Factors affecting the improvement of hill land dominated by bracken (*Pteridium aquilinum* (L.) Kuhn).

by

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3. ABSTRACT

The work described was carried out between 1978 and 1981, and continues the extensive studies of The West of Scotland Agricultural College into methods of controlling bracken (*Pteridium aquilinum* (L.) Kuhn) and subsequent sward improvement. Bracken frond growth is readily controlled with the herbicides asulam (Asulox) and glyphosate (Roundup) but the quality of the resulting sward is frequently poor as a large area of ground is covered with frond litter. The recolonisation of this litter by indigenous species can be slow and may result in a high proportion of plants of little grazing value, but conventional re-seeding methods involving ploughing are not usually possible because the ground is too steep or too rocky. The main aim of this study has therefore been to examine some of the factors affecting sward development from either indigenous or introduced species, following frond clearance, in order to assess other methods by which swards may be improved.

Field surveys of a large number of bracken-infested hill sites in the West of Scotland showed that the main species in the sward were *Agrostis tenuis*, *A. stolonifera*, *A. canina*, *Anthoxanthum odoratum*, *Festuca rubra*, *Holcus mollis*, *Poa pratensis*, *P. trivialis* and *Galium saxatile*, and to a lesser extent, *Digitalis purpurea*, *Viola palustris*, *Luzula campestris* and *Potentilla erecta*. The amount of uncolonised ground covered with bracken litter varied greatly from site to site.

The main species found as viable seed in the soil were *Erica cinerea*, *Calluna vulgaris*, *Digitalis purpurea*, *Juncus bufonius*, *J. effusus* and *Agrostis* spp. Large numbers of viable seeds were found at some sites but there was much variation (approximately 3,000- 24,000 seeds/m^2). Sampling to a depth of 3 cm was considered to account for 74% of the seeds present. Species which were well represented in the buried seed population frequently had very small seeds and there

were far fewer seeds of grasses than of non-grasses. The composition of the soil seed bank and of the sward above frequently did not correspond.

Two sites were examined where frond clearance with herbicides had taken place and where there had been subsequent soil disturbance from the winter feeding of cattle. The composition of the sward and the seed bank at these sites differed from that of untreated sites and probably reflected the introduction of species from the feed.

Data from a variety of experiments produced evidence of changes in the buried viable seed population. Both short-term (month to month) and long-term (year to year) changes in the population as a whole and in the individual species were noted.

The results of these studies on soil seed populations have been related to those of other workers who have examined the survival of seeds in soil. They found that several factors affected the period of survival including the depth of burial, the soil type and its moisture content, the dormancy characteristics of the individual species and the extent to which the soil was disturbed. The problems associated with the estimation of buried viable seed populations have been discussed.

Many of the seeds found during the surveys were not described in standard reference works and had to be germinated and grown on before they could be identified. Photographs and descriptions of these seeds have been included.

A trial was set up to examine the changes in the composition of the sward following frond control with either asulam or glyphosate, and the role of the buried viable seed population. Whilst asulam adversely affected only *Agrostis* spp., many more species were affected by glyphosate. The only species present in the seed bank in any quantity were *Agrostis* spp. and, to a lesser extent, *Galium saxatile*. There was little evidence that the buried viable seed population was playing a significant role in the recovery of the swards, particularly on the glyphosate-treated plots. Sward development following frond control was therefore dependent upon the existing species and their ability to tolerate or recover from the effects of the herbicides.

Previously published work has attributed allelopathic properties to bracken, which would mean that the presence of frond residues could inhibit the establishment of indigenous or introduced species. Leachates collected from bracken fronds at various stages of growth were therefore applied to seed of Trifolium repens and Lolium perenne (species included in re-seeding mixtures), and Festuca rubra, Agrostis tenuis, Poa pratensis and Poa trivialis (species frequently found in association with bracken) to assess their effect on germination, establishment and seedling growth. Soil from below a bracken stand was also tested. Leachate from dry green glasshouse-grown fronds had an adverse effect on seed germination in petri dishes but the six species did not respond in the same way and the results of several similar trials were not consistent. None of the other solutions or materials had any effect on germination or seedling growth either in petri dishes or in soil. Seedling establishment was inhibited by the physical presence of a surface litter layer and this physical effect is probably much more important under British conditions than any allelopathic effect.

An investigation was made of the effect of different after-treatments on the establishment of introduced species and sward composition following frond control with asulam. The layer of bracken litter was removed by raking, burning or incorporation by digging, and lime, fertiliser, and grass and legume seed was applied. Two cutting regimes were imposed, with cutting every 4 or 12 weeks in the first season and every 4 or 6 weeks in the second season.

Over two seasons, the different methods of removing litter had little effect on sward composition or dry weight yields in plots which did not receive fertiliser, lime and seed. In those plots which received fertiliser, lime and seed, digging stimulated the germination of large numbers of weed seeds. Many weed plants established in the first season but had ceased to be a problem by the second. Digging also provided the best conditions for the establishment of sown species, which showed a significantly greater cover and dry weight yield at the end of the first season than where other methods of removing the litter were used. Holcus mollis rapidly recolonised burnt plots. In the second season, both burnt and dug plots gave significantly greater dry weight yields of sown grasses compared with the control, although there was no difference in the percentage cover of these species. Where the sown grasses did not establish well even though lime and fertiliser had been applied, the dry weight yield of grasses in both seasons was no higher than where no such after-treatment had been made. Where the sown grasses established in quantity the grass dry weight yields from the plots receiving lime and fertiliser were significantly increased in the second season relative to those plots receiving neither lime nor fertiliser. Ranunculus repens was the most important herb on all the treatments. It was particularly prevalent where litter had been removed by raking, and to a lesser extent, on control plots.

The more frequent cutting regime significantly affected only the dug treatment which had received fertiliser, lime and seed. The cover of sown grasses was increased but dry weight yield decreased.

It is concluded that although there may be many buried seeds in bracken-infested areas, they are unlikely to affect sward development following frond clearance unless cultivations are undertaken. In the absence of cultivation, litter on the soil surface presents a physical barrier to seed germination. Removal of the litter without any other treatment has little effect on recolonisation following frond clearance with asulam, although the effect of burning in killing other vegetation may allow rhizomatous species such as Holcus mollis to spread. If lime, fertiliser and seed are applied, cultivation of the soil gives the best establishment even allowing for the presence of numerous weed seedlings. The finding that in the second season, swards established after burning the litter gave dry matter yields of sown grasses equivalent to those from swards established by cultivation is interesting, and requires further investigation to establish whether burning as a pre-treatment is a suitable alternative to ploughing in uncultivable areas.

4. INTRODUCTION

Bracken (Pteridium aquilinum (L.) Kuhn) has been estimated to infest between 150,000 and 200,000 hectares of hill land in Scotland (Hendry, 1958; McCreath, 1981),much of which is the better drained mineral soils. Apart from the utilisation of space which could otherwise be used for grass growth, bracken makes shepherding difficult and can cause stock poisoning. In the West of Scotland much of the bracken is so dense that there is little vegetation beneath the canopy. Even where there is a good grass cover beneath the bracken, a proportion of the ground is covered with litter.

Early attempts to control bracken were labour intensive and involved the cutting, slashing or bruising of fronds, or ploughing where the ground was accessible and suitable for the use of machinery. Although bracken cutting was widespread in the 1950s, as labour costs increased less ground was cleared. From a peak of 16,000 hectares in 1952 there was a continuous and steep decline in clearance to only about 200 hectares in 1970 (McCreath, 1981). Many herbicides for frond control were tested and although several gave good control in the first year after treatment, most gave poor results in subsequent seasons. The herbicides currently recommended for the control of bracken in grassland are asulam (Asulox) and glyphosate (Roundup). Whilst asulam causes little permanent damage to the underlying sward, glyphosate, having a wider spectrum of activity, tends to kill most of the understory.

Williams (1980) updated the cost/price relationship of frond control in the 1950s to 1976 prices and found that land application of asulam was competitive with machine cutting whilst aerial application cost £5 more per hectare. In order to qualify for the 50% grant towards spraying costs, a minimum application of 375 kg/ha of 29% ground mineral phosphate is usually necessary and this significantly alters the cost/price relationship. Many farmers consider that follow-up treatment with lime or fertiliser is either unnecessary in practice or not worthwhile financially and as a result some farmers have sprayed and foregone the grant whilst others have not sprayed at all.

The composition of the sward which develops following bracken clearance depends upon several factors which include the type of species in the sward prior to spraying, the tolerance of these species to the herbicide, their ability to recover after spraying, the type of species present as viable seed in the soil and the grazing pressure imposed by mammals such as rabbits, sheep and cattle. The percentage increase in grass yield resulting from bracken removal depends upon the density of the original cover and the amount of litter present. However, an increase in summer production which allows an increase in stocking rate is of little value unless provision can be made for the extra animals during the autumn and winter. Many hill grasses have their maximum period of productivity in mid-summer and thereafter their digestibility declines significantly.

Although re-seeding of cleared ground allows an increase in the length of the grazing season as well as providing improved dry matter yields and quality, the control of bracken frond growth in Scotland with herbicides is seldom followed by re-seeding. Farmers often feel that money for follow-up treatment is better spent on fertiliser than on re-seeding although Newbould (1981) commented that unless the composition of the sward was altered markedly there was little evidence that hill pastures responded with extra dry matter production to the application of lime and phosphate.

Difficulties arise in establishing sown species in hill land partly because of the adverse climate and partly because of the inability to prepare a suitable seed bed. Hill soils are relatively acid (pH 3.5-5.0) and rainfall in these areas is high. Decomposition of organic matter is therefore slow, there is often a mat of undecomposed vegetation or bracken litter of varying depth present and the subsoil is largely infertile as a result. Many hill soils are also fairly shallow and/or stony and ploughing is therefore impossible or of little value. Lime and fertilisers are necessary to establish the species most frequently used in hill land reseeding programmes and in order to maintain them, further periodic applications are required. The costs of application as well as the costs of the materials are continually increasing. Because hill land is frequently of low potential productivity, it is often hard to justify the expense of such after-treatments. As a result there is some interest in the development of techniques of improvement which are less expensive and in the improvement of the existing techniques.

This study was designed to examine some of the factors which might affect sward composition after bracken clearance and to consider possible improvements. The tolerance of individual species to the herbicide employed for frond control and the ability of viable seeds buried in the soil to establish after bracken clearance are important factors when improvements in the sward are based upon the manipulation of the indigenous species. The composition of the sward and the buried viable seed population of a number of bracken-infested hill sites was therefore examined to determine the types of swards which might develop after spraying. The role of the seed population in sward development was assessed in a trial where frond control was achieved using asulam or glyphosate. Previous workers have found bracken to contain water-soluble phytotoxins which are capable of reducing the germination and growth of certain herbaceous species. Trials were designed to determine whether bracken in the West of Scotland influenced the indigenous species or was likely to influence the fate of sown-in species by the release of toxins. The presence of a layer of bracken litter often several centimetres deep emerged during the study as a factor likely to be important in sward development and in the establishment of surface sown species. The effect of various methods of removing this litter were therefore examined.

5. REVIEW OF LITERATURE PERTAINING TO BURIED SEED POPULATIONS.

5.1 *Numerical estimations of buried seed populations*

Many such determinations have been made both in the United Kingdom and abroad although fewer data are available for pasture or grassland situations than for arable land. Kropáč (1966), Jensen (1969) and Harper (1977) have summarised many of these estimates. Table 1 indicates some of the data for grassland situations in the United Kingdom. Problems which arise when estimating seed populations are considered in Section 5.3.

5.2 *Techniques for estimating populations of seeds in the soil*

These may be divided into techniques which involve sieving, sometimes followed by flotation, and a viability determination of the seeds recovered, and those which rely upon a direct assessment of the seedlings arising from the soil samples.

The germination technique involves placing the samples in shallow containers under a regime of fluctuating temperatures and with periodic soil disturbance. Seeds which are stimulated to germinate are identified, recorded and removed. This technique has been adopted by many workers: initially by Chippindale and Milton (1934), Milton (1936, 1939, 1943, 1948), Oosting and Humphries (1940), Prince and Hodgdon (1946), Champness and Morris (1948) and Champness (1949a) and later by Major and Pyott (1966) and Roberts and his co-workers (Roberts, 1964; Roberts and Feast, 1972, 1973b; Roberts and Dawkins, 1967; Roberts and Neilson, 1980, 1981). The technique was modified by Brenchley and Warrington (1930, 1933, 1936) who reduced the bulk of the samples by washing prior to sowing them out in pans.

Using slightly more elaborate equipment, Thorsen and Crabtree (1977) and Fay and Olsen (1978) opted for washing the soil away from the seeds prior to hand sorting of the debris, whilst Kropáč (1966) and

Jensen (1969) washed their samples through a series of sieves to remove the organic material and the majority of the seeds (this fraction being subsequently sorted by hand) and then placed the soil residue in pans in the greenhouse. Following wet sieving, Standifer (1980) suggested that seed might be separated from the organic debris using an air stream of different velocities to blow the samples into fractions depending upon the weight of the different seeds.

Various chemicals have been employed to float off the fraction of the sample which contains the seeds. Hyde and Suckling (1953) extracted clover and other legume seeds from agricultural soils in New Zealand. The samples were washed initially over two wire sieves followed by the flotation of light material and seeds in carbon tetrachloride [CCl_4]. Ivens (1978) used this method successfully to extract Ulex europaeus seeds from soil samples. In America, a soil dispersing solution of potassium carbonate [K_2CO_3] was used to float off organic matter and seeds in a study on witchweed seed (Striga asiatica) (Robinson and Kust, 1962). Kropáč (1966) also used this chemical when separating out seeds from heavy, clay soils, after the bulk of the sample had been reduced by washing. Malone (1967) described a method involving the use of a solution containing sodium hexametaphosphate [$Na(PO_3)_6$], magnesium sulphate [$MgSO_4.7H_2O$] and sodium bicarbonate [$NaHCO_3$] which he suggested was suitable for the extraction of seed of a variety of sizes. Barralis and Chadoeuf (1980) used Malone's solution in a study on weed seeds in arable soils. Rodriguez Bozán and Álvarez Rey (1977) employed a flotation technique to extract seeds from a sandy soil. Saturated sodium bicarbonate, a bromoform/benzene or a bromoform/ethanol solution were used. A solution of calcium chloride [$CaCl_2$] has also been found to be effective in separating seed of a wide range of sizes (Johnson et al, 1978; Roberts and Ricketts, 1979; Visser and Wentzel, 1980).

With all these chemicals a test must be made to ensure that seed viability is not adversely affected or subsequent germination tests may produce an under-estimate of the true population of viable seeds.

The washing and sieving, and chemical techniques, give an estimate of the total number of seeds present but the data are really only of value if a subsequent test of seed viability is made. A direct examination of the seed embryo may be made or a chemical test which indicates metabolic activity may be used, for example, tetrazolium chloride. Placing the seeds in special environmental conditions to induce germination and to break seed dormancy is also acceptable, for example, the use of alternating temperatures in combination with periods of light and darkness or the addition of stimulants such as a 0.2% solution of potassium nitrate (Kolk, 1962).

Only two examples were found where seeds were removed visually with no pre-treatment to reduce the bulk of the sample (Mal'tsev, 1909; Olmsted and Curtis, 1947).

Early attempts to separate seeds from soil by physical and chemical methods were reviewed by Kropáč (1966).

5.3 *Problems encountered when estimating buried seed populations*

5.3.1 Depth to which the samples are taken

Table 1 shows the range of depths to which these selected workers took their samples. It is not possible to standardise these estimates because, in undisturbed soil, the number of seeds decreases with increasing depth (Chippindale & Milton, 1934; Robinson & Kust, 1962; Major & Pyott, 1966). This rate of decrease is not necessarily the same for all soils. In cultivated soils the horizons are repeatedly mixed which tends to create a more uniform distribution of seed. Therefore, comparisons of estimated seed populations in disturbed and undisturbed soils, even to comparable depths, may be misleading.

Table 1 Estimates of buried seed populations in various types of grassland.

Source	Analysed depth (cm)	No. of viable seeds/m^2	Site description
Brenchley (1918)	23.00	18,800	Pasture
Chippindale & Milton (1934)	35.00	21,250 69,871	Pasture 50 years old Pasture formerly arable
Milton (1936)	17.50	24,201 1,912	Young ley *Agrostis/Festuca* sward
Milton (1948)	17.50	7,040 36,665	Dry grassland Wet grassland
Champness & Morris (1948)	16.25	2,364 10,001	Ley Tor grass field
Champness (1949a)	18.75	18,839 4,938-9,728	Ungrazed ley Grazed leys
Douglas (1965)	15.00	11,362 415	Ryegrass ley Old permanent pasture
King (1976)	5.00	9,150	Acidic grassland
WRO (1980)	15.00	10,000	Old indigenous pasture
Eadie & Black (1981)	5.00	460 919 2,149	*Agrostis/Festuca* sward *Molinia* hill land *Nardus* hill land

Because of the variation in the degree of coherence of soils of different texture even when samples are taken to a standard depth, the volume of soil recovered will not be constant (Chippindale and Milton, 1936).

5.3.2 Size of sample

Major and Pyott (1966) found in their literature review that surface area varied from 4.15 cm^2 (Roberts, 1958) to 929 cm^2 (Olmsted and Curtis, 1947). In theory, the size of the sample should be adapted to take account of the pattern of the vegetation.

5.3.3 Number of samples

The distribution of seed in the field tends to be uneven; much of the seed shed enters the seed bank close to the mother plant. The result is that samples often contain seed of one species predominantly and from sample to sample the total number of seeds, as well as the number of seeds of individual species, may vary enormously. As for the size of the sample, the number of samples taken should take into account the distribution of the species rather than the size of the sample area.

Problems arise when trying to analyse the data statistically because most of the commonly used tests assume that the variate is normally distributed. Champness (1949b) transformed each of her figures (n) to $\sqrt{(n + \frac{1}{3}n)}$ which had the effect of stabilizing the variance. She established a relationship between the mean and the variance of her samples which enabled her to calculate the number of samples which she would require in order to estimate her seed population to within 10% of the standard error of the mean. For all the species together, 70 samples were required, and for Ranunculus repens alone 300, in order for the standard error of the population, or of R. repens, to be within 10% of the mean. Roberts (1958) used a square root transformation to normalise his data but found that this made an interpretation of the results difficult.

It is almost always impossible to take the number of samples which statistics dictate will give a reasonable degree of accuracy; the time to process them would be prohibitive. Roberts (1958) and Kropáč (1966) both concluded that a large number of small samples should be taken in preference to a small number of large samples.

5.3.4 Date of sampling

Seed populations show pronounced fluctuations from year to year depending on the opportunities for the production of fresh seed (Brenchley and Warrington, 1933, 1945; Roberts, 1958, 1963; Rabotnov, 1956). These workers considered that any estimate of a seed population would apply to that year only. Rabotnov (1969) felt that the time of year at which the samples were taken was also important. Sampling in the autumn immediately after many plants had shed their seeds, he felt did not reflect the normal buried seed population. Because of these temporal fluctuations if estimates from a number of sites are to be compared, samples should be taken from each as far as possible at the same time.

5.3.5 Conditions of storage of samples

Once the samples have been collected they are generally transferred to a laboratory or greenhouse until they can be processed. The samples may be stored at low temperatures (0°-4°C), a technique used by Oosting and Humphries (1940). This may encourage some seeds into a state of enforced dormancy although for other species this treatment may satisfy a chilling requirement before germination is possible. Olmsted and Curtis (1947) air dried samples and held them in this condition until they could be analysed. Some species are known to remain viable for longer in dry storage than others (Kjaer, 1940, 1948).

Whatever storage procedure is adopted it should be reduced to the minimum length of time possible.

5.3.6 Choice of technique for estimating the seed population

Some of the techniques available for estimating seed populations from soil samples have been outlined in Section 5.2. The efficiency and accuracy of these techniques varies.

Visual sorting with no pre-treatment is an exceedingly slow process and not to be recommended.

Chemical methods may be costly, may have a detrimental effect on seed viability and may be time consuming. For example, in Robinson and Kust's (1962) technique it takes 30 minutes for the organic fraction containing the seeds to float away from the soil. One advantage of the chemical methods is that it is easier under laboratory conditions to control and to vary the environmental conditions used to break dormancy and stimulate germination than it is under greenhouse conditions where the soil is in relatively large, bulky pans.

The most obvious disadvantage with the germination technique is that the samples must be kept for a considerable period of time in order to ensure that the majority of seeds have germinated. Brenchley and Warrington (1930) recommended that samples were kept for a period of three years. When subject to fluctuating temperatures and stirring, most species were found to germinate in the first year (Snell, 1912; Brenchley and Warrington, 1930; Champness and Morris, 1948; Budd et al, 1954). Hyde and Suckling (1953) felt that unless samples were kept for more than two years, 'hard' seeds, such as clovers, would be underestimated in the results. After three years Roberts and Feast (1973b) found the number of seeds which germinated was small. A cautionary note was made by Guyot (1960) who found that some of his species had their maximum period of emergence between the third and seventh years of the experiment. Samples are not held for a standard period of time in such experiments.

Feast and Roberts (1973) suggested that there was no ready means for speeding up the estimate of viable seeds by seedling emergence methods when a range of species was present. Since burial at depth and excess soil moisture are known to favour seed preservation (see Section 5.5.3), the soil in the pans should be fairly shallow and attention paid to soil moisture.

The germination method may not be as efficient in estimating viable seed populations as the extraction techniques (Feast and Roberts, 1973) as a certain proportion of dormant seeds will not be stimulated to germinate and hence will not be recorded. Jensen (1969) compared the population estimates he obtained by processing soil samples three different ways. Separating seeds by washing and subsequently testing viability gave the highest average estimate of viable seed numbers (50,000/m^2). Sowing the samples in boxes in the greenhouse in the autumn gave a mean estimate of 19,000 viable seeds/m^2. This method had the advantage of demonstrating the presence of more individual species than the other two methods. Sowing soil in boxes outdoors in either autumn or the following spring suggested populations averaging 8,000/m^2 and 11,000/m^2 respectively.

Although no one method stands out as vastly superior to the others, it seems that a technique which incorporates the following features will be the most efficient: reducing the bulk of the sample by washing, removing the majority of the seeds in the organic fraction, from which they may then be picked out visually, and finally sowing out the soil residue in pans in the greenhouse where, under fluctuating environmental conditions and periodic disturbance, the remaining viable seeds may be stimulated to germinate and then recorded.

5.3.7 Type of seed population estimate obtained

Many published estimates of seed numbers relate to the total number of seeds recovered and no determinations were made as to what proportion were viable seeds (for example, Kropáč, 1966; and several Russian workers cited in Kropáč (1966) from Kott (1947)). In these cases it was a washing/flotation technique which was employed. Where the seedling emergence technique is used, only an estimate of viable seed numbers is obtained (for example, Milton, 1936). The two types of estimate are not comparable.

5.4 *Longevity of seeds*

The contamination of soil by weed seeds, particularly in such large numbers, can be a significant problem in that some species, through mechanisms such as dormancy cycles or hardness of seed coat, can remain viable for many years.

The longevity of seeds has been illustrated by several workers, amongst them Becquerel (1907) and Ewart (1908). Becquerel tested seeds held in the Paris Natural History Museum and found 50 of the 500 species he tested produced seedlings. The seeds which gave rise to these seedlings were aged between 48 and 87 years of age. Ewart tested 1,400 seeds sent from Kew Gardens and kept in a locked cupboard in the botanical laboratory at Melbourne, Australia. Of these, 58 had retained their viability for over 50 years. With a review of the literature he gave the results of tests on seeds of various ages for over 4,000 species. Ohga (1923) reported the viability of Indian lotus (Nelumbo nucifera) plant seed which had been recovered from a peat bed. Libby (1951) using a ^{14}Carbon test estimated that these seeds were 1040 $\pm$ 210 years of age. This was challenged by Godwin and Willis (1964), who also used a ^{14}Carbon test and who suggested that the seeds were only 100 $\pm$ 60 years of age. Wester (1973) reviewed the literature on these seeds and gave the age of the seeds as about 1024 years which supported the data of Libby (loc cit). Doubt probably still exists about the true age of these seeds. Cassia multijuga seed collected in 1776 and held in dry storage was germinated by Becquerel in 1934 whilst seed of Albizzia julibrissin collected in China in 1793 and stored in the British Museum, germinated in 1940 after 147 years storage (Ramsbottom, 1942). More recently, Harrington (1972) reported that seeds of Trifolium repens from below a 600 year old church were viable.

Other examples of long lived seeds are given by Turner (1933), Barton (1961), Ødum (1965) and Justice and Bass (1979), including several cases where the ages 'claimed' for the seeds are somewhat suspect. With the exception of the Indian lotus seeds and perhaps Harrington's clover seed, these examples of long lived seeds relate to samples held in dry storage.

The topic of seed survival in undisturbed soil has been approached in several ways and was considered as early as 1893 by Peter who found that whereas soil from beneath ancient forests contained few viable seeds that from younger forests contained a large number of viable seeds of species characteristic of grassland or cultivated fields (Peter, 1893). Brenchley (1918) examined the viable seed content of fields at Rothamsted, England, which had been grassed down for between 10 and 58 years and found viable seed of several arable weed species. Chippindale and Milton (1934) showed how arable land sown down to pasture between 6 and 50 years prior to examination still contained viable seed of arable species and Milton (1943) found viable seed of cultivated species beneath 20 year old pastures in Wales. Milton (1936, 1948) and Snell (1912) found seed of Digitalis purpurea, a species characteristic of disturbed woodland, to persist following clearing and cultivation whereas species of arable soils persisted in planted woodlands. Oosting and Humphries (1940) sampled a successional series following old field abandonment and found species typical of open fields as viable seed in wooded habitats in which the parent plants had not grown for several decades. Turrill (1957) found buried arable weed seeds in grassland soil which had not been cultivated for periods between 30 and 40 years, and even up to 300 years in one instance and Guyot (1960) found seeds of crop weeds in soil which had not been cultivated for 20 to 50 years. Livingston and Allessio (1968) carried out a similar survey of a series of abandoned field and forest sites of known history. The results of both studies estimated that seeds of certain species had survived buried in the soil for approximately 50 to 70 years.

There is always the possibility that seeds were introduced after the pastures were laid down or after the forests matured, but Roberts (1970) suggested that if a consideration were made of the number of seeds involved, of the relative frequency of seeds of different species and of their distribution in the soil profile, there was a strong case to suggest that the seeds and seedlings derived were in fact from naturally buried populations.

More direct experimental evidence on the survival of seeds in undisturbed soil was provided by trials initiated by Beal in 1879 (Darlington and Steinbauer, 1961; Kivilaan and Bandurski, 1973) and by Duvel in 1902 (Goss, 1924; Toole and Brown, 1946). Both trials were based upon the burial of many samples of weed seeds and a periodic determination of their viability.

Beal's trial involved the burial of 20 lots of 50 freshly collected seeds of each of 23 locally common weed species. Each set of 50 seeds was well mixed with moist sand and placed in an open mouthed bottle which was buried in an inverted position at a depth of 51 cm. Bottles were dug up every five years until 1920; thereafter bottles were recovered at ten year intervals. The contents of each bottle were spread onto sterilised soil in a greenhouse and watered daily. Seedlings which emerged were identified and counted. Of the 20 species buried in 1879, only three (Rumex crispus, Oenothera biennis and Verbascum blatteria) had survivors as viable seeds in 1960 after 80 years' burial (Darlington and Steinbauer, 1961). Of these three species, only Verbascum blatteria had viable seeds (20%) in 1970. No other species germinated. All ten seeds of this species were grown to maturity and the seed collected gave rise to apparently normal progeny (Kivilaan and Bandurski, 1973). This trial has not yet been terminated; the most recent bottle to be recovered was in 1980 and the results are not yet published.

Duvel's work, incorporating an examination of the effect of burial at different depths, commenced in 1902, when he buried seeds of 107 different crop and weed seeds. Two hundred seeds of each species were mixed with sterilised soil in porous pots and buried at depths of 20, 56 and 107 cm. The porous nature of the pot allowed free access to the seeds of both air and water circulating in the soil. At intervals pots were removed and examined. Goss (1924) found that after twenty years burial, 37 species were viable and after 39 years, Toole and Brown (1946) reported that 36 species were still viable although of these, 18 had less than 6% germination. The trial terminated in 1941. It was noted that the weed seeds retained their viability far better than the crop seeds.

Similar experiments were set up by Kjaer in 1934 using common crop species and weed species of arable land (Kjaer 1940, 1948). Four hundred seeds of each of 37 species were buried in soil at a depth of 25 cm in porous clay pots which were recovered annually. After ten years burial practically all the crop seeds in the experiment had completely lost their viability whilst the weed species were continuing to germinate in considerable numbers. More recently, Lewis (1958, 1973) carried out experiments on the effect of burial upon seed survival over a 20 year period and found, with the exception of Phleum spp., that the grass seeds were relatively short lived whilst those of Ranunculus repens, Chenopodium album and Rumex crispus had the highest percentage survival rates (53%, 23% and 18% respectively). In 1972 a study designed to extend over a period of 50 years was initiated in Mississippi, when seed of twenty local weed species was buried at depths of 8, 23 and 38 cm (Egley and Chandler, 1978). The burial in

1971 of 200 seeds of ten weed species mixed with sterilised soil and placed in plastic cylinders 20 cm deep in the soil was reported by Takabayashi and Nakayama (1978). Samples were recovered periodically and seed viability determined. Grass species were again found to be shorter lived than the weed species.

Although valuable information is again derived from these experiments, they do have certain limitations. All the seeds used in these experiments were of a uniform age at the start of the experiment and this does not reflect a natural seed population. Placing the bottles in Beal's experiment in sand in an inverted position does not subject the seeds to the same conditions as naturally buried seed.

Roberts and his co-workers have worked extensively on seed populations in arable land and they have published data on the rate of loss of viable seeds from the seed banks of naturally occurring populations. Further input of seed was prevented during the work and in the populations they examined viable seed numbers were found to decrease exponentially from year to year at rates of 22% (Roberts and Dawkins, 1967), 12% (Roberts and Feast, 1973a) and 34% (Roberts and Feast, 1973b). Similar data for naturally occurring seed populations in grassland are not available.

5.5 *Factors affecting seed longevity in soil*

5.5.1 Physiological properties of the seeds

Viable seeds prevented from germinating by purely external environmental limitations which, once removed will allow the seed to germinate, are said to be in a state of enforced dormancy. Soil disturbance brings many seeds to the soil surface where, providing the environment is able to supply the requirements for germination, it is either an innate - or an induced - dormancy mechanism which governs whether a viable seed will germinate or not. Innate dormancy is genetically determined for each species and requires a specific stimulus or after-ripening process to be completed before germination can take place whilst induced dormancy is imposed upon a non-dormant seed by certain conditions (for example, high carbon dioxide levels in the soil), the removal of which plus a further specific stimulus is required for dormancy to be broken. Most stimuli breaking dormancy are most active at the soil surface (Harper, 1957). The survival of buried viable seeds depends upon the nature and degree of innate dormancy of the particular species, whether or not induced dormancy can develop and the ability of the seed to persist when dormancy is enforced (Harper, 1957).

These physiological characteristics interact with physical characteristics of the environment such as the depth at which the seeds are buried, the type of soil in which they are buried and its moisture content, and the depth, frequency and timing of any soil disturbance in relation to both environmental conditions and the peak periods of emergence for particular species.

5.5.2 Depth of burial

Although conflicting evidence exists with respect to the effect of depth of burial upon seed survival, the majority of data suggest that increasing the depth of burial increases the period of survival.

Duvel (1905) suggested that seed viability increased with depth of burial but Goss (1924) upon examination of the same data suggested that depth of burial affected seed viability little. Crocker (1938) suggested that depth of burial had no effect upon the life span of seeds, as did Lewis (1958). Kjaer (1940) found that depth of burial had little influence on seed longevity over a limited period of time and Egley and Chandler (1978) found after two and a half years that storage in soil at depths of 8, 23 and 38 cm had no effect on seed viability.

Toole and Brown (1946) reporting on the final results of Duvel's experiment where seed samples had been buried 20, 56 or 107 cm below ground level found that whilst germination from the different levels had often been very irregular, there was a general tendency for seeds from the 20 cm depth to germinate less than those from the 107 cm depth. Dorph-Peterson's experiment, begun in 1904 with eight crop and eight weed species buried at depths of 8, 20 and 30 cm, showed that after a period of six years seeds at the 8 cm depth were the least viable (Dorph-Peterson, 1910). In another of the early investigations, Waldron (1904) found that after three years none of the seven species sown at depths down to 5.2 cm had survived whilst three species were still viable at depths down to 25 cm. With the exception of Salsola pestifer, Chepil (1946b) found in his work that the deeper the seeds were buried the lower was their emergence and hence the higher was the number of seeds which survived the burial period. Bibbey (1948) demonstrated that seed of Brassica arvensis buried between 5 and 12.5 cm deep survived better than seed at a depth of 0-5 cm and Thurston (1961) working with species of Avena found that seeds of Avena fatua survived longer at a depth of 15 cm than in the top 5 cm of soil. Taylorson (1970) found that seeds buried at depths of 2.5, 7.6 and 15.2 cm and recovered after six months had lost their viability to a greater degree the more shallowly they had been placed at burial and Roberts and Feast (1972) showed seedling emergence decreased with increasing depth and conversely seed survival increased with increasing depth of incorporation. Thomas et al (1978) also reported that the deeper seeds were buried the better they survived.

5.5.3 Soil moisture and soil type

A significant amount of data exists which suggests that moisture and soil type are important factors in the preservation of seed in the soil although some data are also available to suggest that this is not the case.

Data were available in 1933 to suggest that continual immersion in water enabled seeds to resist deterioration until favourable conditions arose for germination (Turner, 1933) and this was supported by the work of Chippindale and Milton (1934) who found a strong indication that more seeds were present in a viable condition in the waterlogged soils which they examined although they felt that they had an insufficient number of samples to establish a definite association. Crocker (1938) also found an indication that seeds of many species were able to retain their viability better when held in moist soil than when held in dry storage in air and Milton (1948) found that areas under permanent swards where the soils were wet had larger seed populations than areas with drier soils.

From the results of his buried seed experiment, Kjaer (1940) was able to divide his test species into four groups on the basis of how well they had retained their viability when held in dry storage and when buried in moist soil, and although he did not determine their moisture contents he did find seed of several weed species which fell into the category of species which lost seed viability quickly in dry storage but which survived well in moist soil. Chepil (1946a) noted that although hard seeds are particularly well adapted to survive long periods in moist soil, many of the weed species having a long life span in soil are not 'hard', and these seeds imbibe water freely. He suggested from further work that irrigation in addition to natural precipitation had no effect on the longevity of seed buried in soil (Chepil, 1946b).

At the end of the buried seed trials of both Beal and Duvel, some of the seeds which had survived were found to have taken up moisture (Toole and Brown, 1946) and Toole and Toole (1953) suggested that the processes leading to seed deterioration might be suppressed in dormant seeds such as these which had taken up water. Lewis (1958) found that certain species, especially those surviving comparatively well in soil, deteriorated more rapidly in a granary store than when in a fully imbibed state in the soil. He also found more viable seeds were recovered from experimental samples held below a water table than from those held above it (Lewis, 1961). More recently, Thomas et al (1978) found that fewer seeds germinated in their seed burial treatments which were irrigated than in those in which the soil had been maintained in a much drier condition.

Milton suggested from his results (1936, 1939, 1943) that the size of the buried seed population was linked to both soil moisture and soil type. He found that seeds survived best under damp, acid conditions and data from Champness and Morris (1948) supported his theory. Turner (1933) also found peat to be a good medium for seed preservation; he suggested that it had certain antiseptic properties which protected the seeds from fungal attack. Champness and Morris (1948) further developed Milton's idea and suggested that the low viable seed populations which they recorded for arable soils (compared with grassland soils) were partly a result of soil conditions. Arable soils tend to be limed more frequently and are hence less acidic, and drainage, and consequently soil aeration, is more closely attended to. The poor survival of seeds in downland may be correlated with the high pH and low moisture contents of these soils. Soils of higher pH are also unfavourable for seed preservation as the bacteria involved in the decomposition of organic matter are encouraged under these conditions.

Lewis (1958, 1973) reported the results of an experiment which involved the burial of seeds of crop and weed species at various depths in mineral and peat soils and he suggested after four years and again after twenty years that deterioration of seed viability had been more rapid in the acid peat than in the mineral soil. In another experiment reported on in 1961, Lewis found that the rapid deterioration of seed viability when buried in peat, noted in the interim results of his previous experiment (Lewis, 1958), was not evident here and that seeds from the peat samples were hard to germinate.

Data from arable situations were provided by Brenchley and Warrington (1930) who found that most of the species common to the neutral clay soils at Rothamsted and to the acid sandy soils of Woburn behaved similarly in pans of each type of soil with respect to seed survival and seed dormancy. Prince and Hodgdon (1946) examining seed populations of old pasture soils, found approximately 30% more seeds in the 'heavy' than in the 'light' grade of soils. Chepil (1946b) found that the number of viable seeds of five Canadian weed species surviving the experimental treatments imposed upon them was scarcely affected by soil type. In an experiment on seed dormancy, Bibbey (1948) buried seed of Thlaspi arvense in a fine sandy loam and a clay soil. After five years the germination of T. arvense seed was 90% and 87% for the two soils respectively. Similar treatment imposed upon Brassica arvensis gave figures of 80% and 98% for the loam and the clay soil respectively. However, in a similar experiment by Cates (1917) wild oats were found not to survive more than two years in heavy clay soils but could survive four to six years in drier sandy soils. Thurston (1960) found that soil type had little influence on seed survival. Stevens (unpublished data in Hill, 1980) found that fewer viable seeds became buried in peat than in mineral soils and those which did become buried soon died. In mineral soils Hill (1979) found much larger numbers of buried viable seeds. Eadie and Black (1981) found that the viable seed population of their drier, less acid Agrostis/Festuca sward was only 40% of that in the wetter, more acid Molinia/Nardus site.

5.5.4 Effect of soil disturbance

That seeds can remain viable in a state of enforced dormancy when buried in soil has been indicated. However, if the soil is disturbed, as in cultivation, buried seeds are often brought into an environment favourable for germination. All of the data available on the effect of soil disturbance on seed numbers have been obtained from work on arable systems. Comparable work on grassland does not appear to have been published. In studies examining the rate of loss of seeds from the soil, the input of fresh seed must be prevented in order to achieve meaningful results. This is clearly quite difficult to achieve in a field situation and although studies using artificially created populations, which involve the mixing of known numbers of seeds with soil in pans, enables conditions to be better controlled, the seed used here will be of a uniform age at the start of the experiment. Estimates of natural seed death can only be obtained by removing samples at intervals i.e. by destructive sampling.

5.5.4.1 Effect of cultivation upon naturally occurring weed seed populations

Brenchley and Warrington (1930, 1933, 1936, 1945) were amongst the first to examine the effects of fallowing and cultivation on the number of viable weed seeds in arable soil. Their work on wheat and barley fields at Rothamsted showed that adequate fallowing caused a considerable decrease in the number of buried weed seeds but that the effect of cultivation varied widely from species to species from a decrease equal to that caused by fallowing to an increase of two or three times the original population. Prolonged fallowing (cultivation in the absence of a crop) over a period of four years reduced the buried seed population but could not eliminate it. The effect of vegetable cropping was examined by Roberts (1958) who found that after one year the viable seed population had been reduced to 38% of its original size and at the end of two years' cropping the population had been reduced to 19% of its original size. Again, the individual species were found to vary in their response to cultivation. In further work (Roberts, 1962) the number of viable weed seeds surviving frequent cultivation was found to decrease exponentially from year to year. Provided that appreciable inputs of fresh seed were prevented, the number of viable seeds present in one year was approximately half that of the previous year. Individual species again showed a variation in the rate of loss of viable seeds ranging from 16% per year for <u>Fumaria officinalis</u> to 60% per year for <u>Veronica arvensis</u>. Roberts and Dawkins (1967) carried out a six year experiment with a naturally occurring weed seed population and they too found an exponential decrease in seed numbers from year to year in the absence of further seed inputs. The individual species also showed an exponential decrease in their numbers although the extent of the decrease varied from species to species. The rate of loss of viable seeds was compared for uncultivated plots, plots cultivated twice a year and plots cultivated four times a year and these were found to be 22%, 30% and 36% per year respectively. Statistical analysis showed a significant reduction in seed numbers had been achieved in the plots which had been cultivated over those which had not but the difference between the two cultivation treatments was not significant. Roberts and Feast (1973a) published the results of a similar experiment in which, over a period of four years, the number of seeds in the top 23 cm of the soil was found to decrease exponentially from year to year and the rates of loss for uncultivated plots, plots cultivated twice a year and plots cultivated seven times a year were 34%, 42% and 56% per year respectively.

Work abroad has produced similar data. In Canada, fallowing operations were found to be effective in reducing viable weed seed populations (Budd et al, 1954) and Kropáč (1966) found that intensive cultivation of heavy soil in autumn led to a reduction in the buried seed bank of 19-32%. He cited the results of several other workers who had also demonstrated significant reductions in weed seed populations as a result of soil disturbance including those of Belozerov (1952) who found that improving soil cultivation techniques over a period of 15 years reduced the total seed store (viable and non-viable seeds) by 71%.

Roberts (1970) examined the data of Brenchley and Warrington (1933, 1936, 1945), Roberts (1962), Roberts and Dawkins (1967) and Budd et al (1954) and showed graphically how the effect of a year's cultivation reduced the number of buried seeds, irrespective of the original population size, by 30-60%.

5.5.4.2 Effect of cultivation upon artificially created weed seed populations

Chepil (1946a) carried out an extensive test of seed survival in a shallow layer of soil subject to fallowing or cropping and found approximately 30 species which survived the three year period in considerable numbers. He showed that periodic cultivation brought seeds to the soil surface and increased the number of buried seeds which germinated. Burial of seed by soil disturbance even at a shallow depth was sufficient to depress germination and he found that the number of viable seeds in the soil at the end of a season was far lower in cultivated soil than it was in uncultivated soil at equivalent depths (Chepil, 1946b).

In a series of three experiments which involved the burial of seed of eleven annual weed species in a 7.5 cm layer of soil which was cultivated five or six times a year for five years, Roberts (1964) found that seedling emergence declined exponentially from year to year. The decline in the number of viable seeds present at the end of the experiment were in accord with expectations based upon the rate of decline found in the field.

Roberts and Feast (1972) examined the effect of depth of seed burial in relation to the effect of soil disturbance on seed of twenty annual species and found that the persistence of viable seed depended upon the depth of burial and upon the depth of cultivation. At all three depths examined the number of viable seeds surviving was less in soil cultivated four times a year than in undisturbed soil. There were approximately four times as many seeds in undisturbed soil at the deeper levels of 7.5 cm and 15 cm than at the corresponding levels in the cultivated soil. Roberts and Feast (1973b) found that the number of viable seeds mixed with soil and then left undisturbed over a six year period decreased exponentially at a rate of 12% per year compared with a rate of 32% per year for soil subject to cultivation. Of the seeds originally sown, 27.5% and 5.9% were still viable in the undisturbed and the cultivated soils respectively.

Roberts and Neilson (1980) reported the results of an experiment involving the burial of seed of ten weed species in a 7.5 cm layer of soil which was subject to cultivation three times a year for five years. The number of viable seeds again declined exponentially and varied from species to species. The number of seeds remaining viable at the end of the experiment ranged from 2.5-16.6% of the original number sown, again depending upon the species; nine of the ten had a relatively high capacity for survival in cultivated soil.

Although the data reviewed here relate to arable situations, the general principles illustrated will also apply to grassland. Generally, where replenishment of the seed bank has been prevented, the number of viable seeds will decrease exponentially from year to year whether the soil is disturbed or undisturbed. Also, the persistence of viable seeds in the soil is less under conditions of cultivation than when the soil is undisturbed. The greater the frequency of soil disturbance and the greater the depth to which this disturbance is made, the greater the rate of loss of seeds from the bank will be.

However, it only requires one or two plants of a species to set seed for the composition and extent of the seed bank to alter in size and composition rapidly and radically.

6. BURIED SEED POPULATIONS IN BRACKEN INFESTED HILL LAND IN 1978

6.1 *Introduction*

The composition of the sward which develops following bracken clearance depends upon several factors which include the type of species already growing in the area, the tolerance of these species to the herbicide employed to remove the bracken, the depth of the bracken litter, the grazing pressure imposed by mammals such as deer, rabbits, sheep and cattle and the type of species present as viable seed in the soil.

Much evidence exists to demonstrate that large numbers of seeds are buried in soil and that these seeds have the ability to remain in a viable condition in the soil for considerable periods of time (see Section 5.4). Seeds such as these may exert a significant influence upon the development of a sward following bracken clearance. This study was undertaken to determine the extent, and composition, of the buried seed population which might be available for the colonisation of land on which bracken frond growth has been controlled by the use of herbicides, and to examine its relationship with the composition of the sward of undisturbed bracken infested hill land.

6.2 *Method*

Twenty sites in the West of Scotland were selected for investigation in the autumn of 1978 and these are described in Appendix 1:A. These sites showed a range of bracken cover, including one area where bracken had been removed by spraying in 1976 with glyphosate (Gatehouse A) and another where frond recolonisation was occurring after fosamine treatment in the same year (Gatehouse B). At each site the percentage cover of all species present was assessed in twenty randomly chosen quadrats, each approximately 1,000 cm^2. Soil samples were taken using a cylindrical sampler which lifted cores approximately 5 cm long and

2.5 cm in diameter, twenty such cores being drawn from positions selected at random at each site.

Previous workers (Chippindale and Milton, 1934; Robinson and Kust, 1962) found that the number of seeds decreased with increasing depth in uncultivated soil. In order to determine to what depth the cores should be taken and subsequently cut in the survey of bracken infested sites, twenty cores were taken from seven different sites to a depth of 10-12 cm. Each core was dried in a warm room at a temperature of 18°C prior to being cut into 1 cm deep sections to a total depth of 7 cm. On the cores collected from certain sites there was a layer, frequently several centimetres deep, of newly fallen bracken fronds. Once the cores had been dried this layer could be flaked away until the humus was reached. Examination had shown that almost no seeds were to be found in this layer of freshly fallen frond material. The first centimetre section was generally a mixture of partly decomposed bracken litter and soil. Dead plant material was also carefully removed from the tops of the cores prior to sectioning. Each section was crumbled into a separate dish and examined under a binocular microscope; any seeds discovered were removed and germinated on filter paper. The soil sections were then moistened and maintained in suitable conditions for germination for four weeks. Any seeds which germinated were retained until they could be identified and counted. The results are summarised in Table 2 and the full results are given in Appendix 1:C:Table 1. One sample was lost during handling.

Table 2. Relationship between soil depth and seed numbers.

Depth of core section	Number of viable seeds recovered	% of total seeds recovered/section	
0-1	13	50.00	88.45
1-2	4	15.38	
2-3	6	23.07	
3-4	1	3.85	
4-5	1	3.85	
5-6	1	3.85	
6-7	0	0.00	
Total	26	100.00	

Only 37 seeds were recovered from the 19 cores and it was considered that the data from one particular core was aberrant and should therefore be omitted from the analysis. This core was found to have 11 seeds in the 1-2 cm section: this was unusual as most of the samples had at most four to five seeds in the entire core. Omitting the data from this core gave a total of 26 seeds in the 18 samples and Table 2 indicates that about 88% of all the seeds recovered were found in the top 3 cm of the cores.

Bearing this figure in mind, the time required to examine each sample and the number which were to be taken (20 per site, 20 sites in all), it was decided that samples would be taken to a depth of 3 cm. Thus, according to the data so far obtained, the estimates of viable seed populations would account for about 88% of the seeds present to a depth of 7 cm.

Cores collected during 1978 and 1979 for various other experiments and which were not used were cut into sections as described above and further data on seed distribution with depth was compiled. The full results are given in Appendix 1:C:Table 2 and the results are summarised in Table 3. Only 28 of the 53 samples were taken to a depth of 7 cm and the estimates of seed numbers at the various depths have been corrected to take account of this. The data given in Table 2 have also been included in Appendix 1:C:Table 2.

Table 3. Relationship between soil depth and seed numbers.

Depth of core section	No. of samples taken to a particular depth	No. of seeds recovered	No. of seeds per 28 cores	% at various depths	
0-1	53	24	12.68	26.21)	
1-2	53	24	12.68	26.21)	74.27
2-3	53	20	10.57	21.85)	
3-4	52	12	6.46	13.36	
4-5	47	7	4.17	8.62	
5-6	31	2	1.81	3.75	
6-7	28	0	0	0.00	

The pattern of seed distribution with depth was similar to that noted in Table 2 and supports the decision that taking cores to a depth of 3 cm would be sufficient to recover the majority of the seeds. The estimate that 74% of the seeds present to a depth of 7 cm were held in the 0-3 cm layer was probably more accurate than the estimate of 88% as it was based on a larger number of samples.

The cores collected in the survey were returned to the laboratory where they were placed on trays in a drying room (at 18°C) for a week, after which they were cut to a standard length of 3 cm and carefully crumbled into separate dishes. Each sample was passed through two wire sieves; the first with circular apertures 2.00 mm in diameter and the second a square mesh with holes of side 0.05 mm. The second sieve was considered to be sufficiently fine to retain any seeds present but as a check on the method for a total of ten samples from different sites, the material which did pass through this sieve, mostly silt and clay, was moistened, placed on filter paper in petri dishes and left in a propagator unit maintained for 8 hours at 20°C with additional light provided and for 16 hours at 15°C in darkness. As no seeds germinated in any of these dishes, this final fraction was in future discarded. The material retained by each of the two sieves was washed separately through the second sieve using a gentle stream of water and the mixture of seeds and soil remaining in each case was filtered by suction through Whatman filter paper in a Buchner funnel. The filter paper was removed, placed in a petri dish and returned to the drying room. The samples were examined under a binocular microscope with a x20 magnification and any seeds located were removed, placed in labelled dishes and retained for identification.

After all the samples from the first site had been examined and all the seeds present supposedly removed, the samples were moistened and the dishes placed in a propagator unit. After only a few days large numbers of seeds germinated. Unfortunately it did not prove possible to maintain the seedlings under such conditions, nor to transfer them to pots of soil and most died before they could be identified. Therefore the results of the soil sampling at this site were discarded and the site resampled. It was clear that seeds were being overlooked, that there were a variety of reasons for this, and that it was necessary for alternative or supplementary techniques to be considered. Although it declined with the number of samples examined, the major problem was an inexperience in the identification of the seeds, many of which were very small, and also in distinguishing these from soil particles. The other significant problem was the time element which made it impossible to make an exhaustive search of each sample.

Three chemical techniques were considered in detail and their efficiency in separating out the seeds was compared, firstly with sowing out the dried, sieved samples directly onto compost, and secondly with drying, washing and sieving the samples as previously described prior to visually examining them and then sowing them out onto compost. The chemical techniques tested were those described by Hyde and Suckling (1953) using carbon tetrachloride [CCl_4], by Roberts and Ricketts (1979) using a saturated solution of calcium chloride [$CaCl_2$] and by Malone (1967) using a mixture of sodium hexametaphosphate [$Na(PO_3)_6$], sodium bicarbonate [$NaHCO_3$] and magnesium sulphate [$MgSO_4.7H_2O$]. The first two techniques employed an initial sieving to create subsamples of varying sizes prior to the samples being added to beakers containing the particular chemical. For all three techniques after a thorough mixing in the particular chemical the organic fraction containing the seeds floated to the surface where it could be decanted off. Both the organic fraction and the sediment were thoroughly rinsed with water over a sieve to remove the chemicals prior to the fractions being dried and examined. The soil which was used was collected from a field site which was known to have a large seed population and which had species with a variety of seed sizes. 5 g of air dried soil was used for each of five replicates per treatment. After the chemical treatment and a visual examination of both the organic fraction and the sediment, the two fractions were combined and sown out onto compost in the greenhouse. Any seeds which germinated were recorded. The results are given in Table 4 and are the total of the five replicates.

The use of carbon tetrachloride [CCl_4] was found to have its disadvantages in that glass rather than plastic petri dishes must be used and, because of the nature of the chemical, the work must be carried out in a fume cupboard. Only 3 seeds were floated off by the chemical although a visual examination of the sediment located a further 15 seeds. The CCl_4 caused the soil particles to aggregate strongly and made the subsequent visual sorting difficult, and no doubt many seeds were not detected for this reason. Indeed, when the samples were sown onto compost a further 45 seeds germinated.

Table 4. Comparison of seed recovery from soil by physical and chemical techniques.

Method	No. of seeds recovered				% of seeds recovered	
	visually		by germination	TOTAL	visually	by germination
	in the organic fraction	in the sediment				
Malone's solution	8	36	26	70	63	37
$CaCl_2$	40		43	83	48	52
CCl_4	3	15	45	63	29	71
Wash, sieve and visual examination	48		38	86	56	44
Wash and sieve only	-	-	60	60	0	100

When calcium chloride [$CaCl_2$] was added to the soil samples, no seeds floated off but 40 seeds were recovered by sorting and a further 43 germinated in the greenhouse.

Malone's solution consists of a mixture of three chemicals which together induce the breakdown of soil aggregates and allow the organic material and the seeds to float off. The ratio of solution to soil suggested by Malone (100 g of soil to 200 ml of solution) proved to be too low and in these trials a ratio of 10-20 g of soil to 100 ml of solution was found to be easier to work with. Eight seeds floated to the surface using this mixture but another 36 were located in the sediment. A further 26 seeds germinated when the sample was sown out.

Malone's solution was easier to handle than the carbon tetrachloride and the bulk of the sample could be considerably reduced by washing the sediment over a sieve after the soil particles had been broken down. The seeds which were recovered by a visual examination of the sediment had been cleaned up and were easier to locate. Since the bulk of the sample had been reduced, it took less time to sort through a sample.

It became clear that whatever chemical was used, the entire sample had to be examined and not just the fraction which was floated off although the object of these chemical techniques is specifically to eliminate the need to examine the sediment. Of the three chemical treatments the greatest percentage recovery by visual examination was in those samples treated with Malone's solution (63% v 48% for calcium chloride treated samples v 29% for carbon tetrachloride treated samples). However, there was only a 7% increase in the number of seeds located in samples treated with Malone's solution prior to visual examination compared with those which were not chemically treated prior to sorting. In this trial, this represents an increased location of about 5 seeds in 5 samples. This increased rate of seed recovery as a result of a reduction in the volume of soil to be sorted and of the seeds being easier to locate did not really justify the extra time to treat the samples chemically prior to sorting. Finally, it was clear that the samples must be sown out onto compost after examination since even in the two most suitable methods (Malone's solution and visually sorting) between 37 and 44% of the seeds were not recovered during the visual examination. It is easier to stimulate the germination of seeds on filter paper in a laboratory as the environmental conditions can more closely be controlled and can be altered more often and more effectively than they can be when seeds are buried in soil and held in a greenhouse. Feast and Roberts (1973) have noted that the germination technique alone may be less efficient than extraction techniques and that it has the further disadvantage that the samples should be kept for some considerable time to ensure the germination of a high proportion of the seeds. This latter point is not a practical proposition in these trials and fewer seeds were recovered by this technique than in the three chemical treatments. The adverse effect which the carbon tetrachloride had on the soil particles probably contributed to the lower total number of seeds recovered here. Despite these differences, statistical analysis found none of the methods to recover significantly different total numbers of seeds but visual sorting prior to sowing out did allow an estimate of the number of non-viable or dormant seeds to be made.

Since it would have taken some time to treat all the samples with Malone's solution, only samples from those sites with either a particularly high silt or clay content or with a large number of small seeds in each sample, were given this additional treatment. A check was carried out on the seed of four species (Juncus bufonius, J. effusus, Digitalis purpurea and Viola palustris) to ensure that extraction in Malone's solution had no adverse effect upon seed germination. Twenty seeds of each species were placed in separate muslin bags tied at the top with string and suspended in a beaker of either distilled water or Malone's solution for five minutes. The seeds were then germinated in petri dishes on filter papers moistened with distilled water. The results, given in Table 5 indicate that immersing the seeds in Malone's solution had no adverse effects upon the germination of seed of any of the species. The trial was not replicated.

In order to complete the seed counts in the survey, once examined, the soil samples were moistened with a 0.2% solution of potassium nitrate [KNO_3] and left in a dark place for 48 hours. The samples were then washed onto pots of steam sterilised Levington compost and placed under conditions suitable for germination in a growth cabinet (8 hours at 22°C with additional lighting and 16 hours at 18°C in darkness) for ten weeks, followed by six weeks in a glasshouse (without supplementary lighting). The results are expressed as the mean number of seeds per m^2 in 20 replicates per site.

Many of the published estimates of buried viable seeds are based upon a direct assessment of the seedlings arising from the samples (e.g.

Table 5. Effect upon seed germination of immersion in Malone's solution for five minutes.

Species	% germination	
	Control-water	Malone's solution
Juncus bufonius	85	85
Juncus effusus	60	70
Digitalis purpurea	55	50
Viola palustris	50	45

Brenchley and Warrington, 1930; Milton, 1936). For this method, two to three years is generally accepted as the minimum period of time for which the samples should be kept in order to obtain maximum germination of dormant seeds and hence the most accurate estimate of seed numbers. However, since it was not possible to retain the samples for this length of time it was felt that a more accurate estimate of seed numbers would be obtained by making a visual search for the seeds and then assessing their viability by inducing germination. Samples were placed on compost under a regime of periodic soil disturbance for a further four months in a final attempt to locate any remaining seeds. The procedures adopted were felt to be the best possible considering the number of samples which had to be examined and the length of time required both to conduct an exhaustive search of each sample and to retain the samples in the greenhouse before analysing the results.

6.3 *Results*

The data obtained on the sward composition and soil seed content of the twenty sites are given in Tables 6-25 and each is discussed. The data for Poa pratensis and Poa trivialis have been combined because it was extremely difficult to distinguish between these species in the field when trying to estimate a percentage cover value for each. The data for Agrostis canina and Agrostis tenuis have also been combined.

During the sampling at Gatehouse in 1981 doubts arose about the accuracy of the identification of the Polygonum spp in the 1978 survey. It is possible that plants of P. persicaria might not have been distinguished from those of P. hydropiper which were recorded at this site and at the Gatehouse of Fleet C site in abundance in 1981. Therefore the estimates of cover for P. persicaria have had to be given as P. persicaria/P. hydropiper. There was no question that plants of P. aviculare had been confused with either of these two species. An examination of the seeds of these three species was made and it was found that seed of P. aviculare was very similar to that of P. hydropiper. (See Section 8 - Plates 42 and 43). If there was an element of doubt that P. hydropiper plants had been present in the sward then there was also reason to question whether it was solely P. aviculare seeds which had been found. Therefore the estimates of numbers of P. aviculare seeds have had to be given as P. aviculare/P. hydropiper.

Any areas not containing living plants were classified as 'litter'. Whilst this category included bare soil surfaces and patches of dead plant material as well as bracken litter itself, these two components made a small contribution to only a few sites.

All the estimates of seed populations in the following tables refer to viable seeds.

Barlaes Hill, Kirkcudbrightshire

This site had a relatively sparse distribution of bracken and was grazed by sheep. The sward was dominated by *Agrostis* spp and *Festuca rubra* (40%) with *Galium saxatile* (23%). The litter layer was limited and covered only 10% of the area sampled.

Seed of *Agrostis canina* and *A. tenuis* made a 14% contribution to the site total of 27,210 seeds/m^2 but the dominant species in the soil seed population were *Erica cinerea* (14,000 seeds/m^2) and *Calluna vulgaris* (7,800 seeds/m^2). These species accounted for 81% of all the seeds present although they formed less than 5% of the sward. On the other hand, *Nardus stricta* which contributed 5% of the sward was unrepresented in the soil seed population. No seed of *Festuca rubra* or *Galium saxatile* was recovered although they were dominant species in the sward.

Table 6. Composition of sward and seed population at Barlaes Hill.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & *Agrostis tenuis*	6.35	13.86	3,770
Agrostis stolonifera	0.60	-	-
Anthoxanthum odoratum	2.50	0.37	102
Calluna vulgaris	3.45	28.84	7,846
Carex spp	0.25	-	-
Deschampsia flexuosa	3.85	-	-
Erica cinerea	2.00	52.07	14,166
Festuca rubra	33.65	-	-
Galium saxatile	23.00	-	-
Hypnum cupressiforme	1.00	-	-
Hypericum humifusum	-	0.37	102
Juncus bufonius	-	0.75	204
Luzula campestris	0.50	1.12	306
Nardus stricta	5.35	-	-
Poa annua	-	0.75	204
Poa pratensis & *Poa trivialis*	-	0.75	204
Potentilla erecta	2.80	0.75	204
Rumex acetosella	-	0.37	102
Sieglingia decumbens	3.75	-	-
Vaccinium myrtillus	1.70	-	-
Litter	9.25	-	-
TOTAL	100.00	100.00	27,210

Dalry, Kirkcudbrightshire

The bracken fronds were fairly low and there was no litter on the ground. The sward was dominated by Agrostis canina, A. tenuis, Anthoxanthum odoratum, Festuca rubra, Galium saxatile and Luzula campestris. These species accounted for over 75% of the sward. Approximately twenty other species were present in relatively small quantities.

The total number of viable seeds/m^2 at this site was 4,789 with almost half of this figure accounted for by Agrostis canina and A. tenuis. With the exception of Galium saxatile, which was present in the sward and in the soil in approximately equal proportions (10.50% and 8.50% respectively), the other main species in the seed population (Calluna vulgaris and Juncus effusus) were poorly represented or absent from the sward. C. vulgaris contributed about 900 seeds/m^2, which was almost 20% of the site total. No seed of Festuca rubra was found.

Table 7. Composition of sward and seed population at Dalry.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds m^2
Achillea millefolium	0.75	-	-
Agrostis canina & Agrostis tenuis	25.65	46.81	2,241
Anthoxanthum odoratum	9.40	-	-
Calluna vulgaris	2.00	19.14	917
Campanula rotundifolia	0.10	-	-
Carex spp	2.45	-	-
Cerastium holosteoides	0.15	-	-
Erica cinerea	0.50	-	-
Festuca rubra	22.40	-	-
Galium saxatile	10.50	8.50	407
Holcus lanatus	1.75	-	-
Holcus mollis	1.50	-	-
Juncus effusus	-	6.38	306
Luzula campestris	9.00	-	-
Plantago major	0.25	-	-
Poa annua	-	4.26	204
Poa pratensis & Poa trivialis	1.25	2.13	102
Potentilla erecta	2.50	4.26	204
Rumex acetosella	2.50	-	-
Sieglingia decumbens	2.00	-	-
Trifolium repens	2.60	-	-
Veronica officinalis	1.30	-	-
Veronica serpyllifolia	-	4.26	204
Viola palustris	1.20	-	-
Viola riviniana	0.25	-	-
Unidentified species	-	4.26	204
TOTAL	100.00	100.00	4,789

Glen Douglas A, Dunbarton

This was a relatively heavily infested site with a 35% ground cover of bracken litter. Agrostis stolonifera and Galium saxatile were the dominant species and together accounted for almost 40% of the sward. Smaller, but significant, quantities of Anthoxanthum odoratum, Digitalis purpurea, Holcus mollis and Molinia caerulea were also present.

The soil seed population was dominated by Juncus bufonius and J. effusus with 5,000 seeds/m^2, which accounted for 69% of the total number of buried viable seeds at this site (7,236/m^2). Erica cinerea, absent from the sward but with 1,000 seeds/m^2 in the soil, accounted for 14% of the soil seed population. The proportion of Digitalis purpurea seed in the soil was approximately twice that in the sward and seed of this species formed 8% of the soil seed population. Although dominants in the sward, Agrostis stolonifera was absent and Galium saxatile was poorly represented in the soil.

Table 8. Composition of sward and seed population at Glen Douglas A.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & *Agrostis tenuis*	-	4.23	306
Agrostis stolonifera	20.50	-	-
Anthoxanthum odoratum	4.50	-	-
Campanula rotundifolia	0.25	-	-
Carex spp	1.75	-	-
Deschampsia flexuosa	3.25	-	-
Digitalis purpurea	4.25	8.46	612
Erica cinerea	-	14.08	1,019
Galium saxatile	17.75	1.41	102
Holcus mollis	4.50	-	-
Juncus bufonius	-	43.65	3,159
Juncus effusus	1.50	25.35	1,834
Molinia caerulea	5.50	-	-
Potentilla erecta	0.75	-	-
Rumex acetosella	0.25	-	-
Stellaria media	-	1.41	102
Veronica officinalis	0.25	-	-
Litter	35.00	-	-
Unidentified species	-	1.41	102
TOTAL	100.00	100.00	7,236

Glen Douglas B, Dunbarton

Bracken litter covered 15% of the ground and the fronds were fairly sparse. Grasses dominated the sward with *Agrostis* spp, *Anthoxanthum odoratum* and *Holcus mollis* responsible for 50% of the ground cover. *Digitalis purpurea* and *Galium saxatile* accounted for a further 21% of the sward.

In the soil, seed of *Digitalis purpurea* accounted for 67% of all the seeds recovered (14,471/m^2) whilst only providing 6% of the sward. *Juncus* spp (*J. bufonius* and *J. effusus*) were also important with 2,500 seeds/m^2. Again, only a very minor role was played by these species in the sward. Although 30% of the sward was claimed by *Agrostis* spp, less than 10% of the seeds recovered were of these species (1,300/m^2). The large quantity of *Digitalis purpurea* seed recovered was largely responsible for the high site total of 14,471 seeds/m^2. No seed of *Holcus mollis* was recovered.

Table 9. Composition of sward and seed population at Glen Douglas B.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
<u>Agrostis canina</u> & <u>Agrostis tenuis</u>	4.25	9.16	1,325
<u>Agrostis stolonifera</u>	24.50	-	-
<u>Anthoxanthum odoratum</u>	6.00	-	-
<u>Carex</u> spp	0.50	-	-
<u>Digitalis purpurea</u>	6.25	66.90	9,681
<u>Galium saxatile</u>	14.75	2.82	408
<u>Holcus mollis</u>	14.50	-	-
<u>Hypnum cupressiforme</u>	5.50	-	-
<u>Juncus bufonius</u>	-	5.64	815
<u>Juncus effusus</u>	0.25	12.67	1,834
<u>Luzula campestris</u>	0.75	-	-
<u>Nardus stricta</u>	2.00	-	-
<u>Oxalis acetosella</u>	1.75	-	-
<u>Poa pratensis</u> & <u>Poa trivialis</u>	-	0.70	102
<u>Polytrichum commune</u>	1.50	-	-
<u>Potentilla erecta</u>	1.50	-	-
<u>Rumex acetosella</u>	0.25	0.70	102
<u>Stellaria media</u>	-	1.41	204
<u>Viola palustris</u>	0.25	-	-
Litter	15.50	-	-
TOTAL	100.00	100.00	14,471

Kirkton Farm A, Perthshire

This site was an isolated area of bracken in an otherwise bracken free pasture. Bracken litter accounted for 13% of the ground cover and several rabbit burrows were present. Almost half of the sward was accounted for by grasses including *Agrostis canina*, *A. tenuis*, *Anthoxanthum odoratum*, *Festuca rubra* and *Holcus mollis*. *Galium saxatile* and *Luzula campestris* were the dominant herbs in the sward and, to a lesser extent, *Rumex acetosella*.

3,261 seeds were found per m^2 of the site, of which 1,500 were those of grasses, particularly *Agrostis* spp. *Rumex acetosella* contributed 300 seeds/m^2 and formed almost 10% of the soil seed population; this was twice its level of representation in the sward. *Juncus bufonius* and *J. effusus* were similarly absent from the sward yet 700 seeds of these species were recovered/m^2 of ground. Several clumps of *Juncus effusus* plants were growing nearby and could have been the source of seeds. No seed of *Holcus mollis* or *Luzula campestris* was recovered and *Galium saxatile* was only present in small amounts.

Table 10. Composition of sward and seed population at Kirkton Farm A.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Achillea millefolium	0.75	-	-
Agrostis canina & *Agrostis tenuis*	18.25	40.63	1,325
Anthoxanthum odoratum	6.75	-	-
Campanula rotundifolia	0.75	-	-
Cirsium arvense	1.10	-	-
Erica cinerea	-	12.48	407
Festuca rubra	9.00	-	-
Galium saxatile	12.00	3.13	102
Holcus mollis	11.25	-	-
Hypnum cupressiforme	1.00	-	-
Juncus bufonius	-	9.38	306
Juncus effusus	-	12.48	407
Luzula campestris	8.00	-	-
Molinia caerulea	0.40	-	-
Poa pratensis & *Poa trivialis*	3.50	6.26	204
Polytrichum commune	0.50	-	-
Potentilla erecta	3.40	3.13	102
Ranunculus repens	0.60	-	-
Rumex acetosella	5.65	9.38	306
Sieglingia decumbens	1.50	-	-
Trifolium repens	1.00	-	-
Vaccinium myrtillus	0.10	-	-
Veronica officinalis	1.50	-	-
Litter	13.00	-	-
Unidentified species	-	3.13	102
TOTAL	100.00	100.00	3,261

Kirkton Farm B, Perthshire

This site was very sparsely infested with bracken as it was fairly damp, at a relatively high altitude (250 m above sea level) and quite exposed. There was no bracken litter on the soil surface. The presence of significant amounts of *Molinia caerulea* and *Carex* spp reflected the dampness of the site. The grasses *Agrostis canina*, *A. tenuis*, *Festuca rubra*, *Molinia caerulea* and *Sieglingia decumbens* occupied 60% of the sward with the herbs *Galium saxatile* and *Potentilla erecta* each contributing 10% to the ground cover. Fourteen other species were present in relatively small quantities.

There were an estimated 3,771 seeds/m^2 at this site. *Anthoxanthum odoratum* contributed 1,600 seeds/m^2 although this species was poorly represented in the sward. Approximately 600 *Rumex acetosella* seeds were recovered/m^2 although this species was absent from the sward. Seed of *Galium saxatile* and *Potentilla erecta* was frequent and both species were represented in slightly greater proportions in the soil than in the sward. The four grasses which were dominant in the sward were either completely absent from the soil seed population or in the case of *Agrostis* spp, very poorly represented.

Table 11. Composition of sward and seed population at Kirkton Farm B.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & *Agrostis tenuis*	16.00	5.41	204
Agrostis stolonifera	-	2.70	102
Anthoxanthum odoratum	1.75	43.25	1,631
Calluna vulgaris	0.75	-	-
Campanula rotundifolia	2.00	-	-
Carex spp	6.65	-	-
Festuca rubra	14.10	-	-
Galium saxatile	11.75	13.50	509
Hypnum cupressiforme	2.50	-	-
Juncus effusus	-	5.41	204
Molinia caerulea	10.00	-	-
Nardus stricta	2.25	-	-
Plantago major	1.25	-	-
Polytrichum commune	0.50	-	-
Potentilla erecta	9.25	13.50	509
Prunella vulgaris	1.75	-	-
Rumex acetosella	-	16.23	612
Sieglingia decumbens	18.25	-	-
Veronica officinalis	0.75	-	-
Viola palustris	0.50	-	-
TOTAL	100.00	100.00	3,771

Sundaywellmoor A, Dumfriesshire

Fronds were fairly dense at this site where 40% of the ground cover was bracken litter. Grasses dominated what vegetation was present with *Agrostis* spp (*A. canina*, *A. stolonifera*), *Anthoxanthum odoratum*, *Deschampsia* spp (*D. caespitosa*, *D. flexuosa*) and *Festuca rubra* being the most important. These seven species accounted for 35% of the ground cover. *Galium saxatile* and *Potentilla erecta* were the most frequently occurring of the thirteen herbs.

An average of 7,236 seeds/m^2 were estimated to be present at this site with over 50% of this figure being seeds of *Agrostis canina* and *A. tenuis*. The remaining grasses were either represented poorly or absent from the soil seed population. Seed of *Calluna vulgaris* and *Erica cinerea* accounted for a further 20% of the soil seed population with an estimated 1,500 seeds/m^2, although both species were absent from the sward.

Table 12. Composition of sward and seed population at Sundaywellmoor A.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & *Agrostis tenuis*	5.75	54.94	3,975
Agrostis stolonifera	5.00	-	-
Anthoxanthum odoratum	6.00	2.82	204
Calluna vulgaris	-	14.08	1,019
Carex spp	2.25	-	-
Crataegus monogyna	0.75	-	-
Deschampsia caespitosa	5.00	2.82	204
Deschampsia flexuosa	5.75	-	-
Erica cinerea	-	5.62	407
Festuca rubra	5.50	-	-
Galium saxatile	6.45	2.82	204
Hypnum cupressiforme	4.90	-	-
Juncus effusus	-	1.41	102
Luzula campestris	2.25	-	-
Poa pratensis & *Poa trivialis*	2.00	-	-
Polytrichum commune	0.25	-	-
Potentilla erecta	4.90	4.23	306
Rhytidiadelphus squarrosus	2.15	-	-
Rumex acetosella	-	7.03	509
Sieglingia decumbens	0.25	-	-
Viola palustris	0.35	-	-
Litter	40.50	-	-
Unidentified species	-	4.23	306
TOTAL	100.00	100.00	7,236

Sundaywellmoor B, Dumfriesshire

The site examined was on a portion of raised ground by the side of a stream where Juncus spp and Molinia caerulea were dominant. Approximately one third of the ground was covered with bracken litter.

The relative wetness of the site was reflected in the presence of significant quantities of mosses in the flora - Hypnum cupressiforme and Rhytidiadelphus squarrosus. A limited amount of Molinia caerulea was present at the edges of the site. The main species in the sward were Deschampsia flexuosa (33%) and to a lesser extent Galium saxatile (6.50%).

Seed of Agrostis canina and A. tenuis, Calluna vulgaris and Erica cinerea dominated the soil seed population with 1,500, 600 and 1,000 seeds being found/m^2 for these species respectively. No Erica cinerea plants were found in the sward and only limited quantities of Agrostis canina, A. tenuis and Calluna vulgaris were present. No Deschampsia flexuosa seed was recovered despite its importance in the sward. A relatively small soil seed population was estimated for this site. (4,280 seeds/m^2).

Table 13. Composition of sward and seed population at Sundaywellmoor B.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & *Agrostis tenuis*	2.00	33.32	1,426
Anthoxanthum odoratum	1.25	-	-
Calluna vulgaris	2.00	14.28	611
Carex spp	0.75	2.38	102
Cerastium holosteoides	-	2.38	102
Deschampsia caespitosa	1.50	-	-
Deschampsia flexuosa	33.25	-	-
Erica cinerea	-	26.20	1,121
Galium saxatile	6.50	-	-
Hypnum cupressiforme	3.75	-	-
Juncus acutiflorus	0.25	-	-
Juncus bufonius	-	7.15	306
Juncus effusus	-	4.77	204
Luzula campestris	3.75	2.38	102
Molinia caerulea	2.25	-	-
Poa pratensis & *Poa trivialis*	2.50	-	-
Potentilla erecta	2.75	-	-
Rhytidiadelphus squarrosus	3.00	-	-
Rumex acetosella	-	2.38	102
Sagina procumbens	-	2.38	102
Vaccinium myrtillus	3.25	-	-
Veronica serpyllifolia	-	2.38	102
Viola palustris	0.25	-	-
Litter	31.00	-	-
TOTAL	100.00	100.00	4,280

New Galloway A, Kirkcudbrightshire

The area sampled was particularly wet with two streams nearby. Bracken litter covered about 20% of the ground. Evidence of burning was found and *Digitalis purpurea* and *Rubus fruticosus*, species which frequently establish following burning, were present. The dominant species in the sward were the grasses (*Agrostis* spp, *Holcus mollis* and *Molinia caerulea*) which together accounted for almost 50% of the ground cover. *Galium saxatile* and *Digitalis purpurea* were the most abundant herbs (9% and 6% ground cover respectively). The presence of *Cirsium palustre*, *Carex* spp and *Molinia caerulea* indicated the moistness of the site, the latter species being distributed in discrete pockets.

Seed of *Agrostis canina* and *A. tenuis* was frequent with approximately 1,000 seeds/m^2 but no seeds of the other grasses dominant in the sward were found in the soil seed population. Nor was seed of *Galium saxatile* or *Digitalis purpurea* located. By far the greatest number of seeds recovered were those of *Juncus* spp (*J. articulatus*, *J. bufonius* and *J. effusus*) of which there were estimated to be 7,500 seeds/m^2; 65% of all the seeds recovered at this site. Less than 1% of the sward was devoted to this genus, although *Juncus* plants were noted growing outside the area sampled. *Erica cinerea* was also absent from the sward but present in considerable numbers in the soil (approximately 2,000 seeds/m^2).

The extremely high number of *Juncus* spp and *Erica cinerea* seeds recovered were responsible for the large estimate of 10,905 seeds/m^2 at this site.

Table 14. Composition of sward and seed population at New Galloway A.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & *Agrostis tenuis*	21.75	10.27	1,121
Agrostis stolonifera	11.50	-	-
Anthoxanthum odoratum	2.25	-	-
Calluna vulgaris	0.25	-	-
Carex spp	4.00	-	-
Cirsium palustre	0.25	-	-
Digitalis purpurea	6.00	-	-
Erica cinerea	-	19.62	2,140
Festuca rubra	2.50	-	-
Galium saxatile	9.00	-	-
Holcus mollis	8.00	-	-
Hypericum pulchrum	1.25	-	-
Juncus articulatus	-	0.94	102
Juncus bufonius	-	2.81	306
Juncus effusus	0.75	64.48	7,032
Luzula campestris	0.75	-	-
Molinia caerulea	4.50	-	-
Potentilla erecta	2.25	0.94	102
Rubus fruticosus	1.75	-	-
Rumex acetosella	3.25	-	-
Veronica arvensis	-	0.94	102
Viola palustris	1.50	-	-
Litter	18.50	-	-
TOTAL	100.00	100.00	10,905

New Galloway B, Kirkcudbrightshire

This site had a mixed gorse and bracken infestation and was heavily grazed by cattle. The resulting input of additional nutrients and the effect of trampling was reflected in the flora and in the soil pH which was slightly higher at this site than at the New Galloway A site. 12% of the ground cover was bracken litter.

Seventy per cent (70%) of the sward was accounted for by Agrostis spp (A. canina, A. tenuis, A. stolonifera), Dactylis glomerata, Holcus spp (H. lanatus, H. mollis), Ranunculus repens and Veronica officinalis. The presence of R. repens and D. glomerata and the traces of Cirsium arvense, Plantago lanceolata, Plantago major and Trifolium repens reflected the effects of increased nutrient and pH levels and poaching. Seed of Agrostis canina and A. tenuis (approximately 1,750/m^2) and Poa pratensis and P. trivialis (600/m^2) was important in the soil although Poa spp were poorly represented in the sward (less than 2% cover). Significant quantities of Sagina procumbens (500/m^2), Juncus effusus (400/m^2) and Viola palustris (400/m^2) were found in the soil although neither Sagina procumbens nor Juncus spp was found in the sward and Viola palustris was practically absent. No seed of Dactylis glomerata was found, nor of Holcus mollis. About 4,800 seeds were recovered per m^2 of ground at this site.

Table 15. Composition of sward and seed population at New Galloway B.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Achillea millefolium	1.00	-	-
Agrostis canina & Agrostis tenuis	24.75	36.16	1,732
Agrostis stolonifera	5.25	-	-
Campanula rotundifolia	0.25	2.13	102
Cerastium holosteoides	-	2.13	102
Cirsium arvense	0.40	-	-
Dactylis glomerata	17.50	-	-
Festuca rubra	1.50	-	-
Galium saxatile	2.50	-	-
Holcus lanatus	4.00	6.38	306
Holcus mollis	8.75	-	-
Hypnum cupressiforme	0.25	-	-
Juncus effusus	-	8.50	407
Luzula campestris	0.50	2.13	102
Plantago lanceolata	0.25	-	-
Plantago major	-	2.13	102
Poa pratensis & Poa trivialis	1.25	12.76	611
Potentilla erecta	0.75	4.25	204
Prunella vulgaris	0.40	-	-
Ranunculus repens	5.20	-	-
Rhytidiadelphus squarrosus	0.75	-	-
Rumex acetosella	0.25	2.13	102
Sagina procumbens	-	10.67	511
Trifolium repens	1.35	-	-
Ulex europaeus	1.65	-	-
Veronica officinalis	9.25	-	-
Veronica serpyllifolia	-	2.13	102
Viola palustris	0.25	-	-
Litter	12.00	-	-
Unidentified species	-	8.50	407
TOTAL	100.00	100.00	4,790

Polharrow Bridge A, Kirkcudbrightshire

The bracken here was dense and 60% of the ground cover was accounted for by bracken litter. Some evidence was found that burning had taken place on this site and the presence of species such as *Digitalis purpurea*, *Epilobium palustre* and *Urtica dioica* supports this observation.

Agrostis spp (*A. canina*, *A. tenuis*, *A. stolonifera*) and *Galium saxatile* were the dominant species in the sward and accounted for 13% and 7% of the sward respectively. Twenty-three other species made up the remaining 19% of the sward.

Erica cinerea seed was frequent (700/m^2) and was responsible for almost 22% of the soil seed population although no *Erica cinerea* plants were recorded in the sward assessment. *Sagina procumbens* was absent from the sward but was by far the most frequently occurring species in the soil seed population (approximately 1,000 seeds/m^2) and accounted for 35% of the seed population. Twenty-eight per cent of the seed population (900 seeds/m^2) was contributed by *Agrostis canina* and *A. tenuis*; about four times their contribution to the sward. No seed of *A. stolonifera* was found, nor of *Galium saxatile*.

Only nine species contributed to the soil seed population and five of these each provided only 3% of the seed. The site total was below average at 3,261 seeds/m^2.

Table 16. Composition of sward and seed population at Polharrow Bridge A.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & Agrostis tenuis	6.25	28.12	917
Agrostis stolonifera	6.65	-	-
Anthoxanthum odoratum	2.00	-	-
Campanula rotundifolia	1.00	-	-
Cardamine hirsuta	3.20	-	-
Carex spp	1.25	-	-
Cerastium holosteoides	-	3.13	102
Digitalis purpurea	0.25	-	-
Epilobium palustre	2.00	-	-
Erica cinerea	-	21.86	713
Galium saxatile	7.25	-	-
Gnaphalium uliginosum	-	3.13	102
Holcus mollis	1.00	-	-
Hypericum pulchrum	0.25	-	-
Juncus effusus	0.35	3.13	102
Lotus corniculatus	0.10	-	-
Luzula campestris	1.50	-	-
Poa pratensis & Poa trivialis	-	3.13	102
Potentilla erecta	0.40	-	-
Rumex acetosella	-	3.13	102
Sagina procumbens	-	34.37	1,121
Stellaria media	0.25	-	-
Urtica dioica	0.50	-	-
Veronica officinalis	1.00	-	-
Viola palustris	3.90	-	-
Litter	60.90	-	-
TOTAL	100.00	100.00	3,261

Polharrow Bridge B, Kirkcudbrightshire

This site was characterised by a dense stand of bracken with over 60% of the ground covered by bracken litter. The dominant species in the sward were Deschampsia flexuosa (7%), Galium saxatile (8%) and Luzula campestris (5%).

About 50% of the soil population was composed of Agrostis canina and A. tenuis seed although less than 2% of the sward was occupied by these species. Poa pratensis and P. trivialis were responsible for a further 17% of the seeds recovered; again only a small proportion of the sward was occupied by these species (1%). Seed of Deschampsia flexuosa was recovered but no Galium saxatile or Luzula campestris seed was found despite the important contribution made by these species to the sward.

Only 3,567 seeds were recovered/m^2, well below the average for the sites examined (8,583 seeds/m^2).

Table 17. Composition of sward and seed population at Polharrow Bridge B.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & Agrostis tenuis	1.55	48.55	1,732
Agrostis stolonifera	1.75	-	-
Campanula rotundifolia	0.65	-	-
Carex spp	1.75	2.86	102
Deschampsia flexuosa	6.65	2.86	102
Erica cinerea	-	11.44	408
Galium saxatile	7.80	-	-
Hylocomium splendens	0.25	-	-
Juncus effusus	-	2.86	102
Lophocolea bidentata	0.30	-	-
Luzula campestris	4.90	-	-
Poa pratensis & Poa trivialis	1.00	17.13	611
Potentilla erecta	3.40	5.72	204
Rhytidiadelphus squarrosus	1.55	-	-
Rumex acetosella	-	2.86	102
Vaccinium myrtillus	0.25	-	-
Veronica chamaedrys	3.75	-	-
Veronica officinalis	1.00	-	-
Viola palustris	1.25	-	-
Litter	62.20	-	-
Unidentified species	-	5.72	204
TOTAL	100.00	100.00	3,567

Melfort House A, Argyll

This site was adjacent to a wooded area and to an area cleared of bracken with asulam. The bracken was patchy in its distribution but there was a considerable amount of litter on the ground (35%). The coastal location of this site with its input of sea salts may have accounted for the increased pH of the soil (5.20) relative to the other bracken sites sampled. A few species indicative of relatively high nutrient levels were found - Urtica dioica, Ranunculus repens and Dactylis glomerata and their presence may also have been a result of the influence of sea salts. Several shade tolerant species (common to woodlands) were found on the site and included Geranium robertianum, Brachypodium sylvaticum, Oxalis acetosella, Lysimachia nummularia, Primula vulgaris, Rubus fruticosus and Silene dioica. Species indicative of moist conditions were also found - Cirsium palustre, Epilobium palustre, Iris foetidissima and Juncus effusus. The main species in the sward were Agrostis canina, A. tenuis, Holcus lanatus, Oxalis acetosella and Rubus fruticosus and these accounted for almost 30% of the sward. The sward was highly diverse with thirty different species present.

The soil population was far less diverse with only eleven species contributing to it. Juncus bufonius and J. effusus together accounted for almost 80% of the soil seed population and were present at a rate of 7,800 seeds/m^2. Although few Juncus plants were found on the site, much of the surrounding area was infested and seed may have come from this source. Poa pratensis and P. trivialis seed occurred frequently (approximately 1,000 seeds/m^2) and contributed 10% of the seed at this site. Few seeds of Agrostis spp or Holcus lanatus were found despite their importance in the sward.

9,783 seeds were recovered per m^2 of ground at this site.

Table 18. Composition of sward and seed population at Melfort House A.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & Agrostis tenuis	11.75	1.04	102
Agrostis stolonifera	0.50	-	-
Brachypodium sylvaticum	1.75	-	-
Cardamine hirsuta	0.75	2.09	204
Carex binervis	-	1.04	102
Cirsium palustre	0.35	-	-
Dactylis glomerata	3.50	-	-
Digitalis purpurea	0.25	-	-
Epilobium palustre	3.50	-	-
Geranium robertianum	2.75	-	-
Galium saxatile	-	1.04	102
Holcus lanatus	6.25	2.09	204
Iris foetidissima	2.75	-	-
Juncus bufonius	-	63.53	6,216
Juncus effusus	3.50	15.62	1,528
Luzula campestris	0.25	-	-
Lysimachia nummularia	3.50	-	-
Oxalis acetosella	5.25	-	-
Plantago lanceolata	0.25	-	-
Poa pratensis & Poa trivialis	0.50	10.42	1,019
Potentilla erecta	0.25	-	-
Potentilla sterilis	1.25	-	-
Primula vulgaris	1.25	-	-
Ranunculus repens	1.00	-	-
Rubus fruticosus	4.60	-	-
Rumex acetosella	2.25	-	-
Silene dioica	3.00	-	-
Stellaria media	0.50	-	-
Urtica dioica	2.75	-	-
Veronica chamaedrys	0.50	-	-
Veronica serpyllifolia	-	3.13	306
Viola palustris	0.25	-	-
Litter	35.05	-	-
TOTAL	100.00	100.00	9,783

Melfort House B, Argyll

This was a steep wooded coastal site 90 m above sea level. Several species typical of woodland were found in the sward - Brachypodium sylvaticum, Endymion non-scriptus, Oxalis acetosella, Teucrium scorodonia and Luzula pilosa - which together accounted for 20% of the ground cover. Anthoxanthum odoratum and Viola palustris were also important species here. Bracken litter covered half of the ground sampled. The sward was again diverse with 24 species present.

None of the above species was found as seed. Juncus effusus was the most common species found as seed and accounted for 32% of the soil seed population with 1,500 seeds/m^2. Seed of Veronica spp was almost as common (1,000/m^2) with significant numbers of Agrostis canina and A. tenuis, Erica cinerea and Potentilla erecta seed also present. Approximately 32% of the soil seed population was accounted for by these species. With the exception of Juncus effusus, which was completely absent, all these species were present in very small quantities in the sward.

4,789 seeds were recovered/m^2 of ground.

Table 19. Composition of sward and seed population at Melfort House B.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & *Agrostis tenuis*	1.75	19.15	917
Agrostis stolonifera	2.75	-	-
Anthoxanthum odoratum	4.90	-	-
Brachypodium sylvaticum	1.25	-	-
Deschampsia caespitosa	1.00	2.13	102
Endymion non-scriptus	0.75	-	-
Erica cinerea	0.25	6.38	306
Festuca rubra	0.75	-	-
Galium saxatile	2.50	2.13	102
Holcus mollis	1.00	-	-
Hypericum pulchrum	1.25	-	-
Hypnum cupressiforme	4.50	-	-
Juncus effusus	-	31.91	1,528
Luzula pilosa	3.00	-	-
Lysimachia nummularia	0.25	-	-
Oxalis acetosella	7.20	-	-
Polytrichum commune	2.75	-	-
Poa pratensis & *Poa trivialis*	-	4.26	204
Potentilla erecta	1.25	6.38	306
Prunella vulgaris	0.50	-	-
Sedum album	0.10	-	-
Stellaria holostea	1.75	-	-
Teucrium scorodonia	8.25	-	-
Trifolium repens	-	2.13	102
Veronica arvensis	-	6.38	306
Veronica officinalis	2.25	-	-
Veronica serpyllifolia	-	17.02	815
Viola palustris	3.65	-	-
Litter	46.40	-	-
Unidentified species	-	2.13	102
TOTAL	100.00	100.00	4,789

Oban A, Argyll

A heavy infestation of tall bracken was found at this site. One third of the ground surface was covered with bracken litter. The soil was quite wet and this was reflected by the presence of three types of moss and a liverwort - Hypnum cupressiforme, Hylocomium splendens, Rhytidiadelphus squarrosus and Lophocolea bidentata respectively, and these species accounted for almost 20% of the sward. Holcus mollis was the dominant grass species, with Viola palustris the dominant herb.

The soil seed population did not reflect the species composition of the sward. Poa spp (P. pratensis and P. trivialis) and Agrostis spp (Agrostis canina and A. tenuis) seed was responsible for almost 30% of the seed recovered, with Potentilla erecta forming 6% and Erica cinerea over 45%. Neither Erica cinerea, Agrostis canina nor A. tenuis was recorded in the sward and Potentilla erecta, Poa pratensis and P. trivialis together formed less than 2% of the ground cover. Seed of few other species was found and then only in small quantities. Since the dominant species in the sward (Holcus mollis and Viola palustris) are both capable of spreading vegetatively, the absence of large seed banks of these species was not unexpected.

A relatively small number of seeds were recovered at this site ($3,057/m^2$).

Table 20. Composition of sward and seed population at Oban A.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & *Agrostis tenuis*	-	10.00	306
Cardamine hirsuta	1.25	3.34	102
Cerastium holosteoides	0.75	-	-
Digitalis purpurea	1.50	-	-
Erica cinerea	-	46.64	1,426
Galium saxatile	2.00	-	-
Holcus mollis	28.75	-	-
Hylocomium splendens	1.50	-	-
Hypnum cupressiforme	3.50	-	-
Juncus bufonius	-	3.34	102
Lophocolea bidentata	2.75	-	-
Luzula campestris	-	3.34	102
Luzula pilosa	1.00	-	-
Poa pratensis & *Poa trivialis*	1.25	19.99	611
Potentilla erecta	0.45	6.67	204
Ranunculus repens	0.25	-	-
Rhytidiadelphus squarrosus	10.40	-	-
Rumex acetosella	0.25	-	-
Stellaria alsine	0.25	-	-
Stellaria media	0.75	-	-
Veronica chamaedrys	0.25	-	-
Veronica officinalis	1.00	-	-
Viola palustris	10.50	3.34	102
Litter	31.65	-	-
Unidentified species	-	3.34	102
TOTAL	100.00	100.00	3,057

Oban B, Argyll

This site was located adjacent to a stream and where 50% of the ground cover was bracken litter. Holcus mollis, Poa pratensis, Poa trivialis, Digitalis purpurea, Cardamine hirsuta and Oxalis acetosella were the dominant species in the sward and accounted for 33% of the ground cover. The remaining fourteen species each made small contributions to the sward.

Oxalis acetosella and Digitalis purpurea were absent from the soil population, as was Holcus mollis. Cardamine hirsuta was present in approximately equal proportions in the soil and in the sward. About 2,250 seeds of Poa pratensis and P. trivialis were present /m^2. This represented 23% of the soil seed population which was approximately three times the representation of these species in the sward. Seed of Juncus bufonius and J. effusus accounted for 52% of the soil seed population with 5,000 seeds/m^2 although J. effusus contributed only 0.75% to the sward and J. bufonius made no contribution. Veronica serpyllifolia, whilst unrepresented in the sward, made a 7% contribution to the seed population (700 seeds/m^2). 9,682 seeds were recovered/m^2 of ground at this site.

Table 21. Composition of sward and seed population at Oban B.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis tenuis & Agrostis canina	-	4.21	408
Agrostis stolonifera	3.50	-	-
Anthoxanthum odoratum	0.50	-	-
Campanula rotundifolia	-	1.05	102
Cardamine hirsuta	4.50	5.27	510
Carex spp	2.25	-	-
Digitalis purpurea	6.75	-	-
Galium saxatile	0.10	-	-
Gnaphalium uliginosum	-	1.05	102
Holcus mollis	9.50	-	-
Hylocomium splendens	0.25	-	-
Hypericum humifusum	-	3.16	306
Hypnum cupressiforme	1.00	-	-
Juncus bufonius	-	13.70	1,325
Juncus effusus	0.75	37.88	3,668
Oxalis acetosella	5.75	-	-
Poa pratensis & Poa trivialis	7.40	23.16	2,242
Ranunculus repens	1.50	2.11	204
Rhytidiadelphus squarrosus	1.25	-	-
Rubus fruticosus	0.50	-	-
Stellaria alsine	2.50	-	-
Urtica dioica	1.00	-	-
Veronica officinalis	1.85	-	-
Veronica serpyllifolia	-	7.36	713
Viola palustris	2.90	-	-
Litter	46.25	-	-
Unidentified species	-	1.05	102
TOTAL	100.00	100.00	9,682

Margrie Farm, Kirkcudbrightshire

The sward of this site comprised a mixture of lowland pasture species (Cirsium spp, Dactylis glomerata and Ranunculus repens) and the more 'typical' bracken land species (Agrostis canina, A. tenuis, Rumex acetosella and Viola palustris). The dominant species in the sward were the grasses which included Agrostis spp (A. canina, A. tenuis), Dactylis glomerata, Holcus lanatus and Poa spp (Poa pratensis and P. trivialis). Viola palustris was the dominant herb with smaller quantities of Digitalis purpurea, Rubus fruticosus and Teucrium scorodonia also present.

Six species (Agrostis canina, A. tenuis, Digitalis purpurea, Holcus lanatus, Poa pratensis and P. trivialis) accounted for nearly 90% of the soil seed population with seven other species contributing to the remaining 10%. D. purpurea seed was by far the most frequently occurring (8,000/m^2) and its contribution to the soil seed population was almost twenty times that of its contribution to the sward. The contribution of Agrostis spp and Poa spp was greater to the seed population than to the sward whilst the proportion of Holcus lanatus was greater in the sward.

The number of seeds/m^2 was estimated to be 13,962/m^2 for the area sampled with almost 8,000 seeds/m^2 contributed by Digitalis purpurea.

Table 22. Composition of sward and seed population at Margrie Farm.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & Agrostis tenuis	5.25	10.95	1,529
Cardamine hirsuta	-	0.73	102
Carex spp	0.25	-	-
Cerastium holosteoides	1.25	0.73	102
Cirsium dissectum	0.25	-	-
Cirsium vulgare	2.90	-	-
Dactylis glomerata	4.75	-	-
Digitalis purpurea	3.50	56.93	7,948
Gnaphalium uliginosum	-	2.19	306
Holcus lanatus	14.25	8.76	1,223
Juncus bufonius	-	1.46	204
Lonicera periclymenum	1.50	-	-
Matricaria matricarioides	-	0.73	102
Poa pratensis & Poa trivialis	5.50	13.14	1,834
Potentilla erecta	-	1.46	204
Ranunculus repens	1.15	-	-
Rubus fruticosus	3.60	-	-
Rumex acetosella	0.35	-	-
Stellaria media	1.65	-	-
Teucrium scorodonia	3.50	-	-
Trifolium repens	0.25	-	-
Ulex europaeus	0.75	-	-
Veronica serpyllifolia	-	0.73	102
Viola palustris	4.35	-	-
Litter	45.00	-	-
Unidentified species	-	2.19	306
TOTAL	100.00	100.00	13,962

Gatehouse of Fleet C, Kirkcudbrightshire

The bracken was quite dense and high and 45% of the ground cover was bracken litter. Sheep and cattle which grazed on the Gatehouse A and B sites had access to this site also and certain of the species found here have quite probably been carried by the animals from these other sites, for example, Polygonum spp and Plantago major.

The main species in the sward were Agrostis canina, A. tenuis, Holcus mollis and Digitalis purpurea and to a lesser extent Viola palustris. These species accounted for 36% of the ground cover. Seventeen other species each contributed small quantities to the sward.

Despite their absence from the sward, Juncus bufonius and J. effusus accounted for 45% of the site seed population of 18,446 seeds/m^2. Juncus plants were noted growing outside the area sampled and some of the seed must presumably have come from this source. Approximately 4,000 Agrostis canina and A. tenuis seeds were found /m^2 of soil and these species were twice as frequent in the soil as they were in the sward. Poa annua and Hypericum humifusum, both absent from the sward, contributed significant amounts of seed to the soil seed population, (1,121 and 2,038 seeds/m^2 respectively). No seed of Holcus mollis or Viola palustris was recovered and only small amounts of Digitalis purpurea. Twelve other species contributed the remaining 3,000 seeds/m^2.

Table 23. Composition of sward and seed population at Gatehouse of Fleet C.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & *Agrostis tenuis*	9.75	22.10	4,076
Agrostis stolonifera	2.00	-	-
Anthoxanthum odoratum	2.25	-	-
Cardamine hirsuta	0.35	1.66	306
Carex spp	0.75	-	-
Cerastium holosteoides	0.40	3.31	611
Deschampsia flexuosa	1.60	-	-
Digitalis purpurea	8.75	1.66	306
Erica cinerea	-	1.11	204
Galium saxatile	0.90	-	-
Gnaphalium uliginosum	-	0.55	102
Holcus mollis	13.60	-	-
Hypericum humifusum	-	11.05	2,038
Juncus bufonius	-	34.81	6,420
Juncus effusus	-	9.39	1,732
Myosotis arvensis	0.50	-	-
Oxalis acetosella	0.50	-	-
Plantago major	-	0.55	102
Poa annua	-	6.00	1,121
Poa pratensis & *Poa trivialis*	0.75	1.11	204
Polygonum aviculare	0.15	-	-
Polygonum persicaria	-	0.55	102
Potentilla erecta	0.25	-	-
Rumex acetosella	-	0.55	102
Rumex obtusifolius	0.75	-	-
Stellaria alsine	0.50	-	-
Stellaria media	3.00	2.76	510
Teucrium scorodonia	1.50	-	-
Veronica arvensis	-	0.55	102
Veronica officinalis	0.50	-	-
Veronica serpyllifolia	-	1.66	306
Viola palustris	4.50	-	-
Litter	46.75	-	-
Unidentified species	-	0.55	102
TOTAL	100.00	100.00	18,446

Gatehouse of Fleet A, Kirkcudbrightshire

This site differed considerably from the previous eighteen sites. This site had in the past been sprayed with glyphosate and the bracken more or less eliminated. No bracken litter remained on the soil surface. The area was heavily poached by cattle in the winter when additional feed was left there by the farmer. The high nutrient input, severe soil disturbance and the possible introduction of foreign species in the fodder have led to the development of a highly diverse sward at this site. The pH of the soil here (5.62) was higher than on any of the other sites examined and this has allowed a further diversification of the flora. How great a contribution the removal of bracken itself has been in the development of this sward is not clear but, relative to the factors already outlined, it is probably quite small. It would be wrong to suggest that this site is representative of one successfully sprayed and cleared of bracken.

Twenty-eight to thirty species were found here with only five contributing more than 5% each to the sward. Agrostis stolonifera, Poa annua, Plantago major, Stellaria media and Veronica spp were the main components of the sward and each formed between 10 and 20% of the ground cover. The presence of Ranunculus repens, Trifolium repens, Urtica dioica and Dactylis glomerata indicated a higher pH and nutrient status than that normally associated with a bracken infested site.

Less than 1% of the sward was occupied by Matricaria matricarioides although it contributed 47% of the seeds in the soil (approximately 56,000/m^2). The second most frequently occurring seeds were those of Juncus bufonius, which, together with J. effusus, contributed approximately 18,000 seeds/m^2. Both species were completely absent from the sward and no Juncus plants were noted in the surrounding areas. This suggests that the seeds had blown onto the site and become buried or had survived in a viable state in the soil since they were shed from plants growing on the site prior to spraying.

Several species characteristic of bare or disturbed ground were present in very high numbers in the soil although often only in relatively low proportions in the sward. Between 800 and 18,000 seeds/m^2 were contributed by each of these species which included Rumex obtusifolius, Cerastium holosteoides, Plantago major, Poa annua, Polygonum spp, Stellaria media, Gnaphalium uliginosum and Veronica spp. The absence of seed of Agrostis stolonifera, despite its importance in the sward, was much as expected in that this species spreads, as its name suggests, by stolon extension.

The estimated number of seeds of all the species in the soil was extremely high at approximately 120,000 seeds/m^2; most of this being contributed by Juncus bufonius, Matricaria matricarioides, Veronica arvensis and Stellaria media (80%).

Table 24. Composition of sward and seed population at Gatehouse of Fleet A.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & Agrostis tenuis	2.50	0.09	102
Agrostis stolonifera	18.70	-	-
Anagallis arvensis	0.40	-	-
Anthoxanthum odoratum	-	0.17	204
Aphanes arvensis	-	0.26	306
Capsella bursa-pastoris	0.90	0.68	816
Cerastium holosteoides	0.50	1.71	2,038
Cirsium arvense	2.15	-	-
Dactylis glomerata	1.00	-	-
Digitalis purpurea	-	0.09	102
Gnaphalium uliginosum	1.55	1.96	2,344
Holcus lanatus	0.50	0.43	510
Holcus mollis	1.00	-	-
Juncus bufonius	-	13.57	16,204
Juncus effusus	-	1.71	2,038
Matricaria matricarioides	0.60	47.13	56,255
Myosotis arvensis	4.55	-	-
Plantago major	13.35	3.42	4,076
Poa annua	20.55	3.67	4,382
Poa pratensis & Poa trivialis	-	0.09	102
Polygonum aviculare	1.10	-	-
Polygonum aviculare & Polygonum hydropiper	-	1.62	1,936
Polygonum persicaria	-	0.26	306
Polygonum persicaria & Polygonum hydropiper	0.15	-	-
Potentilla anserina	1.30	-	-
Prunella vulgaris	0.50	-	-
Ranunculus repens	3.95	0.17	204
Rumex acetosella	0.50	0.09	102
Rumex obtusifolius	3.25	0.68	815

Cont ....

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Sagina procumbens	–	0.51	611
Sonchus arvensis	0.70	–	–
Spergula arvensis	0.20	0.09	102
Stellaria media	10.30	5.81	6,930
Trifolium repens	0.10	–	–
Urtica dioica	0.10	0.26	306
Veronica arvensis	3.20	13.31	15,898
Veronica persica	6.40	1.62	1,936
Veronica serpyllifolia	–	0.34	408
Unidentified species	–	0.26	306
TOTAL	100.00	100.00	119,338

Gatehouse of Fleet B, Kirkcudbrightshire

This site was in the past sprayed with fosamine to clear the bracken but frond reinfestation has since taken place and the fronds are now quite dense and very tall. The Gatehouse A site was not far removed from this site and the free access of cattle to both sites has influenced the species composition of both the sward and the soil. Bracken litter covered about 16% of the site.

The sward composition reflected both the increased pH of the soil (relative to the untreated bracken sites) and the effect of severe poaching by cattle. The species diversity was again higher at this site than on the more 'typical' bracken sites and no one species was overwhelmingly dominant. Cardamine hirsuta, Holcus mollis, Poa spp (Poa pratensis and P. trivialis), Ranunculus repens and Stellaria media all contributed between 10 and 15% to the sward, with a lesser contribution from Myosotis arvensis (6%). Nineteen other species accounted for the remaining 17% of ground cover.

The dominant species in the soil was Juncus bufonius with over 4,000 seeds/m^2 and this figure represented 28% of the site total of 14,267 seeds/m^2. Each of Cardamine hirsuta, Cerastium holosteoides, Myosotis arvensis, Polygonum aviculare/P. hydropiper, Sagina procumbens and Stellaria media contributed over 1,000 seeds/m^2 to the soil seed population. No Juncus bufonius or Sagina procumbens were found in the sward whilst Polygonum spp and Cerastium holosteoides were barely represented. Stellaria media and Myosotis arvensis were more frequent in the sward than in the soil. Ranunculus repens, Holcus mollis and Poa spp, all important in the sward, were absent from the soil. Cardamine hirsuta was twice as frequent in the sward as in the soil where it contributed 8% of the seed in the soil.

Table 25. Composition of sward and seed population at Gatehouse of Fleet B.

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina & Agrostis tenuis	1.75	1.43	204
Agrostis stolonifera	1.75	-	-
Aphanes arvensis	0.25	2.86	408
Cardamine hirsuta	13.25	7.86	1,121
Cerastium holosteoides	0.50	12.86	1,834
Cirsium arvense	0.50	-	-
Digitalis purpurea	2.50	-	-
Galium aparine	2.00	-	-
Geranium molle	0.50	-	-
Gnaphalium uliginosum	-	4.29	611
Holcus lanatus	-	2.14	306
Holcus mollis	12.00	-	-
Juncus bufonius	-	25.58	4,076
Matricaria matricarioides	-	0.71	102
Myosotis arvensis	6.00	3.57	510
Plantago major	0.50	0.71	102
Poa annua	-	0.71	102
Poa pratensis & Poa trivialis	10.25	-	-
Polygonum aviculare	2.10	-	-
Polygonum aviculare & Polygonum hydropiper	-	7.86	1,121
Polygonum persicaria	-	4.29	611
Polygonum persicaria & Polygonum hydropiper	0.75	-	-
Prunella vulgaris	0.75	-	-
Ranunculus repens	10.50	-	-
Rumex acetosella	0.75	-	-
Rumex obtusifolius	0.50	-	-
Sagina procumbens	-	9.29	1,325
Sonchus asper	-	0.71	102
Stellaria media	14.40	7.86	1,121

Cont ....

Species	Vegetation % cover	Seed population % contribution	No. of viable seeds/m^2
Trifolium repens	0.25	-	-
Urtica dioica	1.25	0.71	102
Veronica arvensis	-	2.14	306
Veronica officinalis	0.25	-	-
Veronica persica	0.25	-	-
Veronica serpyllifolia	-	0.71	102
Viola palustris	0.25	-	-
Litter	16.25	-	-
Unidentified species	-	0.71	102
TOTAL	100.00	100.00	14,267

A total of ninety-one different species, comprising seventeen grasses and sixty-nine herbaceous species, four mosses and one liverwort, were found in the swards of the various sites. Of this number, only six were confined exclusively to the sites which had been sprayed (*Mentha arvensis*, *Plantago major*, *Poa annua*, *Polygonum hydropiper*, *Veronica arvensis* and *Veronica persica*). A complete list of the species found in the swards of all the sites is given in Appendix 1:C:Table 4. The fifteen species listed in Table 26 were found with sufficient frequency to be considered 'typical' of bracken infested land.

Table 26. Sward cover of main species in untreated bracken sites.

Species	Mean % cover/site of occurrence	
Agrostis canina & *Agrostis tenuis*	10.74	Present in 12 or more sites
Galium saxatile	8.42	
Agrostis stolonifera	7.04	
Anthoxanthum odoratum	3.85	
Viola palustris	2.37	
Potentilla erecta	2.30	
Carex spp	1.91	
Festuca rubra	11.18	Present in more than 7 but fewer than 12 sites
Holcus mollis	10.51	
Digitalis purpurea	4.17	
Luzula campestris	2.92	
Hypnum cupressiforme	2.79	
Poa pratensis & *Poa trivialis*	2.45	
Veronica spp	1.76	
Rumex acetosella	1.67	

There was considerable variation in the amount of litter present (9.25-62.20%) but on average this accounted for 30% of the ground cover at each site and was of variable thickness.

All the estimates of seed numbers refer to viable seeds. For each species the number of viable seeds recovered in the twenty samples from that site was determined. Each of these figures was composed of two elements; firstly, those seeds which were recovered from the samples during the visual examination and which germinated when placed on moist filter paper under various environmental conditions, and secondly, those seeds which germinated when the sample was sown out onto pots of compost. Each of these figures was converted to an estimate of viable seed numbers per m^2. (See Appendix 1:B for conversion formula).

For certain species (Polygonum spp, Ranunculus repens, Rumex spp, Trifolium repens, Urtica dioica and Gnaphalium uliginosum) although large quantities of seed were recovered, the germination tests suggested that many were either dormant (and could not be stimulated to germinate) or were non-viable. All these species had hard testas. The total number of seeds recovered per site is given in Appendix 1:C:Table 3 and the viability of the seeds of the various species is given in Appendix 1:C:Table 5.

The seed populations at the various sites consisted of ten grasses and thirty-seven herbaceous species. Seed of Aphanes arvensis, Capsella bursa-pastoris, Myosotis arvensis, Polygonum aviculare/Polygonum hydropiper, Rumex obtusifolius, Sonchus asper, Spergula arvensis, Urtica dioica and Veronica persica was recovered only from samples from the two sprayed sites. Table 27 indicates the main species present in the soil of the untreated bracken sites. Species such as Calluna vulgaris, Digitalis purpurea, Hypericum humifusum and Sagina procumbens were important in that, although they occurred in only a limited number of sites, they were present in sufficient quantities to have the potential to cause localised weed problems following frond clearance. The remaining herbaceous species which occurred in significant quantities (Erica cinerea, Galium saxatile, Juncus bufonius, Juncus effusus, Potentilla erecta, Rumex acetosella and Veronica spp) were present sufficiently frequently to have the potential to cause more widespread problems following bracken removal. Those species which might be deemed to be agriculturally important with respect to their palatability and nutritional value for the grazing animal were the grasses: Agrostis spp, Poa spp, Anthoxanthum odoratum and Holcus lanatus. These last two species tended to occur less frequently and were of lesser importance than the other grasses.

Table 27. Main species found as seed in soil samples from untreated bracken sites.

Species	Mean no. of viable seeds/site of occurrence (no./m^2)	Mean % contribution to seed population/ site of occurrence	Frequency
Erica cinerea	2,031	19.78	Present in 8 or more sites
Juncus bufonius	1,763	16.93	
Agrostis canina & Agrostis tenuis	1,525	22.17	
Juncus effusus	1,401	16.16	
Poa pratensis & Poa trivialis	620	8.84	
Veronica spp	502	3.75	
Galium saxatile	242	4.42	
Potentilla erecta	232	4.66	
Rumex acetosella	214	4.47	
Digitalis purpurea	4,642	33.49	Present in fewer than 8 sites
Calluna vulgaris	2,602	19.09	
Hypericum humifusum	816	4.86	
Anthoxanthum odoratum	646	15.49	
Holcus lanatus	578	5.74	
Sagina procumbens	578	15.79	
Poa annua	510	3.69	

At the sites where the bracken had been sprayed (Gatehouse of Fleet A and B) a greater diversity of species existed even if frond recolonisation was taking place (Gatehouse B). This is clearly illustrated in Table 28 which compares the sward composition and soil seed populations of the Gatehouse A and B sites (sprayed) with that of a more 'typical' bracken site - Sundaywellmoor A (untreated). The severe poaching inflicted by sheep and cattle which have free access to both the Gatehouse sites together with the introduction of seeds with supplementary feed left by the farmer during the winter have probably been the major factors which determined the composition of both the sward and the soil populations of these two sites.

6.4 *Discussion of results*

The main species associated with the untreated bracken sites as plants in the sward were Galium saxatile and the grasses, and to a lesser extent Digitalis purpurea, Luzula campestris, Potentilla erecta and Viola palustris. In the soil, the number of seeds of herbaceous species far exceeded the number of seeds of graminaceous species with seeds of Calluna vulgaris, Digitalis purpurea, Erica cinerea, Juncus bufonius and Juncus effusus outnumbering those of Agrostis canina, Agrostis tenuis, Holcus lanatus, Poa annua, Poa pratensis and Poa trivialis by five to one. With perhaps the exception of Agrostis canina and Agrostis tenuis, the number of grass seeds found in the soil samples was much lower than that expected considering their dominance in the sward. The extent of the seed banks of species such as Calluna vulgaris, Digitalis purpurea, Juncus bufonius and Juncus effusus was quite unexpected. With the exception of Digitalis purpurea, these species were practically absent from the vegetation cover, yet each contributed over 1,400 seeds per m^2 to the soil seed population. Several papers have considered the relationship between the representation of a species in the sward and its representation in the soil.

Table 28. Main species of sward and seed population of successfully sprayed (Gatehouse A), unsuccessfully sprayed (Gatehouse B) and untreated (Sundaywellmuir A) sites.

Species	Gatehouse A			Gatehouse B		
	Sward % cover	Seed population % contribution	No. of viable seeds/m^2	Sward % cover	Seed population % contribution	No. of viable seeds/m^2
Agrostis canina and Agrostis tenuis						
Agrostis stolonifera	18.70	-	-			
Anthoxanthum odoratum						
Calluna vulgaris						
Cardamine hirsuta				13.25	7.86	1,021
Cerastium holosteoides	0.50	1.71	2,038	0.50	12.86	1,834
Deschampsia caespitosa						
Deschampsia flexuosa						
Erica cinerea						
Festuca rubra						
Galium saxatile						
Gnaphalium uliginosum	1.55	1.96	2,344			
Holcus mollis				12.00	-	-
Juncus bufonius	-	13.57	16,204	-	28.58	4,076
Juncus effusus	-	1.71	2,038			
Matricaria matricarioides	0.60	47.13	56,255			
Myosotis arvensis	4.55	-	-	6.00	3.57	510
Plantago major	13.35	3.42	4,076			
Poa annua	20.55	3.67	4,382			
Poa pratensis and Poa trivialis				10.25	-	-
Polygonum aviculare	1.10	-	-	2.10	-	-
Polygonum aviculare and Polygonum hydropiper	-	1.62	1,936	-	7.86	1,121
Polygonum persicaria and Polygonum hydropiper				0.75	-	-
Polygonum persicaria				-	4.29	611
Ranunculus repens	3.95	0.17	204			
Rumex acetosella						
Rumex obtusifolius	3.25	0.68	815			
Sagina procumbens	-	0.51	611	-	9.29	1,325
Stellaria media	10.30	5.81	6,930	14.40	7.86	1,121
Veronica spp	9.60	14.95	17,834	0.50	2.85	408
Litter	0.00	-	-	16.25	-	-
Other species	12.00	3.11	3,671	24.00	12.84	1,834
TOTAL	100.00	100.00	119,338	100.00	100.00	14,267

According to Chippindale and Milton (1934) and Milton (1936, 1939) with the exception of Holcus lanatus, Agrostis spp, Poa annua, Poa pratensis and Festuca ovina, most grasses rely on vegetative growth to colonise new ground and hence have a relatively low representation in the soil population, whilst Champness and Morris (1948) included Poa trivialis in the above list and suggested that Holcus lanatus and Anthoxanthum odoratum were represented in approximately equal proportions in the soil seed population and in the sward. Mortimer (1976) showed that only about 13% of Holcus lanatus seed actually entered the seed bank; this presumably might lead to a greater representation of this species in the sward and Watt (1978) indicated that seed of this species germinates readily soon after it is shed. Thompson and Grime (1979) classified Holcus lanatus, Poa annua and Poa trivialis as species having persistent seed banks (although many of the seeds germinate soon after release, the remainder become incorporated into a persistent seed bank). This might lead to significant quantities of buried seeds occurring in the soil and hence to a greater representation of these species in the soil than in the sward.

Thompson and Grime (1979) found Dactylis glomerata and Festuca rubra to have transient seed banks (where none of the seed output persists in the soil in a viable condition for more than one year); a fact which would give rise to a greater contribution to the sward than to the soil population. Champness and Morris (1948) found both these species to be better represented in the sward, as did van Altena and Minderhoud (1972) and similar comments were made with respect to Festuca rubra by Dore and Raymond (1942) and Howe (1980). Harberd (1961) suggested that many populations of Festuca rubra were actually clones of very great age and the absence of buried viable seeds in many soils lends credence to his theory. Mortimer (1976) showed that only small proportions (8%) of Dactylis glomerata seed became incorporated into a seed bank.

Both Milton (1943) and Champness and Morris (1948) found smaller quantities of Deschampsia caespitosa in the soil than in the sward. This species has a tufted growth form and probably does rely heavily on seed production for its spread to fresh ground. It seems that much of the seed shed by these plants germinates on the soil surface and most of the seeds do not succeed in entering the soil (Milton, 1943). Thompson and Grime (1979) suggested that this species had a persistent seed bank and Chancellor (1979) found that this species has prolonged dormancy and one might therefore expect significant quantities of seed in the soil where this species occurs in the sward.

Few buried seeds of Molinia caerulea or Nardus stricta were found even where they were the chief components of the swards examined (Chippindale and Milton, 1934; Milton, 1936, 1939). Milton (1936) suggested that certain natural causes prevent large quantities of seed of these species from entering the soil and remaining there in a viable condition. Jeffries (1915) working with Molinia caerulea, found that a large number of the seeds germinated on the soil surface so few were available to form a buried seed bank. Although Champness and Morris (1948) allocated Molinia caerulea to that group of species which made a greater contribution to the sward than to the soil seed population, Eadie and Black (1981) found significant quantities of Molinia caerulea and Nardus stricta seeds in a site which was dominated by these species.

Champness and Morris (1948) allocated Holcus mollis to that group of species which made a greater contribution to the sward than to the soil population. Hill (1980) found that in forest soils seeds of Deschampsia flexuosa survived for only short periods of time and that the species relied heavily upon established plants for its survival and Thompson and Grime (1979) found few seeds of Deschampsia flexuosa in the soil even where this plant was an important component of the sward. At one of their sites these authors noted that both Holcus mollis and

Deschampsia flexuosa produced little seed during their study and Al-Mufti et al (1977) found that in shaded situations both species exhibited low levels of flowering.

Tables 26 & 27 indicated, for the untreated bracken sites in this study, the main grass species associated with the sward and with the soil seed population respectively. Poa annua was not considered to be amongst the most important species in the sward yet considerable quantities of seed were recovered from the soil (500/m^2). Agrostis tenuis and A. canina contributed approximately 22% of the seeds in the soil at the sites where they were recorded (1,500/m^2); double their contribution to the sward. Similarly, Poa pratensis and Poa trivialis accounted for 8.84% of the soil seed population (600 seeds/m^2) but only 2.45% of the sward. These results are in agreement with the findings of previous workers, which are outlined above. Holcus lanatus provided 6% of the seed population (600 seeds/m^2) and approximately 3.25% of the sward. Anthoxanthum odoratum accounted for 15.50% of the seed population (650 seeds/m^2) but only 3.85% of the sward. These species were both considered to be present in approximately equal amounts in the sward and in the soil by Champness and Morris (1948). However, the authors did stress that the data upon which they had based the assignment of these two species to this category were variable, that the species were often present in only small amounts and that further work might permit a reclassification of the species. Whilst Holcus mollis was responsible for 10% of the sward, no seed of this species was recovered in the untreated sites. This was in accordance with the data of Champness and Morris (1948) and the general observations of Thompson and Grime (1979) and Al-Mufti et al (1977).

Other grasses which were important constituents of the sward were Agrostis stolonifera and Festuca rubra. Like Holcus mollis, Agrostis stolonifera is a species with a predominantly creeping habit and the absence of seed of this species is again not surprising. Although Chippindale and Milton (1934) and Milton (1936, 1939) noted that Agrostis spp were excepted from the general observation that most grasses relied on vegetative growth to colonise new ground, they made no distinction between Agrostis stolonifera, which relies on stolon extension for growth, and other Agrostis species such as Agrostis tenuis, which rely on seed production to spread. Howe (1980) found that Agrostis stolonifera seed had some innate dormancy and also that dormancy was readily enforced by burial which suggests that when seeds are shed they have a good chance of entering the seed bank. The absence of seed of Festuca rubra supports the findings of many other workers, which have been outlined previously. This species germinates freely and is therefore unlikely to become a major component of the seed bank (Howe, 1980). Molinia caerulea and Nardus stricta were both recorded in the swards of a few sites but no seed of either species was recovered; Deschampsia caespitosa was also infrequent in the sward and only a very limited quantity of seed of this species was recovered. Insufficient data were obtained to make it possible to place these three species in the various categories according to their relative contributions to the sward and to the soil.

With respect to the non-grass species, published data (Chippindale and Milton, 1934; Milton, 1936; Champness and Morris, 1948; WRO, 1980) suggest that Calluna vulgaris, Erica cinerea, Juncus spp and Sagina procumbens have numbers of viable seeds in the soil greatly in excess of their proportional representation in the sward. Thompson and Grime (1979) added Potentilla erecta and Digitalis purpurea to this list on the basis that they had persistent seed banks and although this did not in itself imply that the representation of seed in the soil exceeded that of plants in the sward, this was in fact the case for Digitalis purpurea in this study. In the present work, (Tables 26 & 27) Juncus bufonius, Juncus effusus, Erica cinerea, Calluna vulgaris, Sagina procumbens and Digitalis purpurea contributed between 15 and 35% of the soil seed population where they occurred with mean seed numbers per m^2 between 500 and 4,600. None of these species, with the exception of Digitalis purpurea (4.2%), made significant contributions to the sward. Potentilla erecta was twice as frequent in the soil (4.66%) as in the sward (2.30%). Whilst Chippindale and Milton (1934) and Champness and Morris (1948) found Luzula campestris, Galium spp and Veronica spp to be present in approximately equal proportions, Milton (1939) and Thompson and Grime (1979) suggested that Galium saxatile was present in far greater proportions in the soil. The results obtained here indicate that Galium saxatile was twice as frequent in the sward (8.42%) as in the soil (4.42%) with approximately 250 seeds/m^2, whilst Luzula campestris was equally frequent in the soil and in the sward and Veronica spp were twice as frequent in the soil (3.75%) as in the sward (1.76%). About 500 Veronica seeds were found per m^2. Rumex spp were considered by Chippindale and Milton (1934) and Champness and Morris (1948) to be present in equal proportions but the data obtained here showed Rumex acetosella to be two and a half times more frequent in the soil than in the sward. Carex spp were frequent in the sward although in quite small proportions (2%/site) and practically no seed of this genus was recovered. The results obtained by earlier workers conflict and insufficient data were obtained here to decide the issue. Chippindale and Milton (1934) and Milton (1939) found the number of Carex seeds in a viable condition in the soil to be far in excess of their proportional representation as plants in the sward; whilst Champness and Morris (1948) suggested that Carex spp made an equally important contribution to the soil and to the sward and Thompson and Grime (1979) noted that Carex spp although frequently present in the vegetation were often absent or present in only small amounts in the soil.

One of the problems which arose when comparing the percentage contributions made by the species to the sward with that made by the seeds to the soil population related to the total number of seeds recorded per site. Half of the untreated sites had less than 5,000 seeds/m^2 and in these situations the location of one extra seed (representing 102 seeds/m^2 - see Appendix 1:B for conversion formula) altered the percentage contribution to the seed population by between 2.12 and 3.33% whilst in those sites with more than 10,000 seeds/m^2, locating one extra seed altered this figure by only 0.37 to 0.93%. Thus, it was easier to suggest that a species made a greater contribution to the soil seed population than to the sward in those sites where the soil seed population was smaller. For example, finding three seeds of a particular species in a sample from Barlaes Hill (total seed population - 27,000/m^2) suggested a 1% contribution to the soil seed population but at Oban A (total seed population - 3,000/m^2) three seeds represented a 10% contribution to the seed population. This bias was not eliminated when the mean contribution per site of occurrence was calculated (Table 27). In particular, at sites where one species accounts for by far the greatest proportion of the seeds, care should be taken when making comparisons between percentage contributions to the sward and to the seed population. This point was also made by Jensen (1969) who found that if he omitted the seed population data for Juncus bufonius the relationship between representation in the soil and the sward was more meaningful for the remaining species. Because relatively few actual seeds were recovered in the samples even where a species was deemed to contribute, for example, 15% of the seeds in the soil, this might in reality have been less than 10 actual seeds. For example, at Polharrow A, Erica cinerea was found to contribute 22% of the seeds in the soil; this figure was based on the actual location of only 7 seeds.

Despite these limitations, the results presented here were in agreement with those of many previous workers (Chippindale and Milton, 1934; Milton, 1936, 1939; Dore and Raymond, 1942; Prince and Hodgdon, 1946; Olmsted and Curtis, 1947; Champness and Morris, 1948; Bruno, 1953; Douglas, 1965; Major and Pyott, 1966; van Altena and Minderhoud, 1972; Jalloq, 1975; Thompson and Grime, 1979; WRO, 1980; Eadie and Black, 1981) who all found that there was frequently a poor correspondence between the composition of the sward and that of the buried viable seed population below it.

The Gatehouse A and B sites were considered separately in that both had been sprayed with herbicides to eliminate the bracken growing on them. Frond reinfestation had taken place on the Gatehouse B site and although at first sight it appeared to be a fairly 'typical' bracken site, many of the features of a sprayed site were still evident (Tables 24, 25 and 28). Many of the species found on these two sites might have been present as a result of several factors other than that of the effect of the chemical treatment of bracken alone. The heavy poaching by cattle had created an ideal environment for species adapted to bare or frequently disturbed ground. Plantago major and Ranunculus repens, although both perennial species, have prostrate growth forms which enabled them to tolerate trampling. Annual species, which are both highly opportunistic and which seed profusely, were frequent and include Cardamine hirsuta, Gnaphalium uliginosum, Matricaria matricarioides, Myosotis arvensis, Polygonum spp, Poa annua, Stellaria media and Veronica spp. The practice of putting out winter feed on these sites had possibly led to the introduction of species with the feed. A higher nutrient level and soil pH had enabled many of the species found here to thrive. It was not possible to determine how great a contribution was made by the removal of bracken fronds and litter to the present sward and soil floras but it was likely to be a less significant contribution than that made by some of the factors outlined above.

The more desirable grasses, Agrostis stolonifera and Poa annua at Gatehouse A and Poa pratensis and P. trivialis at Gatehouse B, accounted for 19, 21 and 10% of the swards respectively with Holcus mollis contributing 12% of the ground cover at Gatehouse B. Less desirable weedy species which were important constituents of the sward were Plantago major (13%) & Stellaria media (10%) at Gatehouse A, Stellaria media (14%) and Cardamine hirsuta (13%) at Gatehouse B and to a lesser extent Veronica spp (10%) at Gatehouse A and Myosotis arvensis (6%) at Gatehouse B.

With the exception of Agrostis stolonifera, Holcus mollis, Poa spp and Myosotis arvensis, the remaining species were well represented in the soil. (Gatehouse A: Plantago major 4,000 seeds/m^2, Stellaria media 7,000 seeds/m^2, Veronica spp 18,000 seeds/m^2; Gatehouse B: Cardamine hirsuta 1,800 seeds/m^2, Stellaria media 1,100 seeds/m^2). Several other species which accounted for only relatively small proportions of the swards (<5%) made significant contributions to the seed population. This group of species included:-

Gatehouse A		Gatehouse B	
Cerastium holosteoides	2,000/m^2	Cerastium holosteoides	1,800/m^2
Gnaphalium uliginosum	2,300/m^2	Juncus spp	4,000/m^2
Juncus spp	18,000/m^2	Polygonum spp	1,700/m^2
Matricaria matricarioides	56,000/m^2	Sagina procumbens	1,300/m^2
Polygonum spp	2,200/m^2		

Because of the very large quantities of seed recovered for certain species (Matricaria matricarioides, Juncus spp, Stellaria media, Veronica spp) the figures obtained for the percentage contribution made to the soil seed population by some of the other species were distorted and it appeared that they made only relatively minor contributions. These figures did not adequately reflect the large numbers of viable seeds of these species. For example, the 3% contribution to the seed population made by Plantago major did not place it in the group of species which made an important contribution to the seed population. However, over 4,000 seeds of this species were estimated to be present per m^2, which was not an insignificant number of seeds. Therefore, the actual numbers of seeds recovered might be more relevant at these sites than the percentage contribution figures.

Chippindale and Milton (1934) and Champness and Morris (1948) considered Cerastium holosteoides, Juncus bufonius and Sagina procumbens to be more frequent in the soil than in the sward and Holcus mollis and Rumex spp to be more frequent in the sward. The results obtained here agree with these findings. Whilst Plantago spp and Veronica spp were thought to contribute equally to the sward and to the soil by these workers, in this study, Plantago major made a greater percentage contribution to the sward and Veronica spp made a greater contribution to the soil. Poa annua, Poa pratensis and Poa trivialis and Ranunculus repens were found to contribute more to the soil than to the sward in previous work (Chippindale and Milton, 1934; Champness and Morris, 1948); the converse was true here. No published data were available with which to compare the relative contributions to the sward and to the soil of the remaining species.

Like Holcus mollis, Agrostis stolonifera reproduces largely by vegetative means and the greater contribution to the sward by this species was as expected. The large numbers of Cerastium holosteoides, Gnaphalium uliginosum, Matricaria matricarioides and Polygonum aviculare/ P. hydropiper were surprising considering their contributions to the sward, and, whilst Veronica spp were important in the sward (9.60%) and a significant seed population was expected, the enormity of it was not

($18,000$ seeds/m^2). Since no Juncus plants were recorded on either site or in their surrounds, the source of the 18,200 Juncus seeds/m^2 is assumed to be either windblown seed from a plant, or plants, some distance away or seed which has remained in a viable condition buried in the soil since such a time as plants were last growing at the site (possibly prior to bracken spraying two years before sampling). Similar cases were found at Oban, Melfort and Glen Douglas where large numbers of Juncus seeds were recovered from the soil although only a small contribution, or no contribution, was made by these species to the sward.

The data from a more 'typical' bracken site (Sundaywellmoor A) are also given in Tables 12 and 28 and the quite significant differences in the composition of the sward and the soil seed population of this site and those which had been sprayed are clearly illustrated. Points which should be noted are the relative number of species which contributed to the sward and to the soil in the sprayed and untreated sites. At the Gatehouse A and B sites 28-29 and 25-28 different species were found in the respective swards but only 17-19 were identified at the Sundaywellmoor A site. In the soil, 26-29, 19-21 and 9-10 species contributed to the seed populations at Gatehouse A, Gatehouse B and Sundaywellmoor A respectively. The mean number of seeds/m^2 was considerably higher for the sprayed sites than for the untreated sites, particularly with respect to the Gatehouse A site. About 120,000 and 14,300 seeds were recovered per m^2 at the Gatehouse A and B sites respectively. The mean number of seeds/m^2 on the untreated sites was estimated to be 8,583/m^2 but, as may be seen from the figures in Appendix 1:C:Table 3 there was much variation between the sites. The site totals ranged from 3,000/m^2 at the Oban A site to 27,210/m^2 at the Barlaes Hill site.

All these figures relate to the number of viable seeds per m^2. Seed viability was about 77% of the total number of seeds recovered.

Attempts to germinate the remaining 23% of seeds were unsuccessful and these seeds were deemed to be either non-viable or dormant. Many of the particularly high estimates of seed numbers for the untreated sites were the result of the extensive populations of one or two individual species such as Juncus bufonius, Juncus effusus, Erica cinerea, Calluna vulgaris and Digitalis purpurea; all species which have relatively small seeds.

6.5 *General discussion*

Clearance of bracken with asulam tends to leave sufficient vegetation for at least a partial colonisation of the exposed ground by the species normally associated with bracken infested hill land and thus without major changes in species composition. The vegetative spread of these species and that of species adjacent to the sprayed plot partially accounts for the changes in sward composition which take place. However, vegetative growth, especially of grasses, is relatively slow (compared with the herbaceous species) and this enables weed species to establish from buried seed. Existing species are at a further disadvantage if their main method of reproduction is sexual since bracken is sprayed in late summer and it is not until the following June that their seed will be ripe. Asulam spraying has little effect on the normal progress of bracken dieback in the autumn of the year of spraying. Some of the species present in the sward will have set seed in June of that year and some of this may have germinated in that same summer. Its growth is likely to be slow because of shading by bracken and the plants are likely to be smothered when the fronds collapse over the winter. Also, seedling grasses are more susceptible to asulam than are established plants (Williams, 1981). It seems likely therefore that, especially in those species in which little seed enters the seed bank or in which viability when buried is rapidly lost, little contribution from seed germination can be expected until their seeds ripen and possibly germinate in the June following spraying. This gives plants establishing from buried seed four to six weeks advantage.

Removal of the canopy is likely to change both the quantity and type of light which reaches the soil surface and this alone may be sufficient to induce buried seeds to germinate whilst the diurnal fluctuations of temperature and moisture which occur on or near the soil surface are known to stimulate the germination of certain species, for example, Holcus lanatus (Watt, 1978).

On average, 30% of the ground below the canopy was covered with a layer of bracken litter of varying thickness. Although it has been suggested that it is not necessary for this to be removed before recolonisation by native species will take place (Williams, 1977) the results of early re-seeding trials with Dactylis glomerata showed that sowing into a mat of existing bracken litter (or vegetation) was ineffective. On those plots where burning had been carried out in the winter following spraying with asulam or glyphosate, the establishment of this species was much improved (Williams, 1976). For some species burning has the effect of stimulating seed germination, for example, Ulex europaeus (Zabkiewicz and Gaskin, 1978) and this may further increase the diversity of the sward which develops. Moss (1980) found that whilst burning stubble killed seeds of Alopecurus myosuroides which were lying in the straw or on the soil surface, those which were shallowly buried were stimulated to germinate. He suggested that burning provided better environmental conditions for the germination and establishment of surviving seeds. A similar situation may result when bracken litter is burnt off. Any after treatment which involves soil mixing will tend to stimulate the germination of buried seeds although a simple inversion of the soil will tend in bracken land to bury seeds and place them under conditions unsuitable for germination where they will either decompose or become dormant because the majority of the viable seeds are to be found in the top 3 cm of soil.

In those sites where seed of Erica cinerea, Juncus bufonius, Juncus effusus, Calluna vulgaris or Digitalis purpurea is present, it is likely to be so in considerable quantities. The data collected here suggest that, providing the herbicide employed has no effect on seed viability, several grass species as well as these less desirable weedy species may be able to establish in quantity from seed following spraying. Cadbury (1976) suggested that the clearance of bracken might lead to infestations of Digitalis purpurea, Cirsium spp and Urtica dioica. However, Digitalis purpurea plants were not evident at the Gatehouse A site or in its surrounds and after spraying no evidence was found of invasion by this species. Similarly, Urtica dioica and Cirsium spp currently form only a relatively small percentage of the surface vegetation and no Cirsium seed and practically no Digitalis purpurea or Urtica dioica seed was found in the soil samples. These species all play but a minor role in both the soil and the sward of the Gatehouse B site. Whilst these species normally only form a relatively small percentage of the sward at the sites where they occur, when seed of Digitalis purpurea is present it is often, as mentioned above, in not insignificant amounts. This suggests that unless the species is part of the normal buried seed population it is unlikely that it will be a serious pest after bracken clearance. This agrees with the findings of Williams (1977).

It has been shown in this study that an estimate of the potential of a particular species to recolonise cleared ground cannot be made on the basis either of the representation of that species in the soil or on the basis of the representation of that species in the sward. Data from both sources is required. This fact was amply demonstrated by the dominance of Galium saxatile in the sward and its almost complete absence from the soil and, vice versa, the absence of species such as Erica cinerea, Calluna vulgaris and Juncus spp as plants in the sward despite their frequency of occurrence as seed in the soil.

It would appear that the recolonisation of litter covered ground from the buried seed population after bracken clearance may sometimes be of little practical value because of the frequency of occurrence of several weed species. It is difficult to decide what constitutes a 'weed' in hill land where there is uncontrolled grazing but some species are of much lower palatability than others. Since Digitalis purpurea and most Juncus spp are not usually grazed by stock, nor Calluna vulgaris or Erica cinerea, except when young shoots, the removal of bracken may result in an increase in the percentage of 'useless' weed species in the sward. Because glyphosate has a wider spectrum of activity than asulam it tends to eliminate almost all of the sward below the canopy and where this herbicide is used to clear bracken it is generally with the intention of re-seeding the ground with more desirable species such as ryegrass and clover. In these cases the buried seed population may provide severe competition for seed of the introduced species. Because more of the sward is killed, the use of glyphosate may also result in a more diverse sward than that which might develop following frond clearance with asulam. It is unlikely that the changes in the sward composition following successful bracken clearance will be as radical in most cases as that seen at the Gatehouse A site, where seed was probably introduced during winter feeding of cattle and where the effects of continual and heavy poaching by cattle during the winter and spring, followed by little disturbance in the summer allowing species to seed freely, has created a somewhat unstable habitat.

Whilst the data obtained here suggest that large populations of viable seeds are present in the soil, it does not necessarily follow that these will all germinate and establish following bracken clearance. Therefore, it would be valuable to determine how far the soil seed population actually influences the sward which develops following bracken clearance with asulam or glyphosate and what additional effects soil cultivation and the removal of bracken litter has upon the germination of seeds buried in the soil and the establishment of surface sown seed. This first point is examined in Section 9 and the latter point in Section 11.

7. VARIATIONS IN BURIED VIABLE SEED POPULATIONS.

7.1 *Introduction*

Data collected during the course of several different experiments in this study revealed variation in seed numbers from site to site and some evidence of temporal changes was also found. Brenchley and Warrington (1933), Roberts (1958, 1963) and Rabotnov (1956), amongst others, have commented on the considerable fluctuations which may occur from year to year in seed populations and many workers (for example, Champness and Morris, 1948) have shown variations from site to site. It was decided to examine this topic in more detail.

7.2 *Methods*

The data considered came from three main sources:

1) Samples collected at Dalry in successive years.
2) Two sites selected for more detailed investigation - Monksfoot and Gatehouse of Fleet A.
3) Samples collected from eighteen other sites in the West of Scotland.

Details of these sites are given in Appendix 1:A and Appendix 2:A (Monksfoot).

7.2.1 Samples collected at Dalry

Cores were taken from this site in August of 1978, 1979 and 1980. The techniques employed in 1978 differed somewhat from those used in 1979 and 1980 and are given in Appendix 2:B.

7.2.2 Samples collected at Monksfoot and Gatehouse of Fleet A

A site at Monksfoot, Lanarkshire and the Gatehouse of Fleet A site (examined in the 1978 seed survey - Section 6) were selected for more detailed sampling. Monksfoot was a bracken covered hill side subject to sheep, and some cattle, grazing at a low level of intensity. The Gatehouse of Fleet A site (referred to in this section as the Gatehouse site) was cleared of bracken with glyphosate in 1976 and was subject to heavy poaching by cattle in the winter months as the farmer left feed for his stock here.

Samples were taken from each site on thirteen occasions on an approximately monthly basis. These dates and the experimental techniques employed are given in Appendix 2:B.

7.2.3 Samples collected at twenty sites in the West of Scotland

Dalry, Gatehouse of Fleet A and eighteen other sites were first examined in 1978 and the methods and full results of this survey are given in Section 6. All the sites were resampled during a two week period in January 1981. The technique employed in 1981 is described in Appendix 2:B.

7.3 Results

7.3.1 Dalry

Table 29 indicates the seed populations in August of each of three years.

Table 29. Number of seeds recovered/m^2 at Dalry in successive years

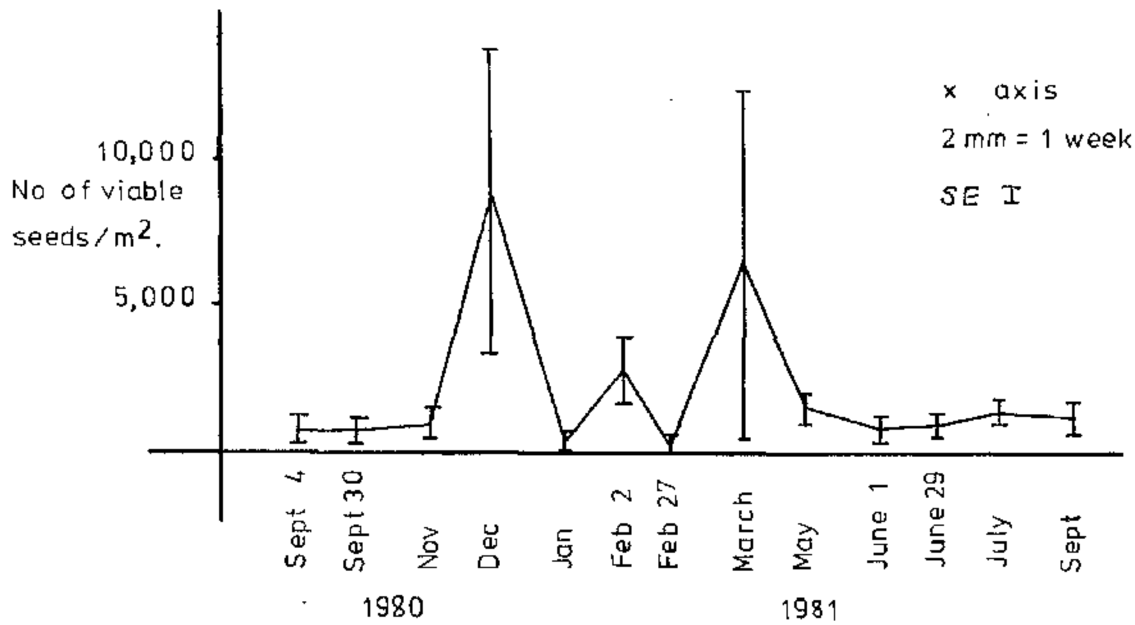
Year	Mean no. of viable seeds/m^2	SE
1978	4,790	$\pm$ 280
1979	2,141	$\pm$ 440
1980	3,050	$\pm$ 419

Differences are statistically significant at $P \leq 0.001$.

7.3.2 Monksfoot and Gatehouse sites

Figure 1 shows the total number of viable seeds recovered between September 1980 and September 1981 at Monksfoot. Few seeds were recovered from the samples (less than one seed per core on average) and the apparently larger seed populations in December 1980 and March 1981

Figure 1. Number of seeds recovered at Monksfoot between September 1980 and September 1981.



were on each occasion the result of a large number of seeds of Juncus spp being recovered in one of the cores. The large standard error of the population mean on these dates reflects the uneven distribution of seeds between the samples.

Only seed of Agrostis spp was found sufficiently frequently to warrant closer examination. Although seed of Agrostis spp was recovered on all thirteen occasions, only 61 seeds were found in the 180 samples and there was no significant relationship between seed numbers and time. Table 30 shows how, because few seeds were recovered, the standard error of the mean tended to be large and in fact ranged from 28% of, to equal to, that of the actual seed population.

Details of the other ten species recovered from the Monksfoot samples are given in Appendix 2:C:Table 1.

Figure 2 shows the total number of viable seeds recovered between September 1980 and September 1981 at Gatehouse. Seed numbers increased significantly ($P \leq 0.01$) between September and 5 November 1980 and decreased significantly ($P \leq 0.001$) thereafter until 27 February 1981. The population increased significantly ($P \leq 0.001$) by the end of May and also decreased significantly ($P \leq 0.001$) by the end of June whereafter it did not alter significantly.

Twelve of the thirty-three species identified in the seed population at Gatehouse occurred sufficiently frequently to be examined in more detail. The data for the other species recovered at this site are given in Appendix 2:C:Table 2.

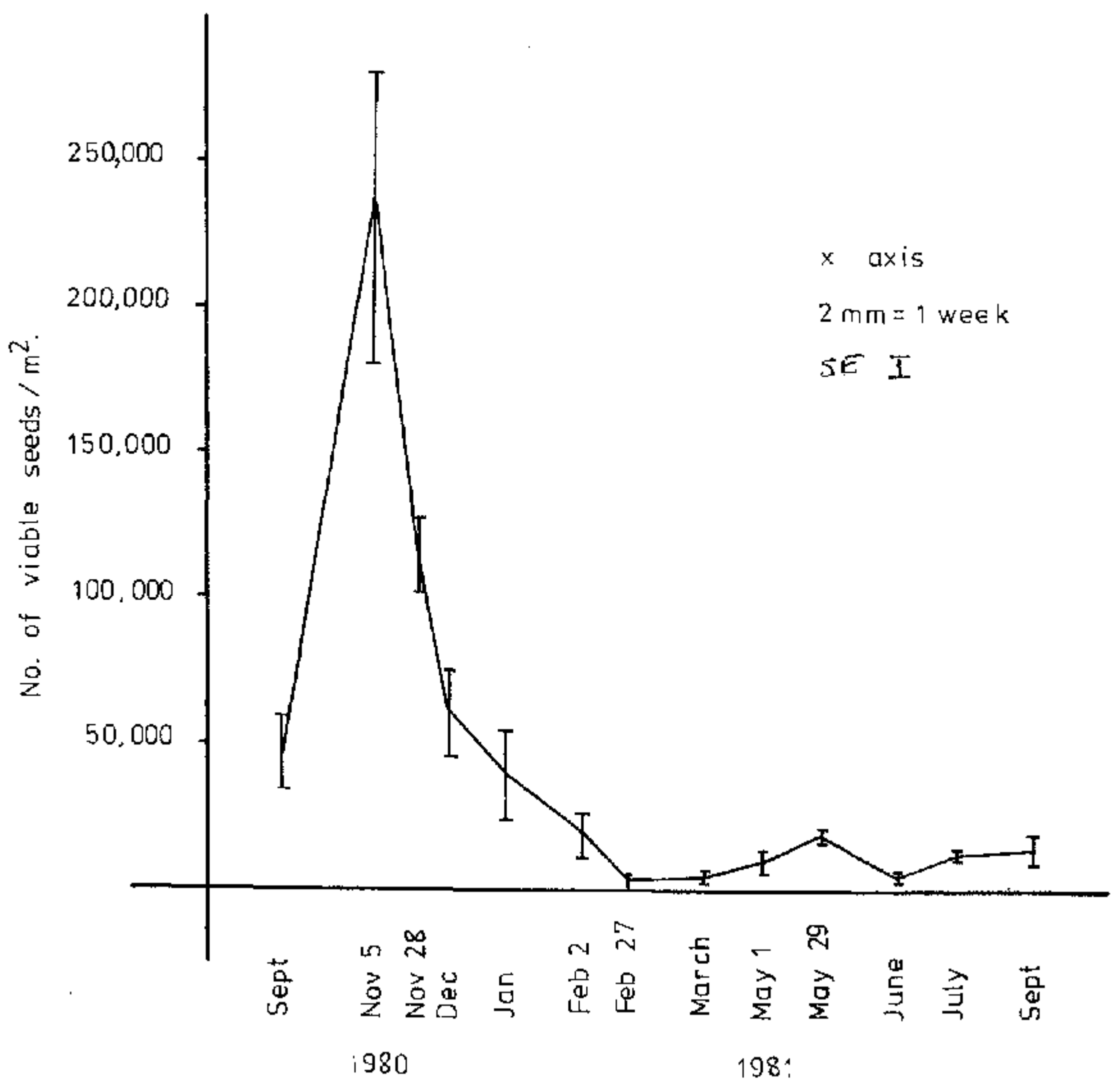
Cerastium holosteoides. Figure 3a

Seed numbers were fairly constant from September 1980 to January 1981 with an average of 2,200 seeds/m^2. Numbers fell to a low level during February (240/m^2) but rose by the end of March and remained at about 860/m^2 until the end of July when they fell to around 350/m^2 in September.

Table 30. Number of viable seeds of *Agrostis* spp recovered at Monksfoot.

Date of sampling	No. of viable seeds/m^2	SE	SE as % of population mean
1980			
4 September	722	506	70.08
30 September	722	361	50.00
November	963	530	55.04
December	8,669	5,298	61.11
1981			
January	482	313	64.94
2 February	2,890	1,276	44.15
27 February	241	241	100.00
March	6,502	5,996	92.22
May	1,565	482	30.80
1 June	843	313	37.13
29 June	963	409	42.47
July	1,445	409	28.30
September	1,204	482	40.03

Figure 2. Number of seeds recovered at Gatehouse between September 1980 and September 1981.



Plantago major. Figure 3b

Numbers rose substantially from September 1980 to 5 November from 0 to 3,850/m^2, falling thereafter in stages to 0/m^2 at the end of February 1981. From the end of March to September the population averaged 385 seeds/m^2.

Gnaphalium uliginosum. Figure 4a

A rise in seed numbers during September 1980 and November to a peak at the end of that month (6,000/m^2) was followed by a fall in numbers to the lowest recorded level in early February 1981 (700/m^2). After this date the population remained at about 1,200/m^2 with peaks occurring at the end of May (3,130/m^2) and the end of July (5,400/m^2).

Sagina procumbens. Figure 4b

The reserves of Sagina procumbens seed varied considerably from sample date to sample date and, as the large standard error of the mean figures indicate, the distribution of seeds from core to core on any one date was also variable. One might distinguish a general increase in numbers from September 1980 to December, falling thereafter until the end of March 1981. The population peaked at the end of May and again in September. Because there was a great deal of variation within each sample it was hard to establish a definite pattern.

Veronica arvensis. Figure 5a

Numbers increased from 2,000 to 9,300/m^2 between the end of September 1980 and 5 November. A gradual decrease by mid-December to 7,000/m^2 was followed by a sharp decline in numbers to 0/m^2 by the end of February 1981. Numbers increased from the end of March, peaked at the end of May and declined to a very low level again by the end of June.

Veronica serpyllifolia. Figure 5b

Numbers increased from September 1980 to 5 November (5,057/m^2) declining sharply by 28 November and gradually thereafter until February 1981 after which the population changed little.

Figure 3. Number of seeds of (a) Cerastium holosteoides and (b) Plantago major recovered at Gatehouse between September 1980 and September 1981.

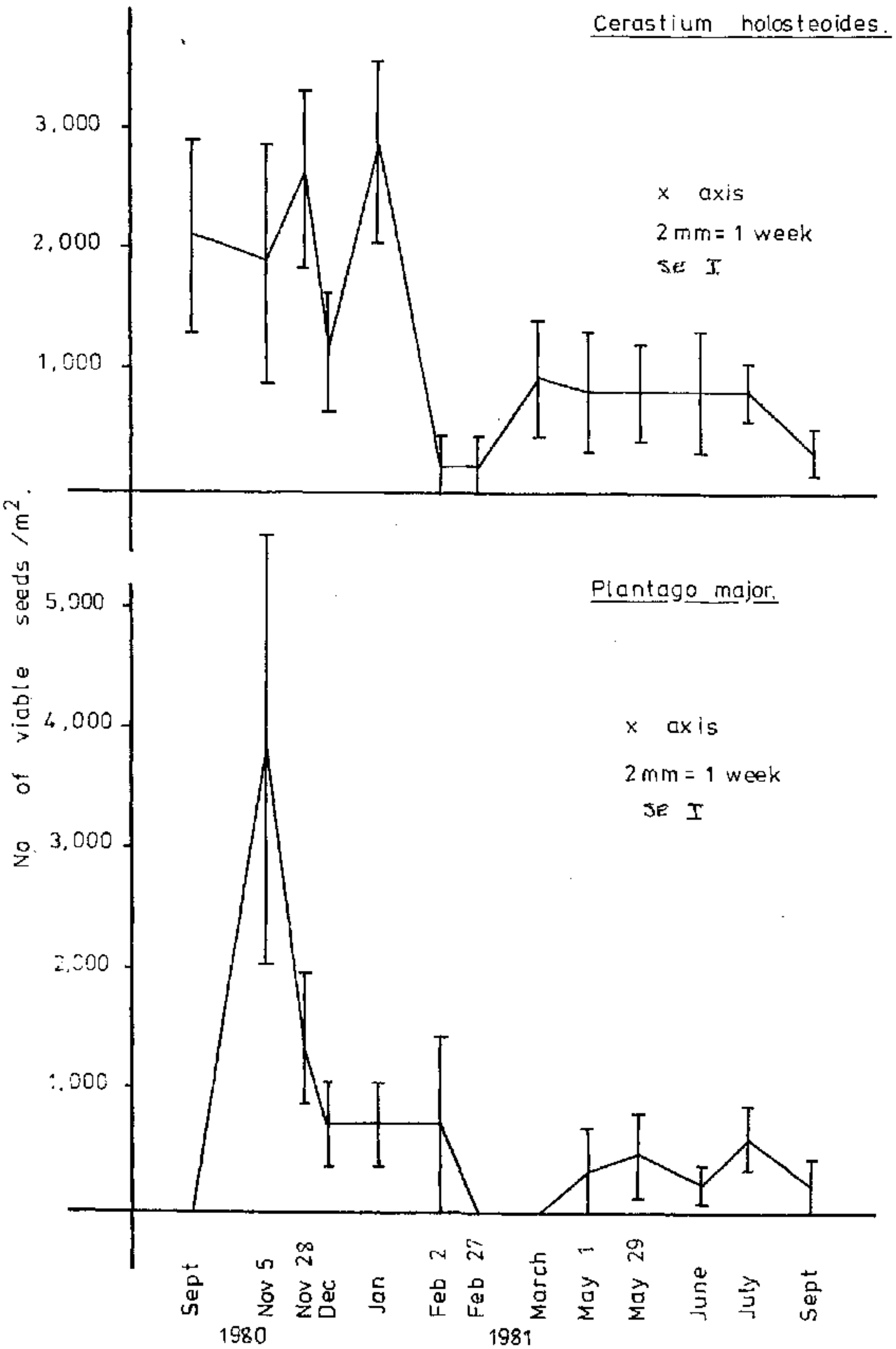


Figure 4. Number of seeds of (a) Gnaphalium uliginosum and (b) Sagina procumbens recovered at Gatehouse between September 1980 and September 1981.

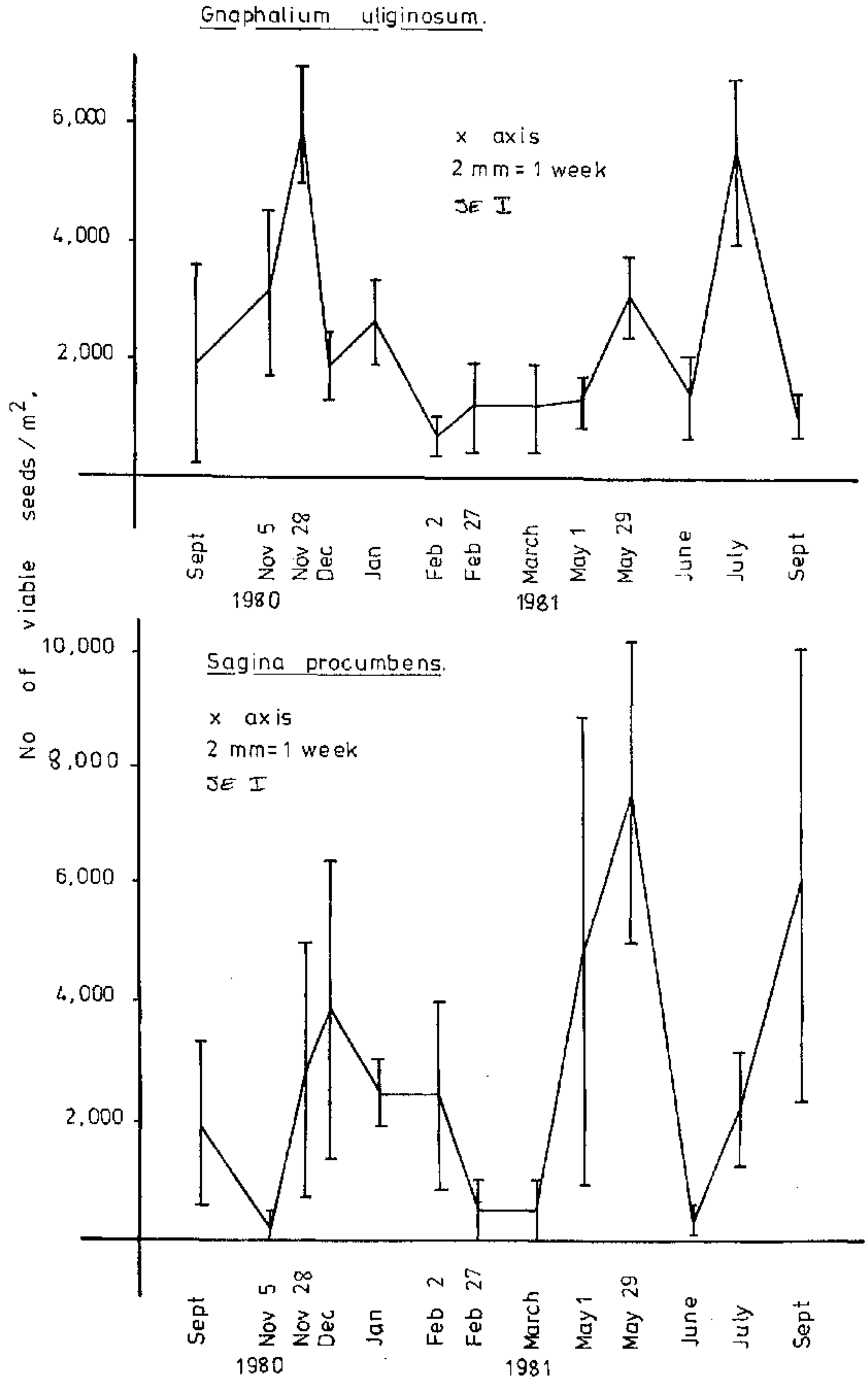
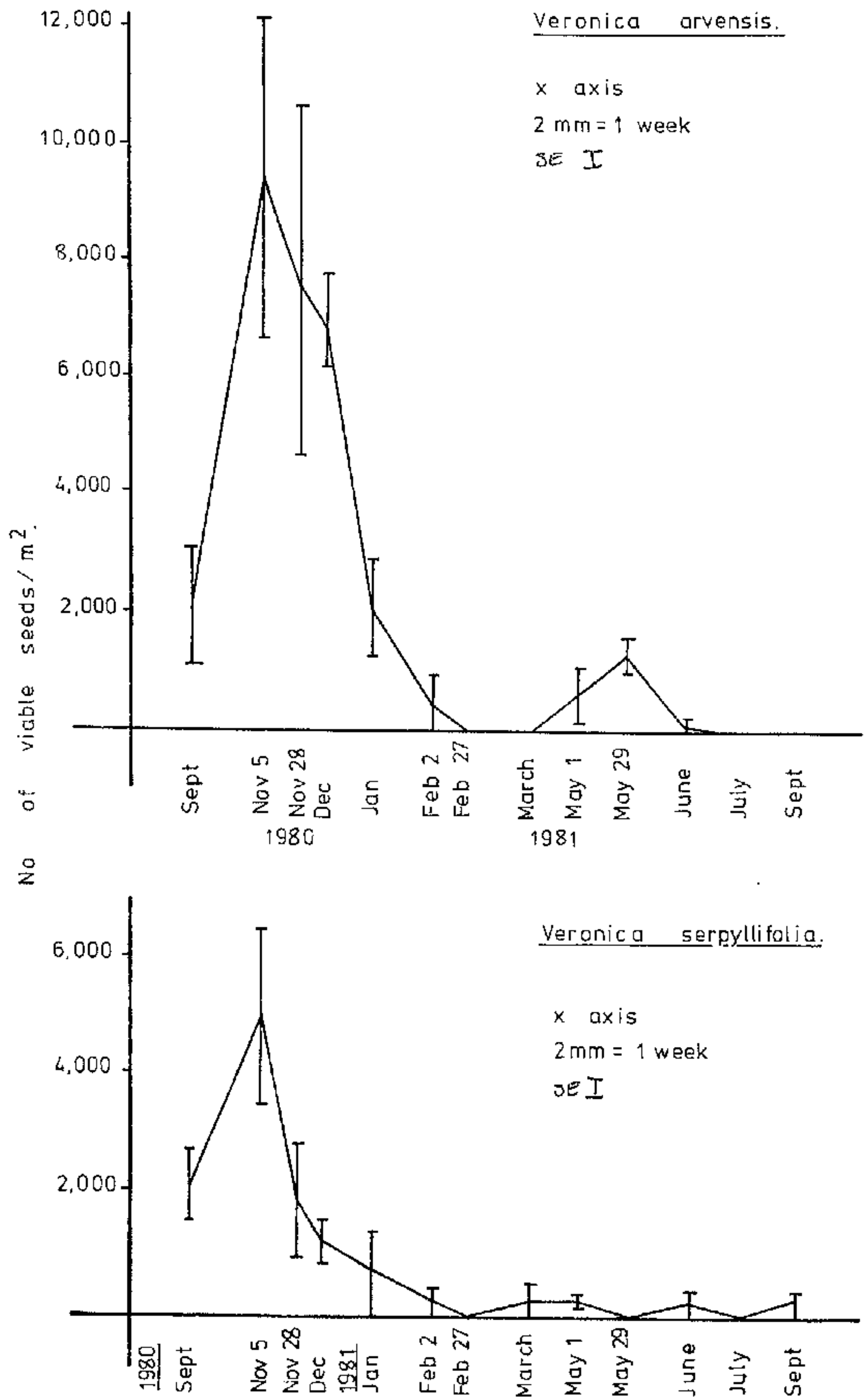


Figure 5. Number of seeds of (a) Veronica arvensis and (b) Veronica serpyllifolia recovered at Gatehouse between September 1980 and September 1981.



Stellaria media. Figure 6a

Seed numbers increased from a low level in September 1980 to an all time high on 5 November (8,900/m^2). There was a gradual decline until 2 February 1981 after which the population fluctuated at a relatively low level until the beginning of September.

Veronica persica. Figure 6b

Numbers increased from September 1980 to 5 November, declining sharply by 28 November and gradually thereafter until February 1981 when the population changed little until September.

Poa spp. Figure 7a

The population increased from September 1980 to its highest level on 5 November (23,000/m^2). It had decreased significantly by the end of November and from December to September 1981 it changed little from an average of 760 seeds/m^2. A slight increase was noted between the end of March and the end of June.

Matricaria matricarioides. Figure 7b

Numbers rose from 1,200/m^2 in September 1980 to a phenomenal 134,600/m^2 on 5 November. The population decreased in stages after this date to only 400/m^2 on 2 February 1981. Apart from a slight increase between May and July, numbers changed little until September.

Juncus spp. Figure 8a

Numbers of Juncus seeds increased from approximately 4,600/m^2 in September 1980 to a peak of 11,700/m^2 at the end of November. Numbers fell to only 900/m^2 in January 1981 and thereafter changed little.

Agrostis spp. Figure 8b

Seed of Agrostis spp was recovered on seven of the thirteen occasions but the pattern observed differed from that of the previous ten species. A larger reserve of seed was indicated to be present at the end of September 1980 than on 5 November although a large standard error was associated with the September population mean. Between the end of

Figure 6. Number of seeds of (a) Stellaria media and (b) Veronica persica recovered at Gatehouse between September 1980 and September 1981.

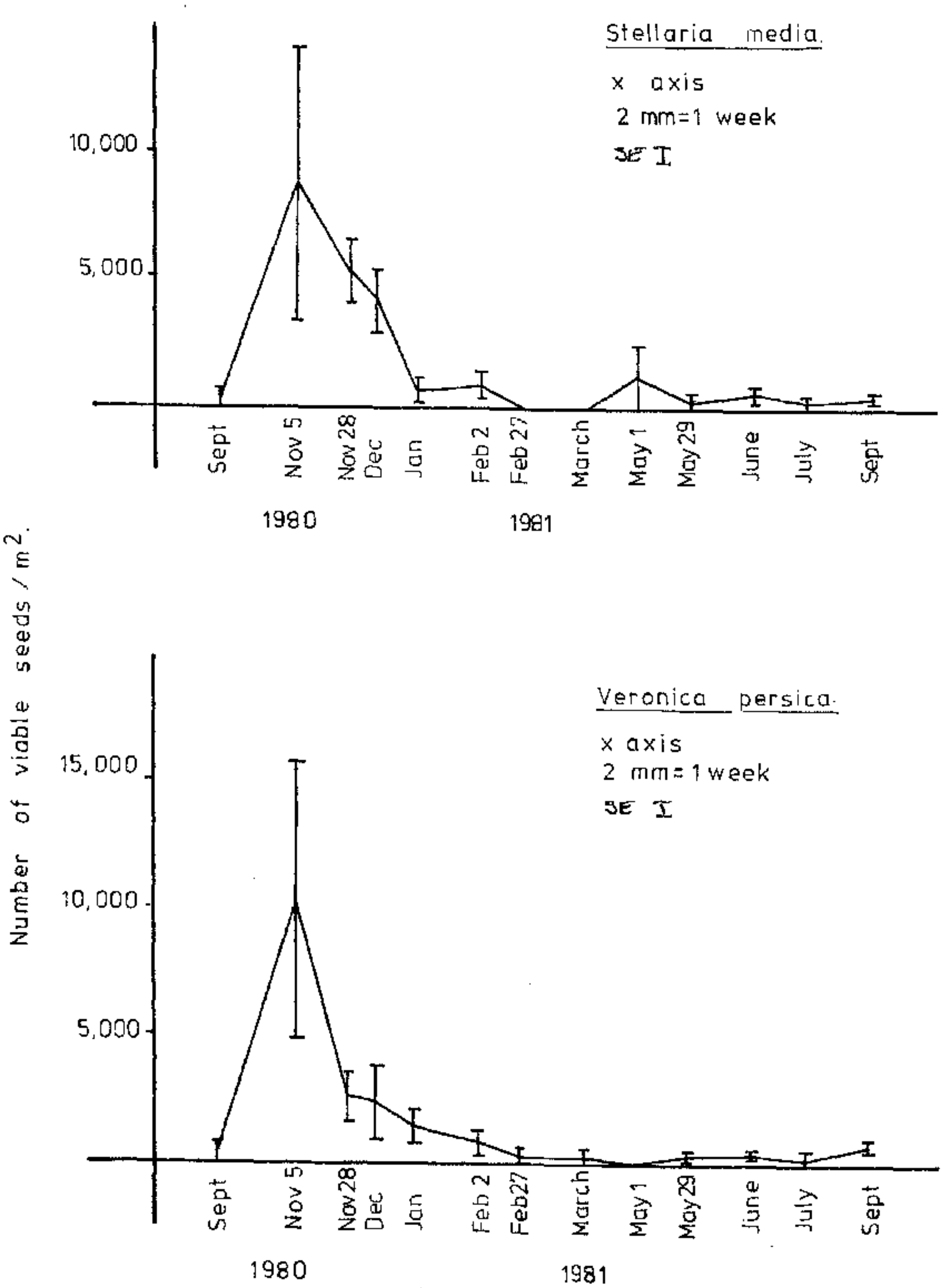


Figure 7. Number of seeds of (a) <u>Poa</u> spp and (b) <u>Matricaria matricarioides</u> recovered at Gatehouse between September 1980 and September 1981.

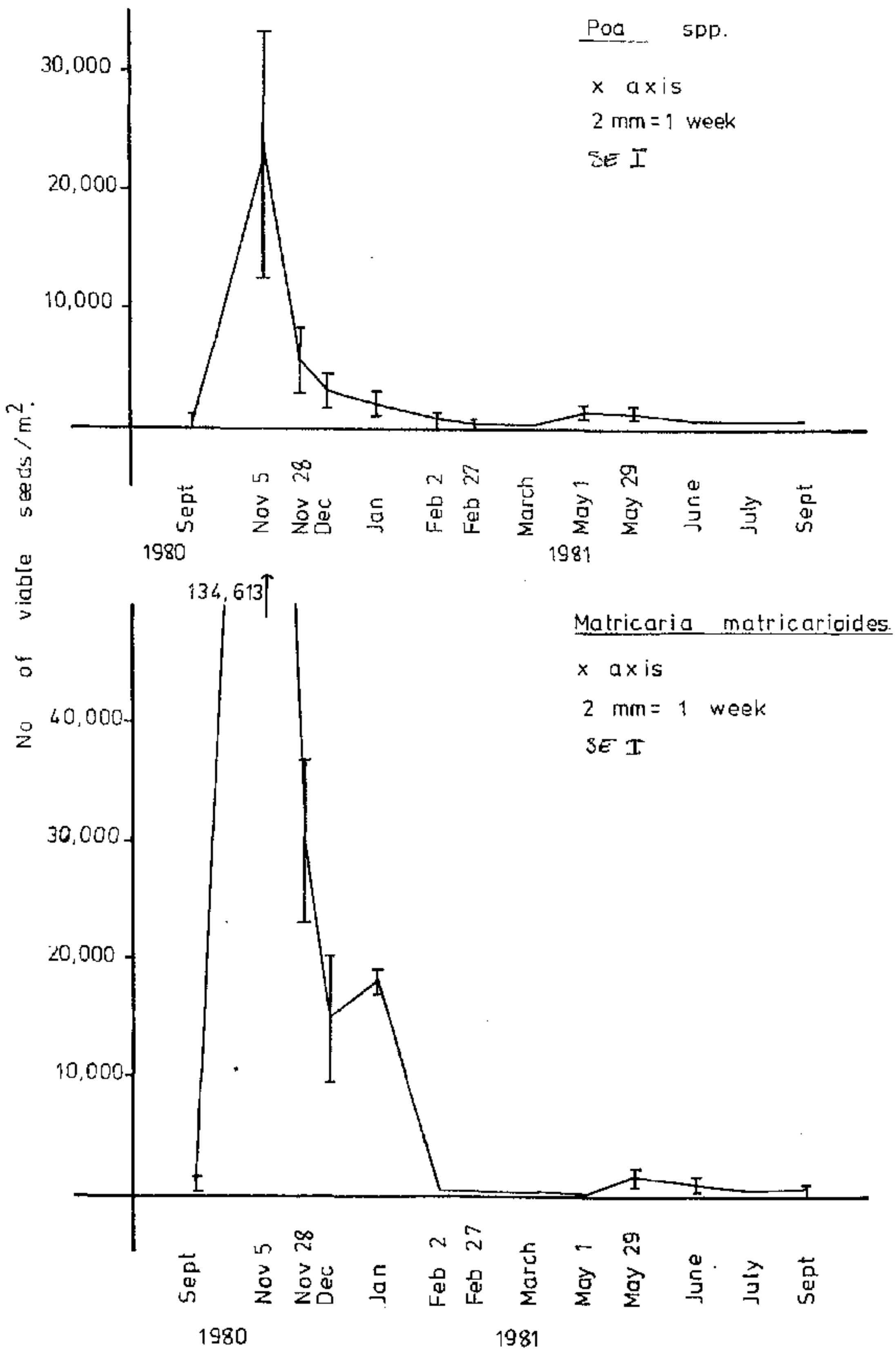
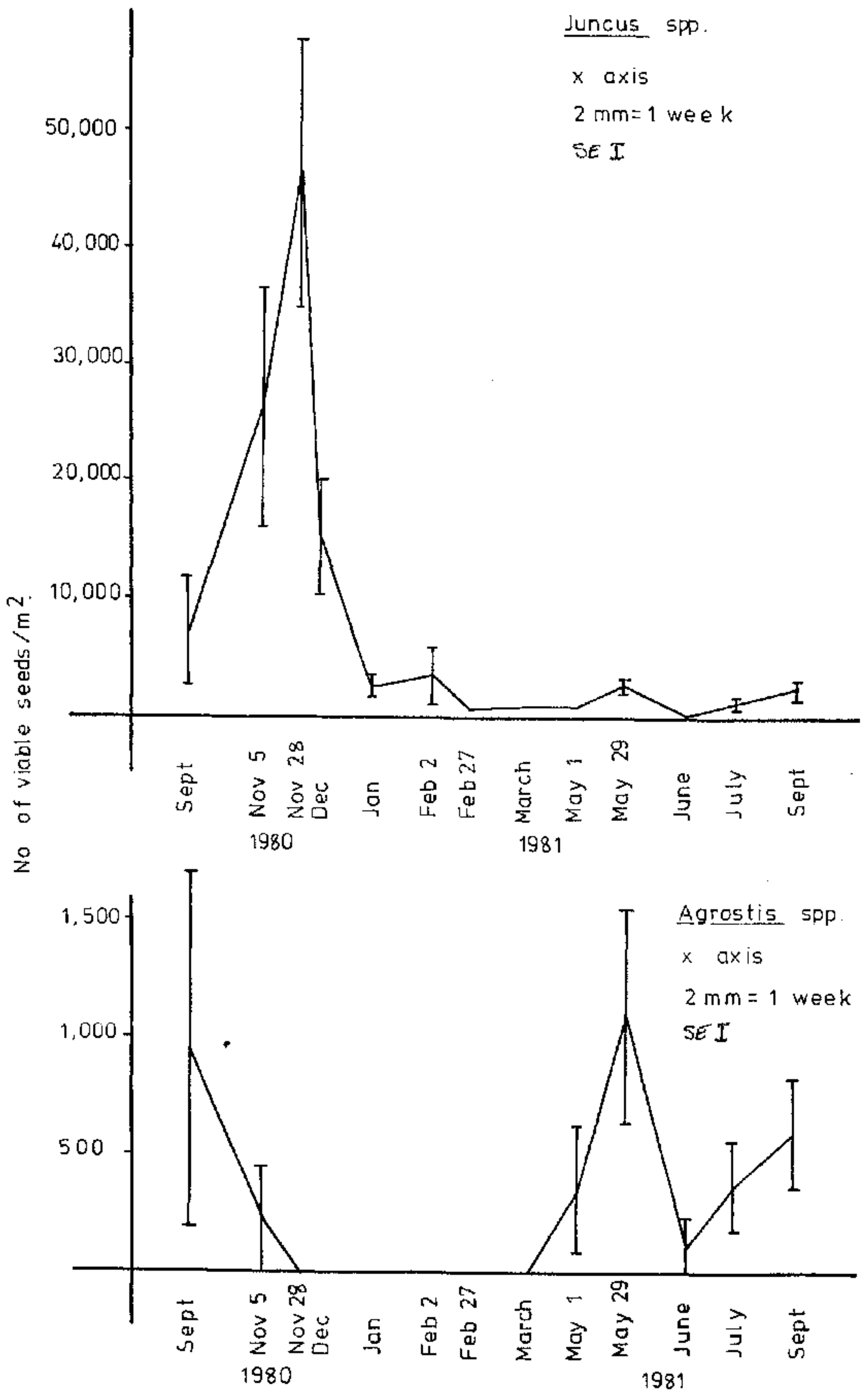


Figure 8. Number of seeds of (a) <u>Juncus</u> spp and (b) <u>Agrostis</u> spp recovered at Gatehouse between September 1980 and September 1981.



November and 1 May 1981, no seed of Agrostis spp was found. The population increased during May and peaked at the end of the month (1,084 seeds/m^2) achieving a level similar to that in September 1980 (963 seeds/m^2). Numbers had declined by the end of June but during July and August began to increase again.

Veronica arvensis, Agrostis tenuis, Sagina procumbens and Gnaphalium uliginosum all showed peaks in seed numbers in late May and whilst Gnaphalium uliginosum peaked for a second time in July, the numbers of Agrostis tenuis and Sagina procumbens continued to increase throughout July and September. The peak in May was reflected in Figure 2 but the September increases were not clearly evident. The number of seeds of the remaining eight species fluctuated during the summer months but throughout the year they conformed largely to the pattern of change noted in Figure 2 for the population as a whole.

Although a more detailed study would be needed to confirm the idea, there is some evidence, Table 31, that the seed population at this site is declining.

Table 31. Seed numbers/m^2 at Gatehouse in September of 1978, 1980 and 1981.

Year	No. of viable seeds/m^2	SE
1978	119,338	33,480
1980	47,680	12,757
1981	15,412	5,769

Differences are statistically significant at $P \leq 0.05$.

7.3.3 1978/1981 seed survey sites

The seed populations estimated to be present at the twenty sites examined in 1978 and 1981 are given in Table 32. The mean seed population in the untreated sites (i.e. excluding Gatehouse A and Gatehouse B) in January 1981 was 2,788 ± 559 compared with a figure of

Table 32. Seed populations at twenty sites surveyed in 1978 and 1981.

Site	Mean no. of viable seeds/m^2		% of 1978 population	Significance ($P\leq$)
	1978	1981		
Gatehouse of Fleet A	119,338	29,739	24.92	0.05
Gatehouse of Fleet B	14,267	5,535	38.80	0.001
Gatehouse of Fleet C	18,446	9,151	49.61	NS
Barlaes Hill	27,210	2,406	8.84	0.001
Dalry	4,789	1,203	25.12	0.001
Glen Douglas A	7,236	3,853	53.25	NS
Glen Douglas B	14,471	1,084	7.49	0.05
Kirkton Farm A	3,261	1,564	47.96	NS
Kirkton Farm B	3,771	1,083	28.72	0.01
Sundaywellmoor A	7,236	2,285	31.58	0.01
Sundaywellmoor B	4,280	1,324	30.93	0.01
New Galloway A	10,905	1,442	13.22	0.01
New Galloway B	4,790	2,890	60.33	NS
Polharrow Bridge A	3,261	3,251	99.69	NS
Polharrow Bridge B	3,567	1,202	33.70	0.05
Melfort House A	9,783	3,973	40.61	0.01
Melfort House B	4,789	1,564	32.66	0.01
Oban A	3,057	8,307	271.74	0.01
Oban B	9,682	841	8.69	0.001
Margrie Farm	13,962	2,769	19.83	0.001
Mean (excluding Gatehouse A and B)	8,583 $\pm$ 1,531	2,788 $\pm$ 559	32.48 (range 7.49-271.74%)	

8,583 $\pm$ 1,531 in 1978.

The individual sites differed in the extent of the change in seed numbers between 1978 and 1981, from a thirteen fold decrease at Glen Douglas B to an almost three fold increase at Oban A. The increase at Oban A was due to larger reserves of Agrostis spp, Juncus spp and Urtica dioica whilst the decrease at Glen Douglas B was due mainly to fewer seeds of Digitalis purpurea and Juncus spp and to a lesser extent, Agrostis spp. For all but five sites (Gatehouse C, Glen Douglas A, Kirkton A, New Galloway B and Polharrow Bridge A) the decrease in the seed population was statistically significant; the increase in seed numbers at Oban A was also statistically significant. The full results of the sampling at each site in 1978 are given in Section 6.3 and in 1981 in Appendix 2:D.

In terms of absolute numbers, the greatest decrease on the untreated sites was noted at Barlaes Hill where there was a reduction of 24,802 seeds/m^2. This was due to an almost total disappearance of seed of Calluna vulgaris and Erica cinerea and to a decrease of 60% in the population of Agrostis spp.

The reductions in the seed populations on the sprayed sites at Gatehouse were comparable to the reductions noted on the untreated sites. The decrease at Gatehouse A was in the order of 89,500 seeds/m^2.

Table 33 gives the total number of viable seeds recovered from the twenty sites for those species having more than a total of 1,000 seeds/m^2. Three of these species - Aphanes arvensis, Urtica dioica and Veronica persica - were found in greater numbers in 1981 than 1978 although the increases were not statistically significant because for each species a large proportion of the seeds was recovered from one particular site. Over 2,500 Potentilla erecta seeds were recovered per m^2 in 1978 but no viable seed of this species was found in 1981; the decrease being statistically significant ($P \leq 0.001$). The remaining species were all found in smaller quantities in 1981. The species which frequently suffered the greatest decrease in numbers on the untreated sites were

Table 33. Number of seeds/m^2 of the principal species recovered in 1978 and 1981.

Species	Mean no. of viable seeds/m^2 (Total of 20 sites) 1978	1981	% of 1978 population
Agrostis spp (A. canina, A. stolonifera, A. tenuis)	27,822	13,242	47.60
*Aphanes arvensis	714	1,806	252.94
Anthoxanthum odoratum	2,141	601	28.07
Cardamine hirsuta	2,345	1,926	82.13
Cerastium holosteoides	4,891	3,371	68.92
Digitalis purpurea	18,649	842	4.51
Erica cinerea and Calluna vulgaris	32,711	2,286	6.99
Galium saxatile	1,936	962	49.69
Gnaphalium uliginosum	3,567	2,890	81.02
Holcus lanatus	2,549	481	18.87
Hypericum humifusum	2,446	240	9.81
Juncus spp (J. bufonius, J. articulatus, J. effusus)	62,773	18,301	29.15
Matricaria matricarioides	56,459	11,679	20.69
Plantago major	4,832	843	17.45
Poa spp (P. annua, P. pratensis, P. trivialis)	14,165	7,224	51.00
Polygonum spp (P. aviculare, P. hydropiper, P. persicaria)	4,076	240	5.89
Potentilla erecta	2,549	-	0.00
Rumex acetosella	2,243	120	5.35
Sagina procumbens	3,670	2,648	72.15
Stellaria media	8,867	2,167	24.44
Urtica dioica	408	3,010	737.75
Veronica arvensis	16,714	3,010	18.00
Veronica persica	1,936	2,047	105.73
Veronica serpyllifolia	3,160	962	30.44
Other species	4,589	3,126	68.12
Unidentified species	1,447	1,442	99.65
TOTAL	288,101	85,466	29.66

*Aphanes arvensis was only recovered at Gatehouse A and B

Digitalis purpurea, Calluna vulgaris, Erica cinerea and Juncus spp, and to a certain extent, Agrostis spp. On the sprayed Gatehouse sites, Matricaria matricarioides, Plantago major, Polygonum spp, Rumex spp, Stellaria media and Veronica arvensis suffered large reductions between 1978 and 1981. Again, because the greater proportion of seeds of each of the species was found on a minority of sites, statistical analyses failed to show any of the decreases in these species to be significant with the exception of Polygonum spp of which species significantly fewer seeds ($P \leq 0.05$) were recovered in 1981 on the sprayed sites.

7.4 *Discussion of results*

Sampling at Dalry in successive years showed how, at a site where the management did not alter and where the ground was subject to little disturbance (in the form of relatively light sheep and cattle grazing) the number of viable seeds in the soil varied from year to year and the differences noted were statistically significant. It was this data largely which prompted a more detailed consideration of the subject of changes in seed numbers; particularly changes with time.

Monksfoot is a site subject to a similar level of disturbance to that at Dalry but it has a much smaller seed population (3,050 $\pm$ 419 seeds/m^2 at Dalry in August 1980 compared with 722 $\pm$ 514 seeds/m^2 at Monksfoot in September 1980). Few seeds were recovered at Monksfoot and on two occasions when a larger seed reserve was indicated to be present, this was the result of several seeds of one particular species (Juncus) being recovered from one of the replicate cores.

Gatehouse differed but is an atypical site in that the fronds have been removed chemically. Several factors have contributed to the development of a quite different flora; one which is perhaps more typical of arable soil where many of the seeds are annual species (such as Gnaphalium uliginosum, Matricaria matricarioides, Stellaria media, Veronica arvensis and Veronica persica) rather than perennial species (Agrostis spp, Anthoxanthum odoratum, Juncus spp and Poa spp). These influencing factors include - an increased soil pH, the effect of heavy stocking in winter followed by little disturbance during the remaining months creating an unstable habitat, increased nutrient levels and possibly the input of seed via winter feed left here by the farmer.

Although a constructive comparison of the two sites was not possible because so few seeds were recovered at Monksfoot, sampling at Gatehouse did produce evidence of changes in seed populations both on a long term basis (Table 31) and over relatively short periods of time. The total seed population changed from month to month and a similar pattern was noted for several of the most frequently occurring species. Large numbers of seeds entered the seedbank in September and November 1980 but many had disappeared by January 1981 and for much of the year the population was relatively small compared with this autumn level. Many of the seeds may have lost viability during the winter whilst some of the reduction in numbers in February and March is probably due to germination, particularly during any mild periods in these months. Increases in the seed population in the May to June period reflect seed production by the established plants, in particular by Gnaphalium uliginosum, Sagina procumbens, Veronica arvensis and Agrostis spp, and the reduction which followed is more likely to represent autumn germination than seed decay.

Sagina procumbens and Agrostis spp showed a peak in numbers in late May and were the only species to show any indication of increasing to levels similar to those noted in the September/November period in 1980. The number of Veronica arvensis seeds remained low after the May peak although large quantities of seed of this species were recovered in September 1980. Gnaphalium uliginosum peaked twice in 1981: in late May and in late July.

Sagina procumbens is a highly opportunistic species which can establish very quickly. It is largely self pollinated and can therefore set seed rapidly. The large variation in seed numbers on each sampling date reflects a high degree of variation between the samples. This is probably partly a result of the patchy distribution of individual plants and partly the result of the large amount of seed produced by each individual plant being shed close to the mother plant. This point was illustrated by the fact that on 1 May, 29 May and 3 September 1981 respectively 51, 64 and 63% of the seeds recovered were in one of the twenty replicate cores. Gnaphalium uliginosum although an annual species takes longer to produce seed than Sagina procumbens and the peak in seed numbers in May might be the result of favourable environmental conditions allowing some of the plants to flower and set seed early. The pattern observed for Agrostis tenuis was based on the recovery of only 26 seeds in 180 samples and although seed distribution between the samples was reasonably even, this is too small a number to determine a true pattern for this species.

These results are, however, based on data collected during only one year and the pattern of change may not be representative. Sampling over several years with an examination of seed input would be necessary to establish a clear pattern.

Thompson and Grime (1979) found that species which had transient seed banks (one where none of the seed output persists in the soil in a viable condition for more than one year) were not recovered from samples taken at certain times of the year. On other occasions, the absence on a particular occasion of a species known to have a seed bank of this type was due to the localised distribution of seed. Species with transient seed banks were often absent in spring and early summer but large numbers were recorded in late summer and autumn (August and September). The numbers of seeds of species having persistent seed banks (where some of the seeds are more than one year old) were often found to fluctuate but never fell to zero; the fluctuations again reflecting the distribution of seeds.

Six species were recorded on all 13 occasions (Cerastium holosteoides, Gnaphalium uliginosum, Juncus spp, Matricaria matricarioides, Poa spp and Sagina procumbens) whilst the other six species which were examined in more detail were absent on between one and six occasions. Thompson and Grime (1979) classified Juncus spp and Poa spp as species having persistent seed reserves whilst Chippindale and Milton (1934) and Champness and Morris (1948) suggested that Cerastium holosteoides, Juncus spp, Poa spp and Sagina procumbens were all better represented in the soil than in the sward, which although in itself does not imply a persistent seed bank, does support the theory. In the 1978 seed survey (Section 6) all these species were found in greater proportions in the soil than in the sward. Plantago major and Veronica spp were found by Chippindale and Milton (1934) and Champness and Morris (1948) in equal proportions in the soil and in the sward, suggesting that the number and distribution of seeds of these species are somewhat dependent upon that of the plants in the sward. Thus, failing to recover seed of these species might partly reflect the distribution of the plants. Agrostis tenuis and A. canina are also thought to have persistent seed banks by these three groups of workers but there was a definite absence of these species during the winter and spring months. No data on the types of seed bank of Gnaphalium uliginosum, Matricaria matricarioides or Stellaria media were available.

Considerable variations were also found in the seed populations of the 18 untreated bracken sites examined in 1978. An average of $8,583 \pm 1,531$ seeds/m^2 were estimated to be present but site totals ranged from 3,057/m^2 (Oban A) to 27,210/m^2 (Barlaes Hill). To a certain extent these differences were related to the differences in seed sizes in that the most abundant seeds were also often the smallest. Thus, sites such as Barlaes Hill, New Galloway A and Melfort A which had large seed populations were also found to have large numbers of seeds of *Agrostis* spp, *Calluna vulgaris*, *Erica cinerea*, *Juncus* spp and *Poa* spp, all of which are small-seeded species.

In 1981 an average of $2,788 \pm 559$ seeds/m^2 were estimated to be present and the site totals ranged from 841/m^2 at Oban B to 9,151/m^2 at Gatehouse C. The most abundant species were again *Agrostis* spp and *Juncus* spp and also *Gnaphalium uliginosum* at Gatehouse C.

The sprayed Gatehouse A and B sites differed slightly in the most abundant species occurring as seed. At Gatehouse A the most numerous species in 1978 were, in order of abundance, *Matricaria matricarioides*, *Juncus* spp, *Veronica arvensis*, *Stellaria media*, *Poa* spp and *Plantago major*, and in 1981 were *Matricaria matricarioides*, *Veronica arvensis* and *Juncus* spp. At Gatehouse B, *Juncus* spp and *Cerastium holosteoides* in 1978 and *Cardamine hirsuta* in 1981 were the most abundant species. Several of these species (*Cardamine hirsuta*, *Matricaria matricarioides*, *Plantago major* and *Stellaria media*) had larger seeds than those species most abundant on the untreated sites (*Agrostis* spp, *Calluna vulgaris* and *Erica cinerea*).

Whilst the total seed population at Gatehouse B was similar to that of several of the untreated sites (although some of the constituent species differed), the population at Gatehouse A far exceeded that of any of the other sites both in 1978 and in 1981.

Although several workers (Chippindale and Milton, 1934; Milton, 936, 1939, 1943; Champness and Morris, 1948) have found that a greater number of seeds are found in a viable condition in moist acid soils, no evidence could be found here that in 1978 the larger seed populations were associated with a lower soil pH (Figure 9). This is not particularly surprising because although there was a wide range of seed populations on the 20 sites, the range of pH values was relatively narrow (from 4.15 to 6.40). A subjective assessment in 1978 of the site and hence of the likely relative soil moisture separates out Glen Douglas B, Sundaywellmoor B, New Galloway A and Oban A as having possibly wetter soils than some of the other sites. Two of these sites (Glen Douglas B and New Galloway A) did have higher than average seed populations but the other two sites had lower than average seed populations.

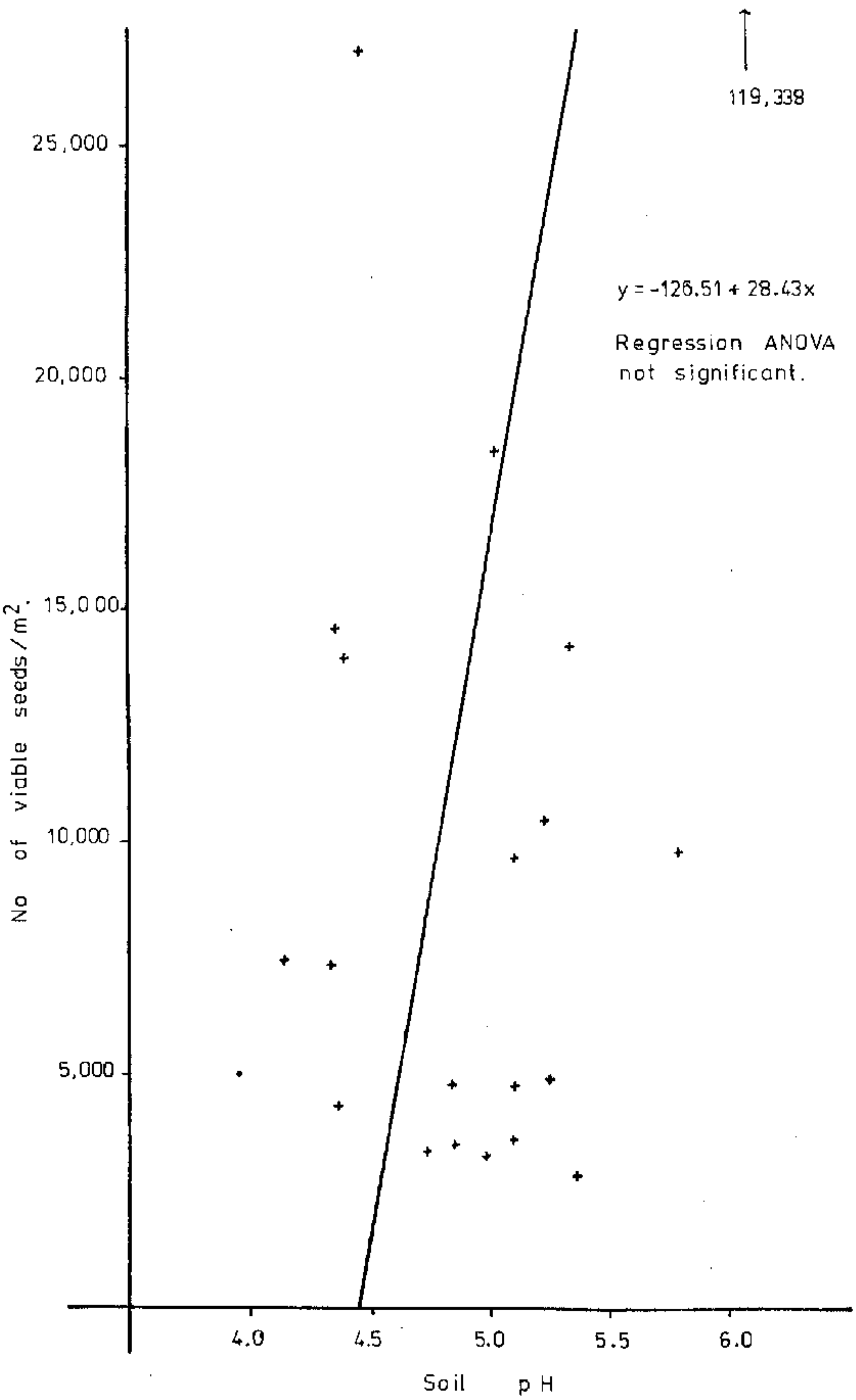
These sites were all sampled over a four month period in 1978 (September to December) whilst the samples taken in 1981 were lifted during a two week period in January. The results of the two surveys are not directly comparable for several reasons:

1. Samples were collected in January in 1981 as opposed to autumn in 1978.
2. Samples collected in 1978 were lifted over a four month period.

The results of the monthly sampling at Gatehouse during 1980 and 1981 has indicated that seed numbers tend to be lower in January than in the autumn and also that during this autumn period numbers can rise and fall considerably.

3. Samples collected in 1978 were visually examined prior to sowing out whilst in 1981 the samples were sown out directly onto compost in the greenhouse.

Figure 9. Relationship between soil pH and number of viable seeds/m^2 for twenty sites examined in 1978.



Feast and Roberts (1973) have noted that the germination technique is often not as efficient in estimating a seed population as a combination of laboratory and greenhouse techniques although in two separate trials significant statistical differences were not recorded in the number of seeds recovered by the two techniques.

4. Samples collected in 1978 were stored for up to several months in a dry room prior to sorting and sowing out.

Kjaer (1940, 1948) has shown that seeds of some species lose their viability faster than others when held in dry storage and it is possible that some seeds were not accounted for in the samples which were kept for the longest periods of time. The order in which the sites were sampled in 1978 is the same as that given in Table 32 but the order in which sorting was carried out was random. The optimum technique is clearly to sample all the sites during as short a period as possible and to treat chemically and/or sow onto compost as soon as possible. If the samples are being visually examined, once sorted they should be stored until they have all been processed and should then be sown out onto compost at the same time.

Calluna vulgaris was one of the species which showed a significant decrease in numbers between 1978 and 1981. Miller (1981) has suggested that seeds of this species probably become dormant when buried and he suggested that oven drying the cores for 72 hours at 30°C before sowing out in the greenhouse might break this induced dormancy. The samples collected in 1978 were held in dry storage at 18°C for up to several months whilst those collected in 1981 were held in similar conditions for only a week or two until the soil had dried sufficiently to be crumbled and sieved. It is possible that some of the losses noted for this species, and for Erica cinerea, a similar type of species, are due to dormant seeds being undetected.

Had all the 1978 samples been collected in one of the four months one might have expected to see a proportional decrease between the 1978 figures and the 1981 figures in Table 32 which would account for the change in seed numbers with the time of sampling. However, no proportional change was noted in 1978 from Gatehouse A to Margrie Farm (the order in which the samples had been taken) nor in the figures indicating what percentage of the 1978 population the 1981 population was. This suggested that the changes which had occurred in the populations were a result of factors which had influenced the individual sites.

Despite these technical criticisms of the methods employed it is clear that fewer seeds were recovered in the 1981 samples and that it was unlikely that all of this reduction was due to the time of year at which the samples had been taken. Large decreases were noted for several individual species (Calluna vulgaris, Digitalis purpurea, Erica cinerea, Juncus spp and Rumex acetosella on the untreated sites and Juncus spp, Matricaria matricarioides, Plantago major, Stellaria media and Veronica arvensis on the sprayed Gatehouse sites). When present in the 1981 samples most of these species tended to germinate readily in the greenhouse and it is therefore thought unlikely that these species were present in the quantities in which they were recovered in 1978 and that they simply failed to germinate.

7.5 *General Discussion*

Many workers, including Brenchley and Warrington (1933), Roberts (1958, 1963) and Rabotnov (1956) have commented on the fluctuations which can occur in seed populations with time.

Seed production at a particular site may vary from year to year. Salisbury (1961) noted that cold wet summers might deplete the seed reserves in the soil and inhibit the production of viable seed whilst cold wet autumns had the effect of shortening the growing season and hence reducing the total amount of seed produced that year. For species relying on wind pollination and possibly also insect pollination, wet weather would reduce the efficiency of the process. Rainfall figures for Auchincruive (Appendix 2:E) indicate that 1978 was a drier than average year whilst in 1977, 1979, 1980 and 1981 the annual rainfall figures were between 16 and 29% greater than the thirty year mean. 1980 was particularly wet (1158.8 mm) and any reduction in seed production during the year as a result of the environmental conditions would have been reflected in the sampling carried out in January 1981 in the second seed survey. Tamm (1956) noted annual differences in the number of flowering individuals on the same plot and Sagar and Mortimer (1976) found that there was variability within the species with respect to the number of seeds produced per plant. For annual species this might be a significant source of variation in the number of seeds added to the soil population in different years. Plant density, both that of the individual plants of a species and that of the plants of different species, is important in that species react differently to this factor. Harper and White (1971) quoted unpublished work by Oxley on <u>Digitalis purpurea</u> which showed that this species reacted to high plant density by a reduction in the proportion of flowering plants. Since individuals of this species can produce vast quantities of seed the failure of one plant to set seed in a given year can significantly alter the seed input for that year for that site. The 1978 seed survey showed that where this species was present in the soil it was in not insignificant quantities and that where plants were absent from the sward very small quantities of seed, if any, were recovered from the soil.

Seed survival on the plant, on the soil surface and once incorporated into the soil may in part be influenced by the palatability and digestibility of the seed and by the incidence of predators (Janzen, 1970, 1971).

Factors which will cause variation in the number of seeds in the soil at a given time, and which are not insignificant, are those of germination and the natural viability of the seeds. The length of time for which seeds can remain viable in soil varies from species to species (Toole and Brown, 1946; Darlington and Steinbauer, 1961) and depends on the nature and degree of innate dormancy, whether or not induced dormancy can develop, and the ability of seeds to persist when dormancy is enforced (Harper, 1957). The factors which influence germination, representing a loss from the seed bank, are numerous and highly variable in time and effect. These factors combined with the differences in seed input each year are alone sufficient to cause large variations in the seed bank of a given site. Not all the losses from the soil may be attributed to germination; Roberts and Dawkins (1967) showed that in populations at a depth of 7.5 cm and which suffered reductions of between 22 and 36% per year, only 0.3 to 9.0% could be accounted for as seedlings.

Soil disturbance, by stock or cultivation, will clearly affect the seed population in a variety of ways. The plants themselves may be damaged physically by trampling which may retard, reduce or prevent seed production. Churning up the soil will bury some seeds and help to preserve them but it will bring others to the surface where they will be stimulated to germinate and will be lost from the seed bank. Roberts and Feast (1972), amongst others, have shown that seed survival is greatest in undisturbed soil. In one particular experiment they found after five years that seed survival at a depth of 2.5 cm in undisturbed soil was 6.8% compared with 2.3% in soil subject to cultivation four times a year.

Grubb (1977) examining the importance of the seed bank in maintaining species diversity, commented on seed dispersal mechanisms and noted that these were dependent upon many factors including wind speed and direction, flooding, the abundance of animal vectors and significantly, the properties of the seeds themselves. Although intra-specific variation in seed morphology occurs it is not a major factor here and with the exception of this factor, the others may vary from time to time.

Seed may be blown onto the site or carried there by animal vectors. Data exist to show that seed eaten by stock is often voided in a viable condition (Takabayashi et al, 1975).

Seed may also be introduced to the site and enter the seed bank as a result of man's activities. For example, at the Gatehouse A site, seed may be entering the system via hay bales left out for the cattle during the winter.

Thus, many factors influence the input of seed in a given year for a particular species at a specific site whilst several factors will affect the subsequent fate of the seed. The combination of all these factors will result in variations in the number of seeds in the soil from time to time, and, as was shown here, both on a short term basis (from month to month) and on a longer term basis (from year to year).

8. PHOTOGRAPHS AND DESCRIPTIONS OF THE SEEDS OF SPECIES ASSOCIATED WITH BRACKEN DOMINATED HILL LAND.

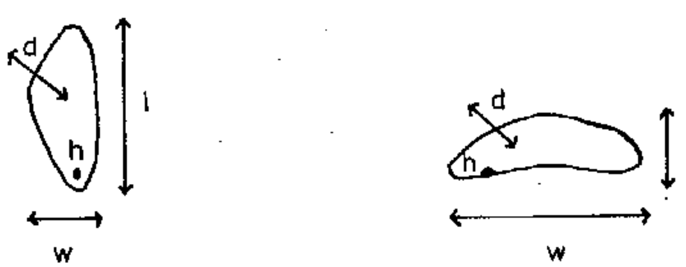
8.1 *Introduction*

Few photographs or drawings exist of seeds of indigenous upland species. It was therefore decided to photograph and describe the seeds of species recovered in the seed surveys and to relate the descriptions to those of previous workers. The references consulted are indicated by code letters which are explained in Section 8.3. Whilst variations in published descriptions are often a reflection of the different geographic sources from which the seeds were obtained, it should be noted that some of the data given by Butcher (1961) appeared to be suspect and although his data on seed sizes have been included, where they are given in parenthesis they should be treated with some caution.

8.2 *Seed Dimensions and Shapes*

The dimensions given in the text are the mean of ten measurements per species and are given in millimetres (mm). The face upon which the hilum was located was considered to be the base of the seed and seed length was measured from the hilum to the apex, as indicated below.

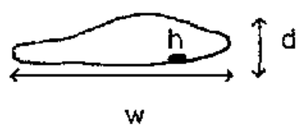
h = hilum
l = length
w = width
d = depth



Several species, for example Urtica dioica, had the remains of a style present as a tip or a small stalk and this was included in the measurement of length. In the case of Ranunculus repens, where the seed has a prominent beak, seed shape was based on measurements of the seed without the beak.

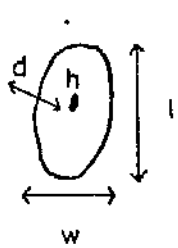
The width of the seed was the horizontal measurement at right angles to the length taken at the widest part of the seed. Depth was taken as the perpendicular measurement at right angles to the length and the width, again at the widest part of the seed.

Certain seeds, for example, Plantago major, are compressed vertically which results in a very wide seed with very little depth and the hilum is thus located on a broad base, as indicated below.



h = hilum
w = width
d = depth

In the case of four of the species in this text - Plantago major, Veronica arvensis, Veronica persica and Veronica serpyllifolia - the length, width and depth measurements were taken as indicated below, rather than with the hilum orientated downwards.



h = hilum
l = length
w = width
d = depth

This orientation allowed a direct comparison to be made with the descriptions given by previous workers who orientated their specimens in this manner.

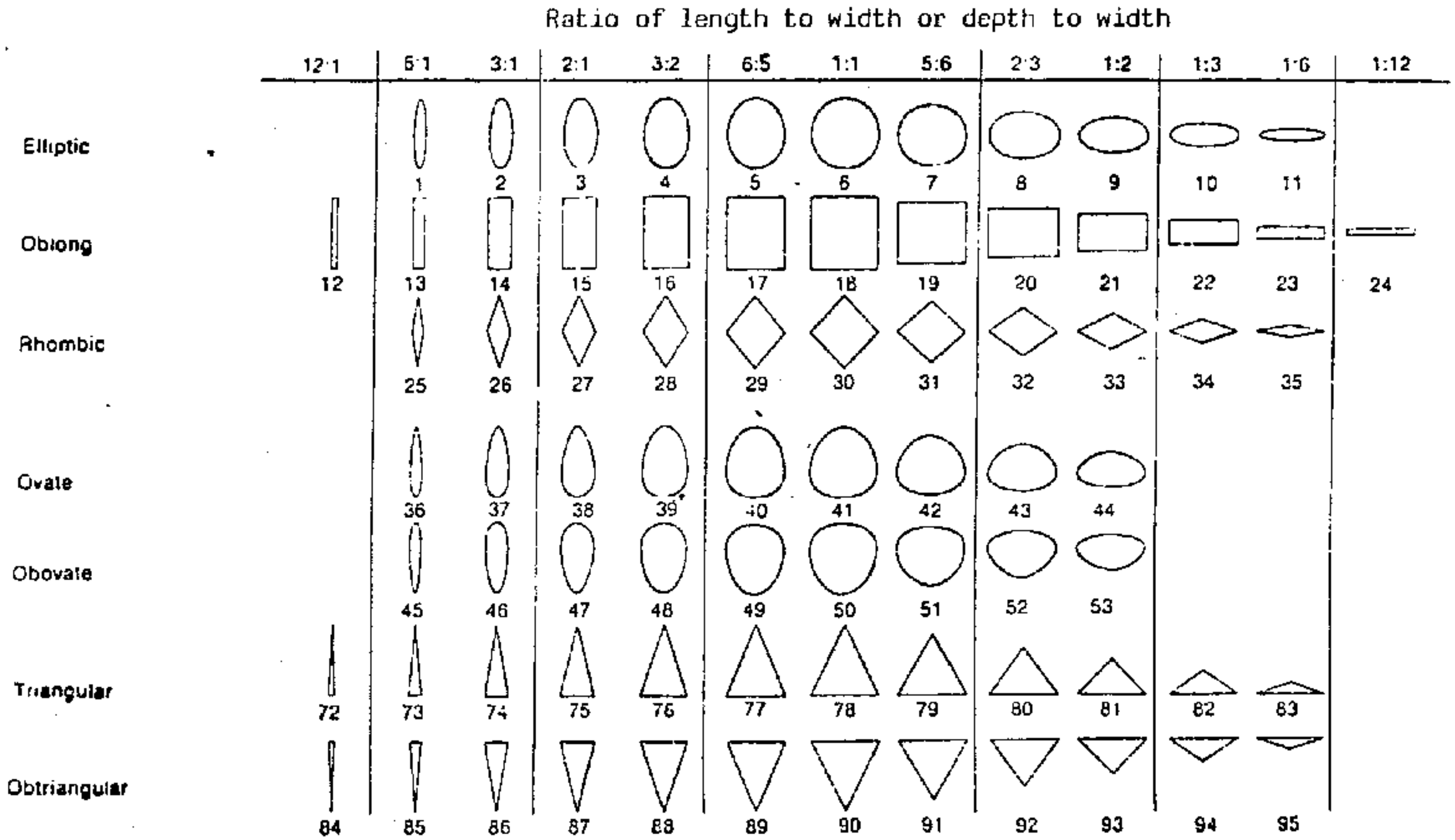
When comments pertaining to the 'dorsal' and 'ventral' sides of the seeds were made, the side on which the hilum was located was termed the ventral side.

The shapes of the seeds were described using the system proposed by the Systematics Association Committee for Descriptive Biological Terminology (1962) which uses mathematical ratios to describe the shapes of the seeds. Montgomery (1977) in his work on the seeds and fruits of eastern Canada and north-eastern United States, used this system and he produced Figure 10 from these descriptive terms. He omitted from the chart diagrammatic representations of the descriptions relating to shapes 54 to 71 inclusive because none of the seeds which he described fell into the two groups (trullate or angular-ovate and obtrullate or angular-obovate) covered by these descriptions. It was possible to allocate each of the seeds examined in this study to one of the shapes given in Figure 10.

The shape of the seed in longitudinal section is given by the ratio of the length of the seed to the width of the seed. Having chosen visually the appropriate 'shape group', given by the lines of shapes running horizontally in Figure 10 and by reducing the ratio of length to width to its lowest terms, given at the top of each vertical column of shapes, a descriptive number for a particular shape may be obtained from the chart. The procedure is repeated to find the shape of the seed in cross section, which is given by the ratio of the depth to the width. In the text, the numbers given in the description of the shape of the seed relate to Figure 10 and 'longitudinal section' and 'cross section' have been abbreviated to ls and cs respectively.

Although some seeds were not symmetrical, for example <u>Aphanes arvensis</u> in longitudinal section and <u>Galium saxatile</u> in cross section,

Figure 10. Seed shapes referred to (by numbers) in the text.



the broad overall shape has been described using the chart and the ratios, and an appropriate comment on the shape has been made.

8.3 References

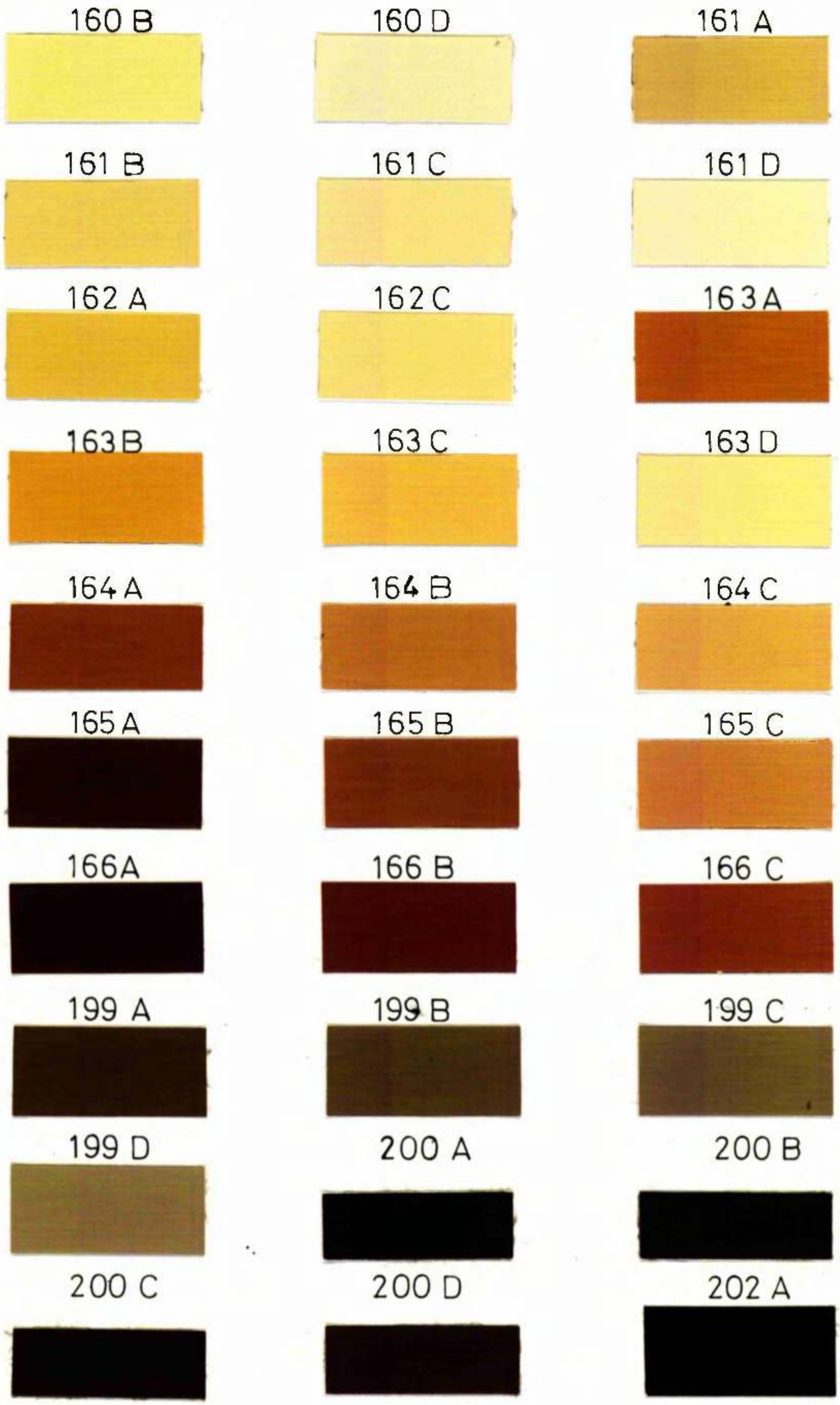
Codes for authors whose work was consulted and included in the range of seed sizes and colours indicated in the text with the photographs, are given below. The full reference for each author is given in Section 14.

Be	Beijerinck (1947)
B & S	Brouwer and Stählin (1975)
vdB	van der Burg et al (1979a, 1979b)
B	Butcher (1961)
CTW	Clapham, Tutin and Warburg (1962)
D	Delorit (1970)
H	Hubbard (1968)
J	Jensen (1969)
J & T	Jermy and Tutin (1968)
K	Korsmo (1935)
KVF	Korsmo et al (1981)
Ma & B	Martin and Barkley (1961)
Me	Mercer (1938)
Mo	Montgomery (1977)
P & S	Parkinson and Smith (1914)
S	Swarbrick (1970)

8.4 Seed Colours

The colours of the seeds were described using the Colour Chart of The Royal Horticultural Society, London (1972). For each species, ten seeds were taken and in turn placed on the coloured cards until the colour upon which each seed was least obvious was determined. Thus, a

Figure 11. Seed colours and codes referred to in the text.



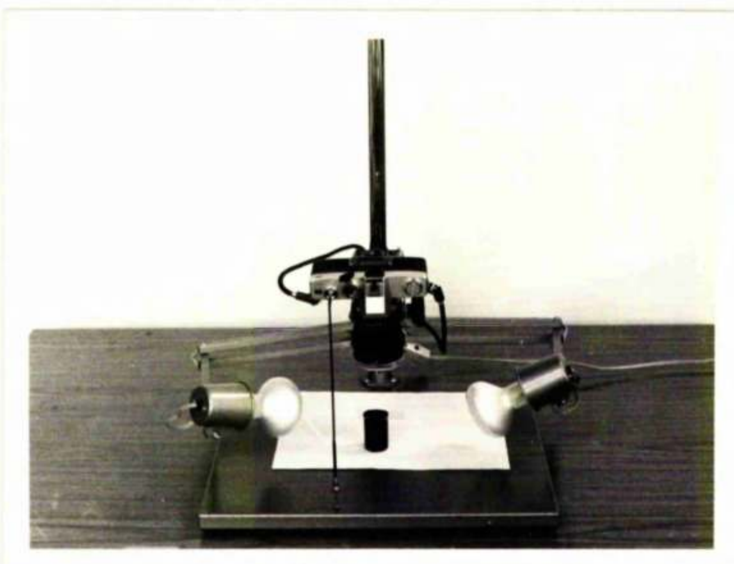
range of colours was found for the seeds of each species. The colour determinations were made under natural daylight conditions as opposed to under artificial lighting. Most of the colours in the Chart do not have a verbal description but each colour is coded with a number and a letter from A to D. These codes are given in the seed descriptions. The colours and the codes which are referred to in this text are given in Figure 11.

8.5 Photographs of the Seeds - Techniques Employed

It was easier to produce photographs of some seeds than it was of others and a variety of techniques and backgrounds was therefore used.

Plate 1 shows one arrangement of the apparatus normally used. In this arrangement the lens was reversed on the camera body.

Plate 1 Arrangement of seed photographic apparatus 1.

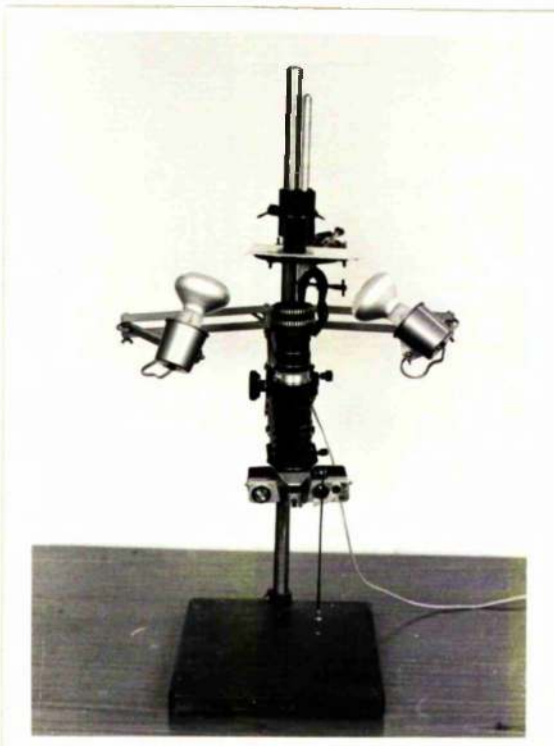


Seeds were placed on a glass slide over an empty upright black plastic film container which provided an excellent uniform black background.

Alternatively, a white card placed beneath a glass slide which was supported at either end on a pencil provided a suitable white background. By raising the slide off the paper, any shadows cast by the seeds resting on the slide were not recorded in the photograph.

Plate 2 illustrates another way of photographing the seeds. By taking the pictures from below and by placing a set of extension tubes and bellows between the camera body and the lens it was possible to obtain a greater magnification.

Plate 2 Arrangement of seed photographic apparatus 2.



A hole was cut in a piece of card with a dark red matt side towards the lens in order to reduce the amount of light reflected back into the lens. A glass slide was secured over the hole, the seeds were placed on the slide and this was covered with an inverted black plastic film container to give the uniform black background.

Because of the variety of techniques employed, the photographs are not of a standard magnification. Below each plate the magnification of the photographs is given and a line equivalent to 2 mm is indicated (1 mm in the case of Plates 33, 35 and 43).

8.6 *Photographs and Descriptions of Seeds*

8.6.1 Index of species

Nomenclature follows Clapham, Tutin and Warburg, 1962.

Agrostis canina L.

Caryopsis

1) Dimensions

Length 1.00 ± 0.03 mm
Width 0.33 ± 0.01 mm
Depth 0.26 ± 0.01 mm

2) Shape

Ovate (37) in ls, elliptic (7) to oblong (20) in cs. Tapers to a point at the apex. Base broader with a blunt tip.

3) Comments

Ventral side has a deep central longitudinal groove running from the apex almost to the base.
Surface longitudinally striate. Caryopsis soft.

4) Colour

Pale brown/brown. 164A, 164B, 165B.

Caryopsis enclosed by lemma and palea

1) Dimensions

Length 1.48 ± 0.04 mm
Width 0.37 ± 0.01 mm
Depth 0.28 ± 0.01 mm

2) Shape

Ovate (38) in ls, elliptic (8) in cs. Base more or less truncate and apex blunt.

3) Comments

Lemma translucent with 5 longitudinal nerves seen most clearly where the lemma exceeds the caryopsis. Palea minute (or absent?). Palea and lemma both longitudinally punctate. Base has a white rim from which short upward pointing hairs arise.
Awn, if present, arises half way up the dorsal side of the lemma from the central nerve. It just exceeds the tip of the lemma and then bends. The lower part is twisted, the upper part has lateral teeth. Total length of awn: 1.86 ± 0.20 mm.

4) Colour

Cream/pale brown. 161B, 161D, 200C, 200D.

Plate 3 Agrostis canina L.

Scale: 2 mm ⊢———⊣
Magnification: x 7.8

Previous descriptions:

1.3-2.2 mm long, 0.2-0.3 mm wide, 0.2-0.3 mm deep (B & S, B).

Caryopsis:

0.8-1.5 mm long, 0.2 mm wide, 0.2 mm deep (B & S, B).
Brown (B & S).

Agrostis stolonifera L.

Caryopsis

1) Dimensions

Length 0.98 ± 0.03 mm
Width 0.37 ± 0.01 mm
Depth 0.31 ± 0.01 mm

2) Shape

Ovate (37) in ls, elliptic (7) to oblong (19) in cs. Tapers to a rounded apex and at the base to a blunt point.

3) Comments

Longitudinal groove on ventral side shallow. Surface longitudinally striate as wavy ridges which are darker than the rest of the caryopsis. Caryopsis hard.

4) Colour

Chestnut brown/brown. 164A, 165A, 165B, 200D.

Caryopsis enclosed by lemma and palea

1) Dimensions

Length 1.68 ± 0.04 mm
Width 0.43 ± 0.01 mm
Depth 0.34 ± 0.01 mm

2) Shape

Ovate (36-37) in ls, elliptic (7) in cs. Pointed towards tip and taperir to blunt base.

3) Comments

Lemma 5-nerved, shiny and with very fine longitudinal striations on the surface. Palea loosely adheres to caryopsis. Is translucent and shiny It covers the entire caryopsis and is about half to two-thirds the length of the lemma. The palea narrows towards the apex where it is bifid. It is faintly 2-nerved.

Basal hairs point upwards.

Awn, if present, is about 1.65 ± 0.05 mm long and twisted along its lengtl It arises on the dorsal side of the lemma near the base. It runs straigl initially, bends away from the seed and then continues parallel to the se edge. The tip bends back towards the seed.

4) Colour

Cream to light brown. 161C, 164B, 165B, 199C. Base cream.

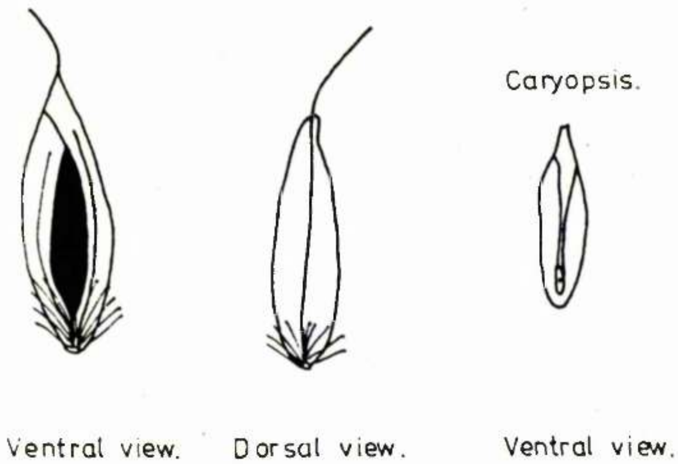
Plate 4 Agrostis stolonifera L.

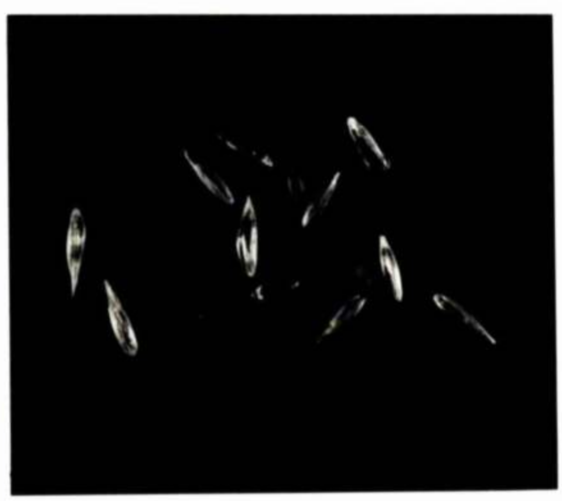
Previous descriptions:

1.5-2.0 mm long, 0.3-0.5 mm wide, 0.3-0.4 mm deep (B & S, B, K).
Greyish yellow to yellowish brown (K).

Caryopsis:

1.0 mm long, 0.2-0.3 mm wide, 0.2-0.3 mm deep (B & S, B).
Brown (B & S, K).





Scale: 2mm

Magnification: x 6.2

<u>Agrostis tenuis</u> Sibth.

Caryopsis

1) Dimensions

Length 1.08 $\pm$ 0.04 mm
Width 0.38 $\pm$ 0.01 mm
Depth 0.32 $\pm$ 0.01 mm

2) Shape

Ovate (37) in ls, elliptic (7) to oblong (19) in cs.

3) Comments

Shallow longitudinal groove on ventral side runs from apex nearly to base. Surface with dark longitudinal striations. Caryopsis hard.

4) Colour

Chestnut brown. 164A, 165A, 166A, 166B. Tip of base below darker hilum is white.

Caryopsis enclosed by lemma and palea

1) Dimensions

Length 1.59 $\pm$ 0.05 mm
Width 0.41 $\pm$ 0.01 mm
Depth 0.33 $\pm$ 0.01 mm

2) Shape

Ovate (36-37) in ls, elliptic (7) in cs.

3) Comments

Lemma 3 to 5 nerved. Between nerves, finely longitudinally striate. Palea half to two-thirds the length of the lemma. It is notched at its apex and adheres tightly to the caryopsis. It extends from the base to within 0.2 mm of the apex of the caryopsis. Base pronounced. Basal hairs longer and more spreading than in <u>A. canina</u> and <u>A. stolonifera</u>.
Awn, if present, arises near base on dorsal side. Is straight as far as apex of lemma when it bends. Awn itself is twisted in its lower part and with lateral teeth in the upper section. Total length of awn: 2.2 $\pm$ 0.19 mm.

4) Colour

Awn yellow/cream. Lemma and palea cream/fawn. 199C, 199D.

Plate 5 Agrostis tenuis Sibth.

Scale: 2 mm

Magnification: x 4.2

Previous descriptions:

1.5-2.0 mm long, 0.3-0.4 mm wide, 0.3-0.4 mm deep (B & S, B).

Caryopsis:

1.0 mm long (B).

Anthoxanthum odoratum L.

Caryopsis enclosed by lemma and palea

1) Dimensions

Length 2.01 ± 0.02 mm
Width 0.53 ± 0.03 mm
Depth 0.64 ± 0.02 mm

2) Shape

Ovate (36-37) in ls, elliptic (5) in cs. Rounded at the base and tapering to a point at the apex. From the side, the ventral edge is more curved than the dorsal and in the upper half of the caryopsis the ventral edge slopes sharply to meet the dorsal edge at the apex.

3) Comments

Caryopsis slightly angular with 5-7 faint longitudinal nerves or ridges. Surface shiny, glabrous and finely longitudinally straite. In upper half of caryopsis, edges of glume overlap. Palea enclosed by lemma, is shorter or as long as lemma. No awn.

4) Colour

Chestnut brown to reddish brown with a lighter tip. 164A, 165B, 166C.

Caryopsis enclosed by lemma and palea is surrounded by two sterile florets represented by the lemmas only

1) Dimensions

Length 3.22 ± 0.07 mm
Width 0.96 ± 0.03 mm
Depth 0.68 ± 0.02 mm

2) Shape

Ovate (37) in ls, elliptic (8) in cs. The sterile florets are arranged facing each other with the awns to the outside. The fertile floret is located between the two sterile florets with its dorsal side towards the lower floret which has a straight awn.

3) Comments

Tips of florets blunt and bifid at the apices. Florets covered with stiff upward pointing hairs which peter out towards the tip.
Upper floret has a geniculate awn which is about 8.45 ± 0.23 mm long inserted near the base of the dorsal side. It is black and twisted to the point where it bends when it becomes dark brown. The lower floret has a 4.88 ± 0.19 mm long straight awn which is chestnut brown and which is inserted in the middle of the dorsal side. The straight awn and the upper part of the geniculate awn have upward pointing lateral teeth.

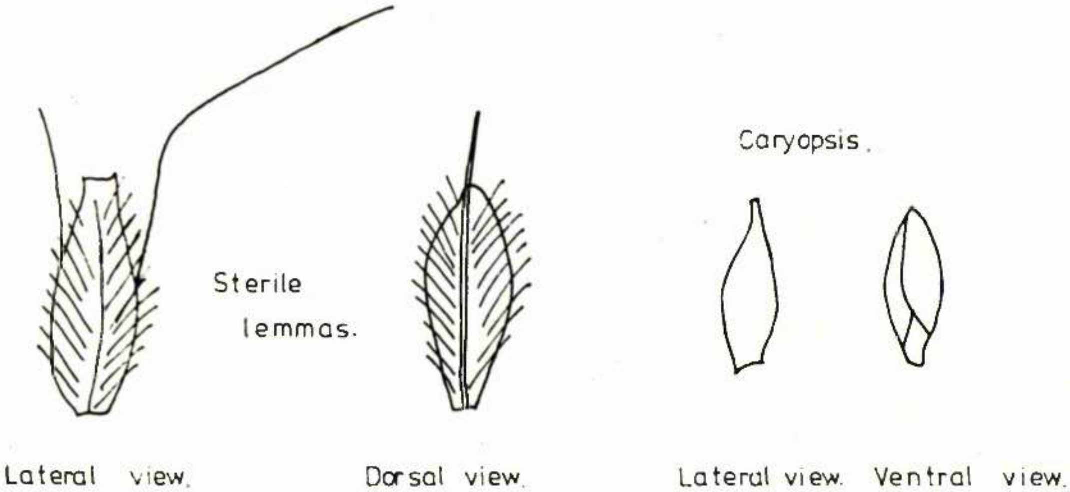
4) Colour

Chestnut brown florets and hairs, lighter tips. 165A, 165B, 200D.

Plate 6&7 Anthoxanthum odoratum L.

Previous descriptions:

2.0-3.5 mm long, 1.0-1.3 mm wide, 0.6-1.0 mm deep (B & S, B, H, K).



Scale: 2 mm
Magnification: x 4.0

Scale: 2 mm
Magnification: x 7.0

Deschampsia caespitosa (L.) Beauv.

Caryopsis

1) Dimensions

Length 1.42 ± 0.03 mm
Width = Depth 0.45 ± 0.01 mm

2) Shape

Obovate (46) in ls, circular (6) in cs. Dorsal side straight to slightly convex, ventral side convex. Apex ends in a white stalk, base as a sharp point. In side view, the ventral side tapers more than the dorsal side towards the base.

3) Comments

Groove on ventral side runs longitudinally. Surface longitudinally striate to slightly ridged with cross markings into squares.

4) Colour

Chestnut brown/brown. 166B.

Caryopsis enclosed by lemma and palea - description compiled completely from previously published work as no seed in the lemma was available for examination.

Lemma oblong, rounded on the back. Apex truncate and jagged. 5-nerved. Bearded at the base. Membranous.
Palea shorter than lemma, glabrous, 2-keeled. Truncate at the base and jagged at the apex. Thin and hyaline.
Fine straight awn arises near the base and slightly exceeds or equals the lemma.

Plate 8&9 Deschampsia caespitosa (L.) Beauv.

Scale: 2 mm

Magnification: x 6.6

Scale: 2 mm

Magnification: x 8.5

Ventral view.

Lateral view.

Caryopsis.

Previous descriptions:

2.9-4.0 mm long, 0.7 mm wide (B, H, K).

Caryopsis:

1.5-2.0 mm long (B & S, B).

Deschampsia flexuosa (L.) Trin.

Caryopsis

1) Dimensions

Length 2.34 $\pm$ 0.08 mm
Width 0.63 $\pm$ 0.02 mm
Depth 0.50 $\pm$ 0.02 mm

2) Shape

Obovate (45-46) in ls, elliptic (7) to oblong (19) in cs. Ventral side flat with both edges marked by ridges extending half way down the caryopsis. Dorsal side convex. Seed tapers to a point at the base and to a dark stalk (= remains of style) at the more rounded or truncate apex.

3) Comments

Surface with rough longitudinal wrinkles and secondary cross veins.

4) Colour

Grey-brown to fawn/yellowish brown. 163C, 164B, 164C, 165B.

Caryopsis enclosed by lemma and palea

1) Dimensions

Length 4.29 $\pm$ 0.08 mm
Width 0.84 $\pm$ 0.04 mm
Depth 0.58 $\pm$ 0.03 mm

2) Shape

Elliptic (1) to obovate (45) in ls, elliptic (8) to oblong (20) in cs.

3) Comments

Lemma finely longitudinally striate ending in a jagged blunt hyaline apex. 4-5 purplish-brown longitudinal nerves. Lemma is toothed. Teeth point upwards, are arranged in longitudinal lines and are longer towards the apex.

Palea slightly shorter than lemma with two rough keels. Long (0.03-0.16 mm) upward-pointing basal hairs.

Awn is inserted on the central nerve near the base of the dorsal side. It is about 5.36 $\pm$ 0.28 mm long. For half the length of the seed it is straight and dark brown. It then bends twice and becomes first chestnut brown and then light brown. The awn is twisted in its lower two parts and laterally toothed and shining in the upper part.

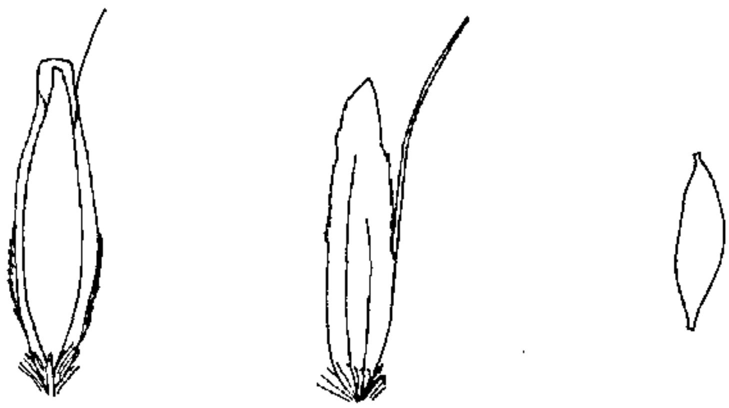
4) Colour

Yellowish brown to light brown. Translucent and shiny at the tip. 162A, 163C, 165A, 165B.

Plate 10   <u>Deschampsia flexuosa</u> (L.) Trin.

<u>Previous descriptions:</u>

2.5-5.5 mm long, 0.5-0.7 mm wide, 0.5-0.6 mm deep (B & S, B, H, K).



Ventral view.   Lateral view.   Caryopsis.

Scale: 2 mm

Magnification: x 4.4

Holcus lanatus L.

Caryopsis

1) Dimensions

Length 1.65 $\pm$ 0.07 mm
Width 0.50 $\pm$ 0.02 mm
Depth 0.66 $\pm$ 0.04 mm

2) Shape

Elliptic (2) in ls, elliptic (4-5) in cs. From a side view, the dorsal side curves more sharply than the ventral side near the base.

3) Comments

Apex truncate and darker. Base darker. Groove on ventral side runs from just below the apex to an oval scar near the base.
Surface smooth with fine longitudinal striations and cross veins forming rectangles.

4) Colour

Chestnut brown to brown. 164A, 165A, 165B.

Caryopsis enclosed by lemma and palea

1) Dimensions

Length 2.42 $\pm$ 0.03 mm
Width 0.61 $\pm$ 0.02 mm
Depth 0.76 $\pm$ 0.02 mm

2) Shape

Elliptic (1-2) to ovate (36-37) in ls, elliptic (7) in cs.
Broadest about a third of the way from the base and tapering to both ends.

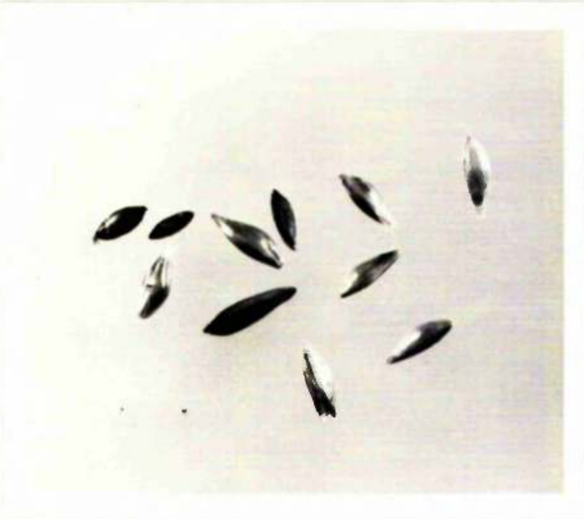
3) Comments

Sharp longitudinal nerve in centre of curved dorsal side. Along ventral side, a groove runs longitudinally almost to the apex from the pedicel which is about 0.7 mm long.
Surface smooth with a longitudinally striate pattern. Palea shorter or equal to lemma.

4) Colour

Shiny. Cream to pale brown. 161B, 163D, 164B, 164C.

Plate 11&12 <u>Holcus lanatus</u> L.

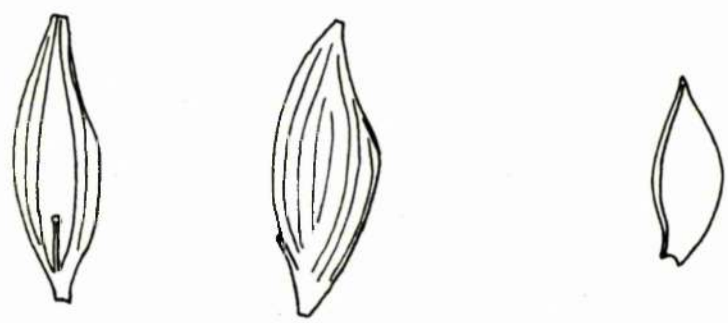


Scale: 2 mm

Magnification: x 4.5

Scale: 2 mm

Magnification: x 6.9



Ventral view. Lateral view. Caryopsis.

Previous descriptions:

2.0-4.0 mm long, 0.7-1.0 mm wide (B & S, B, H, K, Me, P & S).

Poa annua L.

Caryopsis

1) Dimensions

Length 1.39 ± 0.04 mm
Width 0.53 ± 0.01 mm
Depth 0.57 ± 0.01 mm

2) Shape

Ovate (37) in ls, ovate (40-41) to triangular (77-78) in cs. Caryopsis pointed towards apex and base. From the side, the ventral edge is more strongly curved than the dorsal edge. Dorsal side is broadly boat-shaped.

3) Comments

Dorsal side wider than ventral side with a central longitudinal shallow depression at the base of which is the hilum. Surface with raised longitudinal striations and secondary cross veins giving a rectangular pattern.

4) Colour

Dark chestnut brown with apex and tip lighter and translucent where remains of lemma and palea still attached. 165A, 166A, 200D. (Hilum dark with a white tip below.)

Caryopsis enclosed by lemma and palea

1) Dimensions

Length 2.74 ± 0.08 mm
Width 0.63 ± 0.01 mm
Depth 0.77 ± 0.03 mm

2) Shape

Ovate (36-37) in ls, ovate (40) to triangular (77) in cs. Seed tapers to a slightly truncate base and more gently to a pointed apex. Seed is broadest a third of the way from the base. From the side, the dorsal edge looks straighter than the ventral edge.

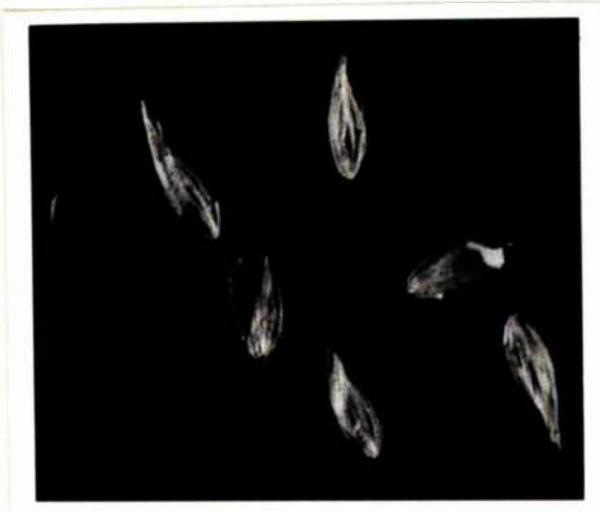
3) Comments

Boat-shaped lemma has 5 nerves running from the base towards, but not reaching, the apex. Central nerve hairy from the base to the middle of the seed. Palea shorter or almost equal to lemma. Margins and tip hyaline. Two longitudinal nerves on palea are hairy from the base to the middle of the seed. Lemma and palea with fine longitudinal striations.

4) Colour

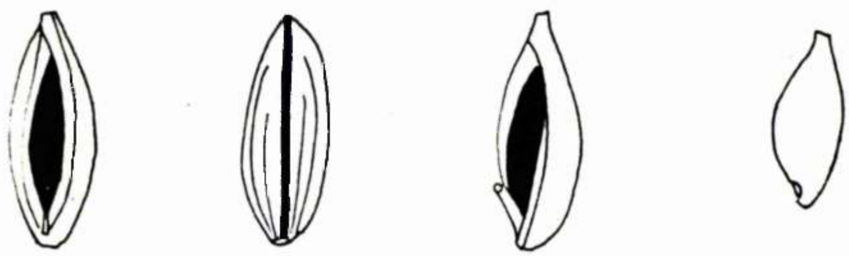
Yellowish-brown to brown. 161A, 199D. Nerves cream coloured.

Plate 13 Poa annua L.



Scale: 2 mm

Magnification: x 6.9



Ventral view. Dorsal view. Lateral view. Caryopsis.

Previous descriptions:

2.2-4.0 mm long, 0.6-1.0 mm wide, 0.5-0.8 mm deep (B & S, vdB, B, H, K).

Poa pratensis L.

Caryopsis

1) Dimensions

Length 1.78 ± 0.05 mm
Width 0.53 ± 0.02 mm
Depth 0.58 ± 0.01 mm

2) Shape

Ovate (37) in ls, ovate (41) to triangular (78) in cs. Apex pointed, base truncate. Dorsal side boat-shaped, ventral side wider and flatter.

3) Comments

Ventral side with a shallow central longitudinal depression. Dorsal side with a sharp central longitudinal ridge. Surface rough with longitudinal and transverse pitting.

4) Colour

Brown with translucent remains where the lemma and palea are still attached. 164A, 165A, 165B. Hilum darker with a lighter point below the hilum.

Caryopsis enclosed by lemma and palea

1) Dimensions

Length 3.03 ± 0.09 mm
Width 0.63 ± 0.02 mm
Depth 0.71 ± 0.02 mm

2) Shape

Ovate (36-37) in ls, ovate (40-41) to triangular (77-78) in cs. In side view, apex flared; in front view, apex pointed. Dorsal side narrowly boat-shaped.

3) Comments

Sharp keeled longitudinal midrib on dorsal side. 5 longitudinal ribs (including midrib) on dorsal side. Palea nearly equals lemma and has 2 longitudinal veins. Lemma and palea with longitudinal striations and less prominent cross veins. Small cottony hairs at base.

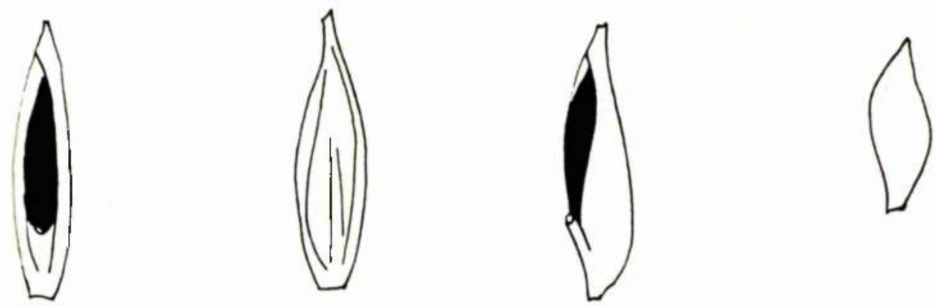
4) Colour

Pale brown to brown. 164B, 165C, 199C, 199D.

Plate 14 Poa pratensis L.

Previous descriptions:

2.2-4.0 mm long, 0.6-0.8 mm wide, 0.3-0.6 mm deep (B & S, vdB, B, H, K).



Ventral view. Dorsal view. Lateral view. Caryopsis.

Scale: 2 mm

Magnification: x 5.2

Poa trivialis L.

Caryopsis

1) Dimensions

Length 1.27 $\pm$ 0.09 mm
Width 0.42 $\pm$ 0.02 mm
Depth 0.49 $\pm$ 0.03 mm

2) Shape

Ovate (37) in ls, ovate (40) to triangular (77) in cs. Base truncate, apex tapers to a point.

3) Comments

Ventral side has a deep longitudinal central depression. Surface finely longitudinally striate with cross veins giving a rectangular pattern.

4) Colour

Brown. 164A, 165A, 166A, 200D. Apex and base darker.

Caryopsis enclosed by lemma and palea

1) Dimensions

Length 2.26 $\pm$ 0.06 mm
Width 0.53 $\pm$ 0.02 mm
Depth 0.59 $\pm$ 0.02 mm

2) Shape

Ovate (36-37) in ls, ovate (40) to triangular (77) in cs.

3) Comments

On dorsal side, 5 sharp longitundinal veins with the central vein very prominent. Palea equals or nearly equals the lemma and has 2 rough longitudinal keels. Cottony hairs at base. Surface of lemma and palea appears mottled but is smooth. Is longitudinally striate with transverse veins giving a rectangular pattern.

4) Colour

Cream, light brown. 161B, 164B, 164C, 165B, 165C.

Plate 15&16 Poa trivialis L.

Scale: 2 mm

Magnification: x 9.9

Previous descriptions:

2.0-3.5 mm long, 0.4-0.6 mm wide, 0.4-0.6 mm deep (vdB, H, B, B & S).

Caryopsis:

1.2 mm long (B).

Scale: 2 mm

Magnification: x 4.7

Aphanes arvensis L.

1) Dimensions

Length 1.32 ± 0.04 mm
Width 0.94 ± 0.02 mm
Depth 0.53 ± 0.01 mm

2) Shape

Ovate (40) in ls, elliptic (8-9) in cs. Rounded base with a short stalk and apex tapering to a point. Stalk and apical point are off-centre giving an asymmetrical ls. Lateral edge nearer to stalk and apex is sharper than opposite edge giving a slightly asymmetrical cs.

3) Comments

Achene surrounded by an indistinct margin. Surface appears lightly wrinkled (but is very finely longitudinally striate and crosswise grooved). Finely longitudinally punctate.

Seed may be found enclosed by sepals which are ridged, covered with upward pointing stiff hairs and which divide into 4 tongues at the top.

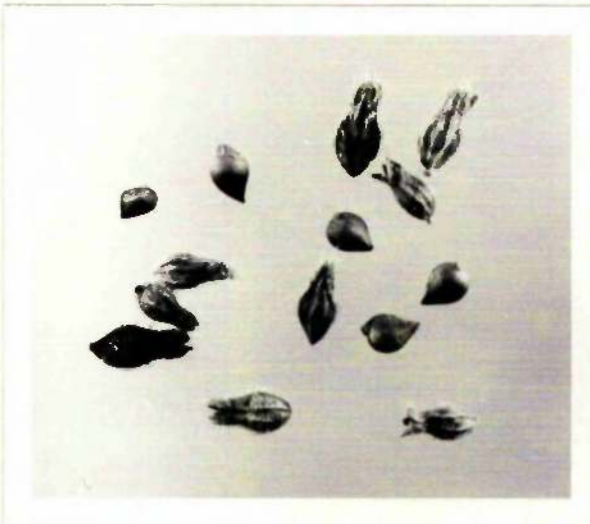
Dimensions: Length 2.26 ± 0.06 mm
Width 1.04 ± 0.02 mm
Depth 0.64 ± 0.01 mm

Shape: Ovate (38) in ls, elliptic (8) to oblong (20) with slightly rounded corners in cs.

4) Colour

Achene pale brown. 161A, 161B. Edge of margin slightly darker giving a crisp outline. When enclosed by sepals - light brown/reddish brown/cream. 161C, 165C, 166B, 200D.

Plate 17 Aphanes arvensis L.



Scale: 2 mm

Magnification: x 5.2

Previous descriptions:

Achene: 1.5 mm long, 1.0 mm wide.
Achene in sepals: 2.2-2.6 mm long. } (B, CTW).

Calluna vulgaris (L.) Hull

1) Dimensions

Length 0.52 ± 0.01 mm
Width 0.34 ± 0.01 mm
Depth 0.22 ± 0.01 mm

2) Shape

Variable. From broadly elliptic (4) to obovate (48) in ls, transversely elliptic (8) in cs.

3) Comments

Hilum situated at base on ventral side.
Seed covered with a raised net-like structure which gives the appearance of pits running longitudinally. Net is often broken above the hilum.

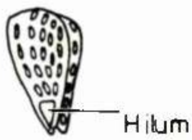
4) Colour

Chestnut brown with a darker net. 164A, 165A. Shiny.

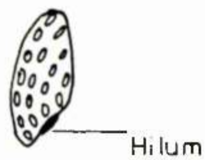
Plate 18 Calluna vulgaris (L.) Hull

Previous descriptions:

0.8-1.2 mm long, 0.2-0.3 mm wide, (0.6 mm wide ?(B)), 0.2-0.3 mm deep. (B & S, B).
Bright brown, brown. (Be, B & S, B).



Ventral view.



Lateral view.

Scale: 2 mm

Magnification: x 7.3

Campanula rotundifolia L.

1) Dimensions

Length 1.07 ± 0.04 mm
Width 0.47 ± 0.02 mm
Depth 0.26 ± 0.01 mm

2) Shape

Elliptic (3) in ls, elliptic (9) in cs. Apex and base truncate.

3) Comments

Wing, of similar colour as seed, runs across one edge and gives seed a twisted appearance.
Surface finely longitudinally striate.

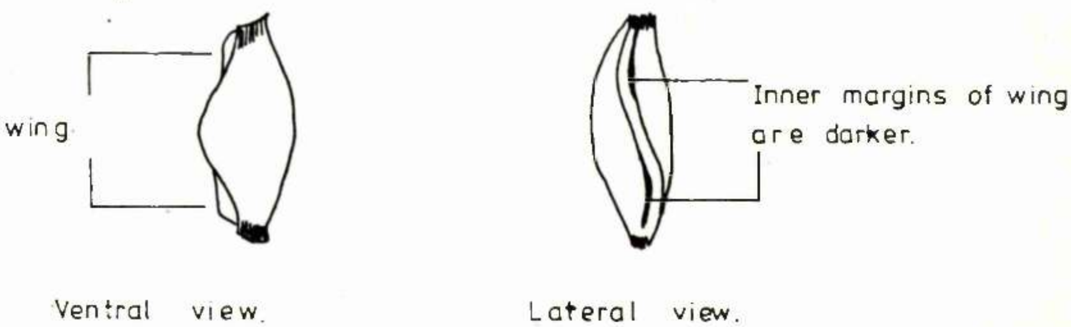
4) Colour

Greenish brown to golden brown. 162A, 163C, 165B. Tip, hilum and inner curves of wing darker than rest of seed.

Plate 19 Campanula rotundifolia L.

Scale: 2 mm

Magnification: x 7.7



Previous descriptions:

0.9-1.5 mm long, 0.4-0.7 mm wide, 0.2 mm deep. (B, Mo).

Light brown, brown. (Be, B, Mo).

<u>Capsella bursa-pastoris</u> (L.) Medic.

1) Dimensions

Length 0.88 ± 0.03 mm
Width 0.47 ± 0.02 mm
Depth 0.30 ± 0.02 mm

2) Shape

Elliptic (3-4) to oblong (15-16) with rounded corners in ls, elliptic (8-9) to oblong (20-21) with rounded corners in cs. Base truncate.

3) Comments

Each face has a groove running parallel to the edge from the base towards the apex and recurving to the base; this indicates the position of the radicle which lies against the flat side of the cotyledons.
Surface finely granular.

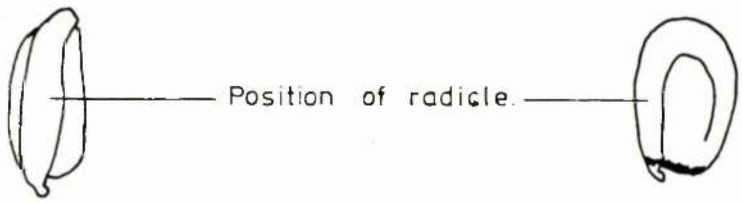
4) Colour

Golden brown, beech brown. 164A, 165A, 165B. Base darker than rest of seed. Seed stalk represented by a white, cream or pale brown tip.

Plate 20 Capsella bursa-pastoris (L.) Medic.

Previous descriptions:

0.8-1.2 mm long, 0.3-0.6 mm wide, 0.3-0.4 mm deep. (B & S, CTW, D, K, Me, Mo, P & S).
Yellow, yellow-brown, ochre, golden brown, pale brown, red-brown, brown. (Be, B, CTW, D, K, Me, P & S).



Lateral view. Ventral view.

Scale: 2 mm

Magnification: x 6.1

<u>*Cardamine hirsuta*</u> L.

1) Dimensions

Length 1.10 $\pm$ 0.03 mm
Width 0.85 $\pm$ 0.01 mm
Depth 0.26 $\pm$ 0.01 mm

2) Shape

Elliptic to broadly elliptic (4-5) in ls, (almost oblong (15-16) with rounded corners); narrowly elliptic (10) in cs. Seed very flat.

3) Comments

Hilum indented on truncate base. From base a groove runs parallel and closer to one of the broad sides towards the apex and then turns back a short way towards the base. This indicates the position of the radicle. Groove more distinct on one side. Narrow margin around seed. Surface with faint longitudinal striations divided by cross veins into rectangles around the edges of the seed. Rest of seed appears granular.

4) Colour

Margin slightly darker than rest of seed, as is hilum. Golden brown to beech brown. 164A, 164B, 165A, 166A.

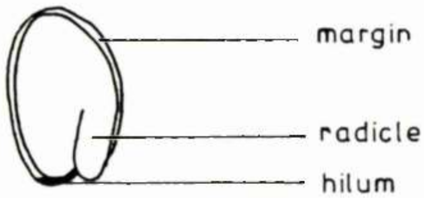
Plate 21&22 Cardamine hirsuta L.

Scale: 2 mm

Magnification: x 9.7

Scale: 2 mm

Magnification: x 7.6



Ventral view.

Previous descriptions:

1.0-1.5 mm long, 1.0 mm wide. (B, CTW).

Light brown, brown. (Be, B).

Carex binervis Sm.

1) Dimensions

Length 2.18 ± 0.05 mm
Width 1.25 ± 0.02 mm
Depth 1.12 ± 0.02 mm

2) Shape

Ovate (38-39) in ls, triangular (78-79) with concave sides in cs.

3) Comments

Faces meet in rounded edges. Remains of stigma indicated by a stalk at the apex. Base ends in blunt snout. Surface longitudinally punctate.

4) Colour

Cream, pale brown. 199A. Base and seed edges lighter. Stalk remains darker.

Nut may be found enclosed by perigynium.

1) Dimensions

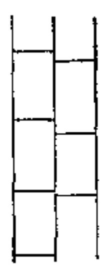
Length 3.71 ± 0.07 mm
Width 1.67 ± 0.04 mm
Depth 1.11 ± 0.02 mm

2) Shape

Narrowly ovate (38) in ls, ovate (43) to triangular (80) in cs, with base concave and lateral faces more or less convex.
Perigynium drawn out into a long neck at the apex which ends in a V or U shaped notch from which the remains of the style may protrude.

3) Comments

Lateral margins broad and sharp. Upper dorsal surfaces with 6-10 longitudinal veins and 2 dark green prominent submarginal nerves.
Dorsal side shiny, longitudinally rectangularly striate. Longitudinal veins are matt, smooth and less obviously scalariform. Veins are absent on ventral side.



4) Colour

Purplish, browny-red with pale brown. 160B, 160D, 161A, 165C, 166A, 200A.

Plate 23 Carex binervis Sm.

Previous descriptions:

3.5-4.5 mm long, 2.0 mm wide. (Nut enclosed by perigynium).
2.0-3.0 mm long, 1.5 mm wide. (Nut).
(B, CTW, J & T).
Pale green, purplish, purple-brown. (CTW, J & T).

Scale: 2 mm
Magnification: x approx. 5.55

<u>Cerastium holosteoides</u> Fr.

1) Dimensions

Length 0.78 ± 0.02 mm
Width 0.76 ± 0.02 mm
Depth 0.47 ± 0.01 mm

2) Shape

Highly variable, sometimes seed broader than long. From rhombic (30) to obovate (50) in ls, elliptic (8) to oblong (20) in cs. Generally broadest below the rounded apex tapering from all sides to the base.

3) Comments

A groove runs from the deeply indented hilum on the base along one edge and fades out on the adjacent edge. Surface covered with blunt elongated tubercles which run from the hilum parallel to the edge on the outermost part of the seed. Further inward the tubercles run towards the base in a less definite pattern.

4) Colour

Reddish brown, brown. Dull. 165A.

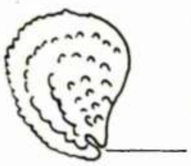
Plate 24&25 Cerastium holosteoides Fr.

Scale: 2 mm

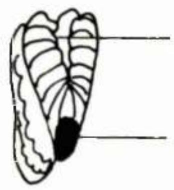
Magnification: x 6.8

Scale: 2 mm

Magnification: x 7.5



Ventral view.



Lateral view.

Previous descriptions:

0.5-0.9 mm long, 0.5-0.7 mm wide, 0.4 mm deep. (CTW, D, K, Me, Mo, P & S).

Red-brown, chocolate-brown, brown. (CTW, D, K, Mo, P & S).

<u>Cirsium arvense</u> (L.) Scop.

1) Dimensions

Length 3.44 ± 0.11 mm
Width 1.01 ± 0.03 mm
Depth 0.66 ± 0.04 mm

2) Shape

Obovate (46) in ls, elliptic (8) in cs. Achene tapers to a truncate base. Axis slightly curved.

3) Comments

Remains of style present as a stalk surrounded by an oblique collar at the apex. Surface smooth with fine longitudinal striations and intervening bands which are also striate.

4) Colour

Main achene body light to golden brown. 161A, 161B, 161C, 164B, 164C. Collar and bands lighter than body. Stalk remnant darker.

Plate 26 Cirsium arvense (L.) Scop.

Previous descriptions:

3.0-4.0 mm long, 1.1-1.5 mm wide. (B, CTW, K, Me, P & S).
Yellow-brown, neutral-brown, silky-brown, dark brown, grey.
(B, CTW, K, Me, P & S).

Scale: 2 mm

Magnification: x 5.9

Digitalis purpurea L.

1) Dimensions

Length 0.89 ± 0.03 mm
Width 0.63 ± 0.02 mm
Depth 0.47 ± 0.02 mm

2) Shape

Obovate (48) in ls, depressed obovate (51-52) in cs. Broadest at apex and tapering towards base. Apex and base truncate.

3) Comments

Groove extends from hilum at base on ventral side almost to apex. Surface covered with a raised honeycomb network.

4) Colour

Greyish brown. 200C, 200D. Network lighter brown.

Plate 27 Digitalis purpurea L.

Scale: 2 mm

Magnification: x 8.5

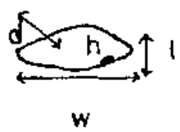
Previous descriptions:

0.6-0.9 mm long, 0.3-0.5 mm wide, 0.3-0.5 mm deep. (B & S, B).
Yellow to brown, brown, grey-brown. (Be, B & S, B).

<u>Erica cinerea</u> L.

1) Dimensions

Length 0.40 $\pm$ 0.02 mm
Width 0.76 $\pm$ 0.02 mm
Depth 0.53 $\pm$ 0.02 mm



2) Shape

Elliptic (9) to obovate (53) in ls, broadly obovate (51-52) in cs.

3) Comments

Hilum located towards one side of broad base. Surface highly sculptured with deep pits running from the hilum in concentric rings.

4) Colour

Beech to golden brown. 164A, 165A. Hilum darker than rest of seed.

Plate 28 Erica cinerea L.

Previous descriptions:

0.6-0.8 mm long, 0.2-0.4 mm wide, 0.2-0.3 mm deep. (B & S, B).
Brown. (Be, B & S, B).

Hilum at base of ventral side.

Lateral view.

Pitted pattern on lateral surfaces.

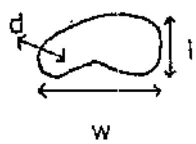
Scale: 2 mm
Magnification: x 5.5

Galium saxatile L.

Seeds are paired on the flowering stalk but are usually found singly or with the partner seed attached but withered. Examples of all three are to be seen in Plate 29. The description is for a single seed with the hilum orientated downwards.

1) Dimensions

Length	0.64 ± 0.03	mm
Width	1.09 ± 0.03	mm
Depth	0.89 ± 0.04	mm



2) Shape

Elliptic (8-9) in ls, broadly elliptic (7) in cs with a depression on the lower side.

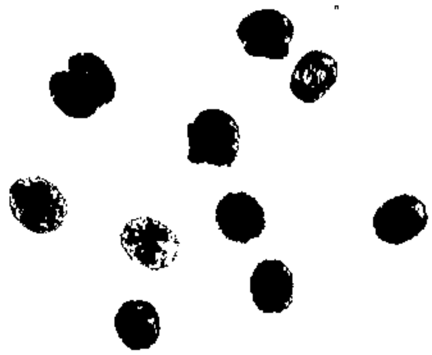
3) Comments

Entire surface covered with high tubercles running longitudinally and dorsal side with longitudinal ridges of tubercles also.

4) Colour

Beech brown to grey. Dull. 165A, 200A, 200B. Seed covered with papery sheath (lighter in colour than the rest of the seed) and tips of tubercles may appear lighter than seed body.

Plate 29 <u>Galium saxatile</u> L.



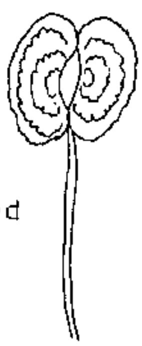
Scale: 2 mm

Magnification: x 6.6

<u>Previous descriptions:</u>

1.5-2.0 mm long, 2.5 mm wide (width across two seeds on stalk). (B, CTW).

Brown. (Be).



Seeds paired on stalk.

Ventral view.

Single seed with withered partner.

Lateral view.

Gnaphalium uliginosum L.

1) Dimensions

Length 0.59 ± 0.02 mm
Width 0.20 ± 0.00 mm
Depth 0.14 ± 0.01 mm

2) Shape

Elliptic (2) to ovate (37) in ls, elliptic (8) to oblong (20) in cs. Base rounded with a short blunt point. Achene tapers towards apex which is drawn into a short stalk like the neck of a bottle.

3) Comments

Lateral faces with a central ridge or wing. Surface longitudinally striate.

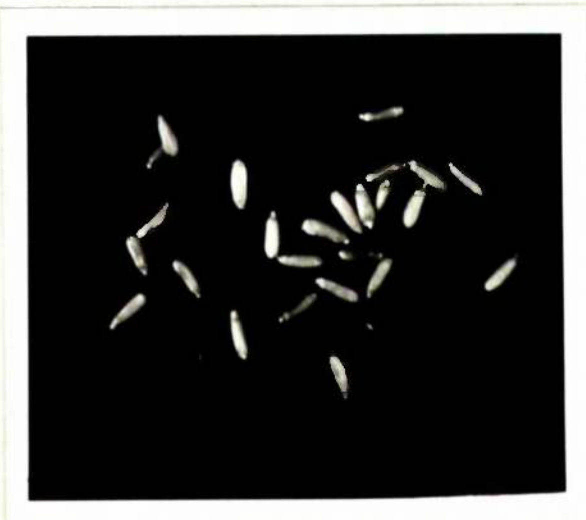
4) Colour

Greyish green. Slightly gleaming. 199A, 199B. Base of neck slightly darker than rest of achene with tip a light brown or cream colour.

Plate 30 Gnaphalium uliginosum L.

Previous descriptions:

0.4-0.7 mm long, 0.1-0.2 mm wide, 0.1 mm deep. (B & S, B, CTW, Mo).
Yellow-brown, brown, dark brown, grey. (Be, B & S, Mo).



Scale: 2 mm

Magnification: x 11.0

Hypericum humifusum L.

1) Dimensions

Length   0.61 ± 0.03 mm
Width = Depth   0.32 ± 0.01 mm

2) Shape

Elliptic (3) in ls, circular (6) in cs.   Small point at each end.

3) Comments

Broad honeycomb-shaped depressions run longitudinally.   Surface shiny.

4) Colour

Dark brown, grey.   200B, 200C, 200D.   Points at either end darker.

Plate 31 Hypericum humifusum L.

Scale: 2 mm

Magnification: x 8.5

Previous descriptions:

0.8 mm long, 0.3 mm wide. (B).

Brown, almost black. (Be, B).

<u>Juncus acutiflorus</u> Hoffm.

1) Dimensions

Length 0.69 $\pm$ 0.03 mm
Width 0.30 $\pm$ 0.01 mm
Depth 0.27 $\pm$ 0.01 mm

2) Shape

Elliptic (2-3) to ovate (37-38) in ls, circular (6) to elliptic (7) in cs. Long axis slightly twisted. Apex sharply pointed. Base bluntly pointed.

3) Comments

Margin along one side. (This may represent the overlap of a glossy sheath surrounding the seed.)
Prominent longitudinal striations divided less obviously into long, narrow rectangles.

4) Colour

Yellow/brown. 164A, 165A, 165B, 200D. Longitudinal veins, margins and apices darker brown than rest of seed. Glossy.

Plate 32 Juncus acutiflorus Hoffm.

Previous descriptions:

0.3-0.5 mm long, 0.2 mm wide. (B, S).

Light brown, yellow-brown, brown. (Be, B, S).

Scale: 2 mm

Magnification: x 6.4

Juncus bufonius L.

1) Dimensions

Length 0.44 ± 0.01 mm
Width = Depth 0.30 ± 0.02 mm

2) Shape

Elliptic (4) in ls, circular (6) in cs. Apex drawn into short stalk, base with small sharp point.

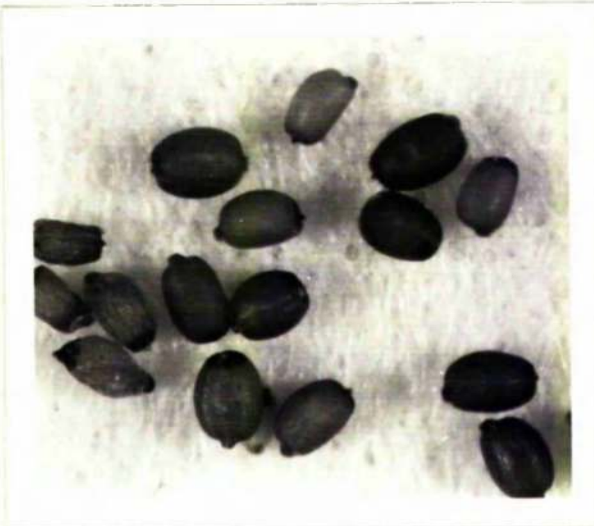
3) Comments

Surface longitudinally striate with undulating ridges and faintly cross rifted. Seed glossy, as if covered with a translucent/ transparent sheath: seen more clearly at the apices.

4) Colour

Seed body yellowy brown 164A, 165B. Apex marginally darker with hilum and point darker still.

Plate 33&34 Juncus bufonius L.



Scale: 1 mm

Magnification: x 27.5

Previous descriptions:

0.2-0.45 mm long, 0.2-0.3 mm wide, 0.2-0.3 mm deep. (B & S, B, K, Mo).

Golden, yellow-brown, light brown, brown. (Be, B & S, B, K).

Scale: 2 mm

Magnification: x 5.9

Juncus effusus L.

1) Dimensions

Length   0.50 ± 0.01 mm
Width = Depth   0.21 ± 0.05 mm

2) Shape

Obliquely obovate (46-47) in ls, circular (6) in cs. Apex drawn out into blunt tip, base drawn into a sharper point.
Viewed from the side, the dorsal side is strongly convex, and the ventral side is straight to slightly convex.

3) Comments

Surface prominently longitudinally striate with fine wavy lines and less obviously cross rifted (into short wide rectangles). Seed surrounded by transparent sheath giving seed a shiny appearance. Sheath clearly visible at apices and as a longitudinal margin on the ventral side.

4) Colour

Seed body yellowish brown 165A, 165B, 166A. Darker towards ends.
Hilum and apex lighter (cream/white).

Plate 35&36 Juncus effusus L.

Scale: 1 mm

Magnification: X 26.8

Previous descriptions:

0.2-0.5 mm long, 0.1-0.25 mm wide, 0.1-0.2 mm deep. (B & S, B, K, Mo, S).

Yellow-brown, red-brown, light brown, brown. (Be, B & S, B, K, S).

Scale: 2 mm

Magnification: x 6.4

Luzula campestris (L.) DC

1) Dimensions

Length 1.50 ± 0.03 mm
Width 0.70 ± 0.01 mm
Depth 0.65 ± 0.01 mm

2) Shape

Ovate (38) in ls, elliptic (6) in cs.

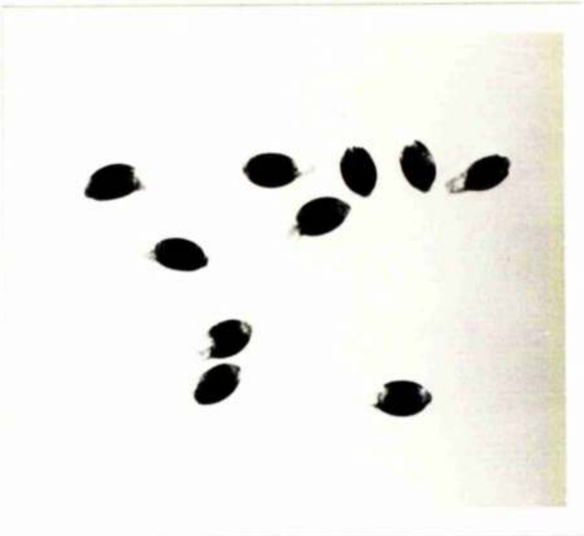
3) Comments

Apex tipped with a prominent translucent/white caruncle which from all 4 sides of the seed appears triangular with a central upright ridge.
Sulcus or groove runs from the base to the caruncle and continues to the apex as a central ridge. Sulcus is on the ventral side.
Surface longitudinally finely ridged below a translucent sheath.

4) Colour

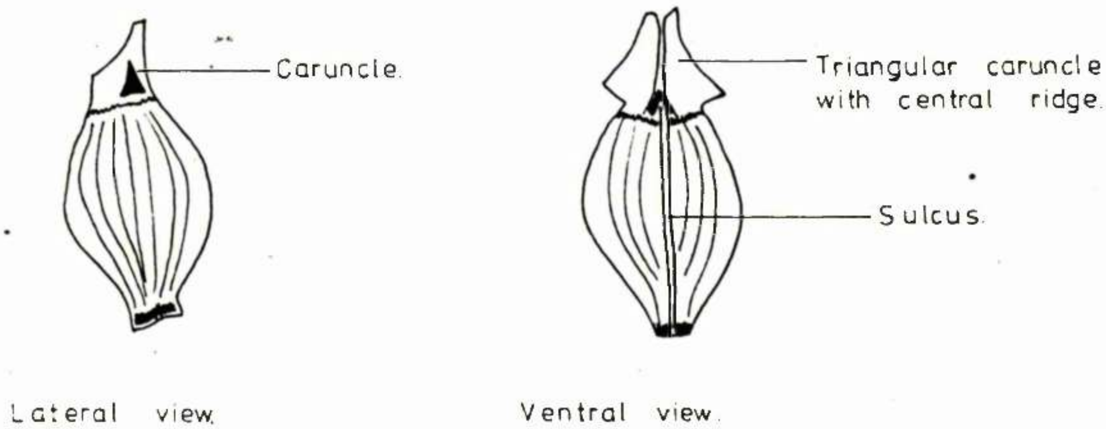
Brown/brownish purple. 165A, 200B, with a translucent sheath.
Base white/translucent but less so than the caruncle at the apex.

Plate 37   Luzula campestris (L.) DC



Scale: 2 mm

Magnification: x 6.7



Previous descriptions:

1.0-2.0 mm long, 0.6-0.9 mm wide, 0.7-0.8 mm deep. (B & S, B, D, Mo).
Reddish, purplish-red, brown, dark brown. (Be, B & S, B, D, Mo).

Matricaria matricarioides (Less.) Porter

1) Dimensions

Length 1.29 ± 0.03 mm
Width 0.48 ± 0.01 mm
Depth 0.37 ± 0.01 mm

2) Shape

Obovate (46-47) in ls, elliptic (7-8) to obovate (51-52) in cs. Axis curved towards ventral side. Apex and base truncate.

3) Comments

Ventral side with 4 longitudinal ribs - 1 at either edge and 2 placed closer together in the centre of the ventral side with a deep groove between them.
Base indicated by a rim and apex by a thick collar. Stalk on apex indicates the point of attachment of the pappus.
Surface appears finely longitudinally striate but is smooth in texture.

4) Colour

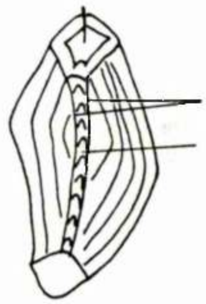
Pale brown. 161B, 161C, 161D, 199C, 199D. Ribs and collar yellowish-brown (i.e. lighter than achene body).

Plate 38 Matricaria matricarioides (Less.) Porter

Previous descriptions:

0.9-1.4 mm long, (B 4.0 mm); 0.3-0.5 mm wide, 0.2-0.3 mm deep.
(B & S, (B), CTW, Mo).
Olive, brownish, dark brown, grey, black. (Be, B & S, B, Mo).

Lateral view.



Ventral view.

Scale: 2 mm

Magnification: x 7.1

Montia fontana L.

1) Dimensions

Length 1.06 $\pm$ 0.02 mm
Width 0.96 $\pm$ 0.01 mm
Depth 0.66 $\pm$ 0.01 mm

2) Shape

Elliptic (5-6) in ls, elliptic (8) in cs.

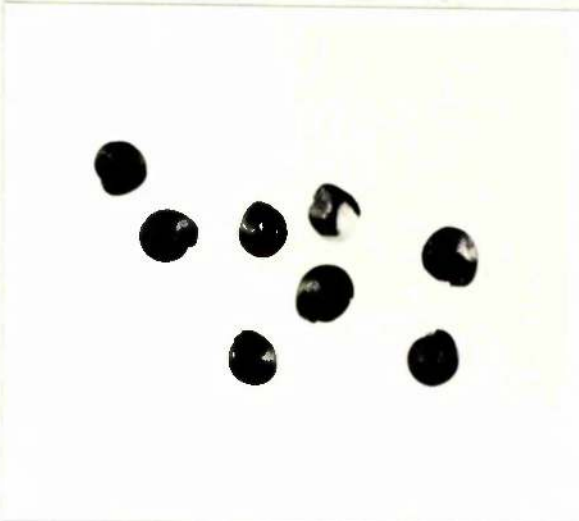
3) Comments

Base appears stepped with hilum and part of base raised relative to the rest of the base. Hilum has a smooth rounded lip. Surface covered with broad rounded protuberances which run longitudinally around the lateral sides of the seed from the hilum and around the edges of the dorsal side and ventral sides. In the middle of the dorsal and ventral sides the protuberances are arranged in lines radiating from the hilum.

4) Colour

Dark brown, 200A, with a lighter hilum. Very shiny.

Plate 39 Montia fontana L.



Scale: 2 mm

Magnification: x 6.5

Previous descriptions:

0.8-1.4 mm in diameter. (B, S).

Brown, dark brown, black. (B, CTW, S).

<u>Myosotis arvensis</u> (L.) Hill

1) Dimensions

Length 1.68 $\pm$ 0.04 mm
Width 1.07 $\pm$ 0.04 mm
Depth 0.65 $\pm$ 0.03 mm

2) Shape

Ovate (39) in ls, obovate (52) in cs. Dorsal side convex. Ventral side with a rounded longitudinal keel (except near the apex where the keel is sharper). Depressions either side of the keel near the apex and near the base almost produce a sector shape in cs.

c.s.

3) Comments

A distinct recurved rim runs from the hilum at the base of the ventral side towards the tip where it becomes downcurved. Hilum has a whitish scar on the ventral side. Surface texture smooth. Surface patterning scalariform.

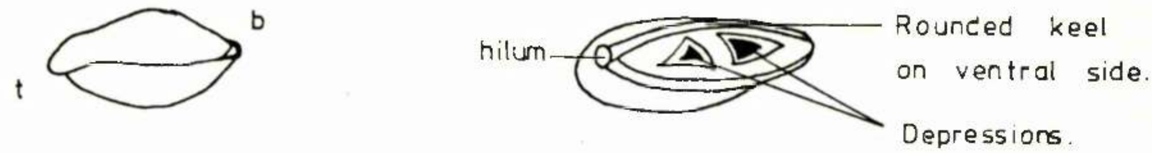
4) Colour

Dark brown to black. 200A. Very glossy.

Plate 40 <u>Myosotis arvensis</u> (L.) Hill

<u>Previous descriptions:</u>

1.0-2.0 mm long, 0.75-1.0 mm wide, 0.4-0.5 mm deep. (B & S, B, CTW, K, Ma & B, Me, P & S).
Light to dark brown, brownish-black, bluish-black, black, jet-black. (Be, B & S, B, CTW, K, Ma & B, Me, P & S).



Rim curves down at tip [t] and upwards at base [b].

Lateral view.

Scale: 2 mm

Magnification: x 6.2

Plantago major L.

1) Dimensions

Length 1.53 ± 0.02 mm
Width 0.83 ± 0.03 mm
Depth 0.42 ± 0.02 mm

2) Shape

In ls, elliptic (3) to oblong (15) with one of the lateral sides obliquely cut off; obovate (53) in cs.
Shape is highly variable and is dependent upon the number of seeds in the capsule. Generally, one edge conspicuously longer than the others, of which 3-4 may be distinguishable.
Seed twisted along its short axis.

3) Comments

Dorsal side flat to slightly convex with low irregular longitudinal ridges. Ventral side rises towards the more or less centrally placed depressed hilum from which threadlike ridges radiate to the seed edges.
Hilum consists of a double scar almost joined by a groove.

4) Colour

Seed body dull. Dark brown 200B, 200C, 200D. Ridges darker. On dorsal side, a broad lighter coloured central band can be detected. White or translucent tissue fragments may adhere to the surface.
Hilum lighter.

Plate 41 Plantago major L.

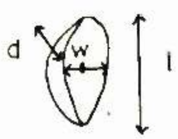
Scale: 2 mm

Magnification: x 5.6

Previous descriptions:

0.8-2.0 mm long, 0.4-1.0 mm wide, 0.4-0.6 mm deep. (B & S, B, D, K, Me, Mo, P & S).

Light brown, brown, dark olive brown, dark brown. (Be, B & S, B, D, K, Mo, P & S).



Polygonum aviculare L.

1) Dimensions

Length	2.88 ± 0.05 mm
Width	1.57 ± 0.04 mm (face 1)
	1.68 ± 0.04 mm (face 2)
Depth	1.18 ± 0.04 mm (base)

2) Shape

Ovate (38-39) in ls, triangular (79-80) in cs. Three faces are unequal, one face being much narrower than the other two (= base). All faces somewhat concave. Seed widest about the middle and tapers to a pointed apex and to a blunter, wider base.

3) Comments

Edges broad and well rounded to within 1 mm of the apex when they become narrower and sharper. Longitudinally finely striate.

4) Colour

Reddish brown to brown. 166A, 200A, 200B. Remains of perianth attached to base are light brown 164B. Seed faintly shiny.

Plate 42 Polygonum aviculare L.

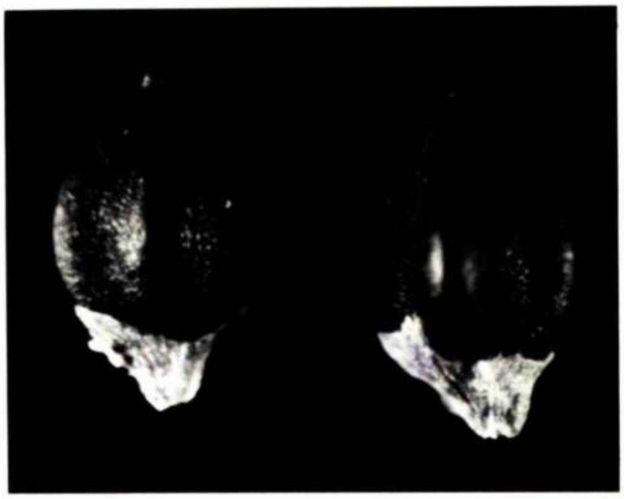
Previous descriptions:

2.0-3.5 mm long, 1.2-2.5 mm wide, 1.3 mm deep. (B & S, B, CTW, D, K, Me, Mo, P & S).
Red yellow, red brown, brown, dark brown, black. (Be, B & S, B, CTW, D, K, Me, Mo, P & S).

Scale: 2 mm

Magnification: x 5.3

Plate 43 Polygonum hydropiper L.



Scale: 1 mm

Magnification: x 15.5

Previous descriptions:

Swarbrick (1970). Achenes 2.5-4.0 mm long; elliptic, ovate or broadly so in outline with parts of the granular perianth often retained around the broadly rounded base and the apex bluntly pointed; triangular or broadly elliptic in section with the edges rounded. Surface finely rough or punctate; matt to shiny; brown to black. The perianth is greenish to pink or brown with prominent embedded scattered grey-brown glands.

Korsmo et al (1981). Achene surrounded by perianth. There are two types of seed:

(a) Seed almost ovate in outline, somewhat pointed at the apex and obliquely elliptic in cs. Surface rough and dull. Colour dark brown.

(b) Similar to (a) but triangular in cs.

Mean size: 2.9 mm long, 1.9 mm wide.

Polygonum persicaria L.

1) Dimensions

Length 2.51 ± 0.07 mm
Width 1.70 ± 0.06 mm
Depth 0.88 ± 0.03 mm

2) Shape

Ovate (39) in ls, elliptic (9) in cs.
Seed flattened with dorsal and ventral sides convex. Apex drawn out into a blunt stalk which ends abruptly.

3) Comments

Remains of perianth still attached to base. Surface with fine scalariform network giving a finely punctate appearance. Texture smooth.

4) Colour

Black, dark brown. 200B, 200C, 200D. Very glossy. Perianth pale brown.

A second type of seed may also be found. It differs in being slightly narrower (by about 0.2-0.4 mm) and in having a large rounded median longitudinal ridge on the dorsal side which gives a triangular cs. The three sides are slightly concave. An example is seen in Plate 44 - the lowest seed on the left hand side.

Plate 44 Polygonum persicaria L.

Scale: 2 mm

Magnification: x 6.0

Previous descriptions:

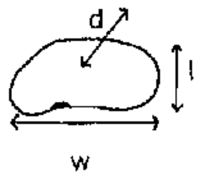
2.0-2.9 (4.0 B) mm long, 1.5-2.1 (3.0 B) mm wide, 0.6-0.8 mm deep. (B & S, (B), CTW, D, K, Me, Mo).

Red brown, dark brown, black brown, black. (Be, B & S, B, D, K, Me, Mo, P & S).

<u>Potentilla erecta</u> (L.) Räusch.

1) Dimensions

Length	0.97 ± 0.03 mm
Width	1.62 ± 0.05 mm
Depth	1.28 ± 0.04 mm



2) Shape

Elliptic (8) to ovate (43) in ls, obovate (48-49) in cs.

3) Comments

Dorsal side as a distinct ridge. Ventral side with hilum towards one side of the base. On lateral sides raised bands radiate in wavy lines (which originate from the edge of the scar tissue on the base by the hilum) up towards the dorsal side where they meet.

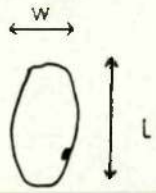
4) Colour

Cream to pale brown with darker patches. 162C, 164B, 199A. Raised bands lighter. Seed apex towards ventral side darker. Scar is yellow/translucent. Unripe seeds paler; greeny-yellow.

Plate 45 <u>Potentilla erecta</u> (L.) Räusch.

Previous descriptions:

1.5 mm long, 1.0 mm wide. (B).
Light brown. (Be).



Scale: 2 mm

Magnification: x 5.9

Ranunculus repens L.

1) Dimensions

Length (including beak)	3.92 ± 0.10 mm
Length (excluding beak)	3.04 ± 0.09 mm
Width	2.54 ± 0.06 mm
Depth	1.04 ± 0.02 mm

2) Shape

Without beak, obliquely obovate (49) in ls (as one edge is more rounded than the other), elliptic (8-9) in cs.

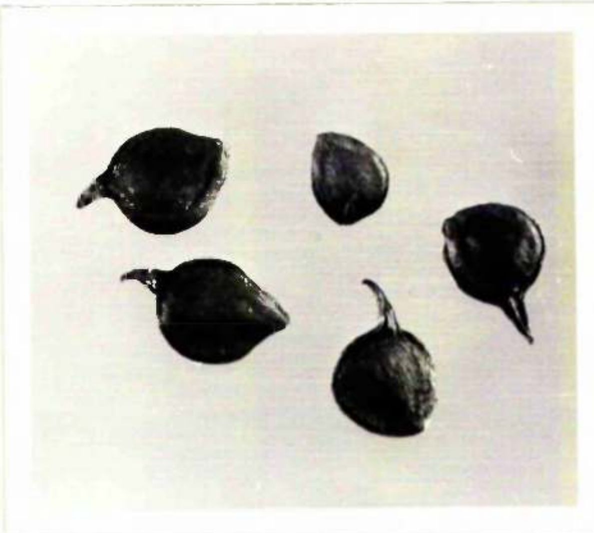
3) Comments

Persistent style present as a curved beak at the apex which itself is a continuation of the broad, well-defined margin which initiates near the base and more or less surrounds the achene. Surface areolate and slightly rough. Longitudinal pitting is evident along the margin. Somewhat pointed near the base where the small, round, white hilum is located.

4) Colour

Light brown, cream, reddish brown. 161A, 164B, 166B, 199A. Margin greenish. Dull.

Plate 46 Ranunculus repens L.



Scale: 2 mm

Magnification: x 5.3

Previous descriptions:

2.4-2.9 mm long, 2.0-2.5 mm wide, 0.7-0.9 mm deep.
(With beak 3.0-3.8 mm long). (B & S, K, Mo).

Light brown, red brown, brown, grey brown, dark brown. (Be, B & S, K, P & S).

Rumex acetosella L.

1) Dimensions

Length	1.11 ± 0.03 mm
Width = Depth	0.90 ± 0.04 mm

2) Shape

Elliptic (5) to ovate (40) in ls, triangular (78) in cs. Three faces approximately equal.

3) Comments

Edges rounded except near apex where they are sharper. Faces slightly concave. Apex with a small point, base rounded but may have a small point. Surface very finely longitudinally striate - difficult to see this feature. Nut looks smooth.

4) Colour

Dark chestnut brown to reddish brown. 166A, 166B. Shiny.

Perianth frequently still tightly attached. Nut looks granular with ridges or wrinkles, has a stalk at the base and the apex is bluntly pointed.

Dimensions:	Length	1.30 ± 0.04 mm
	Width = Depth	0.99 ± 0.03 mm

Colour: Dull. Brown or light brown. 165A, 200D.

Plate 47 Rumex acetosella L.

Previous descriptions:

0.7-1.5 mm long, 0.6-1.1 mm wide, 0.8-1.0 mm deep. (B & S, D, J, K, Me, Mo, P & S).

Light brown/pale brown, red-brown, brown, dark brown. (Be, B & S, B, D, J, K, Mo).

Scale: 2 mm

Magnification: x 9.2

<u>*Rumex obtusifolius*</u> L.

1) Dimensions

Length	2.26 ± 0.04 mm
Width	1.23 ± 0.03 mm
Depth	1.18 ± 0.03 mm

2) Shape

Ovate (38) in ls, triangular (78) in cs. Apex tapers to a blunt point. Base more rounded with a short stalk.

3) Comments

Sides convex near the base and concave towards the apex with sharp edges which are almost ridged. Surface finely longitudinally striate and cross veined. Looks longitudinally punctate.

4) Colour

Chestnut brown with edges lighter. Shiny. 165A, 200D.

Plate 48 Rumex obtusifolius L.

Scale: 2 mm

Magnification: x 5.9

Previous descriptions:

2.0-3.0 mm long, 1.0-1.8 mm wide, 1.1 mm deep. (B & S, B, D, J, K, Me, Mo, P & S).

Light brown, chestnut brown, reddish brown, chocolate brown, chocolate, brown, dark brown. (Be, B & S, B, D, J, K, Me, Mo).

Sonchus asper (L.) Hill

1) Dimensions

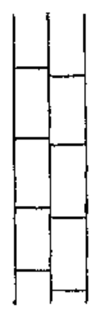
Length 2.60 $\pm$ 0.30 mm
Width 1.00 $\pm$ 0.02 mm
Depth 0.28 $\pm$ 0.01 mm

2) Shape

Elliptic (2-3) to ovate (37-38) in ls, elliptic (10) in cs. Very flat. Longitudinal axis slightly curved.

3) Comments

Three longitudinal ribs located on dorsal side and three on ventral side. Both margins are ribbed making five ribs visible from each side. Ribs meet at the apex in a blunt collar, to which the white pappus of simple hairs was attached, and at the somewhat truncate base as a stout rim. Margins are finely toothed. Between the ribs the achene appears smooth but is finely marked into longitudinal rectangles.



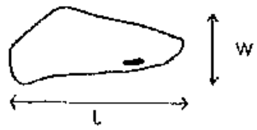
4) Colour

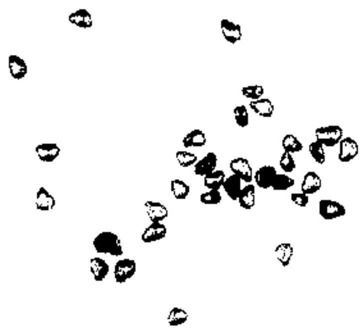
Dull brown, pale brown 165A, 165B, 200D. Apical collar, basal rim and ribs are lighter.

Plate 49 Sagina procumbens L.

Previous descriptions:

0.25-0.50 mm long. (B, CTW).
Brown. (Be, B, CTW).





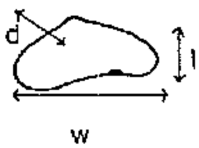
Scale: 2 mm

Magnification: x 7.2

Sagina procumbens L.

1) Dimensions

Length 0.31 ± 0.01 mm
Width 0.39 ± 0.01 mm
Depth 0.23 ± 0.01 mm



2) Shape

Seed appears to have three longer sides joined either roundly and directly or by smaller sides giving an irregular and variable shape, from broadly ovate (42) to broadly triangular (79) in ls, elliptic (8) to oblong (20) in cs.

3) Comments

Hilum located to one side of broad base. A groove is located around the edges of the seed except along the base. Lines of roundly oblong or honeycomb cells radiate from the hilum.

4) Colour

Brown. 165A. Hilum darker.

Plate 50 Sonchus asper (L.) Hill

Scale: 2 mm

Magnification: x 5.4

Previous descriptions:

2.5-3.4 mm long, 0.8-1.6 mm wide, 0.2-0.3 mm deep. (B & S, CTW, K, Ma & B, Me, Mo, P & S).

Light brown, pale brown, brown. (Be, CTW, K, Ma & B, Me, P & S).

Spergula arvensis L.

1) Dimensions

Length = Width 0.92 ± 0.02 mm
Depth 0.69 ± 0.02 mm

2) Shape

Circular (6) in ls with an equatorial ring, elliptic (7-8) in cs.

3) Comments

Wing has a notch at one point which extends slightly into the seed body. Surface covered with club-shaped protuberances which point towards the rim. These may have been weathered away. Surface granular.

4) Colour

Greyish black to black. 202A. Dull. Wing and protuberances dull orange/yellow to yellow.

Several varieties are recognised and the variation in the descriptions may reflect this.

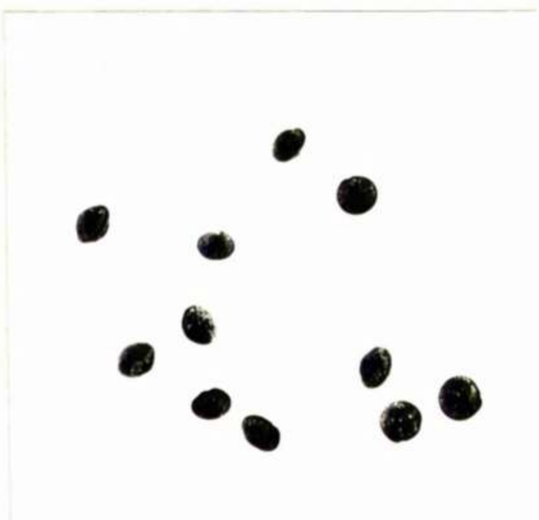
Plate 51&52 Spergula arvensis L.

Scale: 2 mm

Magnification: x 9.7

Previous descriptions:

1.0-2.0 mm long, 0.9-1.7 mm wide, 0.7-1.0 mm deep. (B & S, B, CTW, D, K, Ma & B, Me, Mo, P & S).
Greyish-black, blackish, black. Wing and flecks - light, light-brown, yellow, white. (Be, B & S, B, CTW, D, K, Ma & B, Me, Mo, P & S).



Scale: 2 mm

Magnification: x 6.1

Stellaria media (L.) Vill.

1) Dimensions

Length 0.97 ± 0.02 mm
Width 0.95 ± 0.02 mm
Depth 0.60 ± 0.02 mm

2) Shape

Circular (6) to obovate (50) in ls with parts of the margins sometimes angular; elliptic (8) to oblong (20) in cs.

3) Comments

Hilum on base indicated by a notch and a deep groove which runs inward and is visible on both lateral faces. Lines of low rounded or flat-topped tubercles, from which fine rays radiate, run from the hilum in concentric rings on the dorsal and ventral sides. Lines of narrow interrupted ridges run from the hilum around the margin of the seed and back to the hilum.

4) Colour

Reddish brown to chestnut brown. 165A, 166A, 200C, 200D.

Plate 53&54 Stellaria media (L.) Vill.

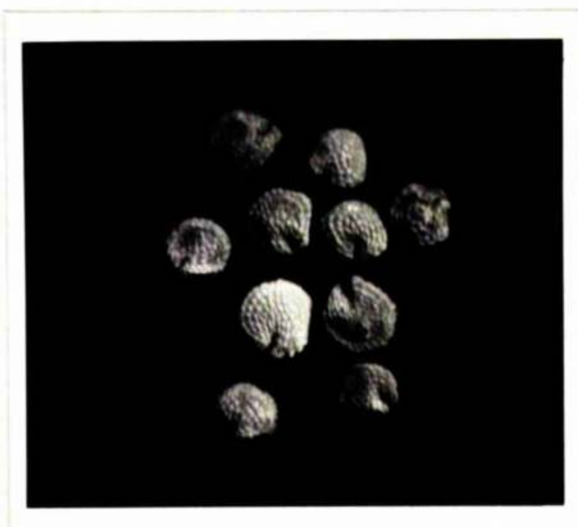
Scale: 2 mm

Magnification: x 6.7

Previous descriptions:

0.9-1.3 mm long, 1.0-1.3 mm wide, 0.5-0.6 mm deep. (B & S, B, CTW, D, K, Ma & B, Me, Mo, P & S).

Snuff, light brown, chestnut-brown, brown, reddish-brown, chocolate-brown, dark brown, grey-brown. (Be, B & S, B, CTW, D, K, Ma & B, Mo, P & S).



Scale: 2 mm

Magnification: x 9.1

Trifolium repens L.

1) Dimensions

Length 1.24 $\pm$ 0.03 mm
Width 1.09 $\pm$ 0.02 mm
Depth 0.73 $\pm$ 0.02 mm

2) Shape

Ovate (40) in ls, elliptic (8) in cs. Approximately heart-shaped.

3) Comments

Hilum situated off-centre on the base in a broad depression. Position of radicle indicated by a lighter coloured groove running from the hilum parallel and closer to one edge. Seed plump. Surface smooth with no discernible pattern.

4) Colour

Golden yellow, light to dark brown, reddish brown. 162A, 163A, 163B, 163C. Depression around hilum darker. Dull or slightly gleaming.

Plate 55 Trifolium repens L.

Previous descriptions:

1.0-1.2 mm long, 0.9-1.25 mm wide, 0.7-0.8 mm deep. (B & S, B, P & S). Sulphur-yellow, golden-yellow, brown-yellow, light to dark brown. (Be, B & S, B, P & S).

Scale: 2 mm

Magnification: x 8.9

Urtica dioica L.

1) Dimensions

Length	1.34 ± 0.03 mm
Width	0.78 ± 0.01 mm
Depth	0.40 ± 0.01 mm.

2) Shape

Elliptic (3-4) to slightly ovate (38-39) in ls, elliptic (9) in cs. Base slightly extended and truncate. Slightly more tapered to broadly pointed apex.

3) Comments

Apex tipped with a short stalk which represents the withered style. Surface areolate. Edges meet in a blunt margin.

4) Colour

Achene fawn, light brown. 199B, 199C. Base, tip and margin lighter with stalk at apex dark brown. Dull.

Achene may be mistaken for Aphanes arvensis which is the same colour (particularly when weathered), basic shape and length but which is slightly wider and deeper. The two may be separated by the fact that Urtica has a blunt rather than a sharp apex although this difference may not be too apparent if the achene of Aphanes is weathered. They may positively be separated by the fact that Urtica is symmetrical in ls where Aphanes is asymmetrical.

Plate 56&57 Urtica dioica L.

Scale: 2 mm ⊢—⊣
Magnification: x 7.6

Previous descriptions:

0.9-1.2 mm long, 0.5-0.9 mm wide, 0.2-0.4 mm deep. (B & S, CTW, D, K, Me, Mo, P & S).
Yellow, yellow-grey, greenish yellow, pale brown, grey to yellow-tan, grey to brownish-yellow. (Be, B & S, D, K, Me, Mo, P & S).

Scale: 2 mm ⊢—⊣
Magnification: x 5.7

Veronica arvensis L.

1) Dimensions

Length 1.04 ± 0.02 mm
Width 0.67 ± 0.02 mm
Depth 0.28 ± 0.01 mm

2) Shape

Elliptic (4) to obovate (48) in ls, elliptic (9) to obovate (53) in cs. Seed somewhat twisted in ls.

3) Comments

Dorsal side flat to slightly convex with downward curving bands of coarse wrinkles running laterally. Ventral side rises towards the central prominent hilum which is surrounded by a ridge. A shallow groove runs from the lower end of the hilum to a notch at the base of the seed. Lines of wrinkles radiate from the hilum to the seed edges.

4) Colour

Yellowish brown, dull. 164A, 165A, 165B. Hilum darker.

Plate 58 Veronica arvensis L.

Scale: 2 mm ⊢——⊣

Magnification: x 6.5

Previous descriptions:

0.8-1.0 mm long, 0.5-0.7 mm wide, 0.2-0.3 mm deep. (B & S, B, K, Mo). Yellow, yellow-gold, yellow-brown, light brown, bright brown. (Be, B & S, B, K).

<u>*Veronica persica*</u> Poir.

1) Dimensions

Length	1.87 ± 0.05 mm
Width	1.29 ± 0.05 mm
Depth	0.84 ± 0.04 mm

2) Shape

Obovate (48) in ls, essentially elliptic (8) in cs with a deep groove on the lower side.

3) Comments

Dorsal side covered with broad deep wavy lateral ridges. Edges of dorsal surface of seed curve under at the top and sides to form three edges of the ventral surface of the seed. Inner surfaces of ventral side of seed are smooth. Large, thin scar runs down the inside of the ventral side with black shrivelled plant remains frequently still attached.

4) Colour

Orange / brown to yellow brown. 164A, 164B, 165B. Dull.

Plate 59&60 Veronica persica Poir.

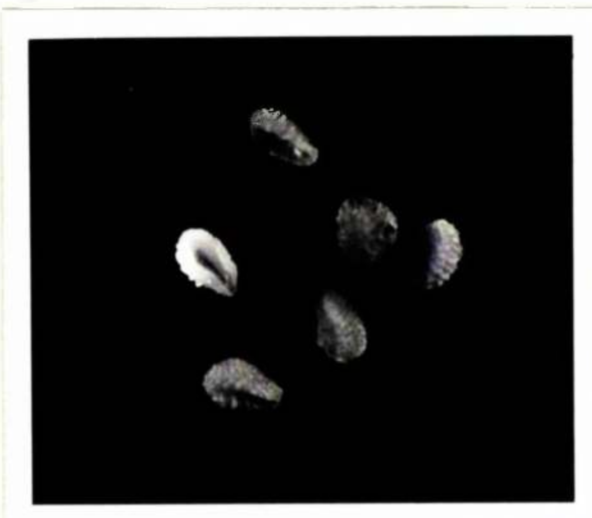
Scale: 2 mm

Magnification: x 8.5

Previous descriptions:

1.4 mm long, 1.0 mm wide. (B).

Brown, grey. (Be, B).



Scale: 2 mm

Magnification: x 5.4

Veronica serpyllifolia L.

1) Dimensions

Length 0.79 ± 0.02 mm
Width 0.56 ± 0.02 mm
Depth 0.23 ± 0.01 mm

2) Shape

Elliptic (4-5) in ls, elliptic (9-10) in cs. Seed slightly twisted in ls.

3) Comments

Ventral side with hilum slightly more convex than dorsal side although seed generally thin and flat. Slight groove indicated by a dark line runs from the lower end of the hilum to the base of the seed which may end in a tip. Surface granular or with very faint striations.

4) Colour

Brownish yellow, light brown. 165A, 165B. Dull. Base and seed edges dark (gives seed a crisp outline). Tip, if present, dark.

Plate 61 Veronica serpyllifolia L.

Previous descriptions:

0.7-1.0 mm long, 0.3-0.6 mm wide, 0.1-0.2 mm deep. (B & S, B, Mo).
Yellow, yellowish brown, light brown. (Be, B & S, Mo).

Scale: 2 mm

Magnification: x 6.1

Viola palustris L.

1) Dimensions

Length 1.88 $\pm$ 0.03 mm
Width = Depth 1.13 $\pm$ 0.02 mm

2) Shape

Ovate (39-40) in ls, circular (6) in cs. Base truncate.

3) Comments

Ridge runs from hilum on ventral side to base of caruncle which is triangular when viewed from the side. Caruncle is withered, pliable and of a white/translucent material. Surface shiny. Patterned initially longitudinally and then crosswise giving a scalariform pattern. Seed looks longitudinally punctate.

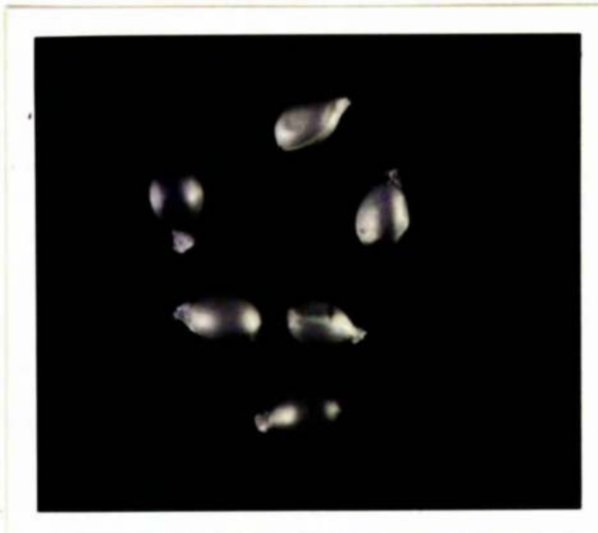
4) Colour

Brownish yellow, golden brown, fawn with dark brown base, ridge and rim around caruncle base. 161A, 161B, 164B, 164C.

Plate 62&63 Viola palustris L.

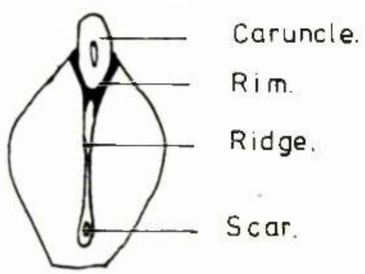
Scale: 2 mm

Magnification: x 7.6

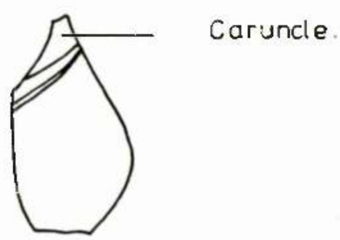


Scale: 2 mm

Magnification: x 6.4



Ventral view.



Lateral view

Previous descriptions:

2.0 mm long, 1.5 mm wide. (B).

Yellow, brownish yellow, brown. (Be, B).

Factors affecting the improvement of hill land dominated by bracken (*Pteridium aquilinum* (L.) Kuhn).

by

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B.Sc. (HONS)

A thesis submitted to the University of Glasgow
for the degree of
Doctor of Philosophy in the Faculty of Science.

Volume 2

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.32-86

9. CHANGES IN SWARD COMPOSITION AND THE ROLE OF THE BURIED SEED BANK IN ITS RECOVERY FOLLOWING BRACKEN FROND CLEARANCE WITH ASULAM OR GLYPHOSATE

9.1 *Introduction*

Asulam and glyphosate are the two herbicides currently in use for the control of bracken. Both have been found to give good control of frond growth (Williams, 1977) but their effect upon the underlying sward differs. The response of a large number of species to both asulam and glyphosate has been established both in pot experiments, where the plants are exposed to the full effects of the spray (Pink & Surman, 1974; Ball et al, 1974; Monsanto, 1977) and in field trials, where the plants are protected to a certain degree by the bracken canopy (Scragg et al, 1974; Cadbury, 1976; Williams, 1977).

Glyphosate has been shown to have a much wider spectrum of activity than asulam and few species show any great degree of resistance to this herbicide (Williams, 1980) whilst many more species are able to tolerate asulam. This difference in activity is reflected in the sward in the spring following spraying when those areas treated with glyphosate appear scorched and brown with very little plant growth. Whilst those areas sprayed with asulam show a slight increase in bare ground much is still occupied by healthy plants. The greater proportion of uncolonised ground (bracken litter and dead plant remains) on the glyphosate plots provides a greater opportunity for species to establish from seed since the competition normally encountered from well established mature plants has been largely removed. The greater potential for sward destruction shown by glyphosate may be a very useful management tool in reseeding ground but it will also provide more favourable conditions for buried seeds.

The results of the seed survey (Section 6.2) showed that large numbers of viable seeds are to be found in the top 2-3 cm of soil and these may contribute to the recovery of the sward. The object of this section of work was firstly to determine the changes in sward composition following the clearance of bracken with either asulam or glyphosate and secondly to assess the extent of the soil seed population and its potential to influence the recolonisation of bare soil or litter covered ground arising as a result of frond clearance.

9.2 Method

A site at Dalry, Kirkcudbrightshire (GR NX 636870) was chosen for examination in 1979. (Plate 64).

Plate 64. Experimental site at Dalry

The site is a south facing hillside 210 m above sea level with a mean annual rainfall of approximately 1,500 mm. A 3-4 cm layer of litter and organic soil overlies a brown mineral soil which has a pH of 4.84. Prior to spraying, the bracken fronds were on average 69 cm high with a mean of 56 fronds/m^2. Grazing by sheep and cattle was unrestricted throughout the experimental period.

A 36 m^2 plot was subdivided into nine 2 m x 2 m plots. Three treatments each replicated three times were arranged in a Latin square. The treatments were:

A. Control-unsprayed bracken;

B. Sprayed with Asulam at a rate of 4.4 kg ai/ha in 400 l of water;

C. Sprayed with Glyphosate at a rate of 2.0 kg ai/ha in 400 l of water.

Spraying was carried out with a hand held sprayer at about the time of full frond development. Any fronds which emerged on the treated plots after spraying were cut by hand.

Immediately prior to spraying the sward composition was assessed by visually estimating the percentage cover of each of the species present within four 2,500 cm^2 quadrats per plot. The edges of the plots were deliberately avoided. The percentage cover values were transformed using the arcsin transformation for statistical analysis. In addition, ten soil cores, 2.3 cm in diameter and 3 cm deep, were collected per plot. These were dried, sieved and washed, redried and then examined visually under a binocular microscope. Any seeds located were identified, recorded and an attempt made to germinate them. After examination the samples were sown out onto compost in the greenhouse where any remaining seeds were given an opportunity to germinate. For each plot, the number of seeds recovered from the ten cores was totalled and a mean per plot was calculated. The figures for the three treatments, given in Tables 35 & 36 are thus the mean of three replicates, each of which is the mean of ten cores. The data are expressed as the number of seeds/m^2. (See Appendix 3:A for conversion factor from seed numbers/core to seed numbers/m^2).

The sward was re-examined on 30/31 July 1980 and the results appeared anomalous (see pages 14 & 15). Therefore the trials were set up again at

Dalry in 1980 with nine 3 m x 3 m plots with a 1 m discard between each plot. The sward was assessed as before and ten cores were taken from each plot prior to spraying. These were stored, washed and examined as before. Spraying was carried out on 31 July 1980 and both trials were re-examined on 9 July 1981.

9.3 *Results*

9.3.1 Sward composition - trial one

Table 34

In August 1979 the overall composition of the control plots was not significantly different from that of the plots designated for treatment either with asulam or glyphosate. The main species present were:

Agrostis spp (A. canina, A. tenuis and some A. stolonifera)

Anthoxanthum odoratum

Festuca rubra

Galium saxatile and

Poa spp (P. pratensis and P. trivialis)

with Potentilla erecta, Carex spp and Luzula campestris, and to a lesser extent Holcus mollis, frequent although in relatively small amounts.

The botanical composition of the control plots altered between August 1979 and July 1980. The cover of Festuca rubra rose significantly ($P \leq 0.001$) and that of Carex spp and Luzula campestris also increased but was not statistically significant. Although the contribution made by Agrostis spp to the sward fell and there were similar reductions in the cover of Anthoxanthum odoratum and Poa spp, the changes were again not statistically significant.

The changes which occurred in the sward composition of the treated plots may be considered in relation to the changes on the control plots. Similar significant increases ($P \leq 0.05$) in the cover of Festuca rubra were noted on the treated plots and the increase in Carex spp and

Table 34. Sward composition (percentage ground cover) at Dalry. Trial one.

Species	Year	Control (Treatment)	Asulam (Treatment)	Glyphosate (Treatment)
Agrostis spp	1979	39.28	35.67	37.22
	1980	26.75	22.75	18.33
Anthoxanthum odoratum	1979	9.72	4.72	9.67
	1980	5.00	6.67	2.17*
Carex spp & *Luzula campestris*	1979	2.50	1.67	3.55
	1980	10.00	8.17*	3.59
Festuca rubra	1979	11.72	14.44	14.17
	1980	29.58***	31.67*	39.33*
Galium saxatile & *Potentilla erecta*	1979	8.81	9.61	12.61
	1980	11.00	9.83	8.33
Holcus mollis	1979	3.78	2.50	0.95
	1980	1.83	2.58	2.25
Poa spp	1979	8.33	15.83	8.39
	1980	4.75	1.67*	0.58**
Other spp	1979	3.28	4.17	4.66
	1980	1.67	3.83	2.92
Bare ground	1979	12.78	11.39	8.78
	1980	9.42	12.83	22.50

* Differences significant at $P \leq 0.05$ Transformed data.

** Differences significant at $P \leq 0.01$ Transformed data.

*** Differences significant at $P \leq 0.001$ Transformed data.

Luzula campestris was significant on those plots treated with asulam ($P \leq 0.05$). The contribution made by Agrostis spp fell on both treatments, but not significantly, whilst the decrease in Poa spp was significant on the asulam plots at $P \leq 0.05$ and on the glyphosate plots at $P \leq 0.01$. Anthoxanthum odoratum was significantly reduced on the glyphosate plots ($P \leq 0.05$).

There was little change in the proportion of uncolonised ground on either the control or the asulam treated plots but the amount of bare ground rose on the glyphosate treated plots from 9 to 23%. This increase was not, however, statistically significant.

9.3.2 Sward composition - trial two

Figure 12a

In July 1980 the composition of the control plots was not significantly different from that of the plots designated for treatment with either asulam or glyphosate. The main species present in the sward were:

Agrostis spp (A. canina and A. tenuis)

Anthoxanthum odoratum

Festuca rubra

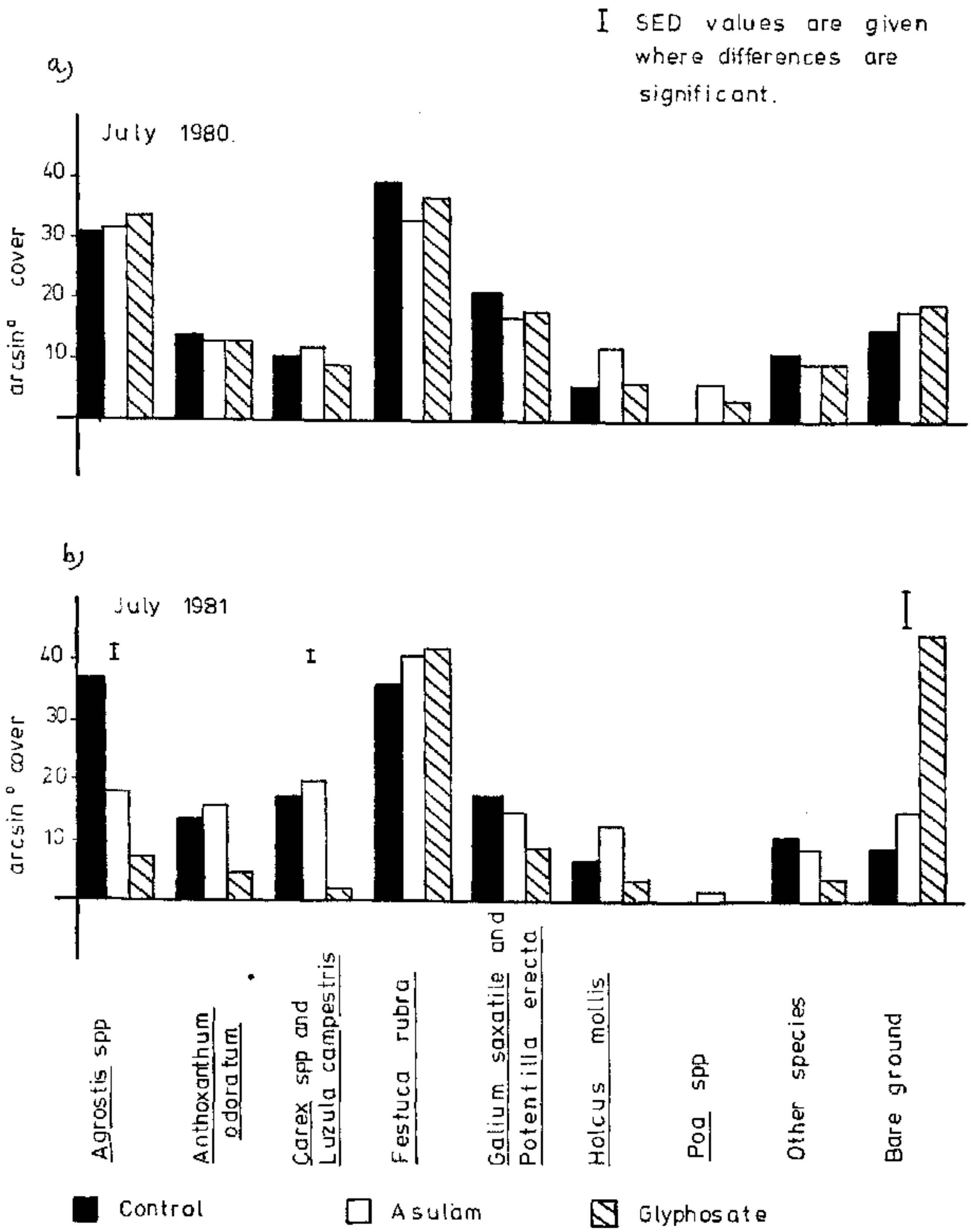
Galium saxatile and

Potentilla erecta

and to a lesser extent Carex spp and Luzula campestris, with Holcus mollis forming a major part of one of the plots designated for treatment with asulam.

During the period July 1980 to July 1981, the composition of the control plots altered with a significant decrease in the amount of bare ground ($P \leq 0.05$) and a corresponding increase in the contribution made by Carex spp and Luzula campestris and Agrostis spp, although these were not significant. On the asulam treated plots the cover of Poa spp

Figure 12. Effect of herbicide application on sward composition at Dalry in (a) July 1980 and (b) July 1981.



fell and the cover of Agrostis spp was reduced by 45% (significant at $P \leq 0.05$). There were non-significant increases in the contributions made by Carex spp and Luzula campestris and Festuca rubra to the sward.

On the glyphosate treated plots, Agrostis spp were reduced by 78%, Carex spp and Luzula campestris by 80%, Anthoxanthum odoratum by 58% and Potentilla erecta by 36%, whilst the amount of bare ground had more than doubled. These differences were significant at $P \leq 0.001$ for Agrostis spp, $P \leq 0.01$ for Potentilla erecta and $P \leq 0.05$ for Carex spp and Luzula campestris and bare ground. There was little change in the cover of Festuca rubra or Galium saxatile.

Figure 12b

One year after treatment, relative to the control plots, the effect of spraying with either asulam or glyphosate was to significantly reduce the cover of Agrostis spp ($P \leq 0.05$) with the decrease being greater on the glyphosate treated plots than on the asulam treated plots. The cover of Carex spp and Luzula campestris was significantly higher on the asulam plots than on the control plots also ($P \leq 0.01$). Glyphosate also reduced the cover of Anthoxanthum odoratum and significantly reduced the contribution made by Carex spp and Luzula campestris relative to both the asulam treated plots and the control plots ($P \leq 0.01$). One year after treatment there was significantly more uncolonised ground on the glyphosate treated plots than on either the control or the asulam plots ($P \leq 0.05$).

Plates 65, 66 & 67 show a control, an asulam treated and a glyphosate treated plot respectively one year after treatment. The asulam treated plot shows a healthy sward with relatively little bare ground whilst that treated with glyphosate shows a much greater proportion of uncolonised ground. The main species present is Festuca rubra but the remaining ground is occupied by bracken litter and plants scorched by the herbicide.

Plate 65

Unsprayed control plot

Plate 66

Asulam treated plot one year after treatment

Plate 67

Glyphosate treated plot one year after treatment

9.3.3 Seed survey - trial one

Table 35

Seed of ten different species was recovered from the three treatments with four species occurring in the soil seed population but not in the sward (Alchemilla arvensis, Digitalis purpurea, Sagina procumbens and Spergula arvensis). Eight species in the sward were unrepresented in the soil, the absence of seed of Festuca rubra being the most significant.

The results appeared to be quite variable and this was partly due to the fact that very few seeds were recovered and partly the result of converting the data from seed numbers per plot to seed numbers per m^2. The recovery of one seed during sampling altered the seed population estimates in Tables 35 & 36 by 80 seeds/m^2 (see Appendix 3:A).

Although the control plots had fewer seeds per unit area than the treated plots, the difference was not statistically significant and was largely due to the different numbers of Agrostis seeds which were recovered. Only the seed of Agrostis spp (principally A. tenuis) was found in any quantity, ranging from 963 seeds/m^2 on the control plots to 2,167 seeds/m^2 on the glyphosate treated plots. No seed of Festuca rubra was recovered although this species was the second most important grass species in the sward (see Table 34). Few seeds of Anthoxanthum odoratum or Poa spp were recovered. Seed of herbaceous species accounted for 12, 25 and 20% of the seed populations on the control, asulam treated and glyphosate treated plots respectively.

9.3.4 Seed survey - trial two

Table 36

Seed of eight different species was recovered including that of Cardamine hirsuta and Juncus bufonius, neither of which was represented

Table 35

Seed populations at Dalry in August 1979. Trial one.

Treatment / Species	Mean number of viable seeds/m^2 Control	Asulam treated plots	Glyphosate treated plots
Agrostis spp (*A. tenuis* & *A. canina*	963	1,525	2,167
Anthoxanthum odoratum	80	80	80
Alchemilla arvensis	-	-	80
Digitalis purpurea	-	-	80
Galium saxatile	80	161	161
Poa spp (*P. pratensis* & *P. trivialis*)	161	80	-
Rumex acetosella	-	80	80
Sagina procumbens	-	80	-
Spergula arvensis	-	-	80
Veronica officinalis	80	241	80
TOTAL	1,364	2,247	2,808
SE $\pm$	401	815	986

Table 36

Seed populations at Dalry in July 1980. Trial two.

Treatment / Species	Mean number of viable seeds/m^2 Control	Asulam treated plots	Glyphosate treated plots
Agrostis spp (*A. canina* & *A. tenuis*	1,926	1,284	1,525
Anthoxanthum odoratum	401	80	80
Cardamine hirsuta	401	161	161
Galium saxatile	883	482	401
Juncus bufonius	241	161	161
Luzula campestris	161	80	-
Poa spp (*P. pratensis* & *P. trivialis*)	161	-	80
Potentilla erecta	161	80	80
TOTAL	4,335	2,328	2,488
SE ±	637	425	526

in the sward. Twelve species which occurred in the sward were not found as seed in the soil and this included Festuca rubra.

Although there was a larger seed population estimated to be present on the control plots than on the sprayed plots, statistical analysis showed the seed populations on the three treatments to be not significantly different from each other. The number of seeds recovered from all the plots was significantly greater ($P \leq 0.001$) in 1980 than in 1979.

Large numbers of Agrostis seeds were recovered on all three treatments and to a lesser extent seed of Anthoxanthum odoratum and Cardamine hirsuta (on the control plots) and Galium saxatile (on all three treatments) was also frequent. On the control and asulam plots, seed of herbaceous species accounted for about 41% of the seed population whilst on the glyphosate plots this figure was about 32%.

9.4 Discussion

An examination of the percentage ground cover data for the trial initiated at Dalry in 1979 suggested that one year after spraying the changes which had occurred in the proportions of the various species on the three treatments had resulted in swards of very similar composition. During the period March 1980 to July 1980 frond regrowth occurred on the sprayed plots and these fronds were cut and removed at regular intervals. By July 1980 it was considered possible that the spraying had been ineffective and the trial was set up again at Dalry.

During 1981, frond regrowth again occurred on the sprayed plots of the first trial but no cutting was carried out and by July 1981 it was impossible to distinguish the treated plots either from each other or from the surrounding hill side. On the sprayed plots of the second trial only a small number of fronds appeared and many of these were stunted and yellowish. On this second trial it was possible to distinguish between the three treatments, Plates 65, 66 & 67.

There were thus several indications that the spraying carried out in August 1979 had been totally ineffective and the changes which had occurred were more likely to have been the result of environmental conditions or of grazing.

The source of the chemicals used in 1980 was the same as that used in 1979 and the herbicides were prepared and applied in the same manner. Had it rained during the six hour period after spraying in 1979 this might have accounted for the lack of frond control. However, had this been the case, the rain would have washed the chemicals off the fronds and onto the underlying sward where their effects would have been more pronounced than normal since the canopy usually protects the underlying sward from the full effects of the chemical.

No reasonable explanation can be offered as to why the spraying was totally ineffective in 1979 yet effective in 1980. There was only a nine day difference between the date of spraying in 1979 (9 August) and that in 1980 (31 July) and this was not sufficiently large an interval to cause these differences. Therefore, only the results from the second trial will be considered in detail.

The susceptibility of Agrostis spp to asulam and the consequent reduction in their cover one year post spraying agrees with the results of, amongst others, Anon (1974), Cadbury (1976), Williams (1977) and Davies et al (1979). Galium saxatile and Potentilla erecta are species which are considered to be tolerant of asulam whilst Anthoxanthum odoratum is slightly susceptible to asulam (Anon, 1974). All three species were found by Williams (1977) to increase in the year following spraying. Although Davies et al (1979) found the cover of Galium saxatile to be reduced one year after treatment, this was thought to be the result of an unfavourable environment. In this trial none of these three species was adversely affected by asulam but neither did they increase their cover. The significant reduction in Agrostis spp was largely compensated for by non-significant increases in Carex spp, Luzula campestris and Festuca rubra, all of which are tolerant of asulam (Anon, 1974), and which were shown to increase post-spraying by Williams (1977). Davies et al (1979) found Luzula campestris was adversely affected by asulam but, as for Galium saxatile, this reduction was thought to be due to adverse environmental conditions. These workers also noted an increase in the cover of Festuca rubra and the absence of any detrimental effects on Carex spp following frond clearance.

In this trial, glyphosate significantly reduced the cover of Agrostis spp, Carex spp, Luzula campestris and Potentilla erecta, all of which are generally susceptible to glyphosate (Monsanto, 1977). Anthoxanthum odoratum when sprayed in mid to late August has been found to be adversely affected by glyphosate although spraying at the start of August leaves it unaffected (Williams, 1977). Spraying at Dalry was carried out at the end of July and after one year there was no significant change in the cover of this species.

In one trial there was little effect of glyphosate on the cover of Galium saxatile, Potentilla erecta, Carex spp and Luzula campestris (Williams, 1974) whilst in a second trial (Williams, 1977) Galium saxatile and Potentilla erecta increased their cover following the application of glyphosate and that of Carex spp and Luzula campestris was reduced. In this trial, the cover of Galium saxatile was not significantly altered. Williams (1977) found Festuca rubra capable of spreading rapidly in the absence of competition following frond clearance with glyphosate. This species appears to be fairly resistant to glyphosate although Oswald (1976) and Monsanto (1977) found this species to suffer a severe check following treatment. In this trial, Festuca rubra did not significantly increase its cover.

There was no significant change in the cover of Holcus mollis on any of the treatments; there was only one plot with more than a 5% cover of this species. Holcus mollis is susceptible to glyphosate (Lanz, 1977) and asulam (Anon, 1974; Pink & Surman, 1974) but Ball et al (1974) and Cadbury (1976) found that this species had recovered well twelve months after treatment with asulam. The site at Dalry is fairly exposed and the clearance of plots of ground within the fairly dense stand (56 fronds/m^2) led to stock concentrating in the area. Although Tansley (1913) suggested that Holcus mollis was able to survive treading, it does not tolerate well either exposure or grazing (Fenton, 1948; Ovington & Scurfield, 1956). This may explain why there was little colonisation by this species particularly on the glyphosate treated plots where, because there was little vegetation remaining after spraying, any plants which established were both unprotected and obvious to a grazing animal. Cadbury (1976) and Williams (1976, 1977) showed that if this species was present in the original sward it had the ability to rapidly colonise ground cleared of bracken with either asulam or glyphosate, particularly in the absence of grazing.

It is difficult to make direct comparisons between these results and those previously published because of differences in the sites and in the time of spraying and because of differences due to geographical location even when spraying dates are similar. Williams has shown in the West of Scotland that the effects of asulam and glyphosate on both frond control and on the underlying sward are influenced by the date of spraying (Williams, 1976, 1977). However, the changes noted in the swards of the sprayed plots are broadly similar to those noted by previous workers.

For those species which are adversely affected by these herbicides the buried seed bank is likely to be of greatest importance in the first year (or two) after spraying, before other species have themselves recovered and before unaffected species have colonised the newly available ground.

At Dalry, the only species present in the soil in any quantity in either 1979 or 1980 as buried seed were Agrostis spp and, to a lesser extent, Galium saxatile. Plants of Galium saxatile were little affected by the sprays but Agrostis spp were significantly reduced on both the asulam and the glyphosate sprayed plots. Despite the large reserves of viable Agrostis seeds, and despite the fact that at least on the glyphosate plots there was considerable bare ground available for colonisation, one year after treatment there was so little Agrostis on the glyphosate plots that it seems very unlikely that the buried seeds were greatly assisting the recovery of this species. The significant increases noted in the cover of Carex spp and Luzula campestris appear to have been a result of vegetative growth since no seeds of Carex spp were recovered and only a small reserve of Luzula campestris seeds was detected.

Work by Howe (1980) showed that species such as Poa trivialis and Agrostis stolonifera whose seed had some innate dormancy and in which dormancy was readily enforced by burial, had larger buried seed banks than species such as Festuca rubra whose seed germinates freely. Plants of Poa spp were only present in two of the nine plots in 1980 and one year later were present in only one plot. There was only a small reserve of buried Poa seeds in the soil.

The available data on the relationship between the soil seed population and the representation of a species in the sward with respect to Luzula campestris and Carex spp is both limited and conflicting (Chippindale and Milton, 1934; Milton, 1939; Champness and Morris, 1948; Thompson and Grime, 1979). No Carex seeds were recovered in 1979 or 1980 and only three Luzula campestris seeds were recovered in 1980. Data collected in the 1978 seed survey was also insufficient to determine the relationship for these species.

Davies et al (1979) found that the consolidation of treated areas by stock during the first year after spraying speeded up the process of sward recovery. It seems that buried seeds must be brought to the soil surface where the conditions necessary for breaking seed dormancy are more frequently encountered before they can contribute to the recovery of the sward and soil disturbance by stock would help to achieve this. The Dalry site was freely grazed by sheep and cattle although at a level which was almost certainly less than that in the trial by Davies et al (1979). Evidence from the Gatehouse site (Section 11.3) also suggested that unless the soil surface was disturbed even a fairly extensive buried viable seed bank played little part in sward recovery. In the absence of a significant contribution from the seed bank the changes in the sward following bracken clearance will largely depend upon the species already growing on the site and their ability to tolerate, or recover from the effects of, the herbicide.

Apart from the significant reduction in Agrostis spp, much of the sward was little affected by asulam and the amount of bare ground was no higher in 1981 than it was prior to spraying in 1980. Recovery of the sward on the plots treated with glyphosate is proceeding slowly because most of the existing species were killed by the herbicide and because the seed population does not appear to be making a significant impact on recolonisation of the bare ground. Glyphosate although clearly suitable for the control of bracken is probably only of value where reseeding is contemplated and where suppression of the native species as well as the bracken is desired.

10. THE CONCEPT OF ALLELOPATHY WITH RESPECT TO BRACKEN

10.1 Introduction

Bracken dominates many types of plant communities and associated species can be severely inhibited or absent. This dominance has been attributed to a variety of factors including the superior competitive ability of bracken for moisture, light and nutrients (Jeffreys, 1917; Salisbury, 1944), the shading or 'smothering' of competing plants by senescent bracken fronds (Jeffreys, 1917; Farrow, 1917b; Long and Fenton, 1938; Tansley, 1939; Salisbury, 1944) and the effect of selective grazing of other species (Farrow, 1917a; Watt, 1955; Gliessman and Muller, 1978). The thickness of the layer of litter may prevent seedling roots from reaching the soil (Vogl, 1964) and physical factors of the environment such as soil pH, soil texture and organic matter content have also been examined (Gliessman and Muller, 1978).

The relative importance of these factors has been much considered but Gliessman and Muller (1972, 1978) have argued that they cannot entirely account for the lack of associated species in bracken stands. They, and several other workers, (Jeffreys, 1917; del Moral and Cates, 1971; Stewart, 1975; Gliessman, 1976) have found that bracken fronds and litter contain water soluble phytotoxins which are capable of reducing the germination and growth of certain herbaceous species. Molisch (1937) coined the term 'allelopathy' to describe any direct or indirect harmful effects by one plant upon another through the production of chemical compounds (phytotoxins) that escape into the environment. Since these toxins may play an important role in the establishment of improved swards in bracken infested areas, the available literature was reviewed and field and laboratory studies were initiated to determine whether bracken in the West of Scotland exerted any allelopathic influences upon other species.

10.2 Literature review

The literature available indicates that water soluble phytotoxins are absent or less effective in green fronds and become more effective as the fronds senesce and turn yellow, with the dry brown fronds being highly toxic (del Moral and Cates, 1971; Gliessman and Muller, 1972; Stewart, 1975; Gliessman, 1976; Gliessman and Muller, 1978). The first rains after frond senescence were found to be the most toxic. After one rainy season the toxicity of the leachate was much reduced and after several seasons the toxic element had been completely removed (Gliessman and Muller, 1972, 1978). These conclusions were derived from work carried out in the Coast ranges of Washington and Oregon on the Pacific coast of the USA (del Moral and Cates, 1971; Stewart, 1975; Gliessman, 1976) and in the Santa Ynez Mountains of southern California, USA (Gliessman, 1976; Gliessman and Muller, 1972, 1978).

As early as 1917, Jeffreys demonstrated active inhibition of associated species by the breakdown of bracken litter (Jeffreys, 1917). Bracken fronds were dug into the subsoil below turves containing Deschampsia flexuosa. After one year the bracken was found to have decomposed and the grass above had died. Fronds lying over a sward of D. flexuosa for the same period of time had not begun to decompose and the sward was healthy. After 18 months decomposition was advanced and the Deschampsia had died. Similar effects were noted for Calluna vulgaris and Nardus stricta. Controls in these experiments took into account the effects of shade on plant growth and in each case it was decomposing fronds which were deemed to be killing the plants. Jeffreys considered that toxins were not likely to be washed out of newly fallen fronds by rain. Konovalov and Luganskii (1970) showed the initial germination of pine and larch seeds was inhibited by bracken extract, the incorporation of dead standing frond material with soil in pots was found by Gliessman and Muller (1972) to reduce root and shoot growth and plant height of Avena fatua seedlings, and Stewart (1975) reported that the incorporation of senescent bracken fronds into soil inhibited the emergence and growth of two shrub species (Rubus parviflorus and R. spectabilis). Horsley (1977) showed that extracts from bracken fronds inhibited the germination of seed of Prunus serotinus. Shoot growth and dry weight accumulation of seedlings which had exhausted their cotyledonary reserves was also inhibited by extracts from bracken fronds.

Gliessman (1976) examined three quite different habitats and found that in southern California toxin release was timed for the start of the wet season and hence the initiation of plant growth. At this time, toxin release was primarily from the dead standing fronds. In the Pacific North-west, toxin release was primarily from the bracken litter and rhizomes at a time when the dormancy of associated plants was breaking in the spring whilst in tropical areas such as Costa Rica, where associated plants were growing throughout the year and green fronds were constantly present, the toxic leachate came primarily from the green fronds. He suggested that bracken had evolved a system of toxin release which concentrated the input of toxins so as to coincide with the start of the rainy season and hence the start of germination of the associated species.

Gliessman and Muller (1978) identified a toxic compound in rain drip which had been collected from below the bracken canopy. They considered it likely that the soil below the bracken fronds might have acquired a significant level of toxicity and they conducted two experiments to examine this theory. In the first of these experiments, soil was collected from below the canopy after the first rain of the season and seed of four species was sown into this. Radicle growth of three of these species (Avena fatua, Hypochaeris glabra and Bromus mollis) was inhibited but that of the fourth species, Bromus rigidus, was unaffected. In the second experiment, soil was collected during the summer from below the bracken stands and from the grassland adjacent. Trays of each type of soil were placed below the canopy and out in the grassland. After the first rains of the winter season the trays were recovered and seeded with Avena fatua. Bracken soil exposed to rainfall in the bracken stand was found to be the most inhibitory to seed germination, with grassland soil exposed to rainfall in the bracken stand also inhibitory but to a lesser degree. Inhibition noted in the tray of bracken soil located in the adjacent grassland indicated that residual toxicity existed in the soil for at least one year. These results supported those of Gliessman and Muller (1972) who found that water extracts of whole fronds when applied to pots of soil were inhibitory to seed of Bromus rigidus and Avena fatua, and those of Gliessman (1976) who collected soil from grassland adjacent to a bracken stand and from below the bracken fronds after the first rains of the season and examined their effect on seed germination. Seeds sown in the soil from below the bracken were inhibited relative to those in the grassland soil. Horsley (1977) found that removing the ground flora of bracken and herbs from orchards did not allow black cherry seedlings to grow during the first year although they were able to do so in the second year. This suggested to him that the resident micro-organisms required some time to decompose the inhibitors or for the inhibitors to be leached away.

Gliessman and Muller (1978) demonstrated how the removal of fronds from bracken stands before rains could leach them resulted in reinvasion by herbaceous species after several seasons and how, conversely, placing fronds over the herbs (supported on a frame to eliminate any effects due to physical smothering) brought about inhibition. A similar frame covered with fabric created a comparable reduction in light intensity to that below the bracken frame and was used as a control. Species susceptible to the frond toxins were reduced in number compared with the adjacent control frame. Results obtained from below the frond frame were comparable with those from below the actual bracken stand.

The toxic compounds in the bracken fronds are thought to be water soluble and work has been concentrated on the phenolic compounds. Whitehead (1964) found that the soil associated with bracken contained p-hydroxybenzoic acid, vanillic acid, p-hydroxycinnamic acid and ferulic acid, Bohm and Tryon (1967) found caffeic acid, ferulic acid and p-coumaric acid in bracken fronds and Glass and Bohm (1969) found bracken fronds to contain p-hydroxybenzoic acid, vanillic acid, p-hydroxycinnamic acid and ferulic acid in high concentrations in the growing season and suggested that rain leaching and decomposing fronds introduced the compounds into the soil. Gliessman and Muller (1972) tentatively identified cinnamic acid, the first requirement for the formation of which is the presence of L-phenylalanine ammonia-lyase which converts phenylalanine to cinnamic acid. Young et al (1966) showed this to be present in high levels in both young and old 'leaves' of P. aquilinum. Gliessman and Muller (1978) separated out several compounds using paper chromatography but did not identify them completely. They found that several of the bands isolated corresponded to phenolic compounds identified from Adenostoma fasciculatum by McPherson et al (1971) but felt that more work was necessary before a final identification could be made. In 1976, Glass grew six species of grass (including barley) and a clover hydroponically in solutions which reproduced the composition and concentration of the major phenolic compounds of the soil associated with Pteridium aquilinum. The presence of these compounds in calcium sulphate [$CaSO_4$] solution severely inhibited root growth as measured by fresh weight, dry weight and root volume of all the species except one grass. There were no obvious effects of these phenolics on barley root growth when they were dissolved in a complete inorganic nutrient medium (Glass, 1976).

10.3 Introduction to experimental work

Many of the experiments carried out to demonstrate the toxicity of bracken leachate employed the 'standard sponge bioassay' described by McPherson and Muller (1969) which consists essentially of a cellulose sponge soaked in the test solution on top of which a piece of filter paper had been placed. The seeds were then arranged on the filter paper, the unit was placed in a petri dish, sealed with parafilm and placed in darkness for 48 hours. Using this technique extracts from various parts of the bracken plant have been shown to inhibit radicle growth and seed germination. Since this creates a somewhat artificial environment, attempts have also been made to demonstrate that these toxins are active in the soil. In the first type of experiment, dead bracken fronds were mixed with soil or placed on the soil surface, to simulate litter accumulation in the field, and any variation in seed germination or seedling growth relative to a suitable control was noted. In a second type of experiment, leachate was extracted and applied to seeds in dishes of soil. The presence of toxins in the soil has also been demonstrated by sowing seed into soil collected from bracken stands.

Some of these experiments have been repeated here to determine whether allelopathy was operating in the bracken ecosystem in the West of Scotland and to consider whether it was likely to be a major factor influencing the distribution of native hill land species or the fate of seed of sown-in species in hill land improvement schemes.

In all these experiments, frond material was collected from well-established plants in the college greenhouse (fresh green material and dry green material) or from the Carrick Hills, South of Ayr (dead standing fronds and bracken litter).

10.4 *Experiment 1. To determine the effect of leachate from fresh green, dry green and dry brown fronds on seed germination in petri dishes*

10.4.1 Method

Leachate was prepared by adding 150 ml of sterile distilled water to 10 g of air dried frond material, or its equivalent in fresh material, and stirring every 30 minutes. At the end of two hours the solution was filtered through a single thickness of muslin.

When fresh green material was being used, three 10 g samples were collected and placed in an oven at 100°C for four hours. Trials showed that after this time no further water loss occurred. The samples were reweighed and the mean percentage water content was calculated. From this figure, a quantity of fresh frond material, equivalent to 10 g of dry frond material, was collected and soaked in 150 ml of sterile distilled water as previously described.

Two pieces of sterile Whatman filter paper No. 4 were placed in each sterile petri dish and the papers were moistened with 4 ml of either leachate or sterile distilled water using sterile disposable syringes. Seeds of various grass species and white clover were surface sterilised with a 0.5% solution of 'chloros' (Sodium hypochlorite) which was shown to have no effect on seed germination (Appendix 4:A:Table 1). Fifty seeds were placed in each dish and for each treatment there were between three and six replicates per species (depending on the trial). The plates were prepared on a lamina flow bench to reduce the likelihood of contamination. The dishes were placed in randomised blocks in an incubator at 22°C in darkness for 48 hours. They were then removed and placed in randomised blocks in a lighted propagator unit maintained at 18°C. Any seeds which had germinated were recorded and removed 48, 72, 96, 120 and 144 hours after seeding, except in the first trial where an assessment at 144 hours was not possible. The filter papers were remoistened as necessary, similar volumes of water or leachate being applied to each treatment as appropriate.

The effect of the different leachates upon the germination of seed of Trifolium repens (white clover), Lolium perenne (perennial ryegrass), Festuca rubra (red fescue), Agrostis tenuis (common bentgrass), Poa pratensis (smooth stalked meadow grass), and Poa trivialis (rough stalked meadow grass) was examined. Several trials were carried out but not all the species were used each time. The dates of the trials are given below.

Trial Number	Date of Trial
1	8 November 1979
2	21 November 1979
3	30 November 1979
4	12 December 1979
5	12 January 1980
6	11 February 1980
7	18 February 1980
8	11 June 1980

In the first trial fungal contamination was found on some of the plates treated with leachate extracted from green frond material which had been allowed to air dry overnight prior to the leachate being prepared. An attempt was made to remove this contamination by passing the leachate through a Sartorius membrane filter (cellulose nitrate composition, 0.2μ pore size) or through sterile Whatman filter paper No. 4.

In the second and third trials for each of the species tested, three replicate plates each of fifty seeds were moistened with leachate (from dry green fronds) which had either been passed through filter paper or through a membrane filter or which was unfiltered. The control plates were moistened with sterile distilled water which was either unfiltered or which had been passed through filter paper or through a membrane filter, as appropriate.

10.4.2 Results

10.4.2.1 Effect of filtration method on fungal contamination and seed germination when using leachate from dry green fronds

Table 37

The results of both trials two and three suggested that there was no significant difference in the number of seeds which germinated on the plates treated with either unfiltered leachate or with leachate passed through either Whatman filter paper or through a membrane filter. Since no contaminants were present on the plates treated with leachate passed through a membrane filter, it was considered unlikely that the fungal contamination, which developed during the course of the experiment, was having a significant or adverse effect upon seed germination. This was the case for each of the species tested. In the light of these two trials it was considered that it would not be necessary to filter the leachate prior to use in future experiments as the presence of fungal contaminants, which arose only periodically, did not appear to contribute significantly to the outcome of the experiments and was unlikely to be a major source of experimental error. There was insufficient evidence to warrant the considerable amount of extra work which would have been involved in filtering through a membrane all the leachate to be used in future experiments.

10.4.2.2 Effect of leachateson seed germination (from fresh green, dry green and dry brown fronds).

Table 38

No significant differences were observed in the number of seeds which germinated when treated with leachate derived from dead standing brown frond material or when treated with sterile distilled water. This was the case for all the species tested.

Table 39

Leachate derived from living green frond material was also found to have no significant effect upon the germination of <u>T. repens</u>, <u>L. perenne</u>,

Table 37

Effect of method of filtering on seed germination in leachate.

Trifolium repens

Trial 2				Trial 3			
hrs	Con	Me	Wh	hrs	Con	Me	Wh
48	24.33	23.33	20.67	48	39.33	35.00	37.67
72	30.00	30.00	27.67	72	40.00	36.00	38.00
96	32.33	32.33	33.00	96	42.67	37.33	38.33
120	43.00	40.33	41.67	120	43.33	37.67	38.67
144	43.67	41.00	42.67	144	43.67	38.00	38.67

Lolium perenne

Trial 2				Trial 3			
hrs	Con	Me	Wh	hrs	Con	Me	Wh
48	42.67	32.00	40.50	48	41.33	41.00	42.00
72	45.33	38.67	44.00	72	42.33	45.00	45.00
96	46.33	43.00	45.00	96	44.00	46.67	46.67
120	47.00	44.67	46.50	120	44.00	46.67	47.33
144	47.00	45.67	46.50	144	45.33	47.33	48.00

Festuca rubra

Trial 2				Trial 3			
hrs	Con	Me	Wh	hrs	Con	Me	Wh
48	4.33	5.33	6.00	48	28.33	30.33	26.67
72	12.33	11.33	13.33	72	34.67	37.33	33.00
96	21.33	19.33	21.67	96	38.00	41.67	38.33
120	31.50	30.33	34.67	120	40.00	43.33	41.00
144	36.50	34.33	35.67	144	41.67	44.33	43.67

Con: Unfiltered leachate: control

Me: Membrane filtered leachate

Wh: Whatman paper filtered leachate

Differences are not statistically significant

Table 37

Effect of method of filtering on seed germination in leachate (cont.)

<u>Agrostis tenuis</u>

Trial 3

hrs	Con	Me	Wh
48	15.00	18.67	19.33
72	17.67	22.67	20.33
96	23.00	28.67	24.67
120	26.00	33.00	26.00
144	30.00	35.33	31.00

<u>Poa pratensis</u>

Trial 3

hrs	Con	Me	Wh
48	0.00	0.00	0.00
72	0.33	0.00	0.33
96	1.33	0.00	1.33
120	3.00	2.00	2.00
144	8.33	4.67	5.33

<u>Poa trivialis</u>

Trial 3

hrs	Con	Me	Wh
48	5.67	7.33	1.33
72	7.33	9.33	4.67
96	14.33	17.00	13.00
120	18.00	20.00	16.67
144	23.33	23.67	22.00

Con: Unfiltered leachate: control

Me: Membrane filtered leachate

Wh: Whatman paper filtered leachate

Differences are not statistically significant

Table 38

Effect of leachate from dry brown fronds on seed germination in petri dishes.

Trifolium repens

Trial 1

hrs	Water	Leachate
48	49.00	46.00
72	49.00	46.67
96	49.00	47.33
120	49.00	47.33
144	-	-

Trial 4

hrs	Water	Leachate
48	38.67	34.33
72	41.00	36.67
96	41.33	36.67
120	41.67	37.00
144	42.00	38.00

Trial 5

hrs	Water	Leachate
48	30.00	30.00
72	30.33	32.00
96	30.33	32.00
120	30.67	33.00
144	30.67	33.00

Trial 8

hrs	Water	Leachate
48	46.75	43.75
72	47.00	43.75
96	47.00	44.50
120	47.00	44.50
144	47.00	44.75

Lolium perenne

Trial 1

hrs	Water	Leachate
48	47.33	44.00
72	48.33	45.00
96	48.67	45.33
120	48.67	46.33
144	-	-

Trial 4

hrs	Water	Leachate
48	45.00	41.67
72	47.67	46.00
96	48.33	46.67
120	49.00	47.00
144	49.00	47.00

Trial 5

hrs	Water	Leachate
48	46.33	46.67
72	46.33	47.00
96	47.00	47.33
120	47.00	47.33
144	47.00	47.33

Trial 8

hrs	Water	Leachate
48	25.75	20.50
72	35.80	32.50
96	39.80	37.80
120	42.80	40.50
144	43.50	41.80

Differences are not statistically significant

Table 38

Effect of leachate from dry brown fronds on seed germination in petri dishes (cont.)

Festuca rubra

Trial 1

hrs	Water	Leachate
48	37.33	29.00
72	44.67	38.00
96	47.00	41.33
120	47.33	44.00
144	-	-

Trial 4

hrs	Water	Leachate
48	30.00	30.67
72	39.33	40.33
96	41.33	42.67
120	42.67	43.67
144	43.33	45.00

Trial 5

hrs	Water	Leachate
48	35.67	30.67
72	40.33	35.67
96	42.67	41.00
120	46.00	43.67
144	46.67	44.33

Agrostis tenuis

Trial 1

hrs	Water	Leachate
48	32.00	30.67
72	43.67	40.33
96	45.67	41.67
120	46.00	42.33
144	-	-

Trial 4

hrs	Water	Leachate
48	11.00	15.33
72	26.67	28.00
96	38.00	38.67
120	38.67	40.67
144	42.00	41.67

Trial 5

hrs	Water	Leachate
48	10.33	10.33
72	13.00	15.67
96	33.33	29.67
120	42.33	42.00
144	43.67	44.00

Trial 8

hrs	Water	Leachate
48	8.00	7.25
72	14.50	13.00
96	36.50	32.75
120	42.00	44.25
144	43.00	45.25

Differences are not statistically significant

Table 38

Effect of leachate from dry brown fronds on seed germination in petri dishes (cont.)

Poa pratensis

Trial 4

hrs	Water	Leachate
48	0.00	0.00
72	0.67	1.33
96	4.67	6.00
120	7.67	7.67
144	10.67	9.33

Trial 5

hrs	Water	Leachate
48	0.00	0.00
72	2.33	2.00
96	9.33	8.00
120	15.33	18.00
144	20.00	21.00

Poa trivialis

Trial 1

hrs	Water	Leachate
48	9.33	7.00
72	21.67	20.67
96	27.00	27.00
120	30.00	29.67
144	-	-

Trial 4

hrs	Water	Leachate
48	1.67	2.00
72	15.67	15.33
96	24.00	21.33
120	29.00	26.67
144	32.00	29.67

Trial 5

hrs	Water	Leachate
48	5.33	5.33
72	11.33	10.67
96	20.00	22.67
120	25.33	27.00
144	28.00	29.67

Differences are not statistically significant

Table 39

Effect of leachate from fresh green fronds on seed germination in petri dishes.

Trifolium repens

Trial 7

hrs	Water	Leachate
48	44.83	44.83
72	45.50	46.00
96	45.67	46.50
120	45.67	46.67
144	45.67	46.67

Trial 8

hrs	Water	Leachate
48	46.80	42.80
72	47.00	46.25
96	47.00	46.75
120	47.00	46.75
144	47.00	46.75

Lolium perenne

Trial 8

hrs	Water	Leachate
48	25.75	22.25
72	35.75	34.00
96	39.75	39.50
120	42.75	41.00
144	43.50	42.00

Festuca rubra

Trial 7

hrs	Water	Leachate
48	27.83	26.50
72	38.50	38.00
96	41.67	43.00
120	43.33	44.50
144	45.17	45.50

Agrostis tenuis

Trial 8

hrs	Water	Leachate
48	8.00	5.25
72	14.50	13.00
96	36.50	26.75
120	42.00	40.00
144	43.00	41.00

Differences are not statistically significant

F. rubra or A. tenuis relative to the control treatments using sterile distilled water.

Figs. 13-17

Significant differences were observed in the number of seeds which germinated relative to the controls only when leachate derived from dry green frond material was used. The six species tested did not respond in the same way and, with respect to the individual species, the results of several similar trials, summarised in Table 40 were not consistent. F. rubra and A. tenuis were the most sensitive species being adversely affected in all but one of the seven trials. Whilst L. perenne was inhibited in two out of three trials the remaining species were only influenced in about one trial in two.

10.4.3 Discussion

On the basis of the dominant stage of the bracken the most likely source of toxins in the autumn and winter would be the senescent and dead standing fronds whilst the fresh green fronds might be the main source in the spring and summer months. By carrying out trials from November 1979 to June 1980 it was hoped that it might be possible to relate any changes in the toxicity of the leachates to the time of year and the growth stage of the bracken.

Dry brown fronds were tested for their effect on seed germination in November, December, January and June but at no time was any evidence found to support that of del Moral and Cates (1971), Gliessman and Muller (1972, 1978) or Stewart (1975), all of whom found that the leachate from dead standing fronds was highly toxic.

The effect of leachate from fresh green fronds was considered in November, February and June but on no occasion was any toxicity demonstrated. This is in agreement with previously published work (del Moral and Cates, 1971; Gliessman and Muller, 1972, 1978).

Figure 13. Effect of leachate from dry green fronds on the germination of <u>Trifolium repens</u> in petri dishes.

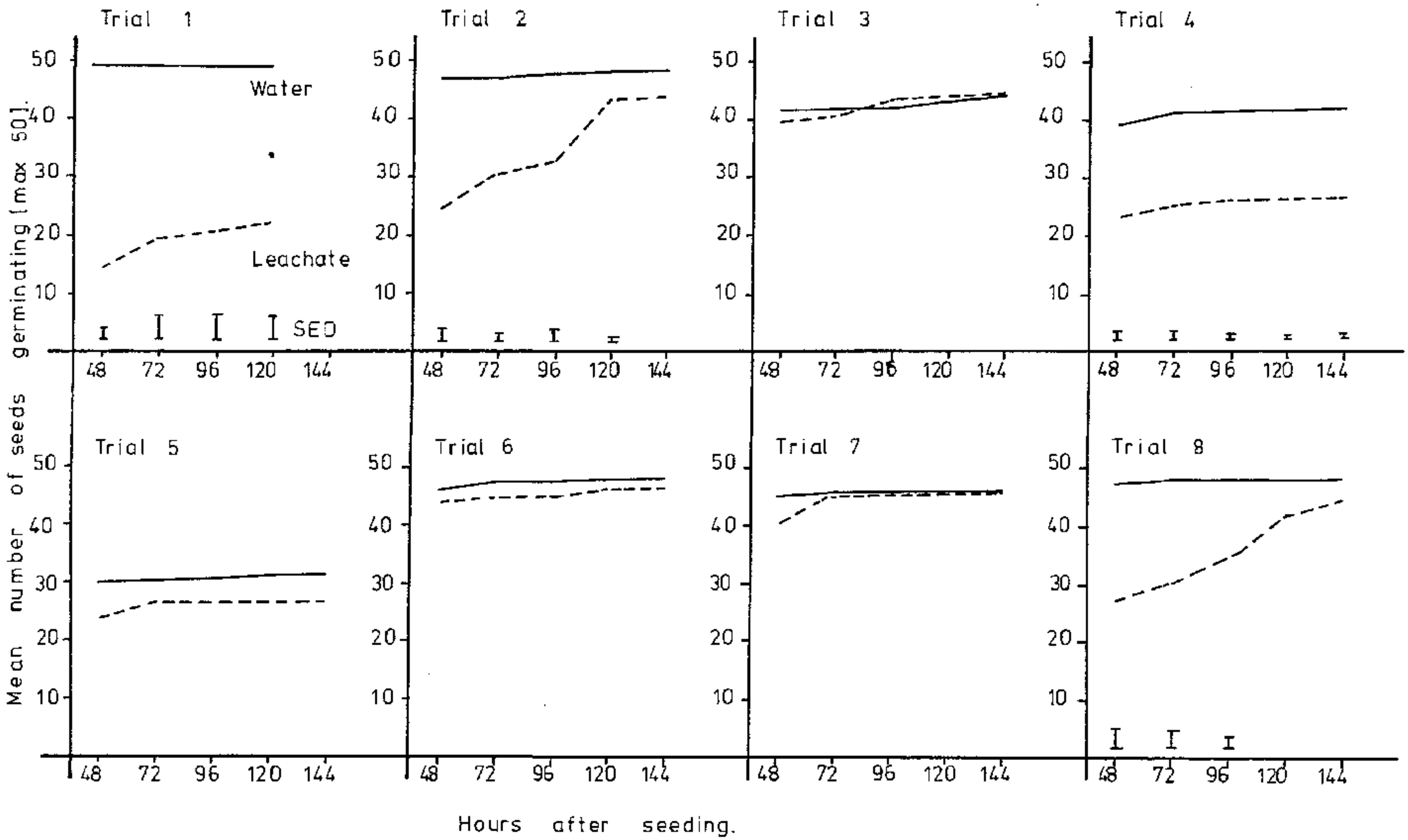


Figure 14. Effect of leachate from dry green fronds on the germination of <u>Lolium perenne</u> in petri dishes.

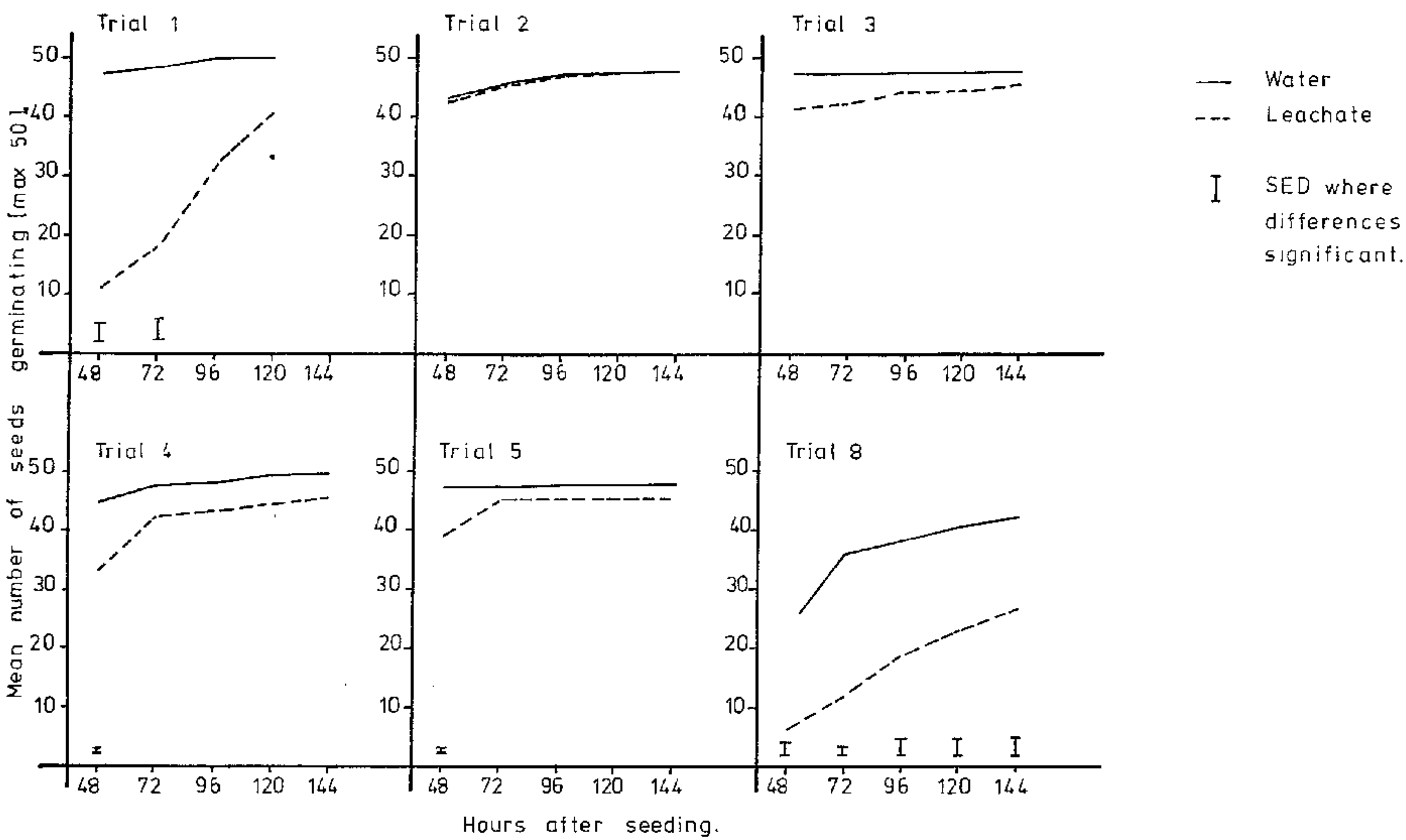


Figure 15. Effect of leachate from dry green fronds on the germination of <u>Festuca rubra</u> in petri dishes.

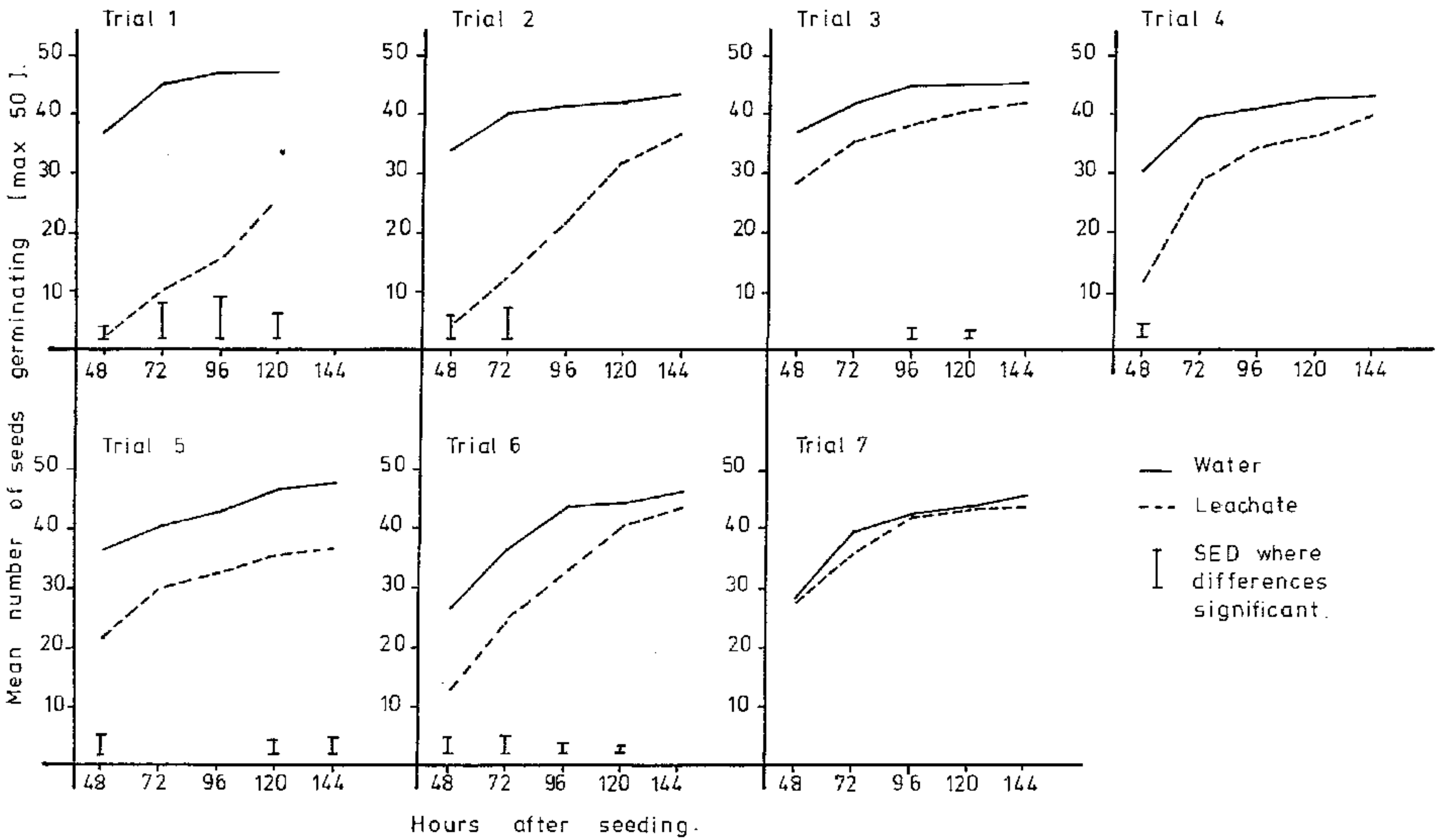


Figure 16. Effect of leachate from dry green fronds on the germination of _Agrostis tenuis_ in petri dishes.

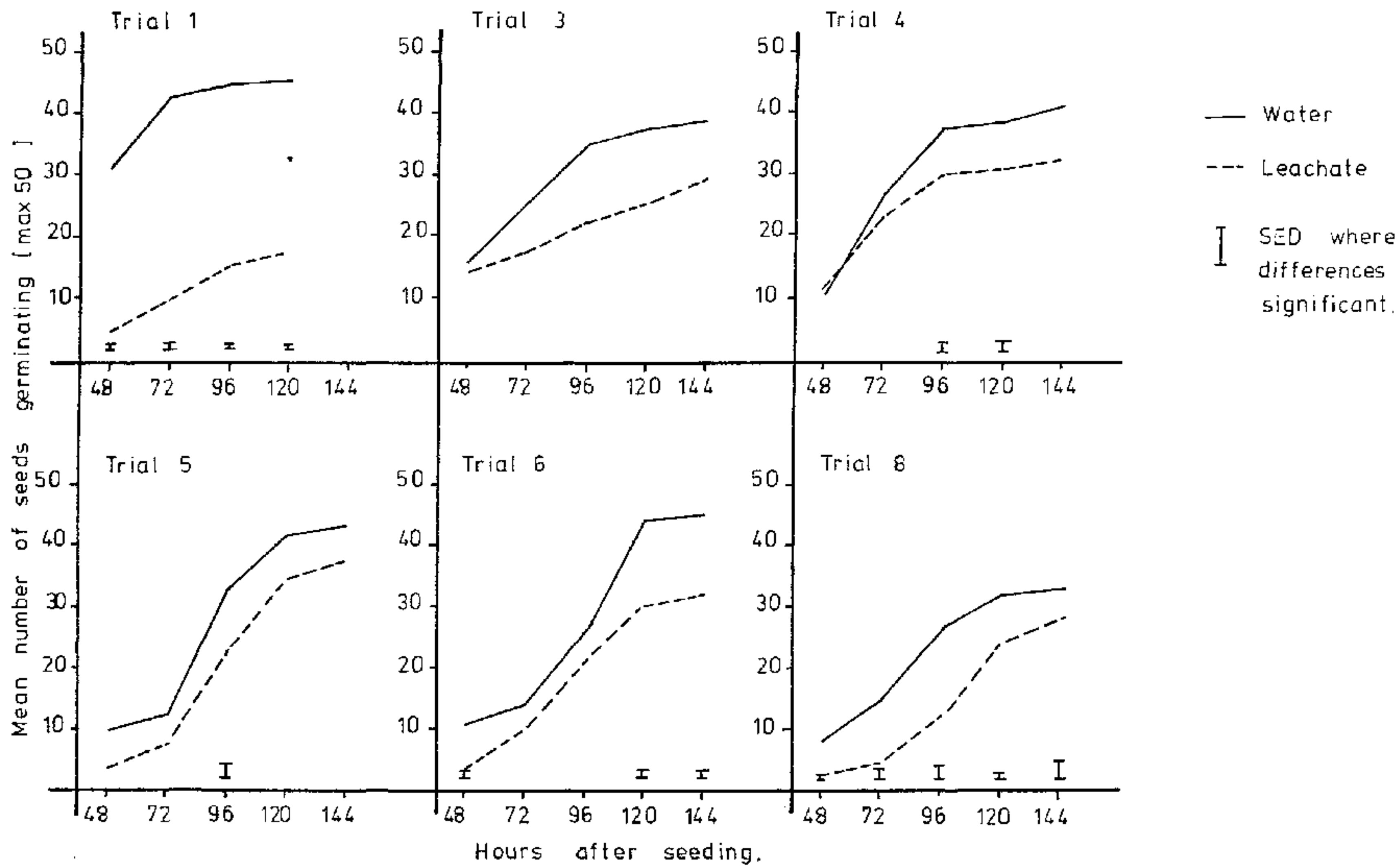


Figure 17. Effect of leachate from dry green fronds on the germination of (a) <u>Poa pratensis</u> and (b) <u>Poa trivialis</u> in petri dishes.

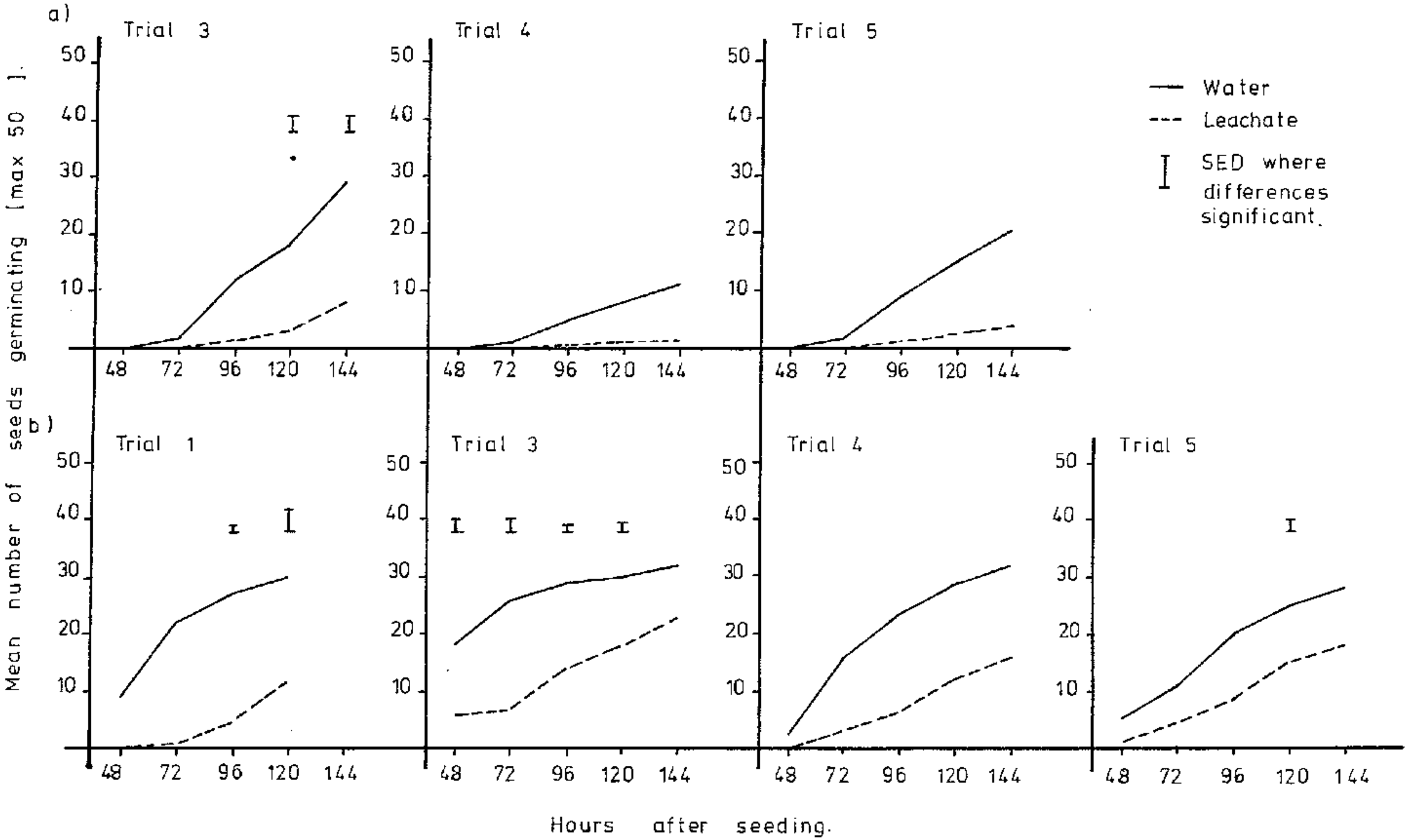


Table 40

Summary of results of trials examining the effect of leachate from dry green fronds on seed germination in petri dishes.

Species	Trial Number 1	2	3	4	5	6	7	8	% of trials demonstrating inhibition
T. repens	*	*	NA	*	NA	NA	NA	*	50.00
L. perenne	*	NA	NA	*	*			*	66.67
F. rubra	*	*	*	*	*	*	NA		85.71
A. tenuis	*		NA	*	*	*		*	83.33
P. pratensis			*	NA	NA				33.33
P. trivialis	*		*	NA	NA				50.00

* Denotes inhibition demonstrated

NA Denotes inhibition not demonstrated

Gaps in the table indicate that a species was not tested in a particular trial

Gliessman, however, found that whilst in southern California leachate from fresh green fronds displayed no toxicity, in Costa Rica, where green fronds were present for most of the year, they provided a significant source of toxin, radicle length of Bromus rigidus being inhibited to 48% of distilled water controls (Gliessman, 1976).

Leachate derived from fresh green fronds which had been allowed to air dry overnight was sometimes found to have a certain degree of toxicity. The results obtained from several similar trials were not consistent and no pattern of changing toxicity with time could be discerned. However, the germination of all six of the species was adversely affected at some point in at least one of the trials.

Whilst a field situation where dry standing green fronds were being leached is not one that would arise under British conditions, these trials were carried out in an attempt to determine whether any phytotoxic influences could be elicited from any kind of bracken leachate.

10.5 Experiment 2. To determine the effect of leachate from fresh green and dry brown fronds on seed germination and seedling growth in soil

10.5.1 Method

Soil was collected from a grassland site adjacent to a bracken site. The soil was air dried and any stones and plant debris were removed. 200 g of soil were added to each of twenty-seven pots. Twenty seeds of Trifolium repens, Lolium perenne or Festuca rubra were placed on the soil surface of each of nine pots. The pots were arranged in three randomised blocks in a greenhouse where three pots of each species were watered daily from above with 25 ml of either sterile distilled water (control), leachate extracted from fresh green fronds or leachate extracted from dead standing fronds. The leachate was prepared freshly each day. The experiment continued for fourteen days at which time the number of seeds which had established was recorded.

Ten seedlings per pot were selected at random, dried at 80°C for 24 hours and then weighed.

A second group of forty-five pots was prepared and set up in the greenhouse as described above, the number of replicates having been increased from three to five per treatment. After eighty-four hours the number of seeds which had germinated was recorded and the radicle length of each germinated seed was measured.

10.5.2 Results

Table 41

No significant differences were observed between the treatments in respect of either the number of seeds which germinated and established or the dry weight of comparable numbers of seedlings.

Table 42

The number of seeds which germinated in the three treatments in the second part of the experiment did not differ significantly for any of the three species, which agrees with the results obtained above. A mean radicle length for each replicate was calculated on the basis of the number of seeds which germinated in that replicate and an overall treatment mean was calculated for the five replicates. The analysis showed no significant differences in the radicle lengths of the germinated seeds in the three treatments. This applied to all three species tested.

10.5.3 Discussion

Gliessman and Muller (1972) suggested that one of the ways in which bracken might suppress associated species was by the release of toxins from the fronds which, being water soluble, would be washed into the soil by rain and hence become available to other plants via the soil water. These workers found evidence that the radicle of _Avena fatua_ seeds was significantly reduced in length when sown in soil treated with frond extract and radicle development of _Bromus rigidus_ seed was inhibited when the extract was concentrated by a factor of four.

Table 41

Effect of leachate from fresh green and dry brown fronds upon seed establishment and seedling dry weight yield.

Species	Test solution	Mean no. of established seedlings	Dry weight of 10 plants (g)
<u>Trifolium repens</u>	Water-control	15.67	0.0151
	Fresh green frond leachate	16.67	0.0137
	Dry brown frond leachate	14.67	0.0123
<u>Lolium perenne</u>	Water-control	17.00	0.0179
	Fresh green frond leachate	17.67	0.0214
	Dry brown frond leachate	17.00	0.0200
<u>Festuca rubra</u>	Water-control	13.67	0.0132
	Fresh green frond leachate	13.67	0.0122
	Dry brown frond leachate	15.00	0.0125

Differences are not statistically significant

Table 42

Effect of leachate from fresh green and dry brown fronds upon seed germination and radicle length.

Species	Treatment	No. of germinated seeds	Length of radicle (mm)
Trifolium repens	Water-control	18.40	6.88
	Fresh green frond leachate	18.80	6.19
	Dry brown frond leachate	18.60	7.63
Lolium perenne	Water-control	16.40	13.30
	Fresh green frond leachate	17.25	11.74
	Dry brown frond leachate	15.80	13.47
Festuca rubra	Water-control	12.00	3.15
	Fresh green frond leachate	14.40	2.84
	Dry brown frond leachate	11.20	2.16

Differences are not statistically significant

These results were recorded after 48 and 72 hours of treatment for A. fatua and B. rigidus respectively.

However, if the release of water soluble toxins from dead standing fronds is to be a major factor determining both the number of seeds which germinate and establish and their subsequent development, then an examination of radicle length alone after at most 72 hours is too early to establish whether any inhibition recorded is going to be either permanent or of major significance in a field situation. No evidence could be found here to suggest that leachate extracted from either dead standing fronds or from fresh green fronds when applied to soil containing seed of the species tested had any adverse effects upon germination or radicle extension. Nor was there any evidence that the dry weight yield or number of established seedlings was adversely affected by either type of leachate relative to the water controls.

10.6 *Experiment 3. To determine the effect of soil source on seed germination*

10.6.1 Method

Soil collected from below a bracken stand and from grassland adjacent to the stand was air dried and stones and plant debris were removed. 200 g of either grassland soil or bracken stand soil were placed in each of fifteen pots. Five pots of each soil type were surface sown with twenty seeds of either Trifolium repens, Lolium perenne or Festuca rubra. The pots were arranged in five randomised blocks in a greenhouse and thoroughly moistened with sterile distilled water. After 72 hours the number of seeds which had germinated was recorded.

10.6.2 Results

Table 43

There were no significant differences in the number of seeds which germinated in the soils from the two different sites. This applied to all three species.

Table 43

Effect of soil source on seed germination.

Species	Soil 'source'	No. of seeds germinated
Trifolium repens	Grassland	17.80
	Bracken stand	18.00
Lolium perenne	Grassland	13.80
	Bracken stand	13.60
Festuca rubra	Grassland	5.80
	Bracken stand	5.80

Differences are not statistically significant

10.6.3 Discussion

Gliessman (1976) reported that fewer seeds germinated in soil collected before the start of the rainy season from below the bracken canopy than in soil from the adjacent grassland. Gliessman and Muller (1978) also demonstrated that soil from below a bracken stand retained an element of toxicity for up to one year.

The results obtained here do not suggest that soil from below a bracken canopy has an inhibitory effect upon seed germination of the species tested relative to soil from an adjacent grassland. The soil from the bracken stand was collected in April 1980 at a time when seed of sown species, and that of some of the native species, might be germinating. The results suggest that the germination of these seeds will be as successful as that of seed sown into grassland soil, all other factors being equal.

10.7 Experiment 4. To determine the effect of dead standing fronds and bracken litter on seed establishment and growth in soil

10.7.1 Method

Soil was collected from a grassland site adjacent to a bracken stand, stones and plant debris were removed and the soil allowed to air dry. 750 g of soil were placed in each of thirty-six pots. 6 g of brown frond material was mixed into the soil of nine pots and a similar amount of bracken was placed on the soil surface of a further nine pots. Untreated wood shavings, which had approximately the same texture and density as dry bracken fronds, were used in the control treatments where they were either mixed with the soil (6 g per pot) or placed on the soil surface to a depth equivalent to that of 6 g of bracken litter (approximately 3 cm). Nine pots of each control treatment were set up. Each of three pots of each treatment were sown with 100 seeds of either Trifolium repens, Lolium perenne or Festuca rubra. The pots were arranged in three randomised blocks in the greenhouse where they were watered periodically with tap water. After ten days the number of seeds which had germinated and established was recorded. Twenty randomly selected seedlings from each pot were removed, dried at 80°C for 24 hours and weighed.

A similar experiment with only two basic treatments (bracken litter incorporated with the soil or bracken litter on the soil surface) was also set up using the same species. (Trial 1: 5 June 1980). The number of seeds which had germinated and established after seven days was recorded and the dry weight of ten randomly selected seedlings was determined after four weeks. The results of this trial will also be considered here.

10.7.2 Results

The results have been tabulated and analysed in sections.

Table 44

The incorporation of bracken fronds did not have a significant inhibitory effect upon either the number of _T. repens_, _L. perenne_ or _F. rubra_ seeds which germinated and established or upon the dry weight yield of the seedlings harvested relative to the control treatment incorporating untreated wood shavings with the soil.

Table 45

Although there were no differences in the yields of the seedlings harvested from the two treatments, significantly fewer seeds of each species established in the pots where bracken frond material covered the soil surface (_T. repens_ $P \leq 0.001$, _L. perenne_ $P \leq 0.05$, _F. rubra_ $P \leq 0.01$) than where untreated wood shavings covered the soil surface.

Tables 46 & 47

The results of the two separate trials, where bracken litter or bracken frond material was either incorporated with the soil or placed on the soil surface, were similar. Significantly fewer seeds germinated in

Table 44

Effect upon seed establishment and yield of incorporating bracken fronds with soil.

Species	Treatment	No. of seeds established	Dry wt. 20 plants (g)
Trifolium repens	Wood shavings	92.33	0.0130
	Frond material	93.66	0.0120
Lolium perenne	Wood shavings	88.33	0.0164
	Frond material	90.00	0.0128
Festuca rubra	Wood shavings	82.66	0.0116
	Frond material	90.66	0.0122

Control treatment = wood shavings

Table 45

Effect upon seed establishment and yield of a layer of fronds on the soil surface.

Species	Treatment	No. of seeds established	SED	Significance	Dry wt. 20 plants (g)
Trifolium repens	Wood shavings	78.66	0.33	$P \leq 0.001$	0.0111
	Frond material	63.00			0.0101
Lolium perenne	Wood shavings	73.33	2.52	$P \leq 0.05$	0.0187
	Frond material	62.33			0.0158
Festuca rubra	Wood shavings	64.00	1.33	$P \leq 0.01$	0.0132
	Frond material	45.66			0.0082

Control treatment = wood shavings

Differences are not statistically significant unless indicated

Table 46 (Trial 1: 5 June 1980)

Comparison of seed establishment and yield when bracken litter was either incorporated with the soil or present as a layer on the soil surface.

Species	Treatment	No. of seeds established	SED	Significance	Dry wt. 10 plants (g)
Trifolium repens	Litter layer	60.66	1.53	$P \leq 0.01$	0.0176
	Litter mixed	79.66			0.0151
Lolium perenne	Litter layer	63.66	1.45	$P \leq 0.05$	0.0243
	Litter mixed	73.33			0.0223
Festuca rubra	Litter layer	40.66	5.17	$P \leq 0.05$	0.0178
	Litter mixed	66.00			0.0177

Table 47 (Trial 2: 16 June 1980)

Comparison of seed establishment and yield when bracken fronds were either incorporated with the soil or present as a layer on the soil surface.

Species	Treatment	No. of seeds established	SED	Significance	Dry wt. 20 plants (g)
Trifolium repens	Frond layer	63.00	2.33	$P \leq 0.01$	0.0101
	Fronds mixed	93.66			0.0120
Lolium perenne	Frond layer	62.33	1.20	$P \leq 0.01$	0.0158
	Fronds mixed	90.00			0.0128
Festuca rubra	Frond layer	45.66	4.16	$P \leq 0.01$	0.0082
	Fronds mixed	90.66			0.0122

Differences are not statistically significant unless stated the pots where bracken fronds or litter itself lay on the soil surface, (T. repens $P \leq 0.01$, L. perenne and F. rubra $P \leq 0.05$, Trial 1: 5 June 1980; T. repens, L. perenne, F. rubra $P \leq 0.01$, Trial 2: 16 June 1980), than in the pots where the fronds or litter had been incorporated with the soil. However, the dry weight of comparable numbers of seedlings did not differ for the two treatments in either trial. This was the case for all three species.

Table 48

A similar significant reduction to that seen in Tables 46 & 47 was noted here in the number of seeds which germinated and established in the pots where a layer of wood shavings lay on the soil surface relative to the treatment where the shavings were incorporated with the soil. (T. repens $P \leq 0.01$, L. perenne and F. rubra $P \leq 0.05$).

10.7.3 Discussion

Gliessman and Muller (1972) incorporated either broken or ground dead fronds with soil (to simulate bracken litter) and compared the yield of Avena fatua roots and shoots and plant height with that of seedlings grown in a mixture of soil and sterile pumice. They found no difference between the plants grown in soil with either type of bracken litter incorporated but both treatments were significantly different from the control plants. Both plant height and the yield of roots and shoots was reduced in the litter treatments. In a longer term experiment, Jeffreys (1917) incorporated bracken fronds with the subsoil below turves containing Deschampsia flexuosa, Calluna vulgaris and Nardus stricta and found one year later, when the fronds had decomposed, that these plants had died.

In these experiments, where wood shavings were incorporated with the soil as a control treatment, broken brown fronds mixed with the soil did not produce significantly different numbers of established seeds nor significantly different yields from the seedlings.

Table 48

Comparison of seed establishment and yield when wood shavings were present as a layer on the soil surface or incorporated with the soil.

Species	Treatment	No. of seeds established	SED	Significance	Dry wt. 20 plants (g)
Trifolium repens	Layer of shavings	78.66	1.20	$P \leq 0.01$	0.0111
	Shavings mixed in	92.33			0.0130
Lolium perenne	Layer of shavings	73.33	3.47	$P \leq 0.05$	0.0187
	Shavings mixed in	88.33			0.0164
Festuca rubra	Layer of shavings	64.00	4.10	$P \leq 0.05$	0.0132
	Shavings mixed in	82.66			0.0116

Differences are not statistically significant unless indicated

The results of a similar experiment by Stewart (1975) are not directly comparable in that the seeds which he sowed onto a mixture of soil and litter were then covered with a layer of sterile pumice. However, he found that one of his three test species (Rubus parviflorus) had a reduced shoot length and reduced root and shoot yields relative to the control treatment (seeds sown onto soil and then covered with sterile pumice).

For all three species tested, significantly fewer seeds germinated in the treatments with bracken fronds on the soil surface than in those where wood shavings covered the soil surface (control treatment) (T. repens $P \leq 0.001$, L. perenne $P \leq 0.05$, F. rubra $P \leq 0.01$). Although the possibility cannot be ignored that toxins leached out of the bracken fronds were responsible for these differences, it was noted during the experiment that the surface of the bracken fronds tended to dry out far more rapidly than did that of the wood shavings and since the seeds were sown onto the surface of the fronds (or shavings) it is possible that more seeds germinated than were able to reach the soil surface and establish before they desiccated. The fact that the yield of comparable numbers of seedlings was similar in both treatments tends to support this idea.

In those treatments where bracken fronds were either incorporated with the soil or left lying on the soil surface, significantly fewer seeds germinated and established in the latter treatment. A similar result was obtained when wood shavings were substituted for bracken fronds. This suggests that it is unlikely to be phytotoxins from the bracken which are causing reduced germination. The yield of comparable numbers of established seedlings did not differ between the 'incorporated' and the 'surface lying' treatments for any of the three species for either bracken fronds or wood shavings.

Jeffreys (1917) suggested that toxins were only leached from decomposing fronds (i.e. litter) and it could be argued that using dead standing fronds to simulate bracken litter is not a valid comparison. However, in the first trial, which used actual bracken litter, similar results were obtained.

Stewart (1975) found that fewer seeds germinated in his experimental treatments where bracken litter was lying on the soil surface and above the seeds than where the litter was incorporated with the soil and then covered with a layer of pumice. He found that one of his three test species was also adversely affected when grown in a mixture of soil plus litter. Since the presence of a layer of bracken or pumice above the seeds makes attributing the differences to moisture stress unlikely, Stewart's suggestion that toxins leached out of the litter layer cannot be discounted.

He further considered that leachate from unincorporated bracken litter should affect germination more readily than incorporated litter because of the positioning of the seeds in relation to the potential source of toxin. After seed germination, seedling growth would be more likely to be affected in those treatments where the plant roots were in close association with the bracken litter as in those treatments where the bracken litter had been incorporated with the soil.

No evidence to support this last point was obtained in the trials carried out here. The layer of bracken litter on the soil surface in these treatments was about 3 cm deep and it is possible that the seeds experienced difficulty in penetrating this layer and reaching the soil surface. The success of surface seeding depends upon the seeds coming into contact with the bare soil and a layer of litter may well hinder this. The following experiment examined this theory.

10.8 Experiment 5. To determine the effect of depth of bracken litter on the establishment of surface sown seed

10.8.1 Introduction

In the previous Section (10.7) it was noted that surface sown seeds might have been experiencing difficulty in coming into contact with the soil. The layer of bracken litter on the soil surface may be several centimetres deep and often forms a more or less continuous cover on the ground in spring. (Plate 68). This experiment was designed to examine this topic.

Plate 68. Litter covered soil surface in spring

10.8.2 Method

Soil was collected from a grassland site adjacent to a bracken stand. Pots 10 cm deep and 20 cm in diameter were filled with soil to a depth of 2, 3, 4 or 5 cm. A layer of dead frond material 4, 3, 2 or 1 cm deep respectively was added to these pots to create a total depth of soil plus litter of 6 cm. The control pots contained soil only to a depth of 6 cm. The pots were surface sown with fifty seeds of either Trifolium repens, Lolium perenne or Festuca rubra and each treatment was replicated three times. The pots were arranged in three randomised blocks in the greenhouse where they were watered regularly from below. After ten days seed establishment was assessed.

10.8.3 Results

Figure 18

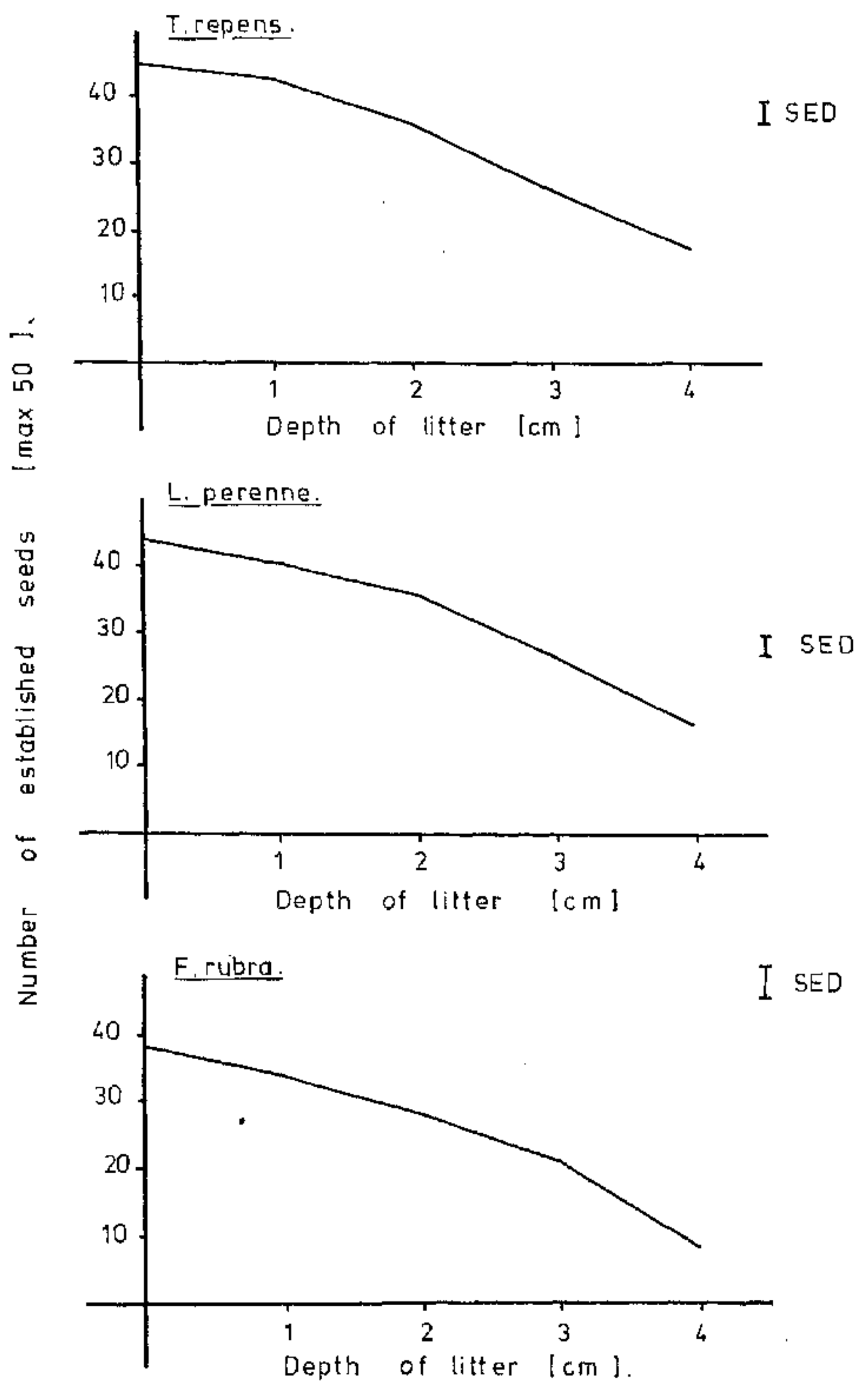
For all three species the number of seeds which germinated decreased as the depth of litter increased. There was not a significant difference between the number of seeds which established in the control pots and in those with a litter layer of only 1 cm deep but significantly fewer seeds germinated where the litter layer exceeded 1 cm in depth. (T. repens and L. perenne $P \leq 0.001$, F. rubra $P \leq 0.01$). Establishment of L. perenne fell more sharply as the litter depth exceeded 2 cm, whilst for T. repens the establishment of seedlings was considerably reduced when there was more than a 1 cm deep litter layer. For F. rubra, seed establishment decreased steadily as the litter depth increased from 0-3 cm but was much reduced when the litter depth reached 4 cm.

10.8.4 Discussion

The success of surface seeding depends chiefly upon the seed coming into contact with bare soil (Williams, 1980) where sufficient moisture is available to permit germination and prevent desiccation of the radicle before it can penetrate the soil surface. The presence of a layer of litter or dead vegetation creates a significant physical barrier to the radicle of a surface sown seedling which is trying to reach the soil surface.

For all three species, a layer of litter on the soil surface caused a reduction in the number of seeds which established but this reduction did not become significant until the layer exceeded 1 cm in depth. In the previous experiment, seed germination was significantly reduced when the seeds were sown into a layer of litter 3 cm deep. The results

Figure 18. Effect of litter depth on seed establishment.



obtained here support the idea that it is the difficulty which the seeds experience in passing through the litter layer which reduces seed establishment rather than any effect of toxins.

10.9 General Discussion

In a field situation, unless the soil is disturbed relatively few buried seeds will be stimulated to germinate and establish. Therefore the seeds most likely to be affected by toxins leaching out of bracken are those shed onto the litter layer during the year. Before they become buried, some of these seeds may encounter suitable environmental conditions that autumn or the following spring (depending upon the species and its dormancy requirements) and at these times it is the dead standing fronds and the dead fronds which have fallen to the ground to form the uppermost litter layer which would be exerting any allelopathic influence which exists. No evidence was found that leachate from dead standing fronds affected the germination of seed either in petri dishes or in soil nor was the growth of seedlings in soil affected. The dead standing fronds used in these experiments (carried out between October 1979 and June 1980) were collected as required from the Carrick Hills, south of Ayr. At no time were any allelopathic effects evident from this material and if toxins were present between the time of frond senescence (September) and October and absent thereafter, then only the autumn-germinating species might be affected.

With respect to the improvement of ground cleared of fronds with herbicides in the autumn, reseeding would not normally take place until the following spring when the bracken litter on the ground would be the most likely source of toxins. No evidence was found in this work to suggest that the germination of surface sown seed would be adversely affected by toxins from bracken litter.

Given suitable conditions for germination during the year, leachate from fresh green fronds might be expected to exert the strongest influence upon seed germination and establishment. Two of the four species tested (A. tenuis and F. rubra) are species frequently associated with bracken but no inhibitory effects of fresh green leachate were found upon seed germination in petri dishes or soil or upon seedling growth in soil for any of the four species. The fresh green fronds used in these experiments were collected from well established plots in the college greenhouse where they were watered from below to ensure that any toxins in the fronds were not washed away. If living green fronds were toxic under field conditions in the West of Scotland it is likely that this fact would have been detected in the results.

The possibility exists that the leachates used in these experiments and in similar work in the past had osmotic potentials sufficiently high to inhibit seed germination. This problem was considered by both del Moral and Cates (1971) and Gliessman and Muller (1978). In each case the osmotic potentials of their test solutions was determined and a control solution of mannitol with a corresponding osmotic potential was prepared. They concluded that the inhibition they noted could not be accounted for by the osmotic concentration of the test solutions used. Stewart (1975) did not measure the osmotic potential of his test solutions but considered that they probably did not have a significant osmotic effect upon germination. No attempt was made in these experiments to measure the osmotic potential of the test solutions as published data seemed to indicate that this does not contribute significantly to the outcome of the experiment.

Surface seeding of cleared bracken land has not been particularly successful and this may in part be due to the fact that the seed is sometimes sown onto a layer of dead vegetation and bracken litter. Whilst Dowling (1976) has reported that the presence of a limited amount of dead indigenous material was beneficial, work carried out here found that seed establishment was significantly reduced when the litter depth exceeded 1 cm and that it fell as the litter depth increased. Whilst the number of established seedlings was less when sown onto a 3 cm deep layer of litter than when sown onto a mixture of soil plus litter, the yield of comparable numbers of seedlings was similar. Since no evidence was found for toxins in the litter or the dead standing fronds, these results suggest that removal of the physical barrier provided by the surface litter layer would improve establishment and that rotavation to incorporate the litter would not produce toxin-related germination problems. However, rotavation would disturb the soil surface and stimulate buried seeds to germinate which would provide competition for sown-in species. Burning would be a suitable alternative since this would not only remove the litter layer but would also destroy any (undetected) toxins.

The differences observed between previously published work and the results obtained here may in part be due to the different varieties of bracken examined. Although not specified by the authors, the variety tested by del Moral and Cates (1971) and Gliessman and Muller (1972, 1978) was probably P. aquilinum subsp aquilinum var pubescens, according to the geographical delimitations made by Page (1976). Stewart (1975) specified that this was the variety of bracken with which he worked. Gliessman (1976) suggested that during his survey he had probably been looking at four or more varieties (as defined by Tryon (1941)) and reference to Page (1976) indicates that this included P. aquilinum subsp aquilinum var pubescens and either P. aquilinum subsp aquilinum var caudatum or P. aquilinum subsp aquilinum var arachnoideum.

In the West of Scotland the only variety of bracken encountered is P. aquilinum subsp aquilinum var aquilinum. These varietal differences possibly coupled with different climatic regimes may explain why allelopathy is either absent or not as easily detected if it is present. The fact that Gliessman found living green fronds to be non-toxic in one environment yet toxic in another illustrates this point (Gliessman, 1976).

Bioassays have frequently been used as a means of demonstrating allelopathic interactions whilst attempting to remove any influence of competition or that of other physical or chemical factors from the outcome of the experiment. However, laboratory and greenhouse bioassays may still be an inadequate method of demonstrating that allelopathy actually occurs in the field (Newman, 1977; Stowe, 1979).

Stowe (1979) examined an old field community and compared the bioassay results he obtained with association patterns in the field. He found that when he tested the seven most abundant species upon each other in nine commonly used bioassays, eight of the nine gave cases of statistically significant inhibition, strong phytotoxicity was exhibited by species which had not previously shown signs of allelopathy in the field and autotoxicity was as high as allotoxicity. His review of the literature revealed that in the few cases which allowed an objective comparison to be made between field patterns and bioassay results, a correspondence between the two was rarely found (Stowe, 1979).

Stowe used his results and his literature review to assess, critically, the problems which arise when relating bioassay results to data from field surveys. He noted that it is very difficult to determine what concentration of an allelopathic agent is appropriate for use in a bioassay. In these experiments the concentration of leachate was based upon that used by Stewart (1975). He used 100 g of dry material in 1,500 ml of water but other workers have used 65 g in 1,500 ml (Gliessman and Muller, 1972, 1978) and 100 g in 1,000 ml (Gliessman, 1976). The length of time for which the material was soaked varied from two to three hours depending upon the worker. Whether the concentration of these leachates was representative of the concentration of the active substances reaching the species normally 'influenced' by bracken leachates in a field situation was not specified in any of the papers.

His second comment was that changes in the toxicity of plant extracts often occur as a result of chemical and physical processes in the soil and as a result of microbial activity in the soil. Differences between soil types, particularly with respect to the rate at which substances might be leached down the profile, are particularly important.

His review noted that in some cases bioassays had been repeated under more natural conditions or with more appropriate controls and had been shown to be invalid as indicators of allelopathy, and that a large proportion of the species tested had given positive results in the bioassays even when no ecological evidence existed to suggest that they were involved in allelopathic activity. He found many examples of species being shown to be autotoxic and that generally a poor correspondence had been found between the results of bioassays and the distribution or succession of plants in the field. Stowe cited the work of several authors to illustrate each of his points.

When reviewing the experimental methods employed in the bioassays, he found that this in itself was a major factor influencing the results obtained regarding the allelopathic potential of the species tested. The choice of material tested was also important. Plant litter (dead, often decomposing shoot material) was found to be more toxic than shoot material or root material, whilst soil was least toxic. Whatever plant material was used, it was least inhibitory when tested whole and most inhibitory when cut up or dried and ground. (In these experiments, dry green fronds were found to be the only type of material to produce leachate with inhibitory properties.). Testing plant extracts on the growth of other plants in water culture or on seed-radicle elongation tended to give positive results, whilst tests on growth of plants in sand or soil were relatively unlikely to show inhibition. He also noted that the extent of dilution of an extract undoubtedly influenced the outcome of the experiment and that substances which were inhibitory in aqueous solution were not necessarily inhibitory in soil.

Another factor which should be considered is the choice of indicator species. As has already been stated, proving in the laboratory that one species can chemically influence the growth and development of another does not necessarily prove that such a relationship operates in the field. Further, the use of sensitive indicator species, such as lettuce or tomato, is more likely to produce a result indicating that a particular species has allelopathic properties if they are not normally found in association with that species in the field. This is because the indicator species will not have had an opportunity to evolve either resistance to, or tolerance of, the toxins. This was a point also noted by Newman and Rovira (1975) who suggested that test plants were often chosen for their convenience rather than any ecological relevance. Seed of _T. repens_ and _L. perenne_, although not normally associated with bracken, was used in this study because they are components of accepted re-seeding programmes. _F. rubra_, _A. tenuis_, _P. pratensis_ and _P. trivialis_ are all species found in association with bracken and _F. rubra_ is also used in re-seeding programmes. The choice of species such as lettuce would have been inappropriate since it is a species not likely to be planted into ground cleared of bracken. . It was however one of the species which Gliessman tested (Gliessman, 1976).

There appear to be several formidable hurdles to overcome in the experimental techniques before the allelopathic properties attributed to bracken may be confirmed or rejected. Although the laboratory and greenhouse studies carried out here were based upon the experimental procedures of Gliessman and Muller (1972, 1978), Stewart (1975) and Gliessman (1976), with some modifications, no data to support their findings was obtained.

The absence of any significant inhibitory effects from the material used in these experiments (which came from only one field area) does not rule out the possibility that some form of allelopathic interaction does exist between bracken and its associated species. However, with respect to the reseeding of cleared ground, it seems unlikely that the effects of any phytotoxins from bracken litter or from living or dead fronds which, if present, were not detected, will be a major factor influencing the establishment of sown-in species.

11. THE IMPROVEMENT OF HILL LAND CLEARED OF BRACKEN WITH ASULAM

11.1 *Introduction*

The application of asulam at 4.5 kg ai/ha is now the most usual method of controlling frond growth and this trial was designed to study the effect of various after-treatments in affecting the subsequent sward composition.

Asulam application may adversely affect species other than bracken. For example, it can cause an initial reduction in the cover of Agrostis spp and Holcus mollis (Williams, 1977). Holcus mollis can recolonise ground rapidly (Williams, 1976) and both species can contribute to appreciable increases in grass cover and yield following bracken clearance (Williams & Fraser, 1979; Davies et al, 1979) but where Holcus mollis is not present, recolonisation of litter covered ground may be slow (Williams, 1976) and there is the possibility that undesirable herbaceous weed species may establish from the large number of viable seeds sometimes known to be present in the soil of bracken dominated hill land (Section 6).

In the absence of fertiliser, Farnworth and Davies (1974) and Davies et al (1979) have shown yields of 2,000 to 3,000 kg/ha dry matter which were significant increases upon the yield from unimproved areas dominated by bracken. Although there is evidence that species such as Agrostis, Holcus and Poa respond to increased fertility by increased production under lowland conditions (Elliott et al, 1974), in the more acid uplands there are data suggesting that the application of lime or phosphate separately are of little value (Robertson & Nicholson, 1961; Munro, 1974; Anon, 1976; Williams & Fraser, 1979). It would appear that some farmers have foregone financial assistance with bracken spraying rather than incur the extra cost of applying ground mineral phosphate where this is a prerequisite for grant aid (Williams, 1980). The application of lime, in particular, poses several problems; high rates of lime are frequently required to raise the soil pH and the remoteness and difficulty of access to many hill land areas creates problems in getting the materials to the sites and then in applying them.

The alternative to improving the native sward by influencing the balance of the indigenous species is to replace them with others which will not only improve the nutritional value of the herbage but which will improve the distribution of productivity during the year, thus overcoming the marked reduction in the digestibility of the native species once their growth has ceased for the season.

The species most frequently used for re-seeding hill land are Lolium perenne and Trifolium repens. In order to establish these species, the application of lime and fertiliser is required in order to raise the soil pH, reduce the mat and reduce the binding of nutrients, in particular in those soils with a high aluminium and iron content. Munro and Davies (1973) and Munro et al (1973) have found that it is often the lack of available nitrogen which is the limiting factor in hill land improvement in the Welsh uplands. Once established, Trifolium repens can provide a continuous and inexpensive source of nitrogen for the sward.

The problem of applying lime and fertiliser has already been mentioned. Re-seeding poses additional problems. Cultivation to prepare a seed bed is often not possible because the ground is either inaccessible or unsuitable for machinery (too steep, soil too shallow or too stony). In these situations surface seeding is employed. The success or failure of this technique depends upon many factors including competition from the indigenous species, both those which are established and those present in the buried viable seed bank.

The effect of various methods of litter removal and seed bed preparation was examined to assess the development of the indigenous flora and to determine whether the establishment of the surface sown species could be assisted. The effect of frequency of cutting (to simulate grazing) upon sward composition and dry weight yield was also examined.

11.2 Materials and methods

A flat to gently sloping site with an easterly aspect at Gatehouse of Fleet, Kirkcudbrightshire (GR NX 578565) was chosen for examination in 1979. Plate 69.

Plate 69. Experimental site at Gatehouse in Spring 1980.

The site had a mean annual rainfall of about 1,400 mm and lay 72 m above sea level. A 2.5 cm humus layer overlay a mineral soil with organic matter 4 cm deep. Below this was a deep clay/mineral soil. The upper soil layers had a pH of 5.04. Prior to both spraying and fencing the site was open to grazing by both sheep and cattle and there were about twenty-five fronds/m^2 which were between 0.50 and 0.75 m tall.

Bracken fronds were sprayed with asulam in August 1979 at a rate of 4.5 kg ai/ha in 400 l of water using a hand held sprayer. In February

1980 a plot 13 m x 13 m was fenced off. Twenty-four plots each 1.25 m x 3 m were marked out in three rows each of eight plots. There was a 0.3 m discard between the plots in each row and a 0.75 m discard between the rows.

There were four litter treatments:

1) Control - litter left lying on soil surface.

2) Raked - bracken litter removed by raking.

3) Burnt - bracken litter removed by burning.

4) Dug - bracken litter and surface vegetation incorporated with the soil by digging: to simulate rotavating.

One set of litter treatments was left unfertilised whilst the other was limed, fertilised and seeded as indicated below:

2.25 kg/ha white clover seed (*Trifolium repens* cv Huia).
13.875 kg/ha creeping red fescue (*Festuca rubra* cv Boreal).
13.875 kg/ha perennial ryegrass (*Lolium perenne* cv Cropper).
Red fescue and perennial ryegrass were included to take account of the wide fertility range.

2 t/ha ground limestone ($CaCO_3$).
26.2 kg/ha phosphorus (P) applied as granular superphosphate which is 21% P_2O_5.

Each treatment was replicated three times and the treatments were arranged as a randomised block. A diagram of the plot design and the actual weights of seed and fertiliser applied per plot are given in Appendix 5:A.

In the text those plots which were fertilised, limed and seeded will be referred to as FLS plots; those which received no such after-treatment will be referred to as non-FLS plots.

At the beginning of April 1980 six plots were dug over to a depth of 30 cm and the bracken litter and surface vegetation of another six was burnt off. The bracken litter was raked away from the surface of a further six plots. One week later the sward composition of each plot was assessed by visually estimating the percentage cover of each of the species present within three 2,500 cm^2 quadrats per plot. In these assessments the category 'bare ground' included bare soil as well as uncolonised litter. During this week growth had occurred obviously on the burnt and dug treatments. Fertiliser, lime and seed was added to twelve of the plots (three plots per litter treatment) after this sward assessment. Plates 70-73 show the four litter treatments shortly after the trial commenced.

Subsequent sward assessments in 1980 were made in three 2,500 cm^2 quadrats on each plot and harvests involved cutting the herbage present in three such quadrats. The edges of the plots were deliberately avoided and once the samples had been taken the remainder of the plot was cut to a similar level and this material was removed from the plots and discarded.

After the first harvest in 1980, it was decided to incorporate into the experiment a more frequent cutting regime to part of each of the plots. A 0.5 m wide strip was marked out across each plot commencing 0.75 m from the bottom of the plot. Sward assessments on the strip were made in two 2,500 cm^2 quadrats. When the herbage on the strip was harvested, about 10 cm at either end was avoided and the strip was cut as one sample (equivalent to two 2,500 cm^2 quadrats). On all subsequent dates, when sward assessments and harvests were taken on the main plot, one quadrat was placed below the strip and two above it.

Each herbage sample was subsampled and sorted into the following components:

a) Dicotyledons.

b) Legumes (clover and other legumes (<u>Lotus uliginosus</u>) separately).

c) <u>Holcus mollis</u>.

Plate 70.

Control treatment in
May 1980.

Plate 71.

Raked treatment in
May 1980.

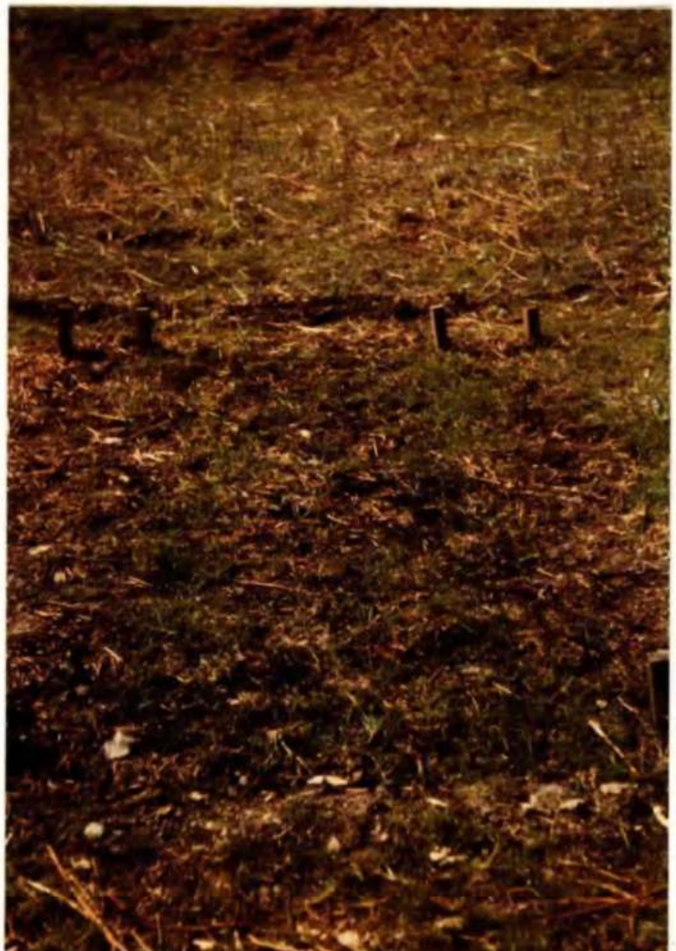


Plate 72.

Burnt treatment in
May 1980.

Plate 73.

Dug treatment in
May 1980.

d) Indigenous grasses other than Holcus mollis (mainly Agrostis tenuis and Poa spp, although Festuca rubra, which established as one clump on one particular unseeded plot, was included here).

e) Lolium perenne and Festuca rubra (only from the FLS plots).

Plant material which was obviously dead was discarded prior to subsampling and each category of each subsample was dried to constant weight prior to weighing.

Sward composition on the main plot was assessed in April, July and October in 1980 and in May, July and September in 1981, whilst the herbage was harvested in July and October in 1980 and in June, July and September in 1981. On the strip, sward composition was assessed in October in 1980 and in May, July and September in 1981, whilst the herbage was harvested in July (see below), August and September 1980 and in May, June, July, August and September in 1981.

When the total dry weight yield was calculated for the various herbage components from the several harvests during 1980, the data collected in July 1980 from the main plot contributed to both the main plot and the strip results (Figures 21 and 24 respectively).

The percentage cover data were transformed using the arcsin transformation for statistical analysis (Appendix 6). The results are expressed as the mean percentage cover per quadrat and the mean dry weight yield in kg/ha in the text.

11.3 Results

11.3.1 Percentage cover between April 1980 and October 1980 (Main plot)

Figures 19 & 20

1) Control treatment.

(a) Non-FLS plots

There was a significant decrease in the amount of uncolonised ground

(P≤0.01) mainly between April and July. The cover of dicotyledons and legumes had increased significantly by October (P≤0.05) with Ranunculus repens the most important species. The cover of Holcus mollis increased but not significantly whilst the cover of the other grasses, and hence the total cover of grasses, increased significantly during the year (P≤0.05 in both cases).

(b) FLS plots

Bare ground decreased mainly between April and July (P≤0.001). There was little change in the cover of the dicotyledons and legumes although Ranunculus repens increased its cover during the year. All the grasses increased their cover significantly, mainly during the first part of the season (P≤0.05 for Holcus mollis and Lolium perenne and Festuca rubra, P≤0.01 for the total grass cover and that of the other indigenous grasses).

2) Raked treatment.

(a) Non-FLS plots

The amount of bare ground decreased significantly (P≤0.01) during the year. Dicotyledons and legumes and Holcus mollis increased their cover slightly but not significantly and the changes in the remainder of the sward were minor. Ranunculus repens was the most important dicotyledon and although its cover increased during the year, the change was not statistically significant.

(b) FLS plots

By July there was no uncolonised ground on these plots, the decrease being significant at P≤0.01. The cover of dicotyledons and legumes and that of Lolium perenne and Festuca rubra increased significantly during the year (P≤0.01 in both cases). The cover of Ranunculus repens, the most widespread dicotyledon, increased significantly between April and October (P≤0.05). The grasses, in particular Holcus mollis, increased their cover but by the end of the season the changes were not large enough to be significant.

3) Burnt treatment.

(a) Non-FLS plots

The amount of bare ground decreased from 95% to 5% during the summer (significant at $P \leq 0.001$). In the April to July period the cover of Holcus mollis and that of the dicotyledons and legumes increased substantially and the amount of bare ground decreased accordingly. In July 30% of the sward was accounted for by dicotyledons and legumes, in particular Stellaria media and Polygonum spp. During the second part of the season the cover of the grasses continued to increase whilst that of the dicotyledons and legumes decreased slightly. Ranunculus repens was the only dicotyledon with more than 5% cover at the end of the season.

The increase in Holcus mollis between April and October was statistically significant ($P \leq 0.01$). The increase in dicotyledons and legumes (significant at $P \leq 0.05$) was largely due to a significant increase in Polygonum spp ($P \leq 0.01$). Grasses other than Holcus mollis contributed little to the sward during 1980.

(b) FLS plots

A significant decrease in uncolonised ground ($P \leq 0.001$) was again accompanied by significant increases in Holcus mollis ($P \leq 0.01$) and the dicotyledons and legumes ($P \leq 0.05$), these increases occurring mainly in the April to July period. The cover of Lolium perenne and Festuca rubra increased in the second part of the season but other species remained little changed during this time. There was, during the year, a significant increase in the total grass cover ($P \leq 0.01$) and in the cover of the sown grasses ($P \leq 0.05$). Polygonum spp and Ranunculus repens were the most important dicotyledons in July and whilst Ranunculus repens continued to increase during the July to October period, the only significant increase during the year for a dicotyledon was in the cover of Stellaria media ($P \leq 0.001$).

4) Dug treatment.

(a) Non-FLS plots

The significant decrease in uncolonised ground ($P \leq 0.001$) was accompanied by significant increases in all the other herbage categories. The dicotyledons and legumes increased substantially between April and July when they accounted for 60% of the sward. Scrophularia nodosa, Galeopsis tetrahit, Stellaria media and Polygonum spp each accounted for more than 5% of the ground flora. Holcus mollis increased slightly during this period. Between July and October the cover of the dicotyledons and legumes decreased although Polygonum spp were still important and Digitalis purpurea appeared in quantity. Whilst the cover of Holcus mollis continued to increase, other grasses were unable to establish.
During the year the increases in the cover of grasses other than Holcus mollis was significant at $P \leq 0.01$ and that in the dicotyledons and legumes, the total grass cover and the cover of Holcus mollis at $P \leq 0.05$. The cover of Polygonum spp and Stellaria media increased significantly ($P \leq 0.01$ and $P \leq 0.001$ respectively) between April and October.

(b) FLS plots

The dicotyledons and legumes increased their cover greatly between April and July when they accounted for 50% of the sward, Stellaria media and Polygonum spp being the most important species. Some Holcus mollis, Lolium perenne and Festuca rubra were able to establish during this time. By October, the cover of dicotyledons and legumes had decreased, whilst that of Holcus mollis had remained similar and that of Lolium perenne and Festuca rubra had increased. The decrease in bare ground during the year was significant at $P \leq 0.001$ whilst the increases in Holcus mollis, Lolium perenne and Festuca rubra, and total grass cover were also significant (at $P \leq 0.05$ for Holcus mollis and $P \leq 0.001$ for the other grass categories).

Figure 19. Composition of sward at Gatehouse during 1980. (Main plot).

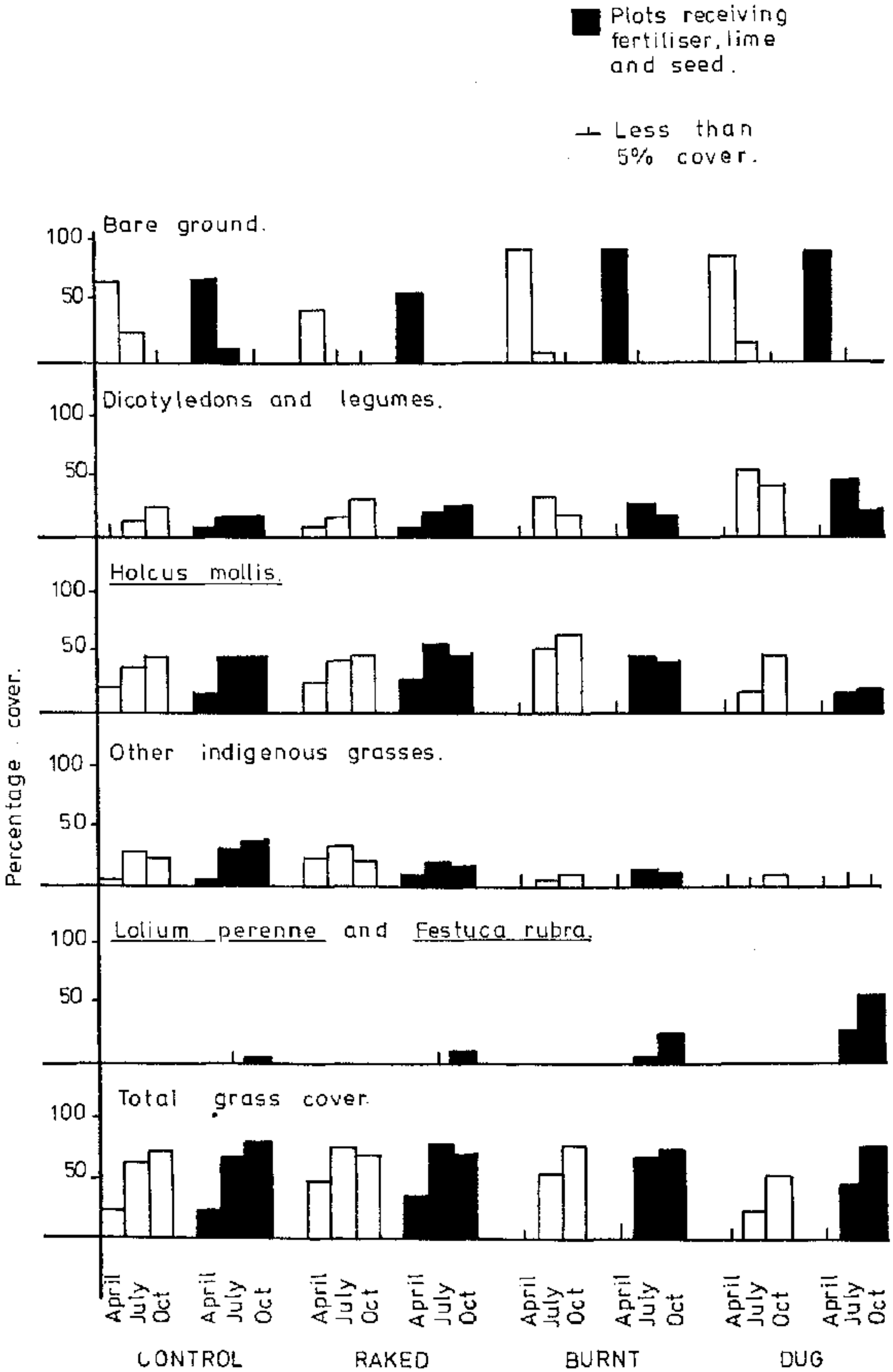
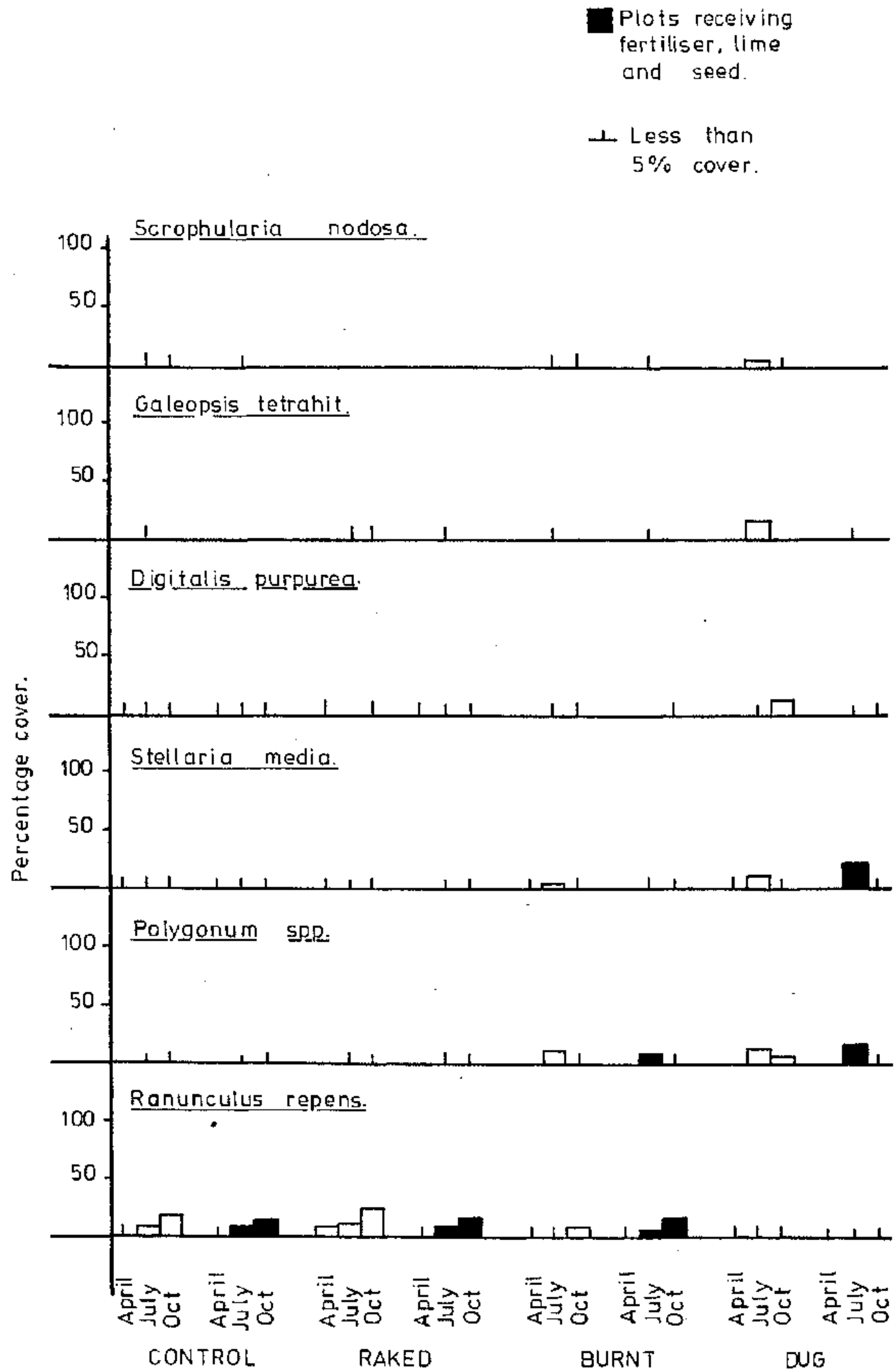


Figure 20. Percentage cover of important dicotyledons at Gatehouse during 1980. (Main plot).



Grasses other than Holcus mollis were unable to establish. Although the contribution made by the dicotyledons and legumes declined between July and October, the increase during the season was significant ($P \leq 0.001$) and the increases in Stellaria media and Polygonum spp were also significant (at $P \leq 0.01$ and $P \leq 0.05$ respectively).

Analysis of the swards in October 1980 showed few differences between the swards of the eight treatments. There were no significant differences in the amount of bare ground, that occupied by dicotyledons and legumes, that occupied by Holcus mollis or that by the grasses as a whole on any of the eight treatments. Lolium perenne and Festuca rubra occurred only on the FLS plots where they had been sown. The cover of these species on the dug treatment significantly exceeded ($P \leq 0.01$) that on the other three litter treatments and the cover on the control treatment was also significantly less ($P \leq 0.01$) than that on the burnt treatment. There were also significant differences in the proportion of ground occupied by grasses other than Holcus mollis. Although there was no difference between the plots which had received lime, fertiliser and seed and those which had not, significantly more of these species were present on the control treatment than on the burnt or dug treatments ($P \leq 0.05$). The raked treatment had a similar cover of these species to that of the control treatment. Although there were no significant differences between the eight treatments in the total cover of dicotyledons, there were significant differences in the cover of Ranunculus repens, Polygonum spp and Stellaria media. There were no differences for any of these species between the plots which had received lime, fertiliser and seed and those which had not, but both Polygonum spp and Stellaria media occupied a significantly greater area on the dug treatment than on the other three treatments ($P \leq 0.01$ for both species). Ranunculus repens was found in significantly smaller amounts on the dug treatment than on the other three treatments whilst the burnt treatment also had a significantly smaller cover of this species than the raked treatment ($P \leq 0.01$ in each case).

11.3.2 Dry weight yield for 1980 (Main plot)

Figure 21

a) Comparison of non-FLS and FLS plots

No significant differences were found between the non-FLS and FLS plots for any of the four litter treatments with respect to the total yield, yield of dicotyledons and legumes, yield of Holcus mollis or yield of other indigenous grasses. Lolium perenne and Festuca rubra occurred only on the FLS plots where they had been sown. Although an overall analysis showed the FLS plots to have a significantly greater total grass yield than the non-FLS plots ($P \leq 0.05$), the yield from the four individual litter treatments was not significantly different between the non-FLS and FLS plots.

b) Comparison of litter treatments

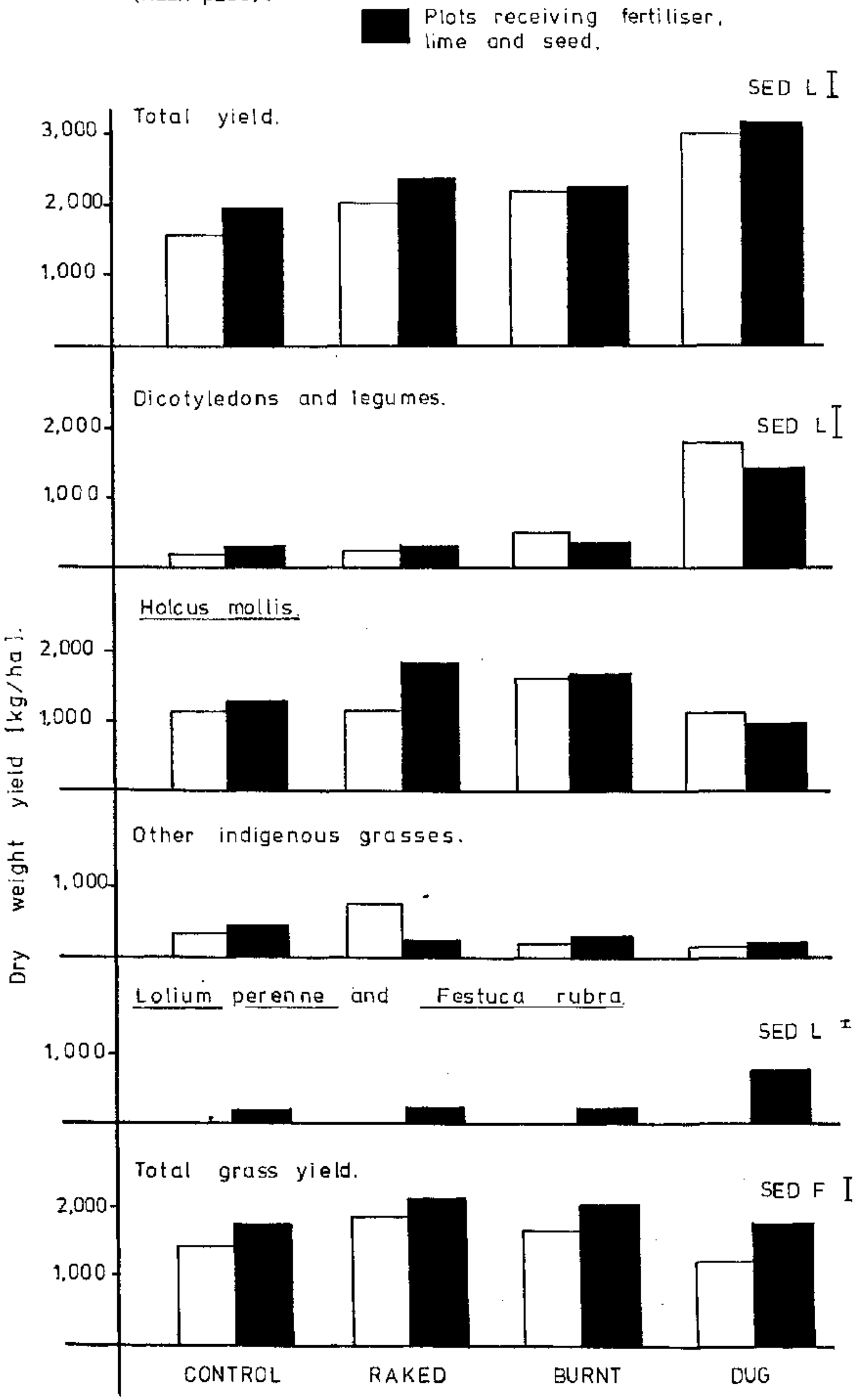
On the control and raked treatments the dicotyledons and legumes and grasses other than Holcus mollis made only small contributions to the yield, as did Lolium perenne and Festuca rubra on the FLS plots. Holcus mollis made the greatest contribution to both treatments. Although there was not a significant difference in the total grass yield on the control and raked treatments, when the contribution made by the dicotyledons and legumes was included, there was a significantly greater total yield from the raked treatment relative to the control ($P \leq 0.001$).

The only significant difference between the control and the burnt treatments was in the total yield figures where the burnt treatment out-yielded the control ($P \leq 0.001$).

There were no differences in the yield of the various components on the raked and the burnt treatments or in the total yield.

On the control and dug treatments the yield of Holcus mollis and that of the other indigenous grasses was similar but the yield of Lolium

Figure 21. Dry weight yield of herbage components at Gatehouse for 1980. (Main plot).



perenne and Festuca rubra was significantly greater on the FLS dug treatment than on the FLS control treatment ($P \leq 0.001$). Despite this difference, the total grass yield was similar for both litter treatments on the non-FLS and FLS plots. Because the yield of dicotyledons and legumes was significantly greater on the dug treatment than on the control treatment ($P \leq 0.001$), the total yield on the dug treatment was significantly greater than that on the control treatment ($P \leq 0.001$).

The raked and burnt treatments differed from the dug treatment in a similar manner. The dug treatment yielded significantly more dicotyledons and legumes than the raked and burnt treatments ($P \leq 0.001$) and the FLS dug treatment also significantly outyielded the FLS raked and burnt treatments with respect to Lolium perenne and Festuca rubra ($P \leq 0.001$). Similar yields of Holcus mollis and other indigenous grasses were recovered from all three litter treatments and the total grass yields were also similar. The total dry weight yields of the three litter treatments were however significantly different ($P \leq 0.001$). The greater total yield from the non-FLS dug treatment relative to the non-FLS raked and burnt treatments was due to the significantly greater yield of dicotyledons from the dug treatment ($P \leq 0.001$) whilst on the FLS dug treatment the significantly greater total yield relative to the FLS raked and burnt treatments was due to the significantly greater contributions made by the dicotyledons and legumes ($P \leq 0.001$) and by the presence of Lolium perenne and Festuca rubra on the FLS dug treatment.

11.3.3 Percentage cover in October 1980 (Strip.)

Figures 22 &23

The composition of the sward on the strip was assessed only once in 1980 and that was in October.

A comparison of the swards showed only a few significant differences between the eight treatments. The cover of Lolium perenne and Festuca rubra was significantly greater on the dug treatments than on the control

Figure 22. Composition of sward at Gatehouse in October 1980. (Strip).

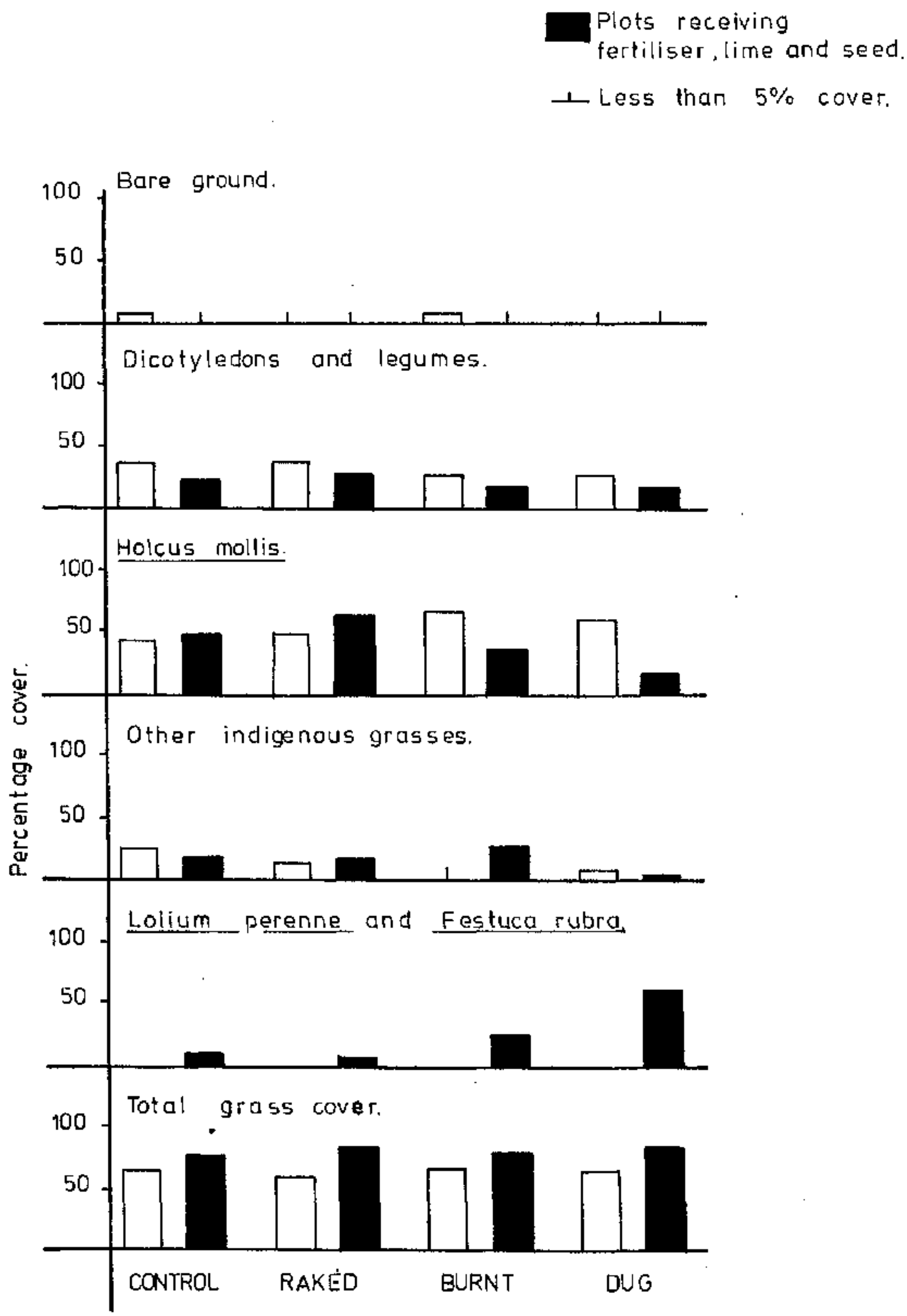
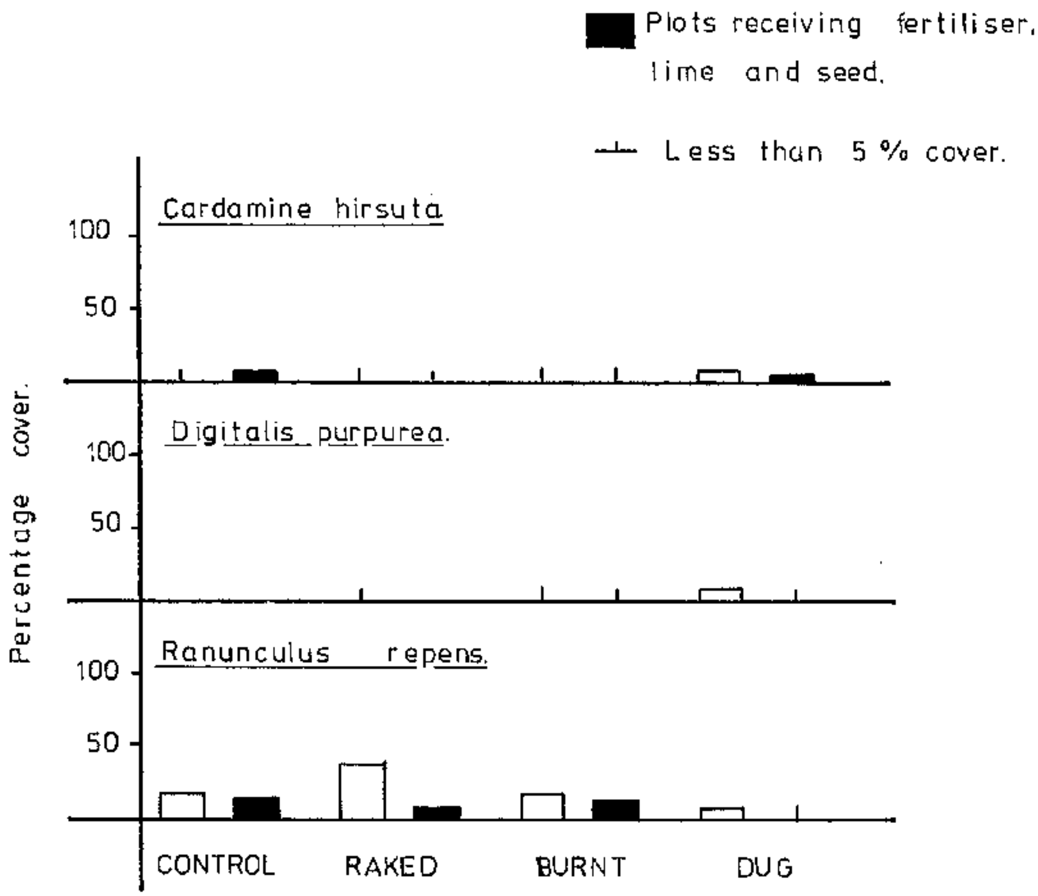


Figure 23. Percentage cover of important dicotyledons at Gatehouse in October 1980. (Strip).



and raked treatments ($P \leq 0.01$). There was no significant difference between the litter treatments with respect to the total cover of grasses but the FLS plots had a significantly greater cover than the non-FLS plots ($P \leq 0.01$). In isolation, there were no significant differences between the FLS and non-FLS plots or between the four litter treatments with respect to the cover of grasses other than Holcus mollis. However, a significant interaction between the two factors was recorded ($P \leq 0.05$) which was largely the result of a significantly smaller cover of these grasses on the non-FLS burnt treatment than on the FLS burnt treatment ($P \leq 0.01$). There were no significant differences in the amount of bare ground, in the cover of dicotyledons and legumes or in the cover of Holcus mollis between the eight treatments.

Of the dicotyledons, only three species were found with more than 5% cover in October. These were Cardamine hirsuta, Digitalis purpurea and Ranunculus repens. The cover of Digitalis purpurea did not differ significantly between the FLS and non-FLS plots but there was significantly more of this species on the dug treatment relative to the control and raked treatments ($P \leq 0.05$). No significant differences were found in the distribution of the other two species.

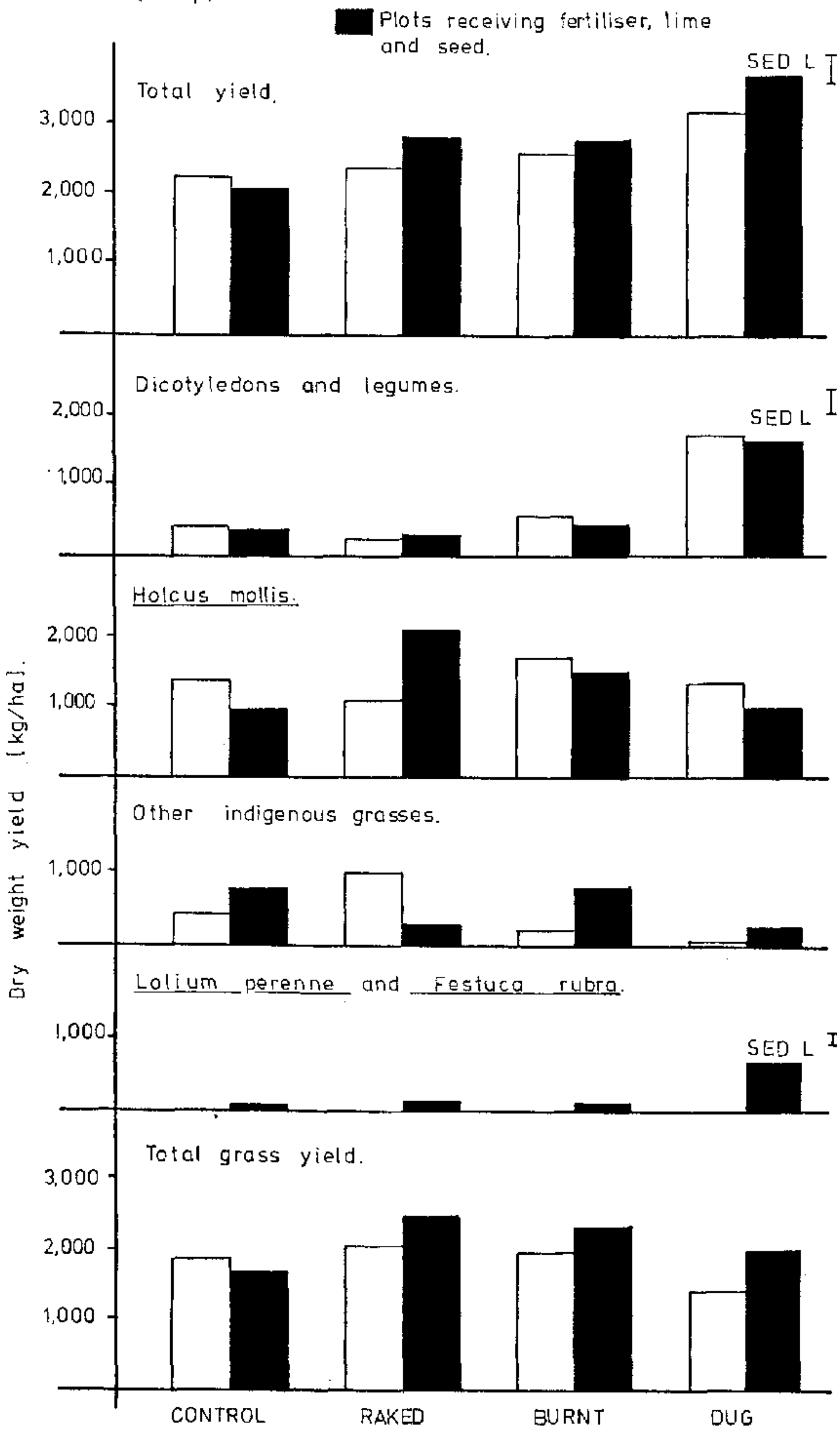
The sward composition of the individual treatments did not differ significantly between the main plot and the strip in October 1980, with the exception of Polygonum spp. These species were not recorded on the strip but were present in significant quantities on the non-FLS burnt treatment ($P \leq 0.01$) and on the FLS dug and non-FLS dug treatment ($P \leq 0.05$ and $P \leq 0.01$ respectively).

11.3.4 Dry weight yield for 1980 (Strip.)

Figure 24

No significant differences were found between the non-FLS and FLS plots for any of the four litter treatments with respect to the yield of any of the herbage components. Lolium perenne and Festuca rubra occurred only on the FLS plots where they had been sown.

Figure 24. Dry weight yield of herbage components at Gatehouse for 1980. (Strip).



The yield of dicotyledons and legumes and that of Lolium perenne and Festuca rubra was significantly higher on the dug treatment relative to the other three litter treatments ($P \leq 0.001$ in both cases). The total dry weight yield from the dug treatment was also significantly greater than from the other three treatments whilst the burnt treatment also significantly outyielded the control treatment ($P \leq 0.001$ in both cases). There were no significant differences in the yield of Holcus mollis, other indigenous grasses or in the total grass yield between the four litter treatments.

The yields of the various categories of herbage were almost always higher on the strip than on the main plot for all the treatments but none of the differences were statistically significant.

11.3.5 Percentage cover between May 1981 and September 1981 (Main plot)

Figures 25 & 26

a) Control and Raked treatments

There was little difference between the two treatments during 1981.

On both the non-FLS and FLS plots, the total cover of grasses showed a decrease between April and July followed by a partial recovery between July and September. There was a parallel increase in the cover of the dicotyledons and legumes followed by a slight decline as the grasses recovered. In July, the dicotyledons and legumes, almost exclusively Ranunculus repens, accounted for about 50% of the sward.

On the FLS plots the cover of Lolium perenne and Festuca rubra increased during the year whilst that of Holcus mollis declined somewhat on both the non-FLS and the FLS plots. The cover of the other indigenous grasses changed little on the non-FLS plots but fell substantially on the FLS plots.

With the exception of the decrease in the cover of grasses other than Holcus mollis on the FLS control treatment which was significant at $P \leq 0.05$, none of the changes which occurred between May and September in the swards of the various treatments (control FLS and non-FLS, raked FLS and non-FLS) were statistically significant. The overall composition of the control and raked FLS treatments was similar as was that of the control and raked non-FLS treatments.

b) Burnt treatment

The dicotyledons and legumes and the total grass cover exhibited a similar pattern of change during the season to that noted on the control and raked treatments and again the cover of Lolium perenne and Festuca rubra increased during the year.

The cover of grasses other than Holcus mollis changed little during the season and was higher on the FLS plots. Holcus mollis, which was present in greater quantity on the non-FLS plots, declined during the season, slightly on the non-FLS plots and significantly ($P \leq 0.01$) on the FLS plots.

With the exception of the significant decrease in Holcus mollis on the FLS plots, none of the other observed changes between May and September were statistically significant.

c) Dug treatment

On the non-FLS plots, the cover of dicotyledons and legumes and that of the grasses other than Holcus mollis increased whilst that of Holcus mollis and the total grass cover declined during 1981. On the FLS plots there was little change in any of the components between May and September. About 60% of the sward was occupied by Lolium perenne and Festuca rubra. There was on the FLS plots a smaller cover of Holcus mollis, other indigenous grasses and possibly also a smaller cover of dicotyledons and legumes, than on the non-FLS plots.

Apart from a significant increase during the season in the cover of Ranunculus repens ($P \leq 0.05$), none of the other changes during the year were statistically significant.

Figure 25. Composition of sward at Gatehouse during 1981. (Main plot).

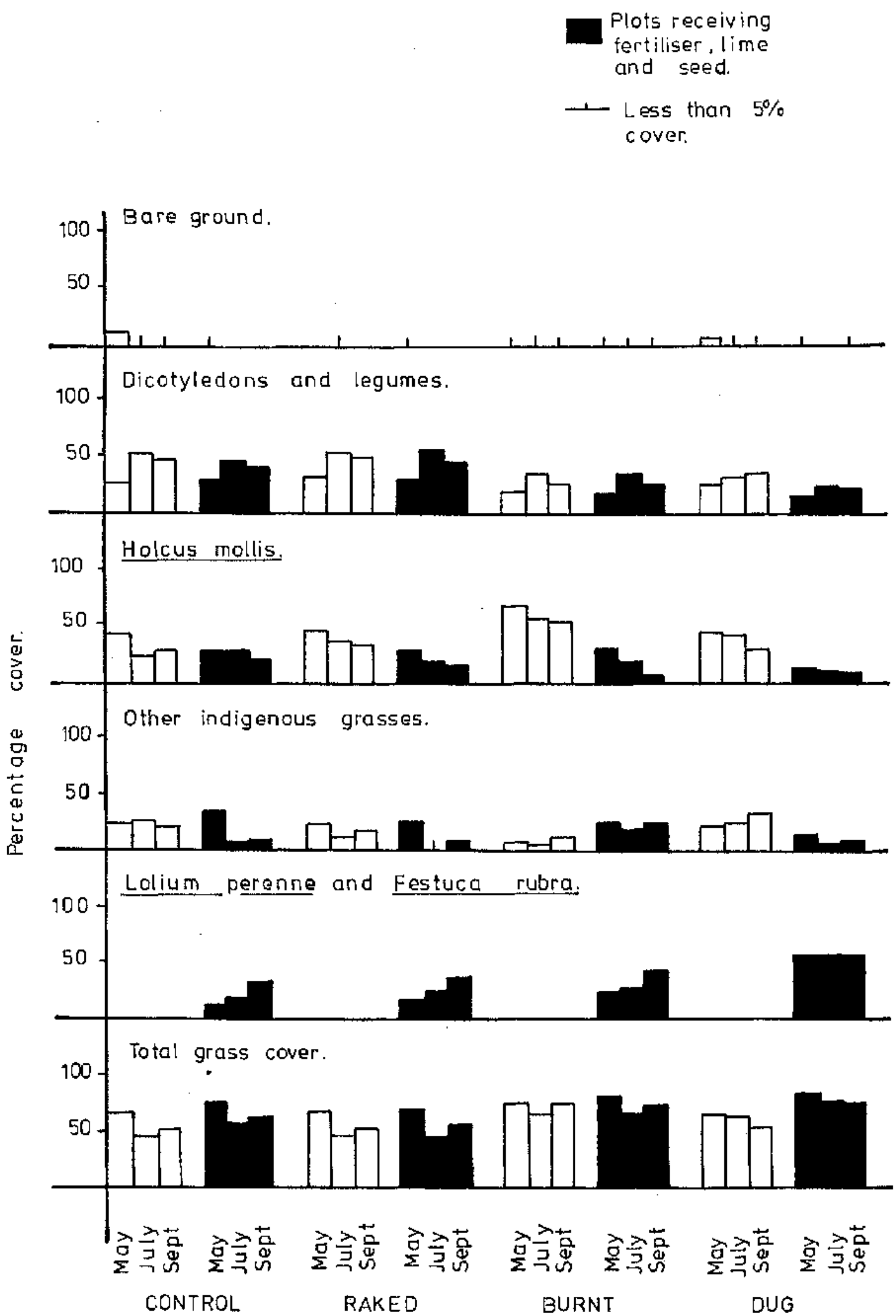
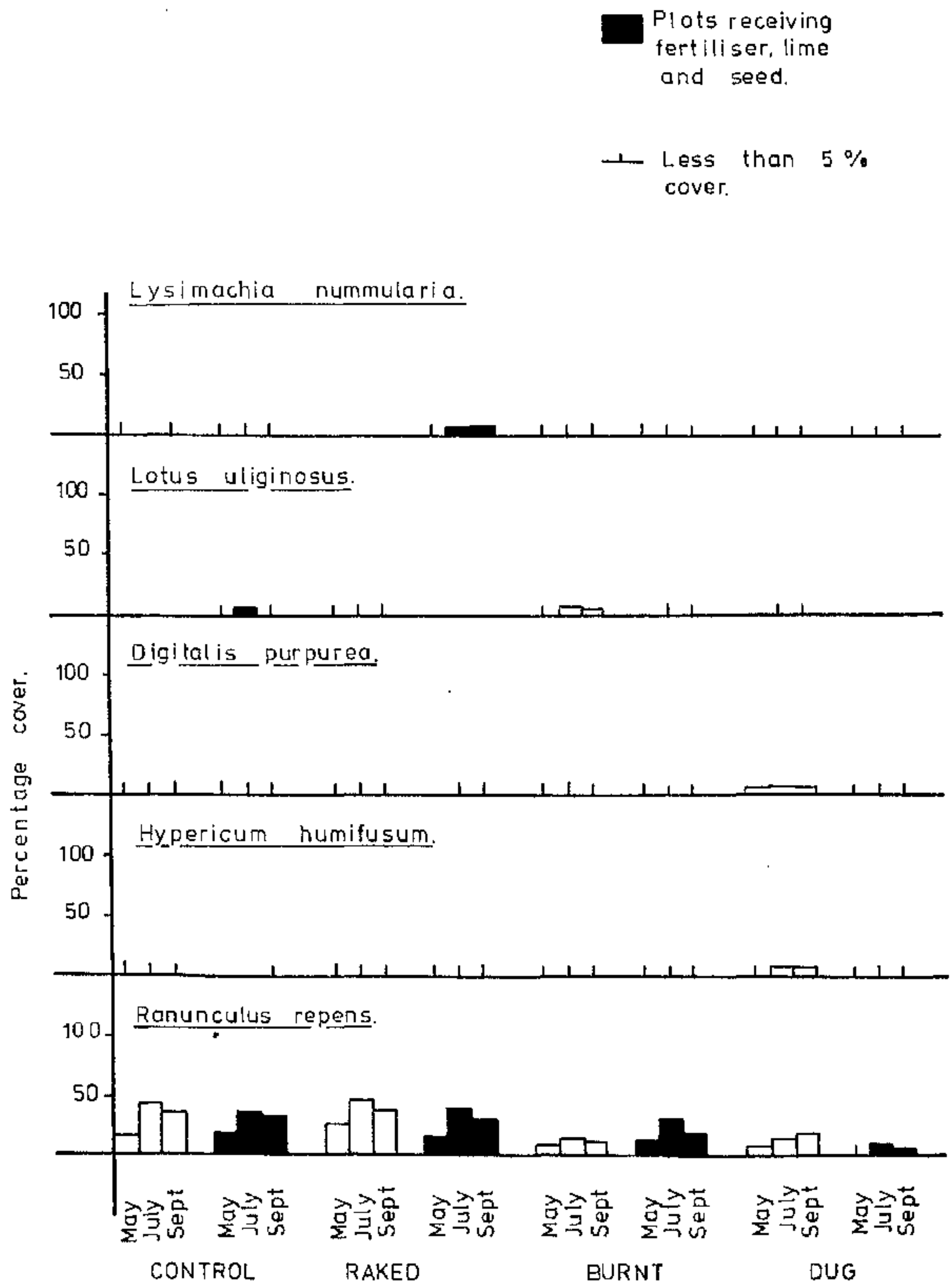


Figure 26. Percentage cover of important dicotyledons at Gatehouse during 1981. (Main plot).



A comparison of the swards in September 1981 (Plates 74 to 82) showed few differences between the eight treatments. Lolium perenne and Festuca rubra were recorded only on the FLS plots where they had been sown but by the end of the season the cover of these species on the four litter treatments was similar. The amount of ground which was occupied by dicotyledons and legumes, by all the grasses, by grasses other than Holcus mollis or which was uncolonised was not significantly different for any of the eight treatments at the end of the season. An overall analysis showed that the cover of Holcus mollis was not significantly different on the four litter treatments but that the FLS plots had a significantly smaller proportion of this species than the corresponding non-FLS plots ($P \leq 0.01$). Of the individual litter treatments the only significant differences were between the non-FLS and FLS burnt plots ($P \leq 0.05$) and between the non-FLS and FLS dug plots ($P \leq 0.01$).

Five dicotyledons were found with more than a 5% ground cover during 1981.

The distribution of both Lysimachia nummularia and Lotus uliginosus was localised and not related to the treatments which the various treatments received. The first of these species occurred in quantity only in plots 17 and 18 (see Appendix 5:A for plot layout) whilst the second species was found only in plots 1, 2 and 3 in substantial amounts. In both cases the plots were contiguous. Since Figure 26 does not represent the true situation for these two species, Table 49 has been included; it shows that where these species occurred they made important contributions to the plots. Further comment will be made with respect to Lotus uliginosus.

Digitalis purpurea showed a significantly greater cover on the non-FLS plots than on the corresponding FLS plots ($P \leq 0.05$) and although there was no significant difference between the four litter treatments this species was only found in quantity on the non-FLS dug treatment.

Plate 74. Experimental site at Gatehouse in autumn 1981.

Plate 75. Control treatment in autumn 1981.

Plate 76. Control treatment (fertilised, limed and seeded) in autumn 1981

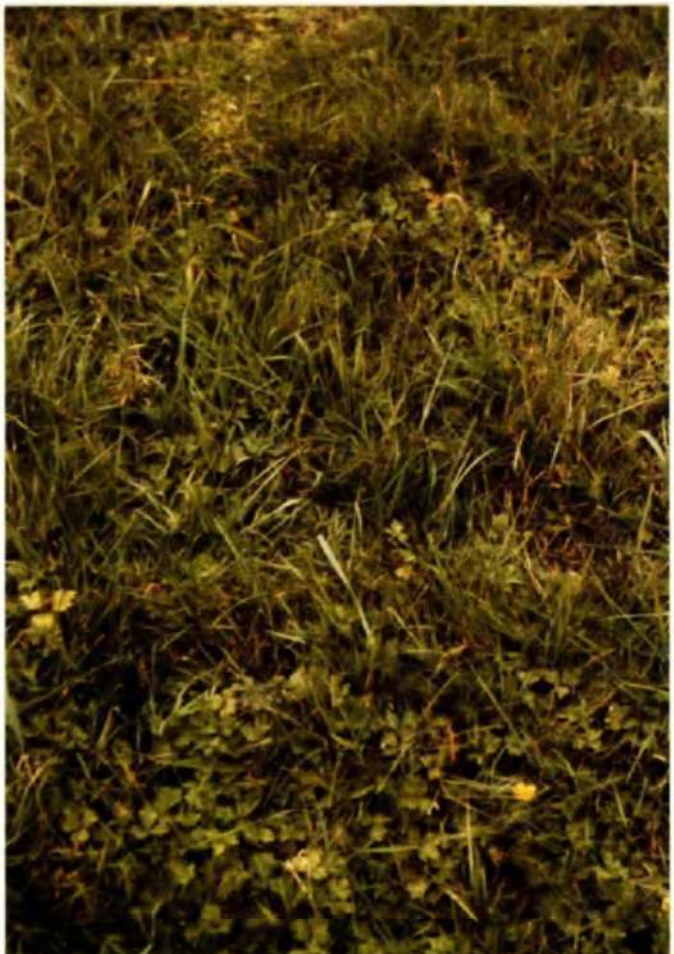


Plate 77

Raked treatment in autumn 1981

Plate 78

Raked treatment (fertilised, limed and seeded) in autumn 1981

Plate 79.

Burnt treatment in autumn 1981.

Plate 80.

Burnt treatment (fertilised, limed and seeded) in autumn 1981.

Plate 81. Dug treatment in autumn 1981.

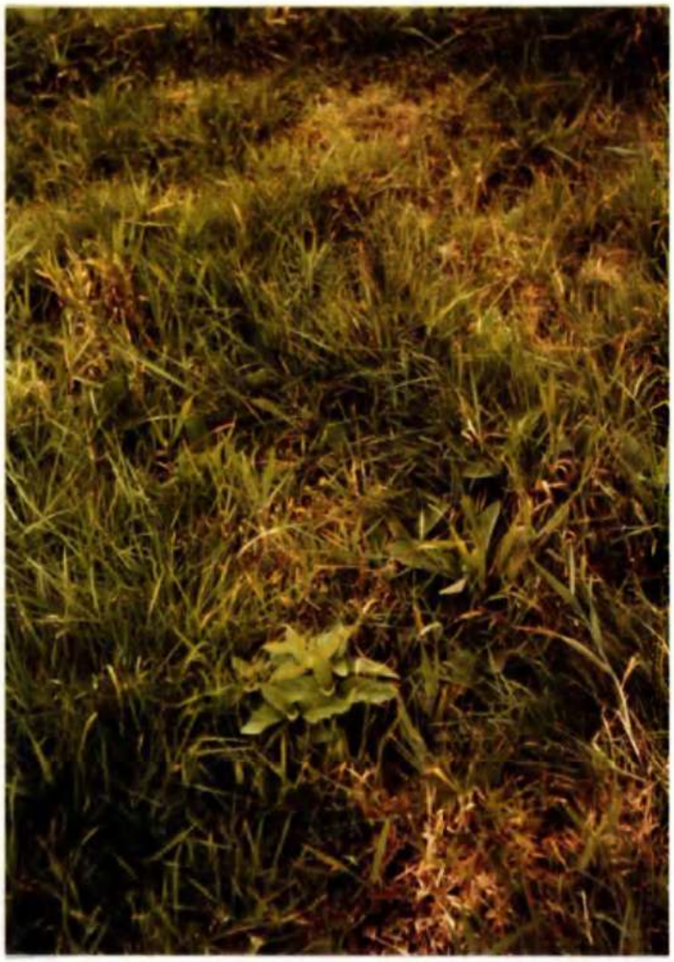


Plate 82. Dug treatment (fertilised, limed and seeded) in autumn 1981.

Table 49. Percentage cover of Lysimachia nummularia and Lotus uliginosus at Gatehouse in 1981 on specific replicates (Main plot).

Lysimachia nummularia

Plot number	Treatment	% cover		
		May	July	September
17	Raked FLS	11.33	18.33	18.33
18	Burnt	5.00	12.33	6.67

Lotus uliginosus

Plot number	Treatment	% cover		
		May	July	September
1	Raked	5.67	14.67	9.33
2	Burnt	7.67	28.33	15.33
3	Control FLS	5.33	15.00	12.00

Hypericum humifusum was found to contribute significantly more to the dug treatment than to the other three litter treatments ($P \leq 0.01$) with no difference noted between the non-FLS and FLS plots.

Ranunculus repens was the only dicotyledon found with a significant cover on all eight treatments. During 1981 this species tended to show an increase in cover between May and July and a slight decline thereafter, generating the pattern noted for the dicotyledons as a whole. The increase between May and September was significant on the FLS dug treatment ($P \leq 0.05$) and in September, although there was no difference between the non-FLS and FLS plots, there was significantly less of this species on the burnt and dug treatments than on the control and raked treatments ($P \leq 0.05$).

11.3.6 Dry weight yield for 1981 (Main plot).

Figure 27

a) Comparison of non-FLS and FLS plots

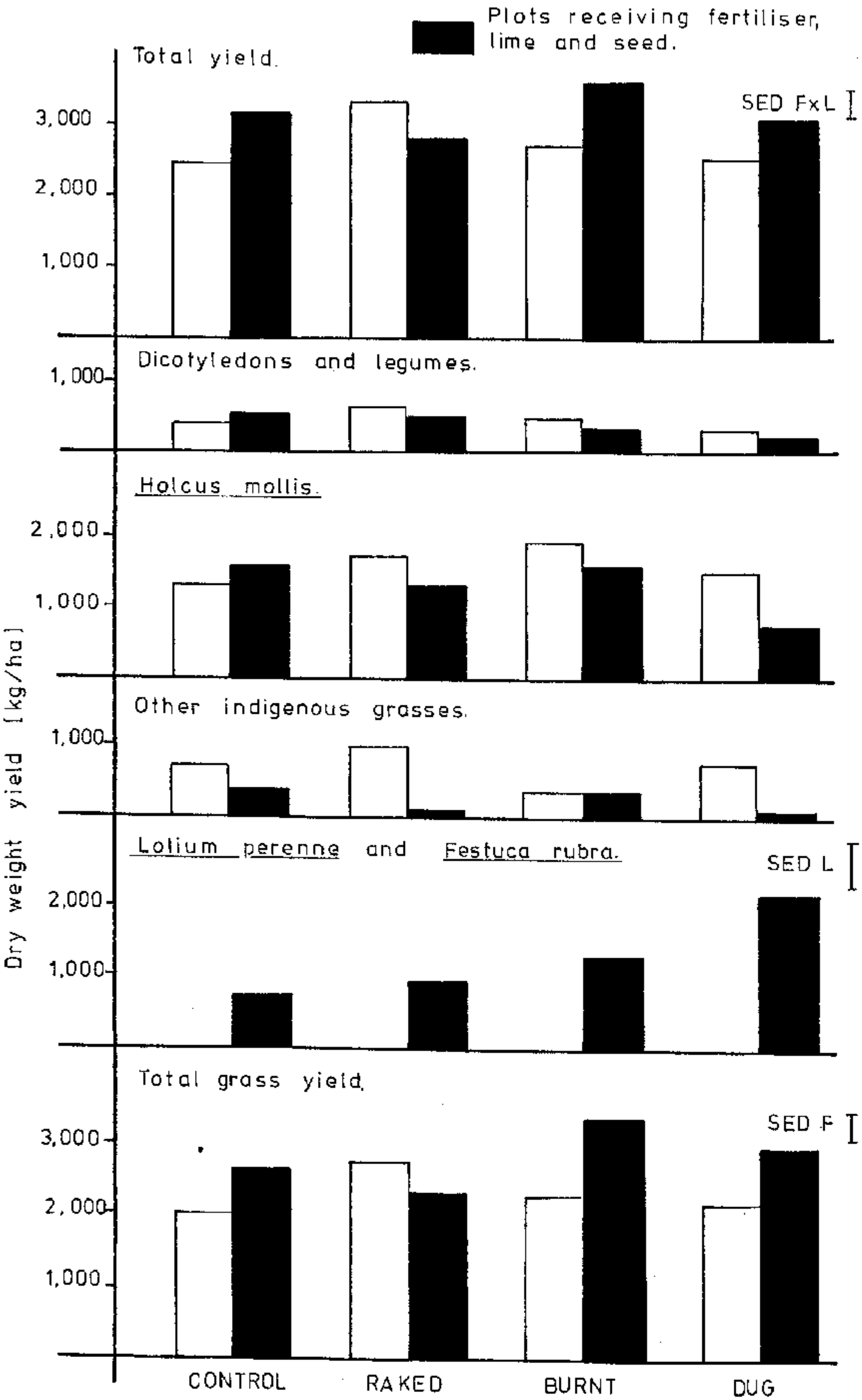
No significant differences were found between the non-FLS and FLS plots for the four litter treatments with respect to the dry weight yield of dicotyledons and legumes, Holcus mollis and other indigenous grasses. Lolium perenne and Festuca rubra were only recovered from the FLS plots where they had been sown. There were overall significant differences between the FLS and non-FLS plots with respect to the total grass yield ($P \leq 0.01$) and the total dry weight yield ($P \leq 0.001$). In both cases the pattern was one of a higher yield from the control, burnt and dug FLS treatments than from the corresponding non-FLS treatments whilst the FLS raked treatment had a lower yield than the non-FLS raked treatment; for the individual litter treatments the pattern was significant for all but the total grass yield for the control and raked treatments.

b) Comparison of litter treatments

There were no significant differences between the four litter treatments with respect to the yield of dicotyledons and legumes, Holcus mollis, other indigenous grasses or total grass yield. The yield of Lolium perenne and Festuca rubra was significantly higher from the dug treatment than from the other three treatments ($P \leq 0.05$) and the yield from the burnt treatment was also significantly higher than that from the control treatment ($P \leq 0.05$).

Although there was no significant difference between the litter treatments with respect to the total grass yield, when the contribution made by the dicotyledons and legumes was included, there were significant differences in the total dry weight yield between the four litter treatments ($P \leq 0.05$) and also a significant interaction ($P \leq 0.001$) between the litter treatments and the application of lime, fertiliser and seed. Thus, with respect to the total dry weight yield on the FLS plots, the burnt treatment significantly outyielded the other three, whilst on the non-FLS plots, the raked treatment significantly outyielded the other three litter treatments.

Figure 27. Dry weight yield of herbage components at Gatehouse for 1981. (Main plot).



The cover and yield of the legumes (chiefly Trifolium repens and Lotus uliginosus) was determined separately from the other dicotyledons. Lotus uliginosus did not play a significant role in the overall yield from the various treatments, but as was previously noted, this species played an important role in a limited number of individual plots. Table 50 shows the yield in 1981 from the three plots in which this species contributed significantly to the sward (9-15% in September). On these plots Lotus uliginosus contributed between 3 and 8% of the total dry weight yield.

Table 50. Dry weight yield of Lotus uliginosus from specific replicates in 1981 (Main plot).

Plot number	Treatment	Dry wt. yield (kg/ha)	% contribution to yield of plot
1	Raked	143.2	3.84
2	Burnt	298.0	8.02
3	Control FLS	183.2	5.54

11.3.7 Percentage cover between May 1981 and September 1981 (Strip). Figure 28 & 29

Analysis suggested that apart from the cover of grasses other than Holcus mollis, the changes which occurred in the composition of the sward between May and September were not statistically significant. The cover of grasses other than Holcus mollis fell significantly on the control, raked and dug FLS treatments ($P \leq 0.05$ in each case).

A comparison of the swards in September 1981 found several significant differences between the treatments.

The amount of bare ground ranged from 0 to 7% on the FLS plots and from 0 to 17% on the non-FLS plots. The FLS control treatment had significantly more bare ground than the corresponding non-FLS treatment ($P \leq 0.05$), whilst the control and dug non-FLS treatments had significantly more uncolonised ground than the raked and burnt non-FLS treatments ($P \leq 0.05$).

There was no significant difference between the non-FLS and FLS plots with respect to the cover of dicotyledons and legumes but the dug treatment had a significantly smaller cover than the control and raked treatments ($P \leq 0.05$). Lolium perenne and Festuca rubra occurred only on the FLS plots where they had been sown. The dug treatment had a significantly greater cover of these species than the other three litter treatments ($P \leq 0.05$).

The cover of Holcus mollis was not greatly different on the four litter treatments but was significantly lower on the FLS burnt treatment than on the non-FLS burnt treatment ($P \leq 0.05$). On the dug treatment the cover of this species was significantly lower in May ($P \leq 0.01$) and in September ($P \leq 0.05$) on the FLS plots relative to the non-FLS plots.

There were no significant differences in the cover of the other indigenous grasses on the four litter treatments but there were significant differences between the non-FLS and FLS plots ($P \leq 0.05$) and there was also a significant interaction between the two factors ($P \leq 0.001$). A greater cover of these species was recorded on the non-FLS control treatment and a significantly greater cover on the non-FLS raked and dug treatments than on the corresponding FLS treatments, whilst the cover on the non-FLS burnt treatment was significantly lower than on the FLS burnt treatment.

The total cover of grasses was similar on the four litter treatments but was significantly greater on the FLS plots than on the non-FLS plots ($P \leq 0.05$).

With respect to the individual dicotyledons, only Ranunculus repens, Lysimachia nummularia and Lotus uliginosus were found with more than a 5% ground cover during 1981. In September there were no significant differences in the cover of any of the species between the eight treatments. However, as noted on the main plot, Lysimachia nummularia and Lotus uliginosus were distributed locally and, as Table 51 shows, these species were important constituents of the plots where they occurred. Lysimachia nummularia was restricted to four contiguous

Figure 28. Composition of sward at Gatehouse during 1981. (Strip).

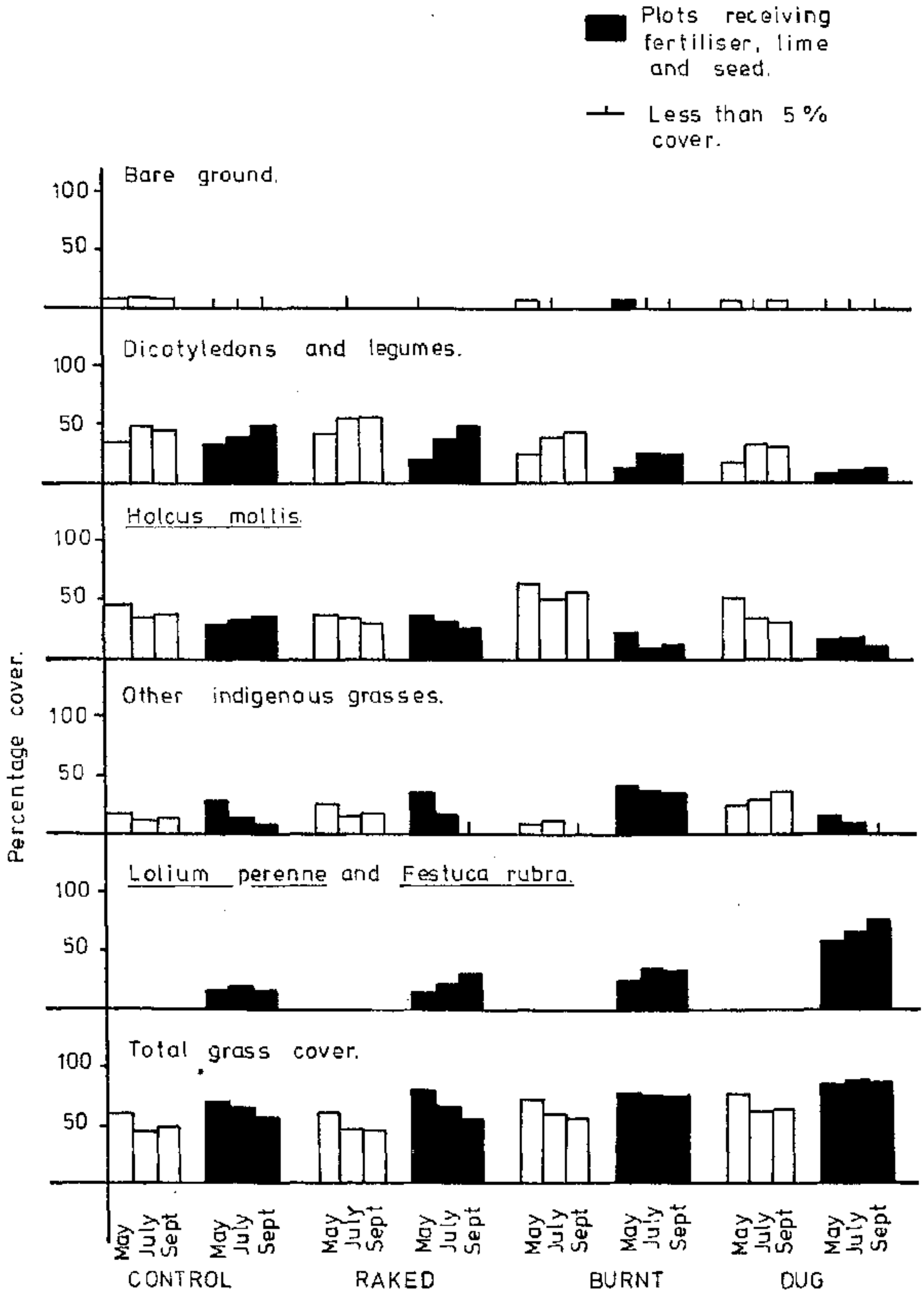


Figure 29. Percentage cover of important dicotyledons at Gatehouse during 1981. (Strip).

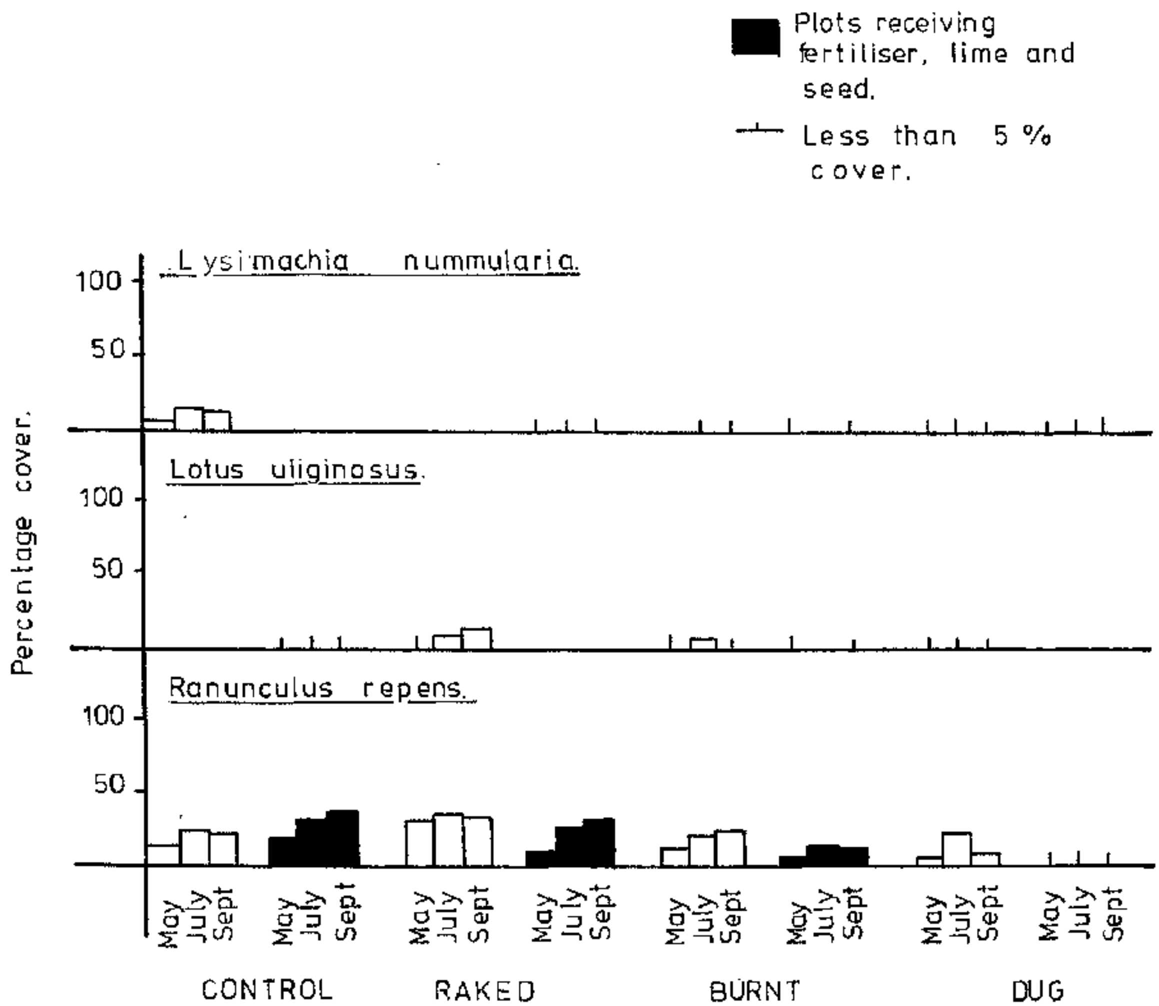


Table 51. Percentage cover of Lysimachia nummularia and Lotus uliginosus at Gatehouse in 1981 on specific replicates (Strip).

Lysimachia nummularia

Plot number	Treatment	% cover May	% cover July	% cover September
10	Control	24.00	40.00	30.00
17	Raked FLS	2.50	7.50	8.50
18	Burnt	0.00	1.00	5.00
19	Control	3.00	7.50	10.50

Lotus uliginosus

Plot number	Treatment	% cover May	% cover July	% cover September
1	Raked	8.50	30.00	39.50
2	Burnt	6.50	19.00	13.50
3	Control FLS	2.50	4.00	10.00
12	Dug	2.00	7.00	12.50

plots (nos. 10, 17, 18 and 19) where it accounted for between 1 and 40% of the swards in 1981, whilst Lotus uliginosus, restricted to three contiguous and one nearby plot (nos. 1, 2, 3 and 12) accounted for between 2 and 40% of these swards during the year.

The only significant differences between the swards of corresponding treatments on the main plot and the strip were seen on the FLS dug treatment. The cover of Lolium perenne and Festuca rubra and of all the grasses was significantly higher on the strip than on the main plot ($P \leq 0.05$ in both cases), whilst Holcus mollis was equally well represented on both the strip and the main plot. Other indigenous grasses, dicotyledons and legumes and Ranunculus repens had significantly greater cover values on the main plot than on the strip ($P \leq 0.01$, $P \leq 0.01$ and $P \leq 0.05$ respectively). The cover of all these components was very similar on the strip and on the main plot for the non-FLS dug treatment. None of the other litter treatments produced significantly different results on the main plot compared with the strip for any of the herbage components and no pattern of differences was evident.

11.3.8 Dry weight yield for 1981 (Strip).

Figure 30

There were no significant differences in the yield of *Lolium perenne* and *Festuca rubra*, in the total grass yield or in the total dry weight yield between the non-FLS and FLS plots or between the four litter treatments. Whilst there were no differences between the non-FLS and FLS plots in the yield of dicotyledons and legumes, the dug treatment significantly outyielded the raked and control treatments ($P \leq 0.05$) whilst the burnt treatment also significantly outyielded the control treatment ($P \leq 0.05$). The yield of *Holcus mollis* was not significantly different on the four litter treatments but the burnt and dug FLS treatments had significantly lower yields than the corresponding non-FLS treatments ($P \leq 0.05$ in both cases). Other indigenous grasses were harvested in greater quantity from the raked FLS treatment than from the corresponding non-FLS treatment ($P \leq 0.05$). The litter treatments alone did not produce significantly different yields of grasses other than *Holcus mollis* but there was an interaction between the litter and fertiliser treatments such that on the FLS plots the burnt treatment significantly outyielded the other three litter treatments ($P \leq 0.05$), whilst on the non-FLS plots the raked treatment significantly outyielded the other three litter treatments ($P \leq 0.05$)..

Lotus uliginosus established in significant quantities on four particular plots where they accounted for between 2 and 40% of the sward. Table 52 indicates that on these plots this species contributed between 1 and 12% of the total dry weight.

Figure 30. Dry weight yield of herbage components at Gatehouse for 1981. (Strip).

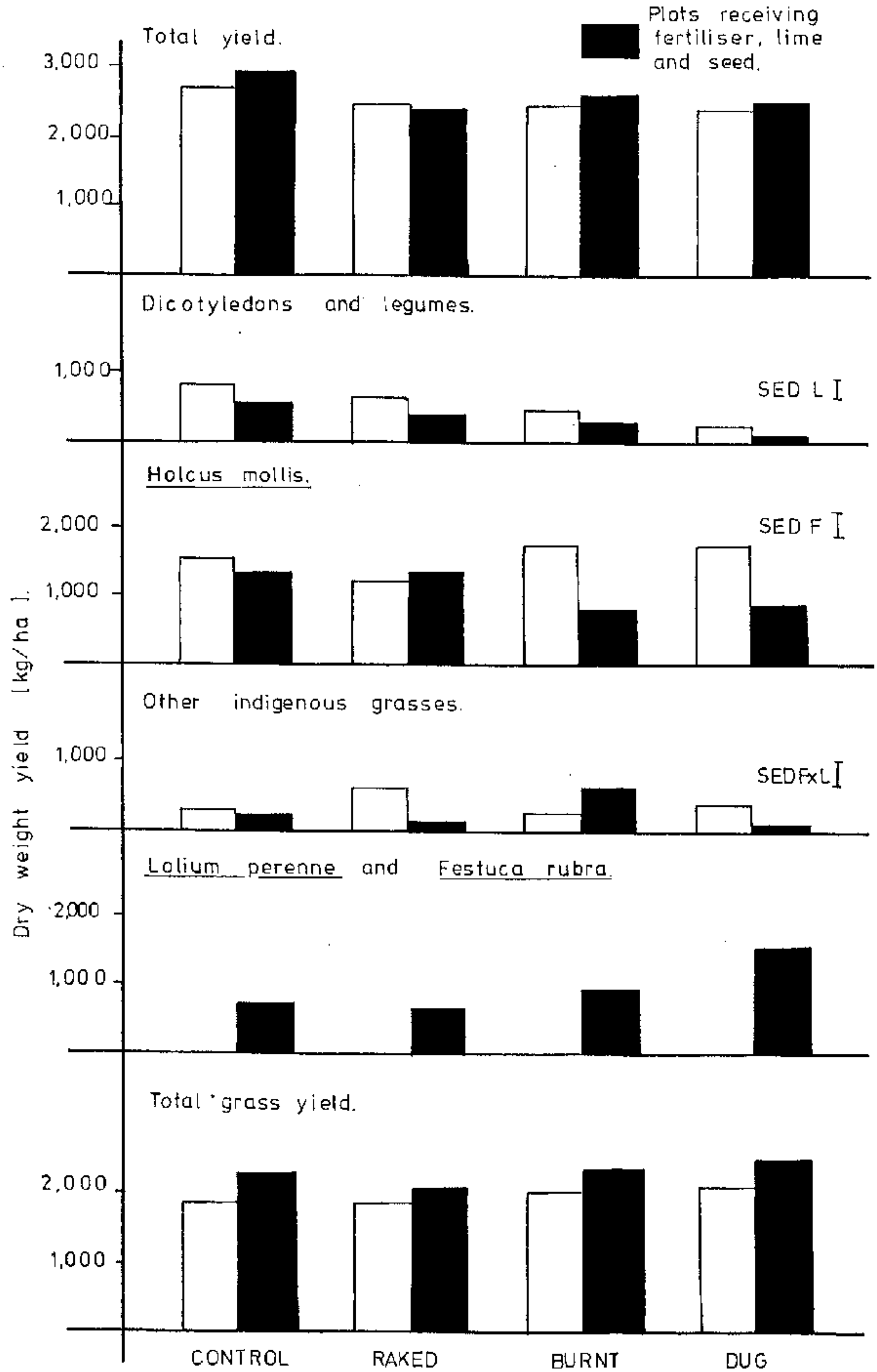


Table 52. Dry weight yield of Lotus uliginosus from specific replicates in 1981 (Strip).

Plot number	Treatment	Dry wt. yield (kg/ha)	% contribution to yield of plot
1	Raked	317.6	12.19
2	Burnt	181.6	6.39
3	Control FLS	168.8	7.02
12	Dug	71.6	1.37

Only three significant differences were found between the yields of the various herbage components of corresponding treatments on the main plot and on the strip. On the non-FLS raked treatment the total grass yield and the total dry weight yield was higher on the main plot than on the strip and on the FLS dug treatment the yield of Lolium perenne and Festuca rubra was higher on the main plot than on the strip ($P \leq 0.05$ in all three cases).

11.4 Discussion of results

After frond clearance with asulam, three different methods of removing the layer of bracken litter were employed, namely raking, burning or digging, and these were compared with control plots where the litter layer was left intact. The effect of removing the litter layer by raking was to increase the amount of bare ground available for colonisation without significantly disturbing the soil. Burning to remove the dead bracken left a larger area available for colonisation because much of the surface vegetation was killed or damaged in the process, although there was again no significant disturbance to the soil surface. Burning also killed some weed seeds lying on or near the soil surface. Digging the plots thoroughly disturbed the soil profile and incorporated both the surface vegetation and the bracken litter with the soil. This procedure effectively created a bare soil surface.

In conjunction with these various methods of litter removal or seed bed preparation, the consequences of applying lime, fertiliser and seed and the effect of frequency of defoliation were considered with respect to various aspects of sward development.

11.4.1 Changes in indigenous grasses

The ability of Holcus mollis to colonise bare ground rapidly was noted on the burnt plots and supports observations made by Jeffreys (1916) who found that this was one of the first species to colonise a burnt area and that where conditions for other plants were unfavourable, this species became a major component of the sward. No seed of Holcus mollis was recovered in any of the soil samples from this, or any other site, on any of the sampling occasions and there was little evidence of flowering on the various sites. It is presumed that this species re-established from pieces of rhizome. Several workers have noted that this species exhibits low levels of flowering and hence seed production (Ovington & Scurfield, 1956; Al-Mufti et al, 1977; Thompson & Grime, 1979) and Ovington & Scurfield (loc cit) found that under shaded woodland conditions reproduction was mainly vegetative and that the amount of seed varied considerably between habitats with the percentage germination of seed frequently very low. Similar shaded conditions might prevail below the bracken canopy which would not favour the development of a seed bank. On the burnt treatment soil disturbance was minimal, fewer weed seeds were stimulated to germinate than on the dug treatment and hence competition from weed species was less severe. Holcus mollis quickly became and remained the dominant species on the burnt non-FLS treatment although on the FLS treatment its expansion was limited. During 1981 its cover decreased significantly on the FLS burnt treatment as the sown species increased ($P \leq 0.01$). On the dug treatments where it might again have established well from rhizome fragments, it was unable to compete with the weed seedlings establishing from seed on the non-FLS plots early in the season, although by October the cover was similar to that on the control treatment, whilst on the FLS plots it could not compete with the dicotyledons initially and with Lolium perenne and Festuca rubra later in the year. During 1981 Holcus mollis was almost completely suppressed by the sown grasses on the FLS plots. Although Ovington (1953) found that Holcus mollis was able to increase in density following the application of lime and superphosphate, Holcus mollis resembles Holcus lanatus, which is suppressed on grazed pastures of reasonable fertility by the more rapidly growing grasses and clovers (Fenton, 1931).

Holcus mollis yielded similar quantities of dry matter in 1980 and 1981 on all eight treatments but the cover of this species in September 1981 was significantly lower on the burnt and dug FLS treatments than on the corresponding non-FLS treatments ($P \leq 0.05$ and $P \leq 0.01$ respectively). This difference was apparent in 1980 but at that time it was not statistically significant.

Although the difference could not be shown to be significant, compared with the other three non-FLS litter treatments, the burnt non-FLS treatment had the highest percentage cover (except at the first assessment in 1980) and dry weight yield of Holcus mollis in both 1980 and 1981.

Grasses other than Holcus mollis, chiefly Agrostis spp and Poa spp, were unable to compete and hence to establish well on the burnt and dug treatments and by the end of 1980 the control treatment had a significantly greater cover of these species ($P \leq 0.05$) although the dry weight yields were not significantly different for the eight treatments. In 1981 there was no significant difference in the percentage cover or dry weight yield of these grasses between the different treatments.

11.4.2 Changes in the herbaceous weed flora

Digging stimulated the germination of large numbers of buried weed seeds in 1980, many of which were able to establish including species not previously recorded in the sward of the control treatment, for example, Galeopsis tetrahit, Polygonum spp and Scrophularia nodosa. By 1981 the overall cover of herbaceous weeds had fallen on the dug treatments to less than that of the control and although Ranunculus repens managed to establish during the year, its cover on the dug treatments was significantly less than that on the control ($P \leq 0.05$) in September.

Where the soil was not significantly disturbed when the bracken litter was removed there was less establishment of the weedy species. On the burnt treatments Stellaria media and Polygonum spp established from seed, as did Ranunculus repens, possibly from seed but more likely from root regeneration. In 1981, whilst this latter species increased its cover, neither Stellaria media nor Polygonum spp reappeared in quantity. Moss (1980) working with seed of Alopecurus myosuroides suggested that although burning might destroy some seeds, those which were shallowly buried might be stimulated to germinate. Alternatively, the increased establishment might simply be a reflection of better environmental conditions for germination. The gradual increase during 1980 and 1981 in the cover of dicotyledons on the raked treatment was almost exclusively due to the spread of Ranunculus repens and in both seasons the cover of this species was significantly greater on the raked than on the burnt or dug treatments ($P \leq 0.01$ in 1980 and $P \leq 0.05$ in 1981). Plate 77 shows the significant presence of Ranunculus repens on the raked treatment in 1981.

By October there was no significant difference in the percentage cover of dicotyledons on the four litter treatments, whether fertilised, limed and seeded, or not, but the dry weight yield was significantly higher on the dug treatment relative to the other three ($P \leq 0.001$) for both the FLS and non-FLS plots. This difference arose because the weed species associated with the dug treatments (Scrophularia nodosa, Galeopsis tetrahit, Digitalis purpurea and Polygonum spp) tend to have an upright growth form whilst the main species associated with the other treatments, Ranunculus repens, was chiefly a prostrate plant. Thus, although occupying similar proportions of the swards, the weeds on the dug treatments had a greater biomass. In order to achieve this greater biomass per unit area, more of the nutritional resources of the soil of the dug treatment would have been required.

By September 1981 the main dicotyledon on all the treatments was Ranunculus repens and although the cover of this species was significantly smaller on the burnt and dug treatments than on the control and raked treatments ($P \leq 0.05$), the cover and dry weight yield of all the dicotyledons was similar on all eight treatments.

There was no significant difference between the plots which received fertiliser, lime and seed and those which did not, for any of the four litter treatments, with respect to the dry weight yield or percentage cover of the dicotyledons as a group, either in 1980 or in 1981.

The development of Ranunculus repens warrants further comment. Established plants were able to take advantage of the improved conditions (increased light, space and fertility) on the control and raked treatments both immediately and rapidly by stolon extension into the open spaces and by the development of large leaves to cover the open patches in the sward. This species tends to respond to changes in environmental conditions by stolon development rather than by seed production (Harper, 1957a). Such plants are likely to be strong competitors under a closely cut or grazed situation in that they can spread rapidly and smother other species yet Ranunculus repens is highly plastic and can adopt an upright growth habit in taller growing vegetation.

Although this species is capable of creating a persistent viable seed bank (Rabotnov, 1969; Sarukhán, 1974; Grime, 1981) it was unable to re-establish on the dug treatment in 1980 partly because germination is normally in the spring (Harper & Sagar, 1953) and partly because of competition. Vast amounts of seed were produced at the site during 1980 (and 1981) and Ranunculus repens was able to establish on the dug treatments in the second season. Recolonisation of the burnt treatments was possible in the first season from undamaged pieces of root but competition from Holcus mollis restricted its spread.

Digitalis purpurea, Cirsium spp and Urtica dioica have been considered by some workers (Cadbury, 1976; Williams, 1977) to be potential weed problems following bracken clearance. No Urtica dioica was recorded and Cirsium spp were found in only small quantities in the various swards. Digitalis purpurea was present on all the treatments but its cover exceeded 5% only on the non-FLS dug treatment where its prominence was the result of seeds being stimulated to germinate as a result of soil disturbance. On the FLS dug treatment it did not seem able to compete well with the faster growing grasses.

Outside the experimental area, flowering plants of Digitalis purpurea were abundant (Plate 83). Since stock are very unlikely to graze this species when grass is available, it may become a nuisance. One plant can produce vast quantities of seed and it is therefore important to control the plant in such a way, or at such a time, as to prevent flowering. Cirsium spp, in particular Cirsium palustre, were also abundant outside the experimental area and a similar argument applies here. Although not normally a component of the sward below the bracken canopy, Polygonum spp, in particular Polygonum hydropiper, were present in significant quantity on the burnt and dug treatments on the main plot in 1980 and outside the experimental area. In the actual trial non-selective cutting controlled all these species but selective grazing will not. Whilst heavy stocking might damage some of the plants sufficiently to prevent flowering, where viable seed is set and the soil disturbed, these species may establish in quantity.

11.4.3 Effect of method of seed bed preparation upon the establishment of sown species

Of the four litter treatments, digging provided the most favourable initial conditions for the establishment of Lolium perenne and Festuca

Plate 83. Infestation of Digitalis purpurea outside the experimental area.

rubra. By October 1980 there was a significantly greater cover of these species on the dug treatment than on the other three ($P \leq 0.01$) and a significantly greater dry weight yield ($P \leq 0.001$). During 1981 the proportion of these grasses in the sward of the dug treatment remained largely unchanged from that in October 1980 at about 60%, whilst the increases noted on the burnt treatment were at the expense of Holcus mollis and on the raked and control treatments were at the expense of indigenous grasses other than Holcus mollis. Although there was no significant difference in the cover of Lolium perenne and Festuca rubra on the four litter treatments by September 1981, the dry weight yield of these species was significantly higher on the dug treatment (2,112 kg/ha) than on the other three (717, 915 and 1,345 kg/ha on the control, raked and burnt treatments respectively) and the burnt treatment also significantly outyielded the control treatment ($P \leq 0.05$ in both cases).

Thus, it took only one season to achieve both a significantly greater cover and dry weight yield of these grasses on the dug treatment whereas on the burnt treatment, although it again only took one season to achieve a significantly greater percentage cover relative to the control, it took two seasons to achieve a significantly greater dry weight yield.

The control of indigenous plants and their capacity to recolonise from viable remains or buried seed are important factors contributing to the successful establishment of sown species. Allen (1966) examined the effects of various seed bed preparations on the flora and buried seed content of an Agrostis/Festuca pasture and on the ability of the indigenous flora to recolonise against a background of sown species. He prepared his seed beds by (a) deep ploughing - to 20 cm, (b) shallow ploughing - to 12 cm, (c) sward destruction with paraquat followed by rotary cultivation - to 5 to 10 cm, or (d) paraquat application only. No lime or fertiliser was applied. After one year the sown species had the greatest cover on the ploughed plots whilst rotary cultivation following sward death could only give a good establishment of a weed-infested crop because the native species regenerated rapidly. The use of paraquat alone allowed little establishment of the sown species and the weeds were most abundant here. A similar result was obtained by Hughes & Nicholson (1961) who found that even where the old sod was effectively destroyed, the subsequent competition from regenerating plants was significant. Rowlands (1966) found that light cultivation did not allow a satisfactory establishment of sown grasses compared with ploughing because the amount of surface disturbance was inadequate to break up the surface mat and allow the seeds to reach the soil and moisture. The strong growth of native species retarded the development of those clover seedlings which did manage to establish and as Chestnutt & Lowe (1970) have pointed out, because clover starts its growth later in spring and because it has a lower growth habit than most grasses, this species is at a disadvantage when grown in association with grasses.

The data obtained in the first year of this study support those of previous workers. Lolium perenne and Festuca rubra were unable to establish effectively on the control and raked treatments because of competition from the established sward and although burning had damaged the native species, regeneration of Holcus mollis was extremely fast and this species severely restricted the establishment of the sown species. On the dug treatments establishment was far superior because the native species had been far more effectively checked, competition had been reduced and the sown species were able to respond faster to the improved soil fertility than the native species. Once established, as the data for 1981 show, the sown grasses were able to increase their cover gradually. Williams (1980) found that once bracken and the associated sward had been killed, a mat of vegetation and frond litter remained and that unless some form of cultivation to form a seed bed, or burning to remove the litter, was possible, surface seeding was unlikely to be successful except in high rainfall areas since the success of surface seeding relies largely upon the seed coming into contact with the soil and remaining there under good moisture conditions (Charles, 1962) and upon the native species being suppressed sufficiently long enough for the seedlings to establish.

Seed of Trifolium repens was sown in April 1980 with the grasses but none established until 1981 and then only in small quantities. It was favoured by the dug treatment (Plate 82) but it never accounted for more than 5% of the sward. This is significant because it is generally acknowledged that the key to hill land improvement and the successful establishment and maintenance of surface sown grasses is the good establishment of clover (Munro, 1974; Munro & Davies, 1974). Clover will not only increase the nutritional value of the sward (Munro & Hughes, 1966) but will also, by the breakdown of roots, nodules and stolons (Cowling, 1961) release nitrogen, which is often the major factor limiting pasture production in the uplands (Munro & Davies, 1973; Munro et al, 1973).

Many factors affect the successful establishment of clover (Chestnutt & Lowe, 1970), including an adequate moisture supply, and the dry spell in April and May following sowing in this trial may have been the reason for the poor establishment of this species (see Appendix 2:E for meteorological data). Under surface seeding conditions in dry years, establishment of less than 10% of the white clover sown is common (Munro, 1981). After this dry spell competition from established plants may have been a contributing factor.

It is only eighteen months since the plots were limed and fertilised and the 60% cover of Lolium perenne and Festuca rubra on the dug treatment may very well not last unless further applications of lime and fertiliser are given or unless the establishment of Trifolium repens improves.

At this site, an alternative legume to Trifolium repens might be Lotus uliginosus. This species was found on several plots where it was thriving (Plate 84). On the main plot it adopted an upright growth form whilst on the strip, where it did not appear to be adversely affected by the more frequent cutting regime, it adopted a highly prostrate growth form. Outside the experimental area this species was found growing in abundance. Although success in the surface seeding of this species on wetter upland areas of western Scotland has been reported (Charlton, 1971, 1975; Gwynne, 1981; Wedderburn, 1981), only Williams (1976) has examined the possibility of sowing this species into land cleared of bracken. Early results suggested that this species was able to establish in the absence of fertiliser and under conditions of uncontrolled sheep grazing and might therefore provide a basis for the improvement of such areas.

11.4.4 Effect of addition of lime, fertiliser and seed upon sward composition and dry weight yield

For each of the four litter treatments, the addition of lime and fertiliser was found, after six months, to have had no significant effect on either the percentage cover or dry weight yield of the various categories of species examined, with the exception of the total grass yields on the non-FLS treatments which were together significantly lower ($P \leq 0.05$) than those of the corresponding FLS treatments but none of the individual corresponding litter treatments were significantly different. Lolium perenne and Festuca rubra established on, and were harvested from, only the FLS plots where they had been sown. The main differences between the treatments were with respect to the method of litter removal.

After eighteen months the addition of lime, fertiliser and seed was found to have had no significant effect upon the percentage cover of the various categories of species examined with the exception of Holcus mollis, which was found in significantly smaller quantities on the FLS burnt and dug treatments than on the corresponding non-FLS treatments

Plate 84. Well established plants of Lotus uliginosus on the dug treatment.

($P \leq 0.01$ in both cases) and Digitalis purpurea, which, although it established in quantity only on the non-FLS dug treatment, showed a significant preference for the non-FLS plots ($P \leq 0.05$). The reduction in Holcus mollis on these treatments was not the result of differences in soil fertility directly but was due to the presence of Lolium perenne and Festuca rubra and the inability of Holcus mollis to compete with these species.

Significant differences were found between the non-FLS and FLS plots with respect to both the total grass yield ($P \leq 0.01$) and the total dry weight yield ($P \leq 0.001$). The total dry weight yield was significantly higher on the control, burnt and dug FLS treatments than on the corresponding non-FLS treatments whilst the relationship was reversed for the raked treatment. A similar pattern was noted for the total grass yield although for the individual litter treatments the only significant differences ($P \leq 0.01$) were between the burnt and dug FLS treatments and the corresponding non-FLS treatments. The addition of lime, fertiliser and seed did not, however, affect the dry weight yield of the individual groups of species.

In both seasons the FLS plots (all four litter treatments together) yielded significantly more grass than the non-FLS plots (1980: 1,515 kg/ha and 1,851 kg/ha on the non-FLS and FLS plots respectively, 1981: 2,329 kg/ha and 2,816 kg/ha on the non-FLS and FLS plots respectively) ($P \leq 0.05$ in both cases). These yields compare favourably with those of Farnworth & Davies (1974), Williams & Fraser (1979) and Davies et al (1979) who all obtained between 2,000 and 3,000 kg/ha of dry matter from indigenous species (including herbaceous species) after frond clearance. Although Copeman & Roberts (1960), Robertson & Nicholson (1961) and Newbould (1981) showed that lime alone could increase the proportion and productivity of Agrostis and Festuca spp, Munro (1974) and Anon (1976) noted that the application of lime and phosphate fertiliser to hill pastures resulted in little extra dry matter production although the nutritional value of the species was increased. For the individual litter treatments the greater yields on the FLS plots were only significant on the burnt and dug treatments in 1981 where significant quantities of Lolium perenne and Festuca rubra had established; this result lending support to the comment of Newbould (1981) that unless sward composition was altered markedly there was little evidence that hill pastures responded with extra dry matter production to the application of lime and phosphate.

11.4.5 Effect of frequency of defoliation upon sward composition and dry weight yield

The strip was cut three times during 1980 (compared with two cuts for the main plot) and, although a fourth cut was planned for mid-October, there had been insufficient growth since the mid-September cut to allow this. Thus, after only six months and one extra cut, major differences in the sward composition and yield were not expected.

By the end of the first season there were no significant differences in the percentage cover or dry weight yield of the various groups of species examined. With respect to the individual dicotyledons, of the species with more than 5% cover in October 1980, significant differences were only noted for Polygonum spp which were more abundant on the burnt and dug treatments on the main plot than on the corresponding treatments on the strip.

The strip was cut five times during 1981, compared with three times on the main plot, and when corresponding treatments on the strip were compared with those on the main plot significant differences in sward composition were found only with respect to the dug FLS treatment. On this treatment, the more frequent cutting regime had resulted in a greater proportion of Lolium perenne and Festuca rubra and a greater total grass cover ($P \leq 0.05$ in both cases) on the strip. There were corresponding smaller proportions of dicotyledons and legumes, chiefly

Ranunculus repens, and grasses other than Holcus mollis ($P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.01$ respectively). The cover of Holcus mollis was similar on the dug FLS treatment on the main plot and on the strip.

With respect to the dry weight yield data, whilst there had been an overall pattern of higher yields for all the herbage categories on all the treatments on the strip in 1980, this pattern was no longer evident in 1981. There were only three significant differences between the main plot and the strip in 1981: the total grass yield and total dry weight yield was higher on the non-FLS raked treatment on the main plot ($P \leq 0.05$ in both cases) and although there was a significantly greater cover of Lolium perenne and Festuca rubra on the FLS dug treatment on the strip, the dry weight yield of these grasses was significantly higher on the main plot than on the strip ($P \leq 0.05$).

Holcus mollis fared as well on the main plot as on the strip and did not appear to suffer adversely in its dry weight yield or percentage cover as a result of the more frequent defoliation. Williams (1980a) suggested that this species might not tolerate hard grazing (simulated here by cutting) and Fenton (1948) found that in woodland conditions Holcus mollis recovered slowly after grazing and that on poorer soils it did not always compete successfully with Agrostis spp.

Thus, the only treatment to be significantly affected by the more frequent defoliation was the FLS dug treatment where more frequent cutting gave a significantly higher cover but a significantly lower dry weight yield of Lolium perenne and Festuca rubra.

11.5 General discussion

The results obtained in this study suggest that where lime and fertiliser were not applied, apart from burning giving a possible advantage to Holcus mollis, there was little to be gained by removing the bracken litter. There was little change in the sward composition but the proportional contributions of the species altered.

One of the problems in improving hill land and increasing its stock carrying capacity is that most native hill grasses have their maximum period of productivity between May and July and thereafter their digestibility declines markedly. Since it is the availability of winter keep rather than summer productivity which ultimately will determine the rate of stocking (McCreath, 1976), one of the aims of any scheme of improvement must be to extend the period of productivity until later in the year and to find some way of offsetting the autumn reduction in digestibility.

Newbould (1974a, 1975) has reviewed the methods of improving pasture in hill areas whilst Williams (1980) has examined these problems with respect to bracken land. In order to improve cleared bracken land it is necessary to alter the species composition but there are several problems to be overcome in order to achieve this. The value of applying phosphate alone, to improve soil fertility, is often limited in acid soils because it is quickly bound and becomes unavailable to plants. Lime to raise the soil pH would be a more useful addition since this would encourage the breakdown of undecomposed plant and animal remains and nutrients would become available. In upland areas where rainfall is high and evapotranspiration low, lime losses are severe and maintenance dressings are necessary (Copeman & Roberts, 1960; Davies, 1980). Evidence from the control and raked FLS treatments, where the sown species failed to establish, suggests that there was an insufficiently large response to justify the application of lime and fertiliser to the native species. Since no change in species occurred, the objective of a better yield distribution during the year had not been realised. Under such conditions it is therefore necessary to replace the native species and those currently used in the majority of re-seeding mixtures are species characteristic of the more fertile lowland soils (Newbould, 1981). These include <u>Lolium perenne</u> and <u>Trifolium repens</u>. In order for these species to establish a minimum application of lime and phosphate is necessary. A further requirement, if the sward is not to revert, is an increase in available nitrogen. Munro & Hughes (1968), Munro et al (1973) and Munro & Davies (1973) have shown that available nitrogen is one of the factors limiting the productivity of upland areas in Wales. Although hill soils rich in organic matter contain large quantities of nitrogen (up to 10,000 kg/ha) only a small part of this (approximately 30 kg/ha) is available for absorption by plants (Floate, 1971). The loss of available nitrogen from the soil is rapid, more so on wetter soils, and it is vitally important to establish a palatable and vigorous nitrogen assimilator to maintain an adequate nitrogen level for the sown grasses.

There are many problems to be overcome in order to establish Trifolium repens in hill land. Chestnutt & Lowe (1970) reviewed the factors affecting the establishment and maintenance of clover, Masterton & Sherwood (1970) have examined the requirements for the formation of an effective symbiotic relationship with Rhizobium trifolii, Munro & Hughes (1966) and Munro (1970) have discussed the limitations to clover performance imposed by climatic, nutritional and Rhizobium deficiencies and Newbould & Haystead (1978) have considered the role of white clover in hill pastures. Countless other papers have described the research being conducted into the value and use of clover in upland areas notably at the Welsh Plant Breeding Station and at the Hill Farming Research Organisation. It is sufficient in this study to mention specific points only.

Clover has three main functions in the sward: (a) to promote an effective nitrogen cycle and help in the mineralisation of nutrients bound in the litter, (b) to improve the feeding quality of the herbage - clover has a higher crude protein content relative to grass, a higher level of digestible energy and a higher mineral content, and (c) to fix atmospheric nitrogen and transfer it to the grasses in the sward. The presence of clover in a sward does not necessarily indicate an effective symbiotic association between clover and Rhizobium trifolii which is necessary for gaseous nitrogen to be fixed.

In order to establish clover it is necessary to apply lime to raise the soil pH; Chestnutt & Lowe (1970) have shown that unless the pH is over 5.5 clover will not make a significant contribution to the sward. Some nitrogen is also usually required for the seed to establish (Davies, 1980). Clover has a higher demand for phosphate, potassium and a more alkaline soil ($\geqslant$5.5) than the sown grasses (Newbould & Haystead, 1978) and periodic applications of lime, phosphate and potassium fertiliser are necessary to maintain this species (Davies, 1968a).

Alternative legumes to clover are being investigated both in the United Kingdom (Welsh Plant Breeding Station) and abroad (New Zealand). Lotus uliginosus has shown promise in wetter upland areas of Scotland (Charlton, 1971; Wedderburn, 1981) and Williams (1976) has examined its potential in bracken land. In this study, although not sown as seed, plants established themselves and became significant components of the swards where they occurred. Although there are no doubt many problems to be overcome in determining the correct management for this species on bracken land, there is evidence from this study and that of Williams (1976) that this species can establish without fertiliser and lime under conditions of cutting and uncontrolled grazing. Lotus uliginosus deserves more attention under these conditions.

Many workers have commented on the advantages and disadvantages of one species relative to another when re-seeding hill land (Thomas, 1934; Copeman & Roberts, 1960; Hughes & Nicholson, 1961, 1962; Munro & Hughes, 1968; Munro, 1974; Newbould, 1974, 1974a, 1975; Herriott, 1975; Haggar, 1976; Younie & Black, 1979) but what is clear is that there are relatively few suitable grasses available for hill land improvement. Several species require high soil fertility (Lolium perenne, Poa trivialis), others are of low digestibility and are unpalatable to stock (Holcus lanatus, Dactylis glomerata), some are palatable but intolerant of grazing (Phleum pratense) whilst species such as Poa pratensis are difficult to establish because they have low seedling vigour.

The weaknesses associated with clover are poor early and late growth and an inability to withstand very high grazing pressure. When Newbould (1974) outlined the features of the grass species which would best complement and make good the deficiencies of clover, he found that a pasture type of Lolium perenne was the best species available. However, because this species has a potential economically unreasonable demand for fertiliser alternative species are required. Although early heading in Festuca rubra is a disadvantage, this species is one of the most suitable alternatives. It tolerates waterlogging but will establish well in dry conditions also. It is winter green and frost tolerant and begins growth one month before Lolium perenne in spring. It tolerates continuous and heavy grazing and is palatable. It utilises both nitrogen and lime more efficiently than Lolium perenne (Copeman & Roberts, 1960; Hughes & Nicholson, 1961; Munro, 1966, 1974; Haggar, 1976; Newbould, 1974). If the poor establishment of Poa pratensis and the intolerance of Phleum pratense to grazing could be overcome these species would be valuable. Unfortunately it is not economic to breed improved varieties of grasses for upland conditions.

Holcus mollis is not grazed when other grasses are available but since it is winter hardy and easy to establish, it may be useful particularly in the first season after frond clearance. It responded well to increased soil fertility (Ovington, 1953) although there was some evidence during this experiment that it was not tolerant of competition from the faster growing grasses on the more fertile soils. Holcus mollis responded well to close cutting in this trial although Williams (1980a) found this species to suffer under hard grazing. Herriott (1975) has advocated the use of Holcus lanatus for hill land and the related species Holcus mollis might well be worth further consideration.

Given that suitable species are available, the establishment of such seed requires consideration. Whilst the plough has a well established role in the preparation of a seed bed, large areasof hill land are too steep, too stony or merely inaccessible for the use of such techniques and it is on the best of these hill soils that bracken is the dominant species. It is on these sites that surface seeding is important. Charles (1962), Dowling et al (1971) and Campbell & Swain (1973) considered the factors affecting the establishment of surface sown pasture species in detail. The main factors which they, and other workers, have raised are:

(a) The importance of reducing competition from the native species to improve the establishment of the sown species (Hughes & Nicholson, 1961; Campbell, 1968; Davies, 1968). This may be achieved by:
   1. Herbicide use (Blackmore, 1957; Campbell, 1968, 1974).
   2. Burning (Hughes & Nicholson, 1961; Robocker et al, 1965).
   3. Hard grazing (Suckling, 1954, 1959).
   4. Cultivation (Copeman & Roberts, 1960; Allen, 1966; Davies, 1980).

(b) The use of stock to break up the vegetation mat remaining after sward control with herbicides and get the seed into contact with the soil (Copeman & Roberts, 1960; Rowlands, 1966; Davies et al, 1968).

(c) The provision of suitable moisture conditions for germination and establishment (Harper & Benton, 1966; Davies, 1968).

(d) The presence of litter as a cover to improve moisture and humidity and to reduce variations in temperature and exposure (Blackmore, 1957; Evans & Young, 1970).

(e) Creation of a suitable microtopography giving a variety of 'safe' sites for the germination of a range of species (Harper, Williams & Sagar, 1965).

(f) Adoption of a suitable management scheme during and after establishment (Chestnutt & Lowe, 1970; Anon, 1976).

The importance of seed bed preparation was clearly shown in this study. Sowing seed into the control or raked FLS plots did not produce a reasonable cover of Lolium perenne and Festuca rubra until perhaps the end of the second season when about a third of the sward was accounted for by these species. Competition from the established native species prevented a good initial establishment of the sown species although given time they responded better to the improved fertility than did the native species and they gradually increased their cover. Burning produced a significantly greater cover of sown species in the first season relative to the control but a significantly greater dry weight yield was not achieved until the second season. Digging gave the best initial establishment although weed seeds which were stimulated to germinate did establish in quantity in 1980. A significantly higher cover and dry weight yield in the first season was obtained, and again in the second season.

Thus, where digging, or some relatively deep form of soil disturbance, is possible this treatment will give the fastest and greatest cover and highest dry weight yield of sown grasses. Where cultivation is not possible prior to re-seeding, burning to remove the litter and reduce competition gives a good but slower establishment. The use of glyphosate, which has a greater spectrum of activity than asulam but which does not seem to affect Festuca rubra (Section 9), might be considered, followed by a spring burn prior to re-seeding.

It is now a question of balancing the cost of repeated applications of lime and fertiliser to maintain species such as *Lolium perenne* and *Trifolium repens* with that of trying new species, such as *Lotus uliginosus* instead of *Trifolium repens*, and the use of seed mixtures combining a large number of species with different characteristics (winter hardiness, a good distribution of annual yield, good seedling vigour etc.), deficiencies in one species being compensated for by the other species.

Where re-seeding is not adopted efforts should be directed towards encouraging the development of swards dominated by *Agrostis* and *Festuca* spp since these species form the basis of a relatively stable sward.

Whatever scheme of improvement is undertaken after bracken frond clearance, the key to its success is a sound management policy.

12. FUTURE WORK

Whether or not bracken land is improved depends largely upon economics and as a result two types of improvement schemes have arisen. A high cost treatment is available based upon the extensive technology for re-seeding with perennial ryegrass and white clover. The expertise for this technique has been built up from work in lowland conditions. In hill land however the basic cost of this treatment is greater because the low soil pH and high rainfall results in a higher requirement for lime and fertiliser to establish and maintain the sown species. The alternative is a low cost treatment involving the manipulation of the sward remaining after frond clearance to produce more valuable grazing land. Minimum inputs of labour, seed and fertiliser are used. In this type of improvement, surface seeding involving little or no cultivation and the use of species which establish better or which require lower fertiliser levels than ryegrass and clover are possibilities for the future.

It is important to improve the establishment of introduced species in order to justify the expense of applying lime and fertilisers periodically to maintain them, particularly whilst ryegrass and clover continue to be the main constituents of re-seeding mixtures for hill land. This study examined some of the factors which might influence sward development after frond control.

Although large numbers of viable seeds were found in the soil below bracken stands (Section 6), it appeared from both the Dalry and the Gatehouse trials (Sections 9 and 11 respectively) that unless the soil was disturbed these seeds were unlikely to germinate and to play a part in the development of the sward. The establishment of the sown grasses was best where the soil had been dug over despite the weed infestations which developed during the first season. Cutting controlled these herbaceous weeds but stock will not graze them and spot applications of herbicides or a cutting regime may have to be adopted during the first season. Ensuring that cultivation is not carried out until after March will result in smaller weed infestations since the greatest number of viable seeds seemed to be present between November and February inclusive (Section 7), although further studies on these temporal changes in seed numbers in bracken land might be of interest.

Very little clover established, possibly because of the dry spell immediately after sowing and later because of an inability to compete with the established plants. The establishment and growth of Lotus uliginosus outside the experimental area and its establishment and tolerance of cutting on both the limed, fertilised treatments and the unlimed, unfertilised treatments suggests that this species deserves further study as an alternative to clover, at least when re-seeding cleared bracken land in the West of Scotland.

Removal of the litter layer was necessary for good establishment of surface sown seed (Section 10) but it was more important to suppress the indigenous species (Section 11). Burning to remove the litter layer suppressed the native species somewhat and eventually gave a good establishment of the sown grasses although the rapid regeneration of Holcus mollis provided some initial competition. The particularly moist climate of the west coast of Scotland can provide something of a problem if the litter is to be burnt off. It is often quite late in the year before the litter is sufficiently dry to burn, particularly where there is a deep litter layer, and the muirburn regulations do not normally permit burning of hill land after 15 April in Scotland.

The use of glyphosate to control frond growth might be considered more often where re-seeding is contemplated and where cultivation is not possible. Because this herbicide has a wider spectrum of activity than asulam, more species are suppressed. Since there is relatively little growth during the winter, a spring burn prior to re-seeding could provide a satisfactory seed bed. This wider spectrum of activity makes drift of glyphosate a potential hazard and there are reservations about its suitability for aerial application. Application to small areas with knapsack equipment might be a possibility.

The success of surface seeding depends upon the seed coming into contact with the soil under conditions of sufficient moisture for germination and establishment and upon the native species being suppressed. Cultivation after frond clearance with asulam, or burning or cultivation after frond clearance with glyphosate, are techniques which may provide suitable seed beds. Although the West of Scotland has a high rainfall (1,000-2,000 mm) and a low rate of evapotranspiration, surface seeding is not always successful because the contact between the soil and the seed is inadequate. There is often a dry spell in April/May, as in this trial, and legume seed in particular appears to be susceptible. The use of stock to trample seed into the ground is possible but this may also increase the weed seed germination rate if poaching is severe. The coating of seed with hygroscopic materials might improve establishment and merits consideration.

There was no evidence however of toxins being leached out of bracken fronds, whether dead or alive, or out of bracken litter, or of any accumulation of toxins in the soil. It is thought unlikely that this phenomenon affects the indigenous species or the sown-in species in the West of Scotland. The physical barrier provided by the layer of litter was a more important factor.

The control of bracken and the improvement of cleared land presents an economic rather than a biological problem. With ever increasing costs of labour, machinery, chemicals and fertilisers it is unlikely that there will be a significant decrease in the amount of bracken on the Scottish hill sides in the near future. The need for a more flexible system of grant aid for spraying has been suggested recently

(Williams, 1980; McCreath, 1981; Martin & Sparke, 1981) and the Department of Agriculture and Fisheries for Scotland is now considering whether a follow-up treatment of fertiliser is necessary in all cases. The removal of this compulsory after-treatment would encourage farmers to increase the amount of spraying carried out. The use of Lotus uliginosus instead of clover, the potential for the improvement of techniques for establishing surface sown seed and the possible use of glyphosate and re-seeding for small areas affords hope that hill swards in the West of Scotland can be improved without resorting to the expense of ploughing and applying large and frequent quantities of lime and fertiliser to establish and maintain ryegrass and clover swards.

13. APPENDICES

Appendix 1

Data pertaining to Section 6. Buried seed populations in bracken infested hill land in 1978.

1:A Photographs and descriptions of sites

1:B Experimental technique

1:C Results of seed survey

Appendix 1:A

At each of the field sites examined in the 1978 seed population survey, 20 soil cores were taken and the vegetation in 20 randomly selected quadrats was visually assessed. Additional background information on each site is given here together with a site photograph.

The Ordnance Survey map provided a grid reference and an estimate of altitude for each site. Aspect was determined with a compass. The rainfall data for 1978 from the nearest meteorological station to each site were obtained from the Meteorological Office in Edinburgh. The grid reference and name of the nearest station to each of the sites is given with the rainfall figures.

A visual examination determined the management regime and an estimate of bracken frond numbers per m^2 was calculated from counts of fronds in ten randomly selected $\frac{1}{4}m^2$ quadrats.

At each site, three samples from the top 5 cm of soil were taken to determine soil pH and a soil profile was dug either to a depth of 30 cm or to the parent bedrock, which ever was reached first. The classification and notation of the soil horizons followed that used in the Forestry Commission Forest Record No 71, 'Soil Groups of Upland Forests' by D G Pyott (1970).

Gatehouse of Fleet A, Kirkcudbrightshire (GR NX 582563)

Date of sampling: 14.9.78

Aspect: Flat

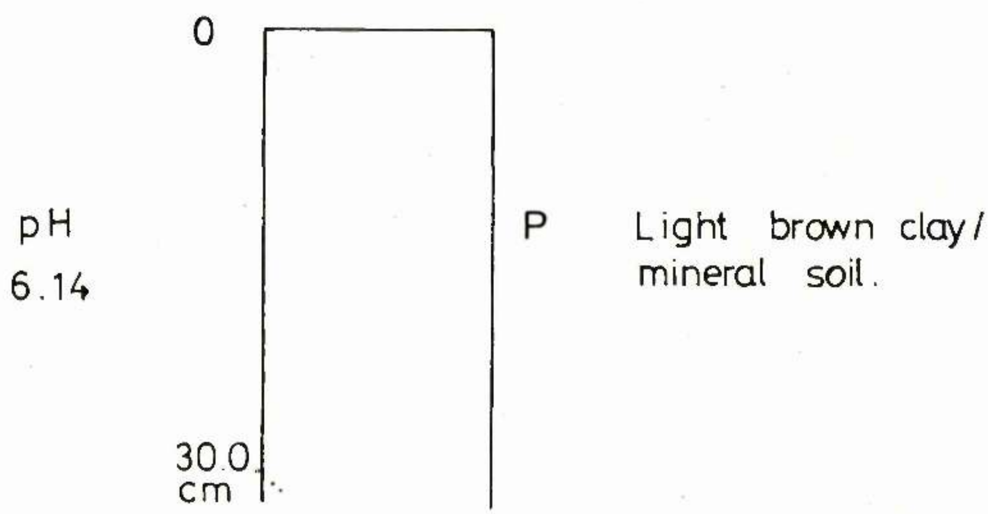
Altitude: 45 m asl.

Total precipitation (1978): 1034 mm (11 months) (Girdstingwood NX 742469)

Management: Sheep and cattle grazing

Frond density: Nil

Soil profile:



Gatehouse of Fleet B, Kirkcudbrightshire (GR NX 583565)

Date of sampling: 14.9.78

Aspect: Flat

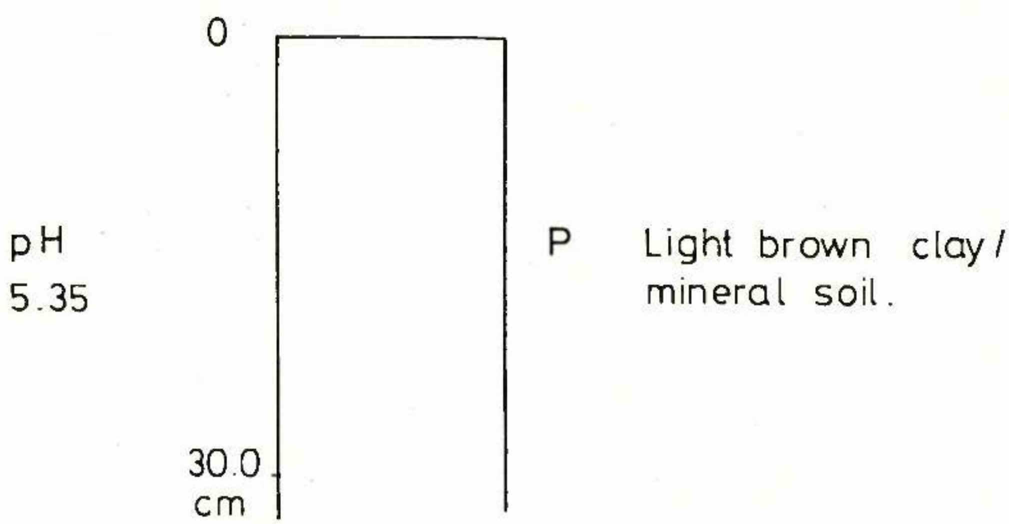
Altitude: 61 m asl.

Total precipitation (1978): 1034 mm (11 months) (Girdingwood NX 742469)

Management: Sheep and cattle grazing

Frond density: $30.3 \pm 0.9/m^2$

Soil profile:



Gatehouse of Fleet C, Kirkcudbrightshire (GR NX 578565)

Date of sampling: 14.9.78

Aspect: Southerly

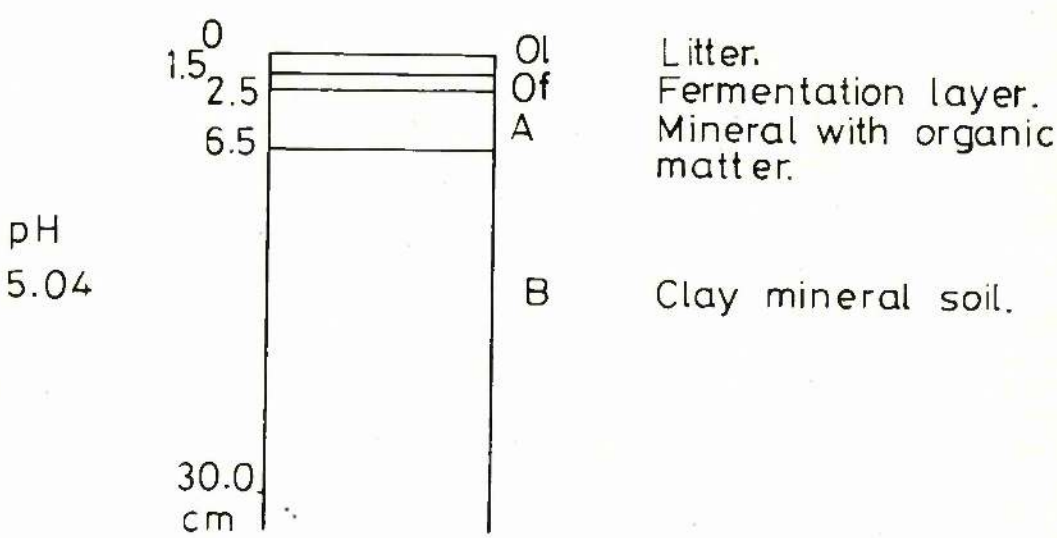
Altitude: 72 m asl.

Total precipitation (1978): 1034 mm (11 months) (Girdstingwood NX 742469)

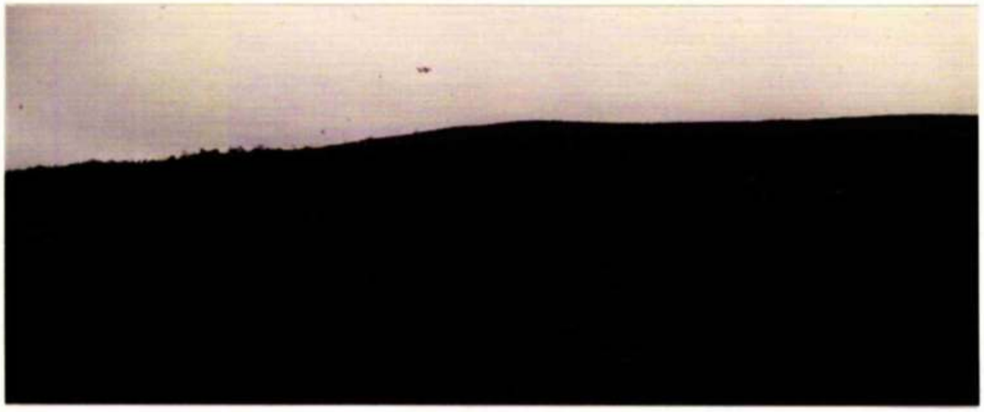
Management: Sheep and some cattle grazing

Frond density: 24.8 $\pm$ 2.6/m^2

Soil profile:



Barlaes Hill, Kirkcudbrightshire (GR NX 622860)



Date of sampling: 26.9.78

Aspect: Northerly

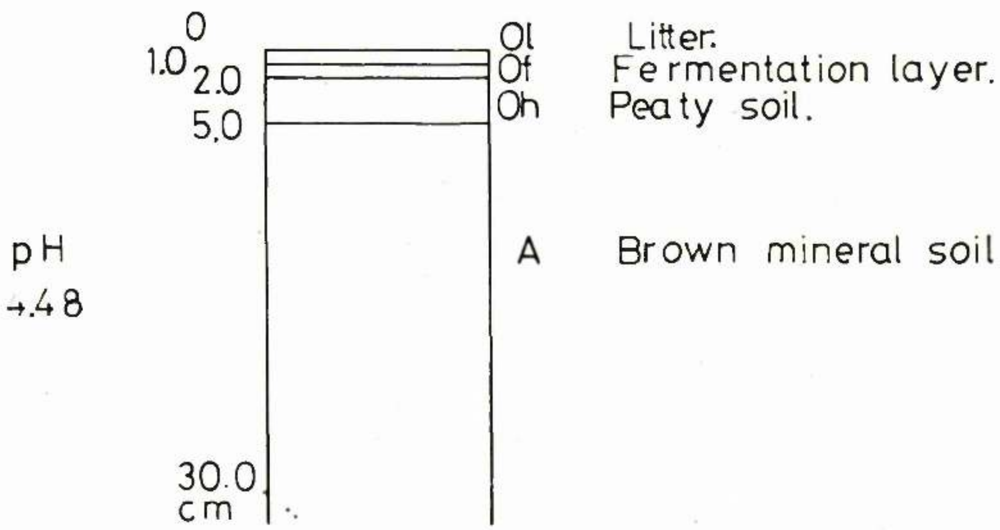
Altitude: 200 m asl.

Total precipitation (1978): 1403 mm (Dundeugh NX 598879)

Management: Sheep grazing

Frond density: 28.8 ± 19.0/m^2

Soil profile:



Dalry, Kirkcudbrightshire (GR NX 636870)

Date of sampling: 26.9.78

Aspect: Southerly

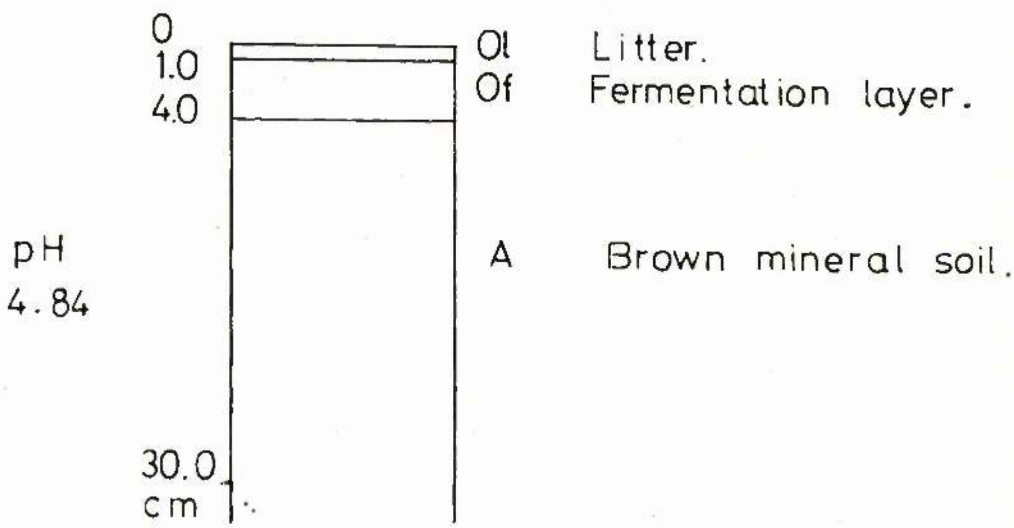
Altitude: 210 m asl.

Total precipitation (1978): 1403 mm (Dundeugh NX 598879)

Management: Sheep and some cattle grazing

Frond density: 40.8 ± 19.1/m^2

Soil profile:



Glen Douglas A, Dunbarton (GR NS 340979)

Date of sampling: 10.10.78

Aspect: Southerly

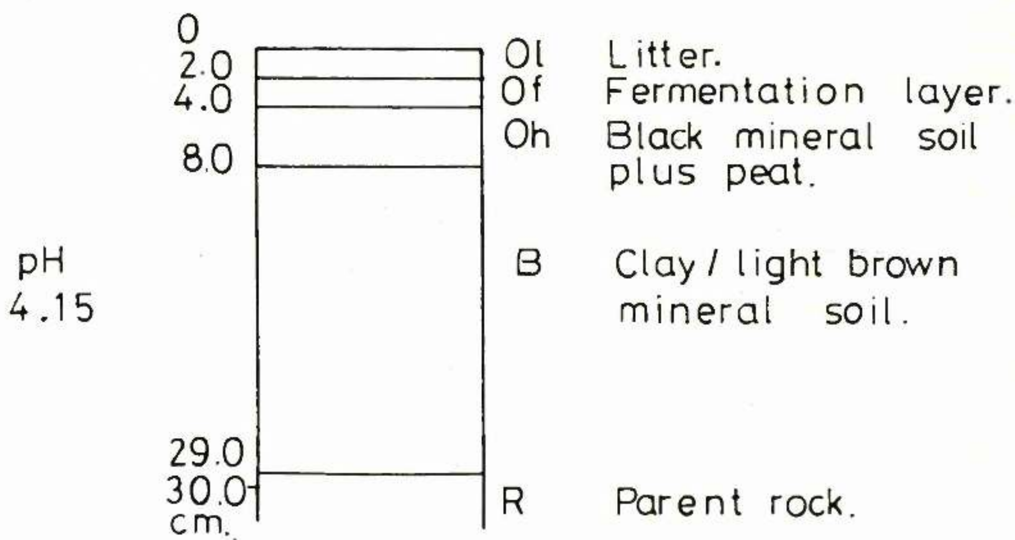
Altitude: 91 m asl.

Total precipitation (1978): 1601 mm (Arrochymore NS 415918)

Management: No grazing evident

Frond density: 29.0 ± 12.5/m^2

Soil profile:



Glen Douglas B, Dunbarton (GR NS 323980)

Date of sampling: 10.10.78

Aspect: Southerly

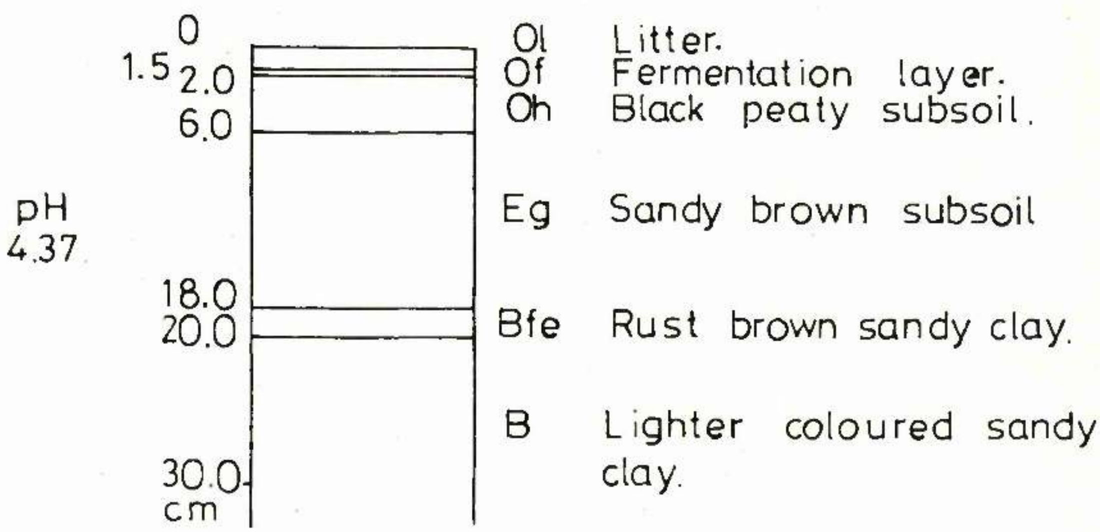
Altitude: 91 m asl.

Total precipitation (1978): 1601 mm (Arrochymore NS 415918)

Management: No grazing evident

Frond density: $7.3 \pm 3.1/m^2$

Soil profile:



Kirkton Farm A, Perthshire (GR NN 361285)

Date of sampling: 18.10.78

Aspect: Rounded hummock

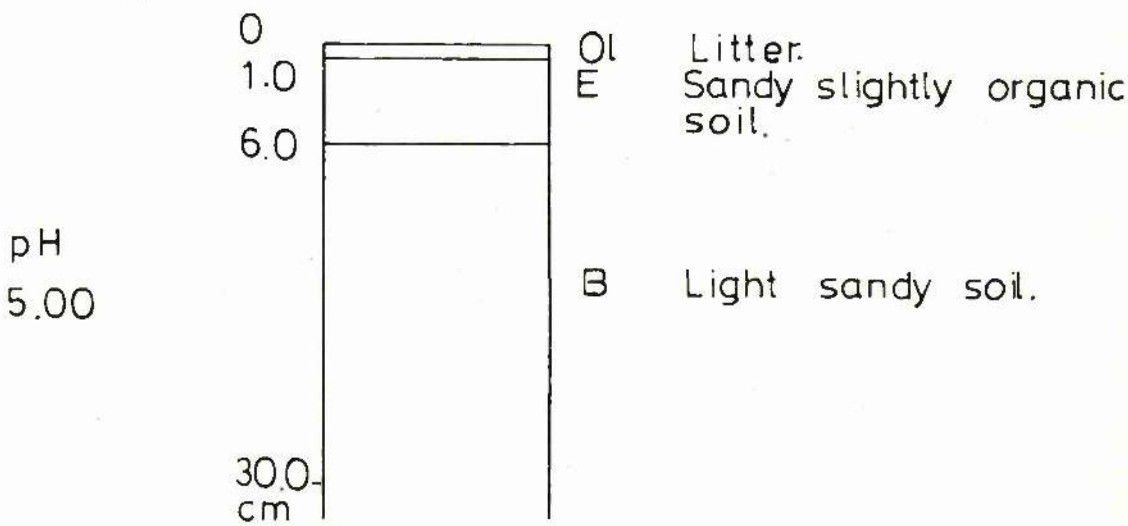
Altitude: 183 m asl.

Total precipitation (1978): 1227 mm (Dall NN 593562)

Management: Sheep grazing

Frond density: 33.1 ± 16.6/m^2

Soil profile:



Kirkton Farm B, Perthshire (GR NN 363287)

Date of sampling: 18.10.78

Aspect: South-westerly

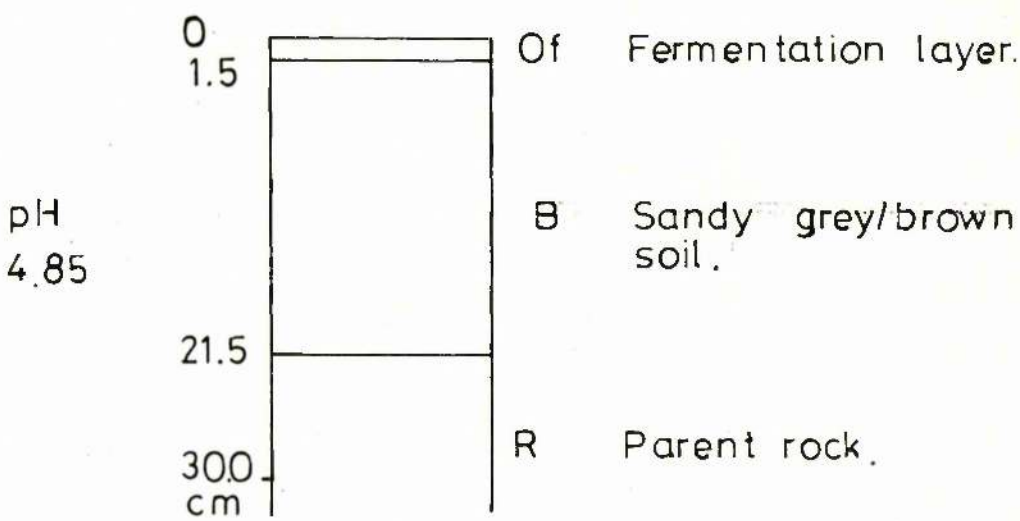
Altitude: 251 m asl.

Total precipitation (1978): 1227 mm (Dall NN 593562)

Management: Sheep grazing

Frond density: $2.0 \pm 1.9/m^2$

Soil profile:



Sundaywellmoor A, Dumfriesshire (GR NX 790845)

Date of sampling: 24.10.78

Aspect: Southerly

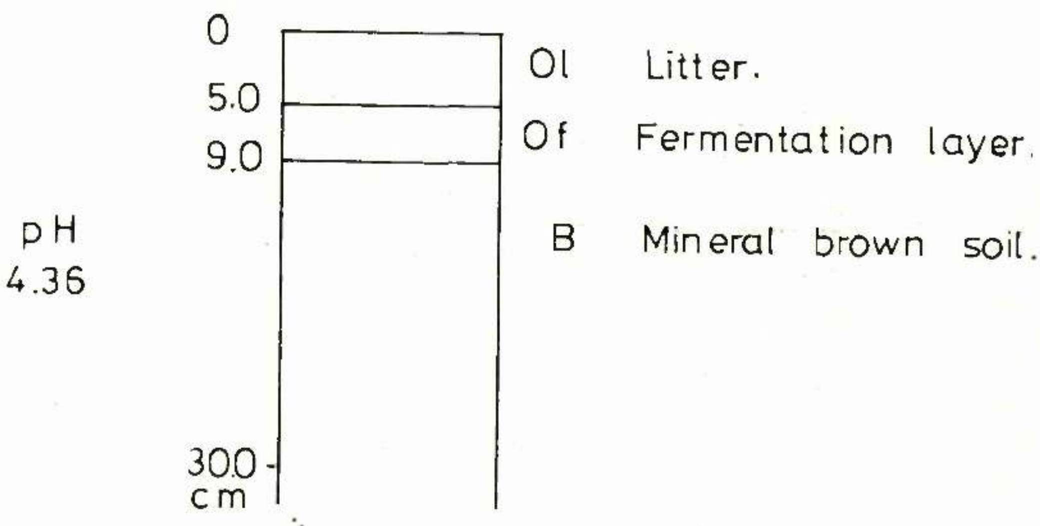
Altitude: 229 m asl.

Total precipitation (1978): 1403 mm (Dundeugh NX 598879)

Management: No grazing evident

Frond density: $30.4 \pm 12.0/m^2$

Soil profile:



Sundaywellmoor B, Dumfriesshire (GR NX 797841)

Date of sampling: 24.10.78

Aspect: South-easterly

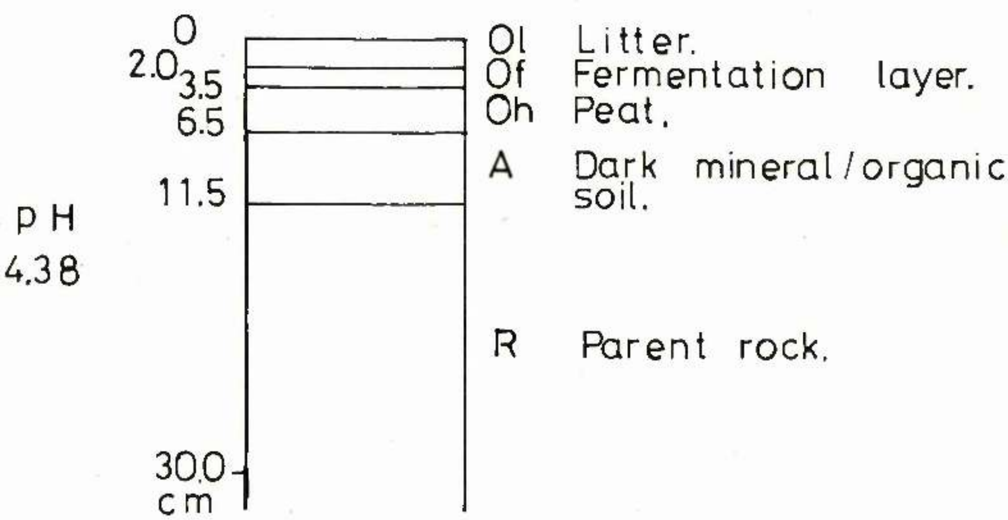
Altitude: 152 m asl.

Total precipitation (1978): 1403 mm (Dundeugh NX 598879)

Management: No grazing evident

Frond density: 29.2 ± 23.9/m^2

Soil profile:



New Galloway A, Kirkcudbrightshire (GR NX 587772)

Date of sampling: 3.11.78

Aspect: Northerly

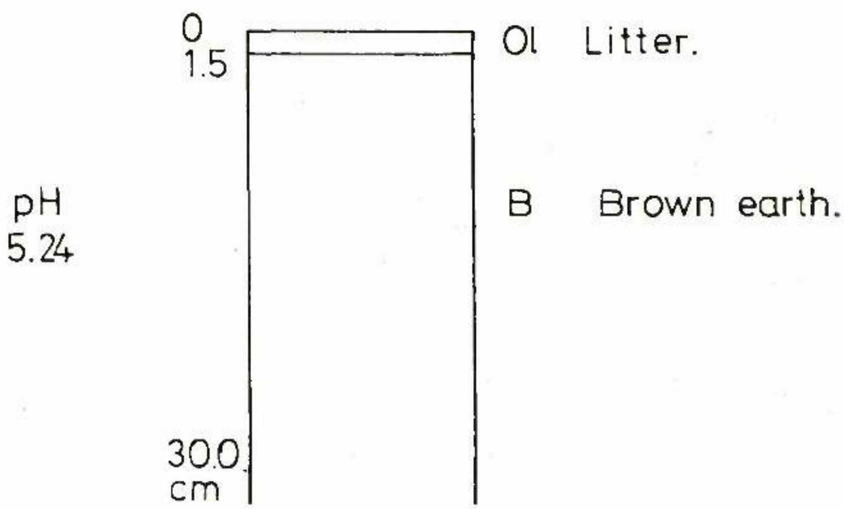
Altitude: 200 m asl.

Total precipitation (1978): 1874 mm (Clatteringshaws NX 554780)

Management: No grazing evident

Frond density: 52.8 $\pm$ 7.7/m^2

Soil profile:



New Galloway B, Kirkcudbrightshire (GR NX 611775)

Date of sampling: 3.11.78

Aspect: South-easterly

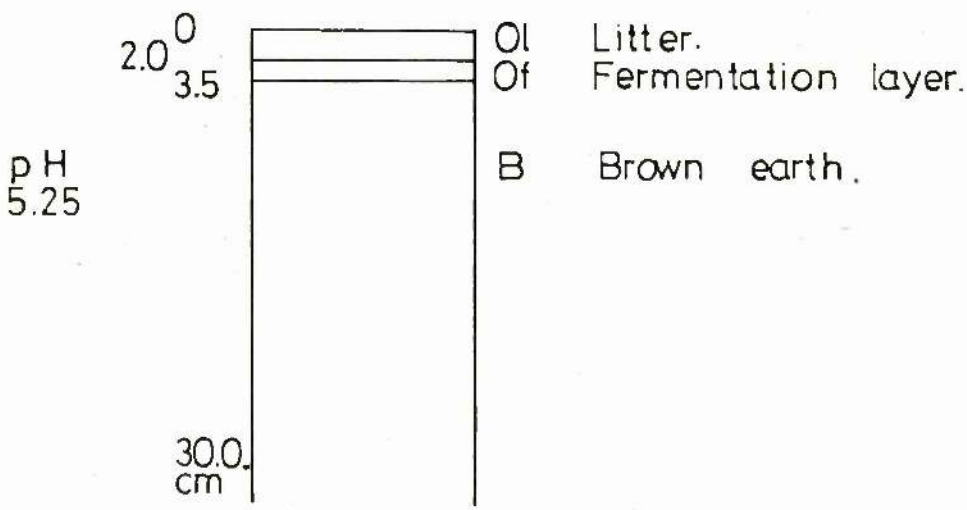
Altitude: 150 m asl.

Total precipitation (1978): 1874 mm (Clatteringshaws NX 554780)

Management: Sheep and cattle grazing

Frond density: $12.0 \pm 7.8/m^2$

Soil profile:



Polharrow Bridge A, Kirkcudbrightshire (GR NX 594844)

Date of sampling: 3.11.78

Aspect: Northerly

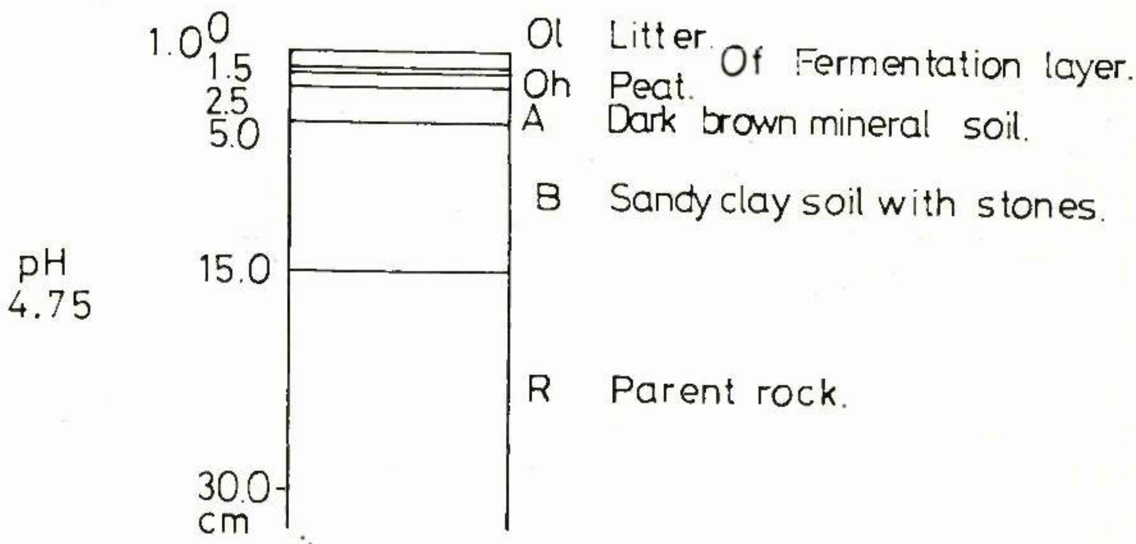
Altitude: 100 m asl.

Total precipitation (1978): 1403 mm (Dundeugh NX 598879)

Management: Sheep grazing

Frond density: 26.8 ± 25.0/m^2

Soil profile:



Polharrow Bridge B, Kirkcudbrightshire (GR NX 593843)

Date of sampling: 9.11.78

Aspect: Northerly

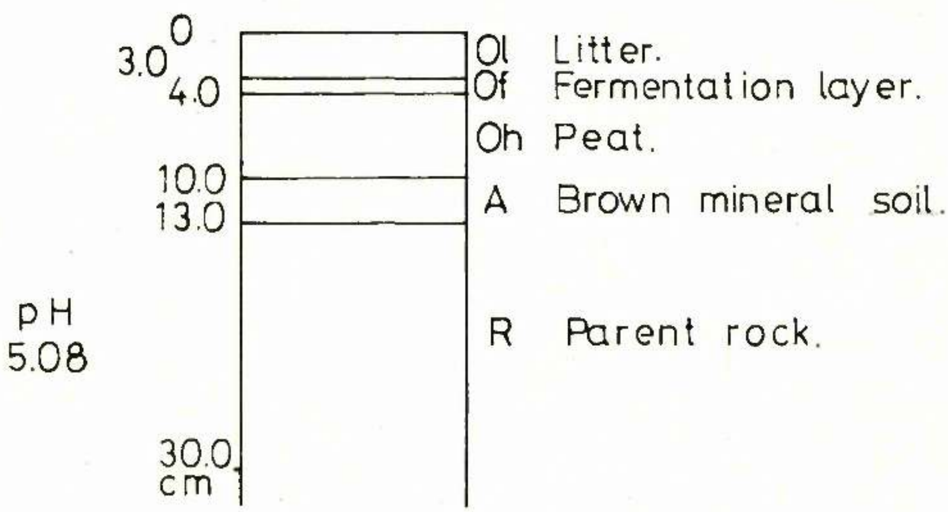
Altitude: 120 m asl.

Total precipitation (1978): 1403 mm (Dundeugh NX 598879)

Management: Sheep grazing

Frond density: $22.4 \pm 10.5/m^2$

Soil profile:



Melfort House A, Argyll (GR NM 821134)

Date of sampling: 8.11.78

Aspect: Southerly

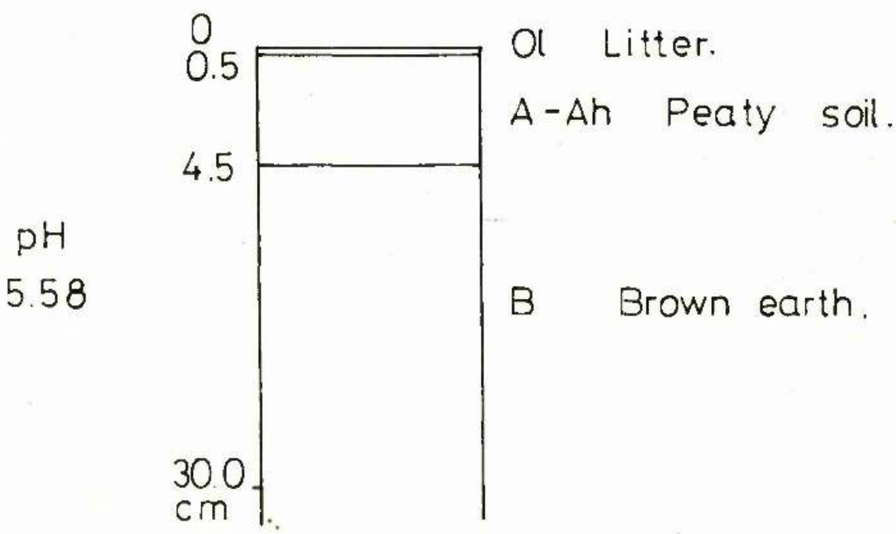
Altitude: 15 m asl.

Total precipitation (1978): 1421 mm (Dunstaffnage NM 881340)

Management: No grazing evident - possibly sheep

Frond density: $25.2 \pm 3.9/m^2$

Soil profile:



Melfort House B, Argyll (GR NM 818137)

Date of sampling: 8.11.78

Aspect: South-easterly

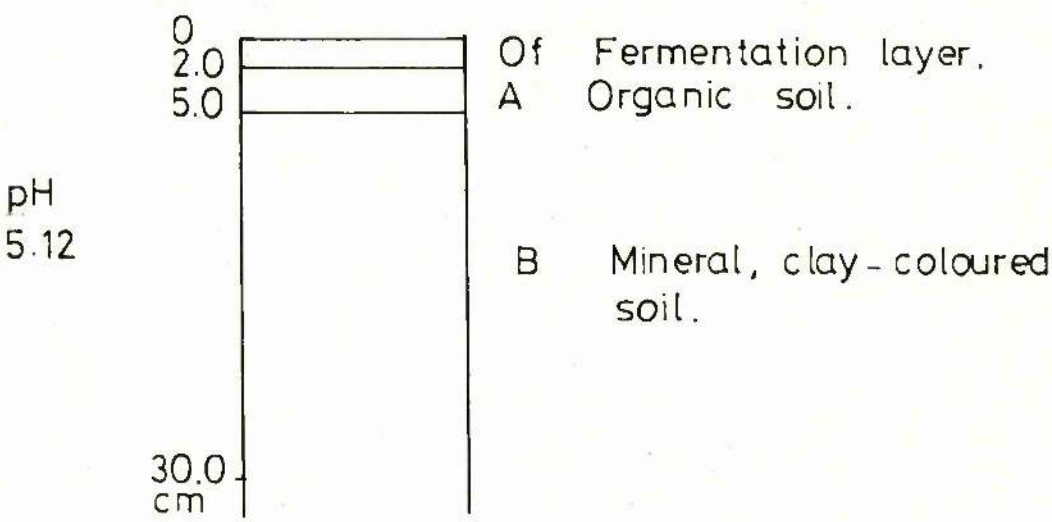
Altitude: 90 m asl.

Total precipitation (1978): 1421 mm (Dunstaffnage NM 881340)

Management: Sheep grazing

Frond density: 16.0 ± 2.8/m^2

Soil profile:



Oban A, Argyll (GR NM 893292)

Date of sampling: 14.11.78

Aspect: North-westerly

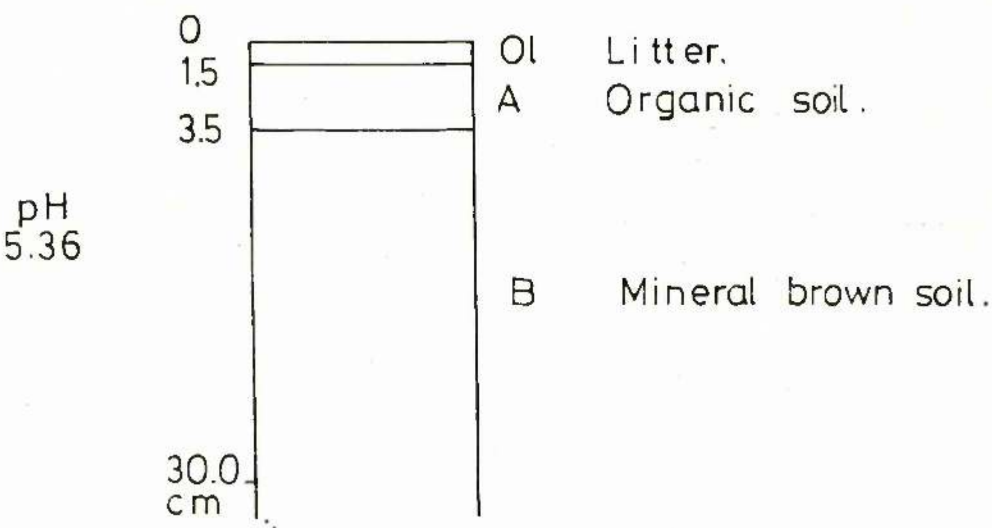
Altitude: 45 m asl.

Total precipitation (1978): 1421 mm (Dunstaffnage NM 881340)

Management: Sheep and cattle grazing

Frond density: $23.6 \pm 9.3/m^2$

Soil profile:



Oban B, Argyll (GR NM 898312)

Date of sampling: 14.11.78

Aspect: Easterly

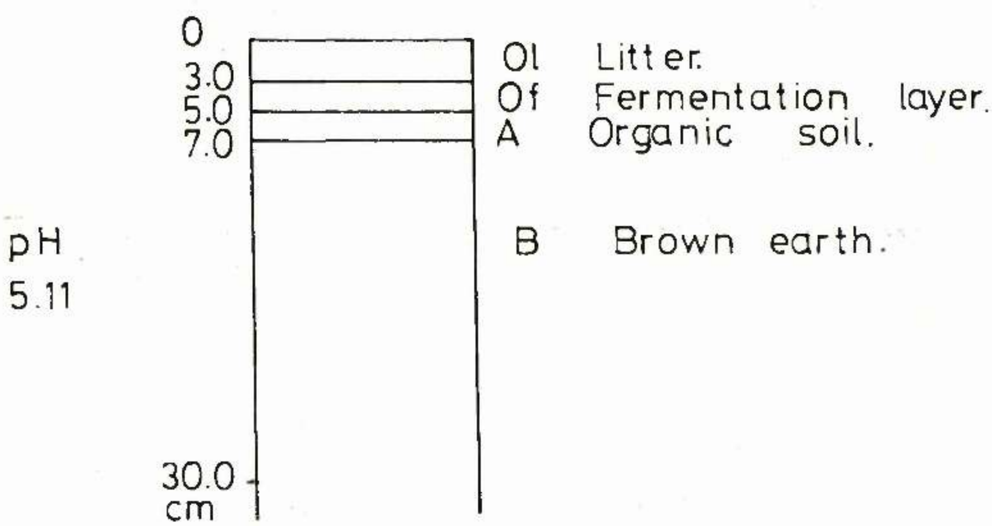
Altitude: 75 m asl.

Total precipitation (1978): 1421 mm (Dunstaffnage NM 881340)

Management: Sheep and cattle grazing

Frond density: $12.0 \pm 6.1/m^2$

Soil profile:



Margrie Farm, Kirkcudbrightshire (GR NX 591505)

Date of sampling: 12.12.78

Aspect: South-easterly

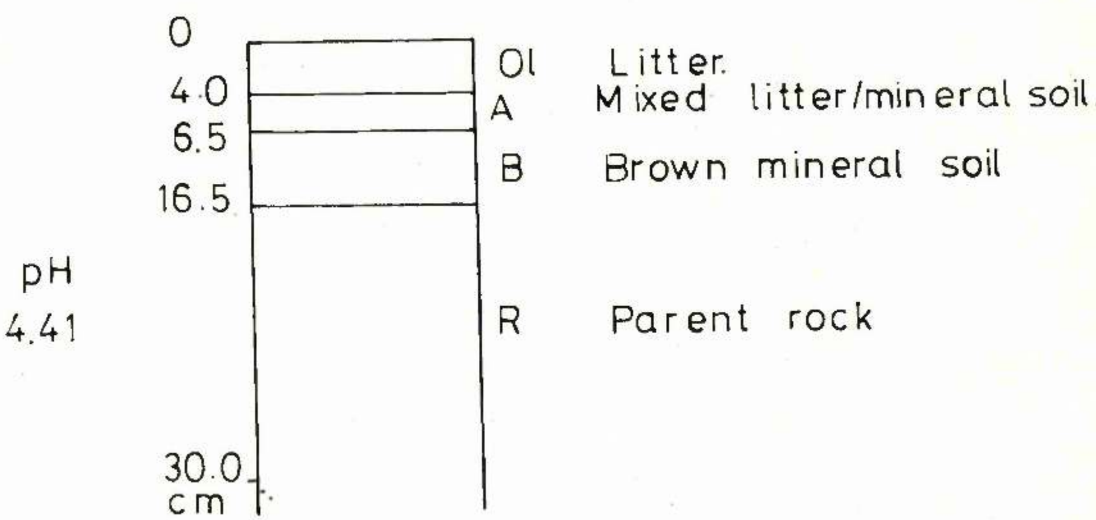
Altitude: 30 m asl.

Total precipitation (1978): 1034 mm (11 months) (Girdstingwood NX 742469)

Management: Cattle grazing

Frond density: $19.0 \pm 2.8/m^2$

Soil profile:



Appendix 1:B

Formula for conversion of mean number of seeds/core to number of seeds/m^2.

Radius of core = 1.25 cm

$$\begin{aligned} \text{Area of core} &= \pi r^2 \\ &= 3.14 \times 1.25^2 \\ &= 4.90625 \text{ cm}^2 \end{aligned}$$

($1\ m^2 = 10{,}000\ cm^2$)

$$\text{Mean number of seeds/core} \times \frac{\text{number of cm}^2/\text{m}^2}{\text{number of cm}^2/\text{core}} = \text{mean number/m}^2$$

$$\equiv \quad \text{Mean number of seeds per core} \times \frac{10{,}000}{4.90625} = \text{mean number/m}^2$$

<u>For example</u>:

Mean number of seeds/core = 15.00

$$\begin{aligned} \text{Mean number of seeds/m}^2 &= 15 \times \frac{10{,}000}{4.90625} \\ &= 15 \times 2038.2165 \\ &= \underline{\underline{30{,}573.25/\text{m}^2}} \end{aligned}$$

Appendix 1:C:Table 1

Number of viable seeds recovered from various depths of soil cores.

Core Number	Site	Depth of core segment (cm) 0-1	1-2	2-3	3-4	4-5	5-6	6-7
1	Gatehouse B					1		
2	Dalry							
3	Dalry		1					
4	Dalry				1			
5	Dalry							
6	Glen Douglas A	1	1					
7	Glen Douglas A	2		1				
8	Kirkton Farm A	4		1				
9	Kirkton Farm A	1						
10	Kirkton Farm A	1						
11	Kirkton Farm A							
12	Kirkton Farm B	1	2	2				
[13	Kirkton Farm B	1	11	1]				
14	Kirkton Farm B	1						
15	Kirkton Farm B							
16	Kirkton Farm B							
17	Kirkton Farm B	1					1	
18	Sundaywellmoor B	1						
19	Polharrow Bridge B			2				
TOTALS [omitting sample no. 13]		13	4	6	1	1	1	0

Appendix 1:C:Table 2

Number of viable seeds recovered from various depths of soil cores.

Core Number	Depth of core segment (cm) 0-1	1-2	2-3	3-4	4-5	5-6	6-7
1	-	-	-	-	1	-	-
2	-	1	-	-	-	-	-
3	-	-	-	1	-	-	-
4	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-
6	1	1	-	-	-	-	-
7	2	-	1	-	-	-	-
8	4	-	1	-	-	-	-
9	1	-	-	-	-	-	-
10	1	-	-	-	-	-	-
11	-	-	-	-	-	-	-
12	1	2	2	-	-	-	-
13	1	11	1	-	-	-	-
14	1	-	-	-	-	-	-
15	-	-	-	-	-	-	-
16	-	-	-	-	-	-	-
17	1	-	-	-	-	1	-
18	1	-	-	-	-	-	-
19	-	-	2	-	-	-	-
20	-	-	-	-	-	-	-
21	-	-	-	-	1		
22	-	-	-	-	-		
23	-	1	-	-	-		
24	1	-	-	2	-		
25	-	-	-	-	-		
26	-	-	-	-	-		
27	-	-	-	-	-		
28	-	-	-	-	-	-	
29	-	-	-	-			
30	-	1	-	1			
31	-	-	2	2	-		
32	1	-	-	-	-	-	
33	1	-	-	1	-		
34	-	-	1	2	-	1	

Core Number	Depth of core segment (cm) 0-1	1-2	2-3	3-4	4-5	5-6	6-7
35	-	-	-	-	-		
36	-	1	-	-	-		
37	1	-	-	-			
38	-	-	1	-			
39	-	-	-	-	-		
40	1	2	1	1	1	-	-
41	-	3	-	-	-		
42	2	-	-	-			
43	-	4	-	1	-		
44	-	1	-	-	2		
45	-	-	4	-	-		
46	3	1	1				
47	-	-	-	-	-	-	-
48	1	4	1	-	-	-	-
49	-	1	2	-	1	-	-
50	-	1	-	-	-	-	-
51	-	-	-	-	-	-	-
52	-	-	1	1	-	-	-
53	-	-	-	-	1	-	-
54	-	-	-	-	-	-	-
TOTALS [omitting sample no. 13]	24	24	20	12	7	2	0

GRAND TOTAL = 89

Appendix 1:C:Table 3

Seed totals for the twenty sites examined in 1978.

Site	No. of viable seeds/m^2	No. of species contributing to total
Gatehouse A	119,338	26-29
Gatehouse B	14,267	19-21
Gatehouse C	18,446	17-19
Barlaes Hill	27,210	11-13
Dalry	4,789	8-10
Glen Douglas A	7,236	7-8
Glen Douglas B	14,471	8-10
Kirkton Farm A	3,261	8-10
Kirkton Farm B	3,771	7-8
Sundaywellmoor A	7,236	9-10
Sundaywellmoor B	4,280	11-12
New Galloway A	10,905	7-8
New Galloway B	4,790	13-14
Polharrow Bridge A	3,261	8-10
Polharrow Bridge B	3,567	8-10
Melfort House A	9,783	9-11
Melfort House B	4,789	10-12
Oban A	3,057	8-10
Oban B	9,682	10-12
Margrie Farm	13,962	11-13
MEAN [omitting Gatehouse A and B]	8,583 $\pm$ 1,531	9-11

Appendix 1:C:Table 4

Complete list of species found in the swards of the sites examined in 1978.

Grasses:

Agrostis stolonifera
Agrostis canina & Agrostis tenuis
Anthoxanthum odoratum
Brachypodium sylvaticum
Dactylis glomerata
Deschampsia caespitosa
Deschampsia flexuosa
Festuca rubra
Holcus lanatus
Holcus mollis
Molinia caerulea
Nardus stricta
*Poa annua
Poa pratensis
Poa trivialis
Sieglingia decumbens

Non-grasses:

Achillea millefolium
Anagallis arvensis
Aphanes arvensis
Calluna vulgaris
Campanula rotundifolia
Capsella bursa-pastoris
Cardamine hirsuta
Carex spp
Cerastium holosteoides
Cirsium arvense
Cirsium dissectum
Cirsium palustre
Cirsium vulgare
Crataegus monogyna
Digitalis purpurea

Endymion non-scriptus
Epilobium palustre
Erica cinerea
Erica tetralix
Galium aparine
Galium saxatile
Geranium molle
Geranium robertianum
Gnaphalium uliginosum
Hylocomium splendens
Hypericum humifusum
Hypnum cupressiforme
Iris foetidissima
Juncus acutiflorus
Juncus bufonius
Juncus effusus
Lonicera periclymenum
Lophocolea bidentata
Lotus corniculatus
Luzula campestris
Luzula pilosa
Lysimachia nummularia
Matricaria matricarioides
*Mentha arvensis
Myosotis arvensis
Oxalis acetosella
Plantago lanceolata
*Plantago major
Polygonum aviculare
*Polygonum hydropiper
Polygonum persicaria
Polytrichum commune
Potentilla anserina
Potentilla erecta
Potentilla sterilis
Primula vulgaris
Prunella vulgaris
Ranunculus repens
Rhytidiadelphus squarrosus
Rubus fruticosus agg.

Sedum album

Silene dioica

Sonchus arvensis

Spergula arvensis

Stellaria alsine

Stellaria holostea

Stellaria media

Teucrium scorodonia

Trifolium repens

Ulex europaeus

Urtica dioica

Vaccinium myrtillus

*Veronica arvensis

Veronica chamaedrys

Veronica officinalis

*Veronica persica

Viola palustris

Viola riviniana

Wahlenbergia hederacea

Species marked with * occurred only in the sprayed sites.

Nomenclature follows Clapham, Tutin and Warburg (1962).

Appendix 1:C:Table 5

Viability of seeds recovered from the twenty site examination 1978.

Species	Mean no. of seeds/m^2 (Total of 20 sites)	Mean no. of viable seeds/m^2	% viability
Agrostis canina & Agrostis tenuis	27,720	27,720	100.00
Agrostis stolonifera	102	102	100.00
Anthoxanthum odoratum	2,549	2,141	83.99
*Aphanes arvensis	714	714	100.00
Calluna vulgaris	10,394	10,394	100.00
Campanula rotundifolia	204	204	100.00
*Capsella bursa-pastoris	816	816	100.00
Cardamine hirsuta	2,345	2,345	100.00
Carex spp	204	204	100.00
Carex binervis	102	102	100.00
Cerastium holosteoides	5,408	4,891	90.44
Deschampsia caespitosa	306	306	100.00
Deschampsia flexuosa	102	102	100.00
Digitalis purpurea	18,649	18,649	100.00
Erica cinerea	24,796	22,317	90.00
Galium saxatile	1,936	1,936	100.00
Gnaphalium uliginosum	6,531	3,567	54.62
Holcus lanatus	2,549	2,549	100.00
Hypericum humifusum	2,446	2,446	100.00
Juncus articulatus	102	102	100.00
Juncus bufonius	49,694	39,643	79.77
Juncus effusus	34,694	23,028	66.38
Luzula campestris	612	612	100.00
Matricaria matricarioides	60,612	56,459	93.15
*Myosotis arvensis	1,122	510	45.45
Plantago major	4,898	4,382	89.47
Poa annua	7,347	6,013	81.84
Poa pratensis & Poa trivialis	8,152	8,152	100.00
*Polygonum aviculare/ Polygonum hydropiper	7,143	3,057	42.80
Polygonum persicaria	2,245	1,019	45.39

Species	Mean no. of seeds/m^2 (Total of 20 sites)	Mean no. of viable seeds/m^2	% viability
Potentilla erecta	3,163	2,549	80.59
Ranunculus repens	1,735	408	23.52
Rumex acetosella	5,612	2,243	39.97
**Rumex obtusifolius*	1,633	815	49.91
Sagina procumbens	4,388	3,670	83.64
**Sonchus asper*	102	102	100.00
**Spergula arvensis*	204	102	50.00
Stellaria media	11,429	8,867	77.58
Trifolium repens	714	102	14.29
**Urtica dioica*	2,755	408	14.81
Veronica arvensis	17,551	16,714	95.23
**Veronica persica*	1,936	1,936	100.00
Veronica serpyllifolia	3,160	3,160	100.00
Viola palustris	102	102	100.00
Unidentified grasses	4,490	1,937	43.14
Unidentified non-grasses	22,653	516	2.25
TOTAL	365,671	288,101	-
Mean viability	-	-	76.92

Species marked with * occurred only in the sprayed sites.

Nomenclature follows Clapham, Tutin and Warburg (1962).

Appendix 2

Data pertaining to Section 7. Variations in buried viable seed populations.

2:A Photograph and description of site at Monksfoot

2:B Experimental techniques

2:C Results of Gatehouse and Monksfoot samplings

2:D Results of 1981 seed survey

2:E Meteorological data for Auchincruive

Appendix 2:A

<u>Monksfoot, Lanarkshire</u> (GR NS 778294)

Aspect: South-westerly

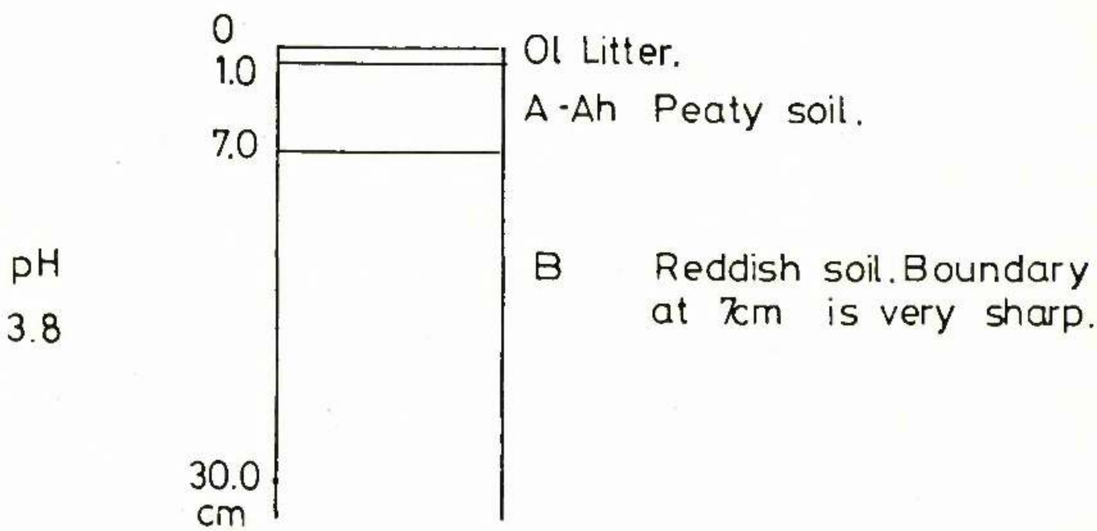
Altitude: 330 m asl.

Total precipitation (1978): 1621 mm (Leadhills GR NS 888151)

Management: Sheep grazing mainly; some cattle grazing also

Frond density: 25 ± 3.60/m^2

Soil profile:



Appendix 2:B

Experimental techniques

Method of sampling at Dalry

The techniques employed in 1978 differed somewhat from those used in 1979 and 1980. In 1978 twenty cores were collected to a depth of 3 cm with a corer 2.5 cm in diameter. These cores were individually dried, washed and sieved, redried and examined under a binocular microscope. Any seeds located were removed, identified and an attempt made to germinate them. After examination the samples were sown out onto compost in the greenhouse where the soil was periodically disturbed and any remaining seeds were given an opportunity to germinate. The samples were arranged in a random order and rotated around the bench at regular intervals. In 1979 and 1980, ninety cores were collected to a depth of 3 cm with a corer 2.3 cm in diameter. Because of the nature of the experiments for which they had been collected, the cores were divided into three replicates each of ten cores. This was equivalent to taking nine samples each of 41.5265 cm^2, compared with twenty samples each of 4.90625 cm^2 in 1978. Allowance was made for these differences when seed numbers/m^2 were calculated. Handling of the samples in the laboratory and the greenhouse in 1979 and 1980 was as for 1978.

Method of sampling at Monksfoot and Gatehouse

Initially only ten cores were collected per site but on 1 May 1981 and thereafter, twenty cores were taken per site, allowance for this being made when the data were converted to seed numbers/m^2. Each core was taken to a depth of 3 cm with a corer 2.3 cm in diameter. Table 1 indicates the dates on which samples were taken at each site.

The cores were dried at 18°C, sieved and washed, redried and examined visually prior to sowing out onto Levington compost in the greenhouse for a period of three months. Any seeds located in the

Appendix 2:B:Table 1

Dates of sampling at Monksfoot and Gatehouse.

Monksfoot	Gatehouse
1980	1980
4 September	29 September
30 September	5 November
5 November	28 November
2 December	12 December
1981	1981
5 January	6 January
2 February	2 February
27 February	27 February
30 March	31 March
1 May	1 May
1 June	29 May
29 June	29 June
27 July	27 July
3 September	3 September

laboratory were identified and an attempt made to germinate them. In the greenhouse the soil was periodically disturbed to stimulate seed germination and seedlings which emerged were identified and recorded. The pots were rotated regularly to ensure that no one treatment was subject to more or less favourable conditions than any other.

Few seeds were recovered from the cores collected at Monksfoot and examined visually and therefore after 5 November 1980 the cores from this site were sown out directly onto compost after drying and sieving.

All the cores collected at Gatehouse in September and on 5 November 1980 were examined visually prior to sowing out. On the subsequent four occasions, five samples were sown out directly and five were visually examined prior to sowing out; the results are given in Table 2. It would appear that significant differences would not arise in the estimates of the seed populations if the samples were sown out directly. Similar non-significant differences in the two techniques were noted in Section 6.2.

Thus, samples collected from Gatehouse from 27 February 1981 to September 1981 inclusive were sown out directly after drying and sieving.

Several workers (Champness, 1949b; Roberts, 1958) found that it was necessary to use a square root transformation prior to analysing their data because the seeds tended to be distributed unevenly between the samples on a given date. Although on several occasions large numbers of seeds of a particular species were found in one or two cores on a sampling date, the transformed data did not appear to have a distinct advantage over the untransformed data in this work.

Method of sampling at the 1978/1981 seed survey sites

The sites were first sampled in 1978 and the methods and full results of this survey are given in Section 6. All the sites were resampled in January 1981 when, at each site, twenty cores were taken to

Appendix 2:B:Table 2

Comparison of seed recovery by visual sorting of Catchouse samples prior to sowing out and sowing out samples directly onto compost.

Date of sampling	Mean number of seeds recovered by visual sorting prior to sowing out	by sowing out directly
1980		
28 November	56.40	40.20
12 December	24.00	26.60
1981		
6 January	11.80	21.60
2 February	10.80	5.40

Differences are not statistically significant

a depth of 3 cm with a corer 2.3 cm in diameter. The cores were dried in a warm room (18°C), sieved to reduce the bulk of the sample and sown out directly onto compost in shallow saucers in the greenhouse. The samples were stirred at intervals and rotated around the bench regularly. Any seeds which germinated over a period of four months were recorded. The data were converted to seed numbers/m^2.

Appendix 2:C:Table 1

Species recovered as seed at Monksfoot from September 1980 to September 1981.

No. of seeds recovered

Species	4 Sept, 1980	30 Sept, 1980	5 Nov, 1980	2 Dec, 1980	5 Jan, 1981	2 Feb, 1981	27 Feb, 1981	30 March, 1981	1 May, 1981	1 June, 1981	29 June, 1981	27 July, 1981	3 Sept, 1981	TOTAL
Agrostis spp		3	2	8	2	6		3	10	7	2	10	8	61
A. odoratum	1			6										7
Betula spp													1	1
Carex spp				1									1	2
G. saxatile				2										2
Juncus spp	1			17		5		24	1			1		49
L. campestris							1							1
Poa spp			1	2		1			2		4	1		11
P. erecta											2			2
R. acetosella	1													1
S. procumbens			1											1
TOTAL	3	3	4	36	2	12	1	27	13	7	8	12	10	138

From 4 September 1980 to 30 March 1981, ten samples were collected on each occasion. After 30 March, twenty samples were collected at each date.

Appendix 2:C:Table 2

Species recovered as seed at Gatehouse between September 1980 and September 1981.

Species	No. of seeds recovered 29 Sept, 1980	5 Nov, 1980	28 Nov, 1980	12 Dec, 1980	6 Jan, 1981	2 Feb, 1981	27 Feb, 1981	31 March, 1981	1 May, 1981	29 May, 1981	29 June, 1981	27 July, 1981	3 Sept, 1981	TOTAL
Agrostis spp	4	1				4			3	9	1	3	5	30
A. arvensis	90	2		7	9		1	1	1	2			1	114
Betula spp			1											1
C. bursa-pastoris		5	5		2									12
C. hirsuta				9	1	30			1		1	1	2	45
C. holosteoides	9	8	11	5	12	1	1	4	7	7	7	7	3	82
C. arvense					1									1
C. palustre											1	1		2
D. flexuosa										1				1
D. purpurea	1													1
G. uliginosum	8	13	25	8	11	3	5	5	11	26	13	45	9	182
Juncus spp	31	110	193	64	10	14	3	4	4	19	1	11	22	486
M. matricarioides	5	559	125	63	76	2	2	2	3	15	10	7	8	877
M. fontana	1													1
M. arvensis												1	3	4
P. major	•	16	6	3	3	3			3	4	2	5	2	47
Poa spp	2	96	24	13	8	2	1	1	11	10	4	4	9	185
Polygonum spp	3	7	1		1				1	2	1			16
P. vulgaris				1	2				2	2		1	1	9
R. repens	2													2

(cont ....)

Species	No. of seeds recovered													
	29 Sept, 1980	5 Nov, 1980	28 Nov, 1980	12 Dec, 1980	6 Jan, 1981	2 Feb, 1981	27 Feb, 1981	31 March, 1981	1 May, 1981	29 May, 1981	29 June, 1981	27 July, 1981	3 Sept, 1981	TOTAL
R. acetosella	12													12
R. obtusifolius		6	5	1										12
S. procumbens	8	1	12	16	10	10	2	2	41	64	3	19	52	240
S. vulgaris				1										1
S. decumbens			1											1
S. arvensis			1			1	1	1	1					5
S. media	2	37	22	17	3	4			1	3	5	2	4	100
T. repens	1													1
U. dioica		1		1		1								3
V. arvensis	8	39	32	29	8	2			5	6	1			130
V. officinalis											1			1
V. persica	2	43	11	10	6	3	1	1	2	3	4	2	6	94
V. serpyllifolia	9	21	8	5	3	1		1			2		1	51
Unidentified species		1												1
TOTAL	198	967	483	253	167	81	17	22	97	173	57	109	128	2752

Between 29 September 1980 and 30 March 1981, ten cores were collected on each occasion; after 30 March, twenty cores were taken on each date.

Appendix 2:D

Results of 1981 seed survey

Barlaes Hill - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (A. canina, A. stolonifera, A. tenuis)	1,565	65.04
Anthoxanthum odoratum	361	15.00
Calluna vulgaris and Erica cinerea	120	4.99
Galium saxatile	120	4.99
Holcus lanatus	120	4.99
Juncus spp (J. bufonius, J. effusus)	120	4.99
TOTAL	2,406	100.00

Dalry - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (A. canina, A. stolonifera, A. tenuis)	361	30.01
Galium saxatile	361	30.01
Poa spp (P. annua, P. pratensis, P. trivialis)	241	20.02
Veronica officinalis	120	9.98
Unidentified species	120	9.98
TOTAL	1,203	100.00

Glen Douglas A - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (A. canina, A. stolonifera, A. tenuis)	602	15.62
Carex spp	120	3.11
Juncus spp (J. bufonius, J. effusus)	3,131	81.27
TOTAL	3,853	100.00

<u>Glen Douglas B</u> - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
<u>Agrostis</u> spp (<u>A. canina</u>, <u>A. stolonifera</u>, <u>A. tenuis</u>)	241	22.23
<u>Calluna vulgaris</u> and <u>Erica cinerea</u>	482	44.46
<u>Juncus</u> spp (<u>J. bufonius</u>, <u>J. effusus</u>)	120	11.08
Unidentified species	241	22.23
TOTAL	1,084	100.00

<u>Kirkton Farm A</u> - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
<u>Agrostis</u> spp (<u>A. canina</u>, <u>A. stolonifera</u>, <u>A. tenuis</u>)	602	38.50
<u>Calluna vulgaris</u> and <u>Erica cinerea</u>	120	7.67
<u>Juncus</u> spp (<u>J. bufonius</u>, <u>J. effusus</u>)	482	30.82
<u>Luzula campestris</u>	120	7.67
<u>Rumex acetosella</u>	120	7.67
Unidentified species	120	7.67
TOTAL	1,564	100.00

<u>Kirkton Farm B</u> - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
<u>Carex</u> spp	120	11.08
<u>Galium saxatile</u>	241	22.26
<u>Juncus</u> spp (<u>J. bufonius</u>, <u>J. effusus</u>)	361	33.33
<u>Sieglingia decumbens</u>	361	33.33
TOTAL	1,083	100.00

Sundaywellmoor A - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (A. canina, A. stolonifera, A. tenuis)	963	42.15
Calluna vulgaris and Erica cinerea	722	31.60
Crataegus monogyna	120	5.25
Luzula campestris	120	5.25
Matricaria matricarioides	120	5.25
Poa spp (P. annua, P. pratensis, P. trivialis)	120	5.25
Unidentified species	120	5.25
TOTAL	2,285	100.00

Sundaywellmoor B - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (A. canina, A. stolonifera, A. tenuis)	482	36.40
Anthoxanthum odoratum	120	9.06
Calluna vulgaris and Erica cinerea	361	27.28
Juncus spp (J. bufonius, J. effusus)	241	18.20
Veronica serpyllifolia	120	9.06
TOTAL	1,324	100.00

New Galloway A - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (A. canina, A. stolonifera, A. tenuis)	722	50.08
Anthoxanthum odoratum	120	8.32
Calluna vulgaris and Erica cinerea	120	8.32
Digitalis purpurea	120	8.32
Galium saxatile	120	8.32
Hypericum humifusum	120	8.32
Unidentified species	120	8.32
TOTAL	1,442	100.00

New Galloway B - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (A. canina, A. stolonifera, A. tenuis)	482	16.68
Holcus lanatus	120	4.15
Juncus spp (J. bufonius, J. effusus)	482	16.68
Poa spp (P. annua, P. pratensis, P. trivialis)	963	33.32
Sagina procumbens	361	12.49
Stellaria media	482	16.68
TOTAL	2,890	100.00

Polharrow Bridge A - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (A. canina, A. stolonifera, A. tenuis)	2,408	74.07
Carex spp	241	7.41
Festuca rubra	120	3.69
Poa spp (P. annua, P. pratensis, P. trivialis)	482	14.83
TOTAL	3,251	100.00

Polharrow Bridge B - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (A. canina, A. stolonifera, A. tenuis)	722	60.08
Calluna vulgaris and Erica cinerea	120	9.98
Carex spp	120	9.98
Hypericum humifusum	120	9.98
Juncus spp (J. bufonius, J. effusus)	120	9.98
TOTAL	1,202	100.00

Melfort House A - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (*A. canina*, *A. stolonifera*, *A. tenuis*)	120	3.02
Cerastium holosteoides	120	3.02
Juncus spp (*J. bufonius*, *J. effusus*)	843	21.22
Poa spp (*P. annua*, *P. pratensis*, *P. trivialis*)	241	6.06
Ranunculus repens	241	6.06
Urtica dioica	2,047	51.52
Veronica serpyllifolia	361	9.10
TOTAL	3,973	100.00

Melfort House B - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (*A. canina*, *A. stolonifera*, *A. tenuis*)	120	7.67
Calluna vulgaris and *Erica cinerea*	241	15.41
Galium saxatile	120	7.67
Juncus spp (*J. bufonius*, *J. effusus*)	120	7.67
Veronica officinalis	361	23.08
Veronica persica	241	15.41
Unidentified species	361	23.08
TOTAL	1,564	100.00

Oban A - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (*A. canina*, *A. stolonifera*, *A. tenuis*)	1,445	17.40
Cardamine hirsuta	120	1.44
Gnaphalium uliginosum	241	2.90
Juncus spp (*J. bufonius*, *J. effusus*)	4,816	57.98
Poa spp (*P. annua*, *P. pratensis*, *P. trivialis*)	722	8.69
Spergula arvensis	120	1.44
Urtica dioica	843	10.15
TOTAL	8,307	100.00

Oban B - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (*A. canina*, *A. stolonifera*, *A. tenuis*)	120	14.27
Cerastium holosteoides	120	14.27
Poa spp (*P. annua*, *P. pratensis*, *P. trivialis*)	361	42.92
Ranunculus repens	120	14.27
Veronica serpyllifolia	120	14.27
TOTAL	841	100.00

Margrie Farm - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (*A. canina*, *A. stolonifera*, *A. tenuis*)	602	21.74
Digitalis purpurea	602	21.74
Juncus spp (*J. bufonius*, *J. effusus*)	241	8.70
Poa spp (*P. annua*, *P. pratensis*, *P. trivialis*)	1,204	43.48
Unidentified species	120	4.34
TOTAL	2,769	100.00

Gatehouse of Fleet C - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (*A. canina*, *A. stolonifera*, *A. tenuis*)	1,445	15.79
Cardamine hirsuta	241	2.63
Cerastium holosteoides	241	2.63
Gnaphalium uliginosum	1,084	11.85
Holcus lanatus	241	2.63
Juncus spp (*J. bufonius*, *J. effusus*)	4,816	52.63
Poa spp (*P. annua*, *P. pratensis*, *P. trivialis*)	602	6.58
Sagina procumbens	361	3.95
Stellaria media	120	1.31
TOTAL	9,151	100.00

Gatehouse of Fleet A - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (A. canina, A. stolonifera, A. tenuis)	120	0.41
Aphanes arvensis	1,686	5.67
Capsella bursa-pastoris	241	0.81
Cardamine hirsuta	361	1.21
Cerastium holosteoides	1,927	6.48
Cirsium arvense	120	0.41
Digitalis purpurea	120	0.41
Gnaphalium uliginosum	1,565	5.26
Juncus spp (J. bufonius, J. effusus)	2,288	7.69
Matricaria matricarioides	11,559	38.87
Plantago major	843	2.83
Poa spp (P. annua, P. pratensis, P. trivialis)	1,806	6.07
Polygonum spp (P. aviculare, P. hydropiper, P. persicaria)	120	0.41
Prunella vulgaris	241	0.81
Sagina procumbens	1,204	4.05
Stellaria media	602	2.02
Veronica arvensis	2,769	9.31
Veronica persica	1,686	5.67
Veronica serpyllifolia	361	1.21
Unidentified species	120	0.40
TOTAL	29,739	100.00

Gatehouse of Fleet B - Viable seed population in 1981

Species	Mean no. of viable seeds/m^2	% contribution to seed population
Agrostis spp (*A. canina*, *A. stolonifera*, *A. tenuis*)	120	2.17
Aphanes arvensis	120	2.17
Cardamine hirsuta	1,204	21.75
Cerastium holosteoides	963	17.39
Juncus spp (*J. bufonius* *J. effusus*)	120	2.17
Myosotis arvensis	120	2.17
Poa spp (*P. annua*, *P. pratensis*, *P. trivialis*)	482	8.71
Polygonum spp (*P. aviculare*, *P. hydropiper*, *P. persicaria*)	120	2.17
Sagina procumbens	722	13.05
Stellaria media	963	17.39
Urtica dioica	120	2.17
Veronica arvensis	241	4.35
Veronica persica	120	2.17
Unidentified species	120	2.17
TOTAL	5,535	100.00

Appendix 2:E

Auchincruive rainfall data (mm).

	1977	1978	1979	1980	1981
January	52.0	79.8	74.7	63.8	105.0
February	67.3	41.3	14.8	54.9	58.7
March	84.7	125.9	96.8	57.8	108.7
April	75.1	20.3	58.0	4.4	18.8
May	50.4	7.2	41.8	22.8	78.5
June	36.1	40.9	45.9	85.7	70.0
July	49.0	47.3	83.2	164.3	88.3
August	136.5	93.6	146.6	157.9	36.5
September	134.4	149.3	65.1	121.4	210.5
October	185.1	66.6	115.1	189.7	173.2
November	135.5	127.1	182.5	101.1	134.1
December	53.1	67.4	121.6	135.0	25.0
TOTAL	1059.2	866.7	1046.1	1158.8	1107.3
% of 30 yr mean	117.69	96.30	116.23	128.76	123.03

30 yr mean = 900 mm

Appendix 3

Data pertaining to Section 9. Changes in sward composition and the role of the buried seed bank in its recovery following bracken frond clearance with asulam or glyphosate.

3:A Experimental techniques

Appendix 3:A

Method of calculating number of seeds /m^2 from number of seeds/core at Dalry, 1979-1981.

Diameter of core: 2.3 cm

Area of core: πr^2

$$\equiv \quad 3.14 \times 2.3^2 \quad \underline{= \ 4.15265 \ cm^2}$$

To convert seed numbers/core to seed numbers/m^2

$$\text{No. of seeds/core} \times \frac{\text{no. of } cm^2/m^2}{\text{no. of } cm^2/\text{core}}$$

$$\equiv \text{No. of seeds/core} \times \frac{10{,}000}{4.15265}$$

$$\equiv \text{No. of seeds/core} \times 2408.1008$$

<u>For example</u> Three samples each of ten cores contain 18, 13 and 4 seeds. The average number recovered from these 30 cores is thus 1.17.

$$1.17 \text{ seeds/core} \equiv 1.17 \times 2408.1008 \text{ seeds}/m^2$$

$$\underline{= 2809.45/m^2}$$

Since 1 seed/core $\equiv$ 2408.1008/m^2, 1 seed/30 cores is $\equiv$ 80.2700/m^2. Therefore finding one extra seed, or one less seed, in a sample at Dalry alters the seed population estimates in Tables 35 and 36 by 80 seeds/m^2.

Appendix 4

Data pertaining to Section 10. The concept of allelopathy with respect to bracken.

4:A Experimental results

Appendix 4:A:Table 1

Effect of a 0.5% solution of 'chloros' on seed germination.

Treatment Species	Water	'chloros'
Trifolium repens	16.00	13.33
Lolium perenne	48.00	48.66
Festuca rubra	46.00	43.00
Agrostis tenuis	29.33	31.00
Poa pratensis	45.00	45.00
Poa trivialis	48.33	49.00

Differences are not statistically significant.

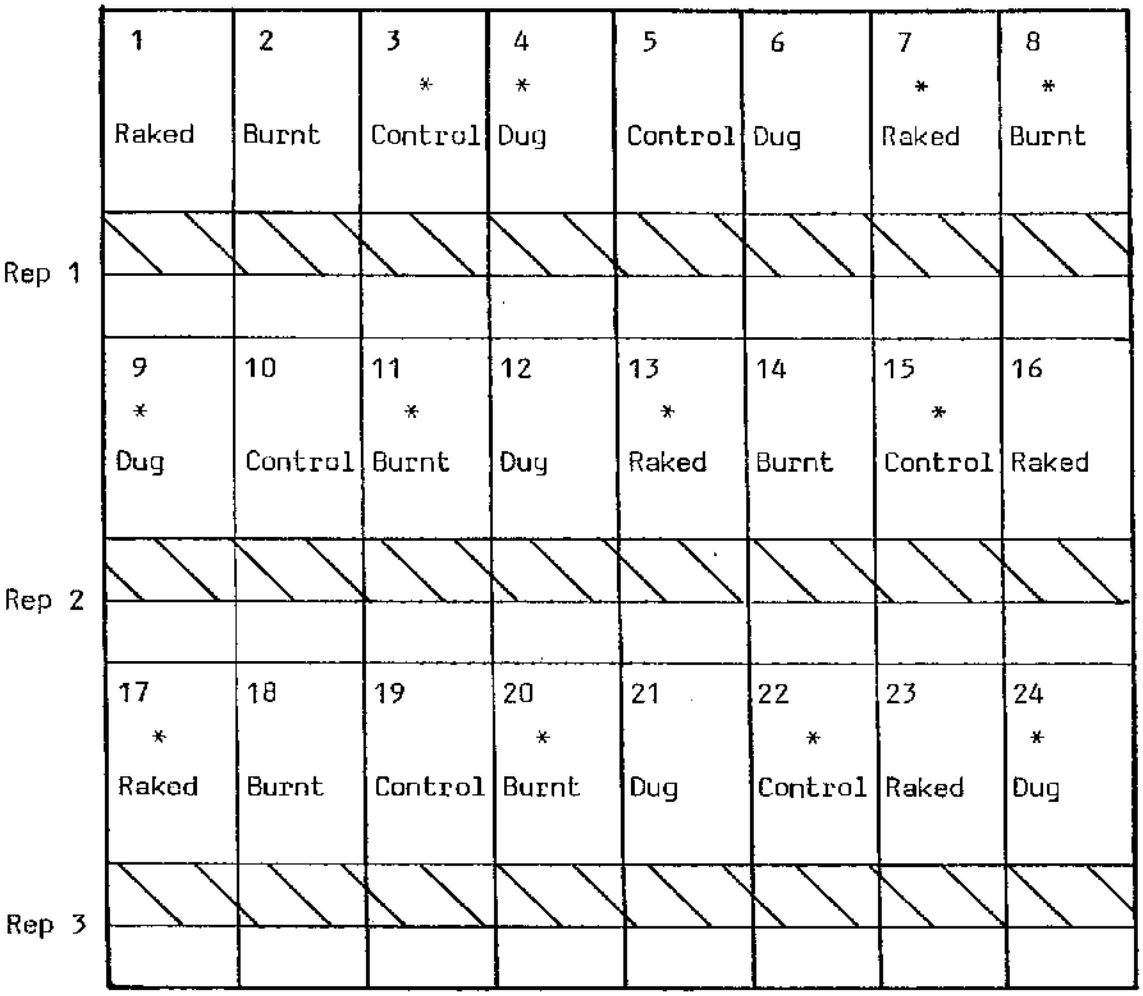
Appendix 5

Data pertaining to Section 11. The improvement of hill land cleared of bracken with asulam.

5:A Experimental design of trial

Appendix 5:A

Experimental design at Gatehouse



* Denotes plots receiving lime, fertiliser and seed.

Denotes position of strip across each plot.

<u>Rates of fertiliser, lime and seed applied per plot</u>

Seed: 0.84 g *T. repens* ≡ 2.25 kg/ha)
5.20 g *F. rubra* ≡ 13.875 kg/ha)
5.20 g *L. perenne* ≡ 13.875 kg/ha)

Lime: 750.00 g $CaCO_3$ ≡ 2 t/ha

Fertiliser: 22.50 g P_2O_5 ≡ 60 kg/ha P_2O_5 ≡ 26.20 kg/ha P.
Granular superphosphate, which is 21% P_2O_5, was used, therefore 107.14 g were applied per plot.

Appendix 6

Statistical techniques

6. Statistical techniques

6.1 *Introduction*

Three statistical tests were employed to analyse the data. These were:

(a) The t test.

(b) The analysis of variance or ANOVA.

(c) The linear regression.

One transformation was used on the data - the arcsin transformation.

The majority of the data were analysed using the ANOVA but one of the assumptions of this test is that each of the variables being compared is independent of the others. Because the percentage ground cover of the species in the autumn was dependent upon the cover in spring, ANOVA could not be used for this or similar comparisons based upon observations at time t and time t + 1 ... n. On these occasions the t test was used, although this technique had the disadvantage that only two means could be compared at any one time.

Linear regression enabled the relationship between two factors, one independent and one dependent upon the other, to be examined. This technique was used to describe the relationship between, for example, soil pH and seed numbers.

The theory behind these techniques, with appropriate examples, is given here but the many individual calculations and analyses of the results obtained during this study are not included in the thesis. Where treatments or relationships were found to be statistically significant, this has been indicated in the text and the level of significance ($P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$) has been stated.

6.2 The t test

This test enables one to compare two treatment means and to ascertain whether differences between them are statistically significant or are due to random chance.

Initially a null hypothesis (Ho) is set up which says that there is no significant difference between the two means. An alternative hypothesis (Ha) automatically exists which says that there is a significant difference between the two means. Each of the two means ($\bar{x}1$ and $\bar{x}2$) is subject to a certain amount of error (SD1 and SD2). The difference between the two means is therefore subject to the error of both means. In order to carry out the calculations the variances ($s^2 1/n$ and $s^2 2/n$) are substituted for the standard deviations (SD1 and SD2) and the square root is calculated. The values obtained so far ($\bar{x}1$ and $\bar{x}2$) and ($\sqrt{s^2 1/n_1}$ and $s^2 2/n_2$) are substituted into the equation:

$$t = \frac{\text{deviation of the difference of the means from zero}}{\text{standard deviation of the difference of the means}}$$

At this point it is useful to introduce some data as an example. In this case the cover of bare ground on two dates is being compared

Variate 1.		Variate 2.	
% bare ground in May.		% bare ground in September.	
$\bar{x}1$	79.13	$\bar{x}2$	6.03
$s^2 1$	22.96	$s^2 2$	28.20
n1	3	n2	3

where $\bar{x}1$, $s^2 1$ and n1 are respectively, the mean, the variance and the number of observations of variate one contributing to $\bar{x}1$ and $s^2 1$. Similar notation has been used for variate two.

Substituting in the equation:

$$t = \frac{79.13 - 6.03}{\sqrt{\frac{22.96}{3} + \frac{28.20}{3}}} = \frac{73.10}{4.13} = 17.70$$

The Ho states that $\bar{x}1 - \bar{x}2 = 0$. However, calculation shows that $\bar{x}1 - \bar{x}2 = 73.10$ i.e. it deviates from the expected value 0 by 73.10 and this amount of deviation is 17.70 times that of its standard deviation. The next step is to determine whether this value of 17.70 is greater than that expected from a normally distributed population.

The tables of the distribution of t give the maximum values of t that may be expected with a normally distributed population. To obtain a value of t from the tables the number of degrees of freedom (df) must be determined. There were three observations per treatment and for the mean value in each case the sum of deviations must equal zero. Therefore for each treatment one value is 'fixed' and not free to vary. Thus the number of df is calculated as $(n1 + n2) - 2$ i.e. $(3 + 3) - 2 = 4$. From the tables for 4 df and $P \leq 0.001$, $t = 8.61$. Therefore one might expect the difference of the means to be up to, but not more than, 8.61 times its standard deviation in 99.9% of cases. Here the difference is 17.70 times the standard deviation, far greater than that expected. For the Ho of no significant difference between the means, and hence the treatments, to be accepted, the difference between $\bar{x}1$ and $\bar{x}2$ must be no greater than $8.61 \times 4.13 = 35.56$. The actual value is 73.10 and the Ho must therefore be rejected in this case.

6.3 *Analysis of variance (ANOVA)*

This technique enables a comparison of several treatments to be made at one time and the majority of the data were analysed by ANOVA.

Each observation recorded for a particular variate deviates from the overall mean. These deviations, or variances, can be divided into a number of component parts each related to different causal circumstances. The analysis calculates the variances about the means of these components and assesses the significance of these variances.

6.3.1 Method of calculation using a worked example

Dry weight of grass (g).

		Litter treatment (L)				
		Control	Raked	Burnt	Dug	Σ
- Fert. (F)	Rep 1	17.19	23.00	14.71	6.71	
	Rep 2	T1 10.97	T2 15.12	T3 3.63	T4 7.50	116.74
	Rep 3	1.23	3.68	6.12	6.88	
+ Fert. (F)	Rep 1	17.74	18.79	14.52	3.55	
	Rep 2	T5 13.65	T6 8.42	T7 8.79	T8 6.19	105.98
	Rep 3	1.76	10.12	0.26	2.19	
	Σ	62.54	79.13	48.03	33.02	222.72

$\Sigma T1 = 29.39$ $\Sigma T2 = 41.80$ $\Sigma T3 = 24.46$ $\Sigma T4 = 21.09$

$\Sigma T5 = 33.15$ $\Sigma T6 = 37.33$ $\Sigma T7 = 23.57$ $\Sigma T8 = 11.93$

ΣRep 1 = 116.21 ΣRep 2 = 74.27 ΣRep 3 = 32.24

A null hypothesis (Ho) of no difference between the means is set up to be tested. The alternative hypothesis (Ha) is that there are differences between the means.

A correction factor (CF) to account for the variation of the observations is calculated:

$$CF = \frac{(\Sigma x)^2}{n} = \frac{(222.72)^2}{24} = 2066.8415$$

S Total $= \Sigma x^2 - CF$

= Corrected sum of squares of all observations.

= 2978.51 - CF

= 911.6685

S Treatment = $(\Sigma T1^2/n + \Sigma T2^2/n \ldots\ldots \Sigma T8^2/n) - CF$

= Corrected sum of squares of the eight treatments.

= $(29.39^2/3 + 41.80^2/3 \ldots\ldots 11.93^2/3) - CF$

= 214.6293

S Replicates = $(\Sigma Rep\ 1^2/n + \Sigma Rep\ 2^2/n + \Sigma Rep\ 3^2/n) - CF$

= Corrected sum of squares of the three replicates.

= $(116.21^2/8 + 74.27^2/8 + 32.24^2/8) - CF$

= 440.6853

S Error = S Total - S Treatment - S Replicates

= Any variation due to random chance and not accounted for by the differences between either the treatments or the replicates.

= 911.6685 - 214.6293 - 440.6853

= 256.3539

The variation due to treatments (S Treatment) can be subdivided into that due to the litter treatment (S Litter) and that due to the addition of fertiliser, lime and seed (or the lack of it) (S Fertiliser) and also into a component indicating any interaction between these two factors (S L x F).

S Litter = $(\Sigma L1^2/n + \Sigma L2^2/n \ldots\ldots \Sigma L4^2/n) - CF$

= $(62.54^2/6 + 79.13^2/6 \ldots\ldots 33.02^2/6) - CF$

= 194.8266

S Fertiliser = $(\Sigma F1^2/n + \Sigma F2^2/n) - CF$

= $(116.74^2/12 + 105.98^2/12) - CF$

= 4.8240

$\mathcal{S}$ F x L = $\mathcal{S}$ Treatment - $\mathcal{S}$ Litter - $\mathcal{S}$ Fertiliser

= 214.6293 - 194.8266 - 4.8240

= 14.9787

The degrees of freedom for each component are calculated as:

No. of observations = 24. No. of df = 24 - 1 = 23.

No. of replicates = 3. No. of df = 3 - 1 = 2.

No. of fertiliser treatments = 2. No. of df = 2 - 1 = 1.

No. of litter treatments = 4. No. of df = 4 - 1 = 3.

No. of df for F x L = No. of df for L x no. of df for F = 3 x 1 = 3.

No. of df for error = 23 - 2 - 1 - 3 - 3 = 14.

ANOVA table

Source of variation	df	S	MS	VR	Signif.
Replicates	2	440.6853	220.3427	12.03	P≤0.001
Fertiliser	1	4.8240	4.8240	0.26	NS
Litter	3	194.8266	64.9422	3.54	P≤0.05
F x L	3	14.9787	4.9929	0.27	NS
Error	14	256.3539	18.3100		
Total	23	911.6685			

Thus, there are significant differences between the replicates (P≤0.001) and also between the litter treatments (P≤0.05).

From the error mean square (EMS) three SEDs (standard error of the difference between means) can be calculated; one for the effect of fertiliser, one for the effect of litter and one for the interaction of the two factors. When the ANOVA examines the effect of the presence or absence of fertiliser, the fact that four litter treatments were also imposed is ignored. Thus, 12 observations contribute to the mean of the treatments receiving fertiliser and 12 to the mean of the observations not receiving fertiliser. Similarly when the effect of the litter treatments is examined, the ANOVA ignores the effect of fertiliser and thus 6 observations contribute to each mean for each litter treatment. When one wishes to compare the effect of the four litter treatments one uses SED No. 2 and when one wishes to compare the effect of fertiliser one uses SED No. 1. If one wishes to compare the eight treatments one with another, one uses the SED associated with the interaction term (No. 3). An SED should ONLY be calculated when the ANOVA shows the factor to be significant. In this example the litter SED (No. 2) is the only one which should be calculated and used. If one wishes to determine whether there are significant differences between the replicates, all other factors are ignored and eight observations contribute to each mean. The SED used in this case is No. 4.

SED No. 1	$\sqrt{EMS \times 2/12}$	=	$\sqrt{(18.31 \times 2)/12}$	=	1.75
SED No. 2	$\sqrt{EMS \times 2/6}$	=	$\sqrt{(18.31 \times 2)/6}$	=	2.47
SED No. 3	$\sqrt{EMS \times 2/3}$	=	$\sqrt{(18.31 \times 2)/3}$	=	3.49
SED No. 4	$\sqrt{EMS \times 2/8}$	=	$\sqrt{(18.31 \times 2)/8}$	=	2.14

Table of means

	Control	Raked	Burnt	Dug	Mean	SED
- Fertiliser	9.79	13.93	8.13	7.03	9.72	1.75
+ Fertiliser	11.05	12.44	7.86	3.98	8.83	
Mean	10.42	19.41	7.99	5.51		
SED	2.47					

Within table SED 3.49

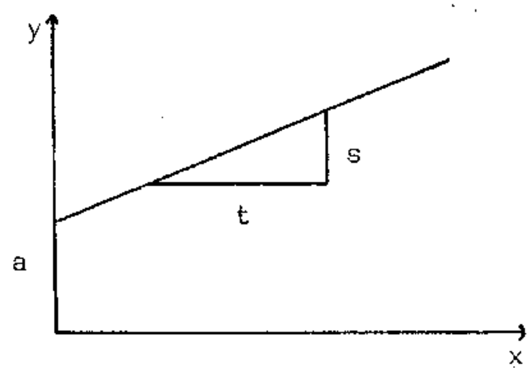
In Section 11, on the dry weight yield figures SED L, F or F x L indicates that the overall ANOVA was significant for the effect of litter, fertiliser or the interaction of the two factors respectively. SEDs have been omitted from the percentage cover figures for the sake of clarity.

6.4 *Regression analysis*

The aim of the analysis is to fit a line between two sets of variables. The equation of a straight line is:

$$y = a + bx$$

where 'a' is a constant and is the intercept of the line $y = a + bx$ with the y axis.



$$b = \frac{s}{t}$$

If a value of x is substituted in the equation $y = a + bx$, a value of y can be obtained and a line plotted. The regression analysis calculates 'a' and 'b' where the line has the smallest amount of deviation from it. The significance of the line can then be tested by an analysis of variance. The analysis of variance (ANOVA) enables a decomposition of the variability exhibited by the dependent variable y into component parts due to regression and residual variation, and thus tests whether or not the regression model explains a significant amount of this variability.

6.4.1 Method of calculation of regression line

The following values must first be calculated:

$\bar{x}$ = mean of the independent variable.

$\bar{y}$ = mean of the dependent variable.

Sxx, Syy and Sxy are the corrected sum of squares.

$Sxx = \Sigma x^2 - (\Sigma x)^2/n.$

$Syy = \Sigma y^2 - (\Sigma y)^2/n.$

$Sxy = \Sigma xy - (\Sigma x \times \Sigma y)/n.$

Using these terms the slope 'b' is: $b = Sxy/Sxx.$

The intercept 'a', since the line must pass through $\bar{x}$ and $\bar{y}$ is

$a = \bar{y} - b\bar{x}.$

In order to draw the line through the scatter of points, two sets of known values are required. Usually $\bar{x}$ and $\bar{y}$ are plotted against each other and any two other points can be found by substitution i.e. substitute a value of x in $y = a + bx$ to obtain the appropriate value of y ('a' and 'b' having been calculated already).

6.4.2 Method of testing for significance of the line

This is done using an analysis of variance table and the values already calculated to draw the regression line.

Source of variation	df	SS		MS	VR
Regression	1	$(Sxy)^2/Sxx$	(1)	(1)	(3)
Error	n - 2	$Syy - (Sxy)^2/Sxx$	(2)	(2)/n - 2	(3)
Total	n - 1	Syy			

The significance of the line is tested by seeing if the variance ratio (VR) is larger than the F value pertaining to 1 regression degree of freedom (df) and n - 2 error degrees of freedom.

6.4.3 Worked example

Soil pH (x axis = independent variable).

Seed numbers (y axis = dependent variable).

Soil pH	Seed numbers/m^2
3.0	205
3.5	310
4.0	450
4.5	260
5.0	500
5.5	540
6.0	610
6.5	650
7.0	720

$\Sigma x = 45.0$ $\quad\quad$ $\Sigma y = 4{,}245$

$\bar{x} = 5.0$ $\quad\quad$ $\bar{y} = 471.67$

$\Sigma x^2 = 240$ $\quad\quad$ $\Sigma y^2 = 2{,}262{,}825.0$

$n = 9$

$\Sigma xy = 23{,}065$

$Sxx = 240 - 45^2/9 = 15$

$Syy = 2{,}262{,}825 - 4{,}245^2/9 = 260{,}600$

$Sxy = 23{,}065 - 45 \times 4{,}245/9 = 1{,}840.0$

$b = 1{,}840/15 = 122.67$

$a = \bar{y} + b\bar{x}$ $\quad\quad$ $a = 471.67 - (122.67 \times 5.0)$

$a = -141.68$

To find two points (other than $\bar{x}$ and $\bar{y}$) to plot the line by:

If $x = 2.0$, $y = ?$

$a = y + bx$ $\quad\quad$ $-141.68 = y - (122.67 \times 2.0)$

$y = 103.66$

Equation of regression line: $\quad y = a + bx$

$y = -141.68 + 122.67x$

ANOVA

Source of variation	df	MS	VR	Signif.
Regression	1	225706.66	38.81	$P \leq 0.001$
Error	6	5815.56		
Total	7			

From F tables at $P \leq 0.001$ with 1 regression df and 6 error df F = 35.00. Since 38.81 exceeds 35.00 the increase in seed numbers with increasing soil pH is not due to random chance and is statistically significant.

6.5 The arcsin transformation

The distribution of a set of percentages is usually not normal. It is assumed in the normal distribution that the tails of the curve extend to infinity on either side of the mean but percentage values must lie in the range 0 to 100%. When the percentages are scattered around 50% their distribution is often approximately normal but at either end of the scale there is a different situation. If, for example, a sample has a mean of 90% it will tend to have a smaller standard deviation than a sample with a mean of 50% simply because the observations greater than 90% cannot be greater than 100%. They are confined by the end of the scale and cannot deviate greatly from 90%. The nearer the mean lies to 100% the more pronounced the effect becomes. The same problem arises at the other end of the scale. Thus the data will not conform to the normal distribution.

The arcsin transformation enables the data to be transformed from a non-normal to a normal distribution, and is specifically used on percentages and proportions. The data may then be analysed using tests such as the analysis of variance.

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