amounts of most nutrients in the vegetation, but as nutrients are released from litter nett nutrient losses from grass components become bound in forb fractions.

Below-ground reserves of *N*, *Ca*, *Mn* and *Zn* are consistently larger than above-ground reserves, *P* and *Mg* vary seasonally, and *K* and *Na* are always in small amounts below ground. Root reserves of nutrients vary although *N* and *Ca* pools are largest during the growing season, and *K*, *Mg* and *Na* largest during winter. Nutrient reserves in detached

roots are generally largest in winter.

Mowing suppresses increases of grasses, roots and rhizomes and limits detached root pools during the first growing season. After this initial period, mowing encourages substantial investments in root and rhizome nutrient pools. Seasonal fluctuations of *K*, *Mg*, *Na* and *Mn* pools in roots, rhizomes and detached roots are particularly affected by mowing regime. Nutrient pools in detached roots were smaller in SG than in LG, during the growing season.

Less than 5% of most nutrients in these ecosystems are contained within the plant sub-system and usually 1% or less of nutrients are removed per annum by mowing, although this represents a large proportion of the nutrients in vegetation. These values are generally higher for *Ca* and *Na*.

The significance of these results in relation to published information is considered in Chapter 8.

CHAPTER 6

ABOVE-GROUND LITTER

Seasonal fluctuations of standing crop of litter and the effects of mowing regime have been considered in previous chapters, together with variations in nutrient concentrations and pools. In particular, surface accumulation of litter has been shown to influence the annual cycle of production, in the absence of mowing. In this chapter, an attempt is made to clarify certain aspects of surface litter decomposition, and particularly of those factors which govern accumulation and breakdown.

6.1 Introduction

Reviews of decomposition studies and methodology have recently been presented (Dickinson and Pugh, 1974*ab*; Schlesinger, 1977; Singh and Gupta, 1977; Swift *et al.*, 1979). One technique which has proved particularly useful is the litter bag method (Shanks and Olson, 1961; Edwards and Heath, 1963), in which litter is enclosed in nylon or wire bags of various size mesh. The technique has been most valuable in studies of the colonization and role of soil animals and micro-organisms during breakdown and the chemical changes brought about, although a number of associated problems and inaccuracies have been identified (Anderson, 1973; Howard and Howard, 1974; Suffling and Smith, 1974). The method has been extensively used in woodland studies, but most investigations in grasslands have utilized the paired-plots method of Wiegert and Evans (1964), or its modification (Lomnicki *et al.*, 1968). Nevertheless, litter bags have been used in grassland studies (Curry, 1969 ; Bleak, 1970; Malone, 1970; Williams *et al.*, 1977; Hunt, 1978, 1979), and were considered most appropriate in the present investigations.

Environmental factors which affect decomposition are described by

Williams and Gray (1974) and Swift *et al.* (1979). Grassland litter is generally less resistant to decay than woodland litter, lacking toughness and accumulations of polyphenols, but resource quality can be a particularly important factor. Although physico-chemical properties of litter determine breakdown, temperature and moisture are the variables of predominant importance (Schlesinger, 1977). Perkins *et al.* (1978) found that rates of litter loss in Snowdonia montane grasslands were positively correlated with rainfall and soil moisture, when air temperature was above 9°C and soil temperature above 7°C. Floate (1970, *bc*) found that moisture content, within the range of 25-100% moisture-holding capacity, has less influence than temperature in controlling the mineralization of *C*, *N* and *P* from decomposing plant materials of Scottish hill pastures.

Experiments were devised to examine the breakdown of the large surface accumulations of litter described. Three litter bag experiments were carried out in the unmown treatments (LG and PAD) during periods when the standing crop of litter was large. The aims were to measure the rates of disappearance, nutrient mineralization and the biotic and abiotic factors which are the most important determinants of breakdown. An elucidation of these processes should provide a further insight into the significance of these surface accumulations, their persistence and importance in the changes of ecosystem structure brought about by cessation of mowing.

6.2 Methods

Litter bag experiments were carried out in LG and PAD at various times between May and December in 1978 and 1979. 15 x 15 cm litter bags were made from 45 µm and 950 µm nylon mesh[1] and 7 mm polyethylene fabric mesh[2], assuming 45 m mesh excludes all soil animals, 950 µm excludes earthworms and 7 mm allows entry to all soil animals (*based on* Edwards and Heath, 1963). Each bag was loosely filled with 2-3 g litter, previously collected from the site and oven-dried. Litter was re-wetted before returning to the field, and spillage inaccuracies were carefully avoided.

1. St Martin's Nylon Mesh; Henry Simon Ltd., Cheadle Heath, Stockport.
2. Grant's Cropguard Shade Fabric; Low Bros. & Co., Dundee.

In *Experiment A* 7 mm litter bags were set out in LG and PAD on various occasions, and collected after periods of between 29-88 days. Litter bags were placed on the soil surface or in the centre of the litter zone, and at least 4 replicates were used in all cases. Each bag was positioned randomly or, where practicable, in the quadrats selected for biomass sampling. Fresh and dry weights were recorded and samples stored prior to chemical analysis.

Experiment B was initiated in early June 1978, in PAD, to examine breakdown from litter bags of varying mesh size. Twelve replicate litter bags of each mesh size were positioned on the soil surface beneath the vegetation, and a further 12 7 mm mesh bags placed in approximately the centre of the litter zone. Six of each set of bags were collected after 49 and 85 days. Fresh and dry weights were recorded and samples stored prior to chemical analysis.

Experiment C was initiated in May 1979, in LG, to examine breakdown in different zones of the litter layer in more detail. A 4 x 15 grid with points 0.3 m apart was marked out, and three 7 mm litter bags fastened at each point with skewers. One bag was positioned on the soil surface, another at the centre of the litter layer, and the third above the vegetation (see PLATE). Four sets of bags were removed after 1, 2, 3, 4, 5, 6, 7, 9, 11 and 15 weeks, after which soil contamination prevented easy removal of litter. Fresh and dry weights were recorded and samples stored prior to chemical analysis.

6.3 Results and Discussion

Rates of breakdown from 7 mm litter bags in *Experiment A* are shown in TABLE 15. Rates were slightly lower in the litter zone than at the soil surface, and lower during the drier summer and cooler winter months.

TREATMENT	POSITION OF LITTER BAG	PERCENTAGE BREAKDOWN PER DAY *(WITH DATES)*				
LG	soil surface	0.878 *(May → Jul) 1978*	0.723 *(Jul → Oct) 1978*	0.696 *(May → Jun) 1979*	0.411 *(Jun → Jul) 1979*	0.770 *(Jul → Aug) 1979*
PAD	soil surface	0.720/0.784*	0.843/0.781*	0.818	1.089	0.553
	litter zone	0.527 *(Jun → Jul) 1978*	0.686 *(Jul → Sep) 1978*	0.815 *(Aug → Oct) 1978*	0.950 *(Oct → Nov) 1978*	0.594 *(Oct → Dec) 1978*

*TABLE 15 : Percentage loss of dry wt. per day from 7 mm litter bags placed on soil surface and in litter zone in LG and PAD (*independent estimates).*

Using similar methods, Curry (1969) recorded breakdown rates of 0.17 to 0.24% per day at an old grassland site in Co. Kildare, Ireland and Perkins *et al.* (1978) measured rates of 0.2 to 1% per day in a montane grassland in Llyn Llydaw, Snowdonia. Clearly, breakdown rates in the present study were high although few recordings were made during the winter months. Litter bag values can be compared to breakdown rates calculated from changes in standing crop of litter (*Section 3.2*) during periods of minimum input into the litter compartment, whilst grass biomass was rapidly increasing (TABLE 16).

LG	0.286 *(Mar-May) 1978*	0.620 *(May-Jul) 1978*
PAD	0.582 *(Mar-Jun) 1979*	0.751 *(Jun-Jul) 1978*

TABLE 16 : Percentage breakdown of litter per day, from standing crop data.

Error will tend to under-estimate these values, thus corroborating the accuracy of litter bag data.

Curry (1969) used much larger weights and also used herbage, rather than litter, in his litter bags (20 g in 22.5 x 18.8 cm bags) which may have given lower breakdown rates. Keele breakdown rates are comparable to those of Perkins *et al.* (1978) in Snowdonia, where temperatures are slightly lower but rainfall much higher (TABLE 17).

	AIR TEMP(°C) MEAN MAX.	AIR TEMP(°C) MEAN MIN.	SOIL TEMP(°C) 15 cms.	RAINFALL (mm annum^{-1})
KEELE (Dec.1978-Nov.1979)	10.9	4.4	8.4	795
LLYN LLYDAW* (1966-71)	9.2	5.1	7.9	2932

*TABLE 17 : Climatological data (*from Perkins, 1978)*

Singh and Gupta (1977) listed breakdown rates of 0.003 and 0.3% per day for temperate ecosystems, although mostly woodland sites. Clearly, breakdown rates of large litter accumulations in LG and PAD were extremely rapid.

Results from *Experiment B* are shown in FIG. 27. Litter disappeared most quickly from 7 mm mesh bags positioned on the soil surface with a 65% reduction after 85 days, illustrating the importance of earthworms in the early stages of breakdown (*see* Edwards and Lofty, 1977). Nevertheless, where earthworms were excluded 30-40% breakdown still occurred and 49% from 7 mm mesh bags in the litter zone, which would have been less accessible to earthworms. Breakdown was slightly slower in 950 µm mesh bags, which allowed access to microarthropods, than in the finest mesh bags. The contributions of these smaller animals to the early stages of decomposition are limited, although the activities of microbivores may be important (see Wallwork, 1970, 1976; Swift *et al.*, 1979).

However, breakdown processes are less straightforward than these dry weight data may indicate. Nutrient changes in confined litter are shown in FIG. 28 and TABLE 18. Nutrient concentrations increased in litter confined in 950 µm and 45 µm mesh bags, but tended to decrease or remain approximately level in litter confined in 7 mm mesh bags, particularly in the litter zone.

Decomposition of plant materials is typically accompanied by increases in the relative concentrations of certain nutrients (*see* Floate, 1970*a-d*), through carbon release in respiration and nutrient immobilization in decomposer tissues. These decomposition processes, together with leaching and some fragmentation, must account for litter disappearance and nett immobilization of nutrients in 45 µm litter bags.

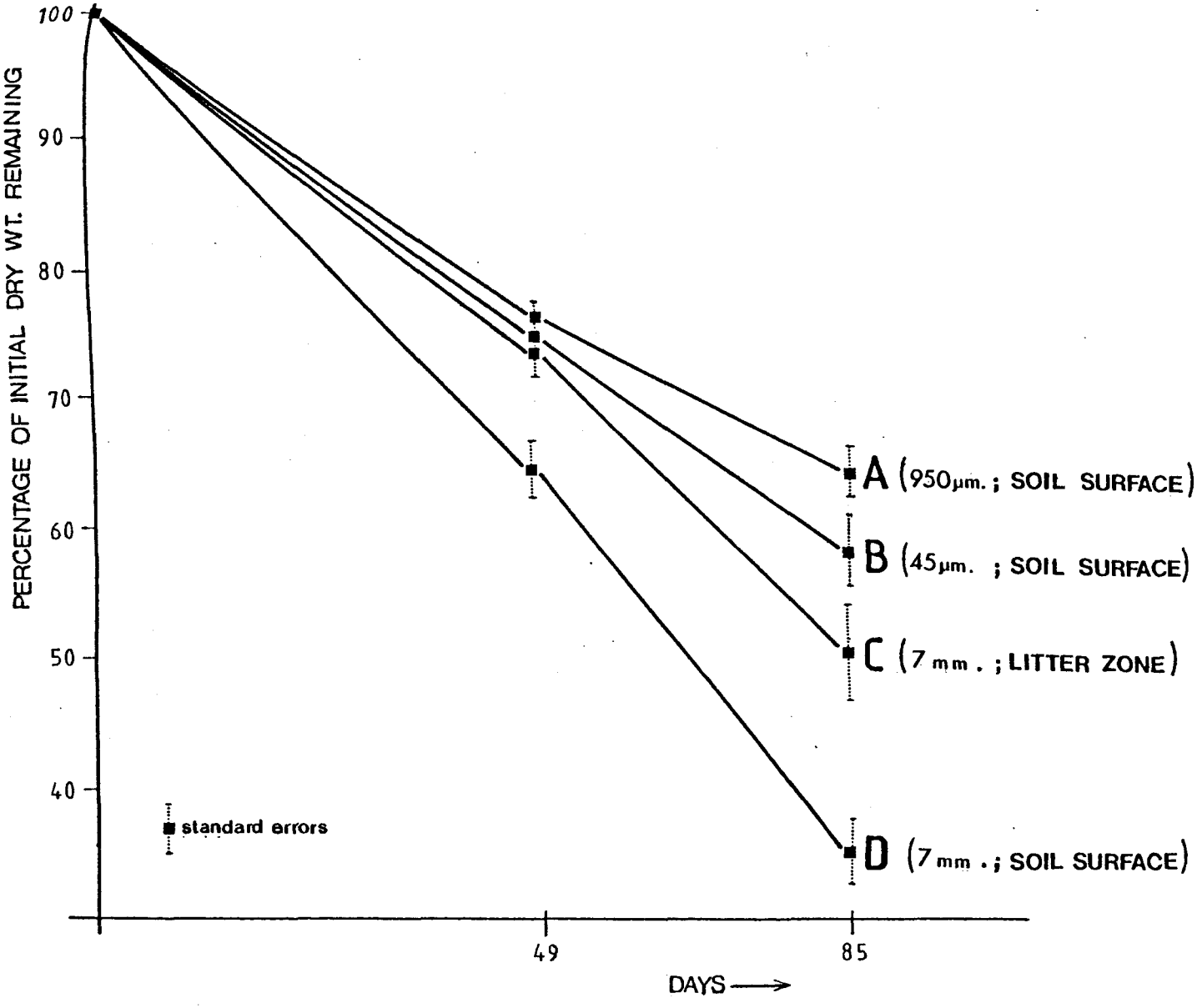


FIG. 27 : Disappearance of litter from 45µm., 950µm. and 7mm. mesh bags (see text). Significant differences exist between treatments, at the 0.001 % level, at t_1 and t_2.

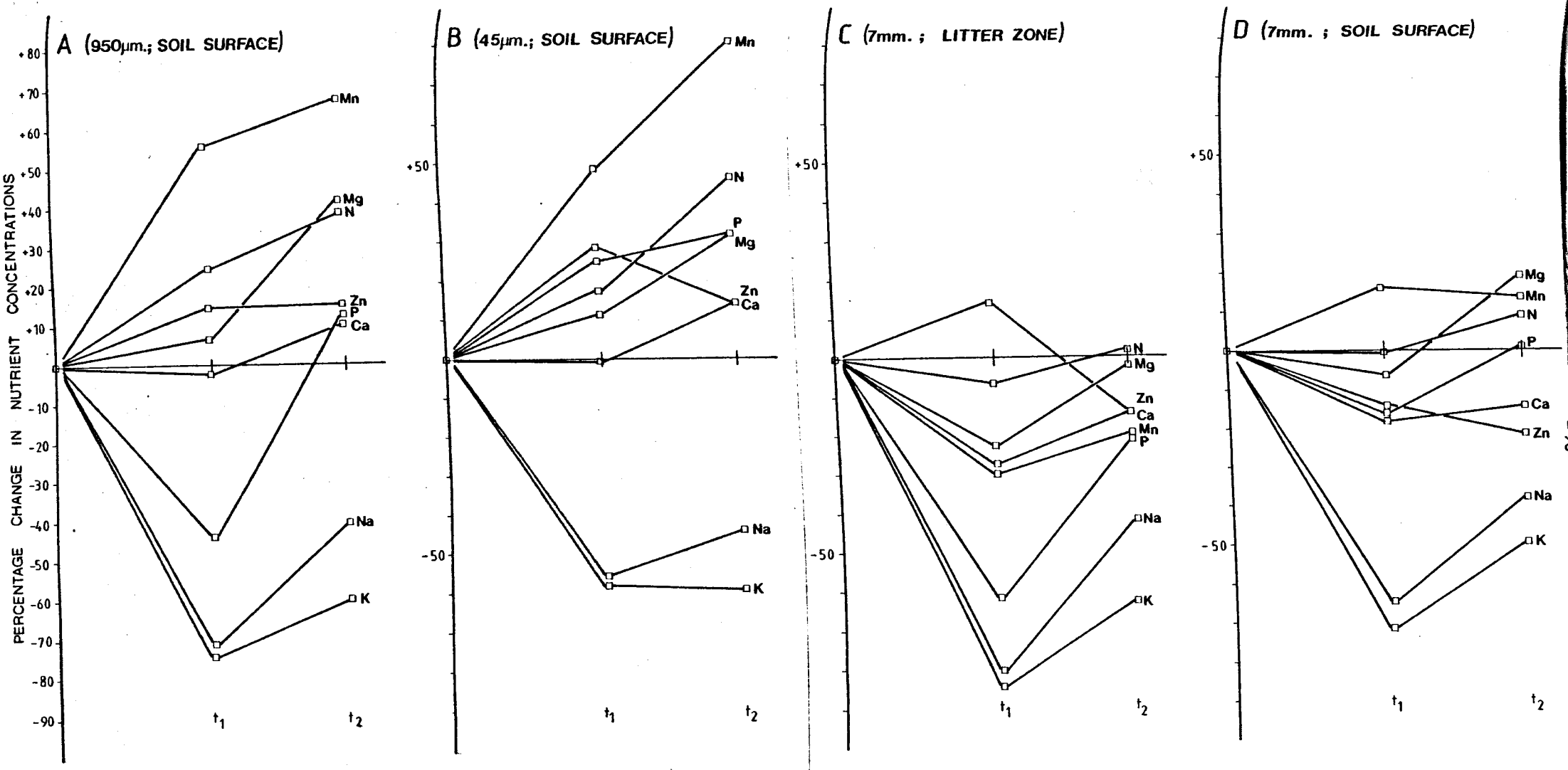


FIG 28 : Percentage change in nutrient concentrations of litter after 49 (t_1) and 85 days (t_2) in 45µm., 950µm. and 7mm. mesh bags.

	PERCENTAGE LOSS PER DAY								
	DRY WEIGHT	*N*	*P*	*K*	*Ca*	*Mg*	*Na*	*Mn*	*Zn*
A. 950 µm soil surface	0.428	0.134	0.333	0.892	0.347	0.109	0.733	-0.085	0.340
B. 45 µm soil surface	0.497	0.178	0.277	0.909	0.400	0.278	0.807	-0.062	0.397
C. 7 mm litter zone	0.607	0.599	0.728	0.971	0.693	0.615	0.850	0.721	0.676
D. 7 mm soil surface	0.782	0.748	0.779	0.984	0.839	0.707	0.938	0.729	0.869

TABLE 18 : Percentage of dry weight and total nutrients remaining in litter from 950 µm, 45 µm and 7 mm mesh bags after 85 days (June-September).

Losses from 7 mm bags would include the effects of litter removal and comminution by earthworms, which probably accelerate nutrient mineralization. *P* and *Ca* were immobilized to a lesser extent in 950 µm than in 45 µm litter bags, which may be an indication of faunal activity (*see* Swift *et al.*, 1979). *Na* and *K* are highly mobile and rapidly leached from plant tissues (Clement *et al.*, 1972; Koelling and Kucera, 1965).

Possible moisture differences between litter in bags of different mesh sizes were examined, since high moisture content during summer months would favour microbial activity and also increase leaching. However, moisture recordings at time of collection were similar for each mesh size, although reduced moisture conditions in 7 mm mesh bags in the litter zone may have contributed to slower breakdown rates:

	PERCENTAGE MOISTURE	
	t_1	t_2
A) 950 µm soil surface	66.7 ± 3.2	79.0 ± 1.9
B) 45 µm soil surface	66.1 ± 4.5	79.0 ± 1.5
C) 7 mm litter zone	35.7 ± 7.7	70.7 ± 3.2
D) 7 mm soil surface	62.6 ± 2.9	76.7 ± 1.8

TABLE 19 : % moisture of litter at times of collection (± s.e.)

Thus, it may be inferred that 55-64% of normal litter breakdown rates can be achieved in the absence of earthworms, through microbial release of carbon. The main contribution of earthworms is probably in burying plant remains, although their activities accelerate nutrient mineralization. The effects of microarthropods in this respect are limited.

Results from *Experiment C* are shown in FIG. 29, with calculated breakdown rates in TABLE 20. Dry weight disappeared from all litter layers at similar rates, but often slower in the air zone.

WEEK NOS	% BREAKDOWN PER DAY		
	AIR ZONE	LITTER ZONE	SOIL SURFACE
0-1	1.96	1.43	1.20
1-2	0.03	0.24	0.36
2-3	0.17	0.59	0.74
3-4	0.43	0.98	0.52
4-5	-0.69	-0.66	-0.37
5-6	0.81	0.87	2.17
6-7	0.14	0.62	-1.53
7-9	0.50	0.02	0.89
9-11	-0.35	-0.55	-0.31
11-15	0.74	1.26	0.77

TABLE 20 : Percentage breakdown per day of litter from 7 mm mesh bags, positioned in air zone, litter zone and on soil surface.

Nutrient concentrations in litter from each set of litter bags are shown in FIG. 30. As with 7 mm mesh bags in the previous experiment, concentrations either remain approximately level or tend to decrease. In most cases, litter in bags positioned above the vegetation (air zone) maintained lower concentrations than in litter bags nearer the soil.

An interesting feature of the varying concentrations of most nutrients is the occurrence of peak levels at week 6. A comparison of these graphs with rainfall and litter moisture levels during the period (*c.f.* FIG. 31) reveals distinct resemblances. Low rainfall for nearly two weeks corresponds with low nutrient concentrations at

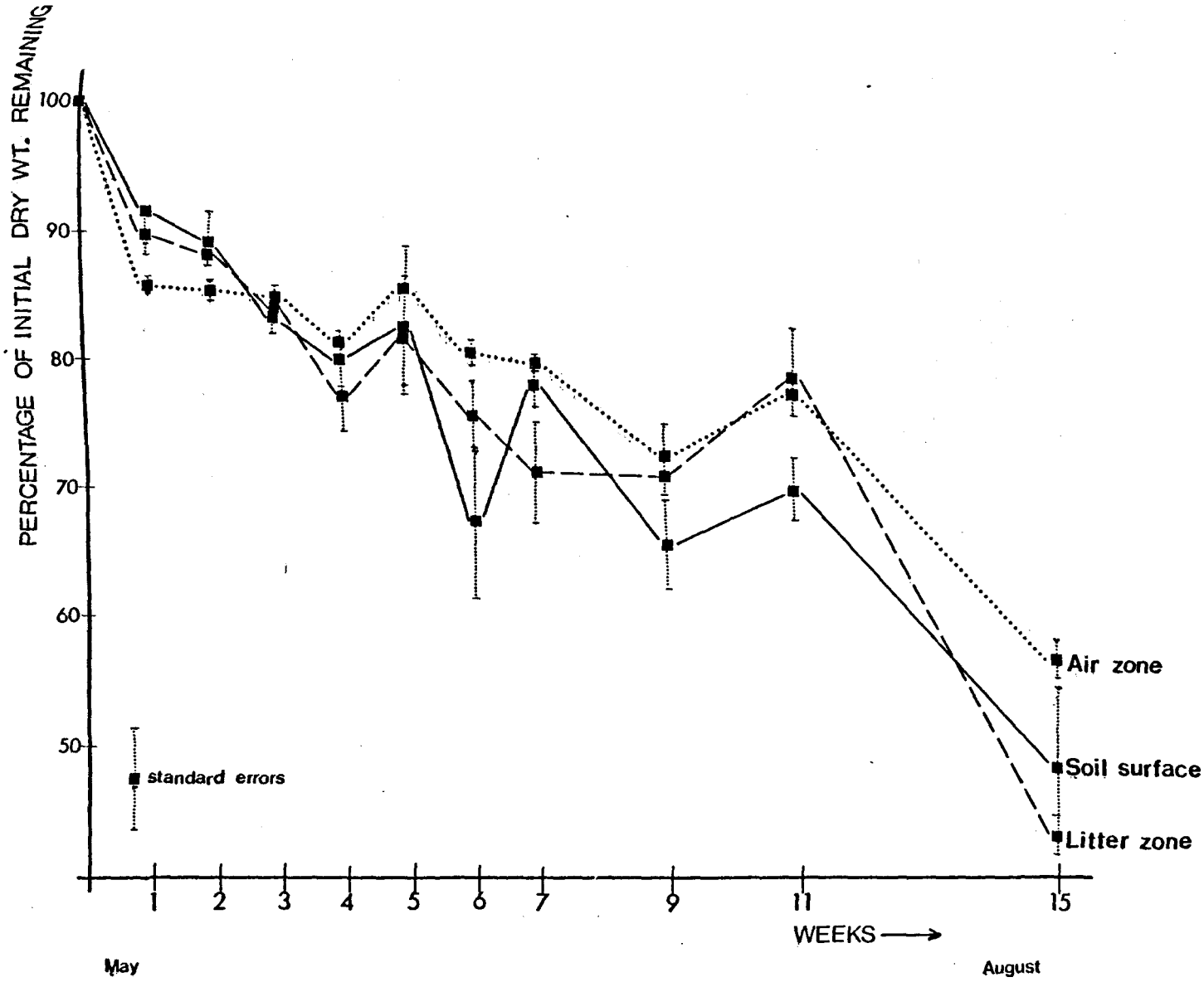


FIG 29 : Disappearance of litter from 7mm. mesh bags placed at different levels in vegetation. No significant differences between zones ($p = 0.2$), except at week 1 where $p = 0.05$.

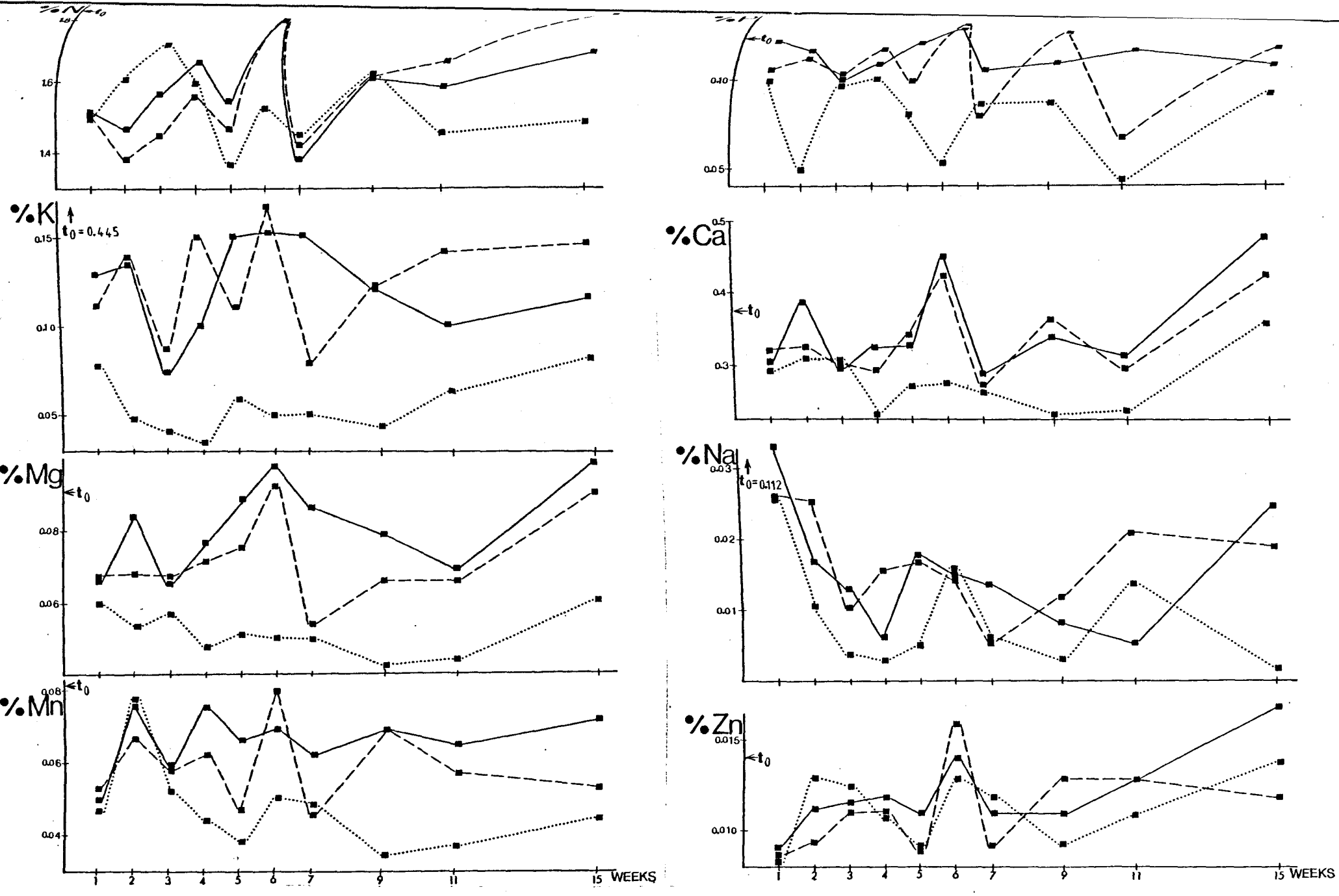


FIG 30 : Nutrient concentrations of litter during breakdown, from mesh bags (7mm) placed on soil surface (■——■) in litter zone (■– – –■) and air zone (■·····■) .

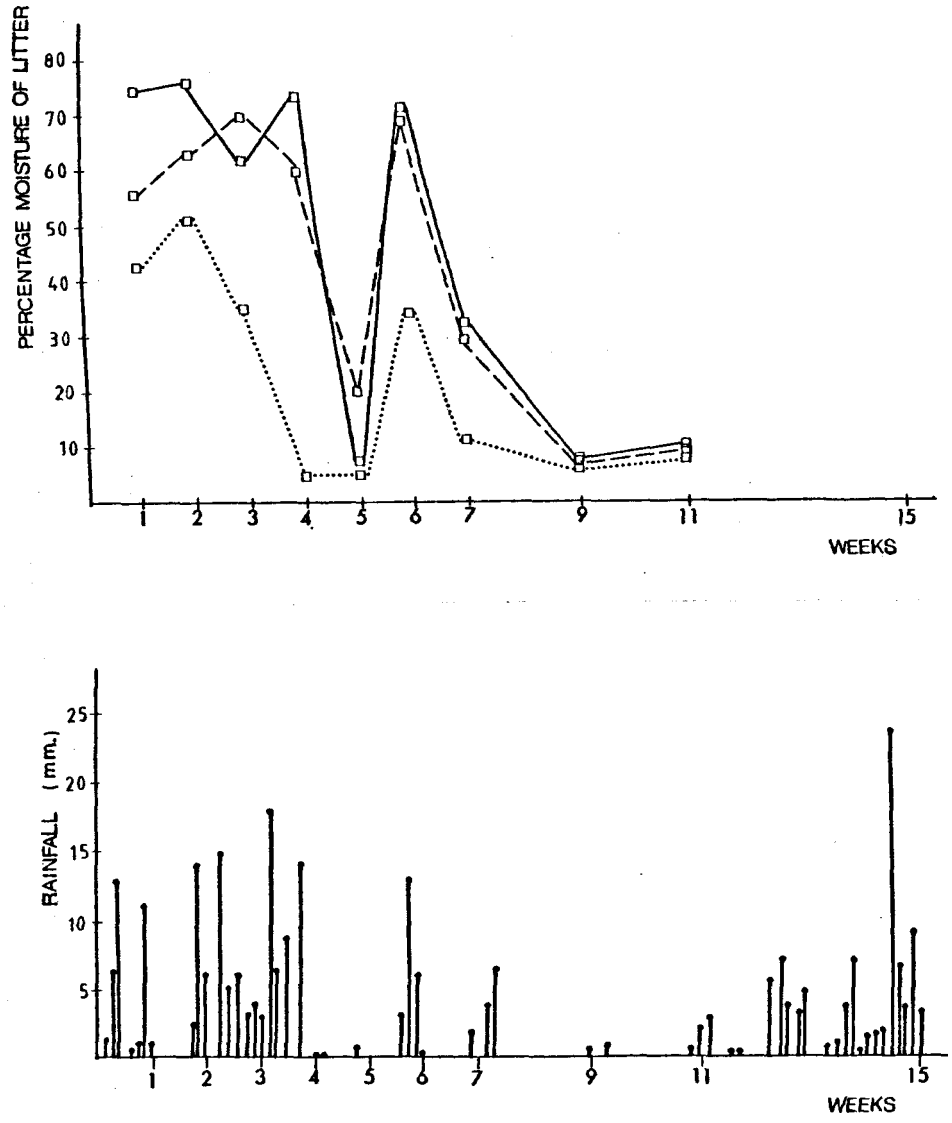


FIG 31 : Moisture content of litter, and climatological data during 15 weeks of breakdown (see figs. 29 & 30).

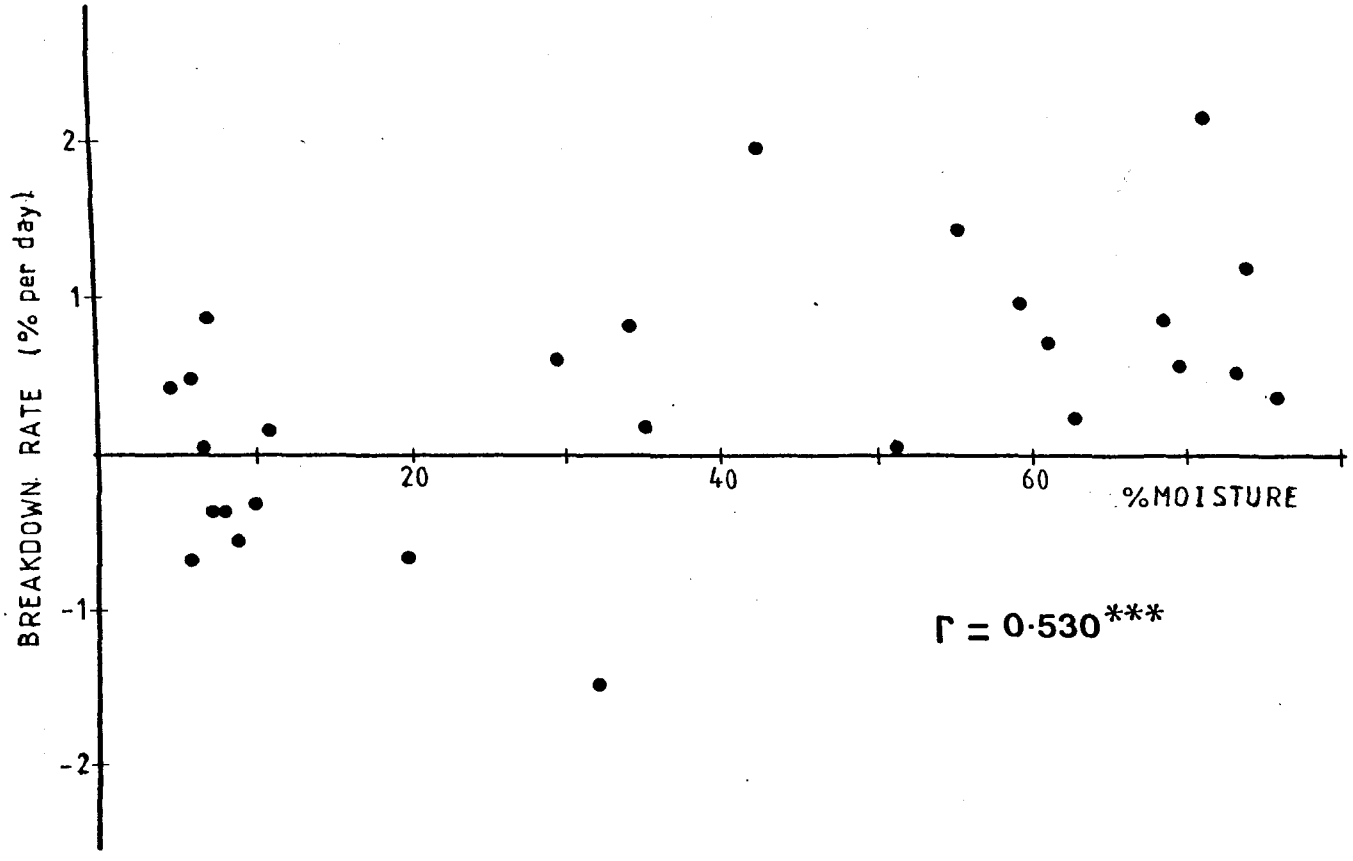


FIG 32 : Breakdown rates versus moisture content of litter. Data from litter bags (7mm.) on soil surface, in litter zone and air zone. (Expmt. B)

week 5, and is followed by three days heavy rain and high nutrient concentrations at week 6. Litter in the air zone was subjected to longer periods of dryness and maintained lower nutrient concentrations. Breakdown rates can be correlated with moisture content of the litter (FIG. 32).

Thus, nutrient concentrations appear to be determined by a balance of immobilization and mineralization, according to prevailing moisture conditions. However, nett immobilization does not continue to increase during long periods of rainfall, so dry periods must be important. Obviously, repeated wetting and drying would increase fragmentation. Oven-drying of litter at the start of the experiment led to *K* and *Na* levels of less than 38% of original values a week later (FIG. 30). It may be speculated that fluctuating moisture conditions could help to maintain microbial populations in a metabolically active juvenile phase, thus enhancing rates of decomposition.

6.4 Conclusions

Breakdown rates of large surface accumulations of litter in LG and PAD were rapid, particularly during spring and autumn. Litter bag experiments indicated that earthworms accelerate breakdown rates, with 65% disappearance recorded after 85 days compared to 30-40% in their absence. The activities of earthworms are accompanied by increased mineralization of nutrients from litter, whereas their absence leads to nett immobilization. Microarthropods also limit immobilization, but do not accelerate the disappearance of dry weight during the early stages of breakdown.

Moisture content of litter is correlated with the disappearance of dry weight, but the principle effects of prevailing moisture conditions on decomposition appear to be more subtle. Besides increasing

fragmentation and leaching, repeated wetting and drying must affect microbial populations on the litter surface, and apparently determine the pattern of mineralization and immobilization.

The combined influence of prevailing moisture conditions and faunal activity determine breakdown rates of litter. Their mutual effects on surface microbial populations are considered to be particularly important.

CHAPTER 7

BELOW-GROUND COMPONENTS

7.1 Introduction

The large below-ground component of primary production emphasizes the importance of a consideration of below-ground dynamics. The paucity of ecological studies concerned with below-ground productivity and associated processes has previously been stressed, together with many of the problems involved in such investigations.

Valid estimates of nett primary productivity (NPP) cannot accurately be derived from changes in biomass (ΔB) over a specified time period ($t_0 - t_1$), but must incorporate some measurement of losses due to breakdown (L) and grazing (G) during that period (Milner and Hughes, 1970; Perkins *et al.*, 1978):

$$NPP^{t_0-t_1} = \Delta B + L + G$$

Below-ground grazing losses may be considered to be quite small in most grassland situations, but breakdown losses cannot be ignored. The aims of this part of the project were to undertake an exploratory investigation of below-ground processes, particularly with respect to breakdown and turnover of root fractions, and to establish techniques appropriate to future research studies. The development of investigations is detailed chronologically.

Initially (*Section 7.2*) experiments were devised in an attempt to obtain estimates of above-ground and below-ground turnover over periods of one week, two weeks and one month. The study was

developed by restricting efforts to a closer examination of the breakdown of root systems in isolated soil cores (*Section 7.3*). Limitations of this technique are the errors caused by the damaging effect of coring to the root system and the artificial isolation of soil cores with above-ground vegetation removed, both of which may tend to over-estimate breakdown rates. Experiments are described which compare the breakdown of living and dead root systems and examine the effects of earthworms on breakdown rates.

In *Section 7.4* a categorization technique is devised for a more detailed investigation of the changes brought about during growth and breakdown, by measuring the size distribution and visual condition of roots. Finally, in *Section 7.5*, possible interactions between earthworms and the root system are investigated with respect to their influence on root growth and breakdown, together with a discussion of their probable significance in grasslands in relation to management regime.

The results are discussed in detail in *Section 7.6*, in perspective with published information.

7.2 Initial Studies on Turnover

7.2.1 Breakdown over one week

In the first experiment, to examine the feasibility of turnover studies, 16 x 1 m^2 plots were arranged in a randomized block design at the Botanic Garden site in June 1977 before the strip-mowing regime had been implemented. Each block was divided into four $\frac{1}{4}$ m x $\frac{1}{4}$ m sections. From one section, vegetation was clipped to ground level, and a second section was covered with 1 cm thick green absorbent felt to prevent photosynthesis. Remaining sections were control plots. Eight above-

and below-ground biomass samples were taken, as described previously, and then 8 samples were taken from each of the treatments and a control plot after 4 days, and again after 7 days. Results are illustrated in FIG. 33.

Errors, caused by high variation between replicates, were large and significance levels were outside acceptable limits. Nevertheless, mean values indicate that below-ground productivity estimates could be considerably underestimated if breakdown is excluded.

7.2.2 Breakdown over one month

In the second experiment in late August 1977, a similar randomized block design was used, again with 8 replicates, but with sampling times increased to 2 weeks (t_1) and 4 weeks (t_2). Additionally, eight 6.7 cm diameter cores were removed and vegetation clipped from the surfaces. Each core was then placed in 1 cm mesh plastic cages and returned to its original borehole immediately, for incubation until t_1 and t_2.

No significant differences could be detected between treatments, with controls or between sampling dates. Carbon and nitrogen concentration ratios in roots and rhizomes to 5 cm depth are shown in FIG. 34, and differ according to treatment. Clearly the experiment was carried out during a period of decreasing biomass of below-ground organs. Nitrogen levels decreased in clipped and dark treatments, with a resultant increase in *C:N* ratios. Results were similar for incubated and control cores, although large mesh cages would permit surrounding roots to grow into the cores.

Labour intensiveness of these experiments was excessive, and further replication impracticable. Therefore, further efforts were redirected towards incubation studies of isolated cores.

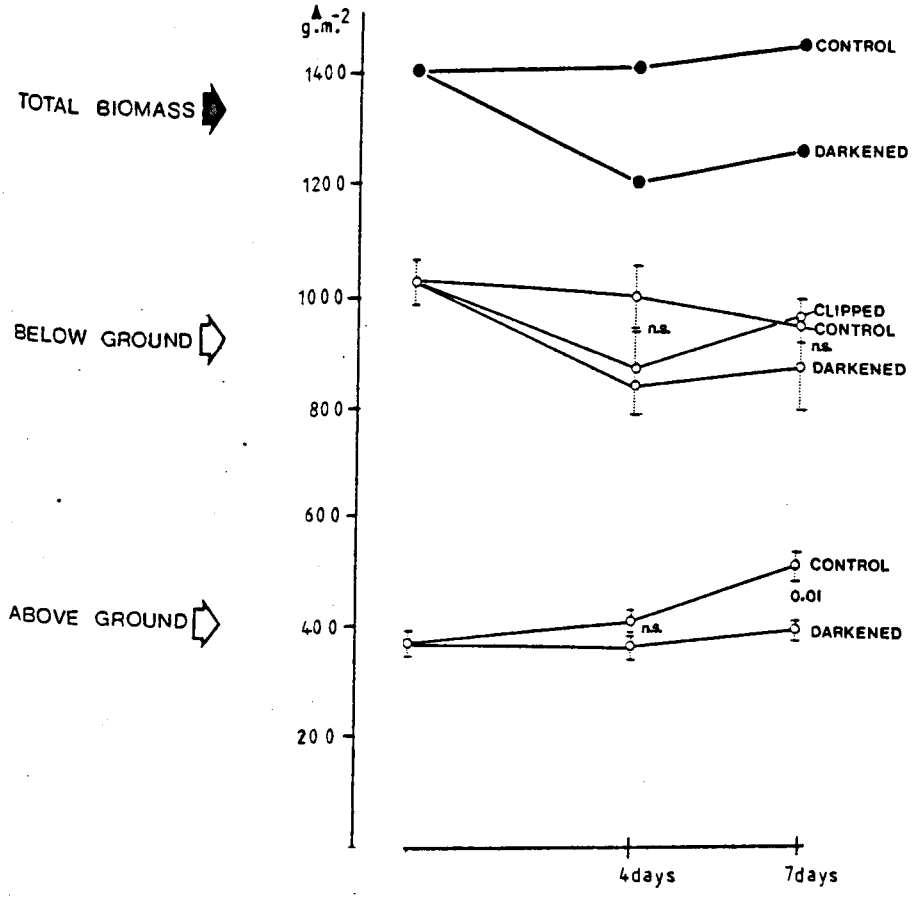


FIG 33 : Standing crop in clipped and darkened plots after 4 and 7 days. Below ground levels are sum of roots and rhizomes (A.F.D.W.). Levels of significance [n.s. = no signif. at 0·05] and standard errors are indicated.

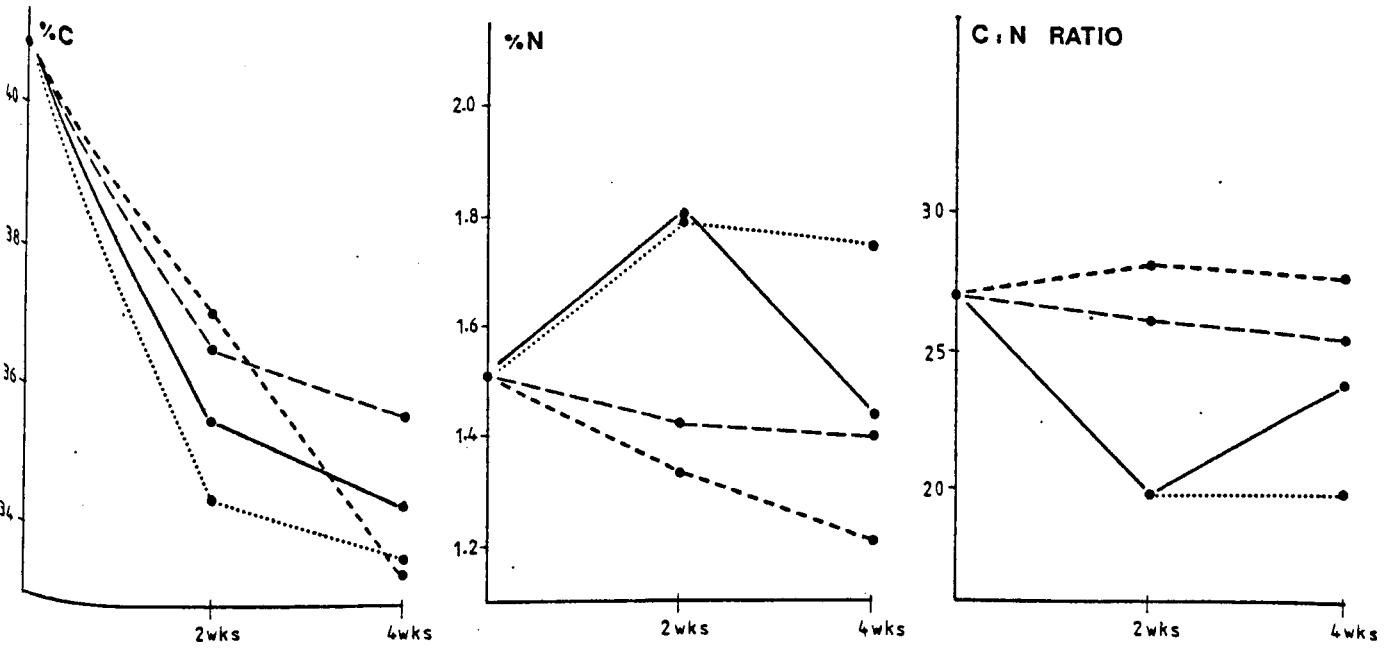


FIG 34 : %C , %N and C : N ratio of below ground organs [roots + rhizomes ; 0 - 5 cms depth] in clipped (●- - - - - -●), darkened (●— — — —●) and control (●————●) plots, and incubated cores (●·····●), after 2 and 4 weeks.

7.3 Field Incubation Studies of Isolated Cores

7.3.1 Introduction

Breakdown of below-ground fractions was examined by isolating soil cores in the field at various times of the year. Additional experiments were carried out to compare breakdown of living and dead root systems, and the effects of earthworms.

7.3.2 Methods

6.7 cm diameter soil cores to 10 cm depth were removed, and vegetation clipped from the surface. A 45 µm mesh nylon sleeve, open at both ends, was fitted around each core before replacement to its original borehole. A green felt disc (1 cm thickness) was then placed on top of each core to prevent regrowth and drying out (FIG. 35). Sleeves of larger mesh size were also tested but, besides allowing surrounding roots to grow into the cores, seemed to encourage earthworm activity.

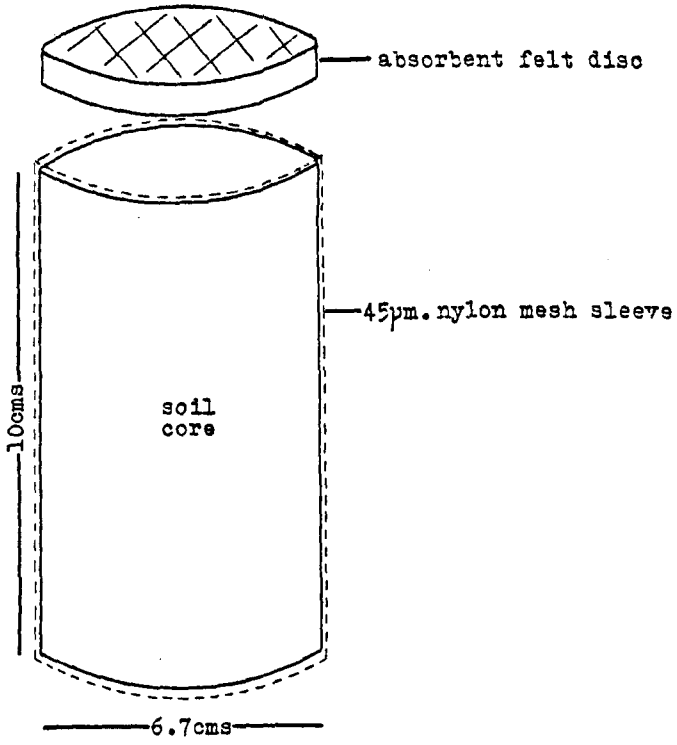


FIG. 35 : Isolated soil core

Twelve replicates were positioned in quadrats selected for biomass sampling in LG, SG and PAD, and collected after periods of approximately two months.

Two additional experiments were carried out, with replication reduced to six but treatment cores positioned as close together as possible in an attempt to improve tests of paired comparison by reducing variability.

In the first experiment, from June to July 1978, six cores were incubated as described and compared with six cores previously frozen overnight at -18°C and thawed, and a further six cores previously frozen and thawed, and then sealed inside mesh sleeves.

In the second experiment, in September 1978, three sets of six cores were frozen at -18°C overnight, thawed and sealed inside mesh sleeves. To one set of cores 1 *Lumbricus terrestris* and 2 *Allolobophora caliginosa* of known weights were introduced, and to a second set 2 *L. terrestris* and 3 *A. caliginosa* were introduced. The third set were control cores, without earthworms. Incubation time was six weeks.

7.3.3 Results and Discussion

Breakdown rates from incubation of isolated cores are shown in TABLE 21. Root breakdown rates were much faster during May to July than in March to May in LG and PAD, and high breakdown rates corresponded to increased amounts of detached roots. Rhizomes have a more active role in primary production in SG than in unmown treatments (Chapter 3), and breakdown rates were faster in SG between March and May. Breakdown rates of roots in May to July were higher than those recorded for surface litter breakdown (*cf.* TABLE 15), but lower in autumn.

It would appear that below-ground breakdown accounts for a substantial proportion of organic matter turnover in grassland ecosystems.

TREATMENT	INCUBATION DATES	PERCENTAGE RATE OF BREAKDOWN PER DAY		
		ROOTS	RHIZOMES	DETACHED ROOTS
SG	14/3/78-16/5/78	0.301	0.741	0.449
LG	14/3/78-23/5/78	0.434	0.283	0.378
	31/5/78-17/7/78	0.967	0.287	-0.427
	14/9/78-26/10/78	0.354 → 0.683	-0.812 → 0.479	-0.481 → 0.092
PAD	13/3/78-8/6/78	0.313	0.621	0.446
	1/6/78-25/7/78	1.015	1.207	-0.292

TABLE 21 : Percentage breakdown per day of below-ground components (dry weight), from field incubation of isolated cores.

Annual below-ground productivity measurements could easily be underestimated by 100% if breakdown were not taken into account. Although these results provide some insight into rates of breakdown, further numerical extrapolation may be inaccurate, but are considered in more detail in *Section 7.4.3.*

Data were disappointing from cores incubated with and without prior freezing, and sealed and unsealed in fine mesh (TABLE 22). Root breakdown was slower in sealed cores, which may indicate that earthworms accelerate breakdown. Interestingly, detached root levels increased in cores not previously frozen, but decreased in cores which had been previously frozen. This corresponds to June/July incubation for unfrozen cores in TABLE 21, and suggests that decomposition processes may differ between a living root system compared to one decomposing en masse.

Incubation experiments with earthworms (TABLE 23) were of little success. Only 54% of earthworms remained after the incubation period and most had lost weight, indicating unfavourable conditions. Nevertheless, data provides further evidence that earthworms accelerate root breakdown.

	t_0	AFTER 6 WEEKS INCUBATION		
TREATMENT		*No Prior Freezing Unsealed*	*Prior Freezing Unsealed*	*Prior Freezing Sealed*
Roots	1.259 ± 0.141	0.687 ± 0.071 (0.01)	0.699 ± 0.051 (0.01)a	0.817 ± 0.021 (0.02)a
Rhizomes	0.918 ± 0.205	0.794 ± 0.098 (n.s.)	0.923 ± 0.081 (n.s.)	0.765 ± 0.068 (n.s.)
Detached Roots	0.753 ± 0.045	0.904 ± 0.089 (n.s.)b.c.	0.554 ± 0.051 (0.02)b	0.630 ± 0.050 (0.10)c

TABLE 22 : Dry weight (g. core^{-1}) ± standard errors of below-ground plant components following field incubation in LG, with and without prior freezing, and sealed and unsealed in 45 µm mesh. Levels of significant differences between treatments and t_0 values are indicated in brackets. Letters indicate significant differences between treatments specified (a = 0.10, b = 0.01, c = 0.05). *n.s.* means no significance at 0.10 level.

	t_0	AFTER 6 WEEKS INCUBATION		
TREATMENT		*Low Nos. Earthworms*	*High Nos. Earthworms*	*No Earthworms*
Roots	0.966 ± 0.066	0.823 ± 0.103 (n.s.)	0.689 ± 0.058 (0.02)a	0.814 ± 0.037 (0.10)a
Rhizomes	0.673 ± 0.131	0.903 ± 0.134 (n.s.)	0.645 ± 0.107 (n.s.)	0.538 ± 0.055 (n.s.)
Detached Roots	0.520 ± 0.050	0.623 ± 0.099 (n.s.)	0.555 ± 0.049 (n.s.)	0.500 ± 0.051 (n.s.)

TABLE 23 : Dry weight (g. core^{-1}) ± standard errors of below-ground plant components, following field incubation in MG with and without earthworms. Levels of significance of differences between treatments and t_0 values are indicated in brackets. a = significant difference (at 0.10 level) between treatments. *n.s.* means no significance at 0.10 level.

7.4 *Root Categorization*

7.4.1 Introduction

A more detailed examination and description of the root system is clearly necessary. Root data have been expressed in terms of dry weight, ash-free dry weight and nutrient contents, although numerous other investigators have measured other parameters such as root length, number, diameter, surface area or number of root tips. Techniques for the measurement of these parameters, and the value of such determinations, are reviewed by Böhm (1979).

Coleman (1976) stresses that different categories of roots should be distinguished, particularly with respect to the probable importance of finer parts of the root system which may be insignificant in terms of weight (*also see* Carlson, 1965; Head, 1970; Ares, 1976).

An attempt is made to develop a quantitative microscopical technique to describe the root fraction and its variations in more detail.

7.4.2 Methods

Small sub-samples of roots, after washing and separation from other below-ground fractions, were teased out on a counting frame marked with a 4 cm^2 grid with 1 mm^2 divisions. Roots were focused beneath 100x magnification and a randomly selected line, 2 cm long, was followed across the grid. Each segment of root touched by the line was measured for diameter on an arbitrary scale (1 unit = 0.00865 mm), using an eyepiece graticule. Visible condition and age of the section of root were recorded according to the scheme of classification in TABLE 24, which approximates to that of Ares (1976). Number of root hairs in the field of view were also counted.

CLASSIFICATION	VISIBLE CHARACTERISTICS
Unsuberized	Translucent or pale white. Vascular stele easily visible.
Suberized	More or less opaque. Vascular stele not easily visible.
Friable	Cortex degenerate.
Diameter	Arbitrary scale (1 unit = 0.00865 mm)
Root hairs	No. in field of view (diam. approx. 0.5 arbitrary units)

TABLE 24 : Classification of sections of root

The line or its perpendicular was followed until 100 recordings of diameter had been made. Five such sets of measurements were recorded, each from a replicated but separate root sample, providing a total of 500 recordings for each set of samples. Substantial amounts of time were saved by verbally recording on to a foot-operated tape recorder. All samples were taken from 0-5 cm depth soil cores, unless otherwise indicated.

The technique was tested by recording the same root samples on three separate occasions, and comparing the frequency at each diameter. Significance levels of correlation coefficients below the 0.1% level were computed, supporting the validity of the technique.

Root material was categorized using this method for numerous samples, including those from incubation experiments. Additionally small pieces of roots (10 replicates) were categorized before and after incubation at $10^{\circ}C$ for one month in fresh soil solution in a 10 ml volumetric flask plugged with cotton wool.

7.4.3 Results

In FIG. 36 categorization data from roots at varying depths are shown. Smaller root categories are most abundant, with most root hairs nearest to the soil surface.

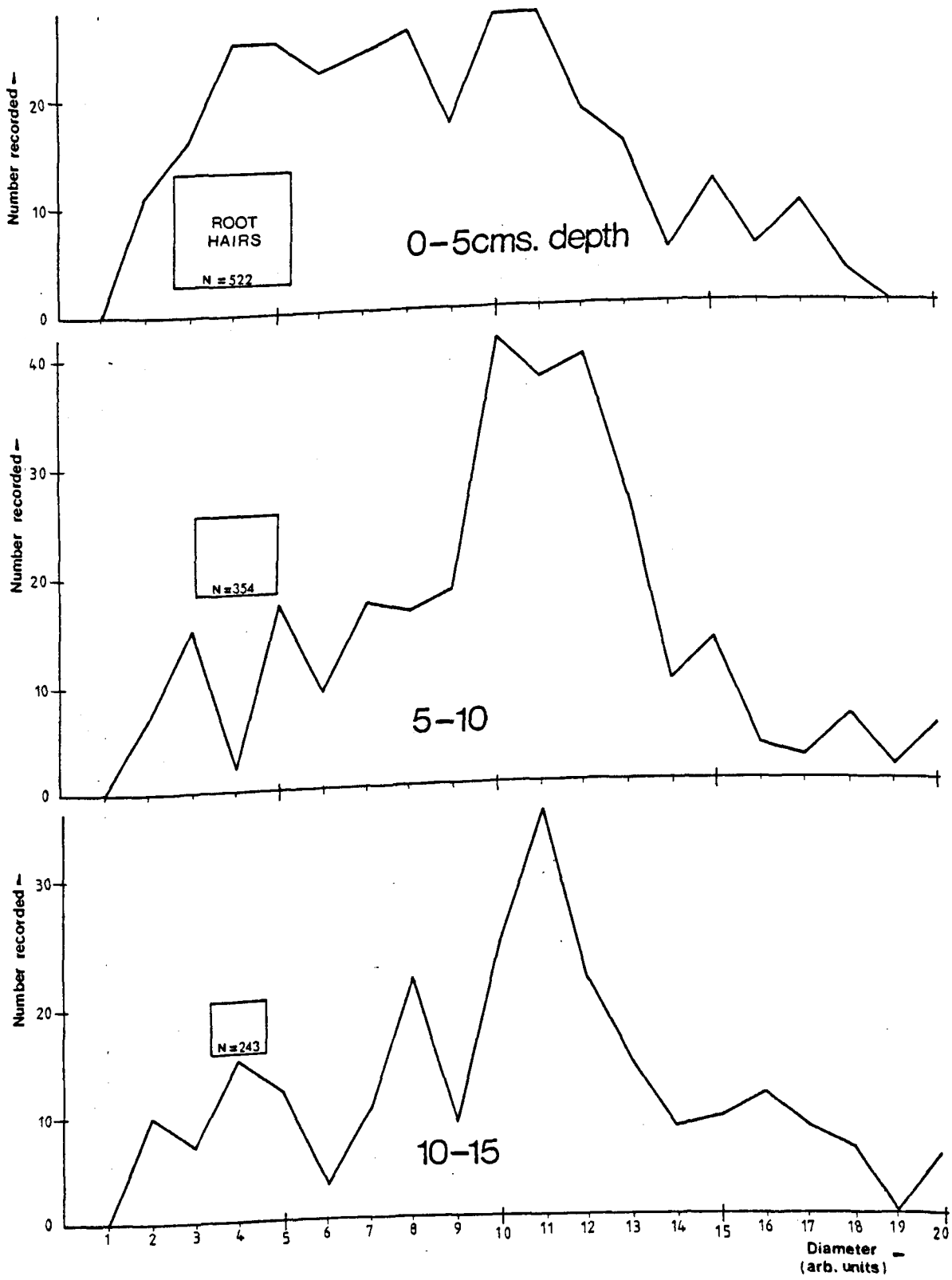


FIG 36 : Distribution of root diameter with varying depth. Recordings (total 500) from Botanic Garden site data in August, 1977. Boxes indicate relative proportions of root hairs at each depth.

Roots from four grassland sites are compared in FIG. 37. Besides the sites previously described, samples were also taken from a field heavily grazed and poached by cattle, in a field adjoining PAD. In SG, the largest frequency of roots were recorded at 10 units diameter (less than 0.1 mm), with large frequencies at lesser diameters. In contrast, roots in the heavily grazed field were distributed in lower frequencies between 5 and 15 units diameter. Fine roots were less frequent in LG than in SG and less frequent in PAD than in LG. Root biomass decreased in the order: SG, LG, PAD (*Section 3.5*), and the heavily grazed site had a substantially lower root biomass than PAD.

Categorization data for roots incubated in soil solution at 10°C for one month are shown in FIGS. 38 and 39. FIG. 38 shows data divided into unsuberized, suberized and friable fractions. Unsuberized roots were distributed around 10 units diameter, and quickly disappeared after incubation (FIG. 39). Smaller suberized roots accounted for most other breakdown. Increased frequencies of suberized roots around 10, 15 and 18 units indicate these fractions are most resistant to breakdown. The same number of root hairs (n = 520) were recorded before and after incubation.

Roots incubated under field conditions from March to May in SG are shown in FIG. 40. Once again, fractions which disappeared most quickly were small suberized roots and larger unsuberized roots. Root hairs decreased by 24%.

Nevertheless, these results must be considered in perspective with the relative weight losses from different categories. Separation of lengths of root of small diameter, large enough to weigh, was extremely difficult. Instead, approximately 1 cm lengths of roots of *Lolium perenne*, grown in nutrient solution, were measured and then dried and accurately weighed. All roots were at stages of early suberization,

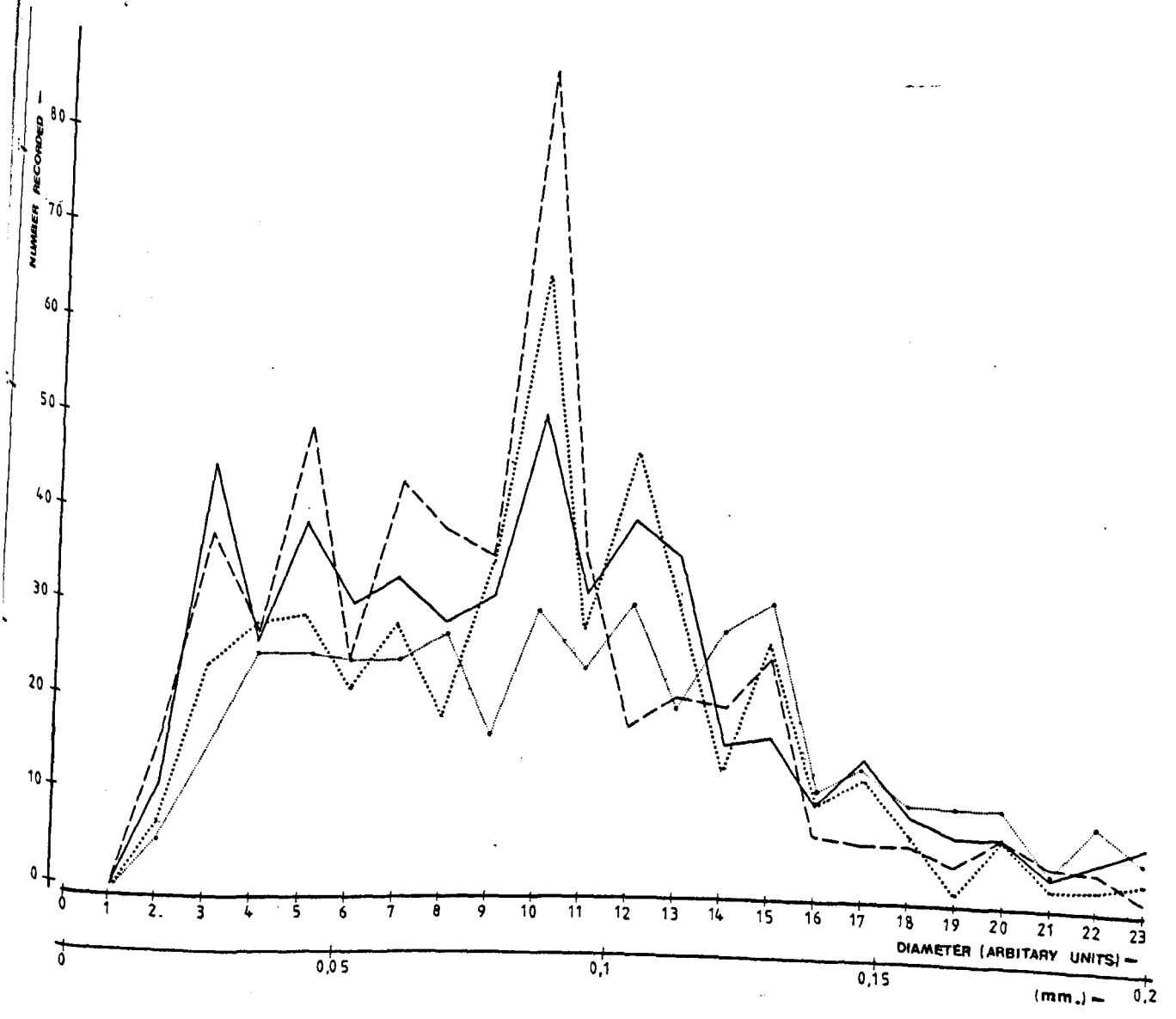


FIG 37 : Diameter distribution of root fractions from 4 grassland sites in January 1978. Sites are LG (————) SG(– – – – – –) PAD(·····) and a nearby sward, heavily grazed and poached by cattle (—·—·—·—).

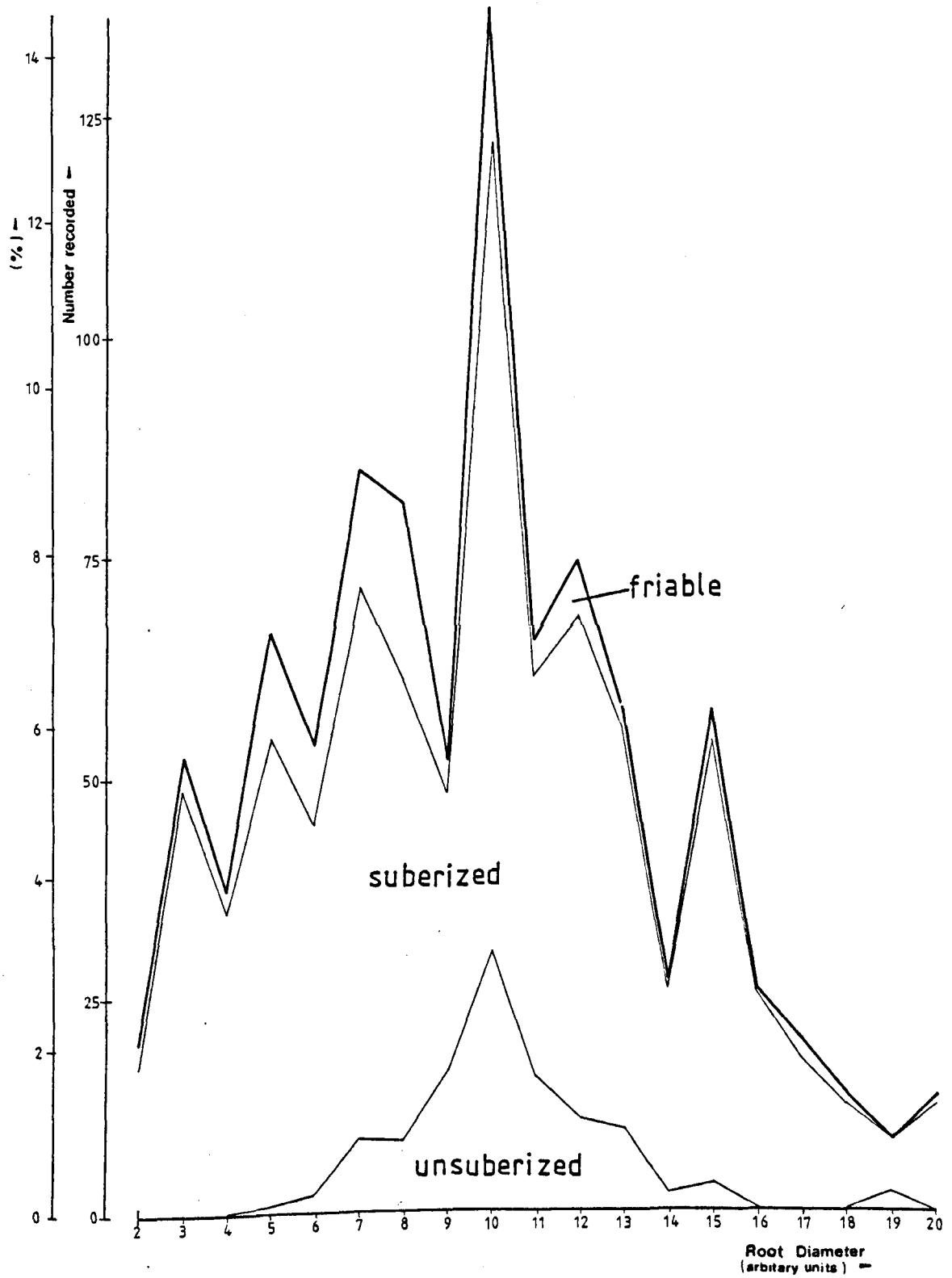


FIG 38 : Distribution of root diameters in September 1978, before laboratory incubation. Thickened line (————) represents total roots, divided into unsuberized , suberized and friable fractions. [940 recordings]

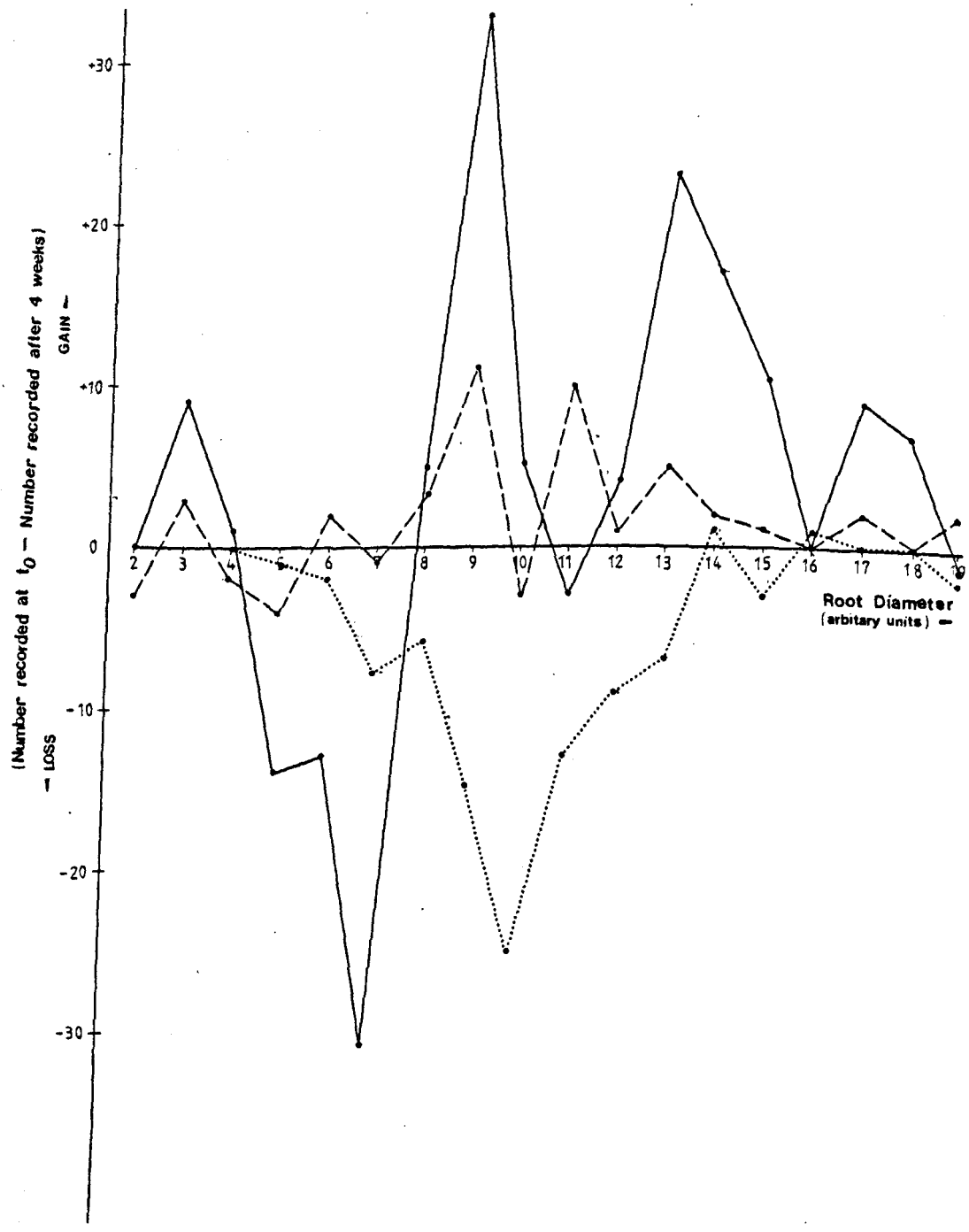
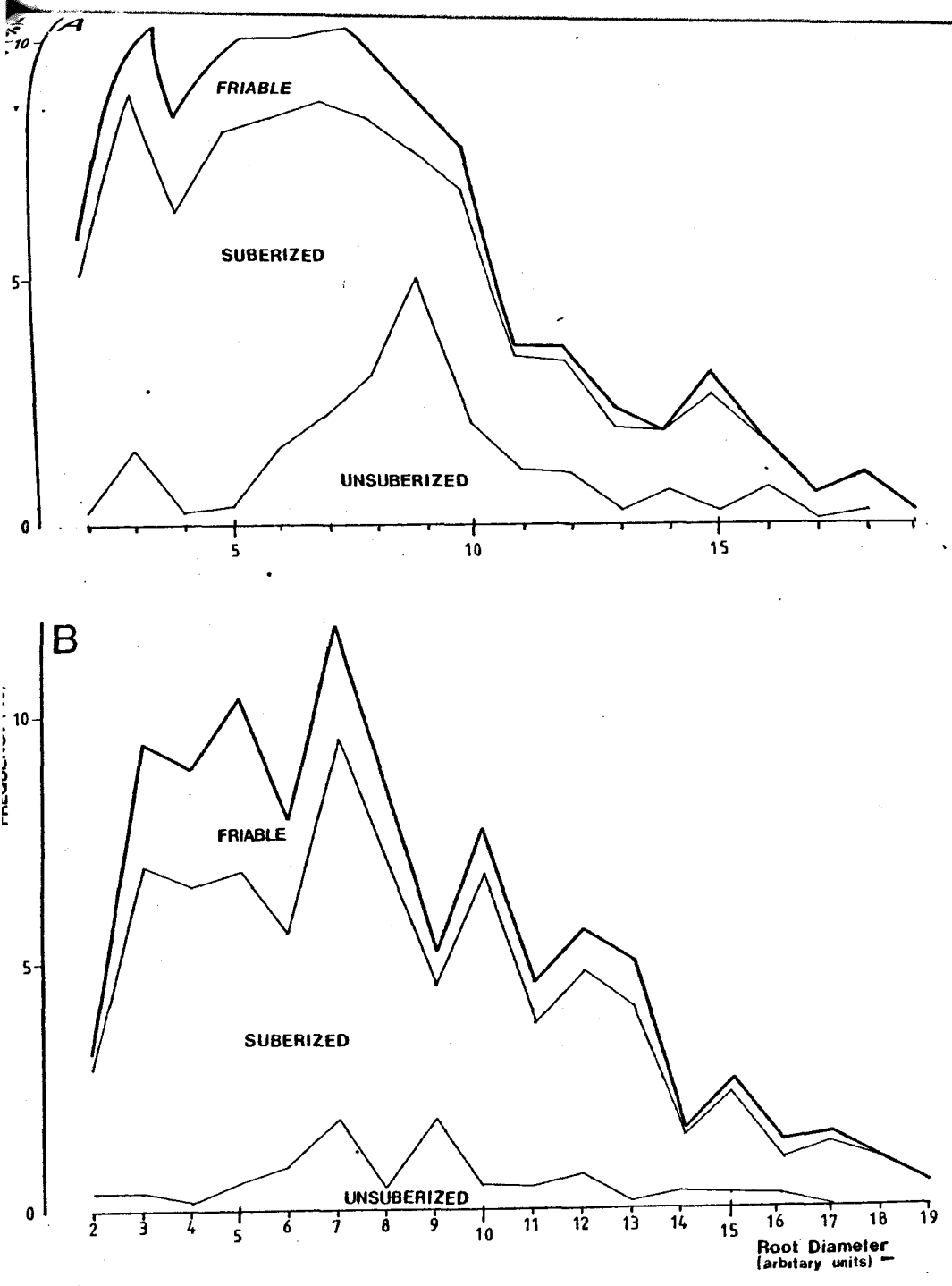


FIG 39 : Change in diameter distribution of unsuberized (•.....•), suberized (•——•), and friable root fractions (•– – – –•), after 4 weeks incubation in soil solution at 10° C [cf. Fig.].



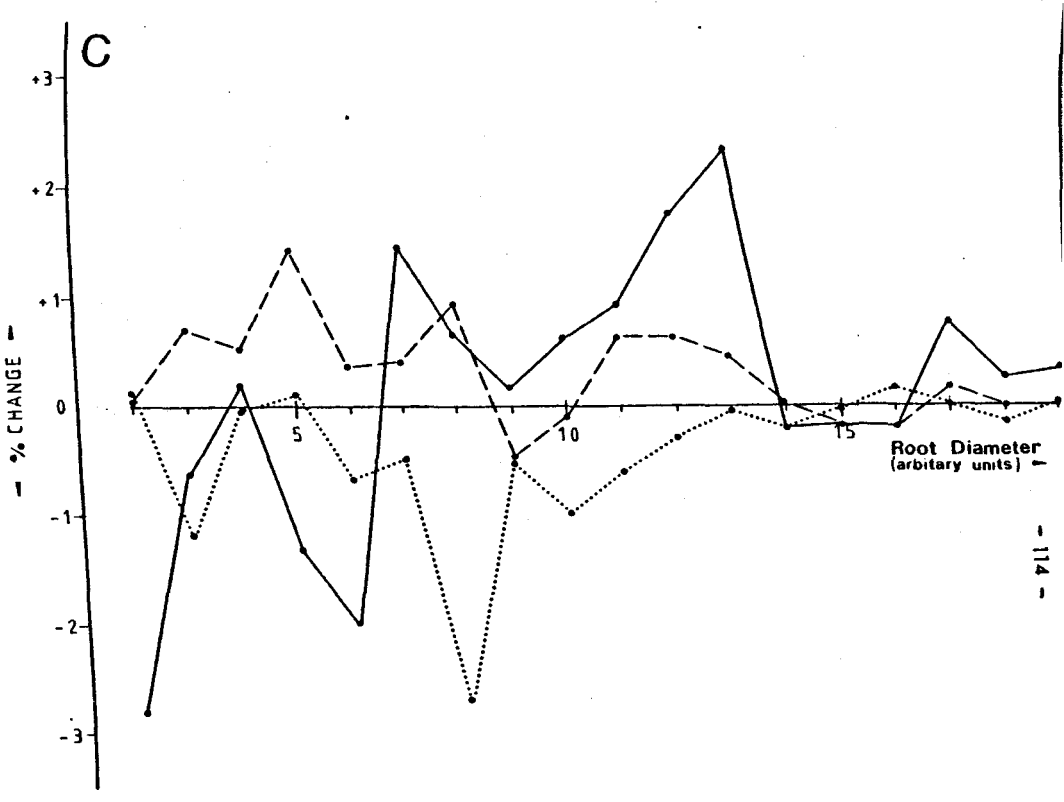


FIG 40 : Before (A) and after (B) March to May field incubation of root fractions in SG. Fig. C shows % change from A to B in unsuberized (•·····•) , suberized (•——•) and friable fractions (•– – –•)

and thus no account was taken of age. A regression of the square root of root weight on diameter provided a good fit (FIG. 41) and the computed regression equation was used to express categorization data in terms of weight. March to May incubation data from SG are thus shown in FIG. 42. Clearly, the breakdown losses of fine roots previously described are also substantial in terms of weight loss.

Finally, categorization data from March to June field incubation experiments in PAD, together with data from normal March and June samples are shown in terms of dry weight in FIG. 43. Unsuberized fractions increased most markedly during the early growing season, with a large proportion becoming suberized, whereas suberized fractions decreased considerably during incubation. Root hairs represent an extremely small proportion of the root system in terms of weight.

Root productivity estimates are calculated from these data in TABLE 25. Estimates which take breakdown into account are 3.6 times higher overall, than estimates based on differences between standing crop.

ROOT CATEGORY	PRODUCTIVITY (*P*) MARCH-JUNE	BREAKDOWN (*B*) MARCH-JUNE	*P + B*
Unsuberized	0.637	-0.031	0.606
Suberized	-0.343	0.753	0.410
Friable	0.014	0.083	0.097
TOTAL	0.308	0.805	1.113

TABLE 25 : Root productivity estimates ($g.m^{-2}.day^{-1}$) in PAD, based on differences between standing crop of dry weight in March and June (*P*), and including breakdown during the period (*P + B*).

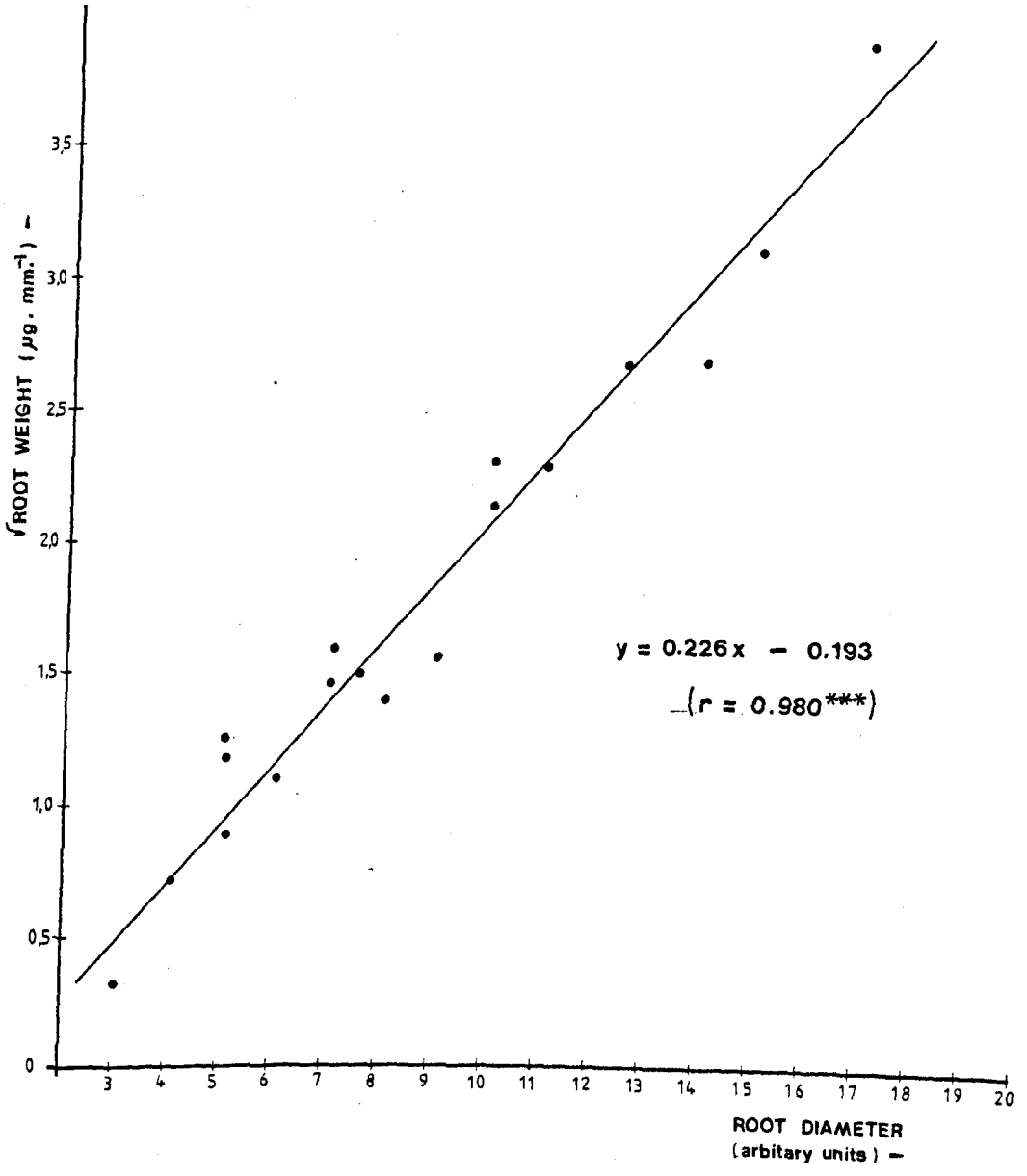
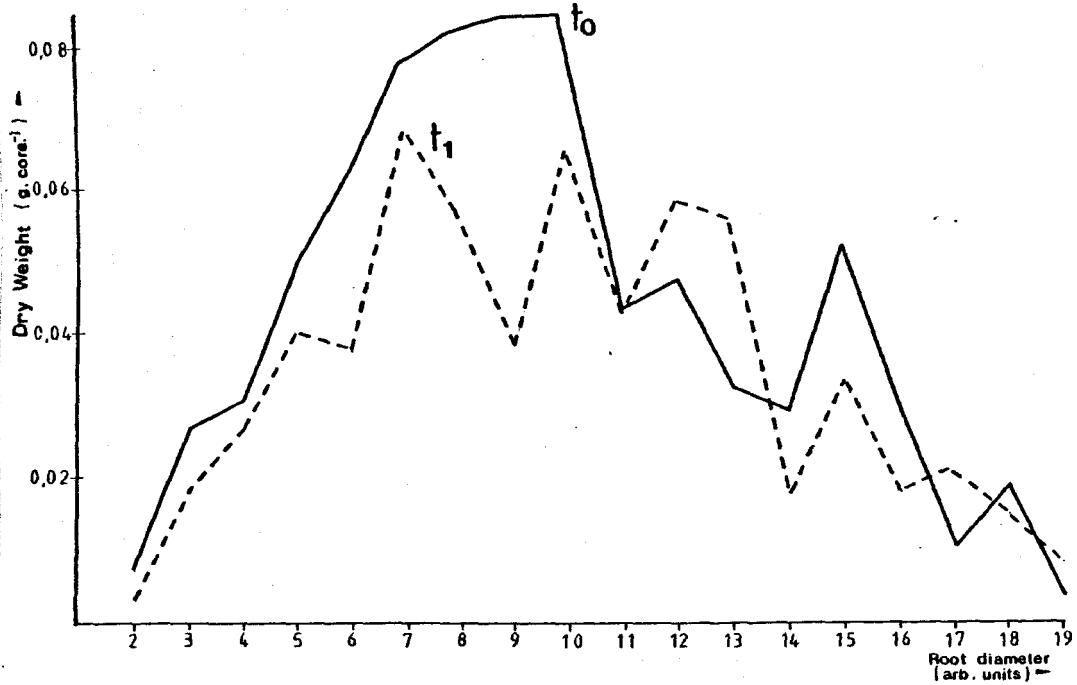


FIG 41 : ROOT WEIGHT / DIAMETER REGRESSION.



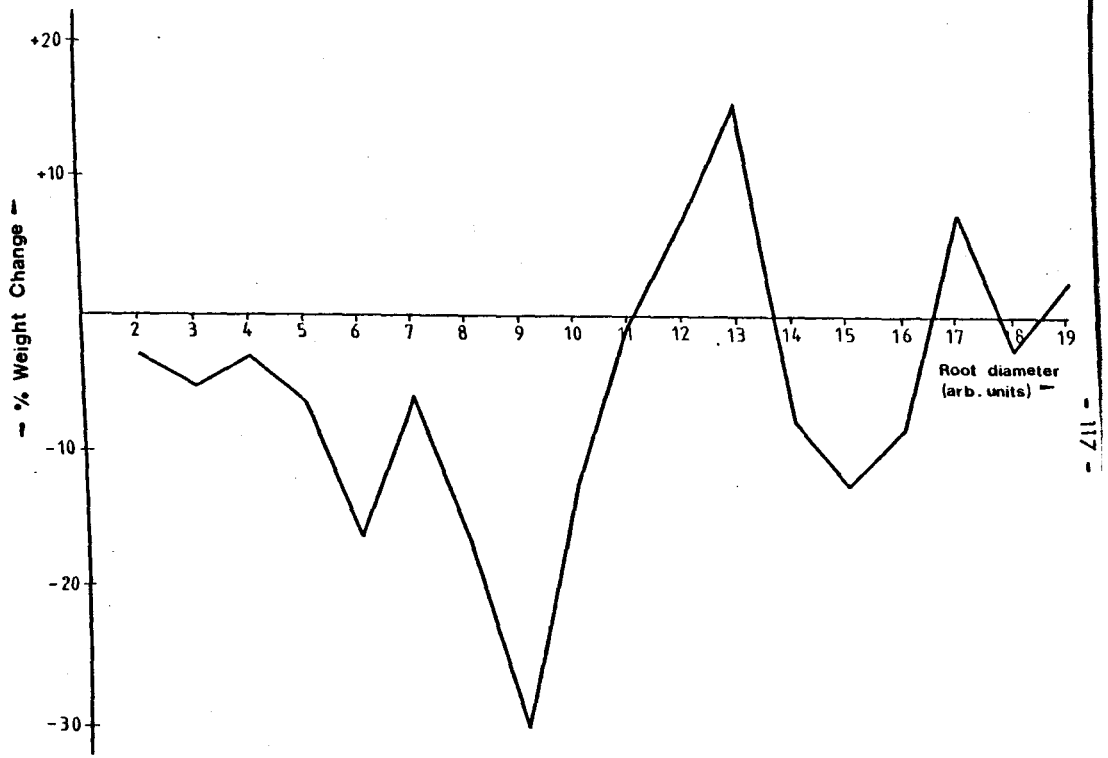


FIG 42 : Weight change of roots at each diameter following March to May incubation ($t_0 - t_1$) in SG, corresponding to Fig .

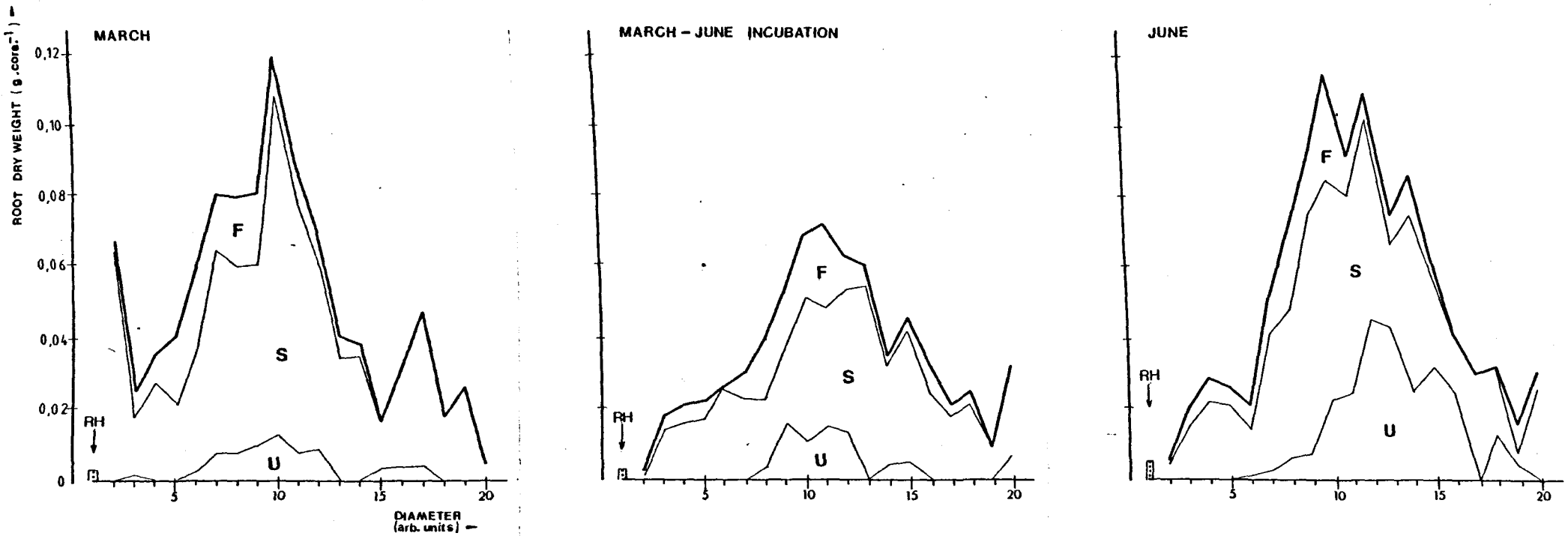


FIG 43 : Dry weight distribution of unsuberized (U), suberized (S) and friable (F) root fractions in PAD in March and June 1978, and after field incubation from March to June (81 days). Approx. wts. of root hairs (RH) are indicated.

7.5 Earthworms

7.5.1 Introduction

The influences of earthworms on surface litter breakdown have been investigated (Chapter 6), and evidence has been presented to suggest that their activities accelerate root breakdown (*Section 7.3*). However, the associations between earthworms and plant root systems are poorly understood.

Results are presented of attempts to discover some of these associations. Their effects on root growth (7.5.2) and breakdown of below-ground components (7.5.3) are examined, together with a comparison of populations in different mowing treatments (7.5.4). The results are discussed in the light of published work in *Section 7.6*.

7.5.2 Earthworms and Root Growth

A) METHODS

Two pot experiments were set up to examine the effects of earthworm activities on root growth.

12.5 cm plastic plant pots were filled to within 2.5 cm of the top with approximately 700 g of steam sterilized soil, previously sieved through 1 cm mesh. A polythene sleeve was fitted to the top of the pots, and the drainage holes covered with fine mesh, to prevent earthworms escaping (FIG. 44).

Earthworms were introduced into the pots and left for one week before 5 young tillers of *Lolium perenne* were transplanted into each pot. In the first experiment 6 pots were set up with high numbers of earthworms, 6 pots with low numbers and 6 without earthworms. In the second experiment 4 pots were set up with each of 4 species of earthworms, and 4 without earthworms (TABLE 26). Approximate densities of earthworms were estimated from field samples and from those used by Phillipson and Bolton (1977).

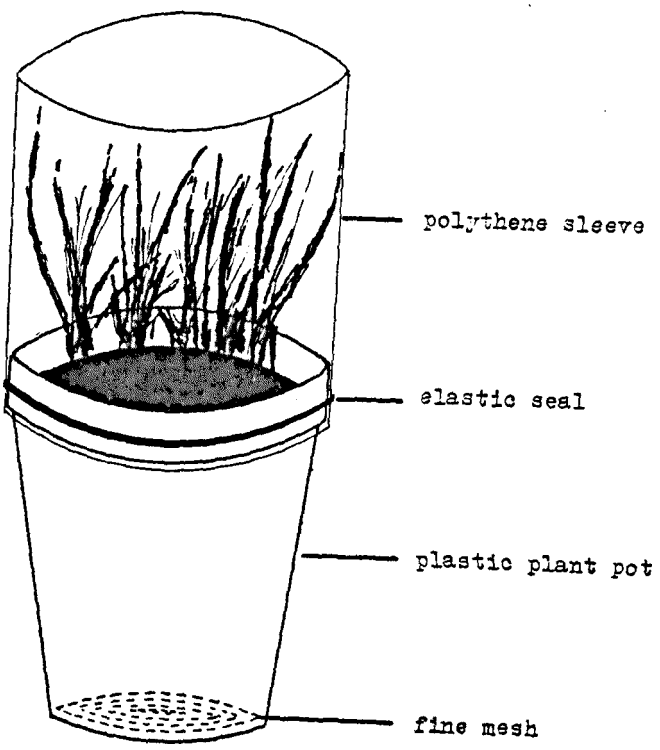


FIG. 44 : Pots used for earthworm/ root growth experiments

SPECIES	EXPERIMENT 1 HIGH NOS.	EXPERIMENT 1 LOW NOS.	EXPERIMENT 2
Allolobophora caliginosa	10	5	20
Lumbricus terrestris	2	1	5
Octolasion cyaneum	2	1	6
Allolobophora longa	2	1	5

TABLE 26 : Earthworm numbers in root growth experiments

Pots for each experiment were randomly positioned in separate controlled environment cabinets at 10°C with 16/8 hours light/dark regime and regular watering. After 12 weeks they were removed and dry weight of plant components, tiller numbers and earthworm numbers were recorded.

B) RESULTS

Data from experiment 1 is presented in FIG. 45. Root dry weight

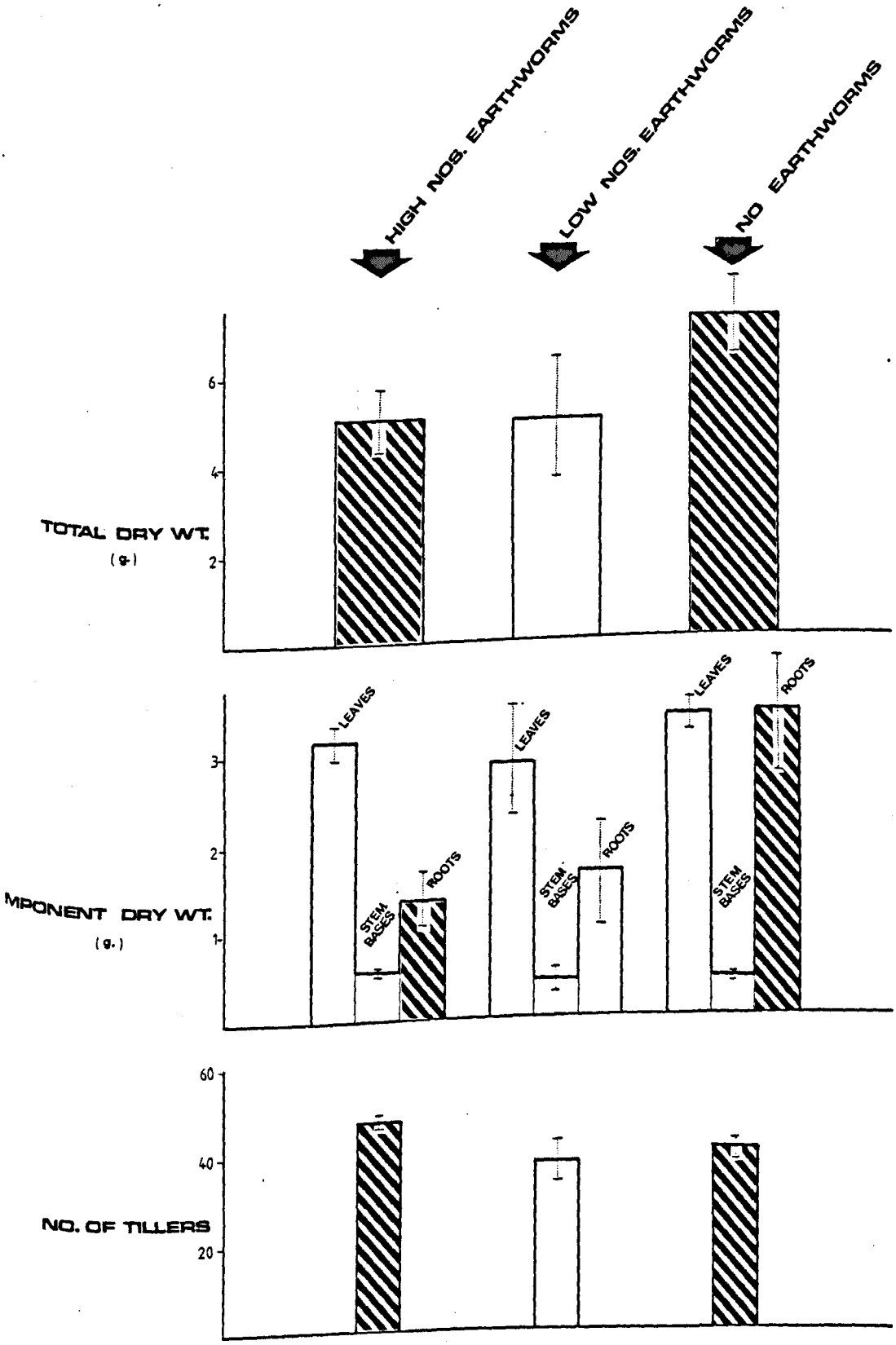


FIG 45 : Growth of Lolium perenne at 10°C after 12 weeks with and without earthworms (see text). Standard errors are shown. Significant differences exist ($p = 0.10$) between shaded treatments.

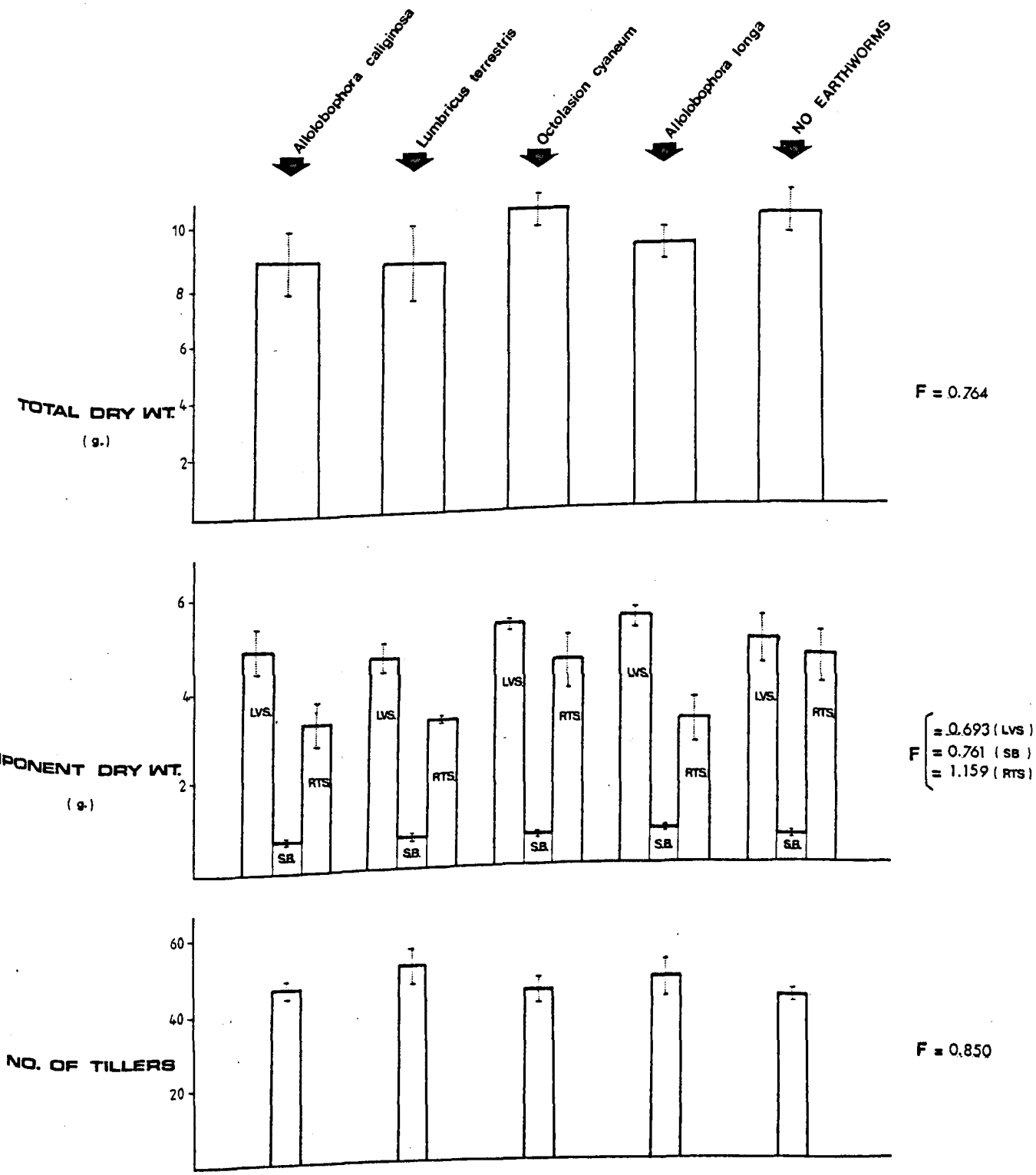


FIG 46 : Growth of Lolium perenne at 10°C after 12 weeks with 4 species of earthworms (see text). Dry wt. (± s.e.) is divided into leaves (LVS), stem bases (SB) and roots (RTS). Variance ratios (F values) are indicated : $F > 2.61$, $p = 0.10$; $F > 1.8$, $p = 0.20$ (4, 10 d.f.). No significant differences.

was lower in pots containing earthworms, although above-ground growth was not impaired. Indeed, tiller number was significantly higher in pots containing earthworms.

Data from experiment 2 is shown in FIG. 46. High residual error masked any treatment differences, but mean values augment the conclusions of the previous experiment, with the exception of *Octolasion cyaneum*.

7.5.3 Earthworms and Breakdown of Below-Ground Components

A) METHODS

Sixty-four 7.5 cm cubic cores were removed from an 8 x 8 sampling grid in SG, with cores taken 7.5 cm apart. Each core was assigned to one of eight treatments (TABLE 27) using a latin square design, then frozen overnight at -18°C, thawed and placed in 10 cm plastic containers sealed with fine mesh. Earthworms were introduced into the containers which were incubated at 12.5°C and moistened occasionally to prevent soil cores from drying out. One treatment and a control were removed after 8 weeks, and the remaining cores after 16 weeks.

TREATMENTS	EARTHWORM NUMBERS	INCUBATION TIME
1. t_0	-	NIL
2. No Earthworms	-	8 wks
3. No Earthworms	-	16 wks
4. Low Nos. Mixed	(1 x *L.t.*, 5 x *A.c.*)	8 wks
5. Low Nos. Mixed	(1 x *L.t.*, 5 x *A.c.*)	16 wks
6. *L.terrestris/A.longa*	(3 individuals)	16 wks
7. High Nos. Mixed	(5 x *L.t./A.l.*, 2 x *O.c.*)	16 wks
8. *A.caliginosa*	(5 individuals)	16 wks

TABLE 27 : Earthworm treatments in incubation experiment

B) RESULTS

Low numbers of earthworms had very little effect on breakdown rates (FIG. 47), although detached roots were significantly less at t_1 in

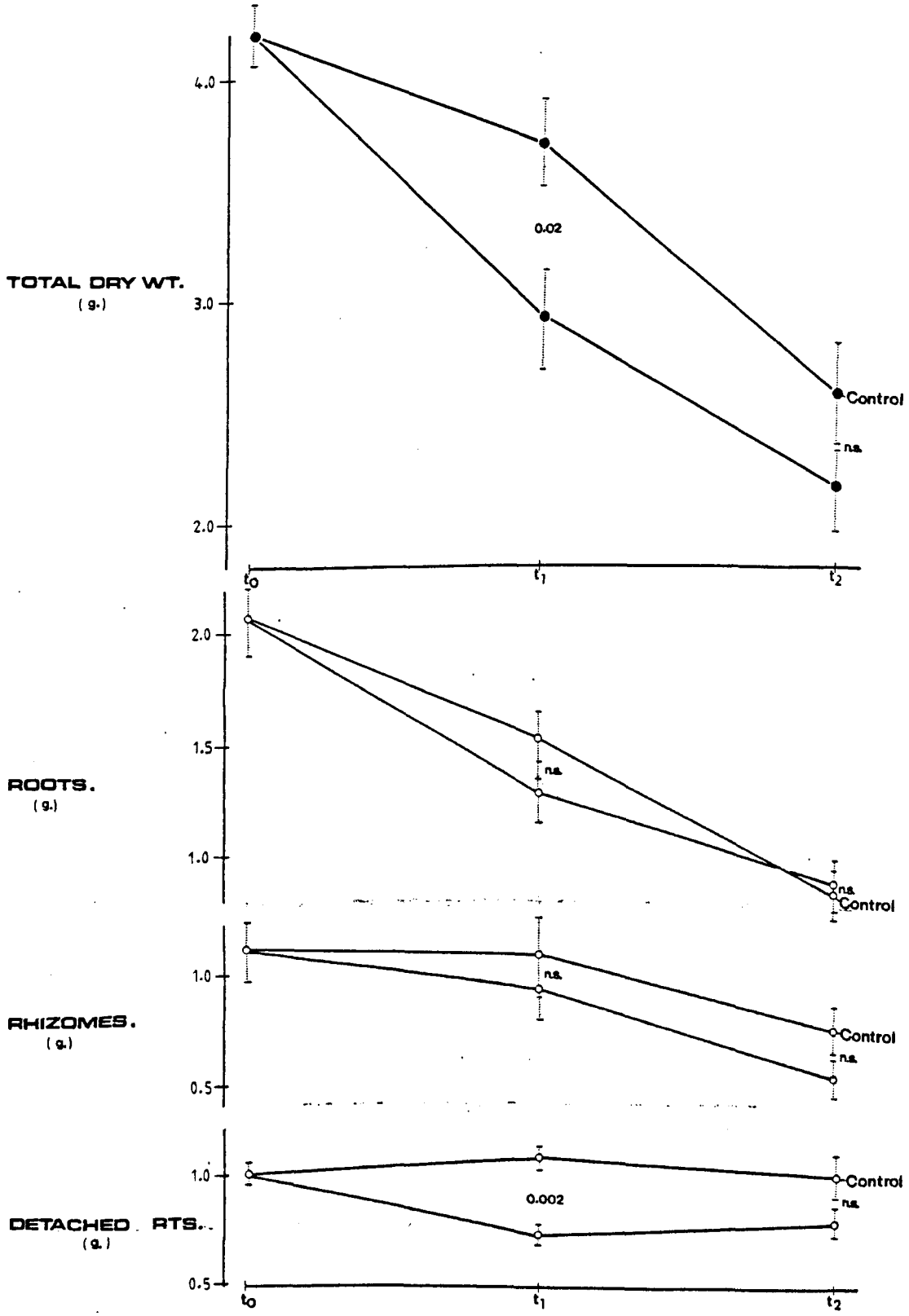


FIG 47 : Breakdown of below-ground components (dry wt ± s.e.) with earthworms and without (control) after 8 (t_1) and 16 (t_2) weeks incubation at 12.5°C. Levels of significant differences are shown (n.s. indicates no significance at 0.1).

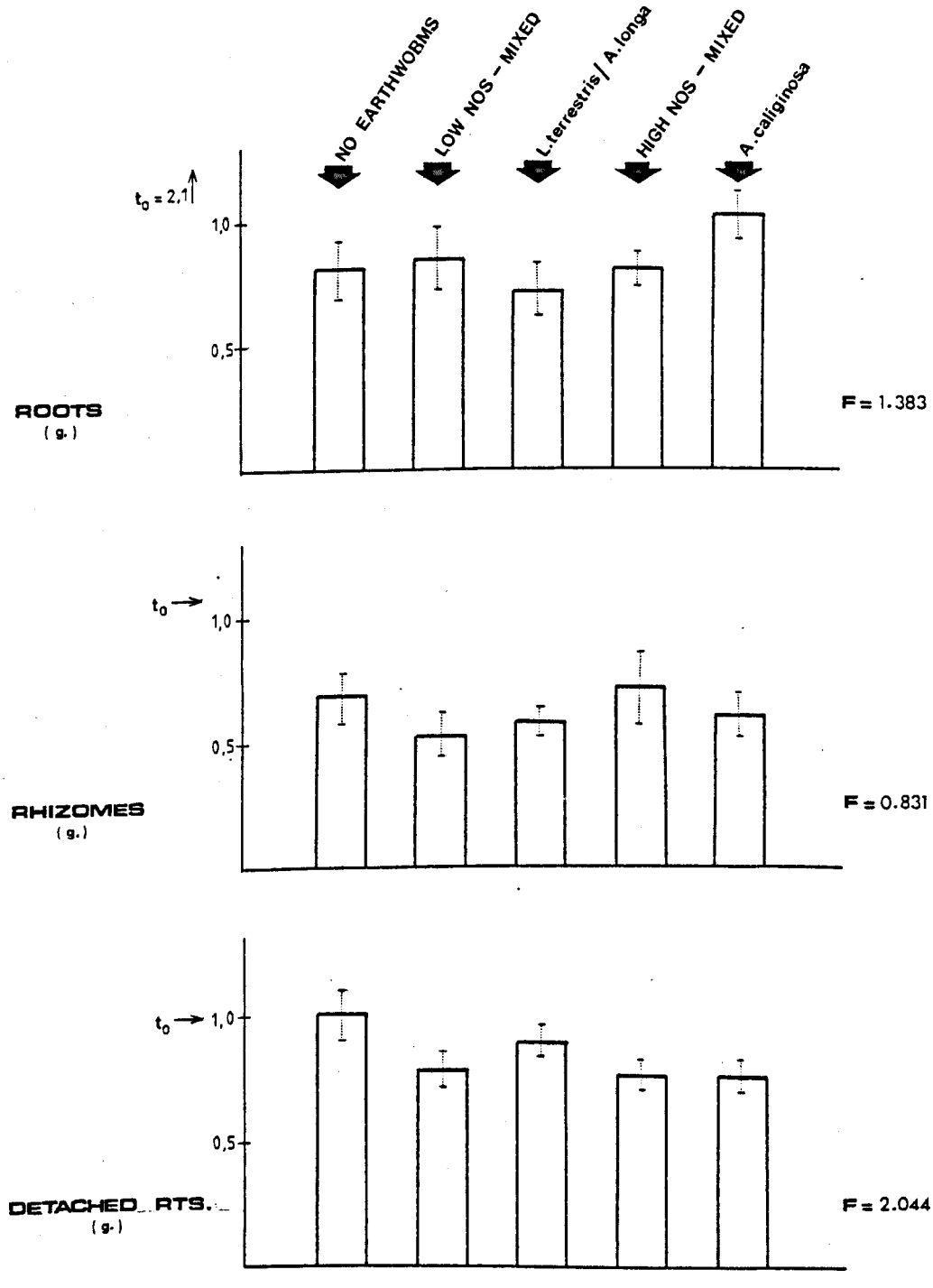


FIG 48 : Dry wt (± s.e.) of below ground components with & without earthworms after 16 weeks incubation at 12.5°C (see text).
Variance ratios (F values) are indicated : $F > 2.12$, $p = 0.10$; $F > 1.6$, $p = 0.20$.
No significant differences.

cores incubated with earthworms. Dry weight of below-ground components after 16 weeks (t_2) are shown in FIG. 48. No significant differences between treatments could be identified, although detached roots tended to decrease when incubated with earthworms. Detached root levels in control treatments remained at similar levels after 16 weeks incubation, whereas root levels had decreased to less than 40%, and rhizome levels to approximately 50% of original (t_0) values.

7.5.4 Earthworms and Mowing Treatments

A) METHODS

Earthworms were extracted using three applications of 4.55 l of 0.275% formaldehyde (*see* Satchell, 1971) on 0.25 m^2 quadrats. One extraction was made from each of the 5 replicated strips of each mowing treatment at the Botanic Garden site, during September, 1979.

B) RESULTS

Results are shown in TABLE 28. Differences are not within acceptable levels of significance, although inspection of raw data revealed unusually large numbers of *Allolobophora spp.* in one sample from LG. Exclusion of data from this quadrat provides significance levels for total numbers and weight within $p = 0.05$. However the validity of data exclusion is questionable.

Nevertheless, earthworm populations in autumn are clearly not enhanced by large surface accumulations of litter. More likely larger populations correspond to a larger standing crop of below-ground components in the mown treatments.

7.6 Discussion and Conclusions

Initial experimental attempts to measure below-ground turnover rates were confounded by the labour requirements of impracticable amounts of replication. The technique of incubating isolated soil

MOWING TREATMENT	*L.terrestris* Nos.	Wt.	*A.longa* Nos.	Wt.	*A.caliginosa gp.* Nos.	Wt.	*O.cyaneum* Nos.	Wt.	TOTAL NOS.	WT.
SG	18	6.7	52	28.1	47	6.6	4	2.9	121 ± 22.3	44.4 ± 3.6
MG	24	10.7	29	16.3	30	3.9	9	7.7	91 ± 10.1	38.5 ± 5.9
LG	10	7.1	30	14.4	19	2.8	1	1.0	61 ± 29.4	25.4 ± 3.0

TABLE 28 : Numbers (per m^2) and fresh weight ($g.m^{-2}$) of earthworms from each mowing treatment in September, 1979. *A.caliginosa gp.* includes small numbers of *A.chlorotica* and *A.rosea* but *A.longa* is listed separately (Gerard, 1964). Standard errors of total values are shown. *F* values for total nos. and wt. are 1.85 and 1.46 (2,12 d.f.) respectively ($F > 1.8$, $p = 0.20$).

cores is more feasible, and annual estimates of below-ground turnover could be achieved in future studies with 12 replicates collected monthly or bimonthly through the year. Annual estimates are not available from this study, but results indicate that below-ground productivity estimates would probably be under-estimated by over 100% if breakdown were not taken into account. Below-ground breakdown rates were higher than those recorded for surface litter breakdown during spring. Between March and June, root productivity estimates which included breakdown were 3.6 times higher than those based on differences between standing crop. Incubation period should be as short as possible, although at least one month, to limit the likelihood of fractions decomposing which otherwise would not. Errors from this source may be unavoidable. Differences were identified between breakdown of living and dead root systems (*ie*: not frozen and frozen prior to incubation), with respect to changes in detached root fractions. Clearly, estimates of turnover must be based on realistic breakdown values (*see* Milner and Hughes, 1970).

Categorization data indicate that fine roots are most frequent near to the soil surface, and represent a larger proportion of the root system in sites with a larger root biomass. Thus, proportions of fine roots appear to be correlated to root activity. Fine roots are known to develop extensively in areas of localized nutrients (Duncan and Ohlrogge, 1958; Drew and Saker, 1975; Fitter, 1976).

Unsuberized roots account for up to 30% of total root weight, being most frequent around 0.07 - 0.09 mm diameter (8 - 10 units). As with fine suberized roots they disappear quickly when growing conditions become unfavourable, which probably explains the presence of fine roots and root tips in detached root fractions and accounts for increased

detached root levels after incubation. Large suberized roots are much more resistant to decay. Friable roots account for approximately 20% of total root weight, with relatively small increases after incubation, and should be considered in association with detached roots (*see* below).

The categorization technique was used as a viable alternative to root observation chambers (*see* Schuurman and Goedewaagen, 1971; Böhm, 1979), and provides a method for obtaining accurate comparative data. Errors may be caused by root damage and loss of root hairs during washing, although Böhm (1979) considered that few root hairs are removed by washing processes. To some extent the method surmounts the problems of distinction between living and dead fractions of the root system, discussed by numerous authors (*see* Böhm, 1979). Perspex wedge observation chambers (Shaver and Billings, 1975) were also tested, but considered unsuitable due to difficulties of maintaining close contact with soil, and in measuring fine roots.

Throughout the study it has been considered valid to describe detached roots as a separate below-ground component, although seasonal variations are often related to those of roots, or less often of rhizomes. For the main part, the detached roots probably represent fractions of decaying roots which become easily detached from the root system.

Results from earthworm studies must be treated with some caution, and further experimentation would have been preferred in certain instances. Nevertheless, a number of conclusions can be drawn from the experiments. Earthworm activities were shown to inhibit root production whilst having no effect on aerial dry weight production, but increasing the numbers of tillers. Edwards and Lofty (1978) found that cereal root growth in soil cores from compacted arable land was concentrated in areas of activity of earthworms, thus demonstrating the benefit of earthworm

tunnelling to root growth in compacted soils. In the present study, with loosely compacted soil, they had the opposite effect.

Earthworms accelerated root breakdown in field experiments, but this could not be substantiated in laboratory experiments. Environmental factors not simulated in the laboratory may enhance the effects of earthworms. Laboratory incubation studies showed that they can accelerate the breakdown of detached roots, and gut analyses revealed that small pieces of fragmented roots can be consumed. Piearce (1978) thought that some species are root browsers, and besides recording small amounts of roots in gut analyses he found large amounts of unspecified fibrous plant materials. Although he does not comment on their origin, these may be derived from below-ground components. Dexter (1978) showed that earthworms tunnel by ingesting the soil ahead of themselves, rather than by pushing loose soil out of the way. By necessity, those species without permanent burrows would consume large amounts of root-derived materials. Waters (1955) suggested earthworm numbers may be correlated with flushes in the availability of dead root material, although Edwards and Lofty (1977) considered there to be few grounds for acceptance, but state that a few species have been shown to feed on dead roots. Comparison of earthworm populations in different mowing treatments in autumn indicated that they are not enhanced by large surface accumulations of litter, but more probably by the larger below-ground biomass in mown treatments.

CHAPTER 8

DISCUSSION AND CONCLUSIONS

The results from the main sampling programme (Chapters 3-5) and their significance are considered in relation to published information, and inferences together with those of the subsidiary experiments (Chapters 6-7) are discussed in perspective.

8.1 Above-Ground Primary Production

Accurate estimates of nett primary productivity (*NPP*) were not sought, but it is worthwhile to compare data from LG and PAD to other similar grassland studies. *NPP* calculated from harvest data by incremental summation of positive increases of total standing crop are compared with results of other studies of British grasslands in TABLE 29. Values for LG are particularly high, with an enormous proliferation

AUTHORITY	GRASSLAND SITE	FREQUENCY OF SAMPLING (per annum)	*NPP* ($g.m^{-2}$ $annum^{-1}$)
Welches & Rawes (1965)	Pennines. Grazed lowland (max.)	12	194.7
	upland (min.)	12	55.9
Williamson (1976)	Sussex. Very lightly grazed lowland	6	213
Perkins *et al.* (1978)	Snowdonia. Grazed upland	9	271
present study	LG	5	549.1
present study	PAD	5	187.7

TABLE 29 : Above-ground *NPP* calculated from incremental summation of positive increases of total standing crop.

of above-ground biomass following cessation of mowing. In fact these

calculated values for *NPP*, although derived by methods recommended by Milner and Hughes (1970), are grossly under-estimated. Williamson (1976) studied a chalk grassland with minimal grazing by rabbits and which was being invaded by scrub. Production parameters were similar to those in the present study, particularly in LG (TABLE 30) and he estimated an improved value for *NPP* of 691 $g.m^{-2}$ $annum^{-1}$ by allowing for leaf turnover. This value is 2.1 times higher than estimates from positive increases in living biomass. Perkins *et al.* (1978) provided an improved estimate for *NPP* of 1143-1145 $g.m^{-2}$ $annum^{-1}$ by including measurements of litter disappearance and living material consumed by sheep and slugs (*cf.* TABLE 29).

Semi-permanent grasslands are not characterized by high productivity, nor is this considered important in amenity grasslands (Grime, 1980). Total removal of cuttings from SG and MG were 200 and 132 $g.m^{-2}$ $annum^{-1}$ respectively. These values are considerably lower than *NPP* estimates in LG, although the efficiency of collecting cuttings after mowing may not be very high. Nevertheless, in agricultural grasslands harvestable dry weight yields in excess of 1000 $g.m^{-2}$ $annum^{-1}$ are obtained from fertilized ryegrass swards (NIAB, 1979; Rhodes and Mee, 1980).

Holiday and Wilman (1965) studied the effects of frequency of mowing (between 2-10 cuts per year) on above-ground dry matter yield of mixed swards, and found that the longer the period between mowings the higher was the yield.

8.2 Effects of Cessation of Mowing

Succession from a plagioclimax (a *plagiosere*) involves an integrated response affecting all components of the ecosystem (Whittaker, 1970; Odum, 1971), and the successional consequences of removal of grazing or mowing pressure are well documented (Duffey *et al.*, 1974).

TABLE 30 : Above-ground production parameters in LG and PAD compared to those in a Sussex chalk grassland (Williamson, 1976)

PRODUCTION PARAMETERS	Williamson (1976)	LG	PAD
Maximum total standing crop ($g.m.^{-2}$)	773	779	448
Maximum living biomass ($g.m.^{-2}$)	355	462	587
Litter as a % of above-ground standing crop	57-89%	17-97%	23-95%
Maximum % of live and dead forb of total above-ground vegetation	8%	6%	57%
NPP from increases in living biomass ($g.m.^{-2}annum^{-1}$)	*310*	*409*	*244*

In the first year following cessation of mowing in the present study, above- and below-ground fractions of grasses increase enormously, until large accumulations of surface litter prevent their continued dominance. The main reason for this is probably the prevention of establishment of new seedlings and tillers by the deep litter layers. Succession towards tall, erect and tussock growth forms is evident in PAD, with *Alopecurus pratensis* and *Dactylis glomerata* particularly abundant (see PLATES). Although large amounts of nutrients are bound in the litter, these represent only a small proportion of total ecosystem nutrients. Below-ground components of grasses decline whilst the litter layer is large, excepting detached roots which increase slightly.

In the second year following cessation of mowing, large accumulations of litter mark the decline of grass communities and favour the proliferation of forbs. *Rumex acetosa* had become established in considerable proportions, above and below ground. Grime (1978, 1980) described the role of plant strategies in vegetation processes. He considered a sequence whereby stress tolerators replace competitors, as a result of resource depletion arising from the development of a large plant biomass.

8.3 Below-Ground Components

Large amounts of replication are found to be necessary to account for the variability of below-ground components. Böhm (1979) echoed the pronouncements of numerous authors that the more accurate the method of root study, the more laborious, tedious and time-consuming it becomes, whilst acknowledging the necessity for the establishment of background information.

Primary production parameters for below-ground components in SG, LG and PAD have been calculated in TABLE 31. In SG annual turnover rates, as indicated by differences between maximum and minimum standing crop,

TABLE 31 : Annual below-ground primary production parameters (ash-free dry wt.; $g.m.^{-2}$) in SG, LG and PAD. Values are means of annual figures between March 1978-March 1979 and June 1978-June 1979.

COMPONENTS	MEAN STANDING CROP ($g.m.^{-2}$)	MAX.-MIN. STANDING CROP	INCREMENTAL SUMMATION OF GAINS OF STANDING CROP	INCREMENTAL SUMMATION OF LOSSES OF STANDING CROP
SG				
Roots	258.5	123.6	134.0	69.9
Rhizomes	241.7	86.9	113.4	86.2
Detached Roots	177.1	35.0	43.9	17.8
Σ	*677.3*	*245.5*	*291.3*	*173.9*
Total Below-Ground Standing Crop	677.3	224.2	249.9	132.5
LG				
Roots	259.5	107.5	37.4	122.4
Rhizomes	231.0	223.2	218.1	233.1
Detached Roots	190.2	50.1	69.0	94.3
Forb Roots	30.0	62.2	54.3	59.4
Σ	*710.7*	*443.0*	*378.8*	*509.2*
Total Below-Ground Standing Crop	710.7	395.7	285.0	415.4
PADDOCK				
Roots	255.2	133.4	56.9	171.1
Rhizomes	176.9	233.6	61.3	233.6
Detached Roots	176.3	100.3	102.6	81.1
Forb Roots	103.1	268.2	291.9	197.3
Σ	*711.5*	*735.5*	*512.7*	*683.1*
Total Below-Ground Standing Crop	711.5	287.7	117.4	287.7

are 33-36% overall. In LG, values are larger (56-62%) mainly due to changes in rhizome biomass and larger losses. Below-ground fractions in PAD reached peak standing crop at different times, and higher production values are obtained from the summation of data for individual components. Large gains are caused by the proliferation of forbs, and differences between maximum and minimum standing crop are 103% of mean standing crop. Using differences between maximum and minimum standing crop, Dahlman (1968) recorded turnover rates of 25% per year in prairie grasslands, Nilsson (1970) recorded 50% in a Swedish hay meadow and Perkins *et al.* (1978) recorded 38-46% in Snowdonia grassland. However, estimates of primary production derived in this way represent the balance of growth and breakdown, and therefore under-estimate true production values. Incubation data indicate that annual turnover exceeds mean standing crop (see below).

Few studies have distinguished between different below-ground fractions. Plewczynska-Kuras (1976) divided underground parts of meadow herbage into three categories of roots, underground parts of stems, underground litter and tillering nodes. The importance of fine root dynamics has been realized in woodland studies (Barnard and Jorgensen, 1977; Santantonio *et al.*, 1977; Cox *et al.*, 1978) and Ares (1976) categorized the root system of *Bouteloua gracilis* (Blue Grama grass). He found that 30-60% of young unsuberized roots decreased within a few weeks of elongation during the spurt of spring growth. Garwood (1967) found that the longevity of adventitous roots arising from the base of tillers of *Lolium perenne* in April and May was often less than one week, whilst those initiated in September to November survived for an average of 5-6 months. Spiedel and Weiss (1974) noted that 54% of observed root tips survived less than one month, whilst only 10-15% survived more than 4 months. In the present study, unsuberized roots are found to

account up to 30% of root weight, and together with fine suberized roots they disappear quickly when conditions become unfavourable, whereas larger suberized roots are more resistant to decay.

The separation of large amounts of detached roots [16-41% ($\bar{x}$ = 28.4%) of ash-free dry weight of total below-ground components] by flotation, after all visible plant material had been picked out, was surprising. Little direct evidence of this fraction has been reported; most authors have used either root washing over sieves or flotation techniques, but not combinations of both. Malone and Swartout (1969) found large proportions of small roots between 297 µm and 1,190 µm in size, and considered that washing through 1 mm screens may under-estimate below-ground standing crop by 50%. The detached root fraction consists mainly of detrital roots, and together with friable categories must account for the largest contribution of organic detritus into the soil. Coleman (1976) reported 20-30% detrital roots in prairie grasslands and Shamoot *et al.* (1968) and Sauerbeck and Johnen (1977), using radio-active tracer methods, found 20-49% more organic debris in soil than could be visibly separated, which they attributed to rhizo-deposition (*also see* Barber and Martin, 1975, 1976). Sloughed root fractions, mucilaginous and soluble materials have not been considered in the present study.

8.4 Effects of Mowing on Below-Ground Components

The greater proportion of biomass in grasslands is held below ground (Bazilevich and Titlyanova, 1980), which represents 54-98% of total biomass in the present study. The morphological and physiological adaptations of grasses provide a certain resilience to grazing or mowing (Langer, 1979) and Nyahoza *et al.* (1973) demonstrated that assimilate redistribution after defoliation between adjacent tillers and between rhizomes and tillers ensures their survival.

Bartos (1971) reviewed the literature concerning the effects of herbage removal on root weight (*also see* Section 2.1), and concluded that most studies showed a reduction in the amounts of roots after herbage removal. For example, Crider (1954) found that removal of half or more of grass foliage stopped root growth for 6-18 days. However, most of these results were derived from experiments carried out in the short term. Pearson (1965) found that grazed areas had more roots than ungrazed areas in desert communities of Eastern Idaho, as did Sims and Singh (1978) in North American grasslands. The present study indicates an increased investment in roots and rhizomes with increased frequency of mowing, although higher levels of roots and rhizomes did not return until the second year following the re-introduction of heavy mowing.

8.5 Nutrient Concentrations

Seasonal changes in nutrient concentrations between components of the vegetation are varied. In broad terms these changes result from movement of nutrients during growth and senescence. Elements differ in their mobility, and translocation particularly affects *N*, *P* and *K* (Allen *et al.*, 1974). Some elements tend to be retained, whilst others are highly mobile and easily leached from tissues. Conclusions of the present study are listed in *Section 4.11*. Seasonal changes in concentrations vary between nutrients and plant components, are altered by mowing regime, and can often be described by dry weight parameters.

Allen *et al.* (1974) described the general seasonal trends of variation of nutrient concentrations in deciduous leaves in temperate climates. They described *N*, *P* and *K* fluctuations as reaching an early spring peak and remaining steady over summer with an autumn decline, which contrasts with the present study in which concentrations were lowest at times of peak biomass and increased through autumn and winter.

Also fluctuations of *Mg* and *Mn* in grasses are better defined than Allen *et al.* suggested, with concentrations increasing through the season to reach an autumn peak. *Ca* concentrations were very high in autumn. Williams *et al.* (1977) found *N*, *P* and *K* concentrations in sheaths and blades of New Zealand tall-tussock grasslands decreased with age, whilst *Ca* and *Mg* increased. Pritchard *et al.* (1964) showed that with progressive maturity of *Phleum* and *Bromus spp.*, leaf and flowering head concentrations of *K* decreased, *Ca* increased and *Mg* remained relatively constant, whilst stem concentrations declined. In the present study, above-ground grass concentrations of most nutrients were highest in mown treatments.

Fluctuations of nutrient concentrations in below-ground components are poorly described in the literature, which provides few comparisons to the present study. Perkins *et al.* (1978) measured *N*, *P*, *K*, *Ca* and *Mg* concentrations in roots and grasses in Snowdonia grassland. They measured higher *Mg* concentrations and lower *Ca* concentrations in roots than in above-ground grasses, both of which were vice versa in the present study. Otherwise, concentrations and relative proportions in grasses and roots were similar in both studies. Troughton (1957) stated that, in general, roots lose *N* at times of rapid herbage growth and gain it during autumn, whereas seasonal concentrations varied only slightly in the present study. Weinman (1942) found *P* concentrations in roots decreased during spring and early summer, and was transferred from leaves to roots in autumn. In the present study, root and rhizome *P* increased through the sampling period in SG and MG and were lowest in autumn in LG.

8.6 Nutrient Cycling

General information and descriptive models of nutrient turnover and circulation are presented by Butler and Bailey (1973), Frissel (1977)

and Clark *et al.* (1980). Briefly, *N* flows readily through plant components, although there is a build up of organic *N* in soil, whilst *P* is in tight circulation, governed by its low solubility, and intra-plant recycling becomes more important. Rapid turnover rates (open circulation) of *K* and *Na* between components of the ecosystem are illustrated by large available pools and leaching losses. Cycling of *Ca* and *Mg* are less well known, although they have important effects on soil properties, and leaching losses may be large (Wilkinson and Lowrey, 1973). *Mn* has been neglected as a nutrient, but soil levels may be low enough to restrict plant growth, and *Zn* is freely available to plants except in very acid soils (Allen *et al.*, 1974).

In the present study, nutrient investment in plant components is shown to differ with management regime. Conclusions are detailed in *Section 5.9*. Release of nutrients from the large accumulations of litter, in the second year following cessation of mowing, are exploited by forb fractions although *Ca*, *Mn* and *Zn* tend to be retained in litter. Mowing encourages substantial investments in root and rhizome pools, and seasonal differences between treatments in the amounts of *N*, *P*, *Ca* and *Zn* in roots and rhizomes tend to follow dry matter differences. Seasonal fluctuations of *K*, *Mg*, *Na* and *Mn* pools in below-ground components differ according to mowing regime.

Perkins *et al.* (1978) recorded largest proportions of *N*, *Ca* and *Mg* in roots, compared to aerial parts, but slightly lower proportions of *P* and much less *K* in roots. Results of the present study are similar, although *P* and *Mg* vary seasonally. Bokhari and Singh (1975) found a greater *N* content in above- and below-ground plant tissues in short grass prairie compared to tall grass prairie.

Jones and Woodmansee (1979) discussed biogeochemical cycling of *N*, *P* and *S* in annual grassland ecosystems. They pointed out that internal

recycling is not important in annual grasslands because most vegetation dies at the end of the growing season, and therefore most nutrients in a current years vegetation are derived from direct mineralization of soil residues. Their comments have some relevance in the present context of perennial grass dominated ecosystems. Translocation of nutrients between plant components during senescence (*ie*: from leaves to rhizomes and roots) is usually assumed, particularly for those elements in limited supply such as *N* and *P*. However, large proportions of nutrients are transferred from grasses to litter (TABLE 32), which indicates that nutrients are poorly conserved by grass communities on an annual basis. Nevertheless, although available nutrients may limit grass production at certain times, those bound in organic matter and soil fractions probably become available as later successional stages develop.

Bradshaw (1980) examined the amounts of nutrients that become available to plants during the growing season, using data of Perkins *et al.* (1978) from Snowdonia grassland. He formulated the total annual requirement of each nutrient, which varied between 1.6-2.6 times the nutrients in capital, assuming the system was in a steady state with complete turnover of capital every year. Similar values are shown for LG in TABLE 33 where annual requirement varies between 0.7-1.5 times the nutrients in capital. The table provides a summary of dry weight and nutrients in capital and production at the Botanic Garden site, together with other relevant measurements. It should be noted that, production values are underestimated in both studies, particularly for below-ground components, and therefore provide an inaccurate measure of nutrient requirements.

Floate (1970 *b*, *d*) examined the modification of nutrient cycles by sheep grazing in Scottish hill pastures, where the supply of available nutrients is frequently low. He considered that increased pasture utilization during the growing season should lead to more efficient utilization of nutrients held in soil organic matter by increasing their availability through faeces and urine.

	N	*P*	*K*	*Ca*	*Mg*	*Na*	*Mn*	*Zn*
Litter concentration as a % of grass concentration at previous sampling date (mean values).	65.2	63.2	37.7	126.0	78.4	56.6	192.7	140.9
Annual Production - Grasses ($g.m.^{-2}$)	4.405	1.141	5.367	2.910	0.703	1.946	0.172	0.022
Annual Production - Litter ($g.m.^{-2}$)	7.723	1.039	2.401	2.523	0.365	0.801	0.420	0.053

TABLE 32 : Comparison of nutrients in grasses and litter in LG. Annual production is calculated from the summation of positive increases in standing crop between March 1978-March 1979

	DRY WEIGHT	*N*	*P*	*K*	*Ca*	*Mg*	*Na*	*Mn*	*Zn*
ABOVE-GROUND									
Biomass (capital)	247.3	3.62	0.62	3.20	1.21	0.32	0.75	0.09	0.02
Production[a]	549.1	4.44	0.83	4.52	2.17	0.49	1.21	0.13	0.04
BELOW-GROUND[b]									
Biomass (capital)	710.7[c]	8.18	0.78	0.21	5.46	0.62	0.16	0.30	0.11
Production	443.7	3.39	0.51	0.34	3.35	0.46	0.12	0.29	0.08
TOTAL									
Biomass (capital)	958.0	11.80	1.40	3.41	6.67	0.94	0.91	0.39	0.13
Production[d]	992.8	7.83	1.34	4.86	5.52	0.95	1.33	0.42	0.12
P/B ratio	*1.04*	*0.66*	*0.96*	*1.43*	*0.83*	*1.01*	*1.46*	*1.08*	*0.92*
Annual litter production-LG[e]	441.0	7.72	1.04	2.40	2.52	0.37	0.80	0.42	0.05
Removal of cuttings-SG[f]	200	4.61	0.62	3.13	1.70	0.38	0.57	0.14	0.01
Nett annual gains or losses in vegetation[g]	+80.5%	+20.0%	+11.4%	+9.7%	-25.0%	+6.2%	+56.1%	+37.7%	+13.0%

TABLE 33 : Dry weight and nutrients in biomass (capital) and production at the Botanic Garden site in $g.m.^{-2}$. Litter production and removal of cuttings are also shown, together with annual gains or losses from vegetation. Values refer to LG, except where indicated, and represent mean annual values.

a. Estimated from incremental summation of positive increases. Accurate estimates including measurements of turnover may be 3x larger (p. 132).

b. Below-ground values are ash-free dry weight.

c Dry weights are mean values from table 31, and nutrients are calculated from incremental summation of positive increases of biomass. Breakdown studies indicate more accurate estimates may be 2-3.6x larger (p. 105).

d. Bradshaw (1980) equates these values to total annual requirements (p. 139).

e. see p. 140.

f. see p. 79.

g. see p. 68.

Less than 5% of the total capital of most nutrients are contained within the vegetation, and usually 1% or less are removed per annum by mowing.

8.7 Decomposition

Organic matter decomposition andthe release of nutrients by mineralization are important parameters of ecosystem function and, in the absence of fertilizer, are controlling determinants of primary production.

Surface litter accumulation and breakdown have been considered in detail, and conclusions are discussed in *Section 6.4*. Breakdown rates of large accumulations of litter following cessation of mowing are rapid, particularly in spring and autumn. The combined influence of prevailing moisture conditions, especially repeated wetting and drying, and faunal activity determine breakdown rates. *In situ* incubation of below-ground fractions showed breakdown rates may exceed those of surface litter, and infer that annual turnover rates are in excess of 100%. Decomposition of below-ground fractions is discussed in *Section 7.6*. Similar incubation techniques were used by Hackney and de la Cruz (1980) to measure decomposition of roots and rhizomes of tidal marsh plants. Otherwise quantitative root decomposition studies have involved the use of ground roots (Herman *et al.*, 1977) or roots previously separated from soil and then buried. Using the latter method Stenina (1964) and Malone and Reichle (1973) recorded breakdown rates of 0.07-0.12% per day. These rates are much lower than those recorded in the present study (*cf.* TABLE 20) and are not really comparable.

The present study has shown that a major proportion of organic matter input into grassland soils is derived from the death of below-ground components (*also see* Schlesinger, 1977; Singh and Gupta, 1977;

Coleman *et al.*, 1980), although the precise contribution made by roots to soil organic matter is largely unknown. Clark *et al.* (1980) considered that the major portion of detrital root nitrogen becomes mineral *N*, and does not go to humus *N*. The accumulation of organic matter in grassland soils has been described (Dahlman, 1968; Floate, 1970*d*; Swift *et al.*, 1979) and Huntjens and Albers (1978) found that the continuous addition of a substrate together with *N* deficiency are probably largely responsible for this accumulation. The substrate is mainly derived from below-ground components.

8.8 Synopsis

The research project has provided background information concerning the structure and function of a semi-permanent grassland ecosystem, according to management regime, although an individual effort on this scale could not practicably embrace all areas of important ecological significance. Certain investigations were initiated but time limitations prevented their continuation. These were mostly concerned with ecosystem inputs and outputs and flow rates between compartments, particularly of soil respiration measurements (although techniques are described in the literature) and nutrient leaching through the grassland canopy. Nevertheless, seasonal biomass dynamics and nutrient variations according to mowing intensity and cessation of mowing are described in detail, with particular emphasis on the dynamics of below-ground components.

The importance of heterotrophic processes to ecosystem structure and function has been stressed. The subsidiary experiments, although often tentative, were instigated in an attempt to examine parameters considered most pertinent to ecosystem dynamics. Breakdown of large surface accumulations of litter is examined in detail and an insight is provided

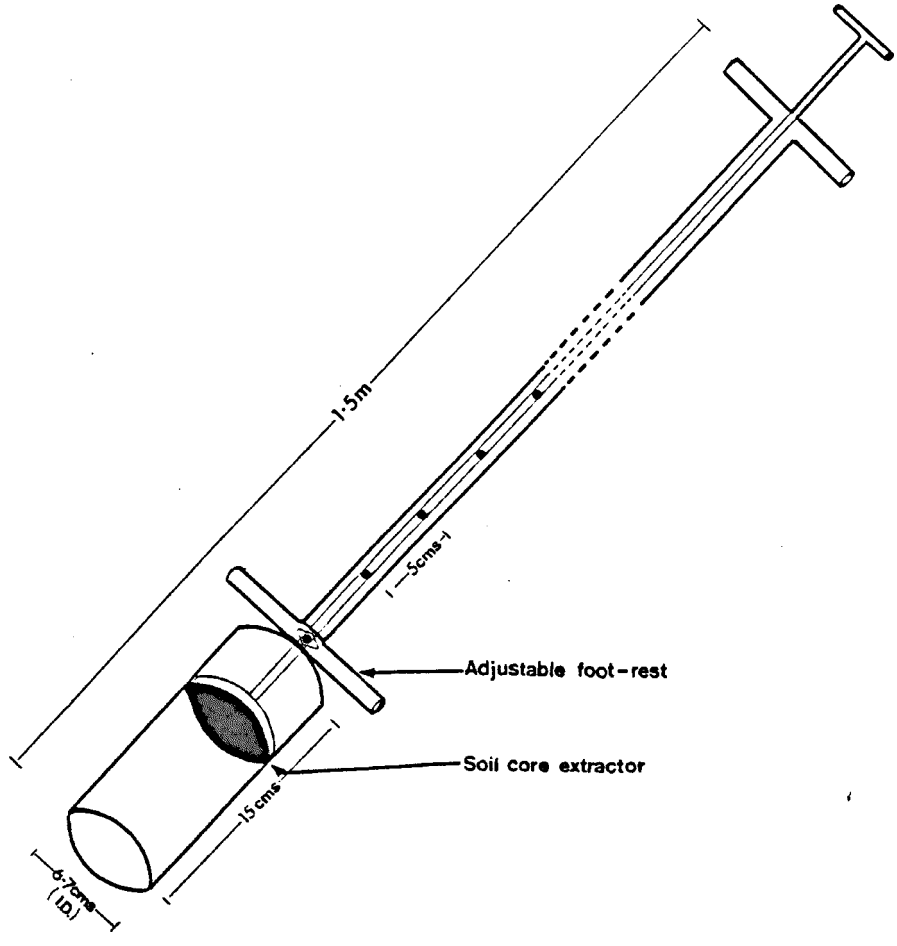
into the breakdown of below-ground components, the importance of fine roots, and the occurrence of detrital roots in soil.

Many aspects of ecological processes in grassland remain largely unknown. For example, Darwin (1881) realized the importance of earthworms in grasslands, but there have been few studies on their associations with plant root systems. The aims of further research should be towards obtaining a unified viewpoint of grassland dynamics, a detailed elucidation of differences between management regimes, and the development of simulation models.

APPENDIX 1 : Physical and Chemical Properties of Soils. Total soil nutrients are percentage of oven-dry weight (see *5.1*). Methods follow those given by Allen *et al.* (1974).

	LG	MG	SG	PAD
pH	5.1	5.0	5.2	5.2
Bulk density	0.823	0.830	0.927	0.965
% sand	73.5	70.5	71.0	73.8
% silt	11.6	10.4	12.1	10.3
% clay	14.9	19.1	16.9	16.1
ISSS Classification	sandy loam	sandy loam	sandy loam	sandy loam
% loss on ignition	7.58	8.00	8.04	6.45
total *C* (%)	3.48	3.87	3.91	3.00
total *N* (%)	0.50	0.65	0.78	0.38
total *H* (%)	0.60	0.65	0.62	0.52
total *P* (%)	0.062	0.039	0.062	0.058
totak *K* (%)	0.329	0.292	0.323	0.271
total *Ca* (%)	0.046	0.054	0.053	0.037
total *Mg* (%)	0.266	0.225	0.254	0.212
total *Na* (%)	0.011	0.012	0.014	0.015
total *Mn* (%)	0.103	0.106	0.135	0.109
total *Zn* (%)	0.008	0.006	0.008	0.006

APPENDIX 2 : STEEL SOIL CORER.



APPENDIX 3

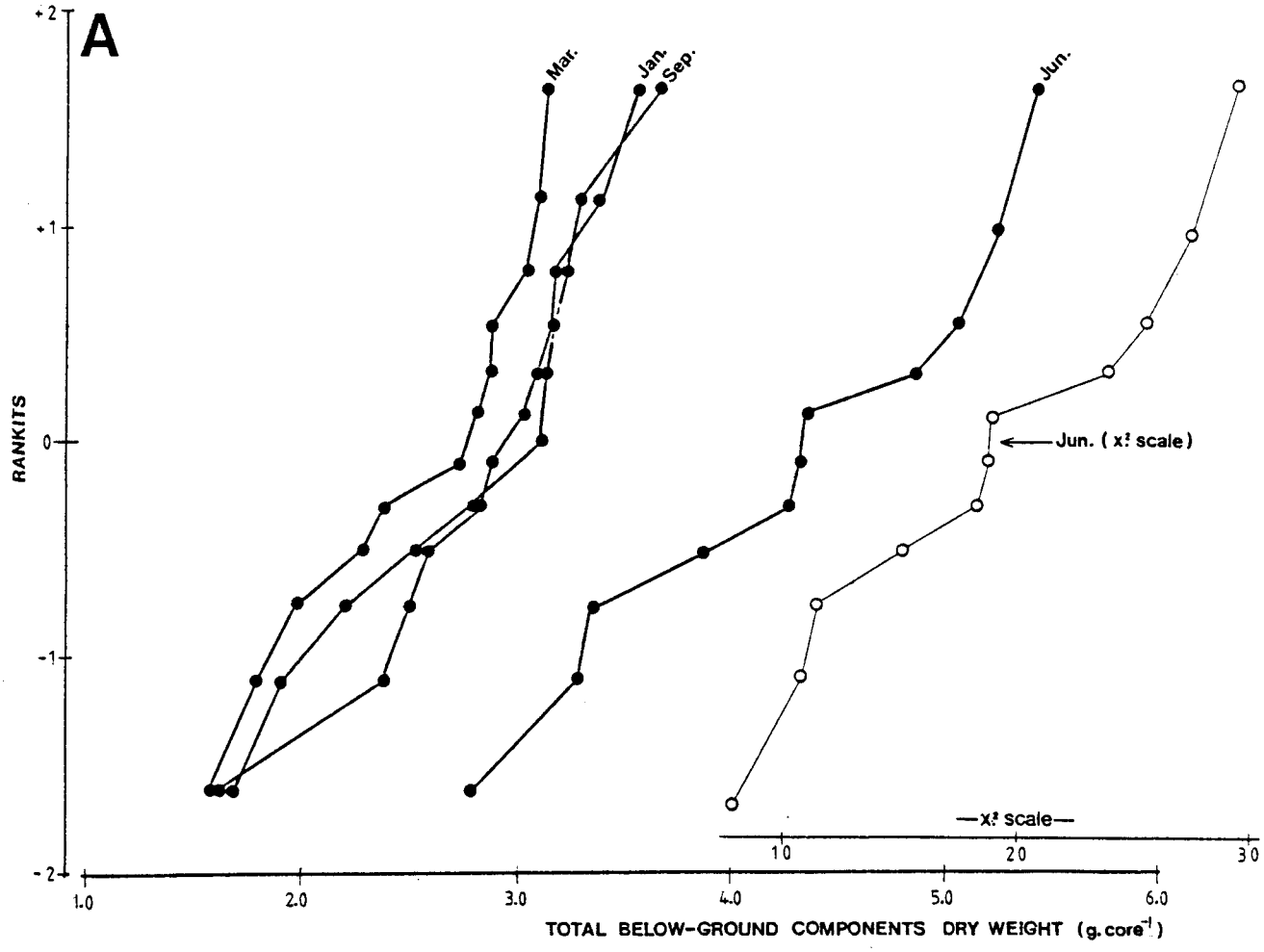
Frequency Distribution and Spatial Distribution of Below-Ground Components

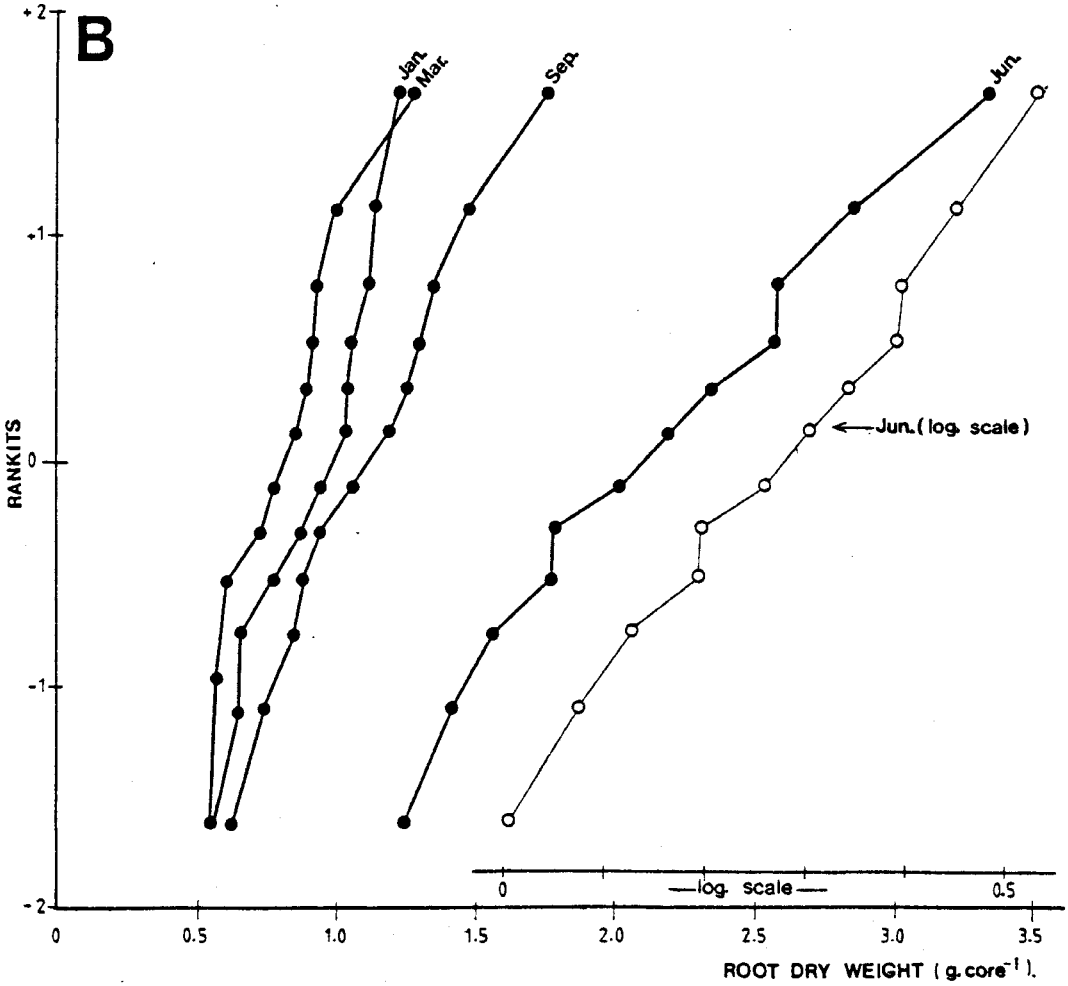
Few published data are available concerning the frequency distribution of below-ground components, and their horizontal spatial dispersion.

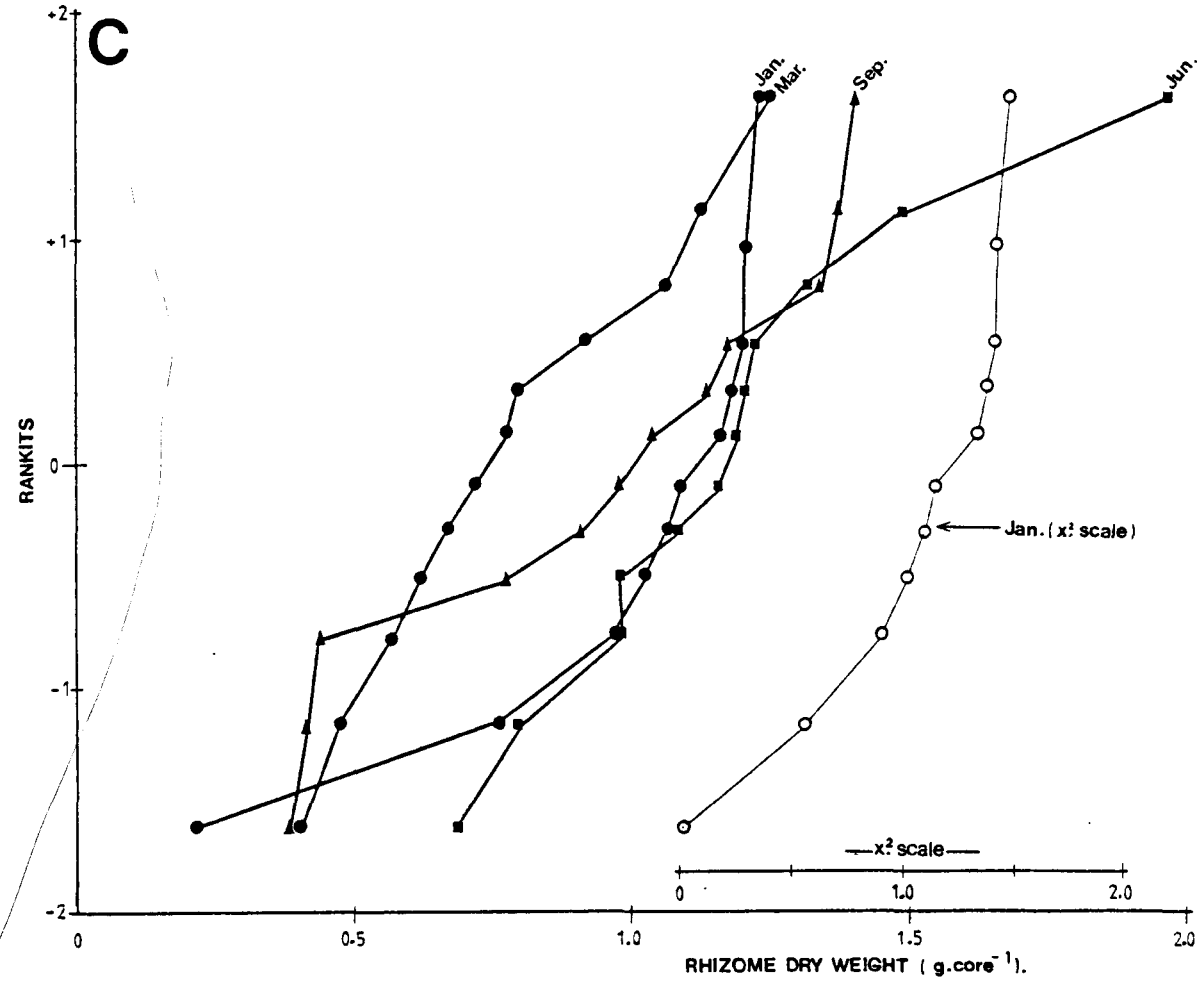
Frequency distributions are examined using *rankit* tests of normality. To pool data indiscriminately into a single distribution could give misleading results, and Bliss (1967) considered that rankit diagrams are the simplest and most sensitive tests of normality. Observations of each sample are arranged in order of increasing size and paired with the corresponding rankit (average deviate for each rank order) drawn from a population known to be normal. Rankit diagrams are shown in FIGS. A-D for below-ground data from SG in four months. A similar linear trend at different months gives a reasonable assurance of normality, but successive points are not independent of each other and tend to weave about the line (*see* Bliss, 1967). In most instances a straight line could reasonably be fitted to the data, although possible transformations are indicated on the graphs.

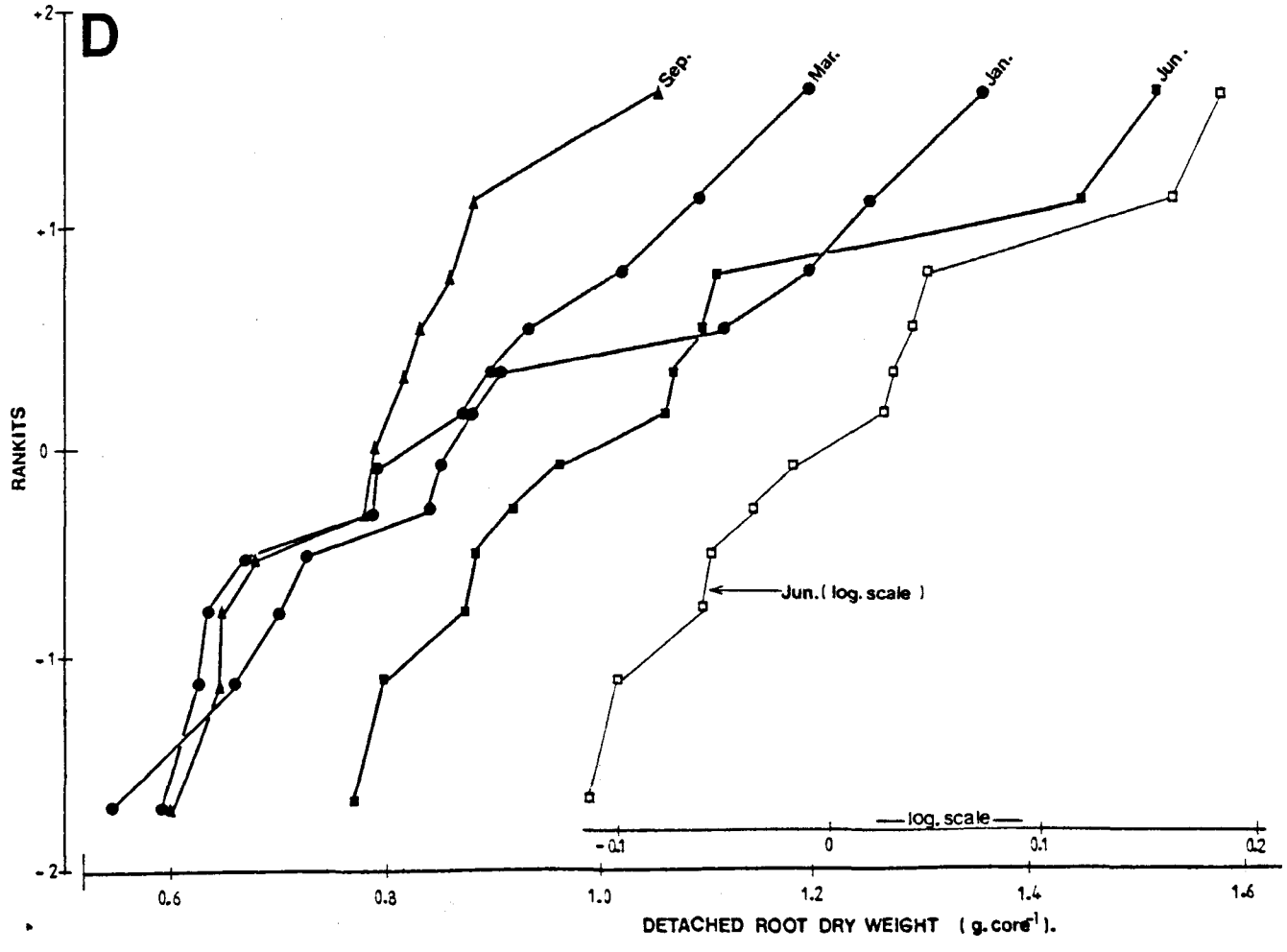
The mean corresponds to rankit 0 and standard deviation corresponds to one rankit unit. It is a property of the normal distribution curve that 95% of observations should fall within 1.96 standard deviations of its mean (*see* Bishop, 1975), which provide a further indication of normality from the graphs. Thus the proposed metameter of normality is not discredited, and statistics which assume a normal distribution are applied to below-ground dry weight data.

It is worthwhile to briefly consider horizonal spatial distribution. Westlake (1968) found that a large number of random samples were needed to overcome the contagious distribution of underground material of reedswamp plants with extensive rhizomes. Although data of the present study are insufficient to examine spatial dispersion, rankit diagrams of rhizomes in January are markedly curvilinear, indicating a frequency distribution skewed to the left. Rhizomes are produced in varying amounts by different species of grasses (Hubbard, 1968), and a more detailed study may indicate some clumping at certain times of the year.


A
+2
+1
0
-1
-2
RANKITS
Mar.
Jan.
Sep.
Jun.
Jun. (x² scale)
—x² scale—
10
20
30
1.0
2.0
3.0
4.0
5.0
6.0
TOTAL BELOW-GROUND COMPONENTS DRY WEIGHT (g.core⁻¹)


B
+2
+1
0
-1
-2
RANKITS
Jan.
Mar.
Sep.
Jun.
Jun.(log. scale)
0
—log. scale—
0.5
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
ROOT DRY WEIGHT (g.core⁻¹).


C
+2
+1
0
-1
-2
RANKITS
Jan.
Mar.
Sep.
Jun.
Jan. (x² scale)
x² scale
0
1.0
2.0
0
0.5
1.0
1.5
2.0
RHIZOME DRY WEIGHT (g.core⁻¹).


D
+2
+1
0
-1
-2
RANKITS
Sep.
Mar.
Jan.
Jun.
Jun. (log. scale)
log. scale
-0.1
0
0.1
0.2
0.6
0.8
1.0
1.2
1.4
1.6
DETACHED ROOT DRY WEIGHT (g.core⁻¹).

APPENDIX 4 : Description of Cluster Analysis and Multiple Regression techniques implemented in Chapters 3 and 4.

A) CLUSTER ANALYSIS

The aims of cluster analysis are to separate data into constituent groups using a number of largely empirical procedures. Objectives and techniques are discussed by Everitt (1974).

*CLUSTAN 1B**, run at UMRCC, was used with options selected for Squared Euclidean Distance Similarity Coefficients, Hierarchic Fusion (Ward's Method) and Centroid Sorting.

Number of clusters was selected by eye on a best of fit basis.

B) MULTIPLE REGRESSION ANALYSIS

A multiple linear regression analysis program in the SPSS** package (version 7) was selected using forward stepwise inclusion with default parameters. Selection criteria are based on the *F* ratio.

All data were transformed to arcsin before computation.

* *'Clustan 1B'*. First Edition (1979)
University of Manchester Regional Computer Centre.

** *'Introduction to SPSS'* (1978) 3rd Edition. NWD2.

APPENDIX 5 : Multiple Regression Equations (LG), with component dry weights as independent variables to describe nutrient concentrations. Levels of significance are indicated (see TABLE 6).

			LEVEL OF SIGNIFICANCE
N%g	=	1.607 - 0.0018G	5%
N%l	=	2.217 - 0.0014G - 0.0012L - 0.0028 RTS	5%
N%rts	=	0.766 + 0.00012G - 0.00113RTS + 0.0008RZM	5%
N%rzm	=	0.803 - 0.00105RZM	5%
N%dr	=	1.151 - 0.00097RZM	0.1%
P%L	=	0.253 - 0.00012G - 0.00009L - 0.00035DR - 0.00006RTS	1%
P%rzm	=	0.067 - 0.000059G	5%
K%g	=	1.917 - 0.0033RZM - 0.0008L - 0.0005G	5%
K%l	=	0.101 + 0.0021RTS - 0.0013RZM	5%
K%rts	=	0.0728 - 0.00023RTS	1%
K%rzm	=	0.101 - 0.00027RTS - 0.00003L	1%
K%dr	=	0.045 + 0.00006L - 0.00023DR	1%
Ca%g	=	0.135 + 0.00063G	5%
Ca%l	=	-0.260 + 0.0019RZM + 0.0007G	5%
Ca%rts	=	0.304 + 0.008RZM	5%
Ca%rzm	=	0.582 - 0.00015L - 0.00111DR	0.1%
Ca%dr	=	0.267 + 0.0007RTS + 0.00018L - 0.0002G + 0.0005RZM	5%
Mg%g	=	0.0618 + 0.000087G	5%
Mg%l	=	0.0798 + 0.00002G - 0.00003L - 0.00009RTS - 0.00002RZM	1%
Mg%rts	=	0.0729 - 0.0001RZM	0.1%
Mg%dr	=	0.035 + 0.00008L - 0.00004G - 0.00009RTS	0.1%
Na%g	=	0.0416 + 0.00052G	0.1%
Na%l	=	0.089 + 0.00066RZM - 0.00109DR - 0.00007L	1%
Na%rts	=	0.019 - 0.000018RTS	5%
Na%rzm	=	0.065 - 0.00011RTS - 0.00002L - 0.00009DR + 0.000007G	5%
Na%dr	=	0.037 - 0.00012DR	1%
Mn%g	=	0.0124 + 0.0001RTS - 0.00005RZM	10%
Mn%rts	=	0.0419 - 0.00008RTS	10%
Mn%dr	=	0.0328 - 0.0002RTS + 0.00033DR	5%
Zn%g	=	0.0323 - 0.000095RTS	1%
Zn%l	=	0.0132 - 0.000006L - 0.000013RZM	5%
Zn%rts	=	0.0055 + 0.000011G	10%

APPENDIX 6 : Multiple Regression Equations (PAD), with component dry weights as independent variables to describe nutrient concentrations. Levels of significance are indicated (see TABLE 7).

			LEVELS OF SIGNIFICANCE
N%g	=	2.009 - 0.00289 - 0.0015RZM	1%
N%rts	=	0.788 - 0.00065RZM	5%
N%rzm	=	0.636 - 0.00061RZM	1%
N%dr	=	1.104 - 0.0014RTS	5%
P%g	=	0.161 - 0.00089RZM + 0.00066L + 0.00015G	0.1%
P%l	=	0.152 - 0.00024RZM	0.1%
K%rzm	=	0.0418 - 0.000047L	1%
K%dr	=	0.131 - 0.00025RTS	10%
Ca%l	=	0.421 + 0.00093G - 0.0014DR	1%
Ca%rts	=	0.539 - 0.00041RZM	5%
Ca%dr	=	0.630 - 0.00088RZM	1%
Mg%l	=	0.078 + 0.00014G - 0.00015RTS	5%
Mg%rts	=	0.083 - 0.000075RZM	10%
Mg%dr	=	0.159 - 0.00024RTS	5%
Na%l	=	0.028 - 0.00047RZM + 0.00026G + 0.0004L - 0.0003DR	1%
Na%rts	=	0.018 - 0.000026RTS	5%
Na%rzm	=	0.006 + 0.000015L	5%
Na%dr	=	0.023 - 0.000048RTS	1%
Mn%l	=	0.0509 - 0.000073L + 0.00006RTS	5%
Mn%rts	=	0.036 - 0.000051RZM	10%
Mn%rzm	=	0.0102 + 0.000018RTS	1%
Mn%dr	=	0.134 - 0.00023L - 0.00015DR - 0.000085G + 0.00007RZM	5%
Zn%g	=	0.0071 - 0.000014G	10%
Zn%l	=	0.267 - 0.000032L - 0.000047DR	5%
Zn%rts	=	0.0036 + 0.000033G - 0.000038RTS + 0.00003L	5%
Zn%rzm	=	0.0035 + 0.000021RZM	5%
Zn%dr	=	0.0137 - 0.000025RTS	10%

APPENDIX 7 : Additional Regression Equations for LG (above) and PAD (below) with nutrient concentrations included with their component dry weights in the list of independent variables (see TABLE 8).

LG

		LEVEL OF SIGNIFICANCE
P%g	= 0.278 - 1.23*P*%rts - 0.000086G	1%
P%l	= 0.057 + 0.073*N*%l	1%
P%rts	= -0.015 + 0.995*P*%dr	0.1%
P%rts	= 0.114 + 0.042*N*%l - 0.451*P*%g	5%
P%dr	= -0.122 + 0.245*N*%dr - 0.898*K*%dr	5%
Ca%dr	= 0.189 + 0.00092RTS + 2.214*Mg*%dr	5%
Mg%rzm	= 0.025 + 0.912*Mn*%rzm	5%
Na%rzm	= 0.022 + 0.266*K*%rzm + 0.786*Mg*%rzm	1%
Mn%l	= 0.031 + 2.985*Mg*%l - 0.574*Na*%l - 14.866*Zn*%l	5%
Mn%rts	= 0.100 + 0.00027RTS + 0.799*K*%rts	5%
Mn%rzm	= 0.018 + 0.829*Mg*%rzm	5%

PAD

N%l	= 0.270 + 5.354*P*%l	5%
P%rts	= 0.0042 + 0.832*P*%dr	5%
P%rts	= -0.0047 + 11.150*Zn*%rts - 0.00013G	5%
P%rzm	= 0.0027 + 0.706*P*%rts	5%
P%rzm	= 0.239 - 0.00028RTS - 0.240*N*%rzm	5%
P%dr	= -0.0905 + 0.337*N*%rts - 0.00042DR	5%
K%g	= 0.425 + 0.0018L + 6.365*P*%rts	5%
K%l	= -0.728 + 14.322*Mg*%l + 0.0012L	1%
K%rts	= -0.051 + 1.282*Mg*%rts	0.1%
K%rts	= -0.029 + 0.079*N*%l	5%
K%dr	= -0.041 + 2.558*Mn*%dr	1%
Ca%g	= -0.439 + 9.683*Mg*%g	1%
Ca%g	= -0.133 + 3.209*Na*%g + 0.00083RZM	1%
Ca%rzm	= 0.367 - 1.808*P*%rzm	1%
Mg%g	= 0.050 + 0.087*Ca*%g	1%
Mg%g	= 0.099 + 0.269*Na*%g - 0.00026DR	5%
Mg%rts	= 0.041 + 0.747*K*%rts	0.1%
Mg%rzm	= 0.053 - 0.217*P*%rzm	5%
Na%g	= 0.043 + 0.305*Ca*%g - 0.00026RZM	1%
Na%l	= 0.0018 + 0.134*K*%l - 0.091*Ca*%l	1%
Mn%g	= 0.044 - 0.084*K*%g + 0.00022L + 0.11*Na*%g + 0.0001DR	5%
Mn%rts	= -0.012 + 0.568*Mg*%rts	5%
Zn%rts	= 0.0013 + 0.097*P*%rts	5%

APPENDIX 8 : One-way analysis of variance tests of difference between treatment means of SG, MG, LG and PAD (nutrient concentrations), corresponding to FIGS. 16-20. Values shown are probability (p) of computed F values exceeding tabulated values.

	GRASSES (Fig.16)	LITTER (Fig.17)	ROOTS (Fig.18)	RHIZOMES (Fig.19)	DETACHED ROOTS (Fig.20)
N%	0.493	0.534	0.615	0.926	*0.064*
P%	0.669	*0.011*	0.475	0.361	0.128
K%	*0.005*	0.113	*0.039*	0.386	*0.003*
Ca%	0.644	0.967	*0.008*	*0.011*	*0.015*
Mg%	*0.002*	*0.003*	*0.039*	*0.072*	0.310
Na%	*0.011*	*0.038*	0.364	0.521	0.768
Mn%	0.164	0.445	0.296	0.404	0.920
Zn%	0.852	0.142	0.606	0.341	0.312

APPENDIX 9 : Spearman correlation coefficients (r) and significan
corresponding to FIGS. 16-20 (spaces indicate $p > 0.$

NUTRIENT CONCNS.	GRASSES (Fig.16)				LITTER (Fig.17)					
	LG v. MG	LG v. SG	MG v. SG	LG v. PAD	LG v. MG	LG v. SG	MG v. SG	LG v. PAD	LG v. MG	
N%			r 1.000 p .001	r .900 p .038	r 1.000 p .001	r 1.000 p .001	r 1.000 p .001		r 1.000 p .001	
P%		r 1.000 p .001		r .821 p .089		*	*			
K%	r -1.000 p .001			r -.900 p .038		*	*			
Ca%	r 1.000 p .001					*	*	r .943 p .005		
Mg%		r 1.000 p .001			r 1.000 p .001	*	*			
Na%	r 1.000 p .001					*	*			
Mn%	r 1.000 p .001			r .900 p .038		*	*			
Zn%			r 1.000 p .001		r 1.000 p .001	*	*			

e levels (p) for pairs of treatments (nutrient concentrations),
; asterisks indicate $n = 2$ and value of r is invalid).

ROOTS (Fig.18)			RHIZOMES (Fig.19)				DETACHED ROOTS (Fig.20)			
LG v. SG	MG v. SG	LG v. PAD	LG v. MG	LG v. SG	MG v. SG	LG v. PAD	LG v. MG	LG v. SG	MG v. SG	LG v. PAD
r -.943 p .005	r 1.000 p .001				r 1.000 p .001	r .771 p .073			r 1.000 p .001	
	r .949 p .052	r -.771 p .073			r 1.000 p .001					
					r-1.000 p .001					
r .943 p .005				r .900 p .038	r 1.000 p .001		r 1.000 p .001	r .886 p .019		
	r 1.000 p .001		r .949 p .052							
r .820 p .046		r .826 p .043				r -.746 p .089	r 1.000 p .001			r .750 p .086
r .783 p .066			r .949 p .052			r .985 p .001				
	r .949 p .052				r 1.000 p .001		r 1.000 p .001			

APPENDIX 10 : Above- and below-ground nutrient concentrations (%) in forb fractions, compared to above-ground grasses and total below-ground components (excluding herb roots). Data from PAD.

ABOVE-GROUND

		1/6/78	21/9/78	21/3/79	19/6/79
N	Forbs	3.895	2.294	4.782	1.056
	grasses	*2.337*	*2.074*	*3.148*	*1.445*
P	Forbs	0.370	0.289	0.526	0.129
	grasses	*0.276*	*0.400*	*0.427*	*0.184*
K	Forbs	3.365	2.543	2.889	1.178
	grasses	*2.692*	*2.216*	*2.223*	*1.997*
Ca	Forbs	0.856	1.859	0.276	0.44
	grasses	*0.544*	*0.959*	*0.178*	*0.183*
Mg	Forbs	0.298	0.238	0.262	0.127
	grasses	*0.145*	*0.172*	*0.108*	*0.103*
Na	Forbs	0.492	0.509	0.192	0.108
	grasses	*0.102*	*0.297*	*0.095*	*0.153*
Mn	Forbs	0.035	0.031	0.029	0.011
	grasses	*0.037*	*0.053*	*0.030*	*0.020*
Zn	Forbs	0.011	0.008	0.010	0.004
	grasses	*0.009*	*0.008*	*0.014*	*0.004*

BELOW-GROUND

		21/9/78	9/1/79	21/3/79	19/6/79
N	Forbs	0.940	1.490	1.850	1.100
	others	*1.333*	*1.380*	*1.524*	*1.502*
P	Forbs	0.102	0.115	0.192	0.082
	others	*0.107*	*0.108*	*0.136*	*0.100*
K	Forbs	0.195	0.075	0.157	0.078
	others	*0.032*	*0.047*	*0.090*	*0.049*
Ca	Forbs	0.936	0.844	0.911	1.030
	others	*0.898*	*0.936*	*0.988*	*0.918*
Mg	Forbs	0.111	0.108	0.123	0.128
	others	*0.114*	*0.109*	*0.150*	*0.118*
Na	Forbs	0.023	0.021	0.027	0.028
	others	*0.021*	*0.021*	*0.025*	*0.022*
Mn	Forbs	0.016	0.024	0.023	0.032
	others	*0.040*	*0.038*	*0.056*	*0.052*
Zn	Forbs	0.005	0.012	0.010	0.010
	others	*0.017*	*0.013*	*0.014*	*0.013*

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REFERENCES

Allen, S., Grimshaw, M., Partinson, J. and Quarmby, C. (Eds.) (1974). *Chemical Analysis of Ecological Materials.* Blackwell Scientific Publications.

Anderson, J.M. (1973). The breakdown and decomposition of Sweet Chestnut (*Castanea sativa* Mill.) and Beech (*Fagus sylvatica* L.) leaf litter in two decisuous woodlands. 1. Breakdown, leaching and decomposition. *Oecologia (Berl.)* 12 (3), 251-74.

Ares, J. (1976). Dynamics of the root system of Blue Grama (*Bouteloua gracilis* (H.B.K.) Lag.). *J. Range Manage* 29 (3), 208-13.

Ares, J. and Singh, J. S. (1974). A model of the root biomass dynamics of a shortgrass prairie dominated by Blue Grama (*Bouteloua gracilis*). *J. appl. Ecol.* 11 (2), 727-43.

Barber, D. A. and Martin, J. K. (1975). Release of organic substances by cereal roots into soil. In: *Letcombe Laboratory Annual Report, 1974.* Agricultural Research Council.

Barber, D. A. and Martin, J. K. (1976). The release of organic substances by cereal roots into soil. *New Phytol.* 76, 69-80.

Barnard, E. L. and Jorgensen, J. R. (1977). Respiration of field-grown Loblolly Pine roots as influenced by temperature and root type. *Can. J. Bot.* 55, 740-43.

Bartos, J. L. (1971). Root dynamics of a shortgrass ecosystem. *Ph.D. Dissertation,* Colorado State University, Fort Collins, 129 pp.

Bazilevich, N. I. and Titlyanova, A. A. (1980). Comparative studies of ecosystem function. In: Breymeyer, A. I. and Van Dyne, G. M. (*op. cit.*) pp. 713-58.

Bleak, A. T. (1970). Disappearance of plant material under a winter snow cover. *Ecology* 51, 915-17.

Bishop, O. N. (1975). *Statistics for Biology.* Second Edition. Longman.

Bliss, C. I. (1967). *Statistics in Biology.* McGraw-Hill.

Böhm, W. (1979). *Methods of Studying Root Systems.* Springer-Verlag, Berlin.

Bokhari, U. G. (1977). Regrowth of western wheatgrass utilizing ^{14}C-labelled assimilates stored in below-ground parts. *Plant and Soil* 48 (1), 115-27.

Bokhari, U. G. and Singh, J. S. (1975). Standing State and cycling of *N* in soil-vegetation components of prairie ecosystems. *Ann. Bot.* 39 (160), 273-85.

*

Bradshaw, A. D. (1980). Mineral Nutrition. In: Rorison, I. H. and Hunt, R. (*op. cit.*) pp. 101-18.

* see addendum

Breymeyer, A. I. and Van Dyne, G. M. (Eds.) (1980). *Grasslands, Systems Analysis and Man.* Cambridge University Press.

Butler, G. W. and Bailey, R. W. (Eds.) (1973). *Chemistry and Biochemistry of Herbage.* Vol. 2. Academic Press.

Cahoon, G. A. and Morton, E. S. (1961). An apparatus for the quantitative separation of plant roots from soil. *Proc. Am. Soc. hort. Sci.* 78, 593-96.

Caldwell, M. M. (1975). Primary production of grazing lands. In: *Photosynthesis and Productivity in Different Environments.* Ed.: J. P. Cooper. IBP 3. Cambridge University Press, pp. 41-73.

Canode, C. L., Hiebert, A. J., Russell, T. S. and Law, A. G. (1977). Sampling technique for estimation of root production of Kentucky Bluegrass. *Crop Sci.*, 17 (1), 28-30.

Carlson, C. W. (1965). Problems and techniques in studying plant root systems. *Proc. 9th. Int. Grassl. Congr.* Sao Paulo, Vol. 2, pp. 1491-93.

Carson, E. W. (Ed.) (1974). *The Plant Root and its Environment.* Univ. Press of Virginia, Charlottesville, Va. 691 pp.

Chapman, S. B. (Ed.) (1976). *Methods in Plant Ecology.* Blackwell Scientific Publications.

Clark, F. E., Cole, C. V. and Bowman, R. A. (1980). Nutrient Cycling. In: Breymer, A. I. and Van Dyne, G. M. (*op. cit.*) pp. 659-712.

Clement, C. R., Jones, L. H. P. and Hopper, M. J. (1972). The leaching of some elements from herbage plants by simulated rain. *J. appl. Ecol.* 9 (1), 249-60.

Coleman, D. C. (1976). A review of root production processes and their influence on soil biota in terrestrial ecosystems. In: *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes.* Eds.: J. M. Anderson and A. Macfadyen. pp. 417-34. Blackwell Scientific Publications.

Coleman, D. C., Andrews, R., Ellis, J. E. and Singh, J. S. (1976). Energy flow and partitioning in selected man-managed and natural ecosystems. *Agro-Ecosystems* 3, 45-54.

Coleman, D. C., Sasson, A., Breymeyer, A. I., Dash, M. C., Dommergues, Y., Hunt, H. W., Paul, E. A., Scheafer, R., Ulehlova, B. and Zlotin, R. I. (1980). Decomposer subsystem. In: Breymeyer, A. I. and Van Dyne, G. M. (*op. cit.*) pp. 609-55.

Coppock, J. T. (1976). *An Agricultural Atlas of England and Wales.* Faber and Faber, London.

Coupland, R. T. (Ed.) (1979). *Grassland Ecosystems of the World: Analysis of Grasslands and their Uses.* IBP. 18. Cambridge University Press.

Coupland, R. T. and Johnson, R. E. (1965). Rooting characteristics of native grassland species in Saskatchewan. *J. Ecol.* 53, 475-507.

Cox, T. L., Harris, W. F., Ausmus, B. S. and Edwards, N. T. (1978). The role of roots in biogeochemical cycles in an eastern deciduous forest. *Pedobiologia* , 18, 264-71.

Crider, F. J. (1955). Root-growth stoppage resulting from defoliation of grasses. *U.S.D.A. Tech. Bull.* No. 1102. 23pp.

Curry, J. P. (1969). The decomposition of organic matter in soil. Part 1. The role of the fauna in decaying grassland herbage. *Soil Biol. Biochem.* 1, 253-58.

Dahlman, R. C. (1968). Root production and turnover of carbon in the root-soil matrix of a grassland ecosystem. In: M. S. Ghilarov *et al.* (Eds.) (*op. cit.*) pp. 11-21.

Dahlman, R. C. and Kucera, C. L. (1965). Root productivity and turnover in native prairie. *Ecology* 46, 84-89.

Darwin, C. (1881). *The formation of Vegetable Mould through the Action of Worms with Observations on their Habits.* John Murray. Reprinted as *Darwin on Humus and the Earthworm* (1945) Faber and Faber, London.

Delwiche, C. C. (1970). The Nitrogen Cycle. *Sci. Am* . 223 (3) 136-46.

Detling, J. K., Dyer, M. I. and Winn, D. T. (1979). Net photosynthesis, root respiration, and regrowth of *Bouteloua gracilis* following simulated grazing. *Oecologia (Berl.)* 41 (2), 127-34.

Dexter, A. R. (1978). Tunnelling in soil by earthworms. *Soil Biol. Biochem.* 10 (5), 447-49.

Dickinson, C. H. and Pugh, G. J. F. (Eds.) (1974). *Biology of Plant Litter Decomposition.* 2 Vols. Academic Press.

Drew, M. C. and Saker, L. R. (1975). Further studies on the modification of root growth and ion uptake brought about by enrichment of phosphate over narrow zones of the root system. *Letcombe Laboratory Annual Report, 1975.* pp. 15-16. Agricultural Research Council.

Duffey, E. and Watt, A. S. (1971). *The Scientific Management of Animal and Plant Communities for Conservation.* Blackwell Scientific Publications.

Duffey, E., Morris, M. G., Sheal, J., Ward, L. K., Wells, D. A. and Wells, T. C. E. (1974). *Grassland Ecology and Wildlife Management.* Chapman and Hall, London.

Duncan, W. G. and Ohlrogge, A. J. (1958). Principles of nutrient uptake from fertilizer bands. II. Root development in the band. *Agron. J.* 50, 605-08.

Edwards, C. A. and Heath, G. W. (1963). The role of soil animals in breakdown of leaf material. In: *Soil Organisms.* J. Doeksen and J. Van der Drift. North-Holland Publishing Company, Amsterdam.

Edwards, C. A. and Lofty, J. R. (1977). *Biology of Earthworms.* Chapman and Hall, London.

Edwards, C. A. and Lofty, J. R. (1978). The influence of arthropods and earthworms upon root growth of direct drilled cereals. *J. appl. Ecol.* 15, 789-95.

Everitt, B. (1974). *Cluster Analysis.* Heinemann Educational Books.

Fitter, A. H. (1976). Effects of nutrient supply and competition from other species on root growth of *Lolium perenne* in soil. *Plant and Soil* 45 (1), 177-89.

Floate, M. J. S. (1970*a*). Decomposition of organic materials from hill soils and pastures. II: Comparative studies on the mineralization of carbon, nitrogen and phosphorus from plant materials and sheep faeces. *Soil Biol. Biochem.* 2 (3), 173-86.

Floate, M. J. S. (1970*b*). Decomposition of organic materials from hill soils and pastures. III: The effect of temperature on the mineralization of carbon, nitrogen and phosphorus from plant materials and sheep faeces. *Soil Biol. Biochem.* 2 (3), 187-96.

Floate, M. J. S. (1970*c*). Decomposition of organic materials from hill soils and pastures. IV: The effects of moisture content on the mineralization of carbon, nitrogen and phosphorus from plant materials and sheep faeces. *Soil Biol. Biochem.* 2 (4), 275-83.

Floate, M. J. S. (1970*d*). Plant nutrient cycling in hill land. In: *Hill Farming Research Organization Vth Report, 1967-70.* pp. 15-33.

Forbes, T. J., Dibb, C., Green, J. O. and Fenlon, K. A. (1977). *Permanent Grassland Studies 1. The Permanent Pasture Project. Objectives and Methods.* Joint GRI/ADAS Permanent Pasture Group. Grassland Research Institute.

Frissel, M. J. (Ed.) (1977). Cycling of mineral nutrients in agricultural ecosystems. *Agro-Ecosystems* 4 (1, 2).

Garwood, E. A. (1967). Seasonal variation in appearance and growth of grass roots. *J. Brit. Grassl. Soc.* 22, 121-30.

Gerard, B. M. (1964). *A Synopsis of the British Lumbricidae.* Synopses of the British Fauna No. 6. The Linnean Society of London.

Ghilarov, M. S., Kovda, V. A., Novichkova-Ivanova, L. N., Rodin, L. E. and Sveshnikova, V. M. (Eds.) (1968). *Methods of Productivity Studies in Root Systems and Rhizosphere Organisms.* Nauka, Leningrad.

Gilmanov, T. G. (1977). Plant submodel in the holistic model of a grassland ecosystem (with special attention to the below-ground part). *Ecol. Model* 3 (2), 149-63.

Green, B. H. (1980). Management of extensive amenity grasslands by mowing. In: I. H. Rorison and R. Hunt (*op. cit.*) pp. 155-62.

Grime, J. P. (1978). *Plant Strategies and Vegetation Processes.* John Wiley, London.

Grime, J. P. (1980). An ecological approach to management. In: I. H. Rorison and R. Hunt (*op. cit.*) pp. 13-56.

*

Harper, J. L. (1971). Grazing, fertilizers and pesticides in the management of grasslands. In: E. Duffey and A. S. Watt (*op. cit.*) pp. 15-31.

Harper, J. L. (1977). *Population Biology of Plants*. Academic Press.

Head, G. C. (1970). Methods for the study of production in root systems. In: *Methods of Study in Soil Ecology*. Ed.: J. Phillipson. IBP/Unesco, Paris.

Heal, O. W. and Perkins, D. F. (1978). *Production Ecology of British Moors and Montane Grasslands*. Springer-Verlag.

Herman, W. A., McGill, W. B. and Dormaar, J. F. (1977). Effects of initial chemical composition on decomposition of roots of three grass species. *Can. J. Soil Sci.* 57 (2), 205-15.

Hess, P. R. (1971). *A Textbook of Soil Chemical Analysis*. Murray.

H.F.R.O. (1979). *Science and Hill Farming. H.F.R.O., 1954-79*. Hill Farming Research Organization. 184 pp.

Holliday, R. and Wilman, D. (1965). The effect of fertilizer nitrogen on frequency of defoliation on yield of grassland herbage. *J. Brit. Grassl. Soc.* 20, 32-40.

Howard, P. J. A. and Howard, D. M. (1974). Microbial decomposition of free and shrub leaf litter. 1. Weight loss and chemical composition of decomposing litter. *Oikos* 25 (3), 341-52.

Hubbard, C. E. (1968). *Grasses*. Reprinted 1976. Penguin.

Hunt, H. W. (1977). A simulation model for decomposition in grasslands. *Ecology* 58, 469-84.

Hunt, H. W. (1978). Decomposition submodel. In: G. S. Innis (*op. cit.*) pp. 257-303.

Huntjens, J. L. M. and Albers, R. A. J. M. (1978). A model experiment to study the influence of living plants on the accumulation of soil organic matter in pastures. *Plant and Soil* 50 (2), 411-18.

Hutchinson, K. J. and King, K. L. (1980). Management impacts on structure and function of sown grasslands. In: A. I. Breymeyer and G. M. Van Dyne (*op. cit.*) pp. 823-52.

Innis, G. S. (Ed.) (1978). *Grassland Simulation Model*. Ecological Studies Vol. 26. Springer-Verlag

Innis, G. S., Noy-Meir, I., Godron, M. and Van Dyne, G. M. (1980). Total-system simulation models. In: A. I. Breymeyer and G. M. Van Dyne (*op. cit.*)

Jones, M. B. and Woodmansee, R. G. (1979). Biogeochemical Cycling in Annual Grassland Ecosystems. *Bot. Rev.* 45 (2), 111-44.

* see addendum

Kelly, J. M. (1975). Dynamics of root biomass in two eastern Tennessee old-field communities. *Am. Midland Natur.* 94 (1), 54-61.

Kelly, J. M., Van Dyne, G. M. and Harris, W. F. (1974). Comparison of three methods of assessing grassland productivity and biomass dynamics. *Am. Midland Natur.* 92 (2), 357-69.

Koelling, M. R. and Kucera, C. L. (1965). Dry matter losses and mineral leaching in bluestem standing crop and litter. *Ecology* 46, 529-32.

Kotanska, M. (1967). Biomass dynamics of underground plant organs in some grassland communities of the Ojcow National Park. *Bulletin De L'Academie Polonaise Des Sciences* 15 (10), 625-31.

Kummerow, K., Krause, D. and Jow, W. (1978). Seasonal changes of fine root density in southern Californian chaparral. *Oecologia* 37 (2), 201-12.

Langer, R. H. M. (1979). *How Grasses Grow.* 2nd Edition. Institute of Biology Studies in Biology No. 34. Edward Arnold.

Lomnicki, A., Bandola, E. and Janowska, K. (1968). Modification of the Evans-Wiegert method for the estimation of net primary production. *Ecology* 49 (1), 147-49.

Malone, C. R. (1970). Short term effects of chemical and mechanical cover management on decomposition processes in a grassland soil. *J. appl. Ecol.* 7 (3), 591-603.

Malone, C. R. and Reichle, D. E. (1973). Chemical manipulation of soil biota in a fescue meadow.. *Soil Biol. Biochem.* 5, 629-39.

Malone, C. R. and Swartout, M. B. (1969). Size, mass and caloric content of particulate organic matter in old-field and forest soils. *Ecology* 50, 395-99.

Milner, C. and Hughes, R. E. (1970). *Methods for the Measurement of Primary Production of Grassland.* IBP Handbook No. 6. Blackwell Scientific Publications.

Morris, M. G. (1971). The management of grasslands for the conservation of invertebrate animals. In: E. Duffey and A. S. Watt (*op. cit.*) pp. 527-52.

N.E.R.C. (1977). *Amenity Grasslands - The Needs for Research.* Natural Environment Research Council. Publications series C. No. 19. NERC, London.

N.I.A.B. (1979). *Recommended Varieties of Grasses 1978/9.* Farmers Leaflet No. 16. National Institute of Agricultural Botany, Cambridge.

Nilsson, J. (1970). Notes on the biomass and productivity of below-ground organs of a South-Swedish hay-meadow. *Bot. Notiser.* 123, 183-94.

Nyahoza, F., Marshall, C. and Sagar, G. R. (1973). The interrelationship between tillers and rhizomes of *Poa pratensis* L. - an autoradiographic study. *Weed Res.* 13, 304-7.

Odum, E. P. (1971). *Fundamentals of Ecology.* 3rd Edition. W. B. Saunders Company, Philadelphia.

Olson, J. S. (1964). Gross and net production of terrestrial vegetation. *J. Ecol.* 52, 99-118.

Parton, W. J., Singh, J. S. and Coleman, D. C. (1978). A model of production and turnover of roots in shortgrass prairie. *J. appl. Ecol.* 15 (2), 515-41.

Pearson, L. C. (1965). Primary production in grazed and ungrazed desert communities of eastern Idaho. *Ecology* 46, 278-85.

Perkins, D. F. (1978). Snowdonia grassland : introduction, vegetation and climate. In: O. W. Heal and D. F. Perkins (*op. cit.*) pp. 289-96.

Perkins, D. F., Jones, V., Millar, R. O. and Neep, P. (1978). Primary production, mineral nutrients and litter decomposition in the grassland ecosystem. In: O. W. Heal and D. F. Perkins (*op. cit.*) pp. 304-31.

Phillipson, J. and Bolton, P. J. (1977). Growth and cocoon production by *Allolobophora rosea* (Oligochaeta: Lumbricidae). *Pedobiologia* 17, 70-82.

Piearce, T. G. (1978). Gut contents of some lumbricid earthworms. *Pedobiologia* 18, 153-57.

Plewczynska-Kuras, U. (1976). Estimation of biomass of the underground parts of meadow herbage in the three variants of fertilization. *Pol. Ecol. Stud.* 2 (4), 63-74.

Pritchard, G. I., Pigden, W. J. and Folkins, L. P. (1964). Distribution of Potassium, Calcium, Magnesium and Sodium in grasses at progressive stages of maturity. *Can. J. Plant Sci.*44, 318-24.

Reuss, J. O. and Innis, G. S. (1977). A grassland nitrogen flow simulation model. *Ecology* 58 (2), 379-88.

Rhodes, I. and Mee, S. S. (1980). Changes in dry matter yield associated with selection for canopy characters in ryegrass. *Grass and Forage Sci.* 35, 35-39.

Rodin, L. E. and Bazilevich, N. I. (1967). *Production and Mineral Cycling in Terrestrial Vegetation.* English translation (ed. G. E. Fogg). Oliver and Boyd, London.

Rorison, I. H. (1971). The use of nutrients in the control of floristic composition of grassland. In: E. Duffey and A. S. Watt (*op. cit.*) pp. 65-77.

Rorison, I. H. (1980). The current challenge for research and development. In: I. H. Rorison and R. Hunt (*op. cit.*) pp. 3-10.

Rorison, I. H. and Hunt, R. (Eds.) (1980). *Amenity Grasslands: An Ecological Perspective.* Wiley.

Russell, R. S. (1977). *Plant Root Systems. Their Function and Interaction with the Soil.* McGraw-Hill.

Santantonio, D., Hermann, R. K. and Overton, W. S. (1977). Root biomass studies in forest ecosystems. *Pedobiologia* 17, 1-31.

Satchell, J. E. (1971). Earthworms. In: *Methods of Study in Quantitative Soil Ecology.* Ed. J. Phillipson. IBP Handbook No. 18. pp. 107-27. Blackwell Scientific Publications.

Sauerbeck, D. and Johnen, B. (1976). The turnover of plant roots during the growth period and its influence on 'soil respiration'. *Z. PFlanzenern. Bodenk.* 3, 315-28.

Sauerbeck, D. R. and Johnen, B. G. (1977). Root formation and decomposition during plant growth. In: *Soil Organic Matter Studies.* Vol. 1. pp. 141-8. International Atomic Energy Agency, Vienna.

Schlesinger, W. H. (1977). Carbon balance in terrestrial detritus. *Ann. Rev. Ecol. Syst.* 8, 51-81.

Schuurman, J. J. and Goedewaagen, M. A. J. (1971). *Methods for the Examination of Root Systems and Roots.* 2nd Edition. Pudoc, Wageningen.

Seligman, N. G. and Arnold, G. W. (1980). Simulation of intensively managed grazing systems. In: A. I. Breymeyer and G. M. Van Dyne (*op. cit.*) pp. 853-80.

Shamoot, S., McDonald, I. and Bartholomew, W. V. (1968). Rhizo-deposition of organic debris in soil. *Proc. Soil Sci. Soc. Am.* 32, 817-20.

Shanks, R. E. and Olson, J. S. (1961). First year breakdown of leaf litter in southern Appalachian forests. *Science*, 134, 194-5.

Shaver, G. R. and Billings, S. D. (1975). Root production and root turnover in a wet tundra ecosystem. *Ecology* 56 (2), 401-09.

Sims, P. L. and Singh, J. S. (1971). Herbage dynamics and net primary production in certain ungrazed and grazed grasslands in North America. In: *Preliminary Analysis of Structure and Function in Grasslands.* Ed. N. R. French. pp. 59-124. Colorado State University, Fort Collins.

Sims, P. L. and Singh, J. S. (1978). The structure and function of ten western North American grasslands. IV. Compartmental transfers and energy flow within the ecosystem. *J. Ecol.* 66 (3), 983-1009.

Singh, J. S. and Gupta, S. R. (1977). Plant Decomposition and soil respiration in terrestrial ecosystems. *Bot. Rev.* 43 (4), 449-528.

Singh, J. S., Lauenroth, W. K. and Steinhorst, R. K. (1975). Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. *Bot. Rev.* 41, 181-232.

Singh, J. S., Trlica, M. J., Risser, P. G., Redman, R. E. and Marshall, J. K. (1980). Autotrophic Subsystem. In: A. I. Breymeyer and G. M. Van Dyne (*op. cit.*) pp. 59-200.

Snaydon, R. W. (1980). Ecological aspects of management - a perspective. In: I. H. Rorison and R. Hunt (*op. cit.*) pp. 219-32.

Spedding, C. R. W. (1971). *Grassland Ecology*. Oxford University Press.

Speidel, B. and Weiss, A. (1974). Untersuchungen zur Wurzelaktivitat unter einer Goldhaferweise (Investigations on the root activity below a Golden Oat meadow). *Angew. Botanik.* 48, 137-54.

Stenina (1964) as cited by J. S. Waid (*op. cit.*).

Suffling, R. and Smith, D. W. (1974). Litter decomposition studies using mesh bags: Spillage inaccuracies and the effects of repeated artificial drying. *Can. J. Bot.* 52 (3), 2157-63.

Swift, M. J., Heal, O. W. and Anderson, J. M. (1979). *Decomposition in Terrestrial Ecosystems*. Studies in Ecology Vol. 5. Blackwell Scientific Publications.

Taylor, S. C. (1979). The leaching of nutrients from plants by water. B.E.S. Winter and Annual General Meeting, 3-5 January, 1979 (*unpublished*).

Torrey, J. G. and Clarkson, D. T. (Eds.) (1974). *The Development and Function of Roots*. Academic Press.

Troughton, A. (1957). *The Underground Organs of Herbage Grasses*. C.A.B. Bulletin No. 44.

Tukey, H. B. Jr. (1970). The leaching of substances from plants. *Ann. Rev. Pl. Physiol.* 21, 305-24.

Van Dyne, G. M. (1978). Foreward: Perspectives on the ELM model and modelling efforts. In: G. S. Innis (*op. cit.*) pp. v-xxvi.

Vickery, P. J. (1972). Grazing and net primary production of a temperate grassland. *J. appl. Ecol.* 9, 307-14.

Waid, J. S. (1974). Decomposition of roots. In: C. H. Dickinson and G. J. F. Pugh (*op. cit.*) pp. 175-211.

Wallwork, J. A. (1970). *Ecology of Soil Animals*. McGraw-Hill.

Wallwork, J. A. (1976). *The Distribution and Diversity of Soil Fauna*. Academic Press.

Waters, R. S. (1955). Numbers and weights of earthworms under a highly productive pasture. *NZJ. Sci. Technol.* 36 (5), 516-25.

Weaver, J. E. (1968). *Prairie Plants and Their Environment*. University of Nebraska Press, Lincoln.

Weinmann, H. (1942). On the autumnal remigration of nitrogen and phosphorus in *Trachypogon plumosus*. *J. S. Afr. Bot.* 8, 179-96.

Welches, D. and Rawes, M. (1965). The herbage production of some Pennine grasslands. *Oikos* 16, 39-47.

Westlake (1968). Methods used to determine the annual production of reedswamp plants with extensive rhizomes. In: M. S. Ghilarov (*op. cit.*) pp. 226-34.

Whittaker, R. H. (1970). *Communities and Ecosystems*. Macmillan, London.

Whittington, W. J. (Ed.) (1969). *Root Growth*. Butterworths, London.

Wiegert, R. C., Coleman, D. C. and Odum, E. P. (1970). Energetics of the litter-soil subsystem. In: *Methods of Study in Soil Ecology*. Ed. J. Phillipson, pp. 93-98. IBP/Unesco, Paris.

Wiegert, R. G. and Evans, F. C. (1964). Primary production and the disappearance of dead vegetation of an old field in southern Michigan. *Ecology* 45, 49-62.

Wildung, R. E., Garland, T. R. and Buschbom, R. L. (1975). The interdependent effects of soil temperature and water content on soil respiration rate and plant root decomposition in arid grassland soils. *Soil Biol. Biochem.* 7, 373-78.

Wilkinson, S. R. and Lowrey, R. W. (1973). Cycling of mineral nutrients in pasture ecosystems. In: G. W. Butler and R. W. Bailey (*op. cit.*) pp. 247-315.

Williams, P. A., Nes, P. and O'Connor, K. F. (1977). Macro-element pools and fluxes in tall-tussock (*Chionochloa*) grasslands, Canterbury, New Zealand. *N.Z.J. Bot.* 15 (2), 443-76.

Williams, S. T. and Gray, T. R. G. (1974). Decomposition of litter on the soil surface. In: C. H. Dickinson and G. J. F. Pugh (*op. cit.*) pp. 611-32.

Williamson, P. (1976). Above-ground primary production of chalk grassland allowing for leaf death. *J. Ecol.* 64 (3), 1059-75.

Woodmansee, R. G. (1978). Critique and analyses of the grassland ecosystem model ELM. In: G. S. Innis (*op. cit.*) pp. 257-81.

Woodmansee, R. G., Dodd, J. L., Bowman, R. A., Clark, F. E. and Dickinson, C. E. (1978). Nitrogen budget of a shortgrass prairie ecosystem. *Oikos* 34 (3), 363-76.

Addendum

Bradshaw, A. D. (1969). An Ecologist's Viewpoint. In: *Ecological Aspects of the Mineral Nutrition of Plants*, I. H. Rorison. Blackwell Scientific Publications.

Hackney, C. T. and de la Cruz, A. A. (1980). In situ decomposition of roots and rhizomes of two tidal marsh plants. *Ecology* 61 (2), 226-31.