A QUANTITATIVE STUDY OF GAP RECOLONIZATION IN TWO CONTRASTED LIMESTONE GRASSLANDS

by

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TO

MUM AND DAD

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SUMMARY

Gaps differing in size, form and season of origin (September 1978 and March 1979) were created artificially in adjacent north- and south-facing grasslands in North Derbyshire.

Detailed measurements revealed marked differences between the two sites in patterns of vegetative regrowth and regeneration from seed. Specific effects of gap type and time of origin were detected on both slopes.

Creation of gaps exerted pronounced effects upon the relative abundance of established components of the north-facing turf. Accumulations of bryophytes were considerably less after three years than in undisturbed turf and *Avenula pratensis* tended to be reduced in comparison with potentially faster-growing species such as *Plantago lanceolata* and *Holcus lanatus*.

Effects of comparable magnitude were not induced on the south-facing slope and it is suggested that this may be related to the high level of disturbance normally experienced by the vegetation on this slope.

On the north-facing slope where seedlings are comparatively scarce in undisturbed turf, gap creation promoted spring germination in species which maintain relatively persistent seed reserves at or near the soil surface. In marked contrast on the south-facing slope, large numbers of seedlings appeared in the autumn in both gaps and control areas. Such patterns are consistent with previous laboratory studies which revealed differences in germination requirements between the species concerned.

On the south-facing slope seedling survival was often highest in areas where resprouting vegetative shoots were relatively dense. However, the benefit of this apparent 'shelter effect' rarely extended to seedling size which tended to decline in close proximity to vigorous vegetative shoots.

In the concluding section of the thesis, the main results of the investigation are reviewed in relation to the influence of aspect upon vegetation structure, current theories on the determinants of 'species richness' and opportunities to control species composition by more informed grassland management.

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CHAPTER 1

INTRODUCTION

Although a considerable proportion of the earth's land surface is vegetated, plant cover is not continuous over large areas, e.g. across deserts or mountain ranges. Similarly, within the many different communities which constitute the earth's green mantle, discontinuities or gaps, of greater or lesser extent, may be observed. A gap may be defined as 'an opening or breach' or alternatively 'a breach of continuity' (Macdonald 1972). In the context of plant communities, vegetation gaps may be thought of as patches of bare ground or breaks in the canopy, resulting from damage to the established vegetation cover.

In most circumstances, gaps are only temporary features of the community, being recolonized, in time, either by the species originally present or by an assemblage of species whose existence within the community is determined, in part, by the continued occurrence of such disturbances in the continuity of plant cover. Which ever alternative is the case, during the recolonization process, the relative importance of different species, plant growth forms and sexual or asexual reproduction, may vary considerably from those found in the established plant community. Foresters have long been aware of this fact. There is an extensive literature, stretching through many decades, which describes the variations in identity, life-history and degree of persistence associated with species characteristic of disturbance episodes in a variety of 'woody' communities (e.g. Morey 1936; Maissurow 1941; Jones 1945; Stearns 1949; Bray 1956; Marks 1974; Fox 1977; Runkle 1981,1982; Van Cleve & Viereck 1981; Gomez-Pompa & Vazquez-Yanes 1981).

Distinct phases in the recolonization process are often described, particularly in the rain forests of the humid tropics (reviewed by Brokaw 1984). Oldeman (1978) recognises at least four phases whose duration may be characterized both by species composition and architectural features of the developing canopy. Species associated with each phase show great variation in many aspects of their biology, e.g. germination phenomena (Ng 1978; Vazquez-Yanes & Orozco-Segovia 1984)), growth rates (Ng 1979; Whitmore & Bowen 1983), palatability (Hartshorn 1978), branching patterns (Hallé et al. 1978).

In systems other than forests, information on gap colonization processes is less readily available. However, descriptions of gap formation and recolonization in various kinds of herbaceous and shrubby vegetation were an important element in the concepts of "Pattern and Process" advanced by A. S. Watt. Watt was amongst the first to recognize the importance of such processes in an understanding of community dynamics. In his classic paper (Watt 1947) the regeneration complex is described in the following manner:

"It consists of a mosaic of patches forming an intergrading series the members of which are readily enough assignable to a few types or phases. The samples of these phases are repeated again and again over the area; each is surrounded by samples of other, but not always the same phases." (Watt 1947).

Clearly included in these sentences is an understanding that vegetation to be found recolonizing gaps differs in character from that of the surrounding vegetation.

Since 1947 there have been relatively few studies of regeneration out of the woodland context. Notable among these is the work of Miles on the role of gaps in the dynamics of Callunetum (Miles 1973a, 1974). In herbaceous vegetation, gap recolonization has been largely ignored as a regulating mechanism in vegetation composition in either time or space, despite obvious implications for the maintenance of diversity. King (1977, 1981) has identified floristic elements characteristic of ant hills in both calcareous and acidic grasslands, and Grubb (1976) suggested that different species of short-lived forbs might be exploiting openings and less dense patches in chalk grassland. A few studies are also available recounting colonization of natural gaps in North American grasslands (Koford 1958; Platt 1975). More recently Verkaar, Schenkeveld & Brand have associated the continued existence of short-lived forb species in chalk grasslands, with the density of vegetation, placing particular emphasis on implications for germination and subsequent growth and establishment of young seedlings (Verkaar et al. 1983; Schenkeveld & Verkaar 1984).

Recolonization of bare areas by vegetative regeneration in damaged plants has been ignored in nearly all studies concerned with gap dynamics whatever the community. A major exception to this generalization is provided by the work of Uhl et al. (1982). This study considered the differential effects of cutting, burning and bulldozing Amazon caatinga forest. Trees with the ability to resprout were found to be disproportionately-represented in forest which had been cut, whereas burning destroyed sprout buds and favoured regeneration from seed buried in the soil.

Gap recolonization has been given more extensive treatment in theoretical studies particularly in relation to the maintenance of diversity. Grime (1973a, 1974), Whittaker (1977), Huston (1979) and Naveh & Whittaker (1980) all include disturbance intensity as one axis in their general models to explain the occurrence of species diversity. Whittaker & Levin (1977) and Miller (1982) specifically discuss gaps and their role in maintaining species diversity. Only one study considers, in detail, the possible importance of gaps and the methods by which they are recolonized, to the maintenance of species richness (Grubb 1977). Grubb coined the phrase 'regeneration niche' to describe the multiplicity of ways in which species co-existing in a plant community might differ not only in their reproductive biology but also in their ability to exploit gaps of varying size, and season of origin. Many data are presented in support of the former contention, less are available for the latter.

Recolonization of gaps and their role in vegetation dynamics has received varying emphasis according to the plant community in question. In woodlands and forests which are long-lived and often relatively stable, disturbance phenomena have attracted much attention. In cyclical vegetation communities such as _Calluna_ heathland, the role of gaps is well understood. In grasslands and other types of herbaceous communities, other influences, particularly competitive interactions between species, have received more attention in attempts to explain community diversity. Data for this type of vegetation are few, and it is the purpose of this thesis to examine quantitatively, gap recolonization phenomena in the context of two very different limestone grassland communities. First, however, it is pertinent to consider the fundamental character of gaps, and their impact on vegetation.

Openings or breaches in the plant canopy result from mechanical or biological damage to the vegetation. Their characteristics and scale vary greatly, e.g. Pickett & Thompson (1978), and reflect the factors which produced them. Extensive areas of bare ground may result from forces such as fire, wind-throw or scouring by flood water, established vegetation being considerably damaged or removed completely. Ant hills and mole hills may be thought of as islands of bare soil of intermediate size, whereas hoof prints or the deaths of individual plants (perhaps as the result of disease or drought) produce small-scale interruptions in the continuity of plant cover. Such examples represent simple situations where the damaging agent and scale of disturbance are clear-cut. There are, however, various combinations possible; thus many small hoof prints in a small area may produce in total, much bare ground. The deaths of individual plants during a continuing, severe summer drought may result in an increasing quantity of bare ground as the months progress. Individual gaps may coalesce, resulting in substantial areas of bare soil. Alternatively, the gap once created may become a force for destruction itself, e.g., by exposing soil to desiccation and therefore placing at risk marginal individuals, or, as in the case of wind-throw in trees, removing support and protection from other members of the group, thus increasing potential instability and greatly increasing the chance of other trees being felled (Sprugel 1976). Conversely, as bare areas are recolonized, a single large opening may become a mosaic of smaller patches.

Openings or breaches in the canopy which are not necessarily accompanied by bare soil beneath them are of particular importance in tall and/or stratified vegetation. In woodlands and forests in particular this type of gap has received much attention and there is a great deal of documentary evidence recounting a variety of responses in the undamaged vegetation (e.g. Hartshorn 1978; Ehrenfeld 1980; Kellman 1980; Whitmore 1982).

Evidence of established communities being subjected to some form of local disruption is not confined to plants. Animal communities in general are not sedentary in nature and as a rule are unlikely to exhibit gap phenomena comparable with those described for vegetation. However, Paine & Levin (1981) in their studies of _Mytilus californianus_ a widespread dominant mussel, on wave-swept rocky inter-tidal shores, state:

"Mussel beds may exist as extensive monocultures: more often they are an ever-changing mosaic of many species which inhabit wave generated patches or gaps." (Paine & Levin 1981).

Their paper then goes on to examine in some detail the role of gap dynamics in maintaining this inter-tidal shore line community, describing many phenomena recognizable in plant communities.

The rate at which gaps in vegetation are recolonized will depend on the severity of damage and the ability of the affected species to recover from it. If a species is severely debilitated or obliterated altogether, the relative abundance of co-existing species may be altered. Silander & Antonovics have demonstrated, by the experimental removal of individual species from a coastal marsh community, that relaxation of competitive interactions allows certain species to expand in the absence of others (Silander & Antonovics 1982).

Recolonization of gaps by vegetative expansion may occur in two ways: (i) the re-sprouting of damaged vegetation, and (ii) lateral invasion by surrounding species. The ability of a species to re-sprout after damage depends on a variety of characteristics. The position of the meristems, possession of root reserves, and the ability to regenerate from small fragments determine recovery potential in the first instance, but growth rate and the timing of damage in relation to the normal phenological pattern of the species are also important considerations. Colonization of a bare area by neighbours may involve a variety of invasion modes, e.g. lateral spread by means of rhizomes and stolons or the re-orientation of aerial parts in response to changed light climate. Alternatively proximal vegetation may simply flop into the gap area in the absence of previously supporting plants. Paine & Levin (1981) describe this phenomenon in mussel beds showing that small patches disappear almost immediately due to a leaning response in neighbouring mussels.

The formation of a canopy gap may alter light, temperature and moisture relations at the ground surface which in turn may promote germination in seeds either at the soil surface or buried in the soil. The inhibition of germination by canopy is a well-recognised phenomenon (Taylorson & Borthwick 1969; Gorski 1975; King 1975; Fenner 1980) and species with buried seed banks may have dormancy broken by both changes in the light climate (Wesson & Wareing 1967; Taylorson 1972) and increased temperature fluctuations experienced in bare soil (Thompson,Grime & Mason 1977; Thompson & Grime 1983). Seed may also be deposited into a gap by agents such as wind, birds, ants, etc., thus creating opportunities for new species to invade.

Pioneer tropical rainforest species provide a classic example of regeneration from seed in gaps. Such species, e.g. Cecropia obtusifolia, Piper auritum and Heliocarpus donnell-smithii, are frequent colonists of large gaps (Vazquez-Yanes 1980; Vazquez-Yanes & Orozco-Sergovia 1982a; Vazquez-Yanes & Smith 1982), where they germinate and grow rapidly. Many pioneer species appear to be particularly sensitive to changes in light quality for both germination and growth and may be excluded from the forest as light intensity diminishes (Nicholson 1960). Denslow (1980) classifies a wide range of tropical forest species according to their requirements for large or small gaps. Gaps which do not cause severe damage to underlying vegetation may, by increasing light intensity and quality, allow previously suppressed seedlings or saplings to grow towards the canopy (Kellman 1980; Whitmore 1982).

A gap then is produced by damage to the vegetation, damage which at least temporarily, and sometimes more permanently, reduces the potential for dominance by the previously established species. Major damage, such as quarrying to take an extreme example, may destroy a community entirely. More usually, however, the potential for some form of recolonization process remains, the extent of which is determined by the type and magnitude of damage to the established plants, and the responses of individual species to it.

Effects of damage have been implicated in attempts to explain the maintenance of diversity in vegetation (Grime 1973a,b; Huston 1979). Where the soil is fertile, damage, unless severe or extensive, will in general provide only a temporary check on the vigour of the associated vegetation cover and very soon the gap will be obliterated by lateral spread of the surrounding vegetation, accompanied by rapid re-sprouting of those plants affected in the first instance. In such circumstances it seems unlikely that individuals of new species will successfully invade the community.

In habitats with moderately fertile to poor soils, however, the situation is likely to be very different. Plants characteristic of communities developed in these situations tend to have lower growth rates (Grime & Hunt 1975) and lower capacities for rapid lateral spread which means that a gap will remain open for a much longer period and is therefore available for recolonization by seedlings arising from either a buried seed bank or seed transported to the site by other means, e.g. wind, birds or ants. If the gap remains open long enough, seedlings of new species may be able to establish and contribute to diversity. The recolonization process therefore depends on an interplay between the sprouting of damaged vegetation, lateral invasion over the ground or through the soil and seedling establishment. In other words, vegetation gaps create opportunity for change and thus may well be of major importance in the maintenance of diversity at a site.

In Britain the most diverse herbaceous communities to be found are grasslands developed on calcareous substrata. These are established on thin, moderately infertile, often summer-droughted, soils and in the past were extensively used for grazing by sheep in particular and more locally by cattle. Rabbits were also widely associated with this type of vegetation before population levels were reduced substantially by myxomatosis. It is a notable feature of these grasslands that once grazing pressure is removed, diversity undergoes a substantial reduction and scrub encroachment often occurs (Thomas 1960,1963; Green 1972; Grime 1973b).

Being so diverse, calcareous grassland has attracted much attention from ecologists in an attempt to explain the mechanisms by which species richness is maintained. One contributory factor has been identified as the influence of grazing animals whose effect is to keep the turf short, thus preventing competitive dominance by taller or more vigorous components of the vegetation (Grime 1973b). Fire has also been implicated, particularly in relation to the limestone grasslands of Derbyshire, which have some of the highest species numbers per unit area in the British Isles. Lloyd's studies on the limestone dales of Derbyshire (Lloyd 1971), have shown clearly that the effect of fire is expressed not through nutrient enrichment but through physical damage to plants and litter removal, again reducing the potential for competitive dominance.

Many calcareous grassland species have low capacities for lateral spread and this characteristic, coupled with the occurrence of miniaturization (Tansley & Adamson 1925) in response to grazing pressure, means that large numbers of individual plants, often of a variety of species, may be found in a small area. Such close proximity of a variety of species has led many to believe that calcareous grasslands contain species showing a high degree of niche differentiation. There is a well developed literature on the concept of the niche and the role of niche differentiation as a mechanism to explain diversity (e.g. Svardson 1949; Dobzhansky 1950; and Williams 1964). In a community at equilibrium it may be argued that every species must occupy a different niche. In other words, each species must make slightly different demands on its environment from the others with which it occurs, such that, in a stable community the species which co-exist will be complementary in their usage of resources (space, light, nutrients etc.).

Leaving aside the problem of defining stability, the idea of niche differentiation is a very attractive proposition for limestone grasslands. Soils are often shallow and, across small areas, may be very variable in depth, nutrient status and exposure to drought. In consequence, it is easy to envisage a situation where deep-rooting forbs penetrating damp crevices might persist side by side with drought-tolerant grasses growing in shallower soil. Sydes (1980) has shown experimentally that such a situation does indeed occur on

Derbyshire limestones. In this study four species, Festuca ovina, Anthoxanthum odoratum, F. rubra and Sanguisorba minor, are shown to have complementary rooting depths which correspond to their abilities to penetrate crevices and so avoid desiccation on surface-droughted soils.

Species may be complementary in time, as well as in space. The greater rooting depth of S. minor described above enables the species to maintain growth throughout the warmest part of the year while shallower rooting species such as F. ovina reach their peak much earlier (Al-Mufti et al. 1977). Winter annuals, such as Arenaria serpyllifolia, Arabidopsis thaliana and Aphanes arvensis, small in stature and adapted to growth at lower temperatures, are able to exploit areas of very shallow soil which dry out in the summer months. These species complete their life-cycle in the cooler months of the year when the soils are moist. The summer drought ensures that such areas are not colonized by more robust vegetation (Ratcliffe 1961) and a buried seed bank enables the species to reappear the following year (Thompson & Grime 1979).

In fact many species found in limestone grasslands, exploit different periods of the year for growth. Furness (1980) has studied the phenological patterns of a number of species occurring in Cressbrookdale, Derbyshire, on a north-facing grassland site developed on limestone. This site has been lightly grazed by cattle and rabbits for over one hundred years and has more than 40 higher plant species per square metre. There is a remarkable degree of complementarity in phenology within this community with some species showing biomass peaks in spring, e.g., Orchis mascula, Primula veris, Anemone nemorosa, early summer, e.g., Anthoxanthum odoratum, Briza media), late summer, e.g., Agrostis capillaris and no obvious peak at all, e.g., Carex flacca, Carex pulicaris.

Understanding of these kinds of patterns has been enhanced by studies such as those of Sydes (1980, 1984) who examined leaf demography in a number of limestone grassland species and found considerable differences in patterns of leaf production and senescence between species occurring together in a small area. More recently the role of genome size as an indicator of the time of year at which different species grow (Grime & Mowforth 1983; Grime, Shacklock & Band 1984) has further elucidated these temporal relationships.

It seems therefore, that it is possible to describe different niches which might be exploited by established plants in limestone grassland, although such arguments are less easily applied in communities of more competitive species developed on fertile soils. However, in a review of mechanisms which might be involved in the maintenance of species richness, Grubb (1977) has drawn attention to the fact that a very important part of the plant life-history is overlooked in discussions of this kind. It is Grubb's assertion that there seem to be almost limitless possibilities for differences between species in their requirements for regeneration, i.e., the replacement of the individual plants of one generation by those of the next. He introduced the term 'regeneration niche' to describe the varied processes by which such replacement might be brought about, suggesting amongst other things that species regenerating from seed might show affinities for gaps of differing sizes or gaps arising at different times of the year. Grubb had previously shown that recognisable groups of short-lived species from chalk grassland seemed to exhibit differences in micro-site preferences (Grubb 1976) while Harper et al. (1965) had demonstrated experimentally that heterogeneity of the soil surface could be an important factor in determining successful establishment from seed. Much of Grubb's evidence for the existence of regeneration niches comes from the forestry literature where there are to be found many examples of shade intolerant trees only occurring in large clearings, e.g., Pincherry (Prunus pennsylvanica (Marks 1974) with smaller openings being colonized by species able to tolerate lower light levels, e.g.Piper hispidum (Vazquez-Yanes & Orozco-Segovia 1982b), Piper aequale (Guevara, personal communication).

Very little is known of the processes by which vegetation gaps in grassland communities are recolonized, and in particular the relative roles of sexual and asexual reproduction. It is the purpose of this thesis to examine this problem in relation to two neighbouring but very different limestone grassland sites and to attempt an assessment of the importance of gaps in the maintenance of diversity in each. The sites are situated on either side of a carboniferous limestone ridge in Millersdale near Litton, Derbyshire (National Grid Reference SK155732; altitude 240 m). Both sites support species-rich vegetation despite continued dereliction and both have been the subject of previous studies, a major consideration in the selection of these areas for further study (Davison 1964; Grime & Curtis 1976; Thompson 1977; Thompson & Grime 1979).

The north-facing slope supports a tall herb community with a large perennial element and dense bryophyte layer. Vegetation cover is more or less continuous throughout the year, although natural gaps do arise from time to time as the result of rodent activity, particularly voles. Local fires also occur periodically at the site but the area selected for study had not been burned for at least three years.

In marked contrast the vegetation of the south-facing slope is much less continuous. Summer droughts, winter frosts, and superficially buried bedrock result in many natural gaps. Annual species are prominent at this site and there are a number of drought-tolerant grasses and deep-rooting forbs. Occasional fires are experienced but in general the amount of bare ground and low quantities of combustible fuel reduce their impact and cause them to be very localized. Again the area selected for investigation had not been burned for at least three years.

These contrasting vegetation characteristics and the physical and climatic differences due to aspect suggest that the germination strategies of the component species and the resilience of the established communities may differ considerably between the two sites. The process of recolonization after damage, therefore, is likely to follow very different courses on the two slopes, one of which seems to be naturally relatively undisturbed, the other of which may be in a constant state of flux.

The bulk of this thesis describes a field experiment conducted at the two sites over a period of three years (from 1978-1981). The study was begun with the aid of L. Staal (a Doctoraal student from Utrecht University) and E. G. Cresswell (a PhD student at Sheffield University), both of whom provide preliminary accounts of the earliest stages of the work in their reports (Staal 1979; Cresswell 1982).In Chapter 2 the established vegetation of the two sites is considered in more detail, and a major experiment designed to examine the effects of creating artificial vegetation gaps of varying sizes and shapes is described. The artificial gaps were created at two distinct periods of the year, autumn 1978 and spring 1979, in order to assess the importance of seasonal effects on germination of seed and longer-term vegetative recovery of damaged plants.

Chapter 3 describes the contribution of vegetative regeneration to the recolonization process. Quantitative analyses of species composition, and changes in the relative abundance of species as a result of damage, are presented for a variety of gap types and undisturbed vegetation on both slopes.

Patterns of germination both within gaps of varying dimensions and between the two different slopes are examined in Chapter 3. Variations in germination phenomena recorded in the autumn and spring periods are also discussed along with a consideration of events occurring in undisturbed turf.

The subsequent survival of seedlings which appeared at the beginning of the experiment is examined in Chapter 5. Rates of mortality in different gap types and final yields attained by survivors are considered in the first part of the chapter and attention is paid to the problem of defining 'success' in terms of percentage survival rates or dry weight acquisition. The second part of the chapter explores in some detail the relationships between germination, seedling survival and re-establishing vegetation cover.

The relative importance of sexual and asexual colonization and Grubb's hypothesis of the regeneration niche(Grubb 1977) are re-examined in Chapter 6 using the results of the field study in Millersdale. Quantitative analyses of the kind described in this thesis, have direct relevance to those interested in the mechanisms by which species richness is maintained, and the conclusions from this study are examined in the light of current theories relating to species diversity. Finally, the importance of the time of year at which gaps arise is considered with special reference to the implications for management of species-rich limestone grasslands.

CHAPTER 2

THE STUDY SITES AND METHOD OF INVESTIGATION

In the preceding chapter it was suggested that the appearance of gaps within a plant community may contribute to the maintenance of species richness. Reduction of potential dominants by damage creates opportunities for change in the relative abundance of particular species and reduced vegetation density may even allow species not found in the undisturbed plant cover to establish from seed. In general terms the recolonization process may be considered to have three main components:

(1) the re-sprouting of damaged vegetation dependent on individual species responses to damage and the severity of damage;

(2) lateral invasion by surrounding species either over the ground surface (stolons), through the soil (rhizomes) or by simple physical movement of aerial parts into the canopy space (overhanging shoots);

(3) establishment of seedlings, from seed in the soil, from seed transported to the bare area by wind, birds etc. or by release of small seedlings previously suppressed by the established vegetation cover.

Particularly in the case of the third component, Grubb (1977) suggests that size and shape of the gap and time of its appearance may have important implications for the establishment of seedlings from different species. It is not unreasonable to predict that seedlings which originate from small seeds may be particularly susceptible to competition and may be unsuccessful in establishment unless the density of surrounding vegetation is greatly reduced. Field studies and laboratory investigations of germination responses to temperature (Thompson & Grime 1979; Grime et al. 1981) have identified a number of species which appear to be obligate autumn or spring germinators. It is also conceivable that mechanisms which result in different degrees of damage to the established vegetation will affect the interplay between and determine the relative importance of the three components of the recolonization process described above. Since grassland species exhibit different patterns of growth throughout the year (Wells 1971; Williamson 1976; Al-Mufti et al. 1977; Sydes 1984) time of damage is likely to affect the course of vegetative recolonization as well as seedling establishment.

This chapter describes an experiment designed to examine some of these processes as they occur in limestone grassland. The method considered below incorporates gaps of differing size, form and season of origin, artificially created at the two sites described in the preceding chapter and in more detail below, and allows an assessment of the relative importance of sexual and asexual reproduction in the recolonization process.

PART I: CHARACTER OF THE STUDY SITES

The two sites selected for study were in close proximity on either side of a carboniferous limestone ridge in Millersdale, Derbyshire. Homogeneous areas of vegetation were identified and it was in these that the experimental investigations took place.Climatic data are not available for Millersdale but measurements made on north- and south-facing slopes over a period of years in neighbouring Lathkilldale (National Grid Reference SK177656) (Rorison & Sutton 1976) show the general pattern of weather which may be experienced by slopes of such different aspect in Derbyshire. The north-facing slope is slightly less steep than the south-facing slope slope which has much thinner soils and more exposed bedrock. With such variation in the physical and climatic characteristics of the two slopes, it is not surprising that species composition and degree of continuity of the vegetation cover on the two slopes differs markedly. Four previous investigations had been conducted at these sites. Davison (1964) investigated seedling establishment particularly on the droughted and unstable soils of the south-facing slope. Summer mortality was found to be a prominent feature of the seedling flora. The studies of Grime & Curtis (1976) considered the interaction of drought and mineral-nutrient stress, a potent factor on the south-facing slope and the investigations of Thompson (1977) and Thompson & Grime (1979) into the soil seed reserves of both sites revealed much variation in the persistence and germination

Fig. 2.1 The vegetation of the north-facing slope in (a) 1975 (redrawn from Thompson & Grime (1979)) and (b) 1978 (data from Staal, Cresswell & Hillier in Cresswell (1982)).

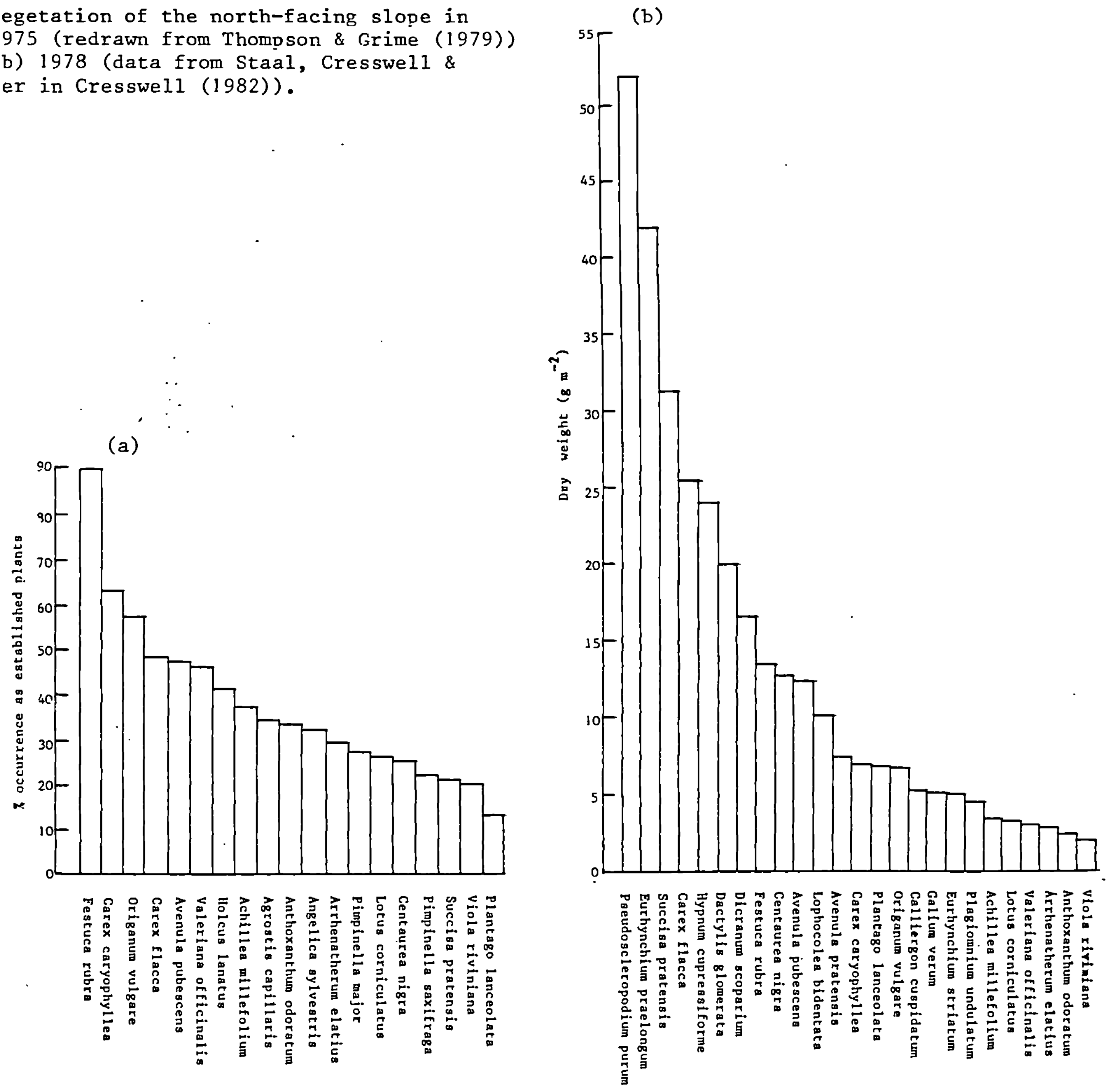
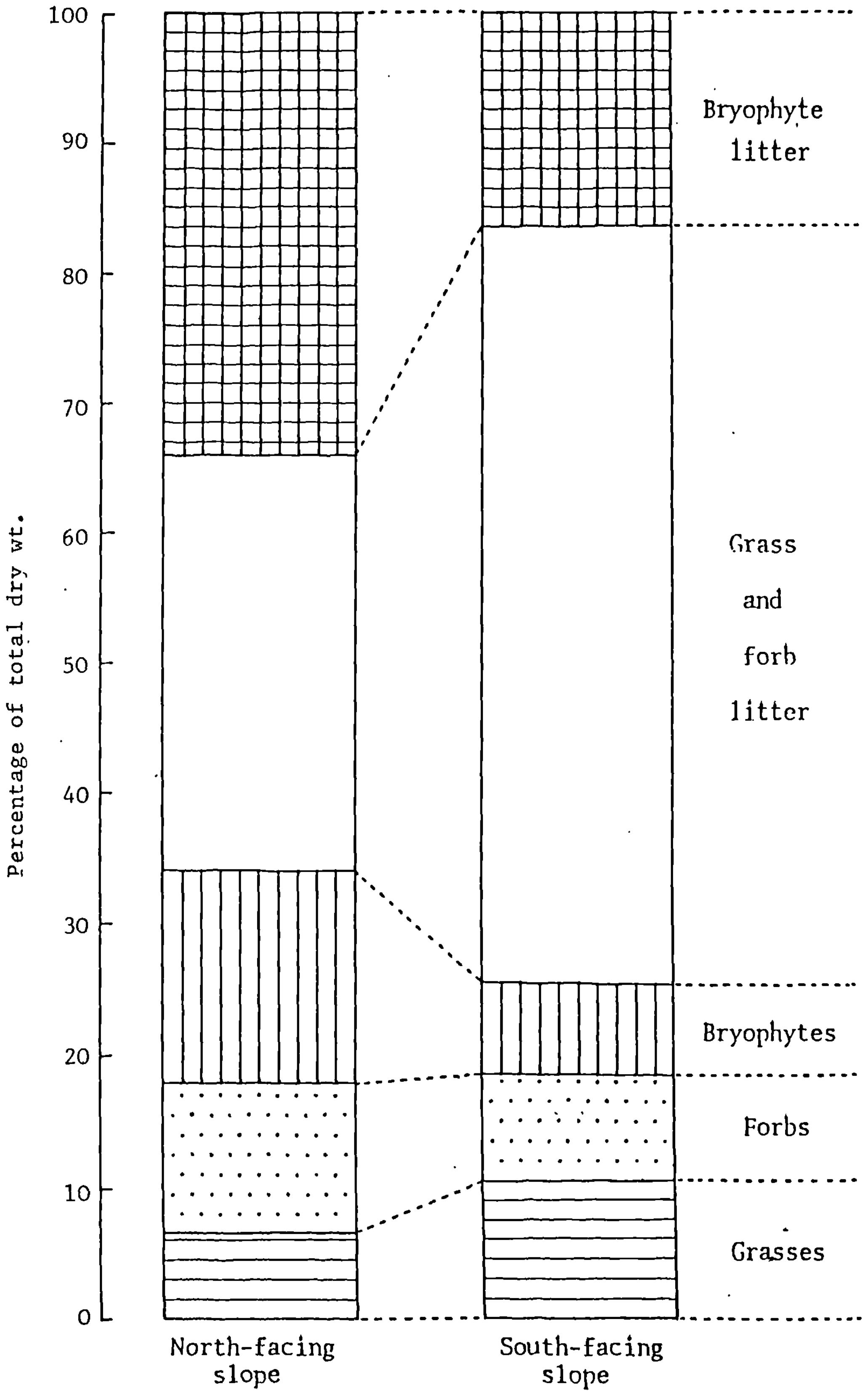


Fig.2.2 Percentage contributions of the different plant groups to the established vegetation of the experimental areas (October 1978).



overhanging the area, may have caused an over-estimate of total plant material to be made, this error then being compounded by multiplication of the values to give grammes per metre square. Nevertheless, a picture of the vegetation composition of the experimental area on the north-facing slope may be gained by consideration of the contribution to total, made by individual species (Figure 2.1(b)) and major plant groups (Fig.2.2).

The most striking feature of the vegetation was the extremely large quantity of living and dead bryophytes, just over 50% of the total dry weight of shoot material and litter. Living material of two species, Pseudoscleropodium purum[1] and Eurhynchium praelongum, was relatively more important than any of the higher plant species recorded from the site, and many other pleurocarpous mosses and the leafy liverwort Lophocolea bidentata made significant contributions to the standing crop. The time of year at which these estimates were made probably favoured bryophytes to a certain extent but the fact that species such as Succisa pratensis, Dactylis glomerata and Centaurea nigra were recorded amongst the ten most important species, and that all three species are frost-sensitive, suggests that the influence of higher plants was still being expressed at the site despite the early autumn and sampling date.

Observations throughout the period of the experiment confirmed the importance of the bryophyte community at all times of the year, pleurocarpous species forming extensive mats effectively insulating

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[1] Nomenclature follows that of Smith (1978) for mosses, Watson (1969) for liverworts and Clapham, Tutin & Warburg (1981) for herbaceous plants.

the soil layer and often retaining moisture at their base in all but the driest periods. The occurrence of moisture-demanding species such as Succisa pratensis, Valeriana officinalis and Angelica sylvestris, at the site appears to be strongly influenced by the northerly aspect,which on the north Derbyshire plateau is conducive to the retention of high soil moisture throughout the greater proportion of the year (Pope 1973), and to a microclimate particularly favourable for bryophyte growth.

Large numbers of Avenula pratensis tussocks were observed in the vegetation but this species did not make a major contribution to the total shoot biomass in 1978. However, comparison of these data with Thompson's earlier work suggests that A. pratensis is increasing in importance at the site, a conclusion supported by both observation throughout the period 1978-1981 and estimates of biomass made at the conclusion of this investigation in 1981 (Chapter 3).

Dead plant material derived from higher plants (32% of total dry weight) and from bryophytes (34%), was found in considerable quantities. Such accumulation reflects the slow decomposition rate of grass and bryophyte litter and the lack of removal by fires, formerly used as a management tool in Derbyshire limestone grassland (Lloyd 1968).

In all, thirty-seven species of higher plants and fourteen species of bryophyte were recorded in the experimental area on the north-facing slope (Appendix 1) This represents a relatively high level of diversity considering that the site has been unmanaged for at least 20 years.

(b) Soil seed reserves

Buried seed reserves present on the north-facing slope in Millersdale have been examined on two occasions. Investigations reported in Thompson (1977) and Thompson & Grime (1979) revealed that of the species prominent in the vegetation in 1975 a considerable number did not maintain detectable seed reserves in the soil throughout the period October 1974 to October 1975, although viable seed was present at certain times of the year. Included in this group were *Achillea millefolium*, *Angelica sylvestris*, *Arrhenatherum elatius*, *Avenula pubescens*, *Carex caryophyllea*, *Carex flacca*, *Centaurea nigra*, *Festuca rubra*, *Lotus corniculatus*, *Pimpinella major*, *P. saxifraga*, *Succisa pratensis* and *Valeriana officinalis*. Conversely, no species absent from the established vegetation were represented as large numbers of germinable seeds, a significant feature if seed reserves in the soil are to be considered as a potential source of diversity. Seeds of five species (*Agrostis capillaris*, *Anthoxanthum odoratum*, *Holcus lanatus*, *Origanum vulgare* and *Plantago lanceolata*), were found in the soil in large numbers which varied little from season to season. These species might reasonably be expected to appear in large numbers after disturbance of the covering vegetation.

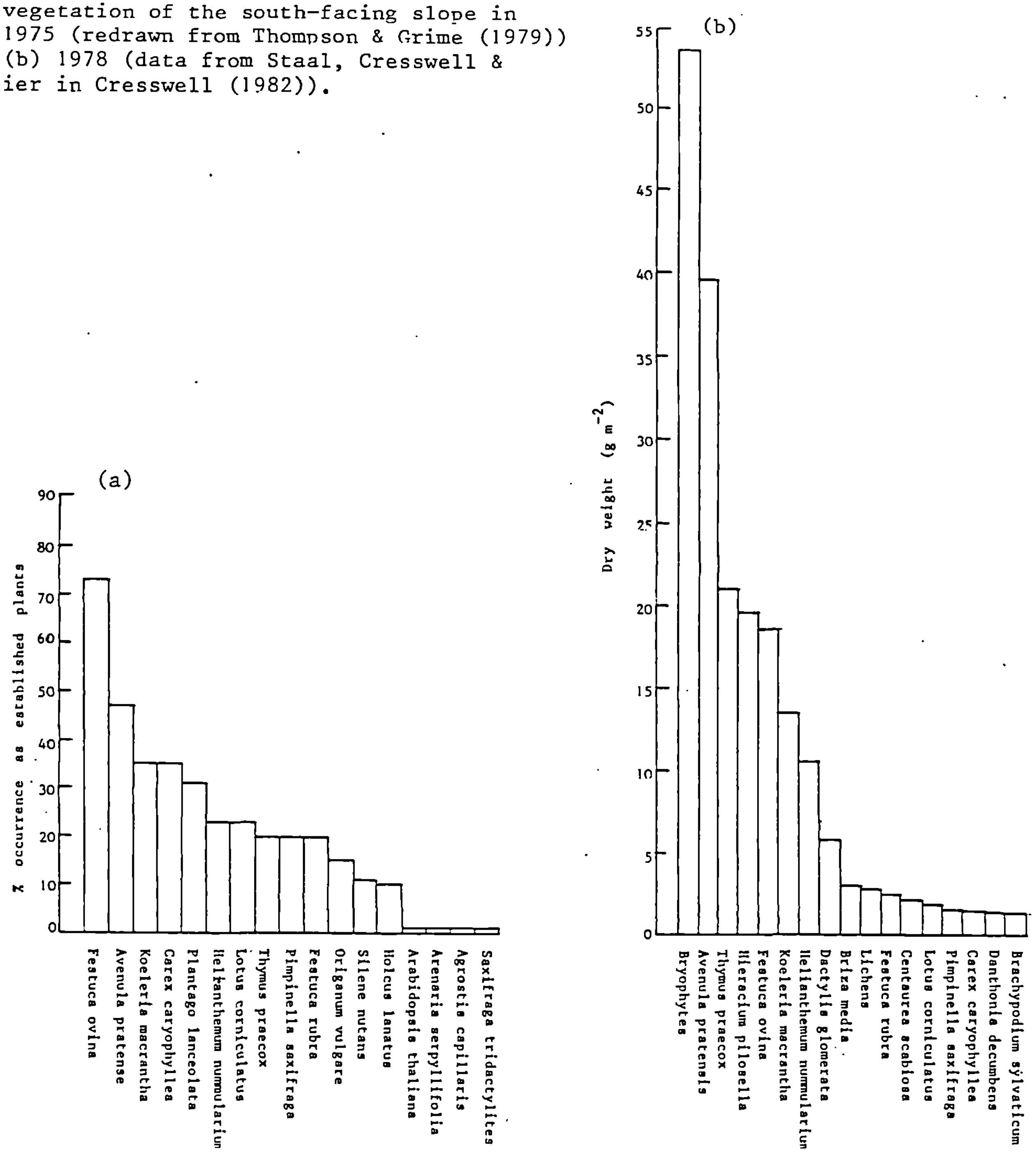
The second investigation of soil seed reserves present on the north-facing slope is contained in a study, complementary to the work described in this thesis, conducted by E. G. Cresswell over the period 1979-1982 (Cresswell 1982). Thompson (1977) had previously examined seasonal variability in soil seed reserves for a small number of species present at the site. The data obtained by Cresswell are more comprehensive, yielding information on most of the important species. Nine species were shown to have detectable soil seed reserves throughout the year, four of these species having been identified already by Thompson. Agrostis capillaris does not appear in Cresswell's list, perhaps due to absence from the more restricted study area. The five additional species found to have detectable soil seed reserves were Danthonia decumbens, Campanula rotundifolia, Centaurea nigra, Hypericum perforatum and Succisa pratensis. Of these species D. decumbens, C. nigra and S. pratensis were probably represented as surface-lying seed since their seed weights (0.87, 2.55 and 1.54 mg respectively) and more particularly the large dimensions of their propagules (length 3.20, 3.85 and 4.50 mmn, width 2.05, 1.70 and 1.60 mm respectively) (Grime et al. 1981) are likely to preclude burial (Thompson & Grime 1979). Five species were found to have detectable soil seed reserves during a proportion of the year: Brachypodium sylvaticum (Aug-Apr), Avenula pratensis (Aug-Feb), Carex caryophyllea (Apr-Sep), Carex flacca (Mar-June) and Serratula tinctoria (Nov-May). A small number of seeds of Chamerion angustifolium were detected over the period August to February and probably originated as wind-blown dispersules from a patch established immediately below the study site.

THE VEGETATION OF THE SOUTH-FACING SLOPE

(a) Established vegetation

The contrasting climate and physical characteristics of the south-facing slope at Millersdale are expressed in a community rather different from that found on the north-facing slope. Thompson &

Fig. 2.3 The vegetation of the south-facing slope in (a) 1975 (redrawn from Thompson & Grime (1979)) and (b) 1978 (data from Staal, Cresswell & Hillier in Cresswell (1982)).



Grime (1979) conducted a general survey of the established vegetation found on the slope in 1975 (Fig.2.3(a)), while data from the studies of Staal, Cresswell and Hillier (Fig.2.3(b) and Fig.2.2) yield information relevant to the actual experimental site. In contrast with the north-facing slope, grasses were found to be relatively more important than forbs, and bryophytes (including litter and lichens) were much less important, comprising only 23% of the total. Bryophyte material for this site was not sorted into species as it consisted mainly of tiny acrocarpous mosses often closely associated with the soil. This feature in itself contrasted markedly with the north-facing slope where pleurocarpous species formed extensive mats often excluding higher plants. On the south-facing slope, the area colonized by bryophytes and their contribution to the plant cover was minor. Total dry weight of plant material was estimated to be 807.6 g m^{-2} subject to the same qualification as that made in relation to the value found for the north-facing slope (p.20).

Of the thirty herbaceous species recorded (Appendix 2) the most important were *Avenula pratensis*, *Thymus praecox*, *Hieracium pilosella*, *Festuca ovina*, *Koeleria macrantha*, *Helianthemum nummularium* and *Dactylis glomerata*. Most of these species exhibit xeromorphic characteristics, and the two sub-shrubs *T. praecox* and *H. nummularium* are deep rooting, as are some of the more minor components of the vegetation, e.g. *Centaurea scabiosa*, *Lotus corniculatus* and *Pimpinella saxifraga*.

Since the samples of vegetation from which these data are derived were collected during the early autumn, two important groups of species were not represented. During the autumn, winter and early spring, winter annual species occur in profusion on areas of exposed soil on rock outcrops. Prominent at this time of the year are Arabidopsis thaliana, Arenaria serpyllifolia, Cardamine hirsuta and Erophila verna. In the spring two short-lived forbs Linum catharticum and Medicago lupulina are to be found.

The plant community on the south-facing slope is far more variable in composition both seasonally and spatially than that of the north-facing slope. Since the site has variable soil depth and is subject to summer drought, plant cover is far less continuous than on the north-facing slope, natural gaps being a prominent feature of the turf.

(b) Soil seed reserves

Again Thompson & Grime (1979) are responsible for much of the information available on soil seed reserves on the south-facing slope. Arrhenatherum elatius, Briza media, Carex caryophyllea, Festuca rubra, Helianthemum nummularium, Koeleria macrantha, Lotus corniculatus and Pimpinella saxifraga, although common components of the established turf, were rarely recorded as seeds in the soil. Agrostis capillaris, Holcus lanatus, Origanum vulgare, Plantago lanceolata, Silene nutans and Thymus praecox were recorded as having persistent reserves of germinable seed which varied little with season. Avenula pratensis and Festuca ovina exhibited strong peaks in late summer and were present only in low numbers or were absent from the site as seeds for the greater part of the year. The largest and most constant numbers of seeds were recorded for the winter annuals Arabidopsis thaliana, Arenaria serpyllifolia and Saxifraga tridactylites. As mentioned above these species are patchy in their distribution and only occur as seedlings and established plants over a restricted period of the year. Populations of these winter annuals fluctuate considerably from year to year (Hodgson, personal communication) and it has been suggested (Thompson & Grime 1979) that their persistence is buffered by the reserves of seeds in the soil.

In addition to the species identified by Thompson & Grime (1979), Cresswell (1982) records Cardamine hirsuta, Crepis capillaris, Hieracium pilosella, Hypericum perforatum and Medicago lupulina as maintaining reserves of seed throughout the year. The seed banks of Crepis capillaris and H. pilosella almost certainly consist of surface-lying propagules. No reserves were detected for Avenula pratensis, A. pubescens, Festuca ovina and Koeleria macrantha. Amongst the other grasses present on the south-facing slope, some seed was found at varying times of year, e.g., Dactylis glomerata (Oct-Nov), Festuca rubra (Oct-May), Holcus lanatus (Aug-Nov), Trisetum flavescens (Aug-Dec). It is a feature of all these species that germination tends to occur within a very short time of seed release. The forbs Linum catharticum (detected Feb-Jun), and Pimpinella saxifraga (Nov-May) both have a chilling requirement before germination will occur (Grime et al. 1981). They germinate in large numbers in Millersdale during the early spring but their capacity for persisting as buried seeds requires further investigation.

Conspicuous in the vegetation of the south-facing slope are certain perennial species which appear to be strongly adapted to the seasonally variable climate. The 'permanent residents' often exhibit features facilitating drought tolerance, e.g. xeromorphic leaves in

Festuca ovina, or drought avoidance, e.g. taproots in *Pimpinella saxifraga* and *Centaurea scabiosa*. In addition, there seems to be a separate 'sub-community' of annual species appearing at distinct times of the year. In these ephemerals the presence of seed reserves in the soil may be an important buffer against failure to produce seeds in a particular year due to exceptional summer drought or winter frost damage.

PART II: METHODS EMPLOYED IN THE INVESTIGATION

A number of approaches are possible to the study of gap recolonization processes, the choice being determined by the aims of the researcher and the degree of control required over events. The aim of this project was to assess the importance of gap recolonization phenomena to the maintenance of species richness in two contrasted limestone grassland communities. As previously described (p.13), the occurrence of gaps is more intermittent at one of the sites selected for study. It was necessary therefore to create artificial gaps in the vegetation in order that recolonization processes might be examined. One of Grubb's hypotheses in his formulation of the 'regeneration niche' (Grubb 1977) was that different species might require gaps of varying dimensions in order to germinate and establish successfully from seed. The obvious way to approach this problem would be to sow seed of known quantity and identity into gaps of particular sizes and shapes. However, recolonization of a gap involves not only seed regeneration but also vegetative recovery of damaged plants. As the aim of this study was to gain as close an understanding as possible of the natural course of events as bare areas are re-invaded, it was decided that the most relevant and informative approach would be to investigate the fate of seedlings arising from seed occurring naturally in the soil or dispersed to the site by vectors such as wind, birds, ants, etc., and their interaction with re-establishing vegetation. While not ideal in leaving the experiment open to the vagaries of weather and spatial variation in soil seed reserves, it was felt that with sufficient replication this approach offered the greatest prospect of insight into the functioning of the natural vegetation and was, therefore, the one adopted. Artificial gaps were then devised which would allow the process of recolonization to take a variety of courses.

CREATION OF ARTIFICIAL GAPS

(a) Size and form of artificial gaps

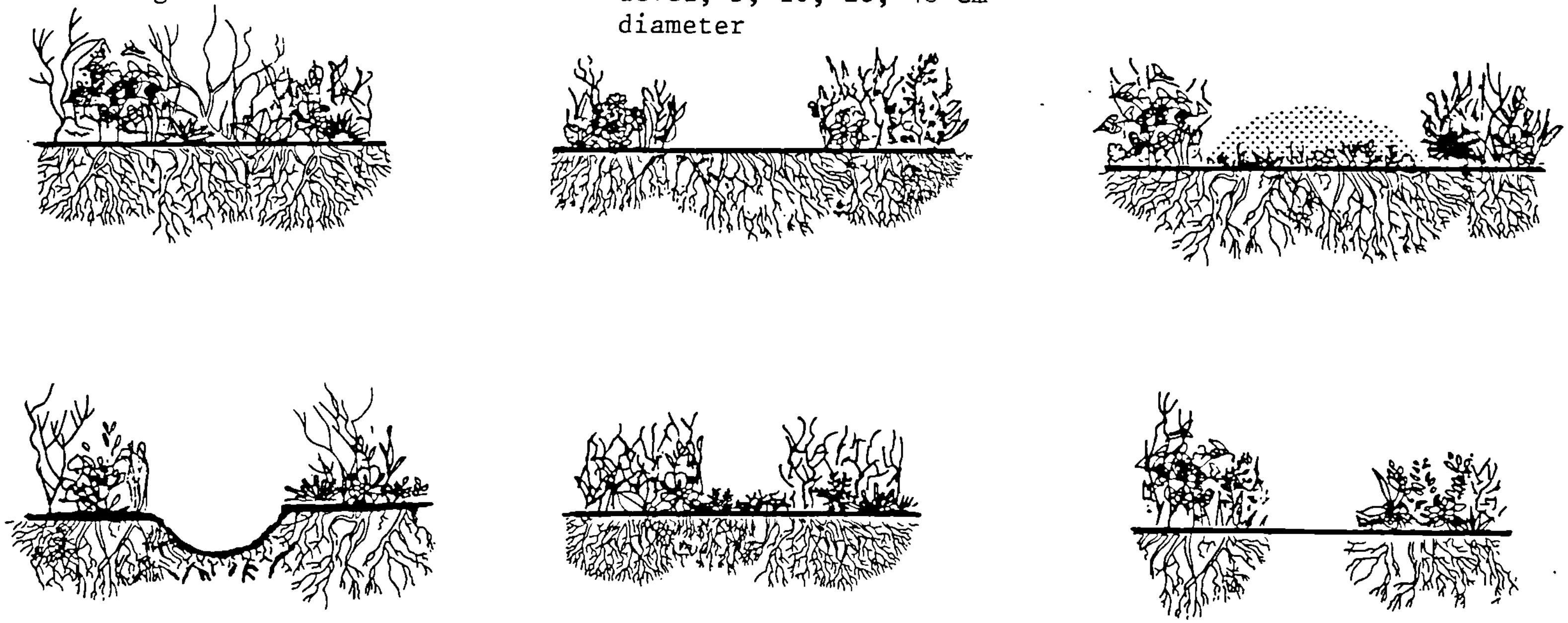
The gaps created in the turf were circular in nature and varied with respect to form and dimensions. In many cases the form of the artificial gap approached that of openings which might arise due to natural processes such as hoof prints and mole hills. Other treatments were purely artificial, enabling closer study of particular recolonization processes. Gaps varied in size from small (5 cm diameter) to bare patches which, with the exception of those arising from fire damage, were considerably larger (40 cm diameter) than any which might occur normally in the two systems under study. In all, twelve treatments were devised including areas of undisturbed

Table 2.1.

Mode of formation and characteristics of artificial gaps
NB. All 'gaps' have circular shape.

Description	Dimensions		Code
(i) Gaps in the canopy created by removing all vegetation to ground level, including bryophytes.	Diameter:	5 cm	5G
		10 cm	10G
		20 cm	20G
		40 cm	40G
(ii) Scrapes created by first removing the vegetation as for gaps and then scraping out the soil to a depth proportional to diameter. Comparable with footprints, hoofprints and rabbit scrapes.	Diameter:	Depth:	
	5 cm	2.5 cm	5S
	10 cm	5.0 cm	10S
	20 cm	10.0 cm	20S
(iii) 'Hills' in which no vegetation was removed but standard quantities of soil were applied according to area, the soil being taken from a position close to the plot to minimise variation in seed banks. Comparable with wormcasts and molehills.	Diameter:	Volume:	
	5 cm	50 cm^3	5H
	20 cm	1000 cm^3	20H
(iv) Root removal, a treatment in which the vegetation was removed as for gaps, the soil then being dug out to a depth below the root layer. Obvious root and rhizome material was removed and the soil replaced.	Diameter:	10 cm	10R
(v) Mowing where the vegetation was removed as for gaps, the bryophyte fraction separated, and the remaining material chopped and reapplied to the gap.	Diameter:	10 cm	10M
(vi) Control. Areas of undisturbed vegetation.	Diameter:	40 cm	C

Fig.2.4 Diagrammatic representation of the character of the artificially-created gaps described in Table 2.1.



C - undisturbed vegetation

G - clearance to ground level, 5, 10, 20, 40 cm diameter

H - hill, 5, 20 cm diameter

S - scrape, 5, 10, 20 cm diameter

M - clipped vegetation re-applied, 10 cm diameter

R - roots completely removed from soil beneath gap 10 cm diameter turf to act as controls. A full description with the dimensions of each gap is contained in Table 2.1, and each treatment is represented diagramatically in Fig.2.4. The margins of each gap were marked with two (four in larger gaps) red plastic pegs. The pegs, 1 cm wide by 5 cm long, were pushed into the soil until only the top 0.5 cm was visible, and were found to be effective permanent markers whose bright colour greatly facilitated identification in dense vegetation.

(b) Season of origin

In field and laboratory seed germination of many species depends upon experiencing particular environmental cues and there may be elaborate systems which determine that germination only occurs under conditions relatively favourable for subsequent seedling establishment. Millersdale species such as Pimpinella saxifraga, and Linum catharticum require chilling before dormancy is broken, a characteristic which may be interpreted as ensuring that the emergent seedling will encounter moist increasingly warm spring weather and not the cold and deteriorating conditions of winter. In other species such as Succisa pratensis, Carex flacca, and Danthonia decumbens, late seed release followed by cool winter conditions enforces dormancy on the seeds until the following spring. In contrast, species such as Festuca ovina and Koeleria macrantha on the south-facing slope show a tendency to germinate profusely in the late summer and autumn.

In Millersdale therefore we may predict that the time of year at which a gap occurs may have important repurcussions for the type of seedling flora which establishes in it. A similar principle applies to the established plants, in that the phenological pattern characteristic of each species will govern the ability of members of the community to re-invade bare areas occurring at different times of the year.

The time of year at which a gap arises was deemed therefore to be as important to potential recolonization processes as its size and form. In order to accommodate this consideration, the disturbance phenomena described in the preceding section were applied to both sites at two distinct periods in the year. The gaps were first created in September 1978, just preceding the autumn burst of germination and a duplicate set were established six months later in March 1979.

Climatic influences vary annually as well as from season to season. In consequence seedlings of species with particular requirements for seed-set and germination may be expected to vary in abundance from year to year. Such variation was assessed by means of a second set of gaps 20 cm in diameter created in September 1979 and March 1980.

EXPERIMENTAL DESIGN

The disturbance treatments were located in experimental blocks replicated seven times on each slope, replicates being separated from each other by paths one metre wide. Each block consisted of thirty plots measuring 50 cm x 50 cm, to the centre of which, individual gap types were allocated at random. Every gap was surrounded therefore by an area of undisturbed vegetation. Autumn- and spring-cut gaps were completely mixed within each block, the positions of each having been determined before the experiment began. The same area of undisturbed turf was used as a control for both the autumn- and spring-cut gaps leaving seven empty plots randomly located within each block. One of these plots in each replicate of the experiment was used to obtain samples of the established vegetation as described on page 20. The remaining six plots contained bare ground in varying proportions caused by cutting different numbers of 10 cm diameter gaps using the method described for 10G in Table 2.1. Thus five gaps produced 15.7%, ten gaps 31.4% and twenty gaps 62.8% bare ground. Duplicates of these treatments were set up in the spring. The inclusion of this sort of disturbance was designed to simulate the effects of different intensities of fire in leaving small patches and tufts of vegetation. However, as work on the rest of the experiment proceeded it was found impossible to record adequately recolonization processes in these plots as well as in those containing the more fundamental gap characters. With great reluctance subsequent work on these more extensive damage treatments was discontinued. The final arrangement of experimental plots showing the position of the 154 gaps and 7 controls on each slope is shown in Figs.2.5 and 2.6.

Events occurring in these gaps may be divided into three types of phenomena: (1) the process of recolonization by vegetative means; (2) initial patterns of colonization by seedlings and (3) survival of seedlings as the bare area is reduced. Chapters 3, 4 and 5 respectively investigate these processes using data derived in the manner described in the succeeding sections in this chapter.

Fig.2.5 The layout of the experiment on the north-facing slope. For treatment codes see Table 2.1.

← 1m →

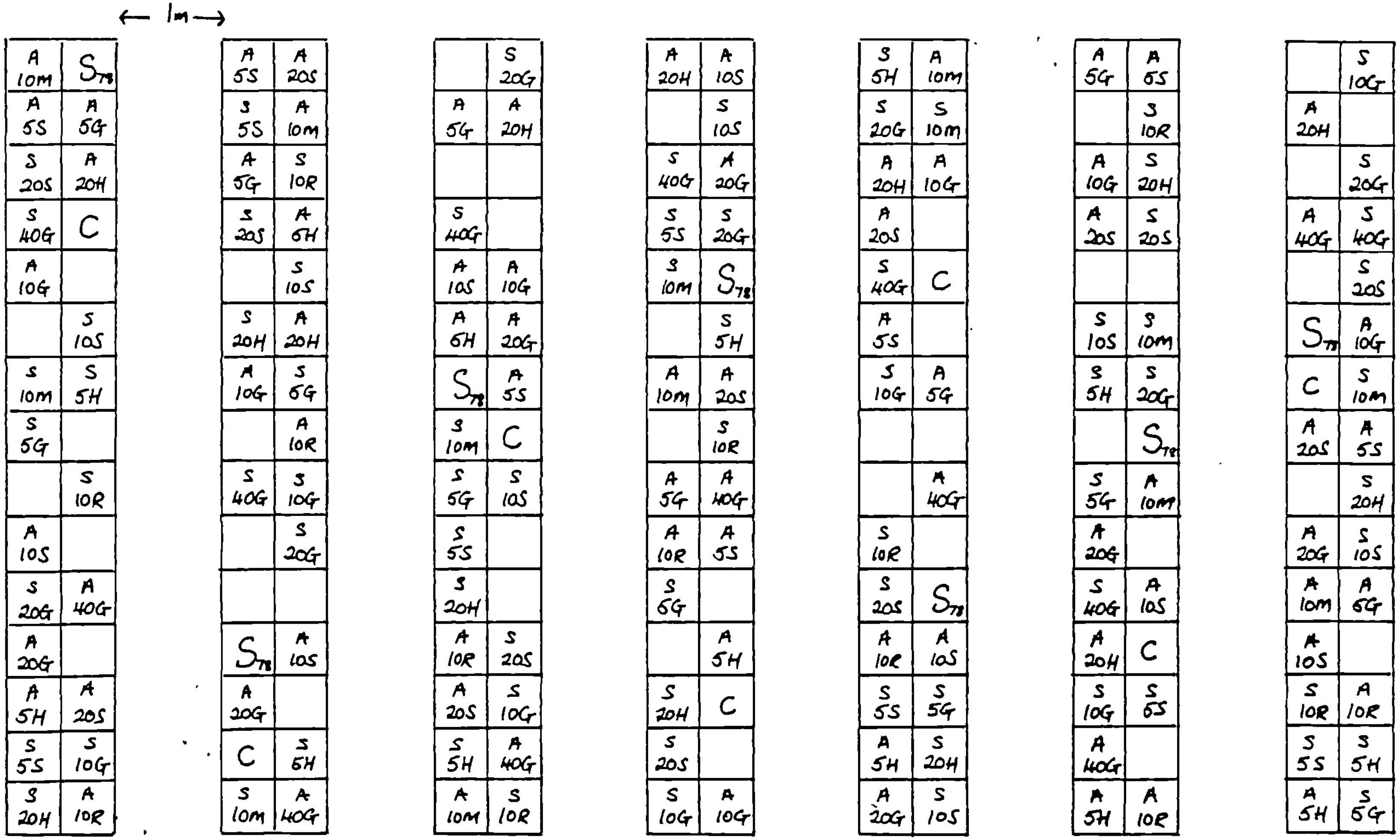
A 40G		S 20G	A 10S	A 5H	A 10S		S 40G	S 20G	C		S 40G	A 20G	A 40G
A 10R	S 40G		S 10G	S 10R			A 20G	A 10S	S 5G	A 5G	S 5H	S 10S	A 10S
A 10G	S 20G	C	A 20S		A 10G	A 10G	A 5G		S 20H	A 20S	A 10M	S 10M	
A 20S	S 10R	S 10S	S 40G	S 10M	A 20G	S 10G	S 20S	A 20H	A 20S	A 5S	A 40G	S 10R	A 5H
A 20G	A 10M	S 20H	S 5S	S 20G		S 5S	A 20H	S 10R	A 5H	A 20H	S 20H	S 20H	
S 5S	S 10S		A 10G	S 5G	S 20H	S 5H	A 5H	S_{78}	A 10M	S 5S	S 5G	S_{78}	S 5G
A 5S	S 20H	A 5G	A 40G	A 40G	S 40G		A 5S	A 5S	S 10S			S 20S	A 10R
S 5H			S 20S		A 5S			A 20G		A 10G		C	S 5H
S 10G	S 10M	A 20H	A 5S	S 10S	S 20S	A 20S		A 10R	S 10M	S 10M	A 10R	A 10G	A 10M
A 5G	A 20H	S 5H	A 10R	A 20S	A 10R	A 40G	S 20G			C	A 10S	A 5G	
			A 10M	S 5S	A 5G	A 10M	S 10R	A 10G		A 5H		A 20S	
A 10S	S_{78}	A 5H	S 10M	S 10G	A 10M	S 10M	S 5G	A 5G	A 40G	S 10S	A 20G	S 10G	A 20H
S 5G		S_{78}	S 5G	A 20H	S 5H	S 20H	S_{78}	S 40G	S 5H		S 10G	S 20G	S 40G
C		S 10R	A 20G		C	C	S 10S	S 10G		S_{78}	S 10R	S 5S	
S 20S	A 5H			S_{78}		A 10S	A 10R	S 20S	S 5S	S 20S	S 20G		A 5S

A - indicates position of autumn-cut gaps.

S - " " " spring-cut gaps.

S_{78} - " " " sample plots.

Fig.2.6 The layout of the experiment on the south-facing slope.
For treatment codes see Table 2.1.



A 10M	S_{78}	A 5S	A 20S		S 20G	A 20H	A 10S	S 5H	A 10M	A 5G	A 6S		S 10G
A 5S	A 5G	S 5S	A 10M	A 5G	A 20H		S 10S	S 20G	S 10M		S 10R	A 20H	
S 20S	A 20H	A 5G	S 10R			S 40G	A 20G	A 20H	A 10G	A 10G	S 20H		S 20G
S 40G	C	S 20S	A 6H	S 40G		S 5S	S 20G	A 20S		A 20S	S 20S	A 40G	S 40G
A 10G			S 10S	A 10S	A 10G	S 10M	S_{78}	S 40G	C				S 20S
	S 10S	S 20H	A 20H	A 6H	A 20G		S 5H	A 5S		S 10S	S 10M	S_{78}	A 10G
S 10M	S 5H	A 10G	S 6G	S_{78}	A 5S	A 10M	A 20S	S 10G	A 5G	S 5H	S 20G	C	S 10M
S 5G			A 10R	S 10M	C		S 10R				S_{78}	A 20S	A 5S
	S 10R	S 40G	S 10G	S 5G	S 10S	A 5G	A 40G		A 40G	S 5G	A 10M		S 20H
A 10S			S 20G	S 5S		A 10R	A 5S	S 10R		A 20G		A 20G	S 10S
S 20G	A 40G			S 20H		S 6G		S 20S	S_{78}	S 40G	A 10S	A 10M	A 6G
A 20G		S_{78}	A 10S	A 10R	S 20S		A 5H	A 10R	A 10S	A 20H	C	A 10S	
A 5H	A 20S	A 20G		A 20S	S 10G	S 20H	C	S 5S	S 5G	S 10G	S 6S	S 10R	A 10R
S 5S	S 10G	C	S 6H	S 5H	A 40G	S 20S		A 5H	S 20H	A 40G		S 5S	S 5H
S 20H	A 10R	S 10M	A 40G	A 10M	S 10R	S 10G	A 10G	A 20G	S 10S	A 5H	A 10R	A 5H	S 6G

A - indicates position of autumn-cut gaps.
S - " " " spring-cut gaps.
S_{78} - " " " sample plots.

RECORDING OF INITIAL SEEDLING COLONIZATION PATTERNS

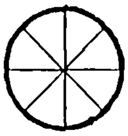
Records of the identity and position of seedlings appearing in the artificial gaps were made on two separate occasions a short time after the gaps had been cut. In November 1978, patterns of recruitment in gaps cut eight weeks previously were examined by means of circular recording frames applied to fixed points on the gap margin. The recording frames were subdivided as in Fig.2.7, the major divisions being arranged in such a way as to facilitate the direct comparison of events occurring in smaller gaps with those in the centres of larger bared areas. Subsections were of equal area in the three outer rings of the largest recording frame. In the two central rings, four small subsections were equivalent in area to one subsection in the outer rings. In the case of scrapes and hills the recording frame was placed horizontally over the gap area and seedlings were assigned to the subsection immediately above them when the gap was viewed in a perpendicular manner.

A similar exercise was conducted for spring-cut gaps in the period mid-June to early-July 1979, ten to twelve weeks after their origin. At the same time the position and identity of spring recruits to the older autumn cut gaps was recorded. In November 1979 and late June 1980, records of seedling number and identity were made in the second set of autumn- and spring-cut 20 cm diameter gaps.

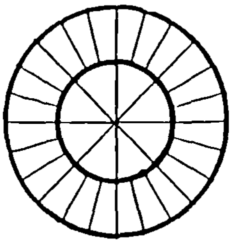
The early onset of winter conditions in 1978 curtailed recording activities on the south-facing slope and as a result replication was slightly reduced for some treatments. Spring recruitment to some of the smallest autumn-cut gaps on both slopes was not recorded in 1979 due to difficulties in recovering their position in the turf.

Data obtained from this phase of the work are examined in Chapter 4.

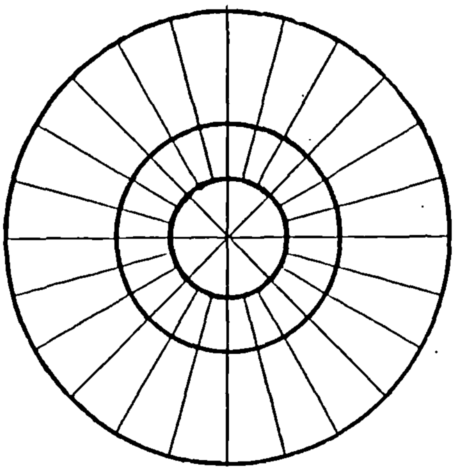
Fig.2.7 Subdivisions of circumrats used in recording seedling patterns.



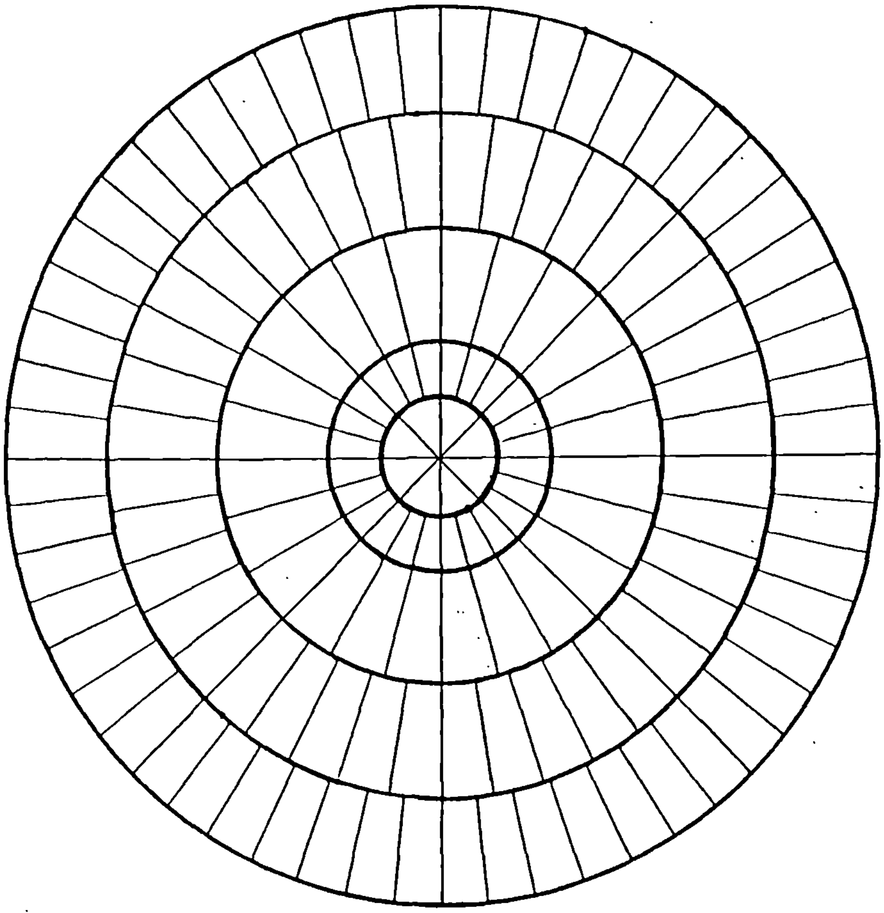
5 cm gaps



10 cm gaps



20 cm gaps



40 cm gaps

RECORDING OF SEEDLING SURVIVORSHIP

(a) Marking of seedlings

Subsequent survival of these early seedling colonists was examined on two further occasions in the summers of 1980 and 1981. Two methods for recording seedling numbers and their changes over a period of time are in popular usage. The first involves the use of a pantograph to record the exact position and identity of seedlings (e.g. Sarukhan 1974) while in the second technique, toothpicks are used to mark seedling position (e.g. Silvertown & Wilkin 1983). In this investigation, due to the possibility of seedling movement especially on the south-facing slope (Davison 1964), it was felt that permanent maps alone would not be sufficient for recording patterns of seedling mortality. For the same reasons the use of toothpicks was not favoured as these might be dislodged from close association with the seedling in question. The technique finally adopted, and found to be highly satisfactory, was to put over each seedling a small, light-weight, plastic-covered wire ring fabricated from multi-coloured transistor cable.

The size of the ring was adjusted according to the size of the seedling and in the case of very small seedlings a short 'tail' of wire was passed into the soil. Fig.2.8 shows the two alternative ring designs in diagrammatic form, their appearance when employed to mark seedlings being visible in Plate 1. In all cases it was found that the rings moved with the seedlings and did not become detached. It was feared that in the case of the smaller seedlings, the 'tail'

Fig.2.8 The design of rings used to mark seedlings.

Plate 1 Representative autumn-cut 40 cm diameter gap on the north-facing slope, showing clearly, coloured rings marking seedling positions.

might anchor the plant, but this was found not to be the case as many rings of this design were found upside down and even buried, with the seedling still inside them, some distance from the point of origin after soil disturbance. As the seedling increased in size, it was possible with this design to alter the dimensions of the ring to allow 'room for growth'. Another advantage was that the cable employed to make the rings is available in a variety of hues. It was possible therefore to 'colour-code' for grasses and forbs and autumn- and spring-germinating seedlings.

All seedling marking took place in early July 1979 due to limitations on time the previous autumn. However, in autumn-cut gaps on the more stable north-facing slope, by reference to the maps obtained previously and careful examination of the seedlings *in situ*, it was found to be possible to distinguish between old and new seedlings, i.e., those which had germinated the preceding autumn and those arising from the spring flush. Such seedlings forming two cohorts were marked accordingly using different colours and in the process mortality patterns during the first six months of life of the first cohort were obtained.

On the south-facing slope in autumn-cut gaps the situation was very different. It was found that winter mortality and soil disturbance due to frost action and rain wash, was very high. In addition spring germination had occurred slightly earlier so that it was not possible to say with sufficient certainty whether a seedling was young or old. Accordingly all seedlings were marked alike regardless of possible time of origin and were treated as one cohort, present in autumn-cut gaps in spring 1979. It was not possible to assess adequately mortality between autumn 1978 and spring 1979 in these gaps; therefore subsequent investigations into seedling mortality in these gaps concerned this one aggregate cohort only.

(b) Assessment of survival

Survival of seedlings in the marked cohorts in all gap types on both slopes was recorded in July 1980 using the same method as that employed to obtain initial patterns of colonization. The coloured rings greatly facilitated this process as it became increasingly difficult to distinguish seedlings from surrounding vegetation as the experiment progressed, particularly in the undisturbed areas of vegetation serving as controls.

In July 1981 all surviving marked seedlings were identified, and their position recorded. They were then harvested destructively by cutting off at ground level. These specimens were removed to the laboratory, dried and weighed to enable survival to be assessed in terms of shoot yield attained as well as proportion of cohort members remaining. Knowledge of the positions of survivors was vitally important to an examination of interactions between seedlings and the proximity and quantity of re-establishing vegetative shoots.

Results and conclusions drawn from this phase of the work are contained in Chapter 5.

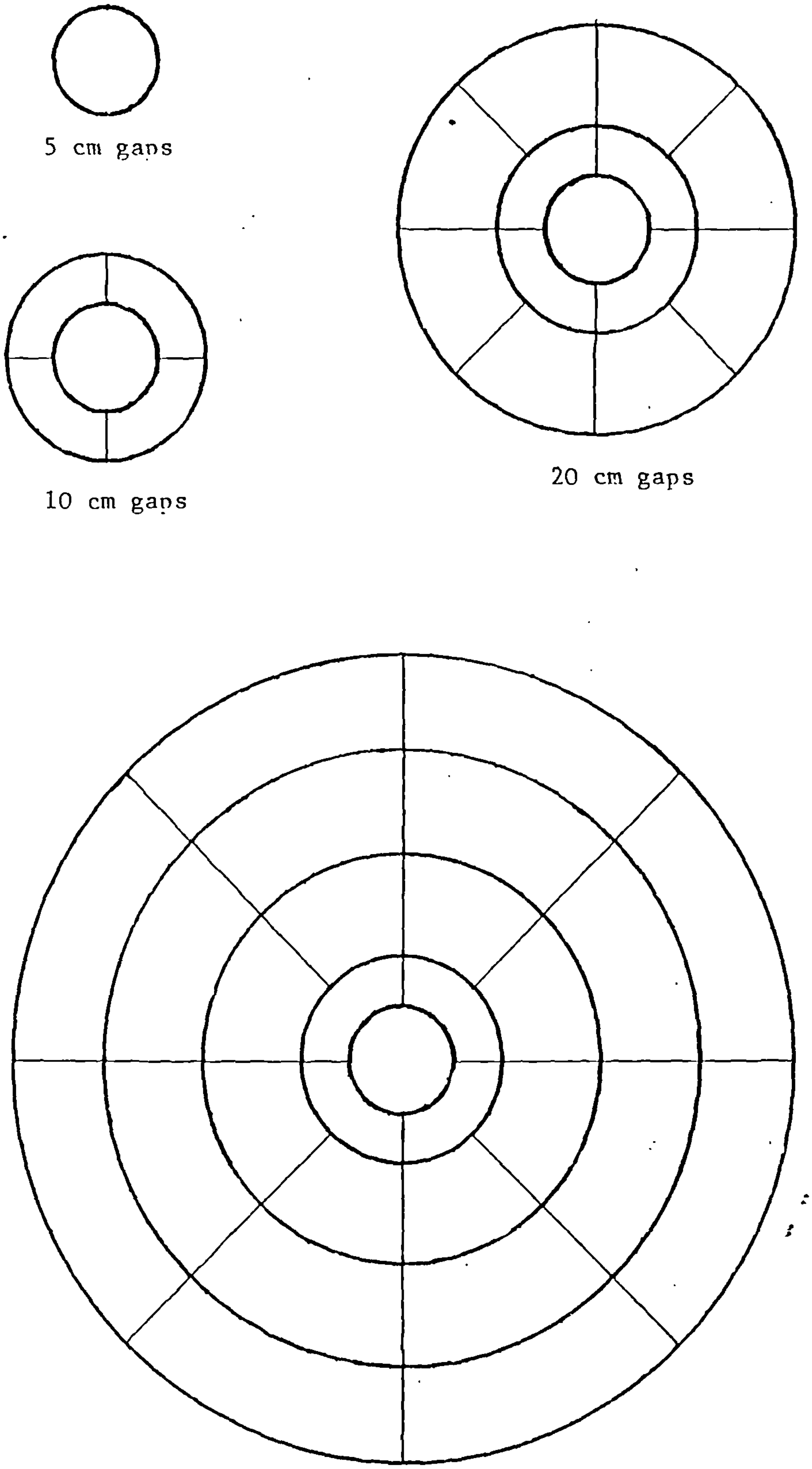
ASSESSMENT OF VEGETATIVE RECOLONIZATION

The invasion of bare areas by plants expanding vegetatively was examined on three occasions. In the autumn of 1978, the distribution of species resprouting from plants damaged at the time of gap creation, or invading the area by means of lateral spread over the ground surface or through the soil, was recorded at the same time as initial seedling colonization patterns. Shoot frequency in the subdivisions of the circular recording frames previously described (page 33 and Fig.2.7) was recorded for all species.

In August 1979, immediately after the recording of spring seedling patterns, colour photographs were taken of certain gap types to avoid unnecessary handling of the turf which might cause damage to seedlings and young tender shoots (see Appendix 7) and thus interference with the recolonization process. All 40 cm diameter gaps and control areas together with all 20 cm diameter gaps, hills and scrapes were recorded in this way. From these photographs estimates of plant cover at this time were made and used in subsequent analyses (see Chapter 5).

In the months of August and September of 1981 after surviving seedlings had been removed, all treatments were harvested destructively by the removal of all higher plant material, litter and bryophytes which had accumulated since 1978 in both gaps and undisturbed turf. Firstly all vegetation overhanging the original gap area or control turf was removed by clipping round a wire template. Gaps were then subdivided as in Fig.2.9 and material was removed in turn from each of these sections by clipping to ground level. Material

Fig.2.9 Subdivisions of gaps, employed in the final harvest of vegetative material.



5 cm gaps

10 cm gaps

20 cm gaps

40 cm gaps

rooted in, but situtated outside the gap area, was not collected. As may be seen from Fig.2.9, subdivisions in smaller gaps correspond with those found in the centres of larger gaps, enabling direct comparisons to be made between sections of different gap types.

In order to facilitate the harvesting procedure, wherever possible turves containing the 'gap' were removed to the laboratory after overhanging material had been collected, and stored for subdivision at a later date (Plate 2). Many of the turves were kept at 5 °C in the dark but the large numbers involved and restricted storage space of this kind caused some turves to be stored in the light at temperatures between 7 °C and 10 °C. Watering was reduced to the minimum required to keep the plant material from desiccating, reducing post-harvest growth to the smallest amount possible. Especially on the south-facing slope, owing to shallow soil or intruding rocks, it was not possible to remove turves intact so the gaps were subdivided and harvested in situ. Once the turves had been subdivided, all material was kept in a state of near desiccation at 5 °C in the dark.

Material from each subsection was hand-sorted into component species, dead and alive bryophytes and herb litter, and dried at a temperature of 85 °C, before being weighed. The quantity of plant material accumulated in this way was extremely large, resulting in a long period of sorting and weighing extending through several months. Preliminary analyses of data obtained in this way are contained in Chapter 3.

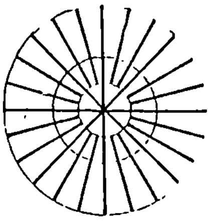
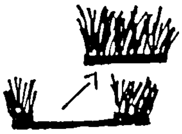
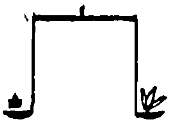
Plate 2. 'Destructive harvesting'. Turves were removed where possible intact to the laboratory. In this photograph a 40 cm diameter gap on the north-facing slope is being removed. Note the extra 'rim' of vegetation which ensured that the 'gap' was removed *in toto*.

SUMMARY

The method employed to investigate gap recolonization processes in Millersdale is summarised in Fig.2.10. The influence of gap size, form and season of origin was studied by means of comparisons between artificial gaps and areas of undisturbed turf. Destructive and non-destructive techniques were adopted where appropriate and yielded information on both sexual and asexual regeneration processes operating at the two sites.

The final phase of the investigation involved the analysis and interpretation of these data in the light of existing information derived from studies of individual species morphology, phenology and laboratory characteristics, e.g., relative growth rate, nuclear DNA content, germination response to light and temperature. By these means an assessment of the role of gap colonisation in the maintenance of species diversity in two contrasted limestone grassland sites is attempted in the concluding chapter of this thesis.

Fig. 2.10 Summary of methods used in the investigation of gap recolonization.

	1978	1979	1980	1981	1982	1983	1984
	Autumn gap cutting Sept.1978	Spring gap cutting Mar. 1979					
	Records of Autumn germination Nov. 1978 and counts of vegetative shoots	Records of Spring germination Jun./Jul. 1979 Photographs	Records of seedling survival Jul.1980	Records of seedling survival Jul. 1981			
		Marking of seedlings Jun. 1979					
				Destructive harvest of surviving seedlings Jul./Aug.1981			
				Destructive harvest of recolonized gaps Jul./Aug.1981			
				Sorting into species, bryophytes and litter →			
				Weighing dried plant material →			
		← - - - - -	- - - - -	- - - - -	Data analysis and interpretation →		

CHAPTER 3

VEGETATIVE RECOLONIZATION

In this chapter vegetative regrowth in the artificial gaps previously described (Chapter 2) is considered and the recolonization process on north- and south-facing slopes in limestone grassland is compared. The contribution of vegetative material to the total standing crop achieved in gaps is assessed and the relative importance of sexual and asexual reproduction discussed. Early patterns of regrowth in both autumn- and spring-cut gaps are described by means of both field mapping and photographs.

The main body of data presented in this chapter is derived from the final harvest of the gap experiment in 1981. By this time the spring gaps were two and a half years and autumn gaps nearly three years old. Particular attention is paid to the influence of both gap size and severity of damage. Recolonization in similarly cleared areas of 10, 20 and 40 cm diameter 'simple' gaps is compared with recovery in scrapes of 10 and 20 cm diameter (the severest form of damage included in the experiment.

Dominance-diversity curves for gaps and scrapes of varying size are used as a prelude to assessments of shifts in relative abundance of species in gaps created at different times of the year, compared with undisturbed turf. The changing role of species in the dominance hierarchy as a result of damage is examined further by consideration of individual species rank order and final biomass attained.

RESULTS

THE IMPORTANCE OF VEGETATIVE REGROWTH IN GAP RECOLONIZATION

The harvests from autumn- and spring-cut gaps in the summer of 1981 were composed of five major types of plant material; bryophytes (including bryophyte litter), herb litter, seedlings (including annuals), living herbs rooted in gap area (including the sub-shrubs *Thymus praecox* and *Helianthemum nummularium*), and vegetation overhanging the gap area. Relative proportions of these groups in 40 cm diameter gaps and areas of control turf (also 40 cm diameter) are shown in Fig.3.1 for the north-facing slope and Fig.3.2 for the south-facing slope.

(a) North-facing slope

In undisturbed vegetation bryophytes constituted 45.5% of the total quantity of plant material harvested and herb litter another 33.2%. Seedlings, including annuals, were a very minor component accounting for only 0.1% of the total. Living herbs were more important than overhanging vegetation (15.7% and 5.6% respectively) but these two categories, together with seedlings, made up only one-fifth of the total.

In autumn-cut gaps bryophytes (21.6%) were much less important and herb litter (46.4%) more important than in undisturbed vegetation. However, these two categories together accounted for approximately the same proportion of the total in each (nearly 70% in autumn gaps and nearly 80% in controls). Seedlings were again a minor component (2%) but were a more prominent feature of the vegetation of gaps than in controls. Living herbs were more

Fig. 3.1 Relative proportions of major groups of plant material at final harvest in 40 cm gaps and controls on the north-facing slope.

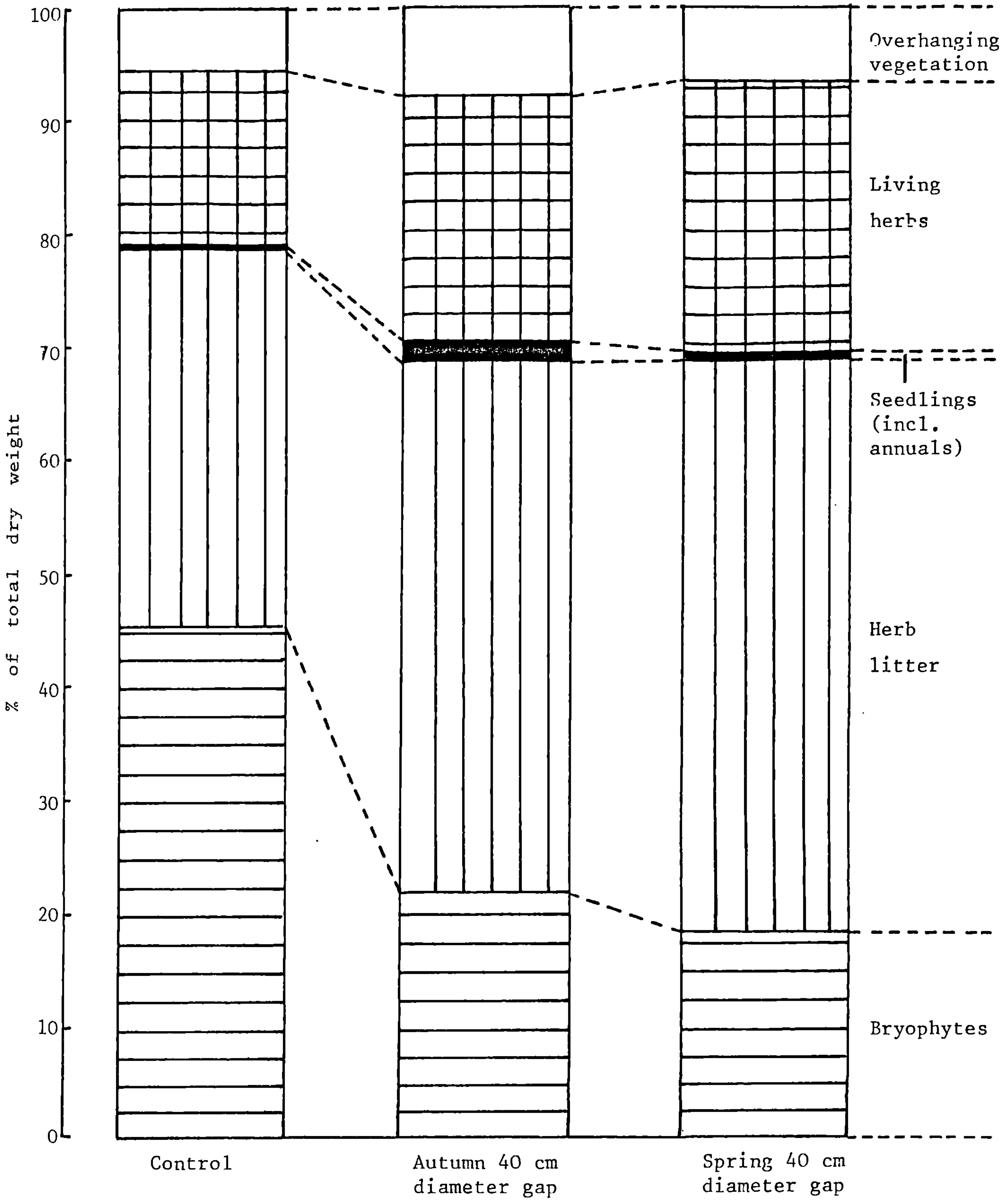
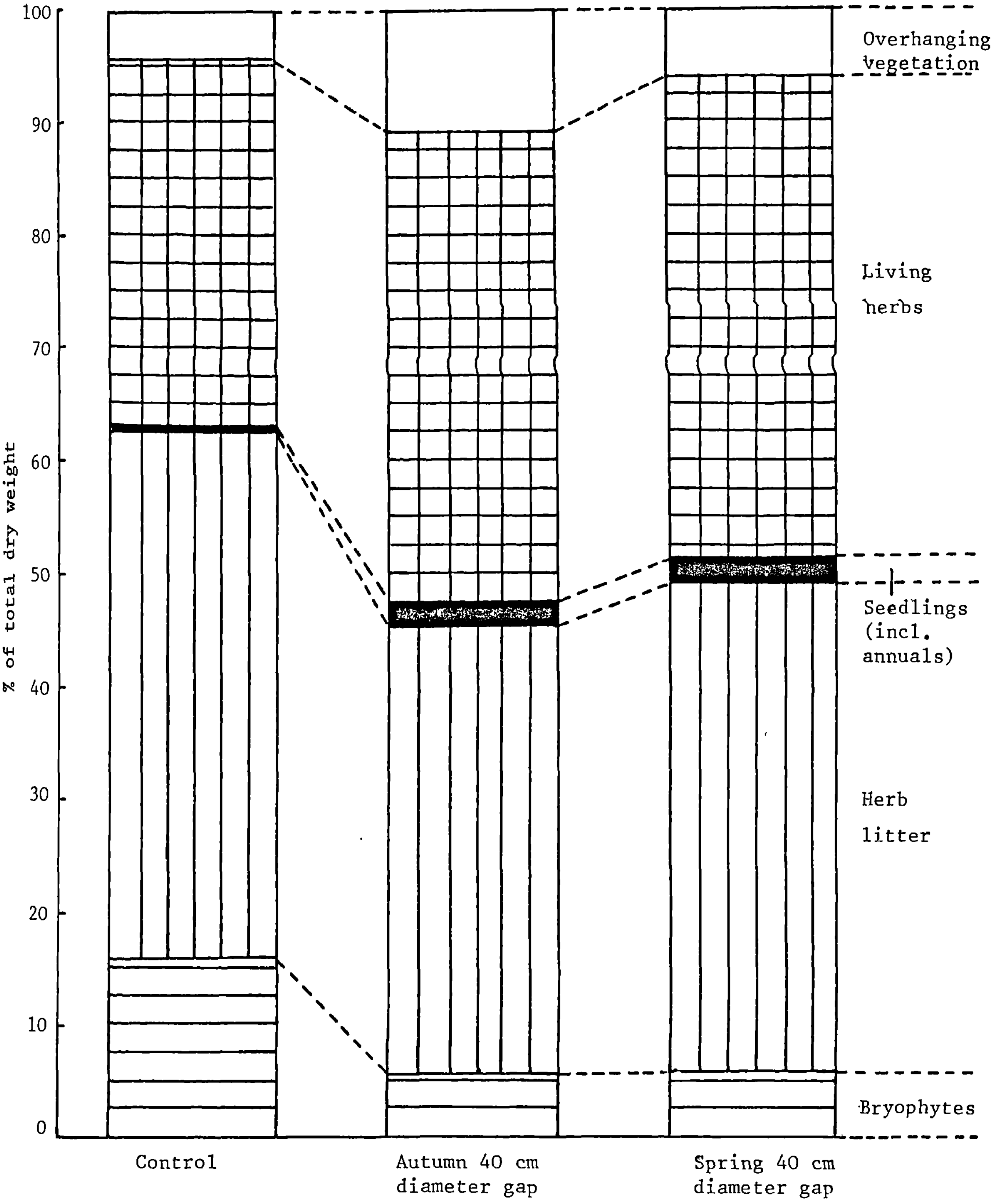


Fig. 3.2 Relative proportions of major groups of plant material at final harvest in 40 cm gaps and controls on the south-facing slope.



important in autumn-cut gaps (21.7%) while the quantity of overhanging vegetation at 8.3% of total was only slightly increased in comparison with undisturbed vegetation.

Spring-cut gaps were remarkably similar in composition to autumn-cut gaps. Seedlings (0.7%) and bryophytes (18.4%) were slightly less important, but together with herb litter accounted for the same proportion of total as in autumn-gaps, as did living herbs and overhanging vegetation.

(b) South-facing slope

Only 16% of mean total biomass was attributable to bryophyte material in undisturbed vegetation on the south-facing slope compared with 45.5% on the north. Living herbs and herb litter together accounted for nearly 80% of the total, while seedlings were again a minor component (0.5%).

The importance of bryophytes in the vegetation was further reduced in autumn-cut gaps (to 5.6%). Seedlings were more prominent (2%) and overhanging vegetation expanded to just over 10% of the total. In common with control plots, living herbs and herb litter together constituted approximately 80% of the total, in equal proportions.

The vegetation composition of spring-cut gaps closely resembled that of the older gaps. Overhanging vegetation was slightly reduced, but all other groups were found in approximately the same proportions as in autumn-cut gaps.

The proportions of major constituents in the plant material harvested from recolonized gaps on both slopes therefore differed in some important respects from the composition of undisturbed vegetation. In particular, bryophytes were less important and seedlings, although remaining a minor component in terms of biomass, became more prominent.

Regeneration from seed is considered in more detail in Chapters 4 and 5, while the remainder of this chapter is devoted to further analysis of the effects of damage on vegetative regrowth.

INITIAL PATTERNS IN AUTUMN-CUT GAPS (1978)

Field mapping of shoot frequency revealed three distinctive responses to gap cutting on both slopes. In Fig.3.3 species invading the cleared area by lateral spread from surrounding vegetation, e.g. Pseudoscleropodium purum and Thymus praecox, may be distinguished clearly from those re-sprouting from damaged tussocks, e.g. Avenula pratensis and Festuca ovina. There were also a number of species of more widespread but less aggregated occurrence in the vegetation which appeared to be able to recover by producing new shoots throughout the gap area, e.g. Festuca rubra and Hieracium pilosella.

The extent of vegetative recovery in 33 individual species on the north-facing slope was estimated from shoot frequency counts. Comparison of species rank order as resprouts in 40 cm diameter autumn-cut gaps with rank order in established vegetation revealed that the status of a number of species changed considerably (Fig.3.4). Notably, Succisa pratensis, Dactylis glomerata and Achillea millefolium were reduced while Campanula rotundifolia, Agrostis capillaris, Poa pratensis, Pimpinella saxifraga and Galium sterneri expanded immediately after cutting.

Fig. 3.3 Three different patterns of vegetative re-invasion of autumn-cut 40 cm diameter gaps
■ indicates shoot present in subsection

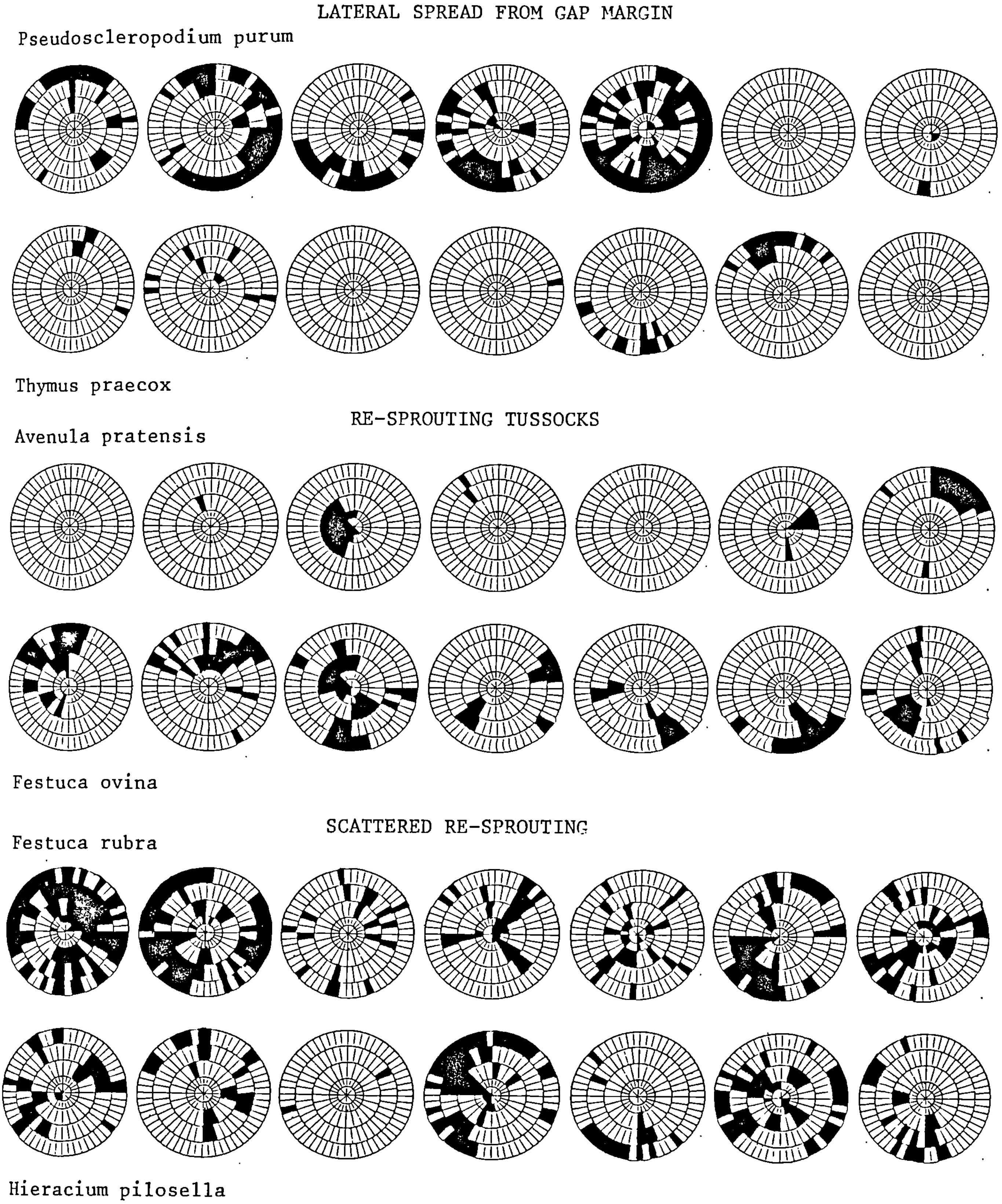
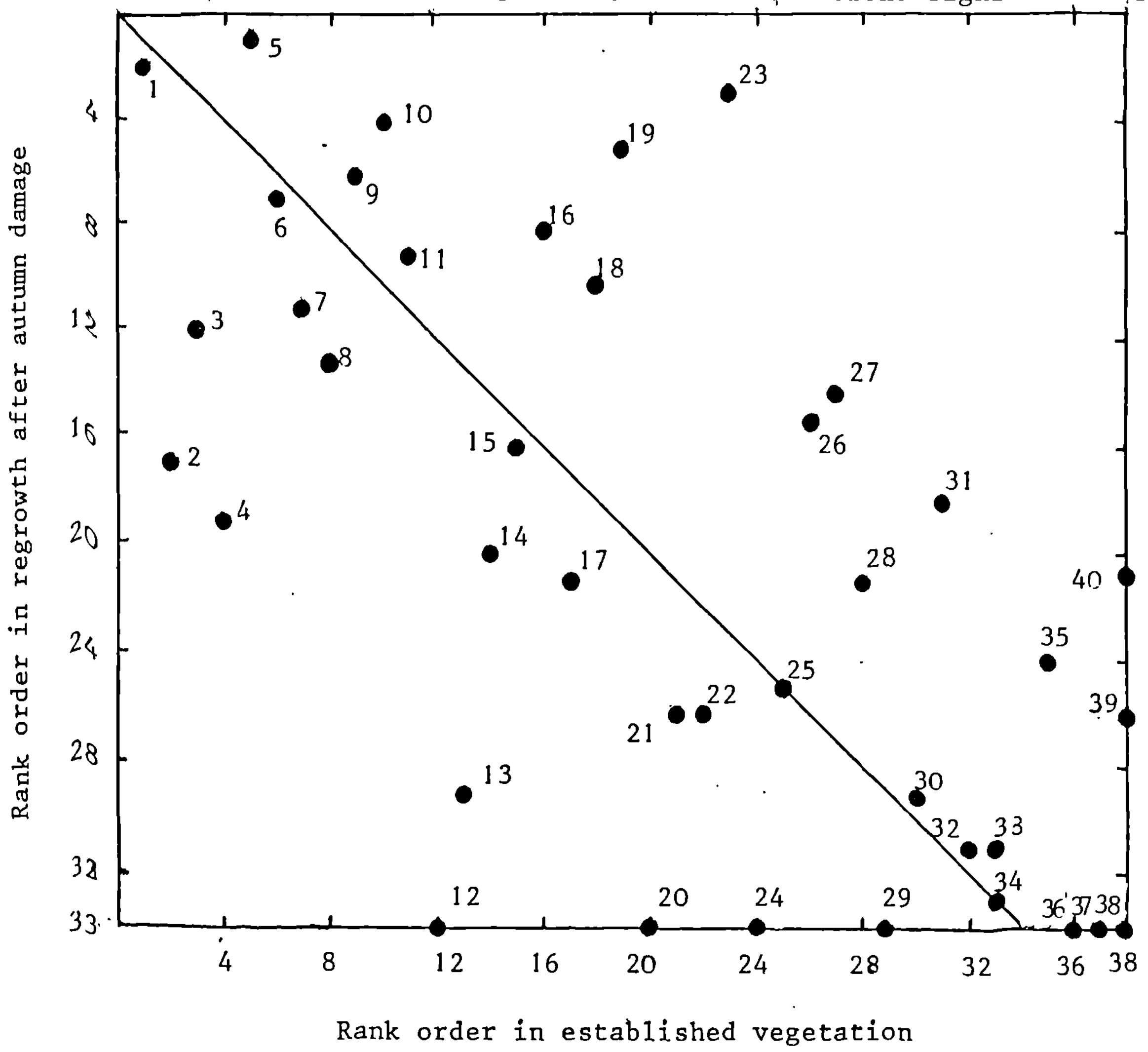
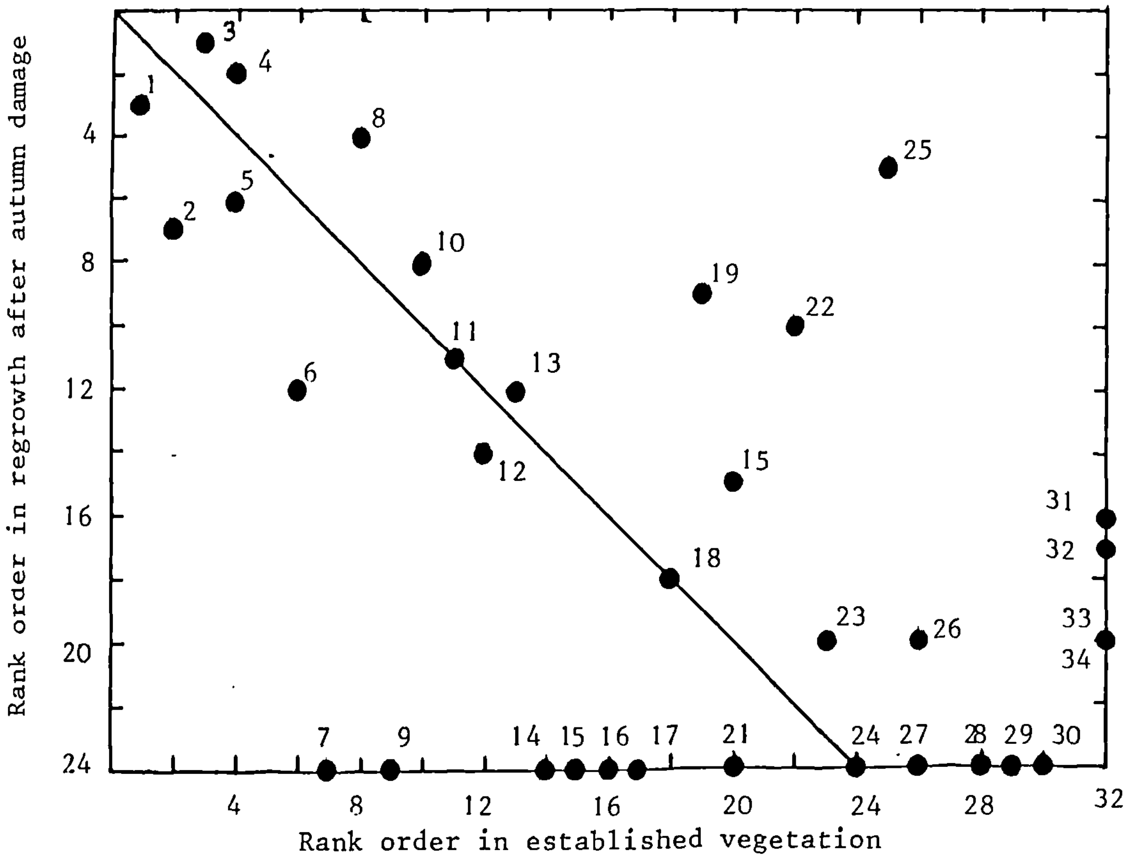


Fig. 3.4 The relative importance of individual species recorded as resprouts eight weeks after creation of autumn 40 cm diameter gaps compared with their status in the established vegetation of the north-facing slope in 1978.
Spearman's rank order correlation coefficient significant at P<0.0005.



1. Pseudoscleropodium purum
2. Succisa pratensis
3. Carex flacca
4. Dactylis glomerata
5. Festuca rubra
6. Centaurea nigra
7. Avenula pubescens
8. Avenula pratensis
9. Carex caryophyllea
10. Plantago lanceolata
11. Origanum vulgare
12. Galium verum
13. Achillea millefolium
14. Lotus corniculatus
15. Valeriana officinalis
16. Arrhenatherum elatius
17. Anthoxanthum odoratum
18. Viola riviniana
19. Agrostis capillaris
20. Danthonia decumbens
21. Holcus lanatus
22. Angelica sylvestris
23. Campanula rotundifolia
24. Pimpinella major
25. Serratula tinctoria
26. Poa pratensis
27. Galium sterneri
28. Trisetum flavescens
29. Hypericum perforatum
30. Festuca ovina
31. Pimpinella saxifraga
32. Potentilla erecta
33. Rumex acetosa
34. Leontodon hispidus
35. Luzula campestris
36. Hieracium spp.
37. Agrostis vinealis
38. Galium saxatile
39. Taraxacum spp.
40. Koeleria macrantha

Fig. 3.5 The relative importance of individual species recorded as resprouts eight weeks after creation of autumn 40 cm diameter gaps, compared with their status in the established vegetation of the south-facing slope in 1978.
Spearman's rank order correlation coefficient significant at $P<0.0005$.



1. Avenula pratensis
2. Thymus praecox
3. Hieracium pilosella
4. Festuca ovina
5. Koeleria macrantha
6. Helianthemum nummularium
7. Dactylis glomerata
8. Briza media
9. Festuca rubra
10. Centaurea scabiosa
11. Lotus corniculatus
12. Pimpinella saxifraga
13. Carex caryophyllea
14. Danthonia decumbens
15. Brachypodium sylvaticum
16. Arabis hirsuta
17. Galium sterneri
18. Plantago lanceolata
19. Arrhenatherum elatius
20. Hieracium spp.
21. Linum catharticum
22. Cerastium fontanum
23. Centaurea nigra
24. Polygala vulgaris
25. Campanula rotundifolia
26. Origanum vulgare
27. Succisa pratensis
28. Avenula pubescens
29. Valeriana officinalis
30. Trisetum flavescens
31. Tragopogon pratensis
32. Taraxacum spp.
33. Festuca arundinacea
34. Leontodon hispidus

On the south-facing slope, only 23 species had recovered vegetatively by mid-November. Comparison of rank order as re-sprouts with rank order in established vegetation (Fig.3.5) revealed that three species, Campanula rotundifolia, Carex flacca and Arrhenatherum elatius were considerably more important and Helianthemum nummularium rather less important amongst the early colonists of gaps. The remaining species changed little in their relative importance although Thymus praecox, which was the second most important species in established vegetation, dropped to seventh position and Briza media, formerly eighth, became the fourth most important species amongst re-sprouts.

On both slopes, a number of species had been recorded as established plants but were not represented as early vegetative colonists of gaps. In most cases these were minor components of the vegetation, but three species of greater importance, i.e. Galium verum on the north-facing slope, and Festuca rubra and Dactylis glomerata on the south-facing slope, appeared to be strongly suppressed by autumn gap-cutting.

INITIAL PATTERNS IN SPRING-CUT GAPS (1979)

Owing to the considerable amount of time spent in recording the spring flush of germination in both autumn- and spring-cut gaps, and marking seedlings for subsequent survival studies, it was not possible to make quantitative estimates of vegetative regrowth in spring-cut gaps. Instead, recolonization patterns were recorded in the form of colour photographs (see below). By late summer 1979, when the spring gaps were six months old, a number of species had succeeded in flowering, despite having been cut back to ground level earlier in the year. These species are listed in Table 3.1.

Table 3.1

Species which succeeded in flowering in the summer of 1979 in spring gaps.

NORTH-FACING SLOPE	SOUTH-FACING SLOPE
Avenula pratensis	Centaurea scabiosa
Carex flacca	Lotus corniculatus
Centaurea nigra	Origanum vulgare
Lotus corniculatus	Thymus praecox
Origanum vulgare	
Succisa pratensis	
Valeriana officinalis	

PHOTOGRAPHIC RECORDS OF VEGETATIVE RECOVERY

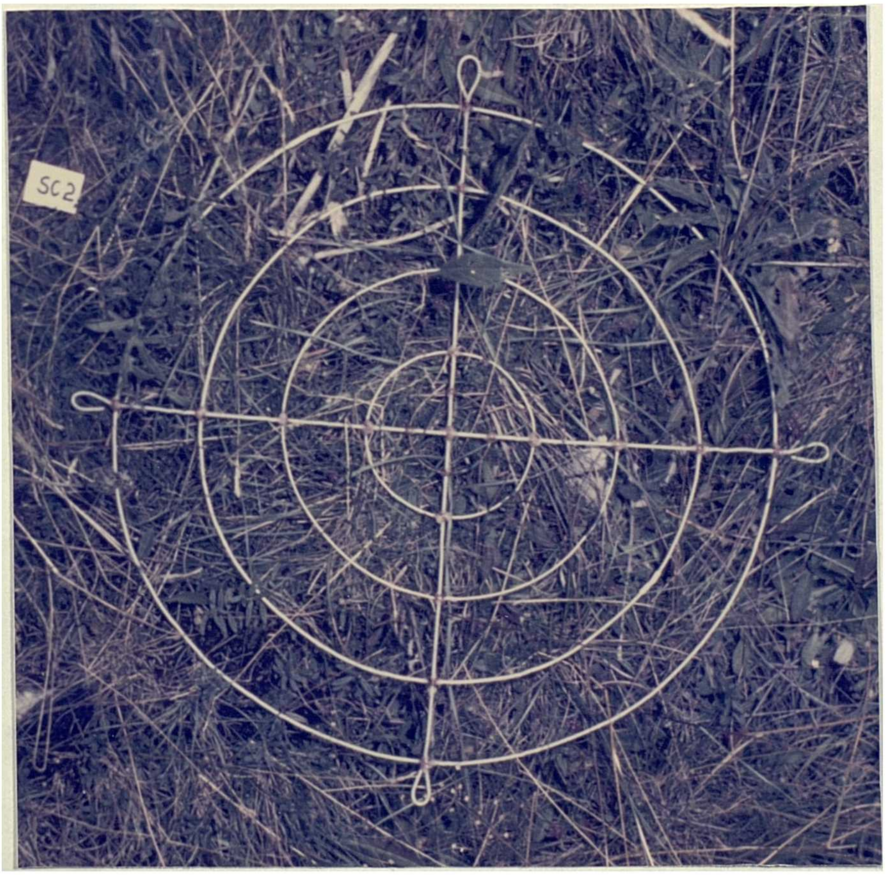
Photographic records of regrowth in both spring gaps and gaps cut the previous autumn were made in August 1979. A representative selection for both slopes is contained in Plate 3 along with photographs of control plots taken at the same time.

Three features are of immediate interest. Firstly the regrowth in gaps on both slopes appeared to be forb-rich in comparison with undisturbed vegetation, regardless of the season at which the gaps were created. Secondly, despite their greater age, autumn-cup gaps were markedly more open ten months after clearance than their four-month-old spring counterparts. Related to this feature is the fact that in both gap types on the south-facing slope, superficially buried rock had been exposed, presumably as the result of frost action and rainwash over the winter and spring periods. It seems

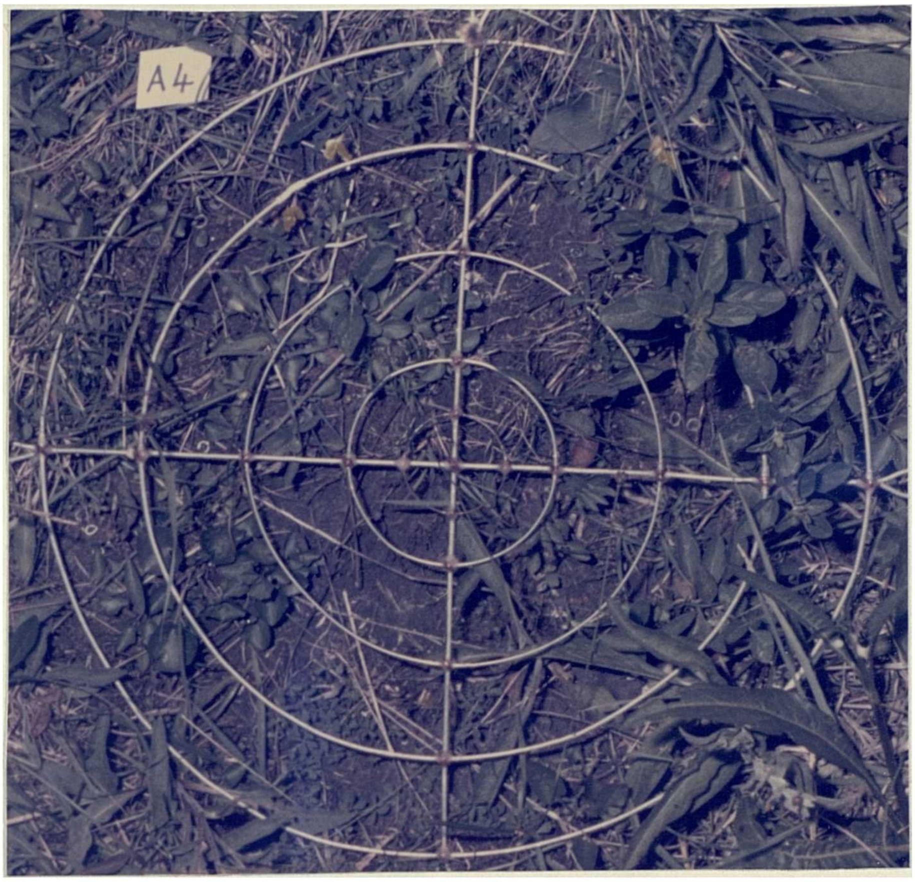
Plate 3 Representative photographs showing the character of the undisturbed vegetation and the extent of vegetative recovery in 10 month old autumn- and 4 month old spring-cut 40 cm diameter gaps on the north- and south-facing slopes in Millersdale. All photographs were taken in August 1979.

Control north-facing slope

Control south-facing slope

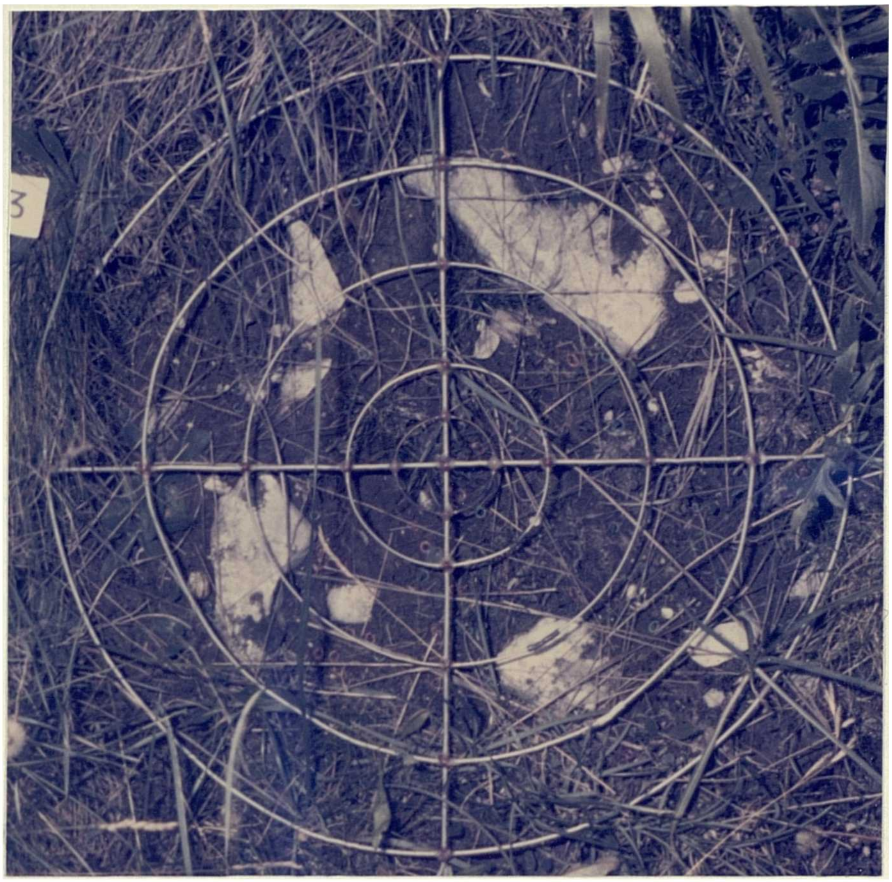


Autumn-cut 40 cm diameter gap, north-facing slope



Spring-cut 40 cm diameter gap, north-facing slope

Autumn-cut 40 cm diameter gap, south-facing slope



Spring-cut 40 cm diameter gap, south-facing slope

likely that secondary damage of this kind, particularly in autumn-cut gaps, may be an important determinant of the subsequent recolonization process. This hypothesis was examined further by quantitative analysis of data derived from harvested vegetative material collected in 1981.

THE COMPOSITION OF VEGETATION IN GAPS AND CONTROL PLOTS IN 1981

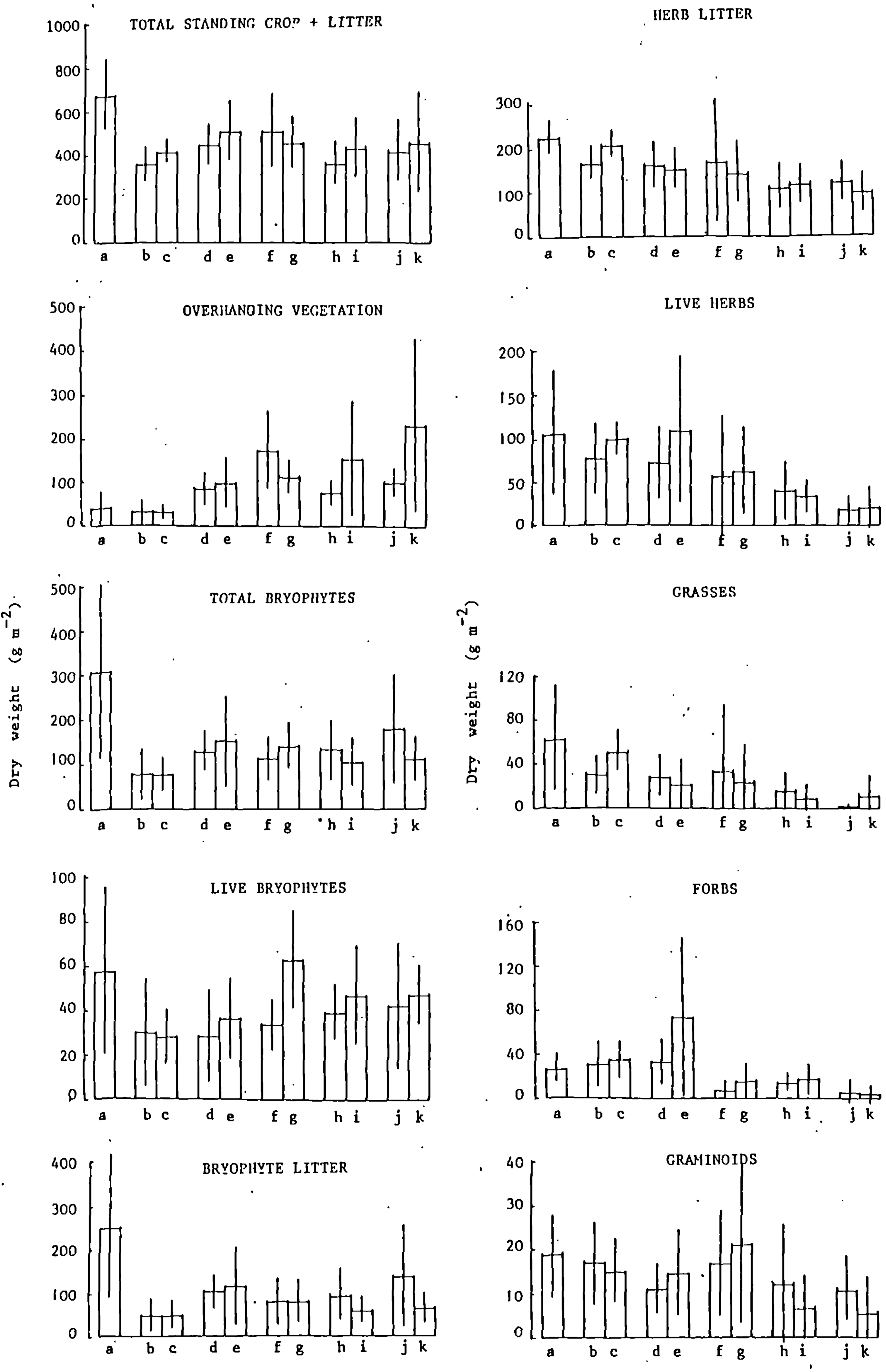
All experimental treatments and control plots were harvested during July and August 1981 by the method described in Chapter 2. At the beginning of this chapter the relative proportions of major components of the plant material in 40 cm diameter gaps and controls were described (pp.41-43 and Figs.3.1 and 3.2). A more detailed presentation of final harvest results is contained in Fig.3.6 and Appendix 3 for the north-facing slope and Fig.3.7 and Appendix 4 for the south-facing slope. Ninety-five percent confidence limits for the means are included with these data.

Data presented are for gaps and scrapes of different sizes which contrast markedly in the severity of damage. Gaps of 5 cm diameter are not included since the relatively low level of replication in relation to their small size produced great variability in the data. Hills are excluded from this analysis as their susceptibility to partial destruction over the experimental period reduced their impact on the buried vegetation.

(a) North-facing slope

After a recovery time of two and a half years for spring-cut gaps and three years for autumn-cut gaps, total standing crop + litter was found to be less in all gap types than in undisturbed

Fig. 3.6 Mean dry weight of major plant groups (as determined by destructive harvest in 1981) in a variety of gap types on the north-facing slope. Respectively, a = controls; b, d, f = autumn 40, 20 and 10 cm gaps; c, e, g = spring 40, 20 and 10 cm gaps; h, j = autumn 20 and 10 cm scrapes; i, k = spring 20 and 10 cm scrapes.
Vertical lines indicate 95% confidence limits for the means.



vegetation. Despite their shorter life-span, spring-cut gaps generally contained slightly more vegetation than autumn-cut gaps but in most cases this difference was not statistically significant. Scrapes (thought to be the severest form of damage) surprisingly contained quantities of material similar to those harvested from gaps.

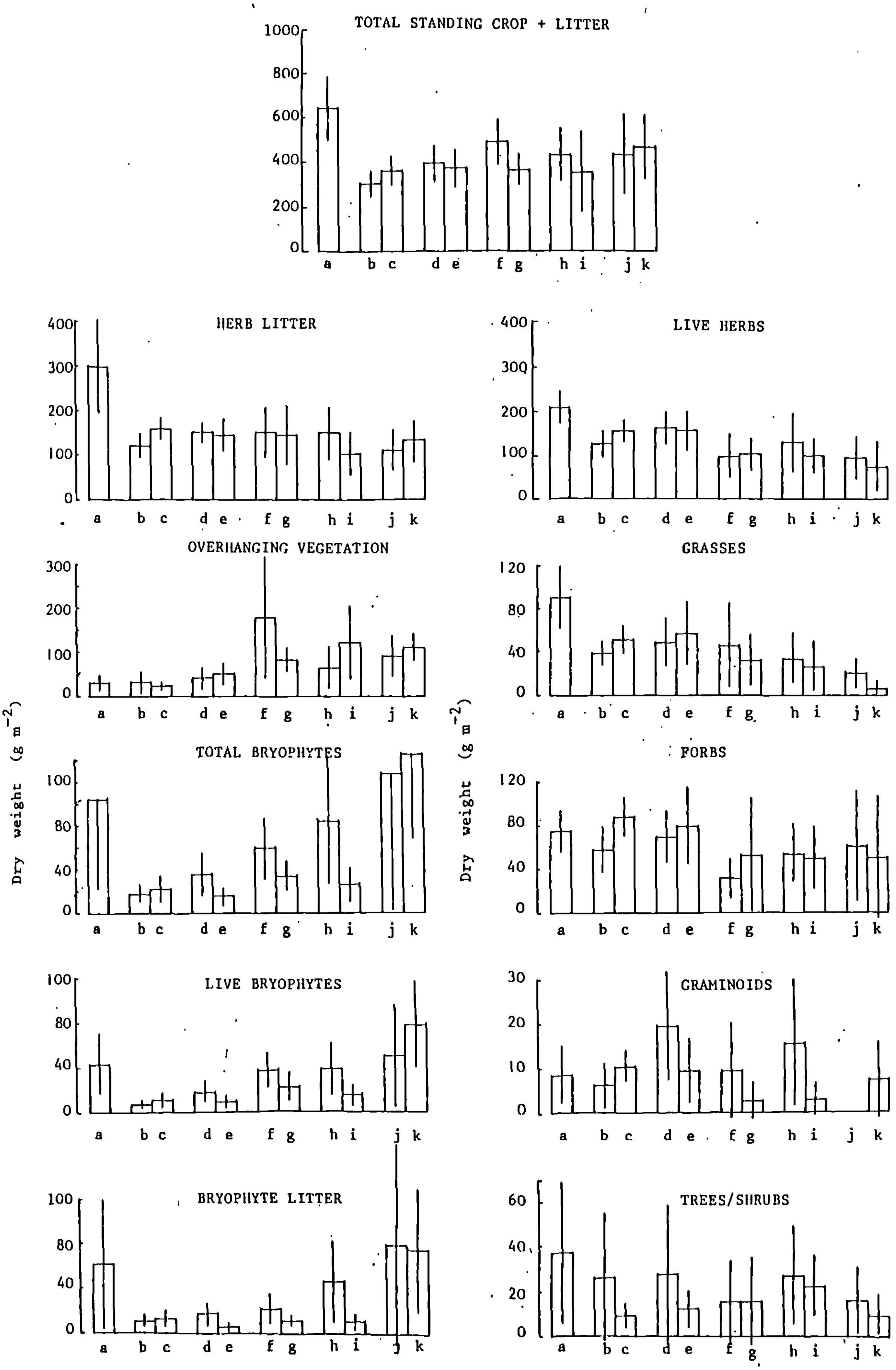
Examination of the composition of the plant material in the various treatments revealed some interesting differences. Scrapes contained significantly smaller quantities of both rooted herbs and herb litter than either gaps or controls. Amounts of herb litter accumulated in gaps were generally less than in undisturbed vegetation, although rooted herbs reached similar quantities in both gaps and controls.

The largest differences between undisturbed vegetation and gaps was found to be in the quantities of bryophyte material, overhanging vegetation and seedlings. The latter are discussed in detail in Chapters 4 and 5 and as they did not make a significant contribution to the vegetation on a dry weight basis, they will not be examined further here. Except in 10 cm scrapes where variability was high, total bryophyte material was considerably less in all gap types than in controls, but was increased somewhat in the smaller gaps and scrapes. While some of this difference could be accounted for by reduced quantities of living bryophyte material, particularly in the larger gaps, the major dissimiliarity between gaps and controls was found in the amount of bryophyte litter accumulated. On a mean dry weight basis undisturbed vegetation contained nearly twice as much bryophyte litter as the autumn-cut 10 cm scrapes (containing the second largest amount) and considerably more than all other gap types. Overhanging vegetation was greatly increased in quantity in smaller gaps and scrapes compared with controls and large gaps. As might be expected, this component showed high variability and was clearly dependent on the nature of the vegetation proximal to the gap area.

Quantities of grasses and forbs were generally reduced in scrapes of both sizes formed at both seasons of the year. Grasses were found in slightly smaller quantities in gaps than in controls, with the exception of the spring 40 cm gaps which contained similar amounts to undisturbed vegetation. The great variability in forb material harvested from spring-cut 20 cm diameter gaps is due to two replicates each of which contained excessive amounts of two species, one of which, Serratula tinctoria, was of very restricted occurrence in the experimental area. In both gaps and scrapes, graminoids varied little in comparison with undisturbed vegetation.

Examination of the vegetation composition of gaps and scrapes revealed therefore, that although the total dry weight of plant material was approximately the same regardless of gap type or season of origin, the relative contribution of various components to the total differed markedly, particularly when overhanging vegetation was considered. The larger quantities of material harvested from control plots seem to be attributable almost entirely to the accumulation of bryophyte material, especially bryophyte litter. A striking feature of the results is the remarkable similarity between autumn- and spring-cut gaps in spite of the disparity in length of the recolonization period.

Fig. 3.7 Mean dry weight of major plant groups (as determined by destructive harvest in 1981) in a variety of gap types on the south-facing slope. Respectively, a = controls; b, d, f = autumn 40, 20 and 10 cm gaps; c, e, g, = spring 40, 20 and 10 cm gaps; h, j = autumn 20 and 10 cm scrapes; i, k = spring 20 and 10 cm scrapes.
Vertical lines indicate 95% confidence limits for the means.



(b) South-facing slope

Data from the south-facing slope were more variable than those from the north-, reflecting the patchier distribution of established vegetation. Nevertheless, estimates of total standing crop and analysis of its components provided some useful information on the nature of gap recolonization at this site. In common with the north-facing slope, seedling biomass is considered in Chapter 5.

There was found to be little difference between gaps and scrapes in the total quantities of plant material accumulated. However, in undisturbed vegetation yield considerably exceeded that in the various damage treatments. In general there were no differences in quantity according to season except in the smallest 'gap' treatment considered (10 cm diameter) where spring-gaps contained less plant material than autumn-cut gaps.

Differences between gaps and scrapes were rather small when rooted herbs alone were considered. However, in all except the 20 cm diameter gaps, the biomass attained by herbs was significantly smaller in gaps and scrapes than in controls. Herb litter accumulation in all damage treatments was also considerably less than in control plots.

Data for the main herbage components were very variable and, with the exception of those relating to grasses, showed little impact of either damage or season. Grasses, however, were significantly reduced in quantity compared with undisturbed vegetation in all except 20 cm diameter gaps and the autumn-cut 10 cm diameter gaps. The shoot biomass of the grasses in 10 cm scrapes was significantly less than in the two larger gap sizes.

For forbs, graminoids and shrubs, season or treatment did not appear to be an important determinant of final biomass and all gap types showed little difference from undisturbed vegetation in these components. However, it is interesting to note that shrubs recolonizing spring-cut gaps showed far less variability in final biomass than in comparable autumn-cut gaps.

There was little difference between controls and the two larger gap sizes in dry weight of overhanging vegetation. In 10 cm scrapes and gaps, plant material of this kind was found in significantly larger amounts than in undisturbed vegetation.

Quantities of bryophyte material harvested from control plots were very variable indeed, reflecting the very patchy distribution of these plants on the south-facing slope. Variability in bryophyte biomass after damage increased inversely with gap size. Thus, 40 cm diameter gaps contained uniformly small amounts of both living and dead plant matter of this kind while the smallest scrapes exhibited huge differences in quantities accumulated. As with shrubs, variability in bryophyte biomass was much less in spring-cut gaps than in their older autumn counterparts.

In common with those of the north-facing slope, gaps and scrapes on the south-facing slope had not accumulated quantities of plant material comparable with those in undisturbed vegetation, during the period of this experiment. However, this generalisation does not apply to all components of the vegetation. Grasses and herb litter were significantly reduced in all treatments regardless of season of origin, but two components - bryophytes and overhanging vegetation - were found to differ considerably in their importance as invaders of canopy gaps on the south-facing slope. While the categories forbs, graminoids and shrubs had reached levels of biomass in gaps comparable with those in undisturbed vegetation, variations in species relative abundance were observed in different gap types. These phenomena are examined further in the following sections.

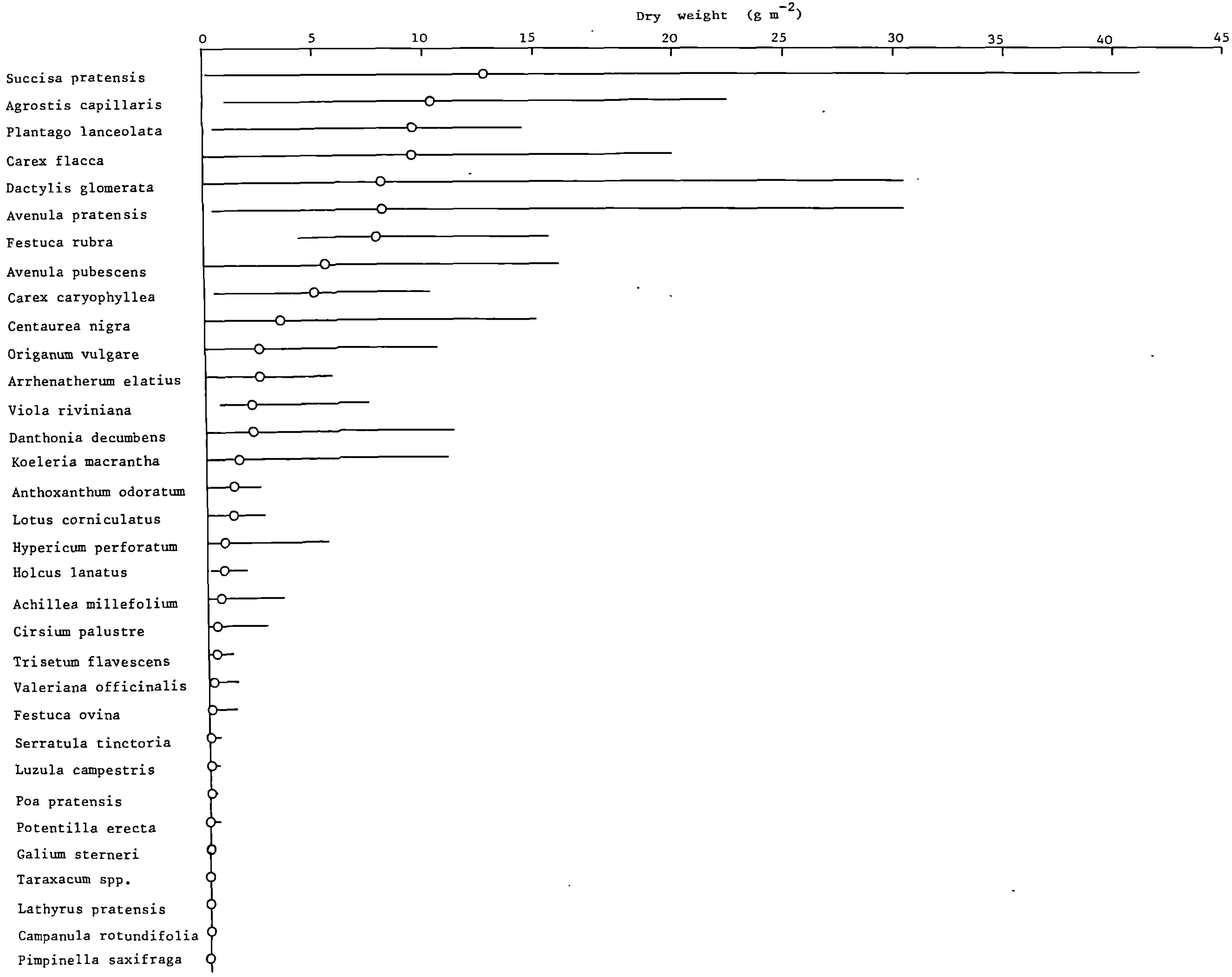
CHANGES IN THE RELATIVE ABUNDANCE OF SPECIES AFTER GAP CUTTING

Earlier in this chapter (pp.43-44) it was noted that species which began to recover vegetatively in autumn-cut gaps were not found in the same proportions as in established vegetation. Such changes in abundance could be a temporary or permanent feature dependent upon the ability of individual species to exploit the changed environmental conditions associated with gaps, e.g. alterations in available nutrients, light and space.

At the species level, replication of results is a particular problem when dealing with natural vegetation, as plant species differ considerably in their patterns of distribution. In this experiment seven replicates of each treatment were found to produce an acceptable level of agreement in results when major groups of plant material were considered (see earlier sections of this chapter). However, there was found to be considerable variation in biomass between replicates in some species, though many were more evenly distributed (see Fig.3.8).

Whilst this feature in itself is of considerable interest, it is desirable to assess the impact of gaps in a more analytical manner. Clearly, mean values for biomass are an unreliable data source for species comparisons. Other methods must be considered.

Fig. 3.8 Range and mean of dry weight values recorded for individual species in seven spring-cut 40 cm diameter gaps on the north-facing slope.



As a first step in addressing this question, dominance diversity curves were constructed for 20 and 40 cm diameter gaps, 20 cm scrapes and undisturbed vegetation on both slopes (Figs.3.9-3.14). These graphs are based on the total shoot biomass in all seven replicates, of individual species, determined by the destructive harvest in 1981 (see pp.38-39 for method).

(a) Hierarchies of common species in gaps and controls

Species which occurred in four or more replicates out of seven were considered to be species of common occurrence in that treatment. Such species were arranged into a hierarchy based on the total shoot biomass of individual species in the treatment in question. Hierarchies for 40 cm and 20 cm diameter gaps, 20 cm diameter scrapes and controls on both slopes are presented in Tables 3.2-3.7. 20 cm diameter gaps and scrapes are compared with the central 20 cm diameter area of control plots to take account of small-scale differences in species distributions.

Many species were found to change little in their relative importance in gaps and scrapes compared with controls. However, a considerable number did show quite dramatic shifts in relative abundance, sometimes in an upward direction, e.g. Plantago lanceolata on the north-facing slope and Leontodon hispidus on the south-facing slope, but more often in a downward direction, e.g. Avenula pratensis and Dactylis glomerata on the north-facing slope and Helianthemum nummularium on the south-facing slope.

Changes in position in the hierarchy are summarized in Table 3.8 for the north-facing slope and Table 3.9 for the south-facing slope. In general, grasses and graminoids were reduced in quantity by gap-cutting while many forb species appeared to increase.

Figure 3.9 Dominance-diversity curve for 40 cm diameter areas of undisturbed vegetation on the north-facing slope, with species responses to damage in autumn (○) and spring (●) 40 cm gaps superimposed.

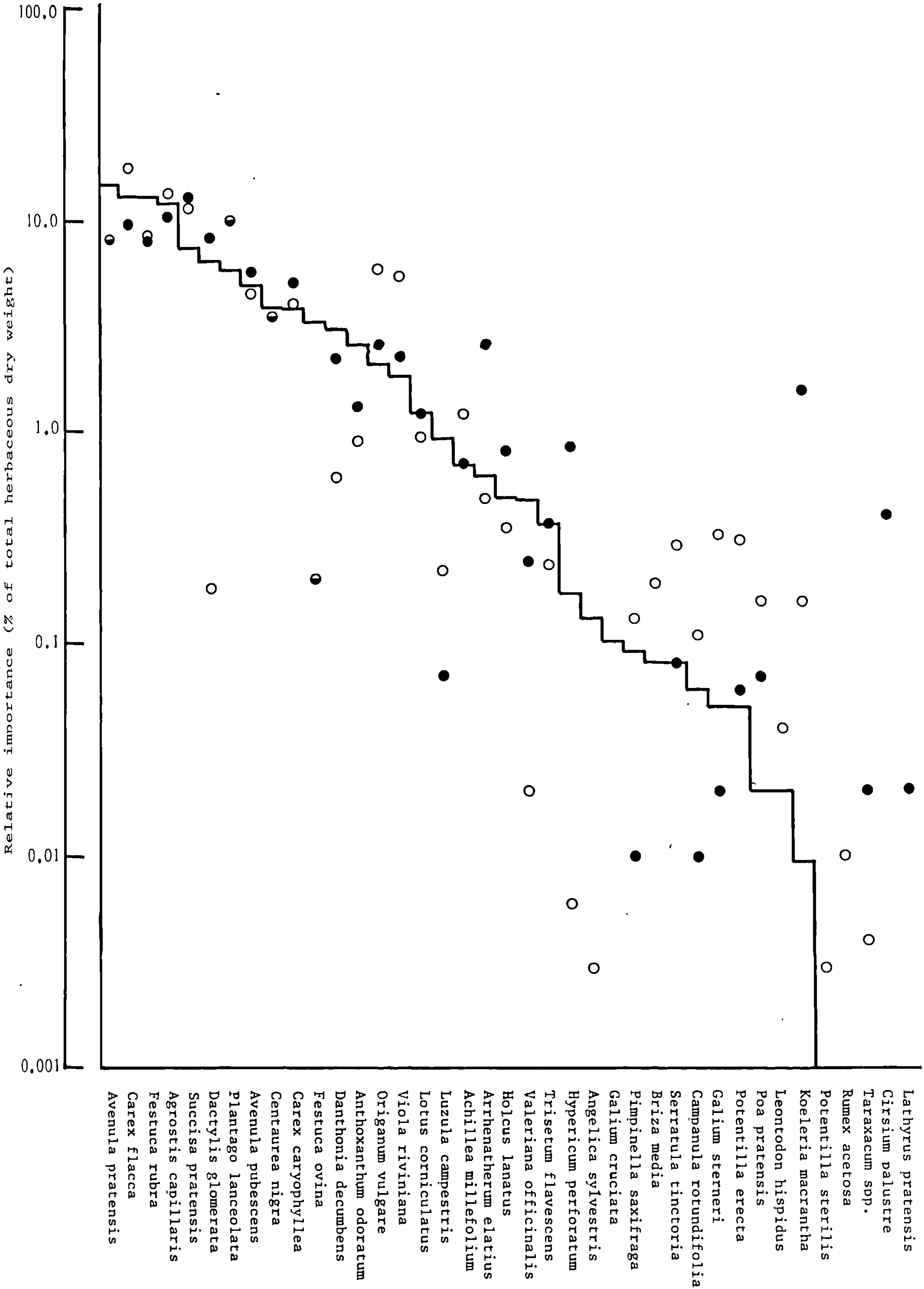


Figure 3.10 Dominance-diversity curve for 20 cm diameter areas of undisturbed vegetation on the north-facing slope, with species responses to damage in autumn (○) and spring (●) 20 cm gaps superimposed.

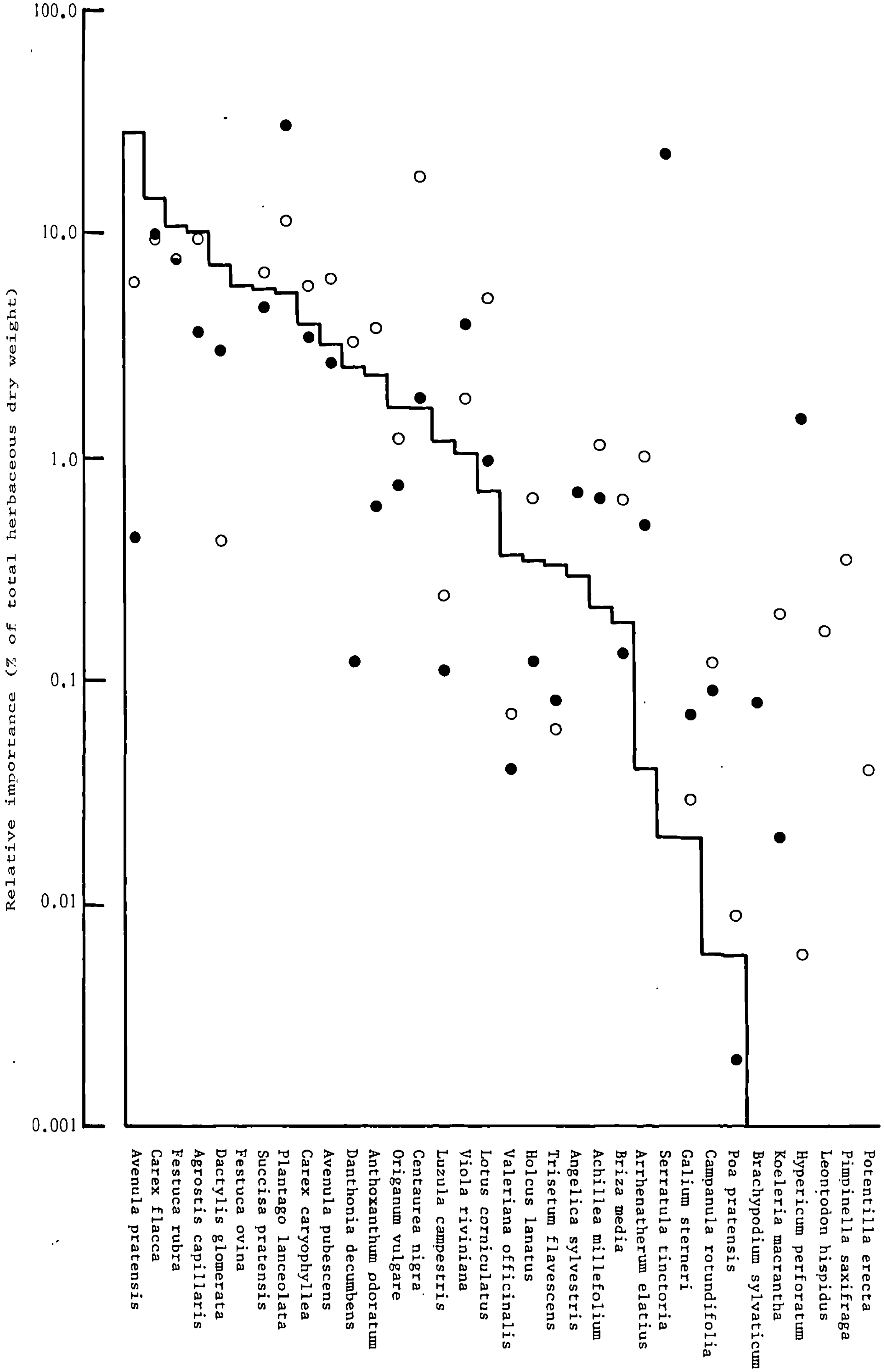


Figure 3.11 Dominance diversity curve for 20 cm diameter areas of undisturbed vegetation on the north-facing slope with species responses to damage in autumn (○) and spring (●) 20 cm scrapes superimposed.

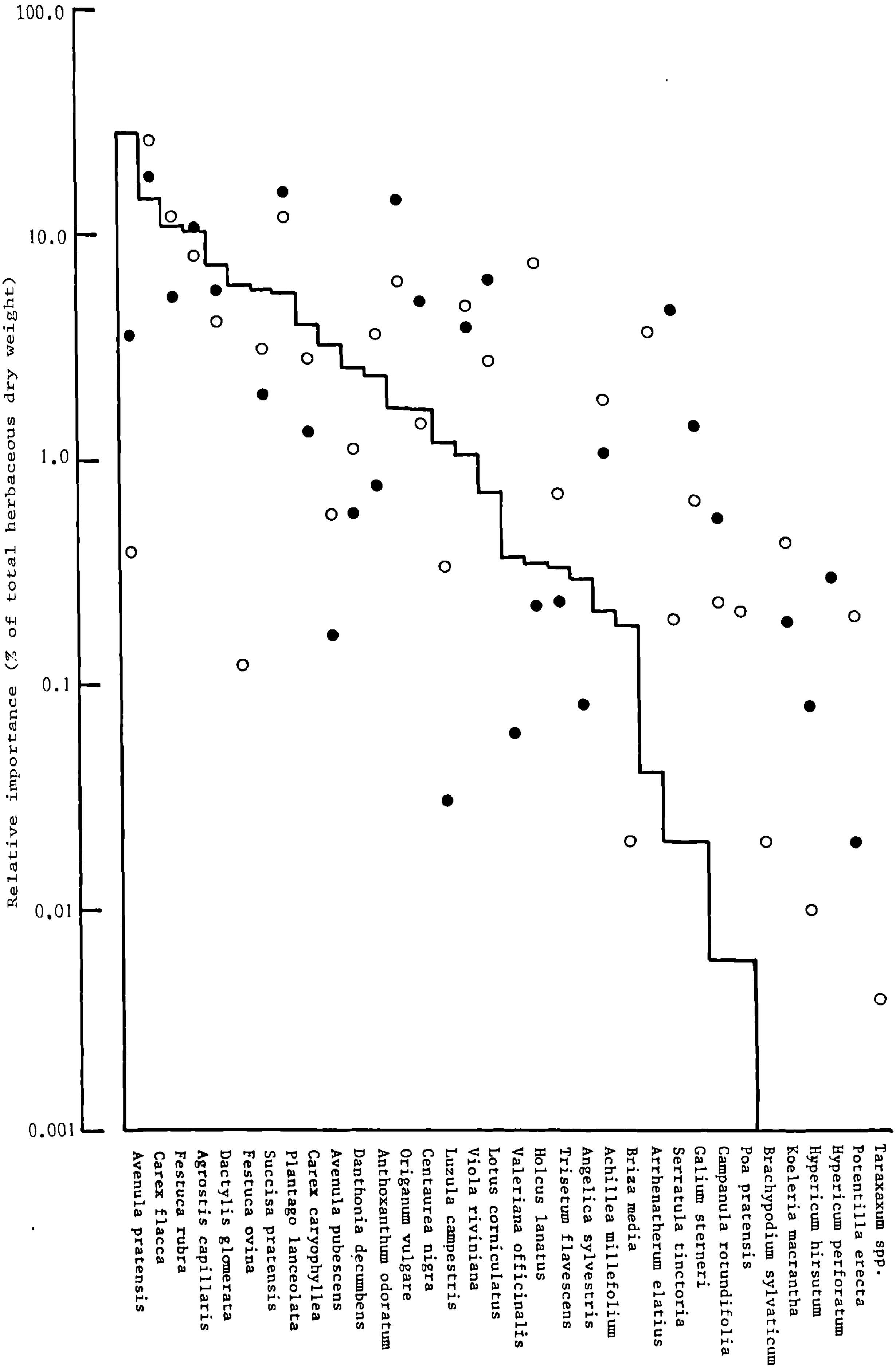


Figure 3.12 Dominance-diversity curve for 40 cm diameter areas of undisturbed vegetation on the south-facing slope with species responses to damage in autumn (○) and spring (●) 40 cm gaps superimposed.

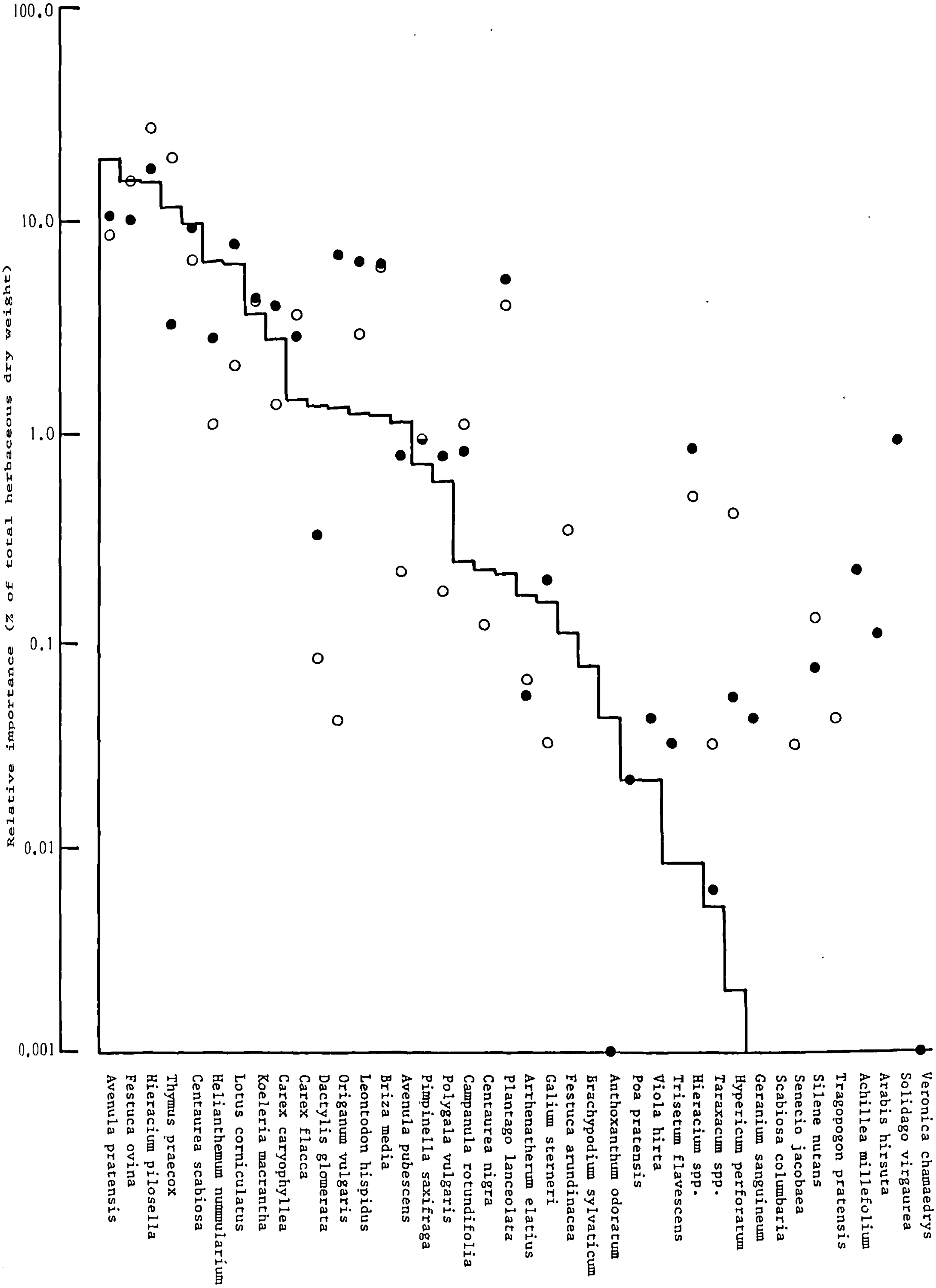


Figure 3.13 Dominance-diversity curve for 20 cm diameter areas of undisturbed vegetation on the south-facing slope, with species responses to damage in autumn (○) and spring (●) 20 cm gaps superimposed.

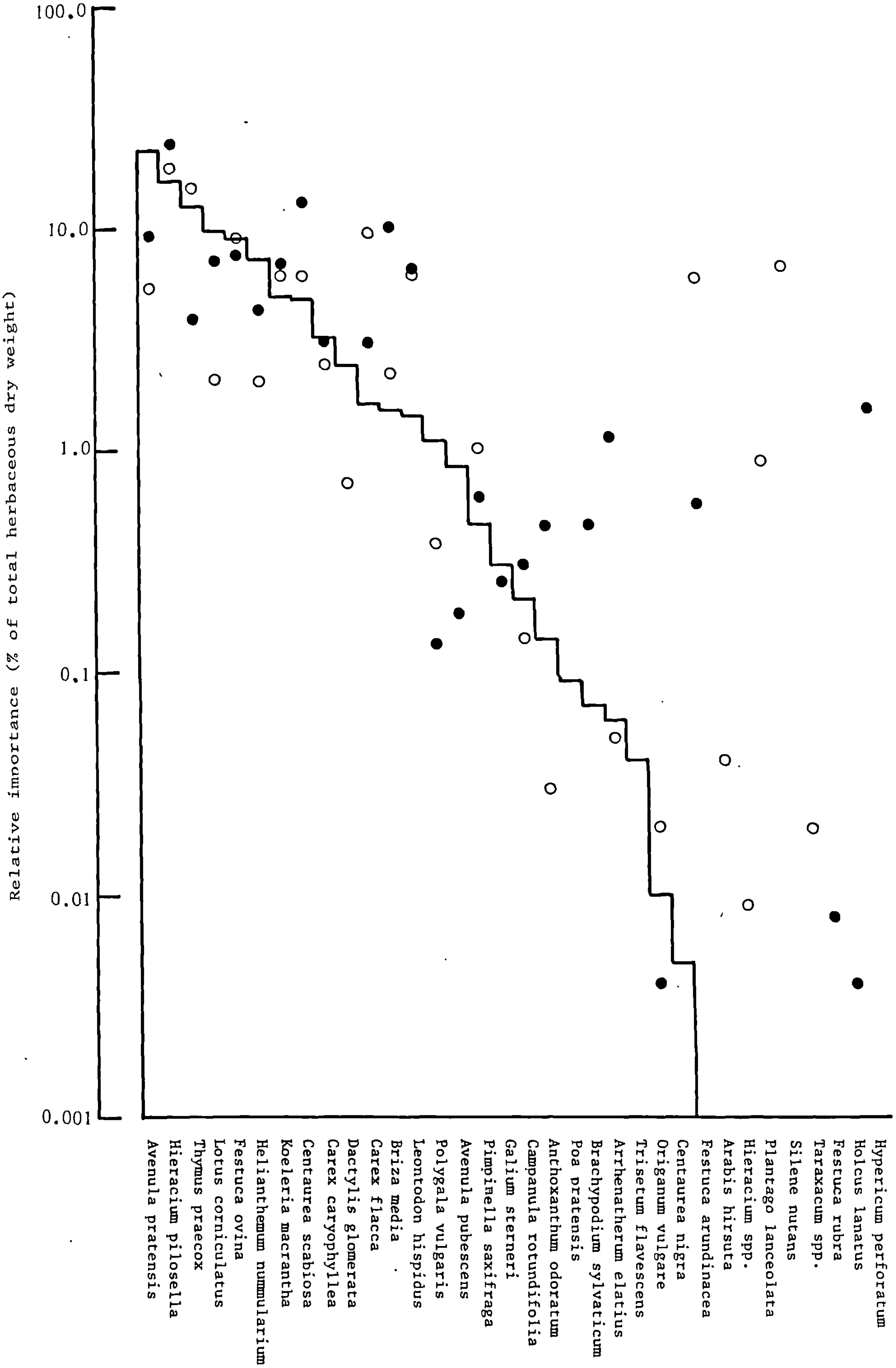


Figure 3.14 Dominance-diversity curve for 20 cm diameter areas of undisturbed vegetation on the south-facing slope, with species responses to damage in autumn (○) and spring (●) 20 cm scrapes superimposed.

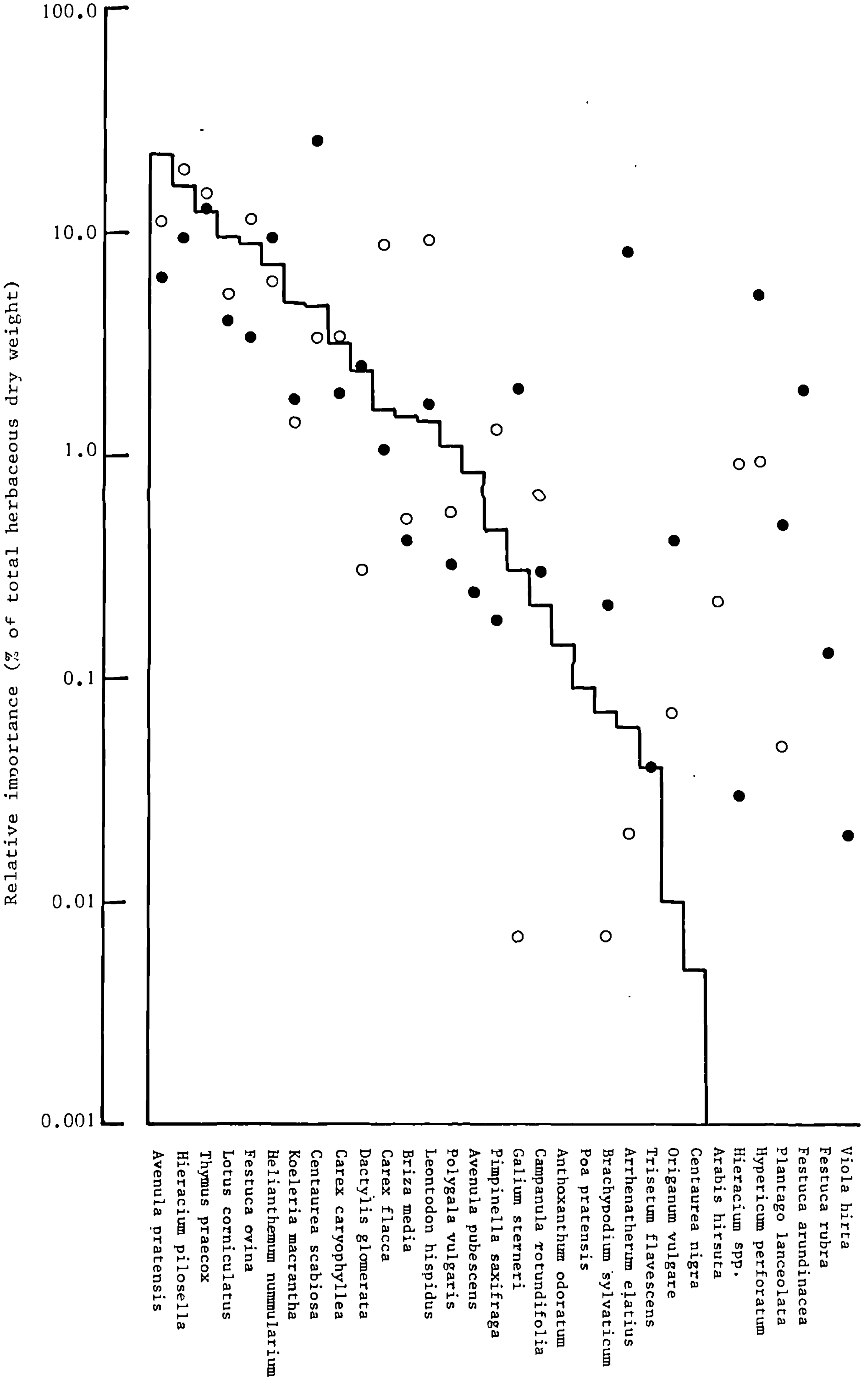


Table 3.2

Changes in the dominance hierarchy of 40 cm diameter gaps compared with 40 cm diameter areas of undisturbed vegetation on the north-facing slope.

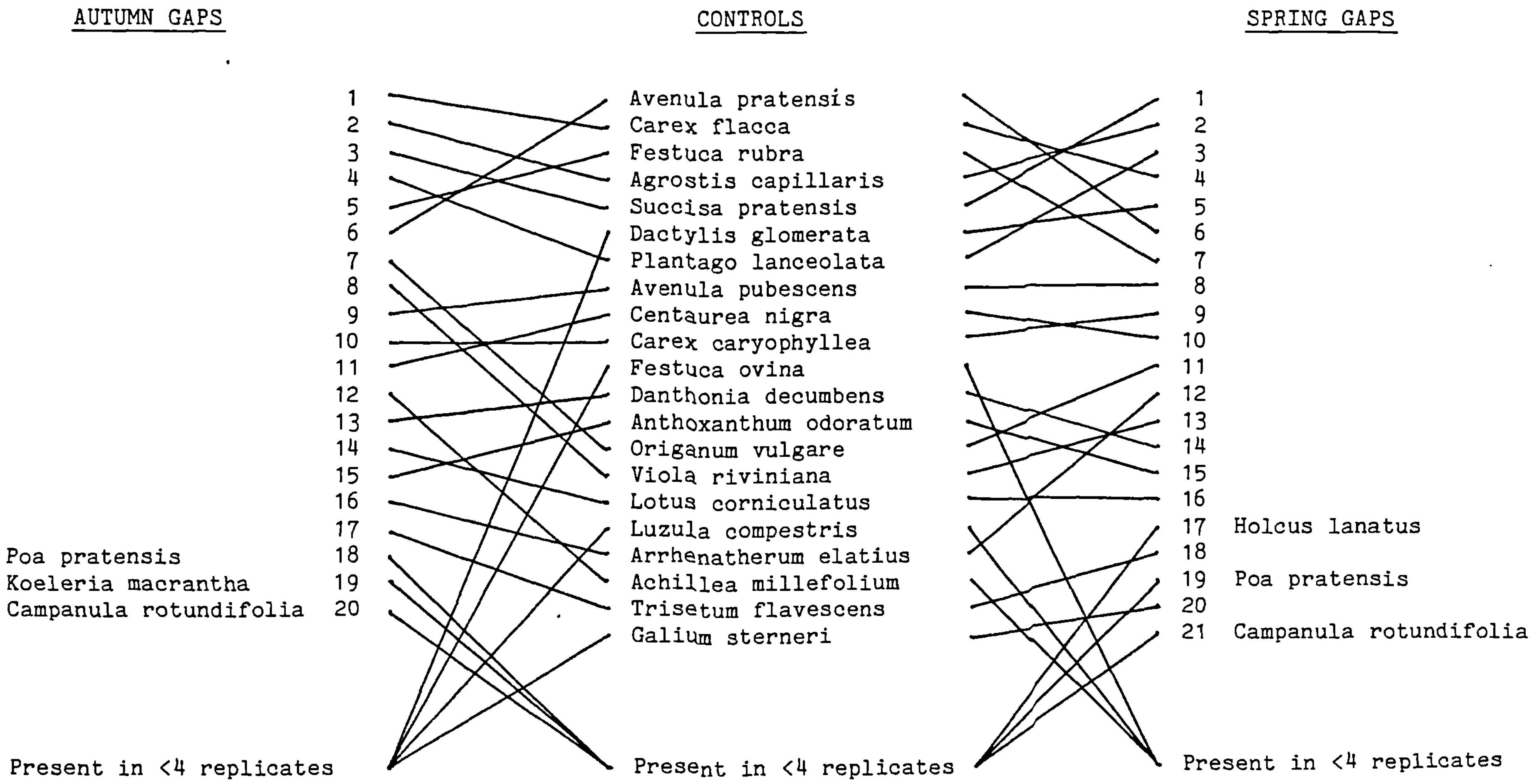


Table 3.3

Changes in the dominance hierarchy of 20 cm diameter gaps compared with 20 cm diameter areas of undisturbed vegetation on the north-facing slope.

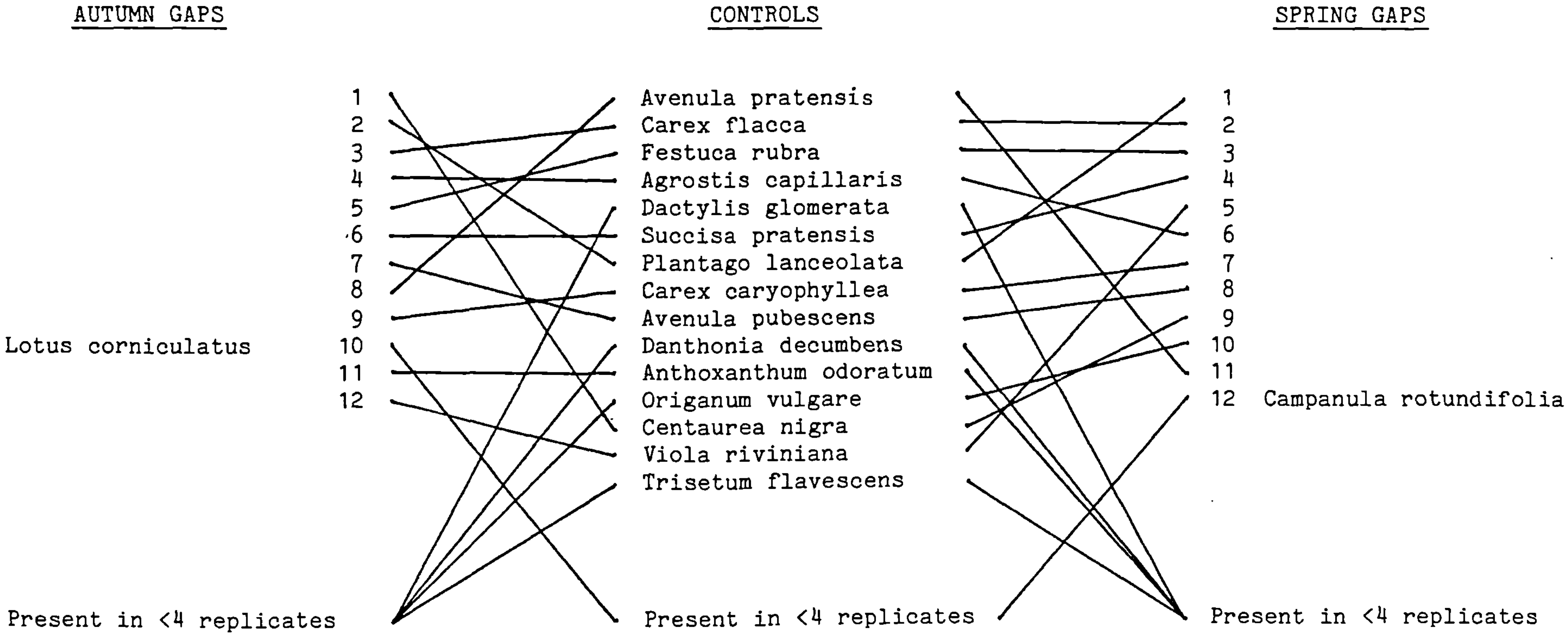


Table 3.4

Changes in the dominance hierarchy of 20 cm diameter scrapes compared with 20 cm diameter areas of undisturbed vegetation on the north-facing slope.

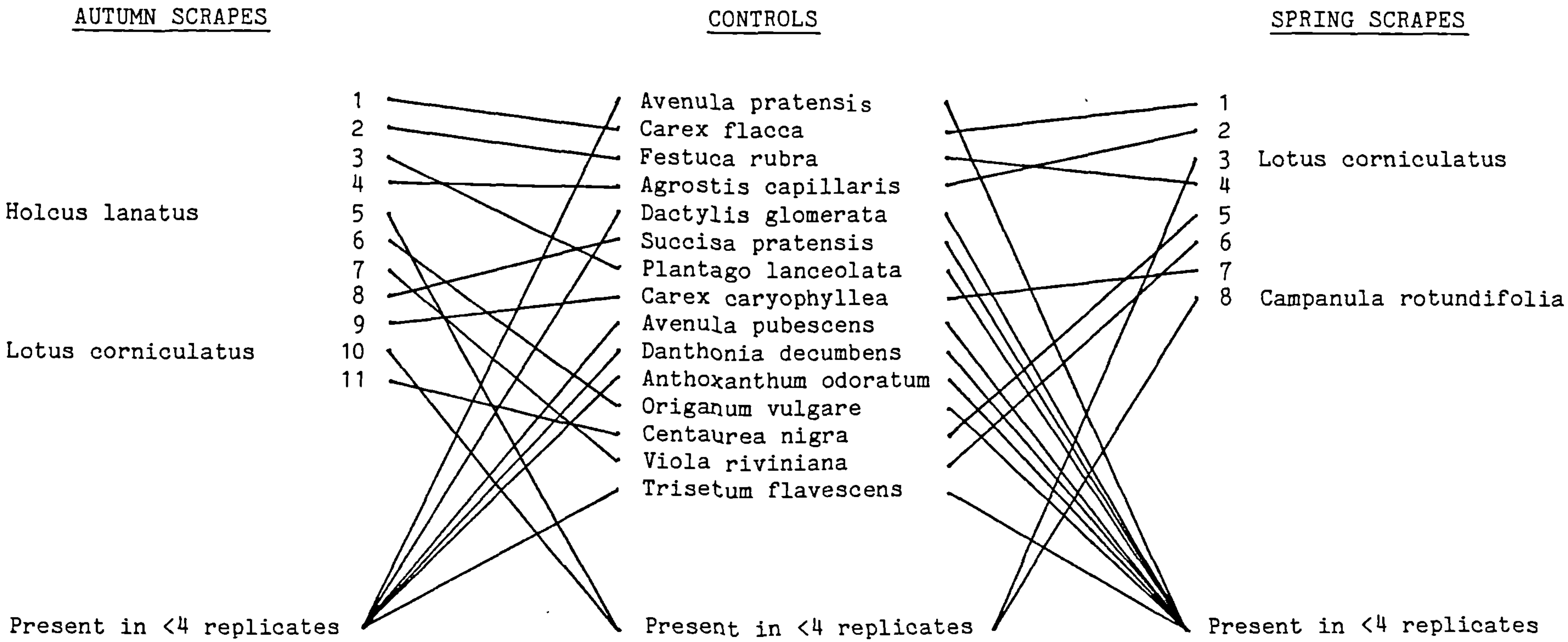


Table 3.5

Changes in the dominance hierarchy of 40 cm diameter gaps compared with 40 cm diameter areas of undisturbed vegetation on the south-facing slope.

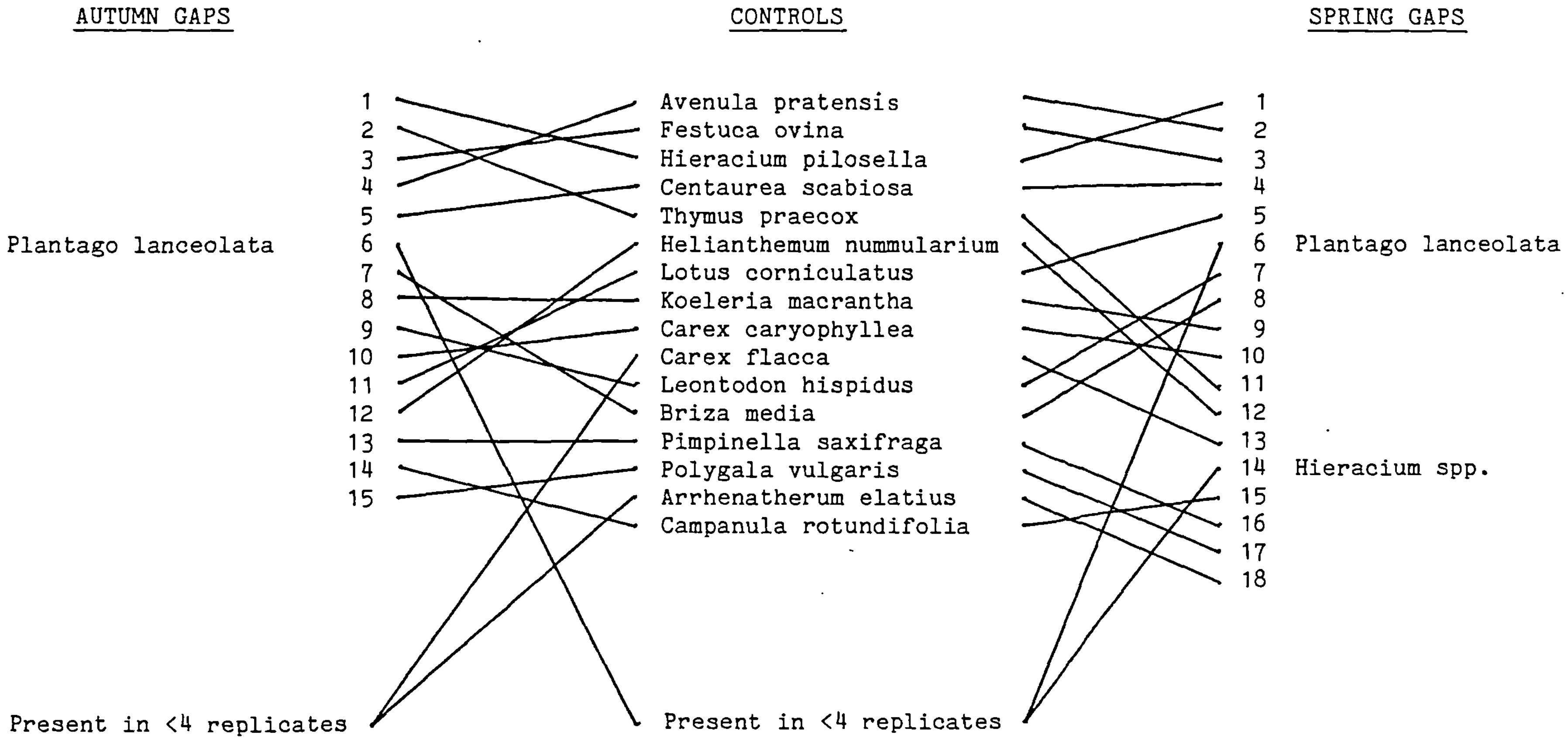


Table 3.6

Changes in the dominance hierarchy of 20 cm diameter gaps compared with 20 cm diameter areas of undisturbed vegetation of similar area on the south-facing slope.

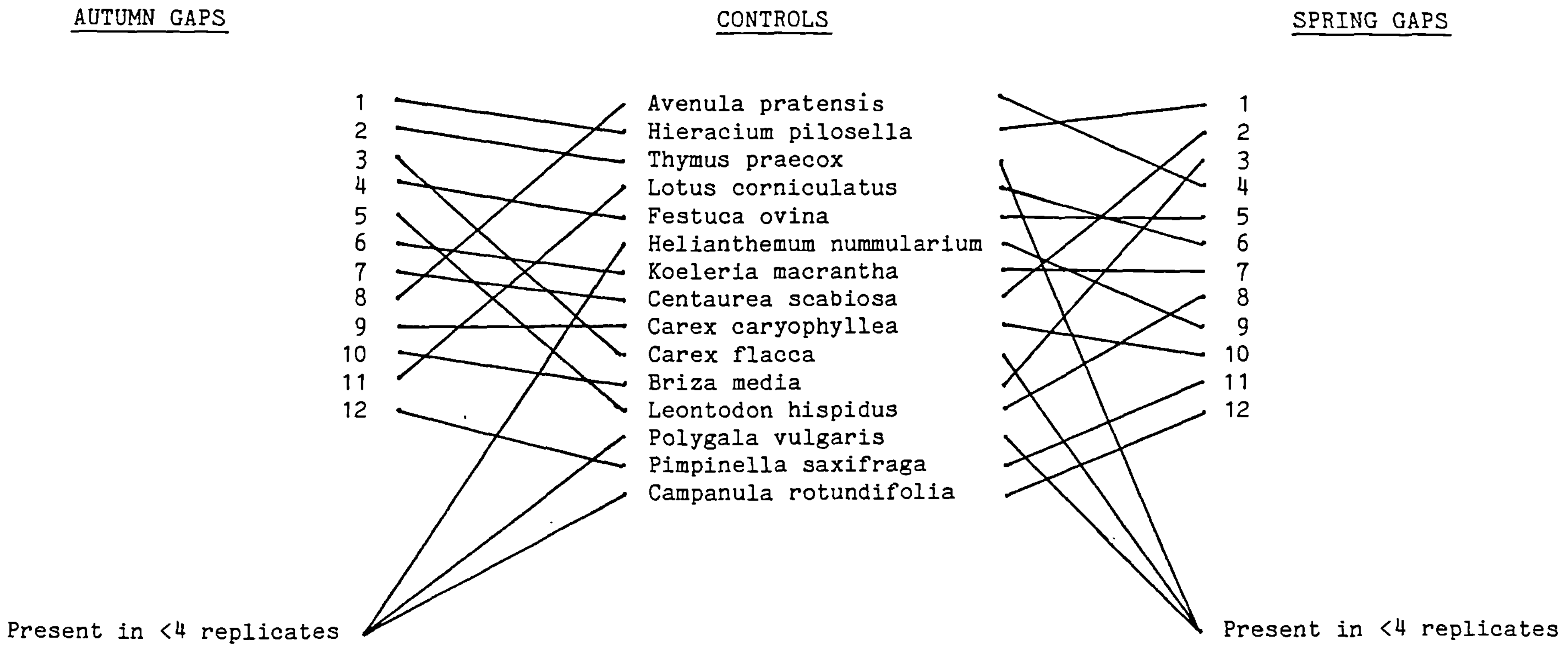


Table 3.7

Changes in the dominance hierarchy of 20 cm diameter scrapes compared with 20 cm diameter areas of undisturbed vegetation of similar area on the south-facing slope.

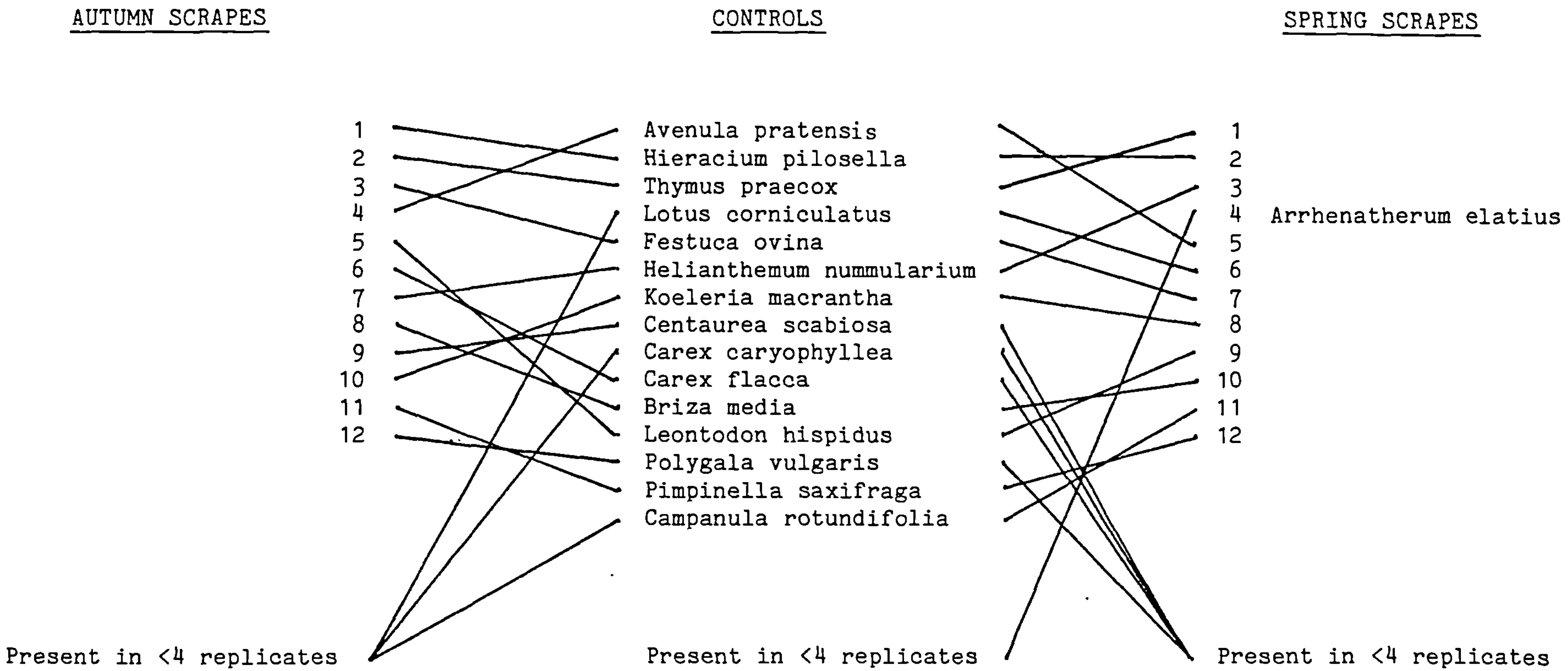


Table 3.8

Summary of changes in the dominance hierarchy in gaps and scrapes compared with controls on the north-facing slope.

	A40G*	S40G	A20G	S20G	A20S	S20S
GRASSES						
Agrostis capillaris	↑	↑	=	↓	=	↑
Anthoxanthum odoratum	↓	↓	=	↓	↓	↓
Arrhenatherum elatius	↑	↑				
Avenula pratensis	↓	↓	↓	↓	↓	↓
Avenula pubescens	=	=	↑	=	↓	↓
Dactylis glomerata	↓	=	↓	↓	↓	↓
Danthonia decumbens	=	↓	↓	↓	↓	↓
Festuca ovina	↓	↓				
Festuca rubra	↓	↓	↓	=	=	=
Holcus lanatus		↑			↑	
Koeleria macrantha	↑					
Poa pratensis	↑	↑				
Trisetum flavescens	↓	↓	↓	↓	↓	↓
GRAMINOIDS						
Carex caryophyllea	=	=	=	=	=	=
Carex flacca	=	↓	=	=	=	=
Luzula campestris	↓	↓				
FORBS						
Achillea millefolium	↑	↓				
Campanula rotundifolia	↑	↑				↑
Centaurea nigra	↓	=	↑	↑	↑	↑
Galium sterneri	↓	=				
Lotus corniculatus	↑	=	↑		↑	↑
Origanum vulgare	↑	↑	↓	↑	↑	↓
Plantago lanceolata	↑	↑	↑	↑	↑	↓
Succisa pratensis	↑	↑	=	↑	↓	↓
Viola riviniana	↑	↑	↑	↑	↑	↑

* codes as in Table 2.1, A = autumn-cut, S = spring cut.

↑ indicates species moved up the hierarchy by two or more positions.

↓ indicates species moved down the hierarchy by two or more positions.

= indicates species moved up or down the hierarchy by less than two positions.

Table 3.9

Summary of changes in the dominance hierarchy in gaps and scrapes compared with controls on the south-facing slope.

	A40G*	S40G	A20G	S20G	A20S	S20S
GRASSES						
Arrhenatherum elatius	↓	↓				↑
Avenula pratensis	↓	=	↓	↓	↓	↓
Briza media	↑	↑	=	↑	↑	=
Festuca ovina	=	=	=	=	↑	↓
Koeleria macrantha	=	=	=	=	↓	=
GRAMINOIDS						
Carex caryophyllea	=	=	=	=	↓	↓
Carex flacca	↓	↓	↑	↓	↑	↓
SHRUBS						
Helianthemum nummularium	↓	↓	↓	↓	=	↑
Thymus praecox	↑	↓	=	↓	=	↑
FORBS						
Campanula rotundifolia	↑	=	↓	↑	↓	↑
Centaurea scabiosa	=	=	=	↑	=	↓
Hieracium pilosella	↑	↑	=	=	=	=
Hieracium spp.		↑				
Leontodon hispidus	↑	↑	↑	↑	↑	↑
Lotus corniculatus	↓	↑	↓	↓	↓	↓
Pimpinella saxifraga	=	↓	↑	↑	↑	↑
Plantago lanceolata	↑	↑				
Polygala vulgaris	=	↓	↓	↓	=	↓

* codes as in Table 2.1, A = autumn-cut, S = spring cut.

↑ indicates species moved up the hierarchy by two or more positions.

↓ indicates species moved down the hierarchy by two or more positions.

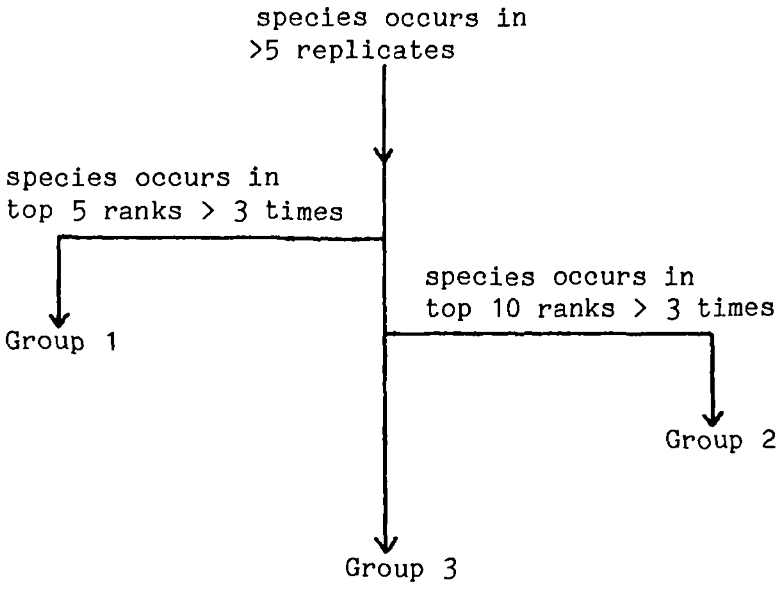
= indicates species moved up or down the hierarchy by less than two positions.

Avenula pratensis declined in importance in all gap types considered on both slopes but appeared to suffer less on the south-facing slope than on the north. Autumn- and spring-cut gaps produced similar patterns of change on the north-facing slope, a generalisation which is broadly true for the south-facing slope, with two notable exceptions. Thymus praecox declined considerably in spring-cut gaps (but not scrapes) while maintaining or elevating its position in autumn treatments. The opposite effect was observed with Lotus corniculatus which was much reduced in importance after autumn damage.

(b) Relative abundance and biomass

Earlier, the variation in species biomass between replicates was discussed and attention was drawn to the fact that the range of values was greater for some species than for others. In part, such dissimilarity in absolute biomass between replicates may be accounted for by small-scale variations in productivity and vegetation structure across the slope, resulting in a general increase or decrease in yield within individual replicates. Despite such fluctuations, particular species may be characteristically minor, major or intermediate components of the vegetation, a feature which is not brought out by consideration of biomass alone.

One method by which this problem may be avoided is to consider the position of species within the rank order for individual replicates. In Tables 3.10 and 3.11 the commonest species on the two slopes are grouped according to their importance in undisturbed vegetation. The criteria for grouping on the north-facing slope were as follows:



For the south-facing slope these divisions gave a disproportionately large group of dominant species and a reduced sub-dominant group. Accordingly, the criterion for inclusion in the first group was amended slightly such that a species must be in the first <u>four</u> ranks on three or more occasions. Groups 2 and 3 were composed as before.

Within these groups, species rank order was plotted against biomass for every replicate of each treatment to give the distributions contained in Figs.3.15 and 3.16 for controls, autumn 40 cm diameter gaps and spring 40 cm diameter gaps on both slopes. In general the three groups remain closely defined regardless of treatment on the north-facing slope but are slightly less compact after gap cutting on the south-facing slope. On this slope, Group 2 (the sub-dominants) is most stable while Groups 1 and 3 show marked expansion of range.

Table 3.10

The commonest species on the north-facing slope grouped according to the method described on p.54.

	Controls	Autumn 40 cm gaps	Spring 40 cm gaps
<u>Dominant species</u>			
Agrostis capillaris	1	1	1
Avenula pratensis	1	2	2
Carex flacca	1	1	1
Festuca rubra	1	1	1
Succisa pratense	1	1	1
<u>'Sub-dominant' species</u>			
Avenula pubescens	2	2	2
Carex caryophyllea	2	2	2
Centaurea nigra	2	2	2
Dactylis glomerata	2	3	2
Danthonia decumbens	2	3	3
Plantago lanceolata	2	1	1
<u>Minor but not inconspicuous</u>			
Anthoxanthum odoratum	3	3	3
Arrhenatherum elatius	3	3	2
Galium sterneri	3	3	3
Holcus lanatus	-	-	3
Lotus corniculatus	-	3	2
Origanum vulgare	3	2	3
Trisetum flavescens	3	3	3
Viola riviniana	3	2	3

- species occurred in less than five replicates.

Table 3.11

The commonest species on the south-facing slope grouped according to the method described on p.54.

	Controls	Autumn 40 cm gaps	Spring 40 cm gaps
<u>Dominant species</u>			
Avenula pratensis	1	1	1
Festuca ovina	1	1	1
Helianthemum nummularium	1	3	2
Hieracium pilosella	1	1	1
Thymus praecox	1	1	2
<u>'Sub-dominant' species</u>			
Briza media	2	2	2
Carex caryophyllea	2	2	2
Centaurea scabiosa	2	2	2
Koeleria macrantha	2	2	2
Lotus corniculatus	2	2	1
<u>Minor but not inconspicuous</u>			
Campanula rotundifolia	3	3	3
Carex flacca	3	2	2
Leontodon hispidus	3	2	1
Pimpinella saxifraga	3	3	3
Polygala vulgaris	3	3	3

Fig. 3.15 Changes in the distributions, with respect to biomass and rank order after gap-cutting, of groups of species in the vegetation of the north-facing slope. Groups, composed in the manner described on pages 53-54, are based on species rank order in undisturbed vegetation.

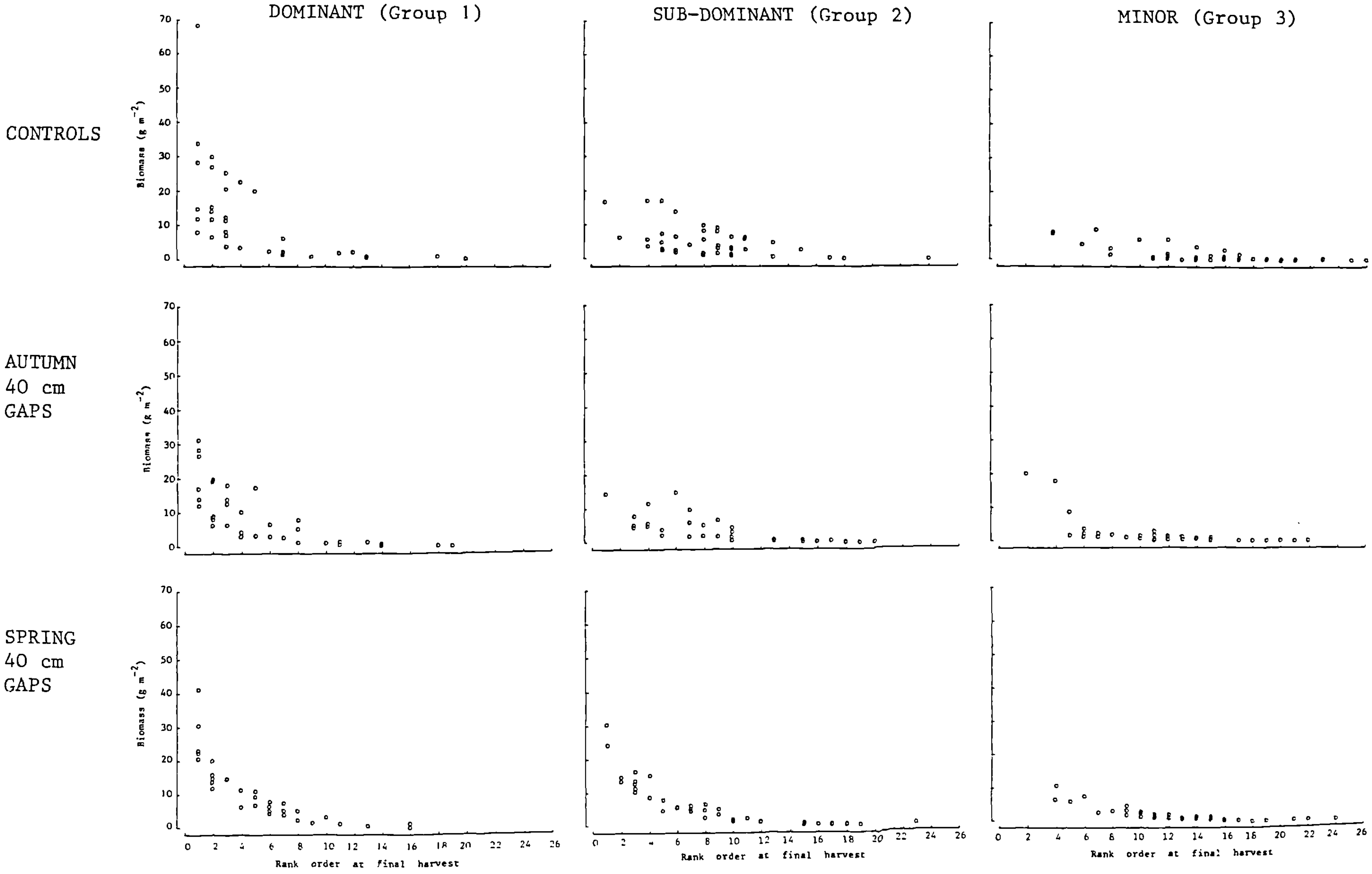


Fig. 3.16 Changes in the distributions, with respect to biomass and rank order after gap cutting, of groups of species in the vegetation of the south-facing slope. Groups, composed in the manner described on pages 53-54, are based on species rank order in undisturbed vegetation.

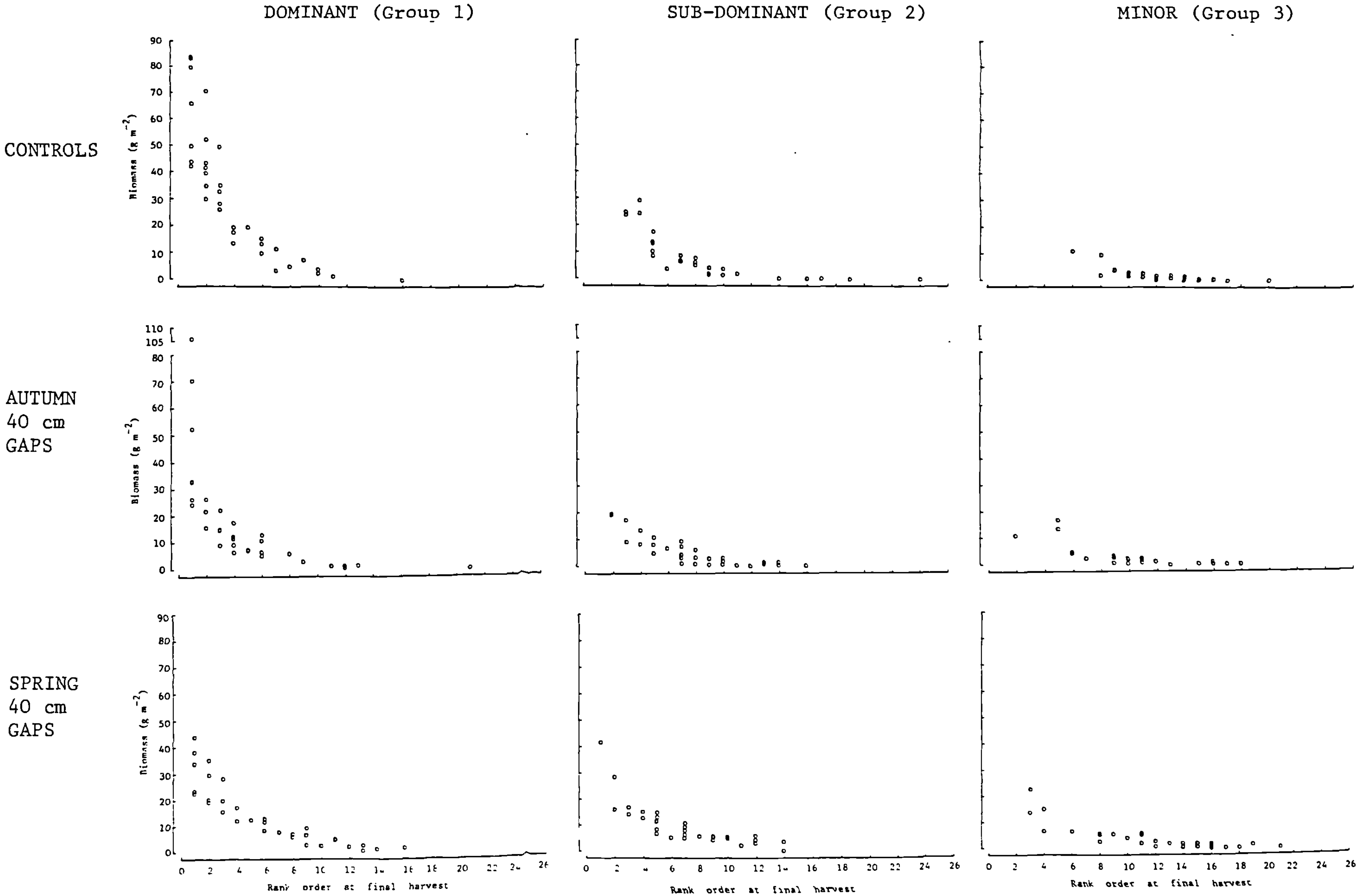
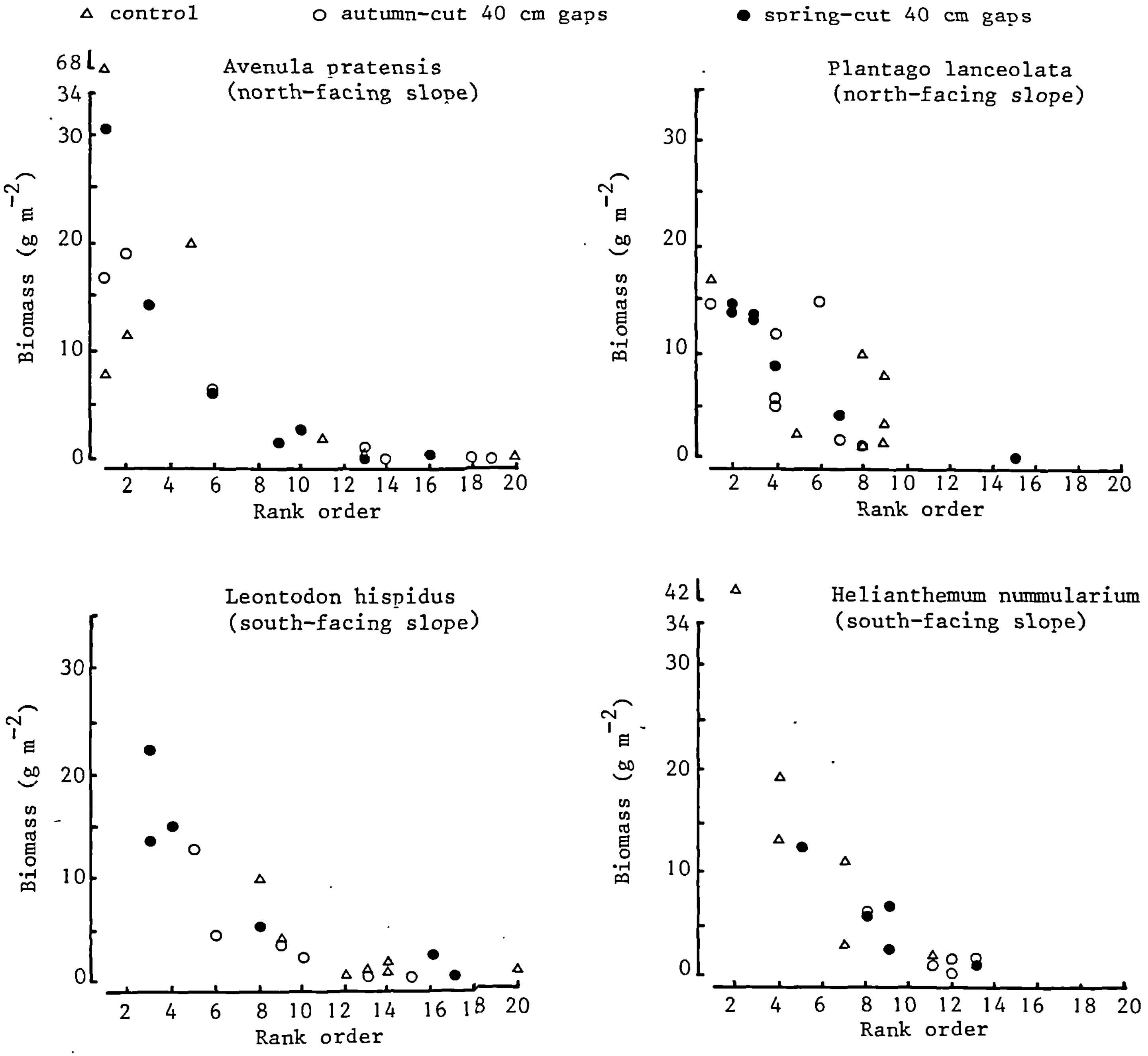


Fig. 3.17 Effects of gap cutting on the distributions with respect to biomass and rank order of four species.



Reference to Table 3.11 reveals that such changes are due to alterations in the relative abundance of one or two component species of each group, e.g. Helianthemum nummularium in Group 1 and Leontodon hispidus in Group 3. On the north-facing slope, Plantago lanceolata (Group 2) and, to a certain extent, Avenula pratensis (Group 1), also showed changes in distribution although these did not appear to affect the cohesiveness of the group as a whole. Changes in abundance of these four species are represented graphically in Fig.3.17.

(c) Initial colonists and their abundance three years later in autumn-cut gaps

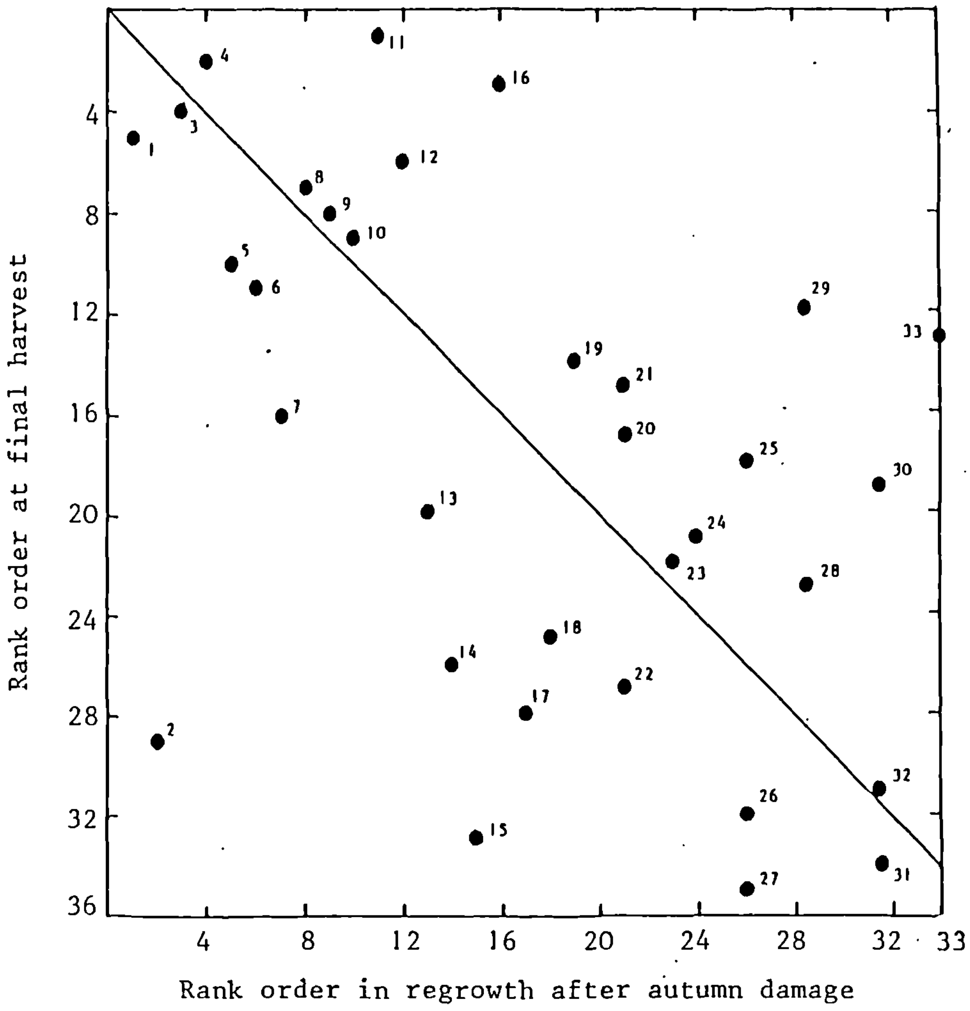
The most satisfactory method by which the impact of gap cutting might be assessed, would be to compare the composition of vegetation removed in the creation of a gap with that which re-established in it, taking due account of general shifts in relative abundance of species occurring at the site in undisturbed vegetation, as the result of competitive interactions or climatic effects. Due to the scale of this experiment, it was not possible to undertake a detailed analysis of species composition in individual gaps at the beginning of this study. A general summary of the vegetation of the two sites was obtained by destructive sampling in 1978 (p.20) but was not considered a suitable basis for comparison due to the possible errors in sampling discussed on pp.20-21.

An alternative approach is to examine the extent to which species alter in their relative abundances as initial colonists when compared with re-established vegetation at a given point in the future. This kind of analysis was not possible for spring-cut gaps since quantitative estimates were not made of early recolonizing vegetation. However, re-sprouting eight weeks after cutting was measured in autumn gaps on both slopes by means of shoot frequency counts (p.37). The rank order of species derived from these data was compared with rank order obtained from quantitative estimates of biomass made in 1981, results being expressed graphically in Figs. 3.18-3.21 for autumn 40 cm gaps and scrapes on the north- and south-facing slope respectively. Spearman's rank correlation coefficients for the four comparisons are contained in Table 3.12.

On the north-facing slope the rank order of species at the final harvest differed in some important respects from the pattern observed soon after gap cutting. Campanula rotundifolia and Arrhenatherum elatius, prominent among the early colonists, were greatly reduced in quantity three years later. Conversely, Succisa pratensis, Carex flacca and to a lesser extent Avenula pratensis, moved up the rank order at final harvest by 13, 10 and 6 places respectively, becoming (in the same order) the first, third and sixth most important species in terms of total biomass. Other species which increased in importance were Potentilla erecta, Achillea millefolium and Holcus lanatus formerly minor contributors in terms of shoot frequency, whilst Valeriana officinalis, Poa pratensis and Pimpinella saxifraga decreased considerably. Danthonia decumbens was the only species which had not been represented as resprouting shoots soon after gap cutting.

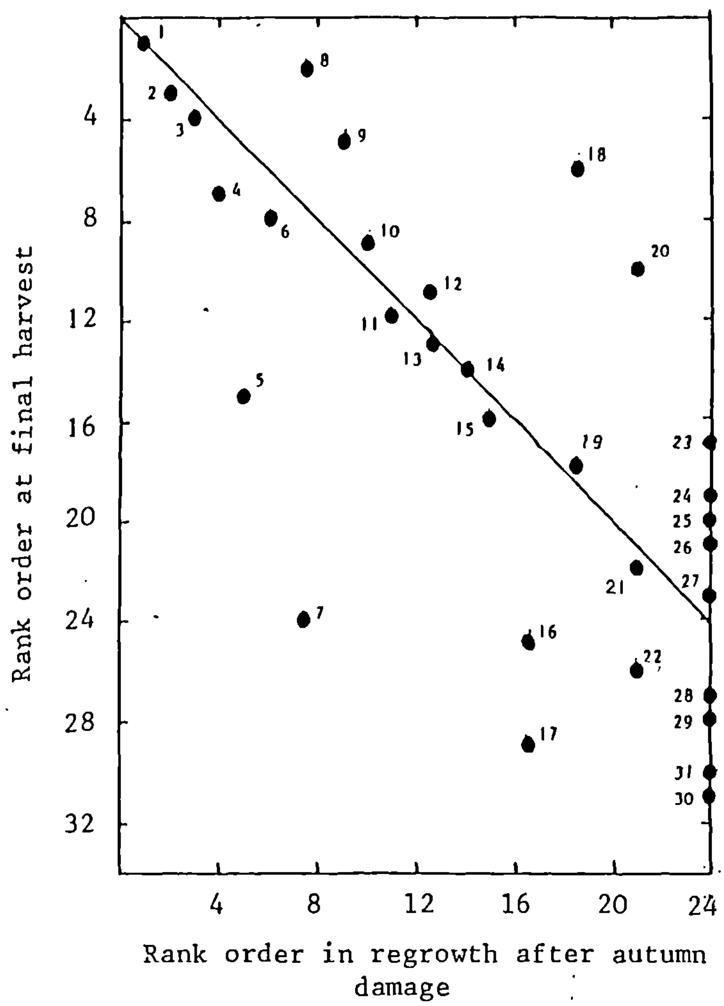
A similar analysis for the south-facing slope revealed a very different state of affairs. Fourteen species out of twenty-three recorded as new shoots, changed little in their rank order over the period of the experiment. This means that for two-thirds of the species which sprouted immediately after autumn gap-cutting on the

Fig. 3.18 The relative importance of species recorded as gap colonists at the time of final harvest in 1981, compared with their relative importance as resprouts 8 weeks after gap creation, in autumn 40 cm diameter gaps on the north-facing slope.



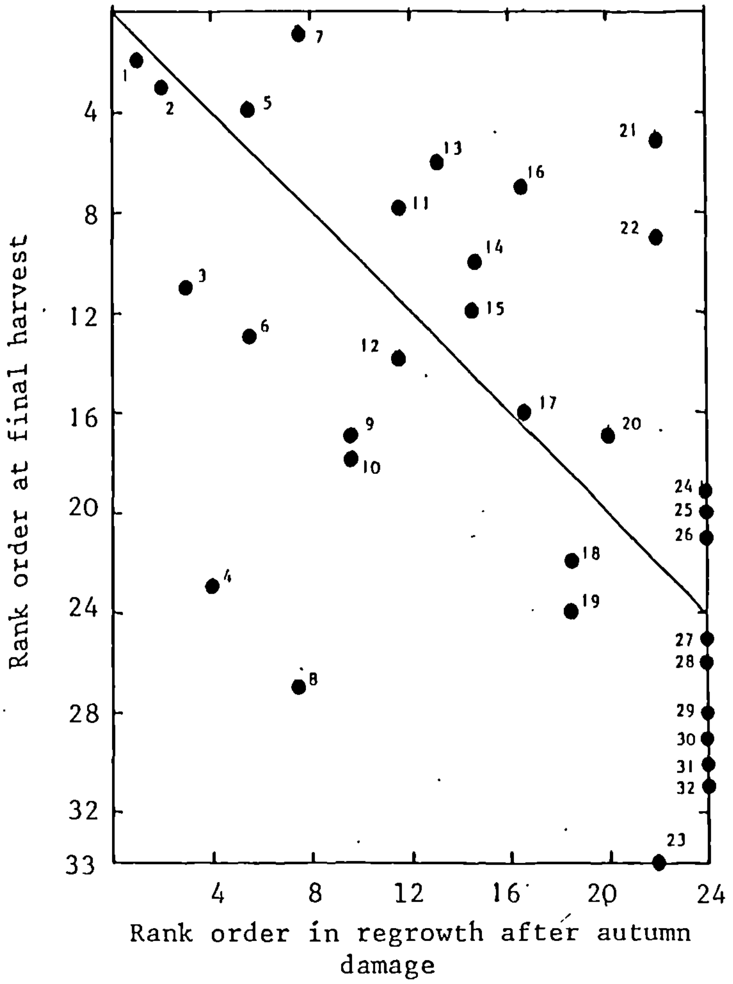
1 Festuca rubra
2 Campanula rotundifolia
3 Plantago lanceolata
4 Agrostis capillaris
5 Carex caryophyllea
6 Centaurea nigra
7 Arrhenatherum elatius
8 Origanum vulgare
9 Viola riviniana
10 Avenula pubescens
11 Carex flacca
12 Avenula pratensis
13 Galium sterneri
14 Poa pratensis
15 Valeriana officinalis
16 Succisa pratensis
17 Pimpinella saxifraga
18 Dactylis glomerata
19 Lotus corniculatus
20 Trisetum flavescens
21 Anthoxanthum odoratum
22 Koeleria macrantha
23 Luzula campestris
24 Serratula tinctoria
25 Holcus lanatus
26 Angelica sylvestris
27 Taraxacum spp.
28 Festuca ovina
29 Achillea millefolium
30 Potentilla erecta
31 Rumex acetosa
32 Leontodon hispidus
33 Danthonia decumbens

Fig. 3.19 The relative importance of species recorded as gap colonists at the time of final harvest in 1981, compared with their relative importance as resprouts 8 weeks after gap creation, in autumn 40 cm diameter gaps on the south-facing slope.



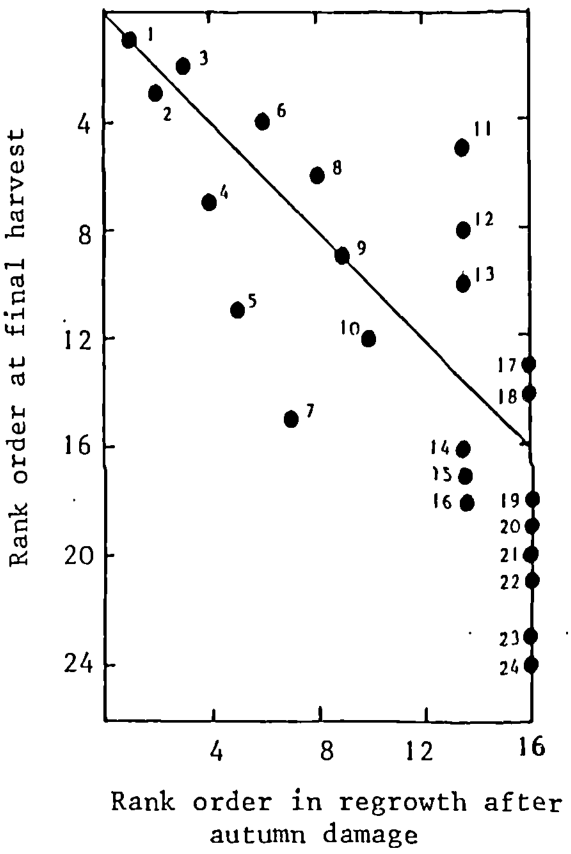
1 Hieracium pilosella
2 Festuca ovina
3 Avenula pratensis
4 Briza media
5 Campanula rotundifolia
6 Koeleria macrantha
7 Arrhenatherum elatius
8 Thymus praecox
9 Centaurea scabiosa
10 Carex flacca
11 Lotus corniculatus
12 Carex caryophyllea
13 Helianthemum nummularium
14 Pimpinella saxifraga
15 Hieracium spp.
16 Tragopogon pratensis
17 Taraxacum spp.
18 Plantago lanceolata
19 Festuca arundinacea
20 Leontodon hispidus
21 Centaurea nigra
22 Origanum vulgare
23 Hypericum perforatum
24 Polygala vulgaris
25 Avenula pubescens
26 Silene nutans
27 Dactylis glomerata
28 Galium sterneri
29 Senecio jacobaea
30 Agrostis capillaris
31 Unidentified forb

Fig. 3.20 The relative importance of species recorded as gap colonists at the time of final harvest in 1981, compared with their relative importance at resprouts 8 weeks after gap creation, in autumn 20 cm diameter scrapes on the north-facing slope.



1 Festuca rubra
2 Plantago lanceolata
3 Carex caryophyllea
4 Campanula rotundifolia
5 Agrostis capillaris
6 Achillea millefolium
7 Carex flacca
8 Festuca ovina
9 Galium sterneri
10 Avenula pubescens
11 Arrhenatherum elatius
12 Centaurea nigra
13 Origanum vulgare
14 Succisa pratensis
15 Lotus corniculatus
16 Vola riviniana
17 Trisetum flavescens
18 Luzula campestris
19 Poa pratensis
20 Danthonia decumbens
21 Holcus lanatus
22 Anthoxanthum odoratum
23 Hypericum perforatum
24 Koeleria macrantha
25 Avenula pratensis
26 Dactylis glomerata
27 Potentilla erecta
28 Serratula tinctoria
29 Brachypodium sylvaticum
30 Briza media
31 Hypericum hirsutum
32 Taraxacum spp.

Fig. 3.21 The relative importance of species recorded as gap colonists at the time of final harvest in 1981, compared with their relative importance as resprouts 8 weeks after gap creation, in autumn 20 cm diameter scrapes on the south-facing slope.



1	Hieracium pilosella	13	Centaurea scabiosa
2	Festuca ovina	14	Polygala vulgaris
3	Thymus praecox	15	Briza media
4	Helianthemum nummularium	16	Arrhenatherum elatius
5	Koeleria macrantha	17	Hypericum perforatum
6	Avenula pratensis	18	Hieracium spp.
7	Campanula rotundifolia	19	Dactylis glomerata
8	Carex flacca	20	Arabis hirsuta
9	Carex caryophyllea	21	Origanum vulgare
10	Pimpinella saxifraga	22	Plantago lanceolata
11	Leontodon hispidus	23	Brachypodium sylvaticum
12	Lotus corniculatus	24	Galium sterneri

Table 3.12

Spearman's coefficient of ranked correlation (r_s) calculated for the comparisons (represented in Figs.3.18 to 3.21) between species rank order as resprouts and rank order at final harvest in gaps and scrapes on the north- and south-facing slopes in Millersdale. Only species represented in both 1979 and 1981 were included in the analysis.

	r_s	significance
North-facing slope		
autumn 40 cm gaps	0.53	**
autumn 20 cm scrapes	0.47	*
South-facing slope		
autumn 40 cm gaps	0.45	*
autumn 20 cm scrapes	0.72	**

* = significant P<0.05
** = " P<0.01

south-facing slope, relative abundance was established at a very early stage and altered little in three years, a situation which contrasts markedly with the north-facing slope.

Eight species which were not recorded as initial colonists had appeared in autumn-cut gaps by the end of the experiment. Of these, four were present in samples of the established vegetation in 1978. All became relatively minor components of gap vegetation and did not significantly alter the relationships previously described.

Two species, *Arrhenatherum elatius* and *Campanula rotundifolia*, showed a marked decline from positions of prominence after three years and three more, *Taraxacum* spp., *Tragopogon pratensis* and *Origanum vulgare*, although relatively minor, also declined. *Thymus praecox* increased from seventh to second position but *Plantago lanceolata* (eighteenth) and *Leontodon hispidus*(twentieth), expanded dramatically to become the sixth and tenth most important species respectively.

For autumn scrapes, on the north-facing slope there was a scatter of points similar to that obtained from large gaps. However, there were some important differences in species relationships. *Anthoxanthum odoratum*, *Holcus lanatus*, *Viola riviniana*, *Origanum vulgare* and, to a lesser extent *Succisa pratensis* and *Arrhenatherum elatius*, increased in importance over the three-year period. *Arrhenatherum elatius* showed a marked decline in gaps. *Viola riviniana* and *O. vulgare* occupied approximately the same position in the final hierarchy in scrapes as in gaps. Species declining in importance included *Achillea millefolium* (which showed considerable expansion in gaps), *Galium sterneri*, *Avenula pubescens*, *Campanula rotundifolia* and

Festuca ovina. Nine of the species recorded at the final harvest had not been present as initial colonists but none of these achieved a position higher than nineteenth.

In common with the north-facing slope, a number of species which had not been recorded in 1978 had established in autumn-scrapes on the south-facing slope. These species were generally of minor importance. Leontodon hispidus increased in relative abundance over the experimental period while Campanula rotundifolia and Arrhenatherum elatius, together with Koeleria macrantha declined. All of the remaining species, recorded as initial colonists, showed little change in status over the three years.

DISCUSSION

GENERAL RESPONSES TO GAP-CUTTING

Destructive harvests of total standing crop (including litter) revealed that vegetative recolonization of gaps on both slopes was considerably more important in terms of plant dry weight than regeneration from seed (Figs.3.1 and 3.2). Nevertheless seedlings provide an important source of both specific and intraspecific diversity and their potential importance in the community must not be under-estimated. The incidence of successful establishment from seed is examined further in Chapters 4 and 5.

The extent of vegetative regrowth in gaps is determined by the ability of individual species to recover from damage which is in turn dependent on a number of characteristics. These may be morphological, e.g. the position of meristems, possession of underground storage organs, rhizomatous or stoloniferous habit, or they may relate to other aspects of growth, e.g. phenological patterns or potential growth rate.

Reference to previous quantitative studies of the seasonal patterns in shoot growth of particular species (Al-Mufti *et al*. 1977; Sydes 1980; Furness 1981) was found to be useful in the interpretation of the colonization process in gaps. Species recovering well immediately after autumn damage included many known to be capable of biomass production later in the year (Jul, Aug, Sept) than those showing poorer responses (May, Jun, Jul). In particular, a strong response was recorded in *Agrostis capillaris* and *Campanula rotundifolia*, both of which tend to peak in shoot biomass in August (Al-Mufti *et al*. 1977; Al-Mashhadani 1979). It seems very likely that many of these successful early colonists were still growing actively at the time at which they were damaged by gap-cutting.

The timing of damage in relation to the phenological cycle therefore, may be an important determinant of species recovery in the initial stages of gap recolonization. Other characteristics may not be excluded however. Thus *Helianthemum nummularium* has a low relative growth rate (Grime & Hunt 1975) and *Dactylis glomerata* is well known for its susceptibility to damage by autumn grazing (Beddows 1959).

The photographs taken ten months after the experiment began strongly suggest that a temporary phase of forb dominance over grasses occurred in the gaps as compared to controls. The explanation seems to lie in the fact that the meristems and a high proportion of the total biomass of grasses are carried above the ground surface and in consequence suffered considerable damage. In contrast, many of the forbs have both reserves and dormant buds below the soil, a growth form which allows vegetative sprouts to develop rapidly once apical dominance is removed.

Secondary damage by frost and rain over the winter months is the most likely explanation for the more open appearance of autumn-cut gaps in the photographs, when these are compared with their younger spring-cut counterparts. Young tender shoots may have been damaged by cold temperatures and areas of bare soil were certainly disturbed by both frost and rain, particularly on the south-facing slope. Quite clearly re-growth in spring-cut gaps occurred under climatic conditions which were likely to be far more favourable for subsequent growth.

Since the experiment extended over three years it was possible to investigate the long-term effects of gap cutting in derelict limestone grassland of very different character, on the two slopes. At both sites, total standing crop (including litter) in all gap types was considerably less than in controls at the end of the period, suggesting that the recovery time for these types of vegetation is in excess of three years. The slower rates of recovery in autumn-cut gaps were still in evidence at the final harvest when the spring gaps contained similar quantities of material to the older autumn gaps. However, examination of the composition of the plant material in gaps (Figs.3.6 and 3.7) revealed that while there were some differences between gap types, e.g. less herb biomass in scrapes on the north-facing slope where damage was most severe and roots had been removed, and more bryophytes in small gaps and scrapes compared with larger gaps on the south-facing slope, the variation between treatments and controls was generally small, with four important exceptions as follows:

(1) The smaller gaps and the scrapes on the north-facing slope were 'overhung' by more vegetation than larger gaps and controls. This situation corresponds to the 'leaning' response identified by Paine & Levin in their study of Patch dynamics in shore-line communities of the mussel Mytilus californianus (Paine & Levin 1981). Small patches in vegetation and mussel beds are most readily colonised by the physical movements of neighbouring individuals which do not necessarily involve growth responses. In stratified vegetation this has important implications for vegetative recovery since reduced light levels and alterations in micro-climate (e.g. humidity) may preclude vigorous growth of damaged plants rooted within the gap.

(2) The greatest difference between undisturbed vegetation and gaps on the north-facing slope was found with respect to the accumulation of bryophyte litter. Most of the bryophyte species identified have rather low potential growth rates (Furness 1981) and accumulate persistent litter relatively slowly. The importance of bryophytes at this site was noted before the experiment began. Pseudoscleropodium purum formed a dense network at ground level and clumps of Dicranum scoparium in excess of 10 cm deep occurred locally. In these only the uppermost 2 cm contained green leaves. Quantities such as these are likely to have a considerable impact in the undisturbed vegetation, particularly in relation to regeneration from seed (see Chapters 4 and 5) but also with respect to competition between bryophytes and higher plant species (Plate 4). Clearly the removal of such accumulations by gap cutting may be of great significance to the recolonization process.

Plate 4 Accumulations of bryophytes on the north-facing slope may become locally dominant. In this photograph a specimen of *Plantago lanceolata* is surrounded by a dense mat of *Pseudoscleropodium purum*.

(3) On the south-facing slope, differences between disturbance treatments and controls were expressed in the biomass of grasses and the quantities of herb litter accumulated, both of which were much reduced. Overhanging vegetation followed a similar pattern to the north-facing slope but to a lesser degree. The poor response to gap-cutting in the grasses may have been due in part to the greater damage sustained and lower resilience, compared with the many tap-rooted forbs on this site (discussed earlier), but may also have resulted from the low potential relative growth rates (Grime & Hunt 1975) and capacities for lateral spread. The tussock grasses _Festuca ovina_, _Avenula pratensis_ and _Koeleria macrantha_, the commonest species on the site, all have these characteristics.

(4) Accumulations of herb litter in undisturbed vegetation on the south-facing slope reflect the absence of fires during and previous to this experiment. It is suggested that patterns of recolonization, particularly in the largest gaps, may bear certain similarities with those which might be expected after burning.

CHANGES IN SPECIES COMPOSITION

Although average quantities of forbs, graminoids and shrubs on both slopes were comparable in gaps and controls, the relative abundance of individual species in these groups and also amongst the grasses was not the same. Neither was the pattern of change recorded for the north-facing slope the same as that for the south.

Avenula pratensis seemed to be less affected by gap cutting on the south-facing slope than on the north. This may be a reflection of differences in the ecology of this species on the two slopes. On the north-facing slope, A. pratensis forms large discrete tussocks, while on the south-facing slope it is a more evenly distributed and less conspicuous member of the vegetation. The tussock growth form affords a certain amount of protection from fire damage as marginal senescent leaves are differentially removed, younger shoots remaining largely unaffected at the centres of the tussocks (Lloyd 1972). However, clipping in the manner employed in this experiment causes severe debilitation of the whole tussock from which recovery is likely to be slow. The increase in importance in Plantago lanceolata was not unexpected since this species is commonly found in more disturbed vegetation such as meadows and pastures.

On the the south-facing slope, Helianthemum nummularium, a slow-growing stress-tolerant sub-shrub, suffered considerably after damage while Hieracium pilosella and Leontodon hispidus were increased. Both these species are commonly associated with less dense vegetation. On this slope too the season at which gaps arise seemed to have more impact when individual species were considered than on the north-facing slope. The poor response in Lotus corniculatus to autumn gap cutting is probably related to frost sensitivity in this species. In contrast, Thymus praecox appeared to suffer more in spring-cut gaps. This species was prominent amongst the earliest colonists of autumn-gaps and although relatively slow-growing, may have been able to expand in gaps, which, it has previously been noted, remained open for a considerable period of time (Plate 3). In spring gaps T. praecox may have suffered competition from denser vegetation.

It has been suggested that the earliest germinators among cohorts of seedlings colonising bare soil are likely to be the most successful in establishment (Symonides 1977; Weaver & Cavers 1979; Cook 1980). In Appendix 7, a laboratory experiment using turves taken from a productive roadside site provides evidence that the same principle applies to vegetative shoots of Elymus repens invading gaps of various sizes. With this evidence in mind, therefore, it was interesting to determine whether the species which were recorded as early colonists of the Millersdale gaps had achieved high relative abundance when the vegetation was harvested three years later.

In fact, the order of species established amongst the early colonists in autumn-gaps on the south-facing slope was broadly reflected in the relative abundance of species at the end of the experiment. On the north-facing slope however, considerable changes in the relative abundance of species in gaps occurred over the three years. These changes appear to be related to the different character of the vegetation of the north-facing slope where the turf contains a number of species, such as Holcus lanatus, Anthoxanthum odoratum and Arrhenatherum elatius, which are more nutrient-demanding, have higher potential relative growth rates and are frequently associated with more productive grasslands. It seems possible that these species which were minor components of the established turf but present amongst the initial colonists, increased in importance as a result of their abilities to exploit nutrients and space released following damage. These species were particularly important in scrapes where they expanded from the margin. Since scrapes involved the removal of soil and root material the potential for recovery from root fragments was severely restricted.

There are in the vegetation of the north-facing slope a number of species, generally of minor importance, which appear to expand in the conditions of greatly reduced competition which result from the creation of gaps. *Campanula rotundifolia* is the best example, but *Achillea millefolium* and *Galium sterneri* were also prominent as early scrape colonists. All these species had declined considerably in importance by the end of the experiment, probably as a result of shading from other more robust species. *Campanula rotundifolia* is recorded by Grime & Lloyd (1973) as persisting in a variety of communities. *Viola riviniana* may have achieved importance in scrapes partly through reduced competition for the same reasons, but also by virtue of the fact that being a shade tolerant species, it is more able to survive under the increased density of overhanging vegetation. Many species not recorded at all as initial colonists of scrapes had established by the end of the experiment. It seeme likely that these expanded from the margins in the absence of vigorous competition.

Amongst the dominant species on the slope, two of them, *Festuca rubra* and *Agrostis capillaris*, recovered quickly from damage but two other species, *Succisa pratensis* and *Carex flacca*, were not abundant as initial colonists. These species are slower-growing and more stress-tolerant (*sensu* Grime 1974) than *F. rubra* and *A. capillaris* and probably built up biomass slowly over the period of the experiment, coming back to prominence as the faster-growing species began to fail as the initial pulse of resources resulting from gap-cutting was depleted. The expansion of *Danthonia decumbens* (a less prominent member of the community) is probably attributable to the same reasons. *Avenula pratensis* did not regain its former importance in the vegetation after damage, for the reasons discussed above.

Perhaps the most interesting group of species at this site are those which may be described as 'sub-dominants'. Included in this group are species such as Luzula campestris, Avenula pubescens, Centaurea nigra, Koeleria macrantha and Briza media, all of which had achieved their final position in the rank order of species soon after gap cutting. These species are common in grazed and/or burned communities (Grime & Lloyd 1973) and may thus be peculiarly well adapted to the types of damage inflicted in this experiment. Despite this, they are never recorded as dominants, either in Millersdale or elsewhere, a feature which merits further investigation.

The north-facing slope therefore, is believed to support a community which contains floristic elements in dynamic equilibrium. The vegetation composition probably does not alter significantly over long periods but damage temporarily promotes forb species while subsequently dereliction tends to exclude them. In the natural situation, the process of dereliction is probably checked by accidential fires but it seems likely that if desirable the same effect could be achieved by mechanical removal of vegetation.

The south-facing slope does not appear to support such a dynamic system. Most species altered little in their relative abundance after damage over the three-year period (Figs.3.19 and 3.21) and only four species showed marked changes. Campanula rotundifolia and Arrhenatherum elatius were both promoted initially by damage but declined in importance as recolonization proceeded. This situation is comparable with the north-facing slope and probably occurred for the reasons suggested for that site. The expansion of Leontodon hispidus and Plantago lanceolata was probably made possible by the generally reduced levels of plant material in the large gaps compared with undisturbed vegetation. The majority of species in the established community may be classified using Grime's system (Grime 1979) as stress-tolerant herbs. Their low growth rates and limited capacity for lateral spread probably result in a lower intensity of competitive interactions than that experienced at a comparable stage of recolonization on the north-facing slope. This appears to have provided opportunities for P. lanceolata and L. hispidus to expand into bare areas. It may be significant also that Hieracium pilosella increased slightly in importance in gaps relative to controls; this low-growing species has considerable capacity for lateral spread over areas of bared ground. (Grindey 1975).

CHAPTER 4

INITIAL PATTERNS OF COLONIZATION BY SEEDLINGS

The aim of the next two chapters is to examine the importance of regeneration from seed on north- and south-facing slopes in Millersdale. Particular attention is paid to the colonization of gaps in the turf by seedlings. This chapter considers temporal and spatial variations in germination phenomena while in Chapter 5 the fate of newly emerged seedlings is described and attempts are made to identify the circumstances conducive to establishment.

Regeneration from seed is a very precarious process which may fail at any one of a number of distinct phases, as described by Grubb in his discussion of the 'regeneration' niche (Grubb 1977). For example, ripe seed may not be produced, dispersal to suitable sites may not occur, or germination may be inhibited by unfavourable weather conditions. The experiment described earlier (Chapter 2) was designed to allow an examination of events succeeding the dispersal of ripe seed but was not concerned directly with mechanisms controlling germination. These are many and varied and have received considerable attention in numerous laboratory studies, e.g. those of Kinzel (1920), Ratcliffe (1961), Vincent & Roberts (1977), Thompson & Cox (1978) and Grime _et al_. (1981).

Most of the species from Millersdale were examined in the general survey of germination characteristics conducted by Grime _et al_. (1981). Responses of many of the species to fluctuating temperatures have been investigated by Thompson (1977) and Thompson, Grime & Mason (1977), while Cresswell has considered the role of light as a controlling mechanism on germination in a number of the more important species in the Millersdale grasslands (Cresswell 1982). Studies such as these provided a source of background information invaluable in the interpretation of the phenomena observed in the field experiment.

Two main hypotheses are examined in this chapter. Firstly, that germination phenomena observed in gaps will differ from those occurring in undisturbed vegetation. Secondly, that the time of year at which gaps occur will affect the species composition of the populations of colonizing seedlings. Data presented are for initial patterns of seedling colonization in artificial gaps and undisturbed turf on both slopes at two distinct periods of the year. Details of experimental design and methods of recording are contained in Chapter 2.

Tables presented in the text are abstracts from Appendices 5 and 6 which contain information on the occurrence of seedlings of individual species, recorded in November 1979 and June/July 1979 in gaps of different character and season of origin on both slopes.

RESULTS

SEEDLINGS IN GAPS AND ESTABLISHED VEGETATION

Records made in the spring of 1979 of seedlings which had appeared in gaps and in undisturbed vegetation showed marked differences between the two slopes (Table 4.1 and Fig.4.1). On the north-facing slope, the creation of gaps produced a nine-fold

Table 4.1

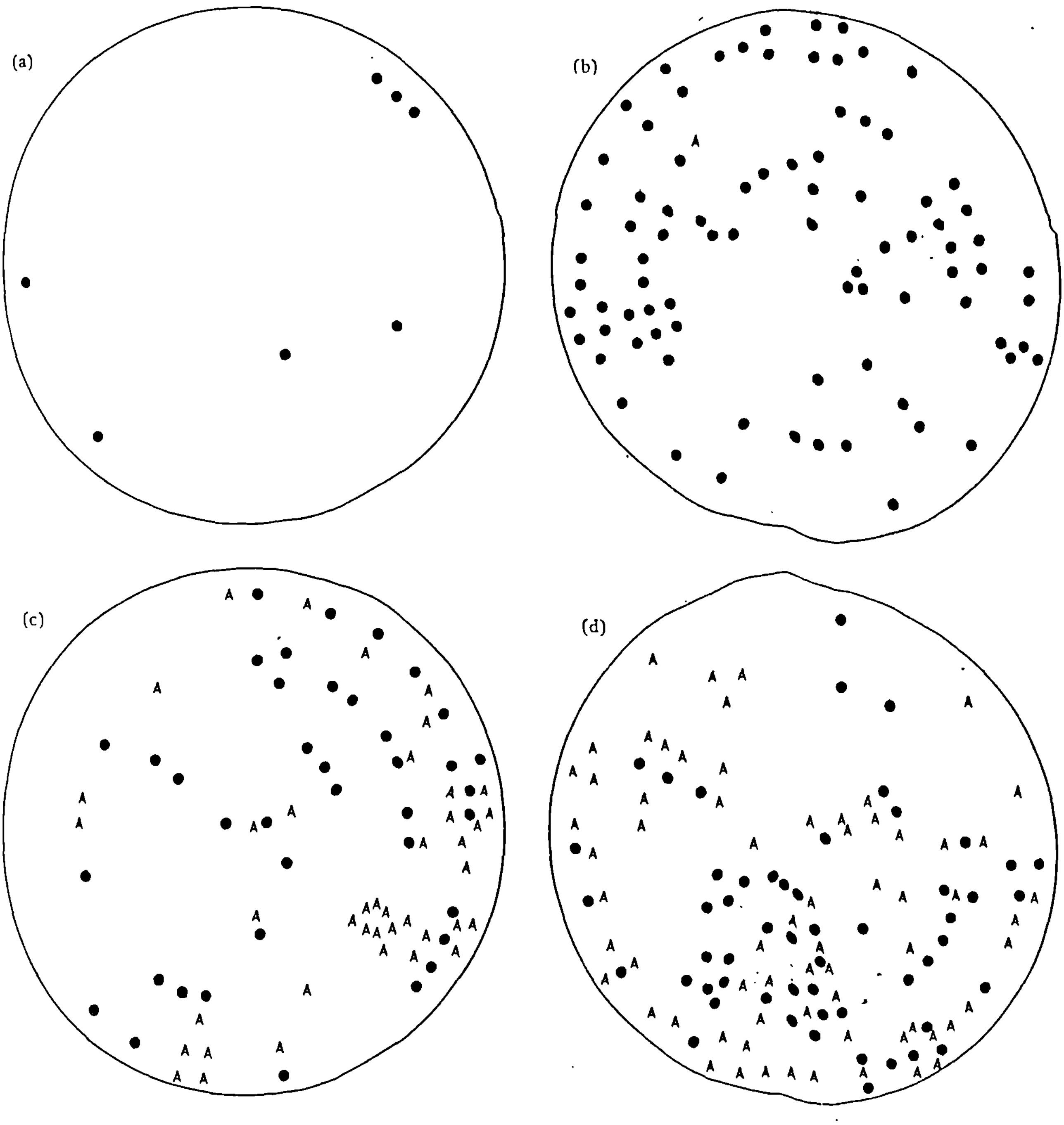
A comparison of the total numbers of seedlings recorded in seven 40 cm diameter gaps and seven 40 cm diameter areas of undisturbed vegetation in June 1979 on the two slopes.

	40 cm controls	Spring 40 cm gaps	
NORTH-FACING SLOPE			
Grasses	11	87	**
Annual forbs	2	7	NS
Perennial forbs	63	572	***
TOTAL	76	666	***
SOUTH-FACING SLOPE			
Grasses	190	84	NS
Annual and biennial forbs	245	242	NS
Perennial forbs+	65	163	*
TOTAL	500	489	NS

+ Including Thymus praecox and Helianthemum nummularium.

Significance levels (Chi-square): NS P>0.05; * P<0.05;
** P<0.01; *** P<0.001

Fig.4.1 Representative diagrams showing patterns of germination and seedling survival in gaps and in undisturbed vegetation at two calcareous grassland sites: (a) undisturbed vegetation, north-facing slope; (b) autumn-cut gap, 40 cm diameter, north-facing slope; (c) undisturbed vegetation south-facing slope; (d) autumn-cut gap, 40 cm diameter, south-facing slope.
Key: ● , seedlings of perennial species present in June 1979.
A, annuals and monocarps present in June 1979.



increase in the number of seedlings recorded. Grasses and forbs were significantly more important in gaps than in established vegetation but the ratio between these two groups of species was not altered by disturbance. Annuals are not an important component of the turf at this site.

In marked contrast, the occurrence of gaps on the south-facing slope had a negligible effect on the total numbers of seedlings recorded. Annual and biennial species (mainly Linum catharticum and Gentianella amarella) constituted 50% of the total in both gaps and undisturbed turf. Seedlings of grasses appeared to be more numerous than forbs in control plots, the reverse being true in spring-cut gaps.

Seedlings of 23 species were recorded in autumn gaps, 34 in spring gaps and 21 in controls on the north-facing slope. On the south-facing slope 27, 35 and 20 species respectively were identified in comparable situations. However, most of the species were represented by only a small number of individuals (Appendices 5 and 6). Even in the largest gaps densities of all but a few species were low. As a result, comparison between gaps and controls at the species level is inconclusive in most cases. Table 4.2 contains information relating to some of the commonest species on the two slopes.

SEEDLINGS IN GAPS ARISING AT DIFFERENT SEASONS

(a) Variations between autumn- and spring-cut gaps

Total numbers of seedlings recorded in a utumn- and spring-cut gaps on both slopes are contained in Table 4.3. Nearly four times as many seedlings appeared in autumn gaps on the south-facing slope than

Table 4.2

A comparison of some of the more common species recorded in spring-cut 40 cm diameter gaps and controls in June 1979 on the two slopes.

Species	40 cm controls	40 cm gaps	
NORTH-FACING SLOPE			
Grasses			
Agrostis capillaris	1	28	*
Anthoxanthum odoratum	0	9	NS
Danthonia decumbens	5	11	NS
Holcus lanatus	1	29	**
Forbs			
Campanula rotundifolia	4	35	*
Carex caryophyllea	0	15	NS
Carex flacca	0	64	NS
Centaurea nigra	2	30	*
Hypericum perforatum	1	9	NS
Origanum vulgare	5	158	*
Plantago lanceolata	22	229	**
Viola riviniana	14	3	NS
SOUTH-FACING SLOPE			
Grasses			
Avenula pratensis	21	7	NS
Festuca ovina	143	42	NS
Koeleria macrantha	20	23	NS
Forbs			
Gentianella amarella	10	0	NS
Linum catharticum	229	237	NS
Lotus corniculatus	5	27	*
Pimpinella saxifraga	31	33	NS
Plantago lanceolata	0	11	NS
Sonchus asper	6	5	NS
Dwarf shrub			
Helianthemum nummularium	4	16	*

Significance levels (Chi-square): NS $P>0.05$; * $P<0.05$
** $P<0.01$; *** $P<0.001$

Table 4.3

Total numbers of seedlings recorded in all treatments on the two slopes in autumn and spring.

NORTH-FACING SLOPE

	Autumn treatments		Spring treatments
Grasses	86	***	160
Annual and biennial forbs	0	***	12
Perennial forbs	258	***	873
TOTAL	344	***	1045

SOUTH-FACING SLOPE

	Autumn treatments		Spring treatments
Grasses	670	***	144
Annual and biennial forbs	316	***	416
Perennial forbs[a]	202	***	418
TOTAL	1188	***	834

[a] Including *Thymus praecox*, *Helianthemum nummularium* and *Ulmus glabra*.

*** Significance level (Chi-square) $P<0.001$

on the north. In spring-cut gaps the north-facing slope supported a larger number than the south. It is clear from Table 4.3 that the relative contributions of grasses, perennial forbs and annuals to seedling total, varied considerably both between seasons and between slopes. Perennial forb species were more important in spring gaps, particularly on the north-facing slope and grass seedlings were considerably more numerous in autumn-gaps on the south-facing slope than in any other situation. Annual and biennial forbs were found in similar quantities at both seasons but in the autumn this group consisted mainly of Arabidopsis thaliana and Gentianella amarella, while numbers in spring gaps are attributable almost entirely to Linum catharticum.

Table 4.4 contains information relating to the most common species on the two slopes together with their temperature requirements for germination as determined from laboratory investigations (Grime et al. 1981). It is clear from these data that the spring germinating perennial forb species on the north-facing slope are characterized by higher minimum temperature requirements and narrower ranges than those of the more numerous autumn germinating grasses of the south-facing slope.

Fig.4.2 reveals that gap season of origin may have effects which extend beyond the first flush of colonizing seedlings. On the south-facing slope, summer seedling totals in autumn-cut gaps were rather different from totals in spring gaps recorded at the same time. In particular, annual species were considerably more numerous in the older gaps. On the north-facing slope in November 1978, eight weeks after gap cutting, seedlings of perennial forb species were

Table 4.4

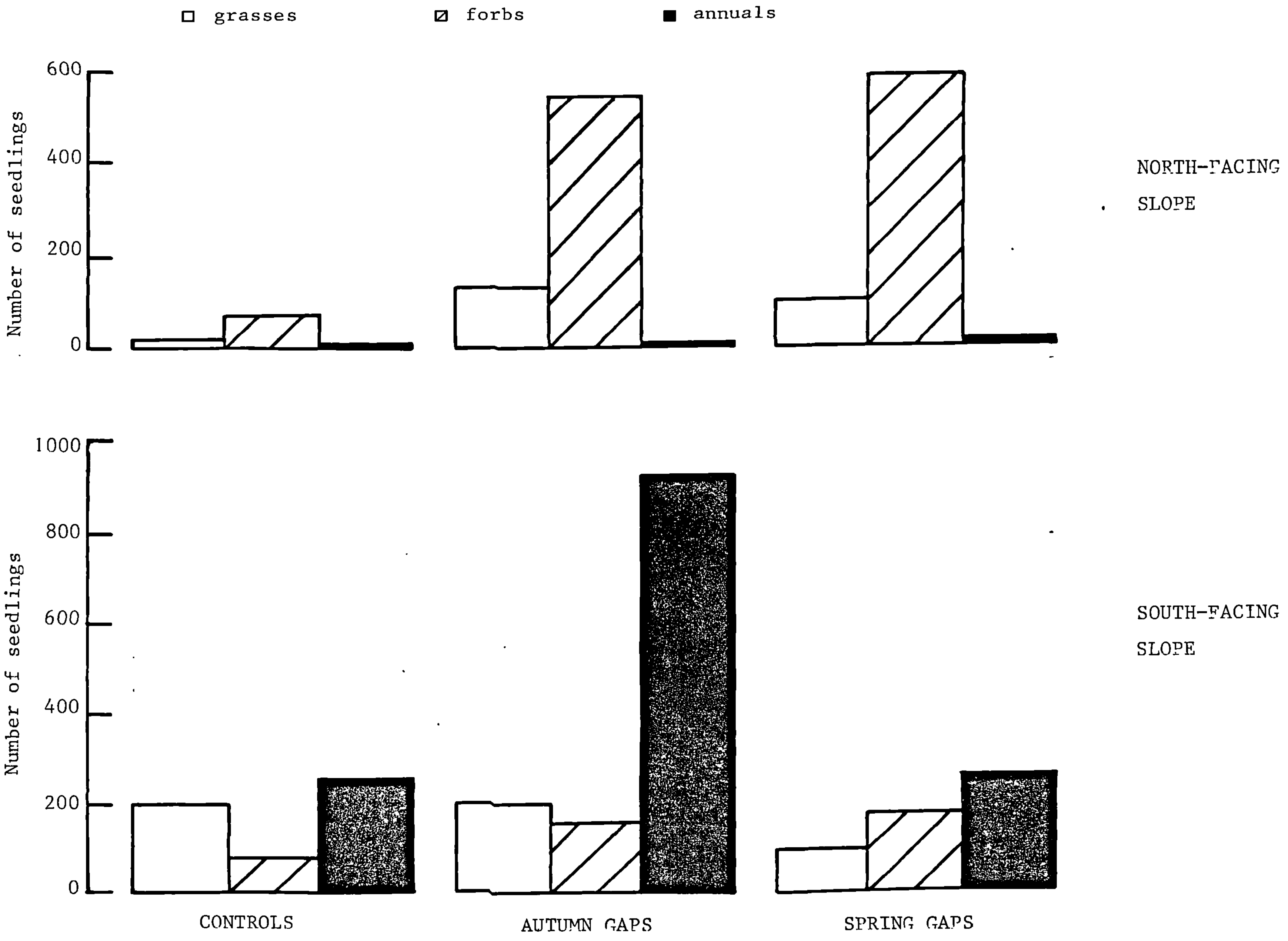
A comparison of some of the more common species recorded on the two slopes in autumn and spring gaps.

Species	Total number of seedlings recorded Autumn gaps		Spring gaps	Temperature range[1] (°C)
NORTH-FACING SLOPE				
Grasses				
Agrostis capillaris	29	*	50	7-31
Anthoxanthum odoratum	2	***	18	7-31
Danthonia decumbens	0	***	20	13-29
Holcus lanatus	36	NS	52	<5-35
Forbs				
Campanula rotundifolia	3	***	51	11-24
Carex flacca	1	***	83	16-28
Centaurea nigra	10	***	54	11-34
Origanum vulgare	95	***	238	13-33
Plantago lanceolata	124	***	349	10-25
SOUTH-FACING SLOPE				
Grasses				
Avenula pratensis	43	**	18	8-26
Briza media	59	***	4	-
Festuca arundinacea	26	***	3	10-32
Festuca ovina	371	***	76	7-33
Koeleria macrantha	146	***	31	6-31
Forbs				
Arabidopsis thaliana	53	***	0	7-31
Campanula rotundifolia	35	NS	29	11-24
Gentianella amarella	241	***	1	-
Hieracium pilosella	48	***	10	6-27
Linum catharticum	1	***	401	7-36[c]
Lotus corniculatus	2	***	48	<5-34[s]
Pimpinella saxifraga	2	***	66	-
Sonchus asper	20	*	9	9-35
Dwarf shrubs				
Helianthemum nummularium	9	*	22	<5-36[s]
Thymus praecox	43	***	14	9-28

[1] Temperatures refer to the range of constant temperatures over which germination in light exceeds 50% of maximum in standardized laboratory tests (Grime *et al*. 1981).

c = seeds germinate only after extended chilling
s = seeds scarified prior to test
- = no available data.
Significance levels (Chi-square): NS P>0.05; * P<0.05
** P<0.01; *** P<0.001

Figure 4.2 Seedling numbers recorded in June 1979 in ten-month-old autumn-cut 40 cm diameter gaps, four-month-old spring-cut 40 cm diameter gaps and 40 cm diameter controls.



few in number. However, by June 1979 the spring flush recorded in spring gaps had also occurred in the older gaps and the seedling total in gaps, for all categories, showed no effects of season.

In Table 4.5 numbers of seedlings resulting from spring germination in selected species are compared for both gap types. Data for the south-facing slope relate to species known to be spring germinators only, due to the difficulties experienced in recording a second cohort in autumn gaps (see p.35).

Gap season of origin had no effect on total numbers of seedlings recorded in many species. Significantly more seedlings of Campanula rotundifolia, Origanum vulgare and Plantago lanceolata were recorded in spring gaps than in autumn gaps. The older gaps supported considerably larger numbers of Linum catharticum and Viola riviniana.

(b) Variations from year to year

On the north-facing slope the total numbers of seedlings recorded in 20 cm diameter gaps cut in the autumn of 1978 were approximately the same as those found after a comparable period in gaps cut on the same date in 1979. However, only three species were found on both occasions (Table 4.6(a)). Comparison between two sets of spring-cut gaps revealed that although eight species were found both in June 1979 and in June 1980, ten species recorded as seedlings in 1979 were not present in newly-cut gaps in 1980 and six species recorded in 1980 were not represented the previous year (Table 4.6(b)). Larger numbers of Origanum vulgare and Plantago lanceolata were found in 1978 autumn gaps and 1979 spring gaps than in comparable gaps created in 1979 and 1980 respectively.

Table 4.5

Effects of gap season of origin on numbers of seedlings recorded as germinating in the spring.

	Autumn gaps (40 cm diameter)		Spring gaps (40 cm diameter)	
NORTH-FACING SLOPE				
Agrostis capillaris	33	a	28	NS
Holcus lanatus	30	a	29	NS
Danthonia decumbens	7		11	NS
Carex flacca	62		64	NS
Campanula rotundifolia	19	a	35	*
Centaurea nigra	30	a	30	NS
Linum catharticum	24		6	**
Origanum vulgare	71	a	158	***
Plantago lanceolata	127	a	229	***
Succisa pratensis	13		6	NS
Viola riviniana	45		3	***
SOUTH-FACING SLOPE				
Hieracium spp.	8		8	NS
Hypericum perforatum	5		10	NS
Leontodon hispidus	1		7	NS
Linum catharticum	845		237	***
Lotus corniculatus	16		27	NS
Pimpinella saxifraga	19		33	NS

a An autumn cohort was also recorded for these species.

Significance levels (Chi-square): NS $P>0.05$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$

Table 4.6(a)

Variations in the seedling flora appearing on the north-facing slope in autumn-cut 20 cm diameter gaps in two different years.

	Number of seedlings	
	1978[a]	1979[b]
Species occurring in 1978 and 1979		
Arrhenatherum elatius	1	2 NS
Origanum vulgare	11	7 NS
Plantago lanceolata	15	9 NS
Species occurring in 1978 only		
Anthoxanthum odoratum	1	
Centaurea nigra	1	
Luzula campestris	1	
Unidentified forb	1	
Species occurring in 1979 only		
Agrostis capillaris		1
Avenula pubescens		1
Dactylis glomerata		1
Holcus lanatus		1
Angelica sylvestris		1
Succisa pratensis		2
TOTAL	31	25 NS

a gaps cut September 1978 and recorded November 1978.

b gaps cut September 1070 and recorded November 1979.

NS significance level (Chi-square) $P>0.05$

Table 4.6(b)

Variations in the seedling flora appearing on the north-facing slope in spring-cut 20 cm diameter gaps in two different years.

	Number of seedlings	
	1979[c]	1980[d]
<u>Species occurring in 1979 and 1980</u>		
Dactylis glomerata	1	1 NS
Danthonia decumbens	6	2 NS
Campanula rotundifolia	9	10 NS
Centaurea nigra	6	5 NS
Hypericum perforatum	3	2 NS
Origanum vulgare	25	19 NS
Plantago lanceolata	56	27 **
Viola riviniana	1	1 NS
<u>Species occurring in 1979 only</u>		
Agrostis capillaris	9	
Anthoxanthum odoratum	6	
Avenula pubescens	1	
Holcus lanatus	12	
Achillea millefolium	1	
Carex caryophyllea	1	
Carex flacca	11	
Cirsium palustre	1	
Scabiosa columbaria	3	
Valeriana officinalis	1	
<u>Species occurring in 1980 only</u>		
Avenula pratensis		1
Koeleria macrantha		1
Unidentified grass		1
Galium sterneri		1
Potentilla erecta		1
Succisa pratensis		1
TOTAL	153	73 ***

c gaps cut April 1979 and recorded June 1979.

d gaps cut April 1980 and recorded June 1980.

Significance levels (Chi-square): NS $P>0.05$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$

Table 4.7(a)

Variations in the seedling flora appearing on the south-facing slope in autumn-cut 20 cm diameter gaps in two different years.

	Number of seedlings	
	1978[a]	1979[b]
Species occurring in 1978 and 1979		
Arrhenatherum elatius	1	2 NS
Avenula pratensis	6	6 NS
Briza media	4	12 NS
Festuca ovina	46	35 NS
Koeleria macrantha	17	6 *
Campanula rotundifolia	3	35 ***
Helianthemum nummularium	1	1 NS
Hieracium pilosella	2	2 NS
Sonchus asper	4	3 NS
Thymus praecox	3	3 NS
Unidentified forb	5	7 NS
Species occurring in 1978 only		
Festuca arundinacea	22	
Poa pratensis	1	
Unidentified grass	2	
Arabidopsis thaliana	1	
Gentianella amarella	155	
Hieracium spp.	1	
Hypericum hirsutum	1	
Leontodon hispidus	1	
Lotus corniculatus	1	
Species occurring in 1979 only		
Anthoxanthum odoratum		1
Trisetum flavescens		1
Arenaria serpyllifolia		16
Linum catharticum		1
Pimpinella saxifraga		2
Silene nutans		8
TOTAL	277	141 ***

a gaps cut September 1978 and recorded November 1978.

b gaps cut September 1979 and recorded November 1979.

Significance levels (Chi-square): NS P>0.05; * P<0.05
** P<0.01; *** P<0.001

Table 4.7(b)

Variations in the seedling flora appearing on the south-facing slope in spring-cut 20 cm diameter gaps in two different years.

	Number of seedlings	
	1979[c]	1980[d]
Species occurring in 1979 and 1980		
Avenula pratensis	3	3 NS
Festuca ovina	18	5 **
Koeleria macrantha	4	1 NS
Campanula rotundifolia	3	9 NS
Helianthemum nummularium	2	12 **
Hieracium spp.	2	14 **
Hypericum perforatum	2	1 NS
Linum catharticum	53	2 ***
Lotus corniculatus	8	1 NS
Origanum vulgare	1	3 NS
Pimpinella saxifraga	14	7 NS
Silene nutans	1	7 NS
Thymus praecox	4	23 ***
Species occurring in 1979 only		
Arrhenatherum elatius	1	
Briza media	2	
Arabis hirsuta	1	
Trifolium campestre	1	
Ulmus glabra	2	
Species occurring in 1980 only		
Anthoxanthum odoratum		2
Arabidopsis thaliana		1
Arenaria serpyllifolia		12
Carex caryophyllea		1
Centaurea scabiosa		6
Epilobium spp.		1
Galium sterneri		7
Hieracium pilosella		8
Leontodon hispidus		2
Plantago lanceolata		2
Sonchus asper		3
Unidentified forb		21
TOTAL	122	154 NS

c gaps cut April 1979 and recorded June 1979.

d gaps cut April 1980 and recorded June 1980.

Significance levels (Chi-square): NS P>0.05; * P<0.05
** P<0.01; *** P<0.001

Annual variations in the seedling flora of gaps were also found on the south-facing slope. Eleven species were found on both occasions in autumn-cut gaps and with the exception of *Koeleria macrantha* and *Campanula rotundifolia* showed little variation from year to year (Table 4.7(a)). However, nine species recorded in the autumn of 1978 were not present in autumn-cut gaps in 1979 and conversely, six species found in 1979 were not represented the previous year. Seedling numbers in these species were small. In spring gaps, grasses were more numerous in 1979 than in 1980 while seedlings of forbs, trees and shrubs were more abundant in 1980 (Table 4.7(b)). Thirteen species appeared in both years and, with the exception of *Linum catharticum* and *Thymus praecox*, showed little variation in numbers. The former was more abundant in spring-cut gaps in 1979, the latter in comparable gaps in 1980. Five species not represented in 1980 were recorded in 1979 while twelve new species appeared in 1980.

SEEDLING NUMBERS IN GAPS OF DIFFERENT SIZE AND SHAPE

(a) Seedling numbers in gaps of different diameter

Total numbers of seedlings recorded in gaps of different diameter on both slopes in autumn and spring are contained in Table 4.8. Comparison between gaps of different size was facilitated by conversion of these data to seedling numbers per square metre, taking account of slight variations in replication (see footnote to table). Densities of seedlings varied little with gap size in the spring on both slopes but autumn records suggest that smaller gaps on the south-facing slope and larger gaps on the north-facing slope contained the most seedlings.

Table 4.8

Total number of seedlings recorded in gaps of different diameter on the two slopes in autumn and spring.

	No. of seedlings				Number per square metre			
Gap diameter	40 cm	20 cm	10 cm	5 cm	40 cm	20 cm	10 cm	5 cm
NORTH-FACING SLOPE								
Autumn								
Grasses	56	2	2	0	63.7	9.1	36.4	0.0
Annual forbs	0	0	0	0	0.0	0.0	0.0	0.0
Perennial forbs	155	30	4	0	176.2	136.4	72.8	0.0
TOTAL	211	32	6	0	239.9	145.5	109.1	0.0
Spring								
Grasses	87	35	8	3	98.9	159.2	145.5	218.3
Annual forbs	7	0	0	1	8.0	0.0	0.0	72.8
Perennial forbs	572	118	31	8	650.4	536.6	563.9	582.1
TOTAL	666	153	39	12	757.2	695.7	709.4	873.1
SOUTH-FACING SLOPE								
Autumn*								
Grasses	448	99	25	12	509.4	525.2	530.5	1222.8
Annual and biennial forbs	69	160	48	0	78.5	848.8	1018.6	0.0
Perennial forbs	132	18	8	1	150.1	95.5	169.8	101.9
TOTAL	649	277	81	13	737.9	1469.5	1718.9	1324.7
Spring								
Grasses	84	28	7	3	95.5	127.3	127.3	218.3
Annual and biennial forbs	242	54	14	6	275.2	245.5	254.6	436.5
Perennial forbs	163	40	12	2	185.3	181.9	218.3	145.5
TOTAL	489	122	33	11	556.0	554.7	600.2	800.3

***N.B.** Total seedling numbers recorded on the south-facing slope in autumn treatments do not represent data from all seven replicates in every case: 20 cm and 10 cm gaps were not recorded in Rep.7, while 5 cm gaps were not recorded in Reps.6 or 7 because of the onset of harsh winter weather conditions. This factor is taken into account in the conversion of total seedling numbers to number m^{-2}.

Seedlings of species known to have buried seed reserves (Thompson 1977; Thompson & Grime 1979) formed a much greater proportion of the total in gaps on the north-facing slope than on the south (Table 4.9) with the exception of autumn-cut 10 cm diameter gaps, a few of which contained large numbers of Arabidopsis thaliana seedlings. Apart from these phenomena, gap diameter appeared to have little influence on the densities of seedlings recruited from species known to develop persistent seed banks in the soil. Seedlings of Plantago lanceolata are excluded from this analysis since soil reserves in this large-seeded species include a surface lying as well as a buried component.

Table 4.9

Density of seedlings (no. m^{-2}) in gaps of different diameter, of species known to have buried seed banks.

		Gap diameter			
		40 cm	20 cm	10 cm	5 cm
North-facing slope	Autumn gaps	114.8	54.6	54.6	-
	% of total	47.9	37.5	50.1	-
	Spring gaps	321.8	322.9	363.9	364.0
	% of total	42.5	46.4	51.3	41.7
South-facing slope	Autumn gaps	70.4	31.8	782.1	72.8
	% of total	9.5	2.2	46.6	5.5
	Spring gaps	50.1	54.7	84.9	-
	% of total	9.0	9.9	14.2	-

Table 4.10

Seedling numbers in gaps, hills and scrapes of diameter 20 cm on both slopes.

		Total number of seedlings								
		Gaps			Hills			Scrapes		
North-facing slope	AUTUMN TREATMENTS									
	Grasses	2		(7.3)	7		(15.9)	13		(29.6)
	Perennial forbs	29		(105.5)	27		(61.4)	25		(56.9)
	TOTAL	31		(112.8)	34		(77.3)	38		(86.4)
	SPRING TREATMENTS									
	Grasses	35	***	(127.3)	3	NS	(6.8)	14	NS	(31.8)
	Perennial forbs	118	***	(429.3)	34	NS	(77.3)	59	***	(134.2)
	TOTAL	153	***	(556.6)	37	NS	(84.1)	73	***	(166.0)
South-facing slope	AUTUMN TREATMENTS									
	Grasses	99		(525.2)	24		(76.4)	18		(47.8)
	Perennial forbs	18		(95.5)	12		(38.2)	13		(34.5)
	Annuals/Biennials	160		(848.8)	10		(31.8)	15		(39.8)
	TOTAL	277		(1469.5)	46		(146.4)	46		(122.0)
	SPRING TREATMENTS									
	Grasses	28	***	(101.9)	6	***	(13.6)	-	***	-
	Perennial forbs	40	*	(145.5)	10	NS	(22.7)	9	NS	(20.5)
	Annuals/Biennials	54	***	(196.5)	16	NS	(36.4)	22	NS	(50.0)
	TOTAL	122	***	(443.8)	32	**	(72.7)	31	**	(70.5)

N.B. Total seedling numbers recorded in autumn treatments on the south-facing slope are based on six replicates for gaps and scrapes and five replicates for hills, due to the early onset of harsh winter weather conditions.

Figures in parentheses represent number of seedlings per square metre. The increased surface area of hills and scrapes and reduced replication of autumn treatments on the south-facing slope was taken into account in the conversion.

Significance levels (Chi-square): NS P>0.05; * P<0.05; ** P<0.01; *** P<000.1

(b) Seedling numbers in gaps, hills and scrapes

Total numbers of seedlings recorded in gaps, hills, and scrapes are presented in Table 4.10. Autumn records revealed that gap form had no effect on seedling numbers on the north-facing slope. On the south-facing slope however, 'simple' gaps supported many more seedlings than either hills or scrapes at this time of the year. In particular grasses and annual species were more numerous. Data for annual species in autumn gaps were very variable and were strongly dependent on records for one gap which contained 148 seedlings of Gentianella amarella. However, the distribution of grass seedlings between replicates was much more uniform. If annual species are removed from the analysis 'simple' gaps still contained over three times more seedlings than either hills or scrapes.

Spring treatments produced similar patterns on both slopes, in that 'simple' gaps contained the largest number of seedlings. On the north-facing slope, gaps supported twice as many seedlings as scrapes and four times as many as hills while on the south-facing slope hills and scrapes contained only one quarter of the total numbers of seedlings recorded in gaps. Grasses were poorly represented on hills on both slopes and were not present at all in scrapes on the south-facing slope.

(c) Seedling numbers in different types of 10 cm diameter gap

The small sample size for 10 cm diameter treatments necessitates some care in the interpretation of the data in Table 4.11. However, features of interest did emerge from seedling records made in these smaller treatments.

Table 4.11

Density of seedlings of perennial species (no. m^{-2}) in 10 cm diameter gaps, scrapes and controls compared with densities in treatments of similar size where roots were removed or clippings re-applied.

		C	10G	10S*	10R	10M
North-facing slope	Autumn	-	109.1	136.4	91.0	36.4
South-facing slope	Autumn	560.3	700.3	178.3	229.2	509.3
North-facing slope	Spring	54.6	709.4	109.2	418.4	291.0
South-facing slope	Spring	272.9	381.9	200.1	236.5	236.4

* Data take account of increased surface area of scrapes.
NB. Annuals were omitted from this analysis due to their extremely patchy distribution on the south-facing slope.

Seedling densities were increased in both autumn and spring gaps of all description, relative to controls, on the north-facing slope. Except in the spring on the north-facing slope, the treatment in which clippings were reapplied to the gap area (10M) produced seedling densities closest to those in controls. Scrapes and treatments in which considerable soil disturbance took place (10R) resulted in lowest seedling densities on the south-facing slope. In spring on the north-facing slope, scrapes and root removal appeared to promote germination relative to controls but resulted in seedling densities considerably lower than those in 10 cm diameter gaps.

(d) Individual species responses

It is difficult to assess the 'preference' of individual species for one gap type rather than another when dealing with natural germination phenomena, due to heterogeneity in the distribution of both surface-lying and buried seeds. Seedling numbers of different species recorded in November 1978 and June 1979, in all treatments on both slopes, are contained in Appendices 5 and 6. In the autumn only 549 cm^2 of undisturbed turf was recorded as a control but this was increased to 8796.2 cm^2 when spring records were made.

Many of the species detected in small numbers occurred only in the largest gaps. It seems likely that seedlings of these species appear only infrequently at the two sites and that their apparent concentration in large gaps is a reflection of the greater total area sampled in this gap category. Only a few species were found in a wide variety of gap types, e.g. Campanula rotundifolia, Carex flacca, Centaurea nigra, Origanum vulgare, Plantago lanceolata, Succisa pratensis and Viola riviniana on the north-facing slope, and Briza media, C. rotundifolia, Gentianella amarella, Festuca ovina, Koeleria macrantha, Linum catharticum, Lotus corniculatus and Pimpinella saxifraga on the south-facing slope.

Seedlings of most of these species were few in number in all treatments. Five species, O. vulgare, P. lanceolata, F. ovina, K. macrantha and L. catharticum were more numerous but in all except the largest gaps, numbers per replicate were low and subject to considerable variability (Table 4.12).

PATTERNS WITHIN GAPS

(a) Centres v. edges in 40 cm diameter gaps

Figs. 4.3 and 4.4 show a general tendency for seedlings to be concentrated at the centres of large gaps cut in both the autumn and spring on the two slopes. The importance of species with buried seed banks on the north-facing slope has been noted previously (p.74). In Fig. 4.3 the distribution of these species is shown separately as is the distribution of Plantago lanceolata, the other main contributor

Table 4.12

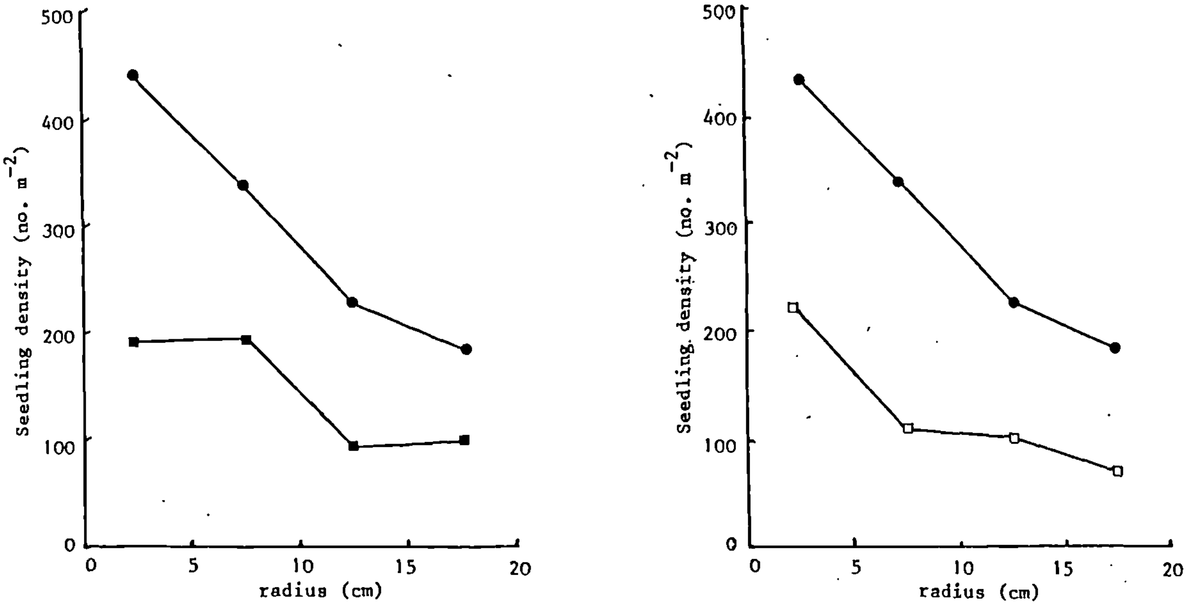
Variability between replicates in numbers of seedlings of five species.

	Replicates								
	1	2	3	4	5	6	7	TOT	No. m^{-2}
<u>40 cm diameter gaps</u>									
Origanum vulgare	60	14	13	37	15	10	9	158	179.6
Plantago lanceolata	13	62	48	38	19	28	21	229	260.4
Festuca ovina+	19	91	54	17	13	45	25	264	300.2
Koeleria macrantha+	7	24	21	7	15	17	3	94	106.9
Linum catharticum+*	80	109	64	118	79	230	165	845	960.8
<u>20 cm diameter gaps</u>									
Origanum vulgare*	11	2	1	2	5	4	0	25	113.7
Plantago lanceolata*	30	4	8	2	8	2	2	56	254.6
Festuca ovina+	11	15	6	5	6	3	0	46	209.2
Koeleria macrantha+	0	2	8	0	4	3	0	17	77.3
Linum catharticum+*	20	13	60	20	72	9	75	269	1223.1
<u>10 cm diameter gaps</u>									
Origanum vulgare*	1	1	0	8	0	0	0	11	200.2
Plantago lanceolata*	7	2	0	0	0	0	0	9	163.8
Festuca ovina+	3	0	5	6	0	0	0	14	254.8
Koeleria macrantha+	0	0	2	0	0	1	0	3	54.6
Linum catharticum+*	4	12	9	4	-	1	6	36	655.1

\- replicate not recorded.
* spring-cut gaps.
\+ autumn-cut gaps.
+* spring germination in autumn-cut gaps.

Fig. 4.3 Distribution of seedlings in 40 cm diameter gaps on the north-facing slope
● all species
■ species known to have buried seed reserves (excluding *Plantago lanceolata*)
□ *Plantago lanceolata*

Autumn-cut gaps recorded November 1978



Spring-cut gaps recorded July 1979

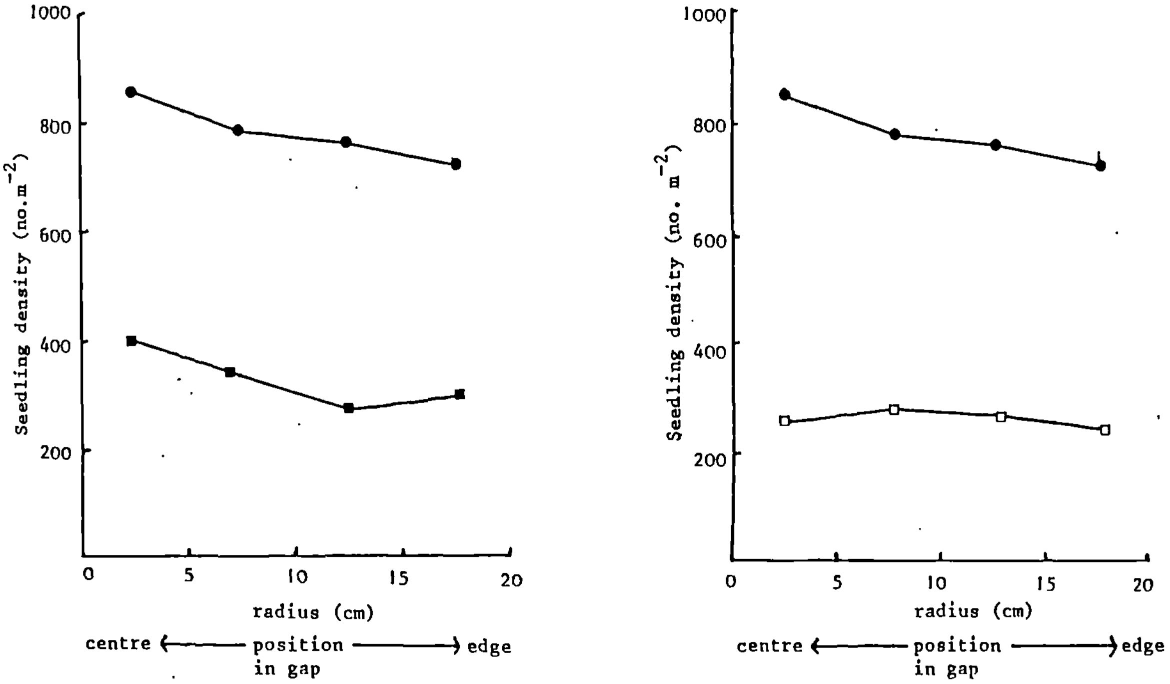
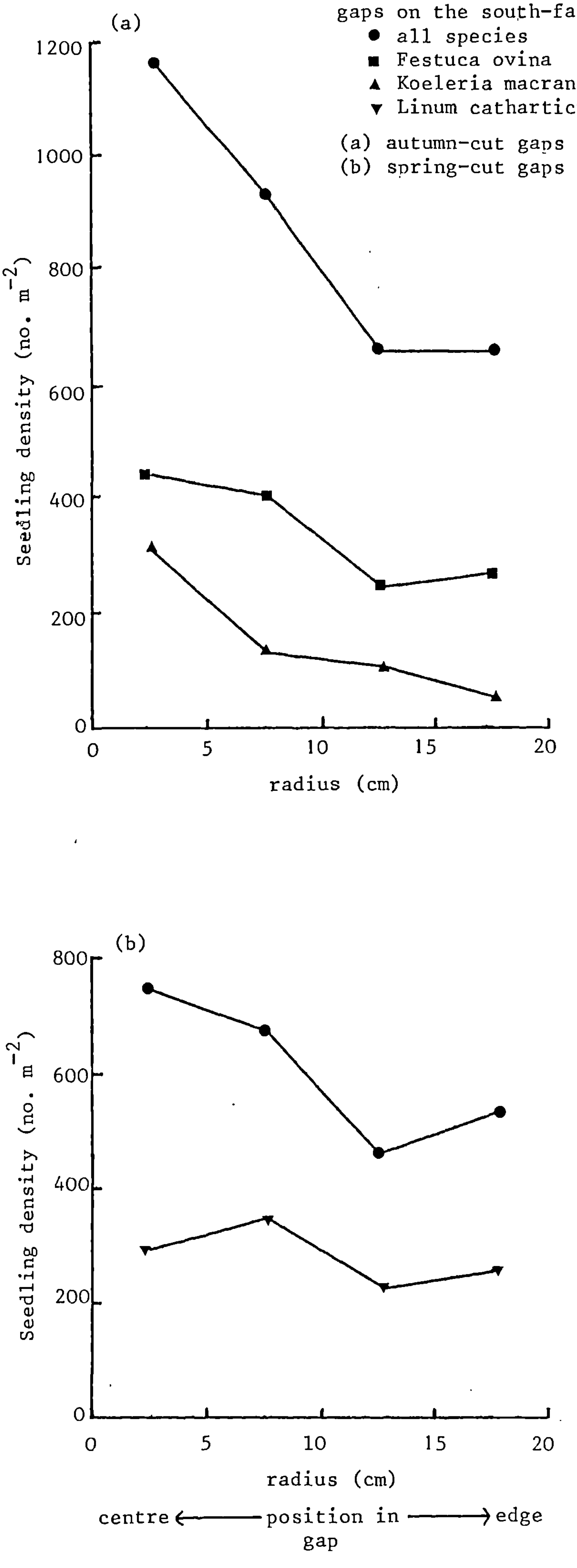


Fig. 4.4 Distribution of seedlings in 40 cm diameter gaps on the south-facing slope.

● all species
■ Festuca ovina
▲ Koeleria macrantha
▼ Linum catharticum

(a) autumn-cut gaps recorded November 1978
(b) spring-cut gaps recorded July 1979



to seedling totals at this site. On the south-facing slope, autumn totals were largely dependent on seedlings of Festuca ovina and Koeleria macrantha whilst Linum catharticum was a major contributor to the spring totals. The distribution of these species is also shown separately in Fig.4.4. With the exception of P. lanceolata and L. catharticum, which were evenly distributed, these species were all more numerous in the centres of large gaps than at the edges.

(b) Rim v. floor in 20 cm diameter scrapes

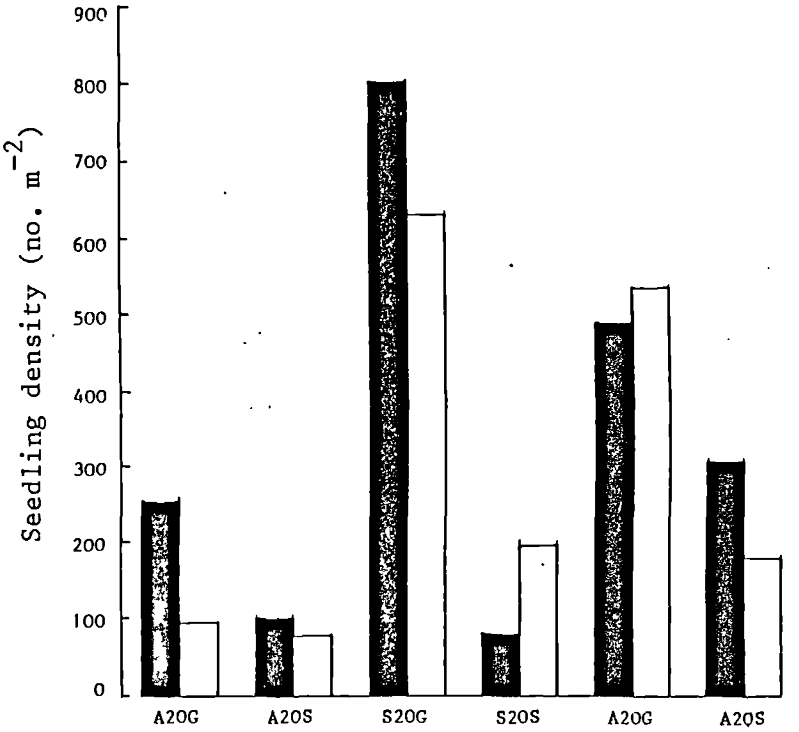
On the north-facing slope spring scrapes contained more seedlings per unit area on the rim than on the floor (Fig.4.5). However, species germinating in the spring in autumn-cut scrapes, were more numerous on the floor than on the rim. In autumn scrapes numbers of seedlings were low and showed little differentiation between floor and rim. In all instances these distributions contrasted markedly with those found when the centres and edges of 20 cm gaps were compared (also included in Fig.4.5). Scrapes on the south-facing slope contained very few seedlings. These showed a slight tendency to concentrate on the rim.

(c) Upslope v. downslope in 20 cm diameter gaps, hills and scrapes

Some interesting differences between the two sites were revealed when their sloping nature was taken into account (Fig.4.6). On the north-facing slope seedlings tended to concentrate in the downslope quadrant of 20 cm diameter scrapes but showed a more even distribution in gaps and on hills. On the south-facing slope such concentration was found in both scrapes and gaps. The difference

Fig. 4.5 Distribution of seedlings in 20 cm diameter gaps and scrapes. Densities in the central 10 cm diameter areas of gaps and scrapes (centres and floors respectively) are compared with densities in the remaining area (edges and rims). Treatment codes as in Table 2.1.

■ indicates centre of gap or floor of scrape



Spring germination

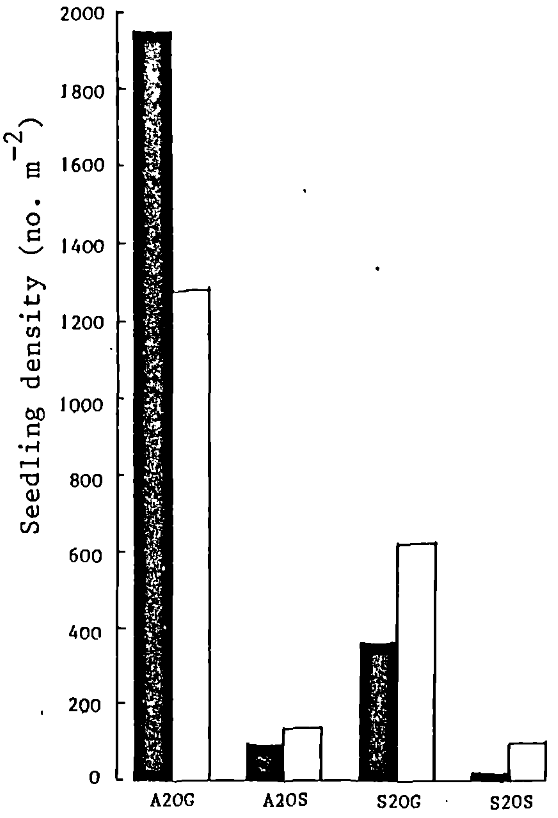
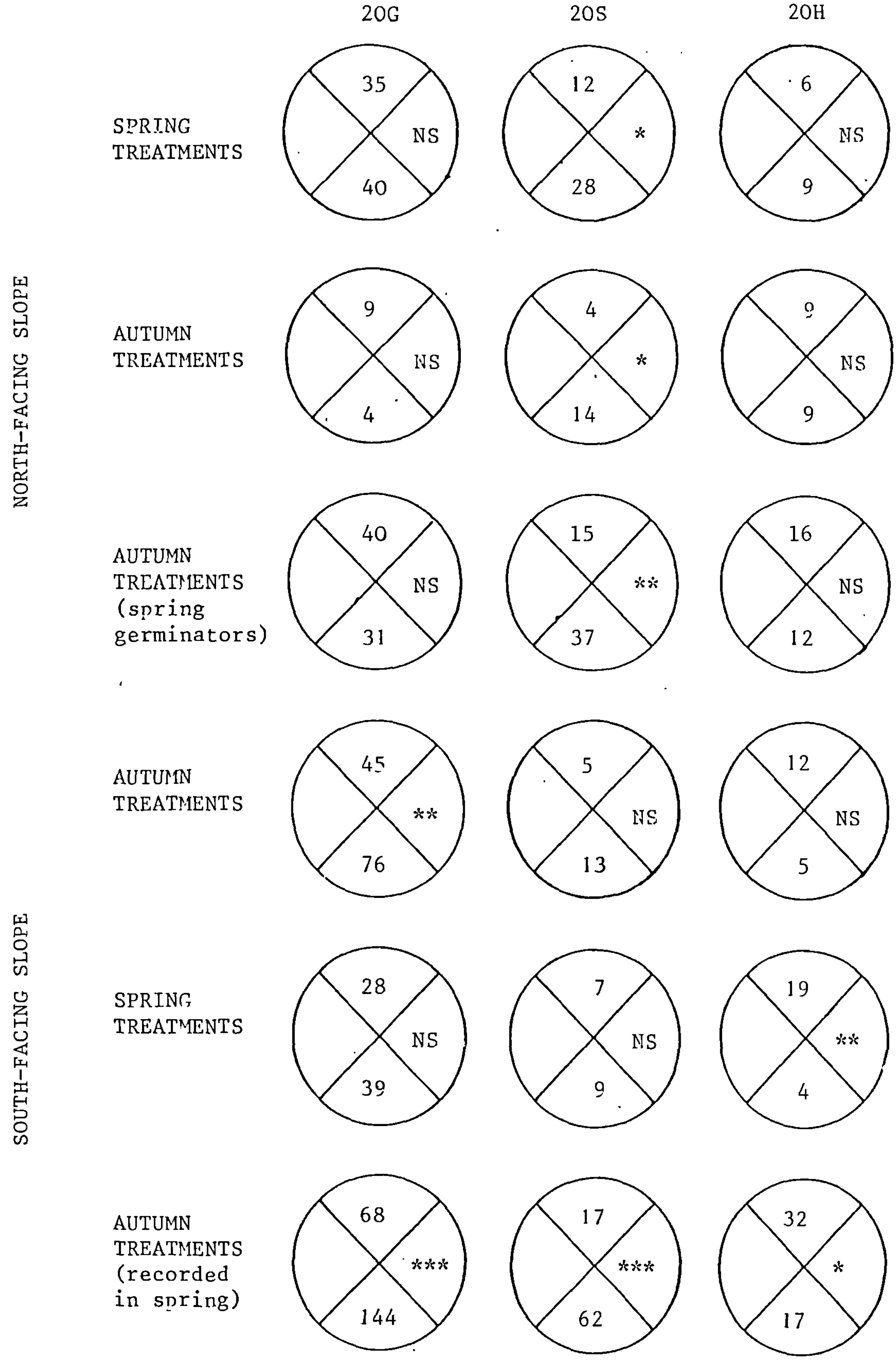


Fig. 4.6 The distribution of seedlings in upslope and downslope quadrants of 20 cm diameter gaps (20G), hills (20H) and scrapes (20S) on the north- and south-facing slopes. The numbers in each quadrant are the total from seven replicates.
Significance conventions: NS - not significant, * - $P<0.05$, ** - $P<0.01$, *** - $P<0.001$



between upslope and downslope quadrants was particularly marked when seedling distributions in autumn gaps were examined in the spring of 1979.

In contrast, 20 cm diameter hills on the south-facing slope contained more seedlings in the upslope quadrant than downslope. Seedlings were evenly distributed in 20 cm diameter areas of undisturbed turf recorded in the spring. On both slopes seed size did not appear to be an important determinant of seedling distribution.

DISCUSSION

Owing to their very different character, the two sites in Millersdale offered very good opportunities for studies of regeneration from seed and in particular of the role which vegetation gaps might play in the process. Data presented in this chapter and its successor were collected as part of an extensive study of gap recolonization processes at the two sites. The work was planned in conjunction with the investigation of vegetative recolonization described in Chapter 3.

It was not possible, nor desirable, to undertake a full-scale demographic analysis of germination and seedling establishment. Such studies, apart from being extremely time-consuming, involve considerable and repeated disturbance of the vegetation in order to obtain data. Laboratory studies (Appendix 7) have shown that the act of recording may have a considerable impact on the process of vegetative gap recolonization, a situation which was to be avoided as much as possible in this work. Accordingly, collection of records of seedling colonization was restricted to two occasions chosen to reflect the main phases of seed germination occurring on the two slopes. It is inevitable, however, that prior to recording, some of the earliest seedling colonists may have perished.

THE IMPORTANCE OF GAPS IN INITIATING GERMINATION

Gaps appear to have a strong controlling influence on the occurrence of seedlings on the north-facing slope. Exposure of the soil by removal of vegetation during gap creation leads to changes in the level and quality of irradiance and to increased soil temperatures or fluctuations thereof. Such changes may have the effect of breaking dormancy in buried or surface-lying seeds. High seedling densities in gaps, probably attributable to changed light intensity and quality, were a feature of the north-facing slope where gap creation often involved removal of a deep bryophyte litter layer. It seems likely that species such as *Origanum vulgare* and *Plantago lanceolata* were stimulated to germinate in this way since these species were prominent in the seedling flora of gaps but were extremely poorly represented in undisturbed vegetation.

No such effects of gaps were apparent on the south-facing slope where the many grass species prominent in the autumn at this site tended to germinate soon after seed release. Most of these grasses are relatively insensitive to light intensity and quality (Grime *et al.* 1981; Cresswell 1982) and it is not surprising therefore, that seeds of so many of them germinated in both gaps and control areas. The two forb species most common in the spring, *Linum catharticum* and *Pimpinella saxifraga*, both exhibit synchronous germination after chilling in darkness in the laboratory (Grime *et al.* 1981) and therefore would not be expected to respond to gap cutting.

TEMPORAL VARIATIONS IN THE SEEDLING FLORA

Gap colonization by seedlings was strongly affected by season on both slopes. Not only did the total number of seedlings alter dramatically with season, but there were also changes in the relative contribution of grasses and forbs to the seedling flora. The germination responses exhibited by Millersdale species examined under laboratory conditions (Grime et al. 1981) were consistent with the different times of year at which seedlings were found in the field.

On the south-facing slope, most seedlings appeared in the autumn and the seedling flora was dominated by grass species, principally Festuca ovina and Koeleria macrantha. Many grass species germinate soon after seed release in the autumn and early winter (Davison 1961, 1977; Thompson & Grime 1979) and reference to Table 4.4 reveals that both F. ovina and K. macrantha have the capacity to germinate at the lower temperatures characteristic of this time of year. It is believed that the early onset of harsh winter conditions in November 1978 curtailed germination of many grasses. These species in consequence, may have been represented to an atypical extent as spring germinators in 1979, dormancy enforced by low temperatures having delayed germination until the spring.

The preponderance of seedlings germinating in the spring on the north-facing slope reflects a variety of seed characteristics. Late seed production and/or release in species such as Agrostis capillaris, Carex flacca, Danthonia decumbens and Succisa pratensis, coupled with the requirement of these and other common species, e.g. Plantago lanceolata, for relatively higher temperatures to initiate germination, correlates with their tendency to appear in the spring.

Large numbers of seedlings appeared in spring gaps on the south-facing slope also. These were attributable in part to considerable quantities of the spring germinating biennial species Linum catharticum and the perennial forb Pimpinella saxifraga. Seeds of both species have a chilling requirement before germination will occur.

Some species, e.g. Linum catharticum, Succisa pratensis and Viola riviniana, although spring germinators, were more abundant in autumn-cut gaps. It seems likely that seeds or newly germinated seedlings of these species were removed by the spring gap cutting operation.

THE INFLUENCE OF GAP CHARACTERICTICS

It was difficult to compare the relative impacts of large and small gaps on regeneration from seed, due to the low total surface area of the latter which made estimates of seedling numbers unreliable. However, comparisons between 10 cm gaps of differing character suggested that soil disturbance reduced seedling numbers and the treatment in which clipped vegetation was re-applied to the gap immediately after cutting, produced seedling densities closest to undisturbed vegetation. This finding, when coupled with the fact that clearance of vegetation down to ground level resulted in the highest seedling densities, tends to suggest that a litter layer alone is sufficient to inhibit seedling emergence. There may be a number of possible explanations for this. A layer of litter causes considerable reductions in light quantity and possibly even light quality, both of which tend to preclude germination. Litter also causes reduced air circulation which may promote 'damping off'.

Alternatively, the presence of litter may simply present a physical barrier to seedling emergence in much the same way as tree litter is thought to affect the woodland ground flora (Sydes 1981).

Lower seedling densities on hills may be due to the mixing of upper and lower soil levels during their creation. Seeds in the soil may thus have been more deeply buried and as such were unlikely either to germinate or to survive as emerging seedlings. Reduced seedling densities in scrapes are likely to be due to even more severe soil disturbance. In the creation of this type of gap, soil and associated seed was removed completely. Reduced light levels caused by overhanging vegetation (see Chapter 3) may also have contributed to the lower seedling densities in scrapes. The largest numbers of seedlings were found in gaps whose character was similar to that of a closely mown or grazed sward.

Seedlings of species occurring in Millersdale, even in gaps, tended to be few in number and patchy in their distribution (Table 4.12). For these reasons attempts to assess affinities of individual species with particular gap types in these sorts of systems are unlikely to be informative using data based on natural germination phenomena.

The increased surface area of 40 cm diameter gaps promoted small numbers of seedlings of species less common in both the established and the seedling flora. However, it was doubtful whether many of these would survive to become established plants. Their fate is explored further in Chapter 5. Even in these larger gaps, significant numbers of new species were not introduced to either system, a reflection of the isolation of the two sites from potential source areas and also of management techniques which altered little in the period prior to dereliction.

SEEDLING DISTRIBUTIONS IN GAPS

The increased densities of seedlings at the centres of large gaps appeared to be a general phenomenon not dependent on the distribution of species making major contributions to seedling totals (Figs. 4.3 and 4.4). The most likely explanation is to be found in the altered temperature and light relations. Centres of large gaps experience generally higher temperatures and/or fluctuations (Thompson & Grime 1983). For many species this cue alone will promote germination. Increased light levels at the centres of large gaps may also contribute to enhanced germination. Alternatively it is possible that the edges of the bare area in being overhung by surrounding unsupported vegetation experience lower red:far-red ratios than centres of gaps and some species may have canopy dormancy imposed on them (e.g. Gorski 1975; Frankland 1981).

Since the creation of 20 cm diameter scrapes caused soil to be removed to a depth of 10 cm and most seeds are contained in the upper 3 cm of soil, it had been expected that scrape rims might support larger quantities of seedlings than their floors, which also tend to experience lower light intensities due to shading by overhanging vegetation. While this prediction was broadly confirmed, re-examination of autumn 20 cm scrapes on the north-facing slope revealed that spring germinating seedlings contained in them had an entirely different distribution, more being found on the floor than on the rim. It was conjectured that some re-distribution of seed had occurred between the time of origin of these scrapes in the autumn of 1978 and the occurrence of spring germination in 1979.

This view was supported by an examination of seedling densities in upslope and downslope quadrants of gaps, hills and scrapes on both slopes (Fig.4.6). On the north-facing slope it seems likely that seeds entering a scrape are effectively trapped and tend to aggregate in the downslope portion. On the south-facing slope seed movements appeared to be a much more general phenomenon. It seems that seeds move freely across bare areas in gaps and scrapes, tending to aggregate in the downslope portion, but on reaching a barrier such as that presented by a hill, further downslope movement is halted. The greater concentration of seeds in upslope quadrants on hills may be due to seeds moving onto the hill from vegetation above or alternatively by differential removal of seed from downslope sections. The former seems to be the most likely cause since seedling densities in the downslope quadrants of hills created in the autumn were not as low as might be expected if seed was being differentially removed from these sections. Such large scale movements are likely to have important implications for seedling survival (Davison 1964).

CHAPTER 5

SEEDLING SURVIVAL

In the previous chapter it was shown that at certain times of the year, large numbers of freshly-germinated seedlings were detectable in artificially-created gaps in the turf at Millersdale. Estimates of dry matter accumulation in the same gaps over the period of the experiment, as determined by destructive harvests (Chapter 3), revealed that a small but measurable quantity of material derived from these early seedling colonists (Appendices 3 and 4). The purpose of this chapter is to explore some of the processes which contributed to this situation.

Survival in marked cohorts of seedlings, over the period of the investigation, was examined in a variety of gap types and also in undisturbed turf on both slopes. An additional measure of success in establishment was obtained by recording the shoot dry weight of surviving seedlings harvested in 1981. Details of the methods employed to obtain these data are given in Chapter 2.

Annual records of the position of marked seedlings in gaps and controls allowed investigation of some of the factors affecting seedling survival in Millersdale. Relationships between the position of seedlings and vegetative regrowth were explored in some detail, in an effort to understand the interplay between regeneration from seed and vegetative recolonization.

RESULTS

PART I : GENERAL PATTERNS OF SEEDLING SURVIVAL

NUMBERS OF SEEDLINGS SURVIVING

(a) All treatments

Total numbers of surviving seedlings in all autumn- and spring-cut gaps on both slopes are contained in Table 5.1. Separate values for the autumn cohort in autumn-cut gaps on the north-facing slope are included. On both slopes autumn-gaps contained the largest numbers of surviving seedlings at the end of the experiment. However, the difference in numbers between autumn-and spring-cut gaps was greater on the south-facing slope.

One quarter of the total number of survivors in autumn-cut gaps on the north-facing slope derived from the autumn-germinating cohort. It is interesting to note that if these are removed from the calculations there is very little difference between autumn- and spring-cut gaps when comparison is made between totals in the two spring cohorts. On the south-facing slope the difference in seedling totals in autumn- and spring-cut gaps is almost entirely due to the large number of grasses. Seedlings of perennial forb species were only slightly more abundant in the older gaps. Table 5.2 contains information relating to the annual and biennial species on the south-facing slope marked at the same time as the perennials. Numbers of seedlings of Gentianella amarella declined considerably over the winter of 1978-79. The large numbers of Linum catharticum seedlings present in 1979 were severely depleted by 1980 but most of those which survived flowered.

Table 5.1

Total number of seedlings surviving in all treatments.

North-facing slope

	Autumn treatments	Spring treatments
Grasses	67 (22)	43
Forbs[a]	207 (38)	196
TOTAL	274 (60)	239

South-facing slope

	Autumn treatments	Spring treatments
Grasses	109	56
Forbs[a]	124	112
TOTAL	233	168

Figures in parentheses are the number of seedlings surviving from the autumn cohort.

a including graminoids and trees/shrubs.

Table 5.2

Depletion of seedling totals of annual and biennial species on the south-facing slope.

	AUTUMN TREFATMENTS			SPRING TREATMENTS	
	1978	1979*	1980**	1979	1980
Arabidopsis thaliana	53	-	-	-	-
Arenaria serpyllifolia	-	4	-	-	-
Gentianella amarella	241	76 (31.5)	22 (9.1)	1	1
Linum catharticum	1	1503	609 (40.5)	401	168 (41.9)
Sonchus asper	20	11 (55.0)	-	9	-
Trifolium campestre	-	-	-	5	-

Figures in parentheses indicate proportion of initial seedling total surviving.

* recorded spring 1979 at same time as spring treatments
** recorded spring 1980 at same time as spring treatments.

The species represented by marked seedlings which were still alive in 1981 are identified in Table 5.3. Totals for autumn gaps and controls on both slopes include survivors from both the autumn and spring cohorts. In these gaps the 1979 total given for comparison represents the number of seedlings in autumn gaps at that time regardless of season of germination. It is evident that many species represented in 1979 no longer formed part of the seedling flora in 1981. Most of these had been found originally in only small numbers but a few, notably Carex flacca, while numerous in 1979 were inconspicuous by the end of the experiment.

One seedling of Leontodon hispidus on the south-facing slope and one of Plantago lanceolata on the north-facing slope, flowered in the period immediately prior to harvest. Both were in 40 cm diameter gaps.

(b) Gaps of different diameter

It is clear from Table 5.4 that gap diameter was more strongly related to seedling survival on the north-facing slope than on the south. Gaps of diameter 10 cm on the north-facing slope, while supporting densities of seedlings in 1979 which were comparable with those in 40 cm diameter gaps, sustained considerably higher levels of mortality over the period of the experiment. The agreement in seedling densities obtained from 10 cm, 20 cm and 40 cm diameter areas of undisturbed turf suggests that the reduction of seedling numbers in 10 cm gaps, when compared with other treatments, was not the result of sampling error. On the south-facing slope, final seedling densities were variable, showing no consistent patterns associated with gap size.

Table 5.3

Identity and number of seedlings surviving at final harvest in 1981.
(a) North-facing slope

	Controls 40 cm diameter	Autumn^a 40 cm gaps	Spring^b 40 cm gaps	Autumn^a other^c treatments	Spring^b other^c treatments
Agrostis capillaris	- (1)	5 (41)	8 (28)	1 (17)	2 (22)
Anthoxanthum odoratum		5 (12)	2 (9)	8 (11)	4 (9)
Arrhenatherum elatius	- (1)	2 (2)		- (2)	1 (1)
Avenula pratensis		- (1)	- (1)	2 (4)	- (2)
Avenula pubescens		1 (3)	1 (2)		- (2)
Briza media				- (1)	
Dactylis glomerata	- (1)	1 (3)	2 (5)	2 (3)	2 (3)
Danthonia decumbens	4 (5)	5 (7)	5 (11)	3 (4)	4 (9)
Festuca ovina	- (1)				
Festuca rubra	1 (1)	2 (2)	1 (1)		
Holcus lanatus	- (1)	25 (48)	8 (29)	5 (22)	4 (23)
Koeleria macrantha		- (1)	- (1)		
Trisetum flavescens					- (2)
TOTAL GRASSES	5 (11)	46 (120)	27 (87)	21 (63)	17 (73)
Achillea millefolium		1 (3)	1 (3)	1 (3)	- (3)
Angelica sylvestris	- (1)			- (1)	
Campanula rotundifolia	1 (4)	3 (21)	6 (35)	1 (15)	6 (16)
Carex caryophyllea		1 (7)	8 (15)	3 (4)	- (3)
Carex flacca		5 (62)	- (64)	- (31)	- (19)
Centaurea nigra	- (2)	19 (33)	10 (30)	7 (21)	7 (24)
Cirsium palustre		1 (1)	4 (4)	- (1)	4 (5)
Epilobium spp.	- (1)	- (3)	- (2)	- (8)	- (3)
Galium sterneri		2 (2)			
Hieracium spp.	1 (2)	- (1)	- (1)	3 (5)	
Hypericum perforatum	1 (1)	- (9)	4 (9)	1 (3)	2 (4)
Leontodon hispidus				- (2)	
Lotus corniculatus		- (3)	- (1)	- (2)	- (4)
Luzula campestris				1 (2)	- (1)
Origanum vulgare	- (5)	10 (105)	34 (158)	16 (91)	13 (80)
Pimpinella saxifraga		- (3)	- (1)	2 (9)	- (1)
Plantago lanceolata	3 (22)	59 (180)	46 (229)	27 (112)	39 (120)
Potentilla sterilis		1 (4)		1 (1)	
Primula veris			- (2)	1 (5)	
Rumex acetosa			- (4)		
Scabiosa columbaria		1 (1)	- (1)		- (3)
Senecio jacobaea		1 (2)			
Serratula tinctoria	- (1)	- (1)		- (2)	
Succisa pratensis	1 (5)	1 (13)	3 (6)	7 (27)	4 (6)
Taraxacum spp.	1 (3)	1 (1)		1 (3)	
Valeriana officinalis	- (2)	- (3)	- (3)	- (1)	- (2)
Viola riviniana	5 (14)	24 (45)	3 (3)	5 (15)	1 (7)
TOTAL FORBS^d	13 (65)	130 (503)	119 (579)	77 (403)	76 (306)
TOTAL SEEDLINGS	18 (76)	176 (623)	146 (666)	98 (466)	93 (379)

Figures in parentheses represent seedlings totals recorded in 1979.

a gaps created September 1978.

b gaps created April 1979.

c scrapes, hills etc.

d including the graminoids Carex caryophyllea, Carex flacca and Luzula campestris.

Table 5.3

Identity and number of seedlings surviving at final harvest in 1981.

(b) South-facing slope

	Controls 40 cm diameter	Autumn[a] 40 cm gaps	Spring[b] 40 cm gaps	Autumn[a] other[c] treatments	Spring[b] other[c] treatments
Arrhenatherum elatius		- (1)		- (1)	- (1)
Avenula pratensis	4 (22)	3 (16)	3 (7)	7 (15)	2 (11)
Brachypodium sylvaticum				- (1)	
Briza media	- (1)	- (2)	- (2)	1 (3)	- (2)
Dactylis glomerata	1 (3)		2 (7)	1 (5)	
Festuca arundinacea			1 (1)	3 (11)	1 (2)
Festuca ovina	40 (143)	31 (129)	18 (42)	38 (120)	6 (34)
Koeleria macrantha	8 (20)	10 (38)	16 (23)	13 (28)	3 (8)
Poa pratensis		1 (1)	1 (1)	1 (1)	1 (1)
Trisetum flavescens		- (1)	1 (1)		1 (1)
TOTAL GRASSES	53 (189)	45 (188)	42 (84)	62 (185)	14 (60)
Arabis hirsuta	1 (1)		2 (3)	1 (4)	- (1)
Betula pubescens		- (1)			
Campanula rotundifolia	4 (12)	8 (34)	4 (21)	2 (16)	3 (8)
Carex caryophyllea			1 (1)		
Centaurea scabiosa			1 (1)	1 (1)	
Galium sterneri				1 (2)	
Helianthemum nummularium	3 (4)	1 (5)	6 (16)	1 (2)	3 (6)
Hieracium pilosella	- (3)	(5) (6)	6 (7)	3 (5)	1 (3)
Hieracium spp.	1 (1)	1 (8)	3 (8)	2 (6)	3 (5)
Hypericum perforatum		1 (5)	3 (10)	- (5)	1 (2)
Leontodon hispidus	2 (2)	1 (1)	4 (7)	3 (5)	- (7)
Lotus corniculatus	1 (5)	7 (16)	9 (27)	4 (15)	5 (21)
Origanum vulgare		- (5)	3 (3)	2 (13)	- (4)
Pimpinella saxifraga	19 (31)	10 (19)	19 (33)	51 (131)	13 (33)
Plantago lanceolata		3 (4)	8 (11)	1 (1)	- (1)
Polygala vulgaris	1 (2)	- (2)	- (3)	1 (5)	2 (2)
Scabiosa columbaria			1 (1)		
Senecio jacobaea		2 (5)	1 (1)	- (2)	1 (2)
Silene nutans	- (2)	- (6)	- (2)	1 (8)	1 (3)
Solidago virgaurea		1 (2)	- (1)	1 (5)	- (2)
Taraxacum spp.	- (1)		- (1)		
Thymus praecox	- (1)	5 (19)	4 (5)	4 (15)	3 (9)
Ulmus glabra					- (2)
Viola hirta		- (1)			1 (1)
TOTAL FORBS[d]	32 (65)	45 (139)	75 (160)	79 (241)	37 (112

Figures in parentheses represent seedling totals recorded in 1979.

a gaps created September 1978.

b gaps created April 1979.

c scrapes, hills etc.

d including the trees/shrubs Betula pubescens, Helianthemum nummularium, Thymus praecox, Ulmus glabra

Table 5.4

Seedling survival in gaps of different diameter.

		Controls			Autumn gaps			Spring gaps		
		No. m^{-2} 1979	No. m^{-2} 1981	% survival	No. m^{-2} 1979	No. m^{-2} 1981	% survival	No. m^{-2} 1979	No. m^{-2} 1981	% survival
(a) <u>North-facing slope</u>										
40 cm diameter	perennial grasses	12.5	5.7	45.6	136.4	52.3	38.3	98.9	30.7	31.0
	perennial forbs	71.6	14.8	20.7	650.3	178.5	27.5	651.0	135.3	20.8
	TOTAL	84.1	20.5	24.4	786.7	230.8	29.3	749.9	166.0	22.1
20 cm diameter	perennial grasses	18.2	9.1	50.0	63.7	36.4	57.1	159.2	45.5	28.6
	perennial forbs	54.6	13.6	24.9	504.7	131.9	26.1	536.6	186.4	34.7
	TOTAL	72.8	22.7	31.2	568.4	168.3	29.6	695.7	231.9	33.3
10 cm diameter	perennial grasses	-	-	-	145.5	-	0.0	145.5	36.4	25.0
	perennial forbs	54.6	18.2	33.3	600.3	109.2	18.2	563.9	36.4	6.5
	TOTAL	54.6	18.2	33.3	745.8	109.2	14.6	709.4	72.8	10.3
(b) <u>South-facing slope</u>*										
40 cm diameter	perennial grasses	216.0	60.3	27.9	213.8	51.2	24.0	95.5	47.8	50.1
	perennial forbs	73.9	36.4	49.3	158.0	51.2	32.4	185.3	85.3	46.0
	TOTAL	289.9	96.7	33.4	371.8	102.4	27.5	280.8	133.1	47.4
20 cm diameter	perennial grasses	268.3	81.8	30.5	381.9	159.2	41.7	127.3	27.3	21.4
	perennial forbs	68.2	18.2	26.7	218.3	74.3	34.0	172.8	50.0	28.9
	TOTAL	336.5	100.0	29.7	600.2	233.5	38.9	300.1	77.3	25.8
10 cm diameter	perennial grasses	200.2	72.8	36.4	297.2	63.7	21.4	127.4	72.8	57.1
	perennial forbs	54.6	-	0.0	191.1	42.5	22.2	218.4	109.2	50.0
	TOTAL	258.8	72.8	28.6	488.3	106.2	21.7	345.8	182.0	52.6

* data for autumn-cut 10 cm and 20 cm diameter gaps are based on 6 replicates.

Table 5.5

Survival of seedlings in 5, 10 and 20 cm diameter gaps of differing form.

	GAP TYPE+	20G	20S	20H	10G	10S	10R	10R	5G	5S	5H
NFS*	Number in 1979	125	109	62	41	33	14	20	9	10	4
autumn	Number in 1981	37	20	13	6	4	3	9	3	-	3
treatments	% survival	29.6	18.3	21.0	14.6	12.1	21.4	45.0	33.3	0.0	75.0
NFS	Number in 1979	153	73	37	39	12	23	16	11	3	7
spring	Number in 1981	51	10	16	4	5	3	1	-	1	1
treatments	% survival	33.3	13.7	43.2	10.3	41.7	13.0	12.5	0.0	33.3	14.3
SFS**	Number in 1979	121[1]	130	32	23[1]	39	17	18	10[1]	21	7
autumn	Number in 1981	44[1]	48	13	5[1]	18	4	4	1[1]	9	1
treatments	% survival	36.4	36.9	40.6	21.7	46.2	23.5	22.2	10.0	42.9	14.3
SFS	Number in 1979	68	16	9	19	22	13	13	5	5	1
spring	Number in 1981	17	6	6	10	5	3	1	2	-	-
treatments	% survival	25.0	37.5	66.7	52.6	22.7	23.1	7.7	40.0	0.0	0.0

* north-facing slope.
** south-facing slope.
\+ for explanation of codes see Table 2.1.
1 data based on six replicates.

The relative contributions of grasses and perennial forb species to the total number of surviving seedlings showed considerable variability on both slopes. No consistent patterns were observed in gaps of different size or season of origin, suggesting that neither factor exerted a strong influence upon the ability of these species to persist as seedlings in gaps.

(c) Gaps of differing forms

Numbers of seedlings surviving in treatments other than 'simple' gaps were small, as may be seen from Table 5.5. In most cases this reflects the small number of seedlings which colonized these gaps in the early phases of the experiment.

SEEDLING MORTALITY OVER THE PERIOD OF THE EXPERIMENT

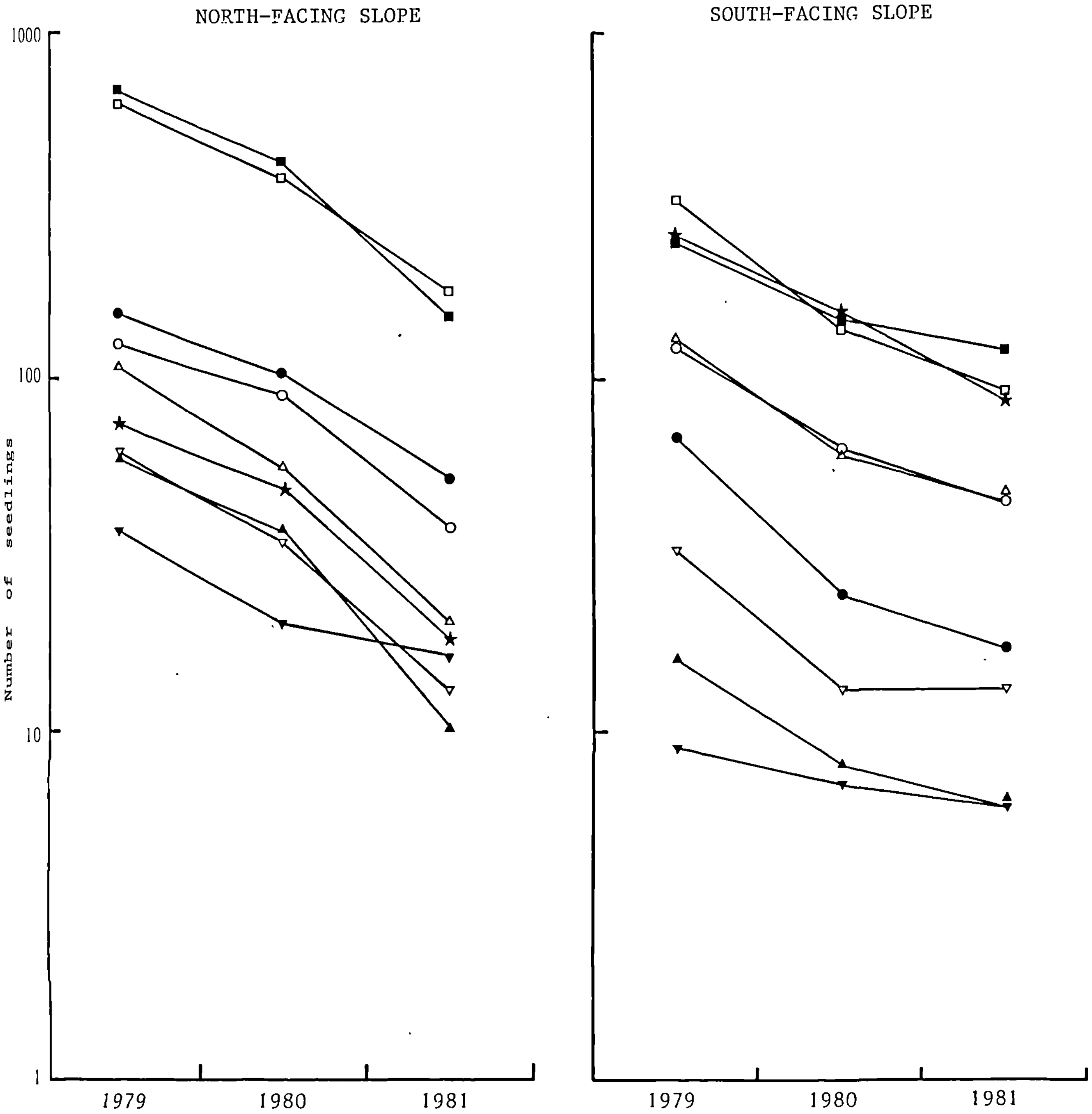
(a) Rates of loss in different treatments

Survival curves for seedlings of perennial species in 40 cm diameter gaps and 20 cm diameter gaps, hills and scrapes, on both slopes, are presented in Fig. 5.1. Data for autumn gaps and controls are derived from seedling numbers present in 1979 regardless of season of germination. It is clear from these curves and Fig.5.9 that patterns of mortality on the north-facing slope differed from those on the south-facing slope in three important respects:

(1) The proportion of seedlings surviving in all comparable treatments was higher on the south-facing slope with the exception of spring-cut 20 cm gaps.

(2) In gaps but not controls the risk of mortality on the south-facing slope was much higher between 1979 and 1980 than between 1980 and 1981. In all treatments on the north-facing slope, the risk of mortality was slightly higher in the latter period.

Figure 5.1 Survival curves for seedlings of perennial species in:
□ autumn-cut 40 cm diameter gaps; ■ spring-cut 40 cm diameter gaps
○ " " 20 cm " " ; ● " " 20 cm " "
△ " " 20 cm " scrapes; ▲ " " 20 cm " scrapes
▽ " " 20 cm " hills; ▼ " " 20 cm " hills
* controls



(3) On the north-facing slope, with the exception of spring 20 cm diameter hills, gap season of origin did not appear to influence rates of loss of seedlings. On the south-facing slope survival was generally higher in spring treatments. This pattern was not observed, however, in the 20 cm diameter gaps.

(b) Rates of loss in cohorts of different age

In autumn-cut gaps on the north-facing slope mortality in two cohorts of seedlings (one from the autumn flush of germination and one from the spring flush) was examined separately. Survival curves for the autumn cohort and spring cohort in autumn-cut gaps are plotted separately in Fig.5.2 for 40 cm diameter gaps and 20 cm diameter gaps, hills and scrapes. Curves for the spring cohort in spring-cut gaps of similar type are included for comparison.

With the exception of the hills, gap season of origin made no difference to the patterns of mortality experienced in spring cohorts. In all treatments considered the proportion of the autumn cohort alive at the end of the experiment was smaller than the proportion remaining in the spring cohort. This difference became most marked in hills and scrapes. Since the autumn cohort contained fewer seedlings originally, the proportion surviving represents a very small number of seedlings. Rates of loss from the autumn cohort accelerated between 1980 and 1981 in all except 40 cm diameter gaps.

(c) Rates of loss in different species

Survival curves for eight species from the north-facing slope and six species from the south- are plotted in Figs. 5.3 and 5.4. It is clear from Fig.5.4 that seedlings on the south-facing slope in all species considered, suffered heaviest mortalities during the period

Figure 5.2 Survival of seedlings from autumn and spring cohorts in a variety of treatments on the north-facing slope.

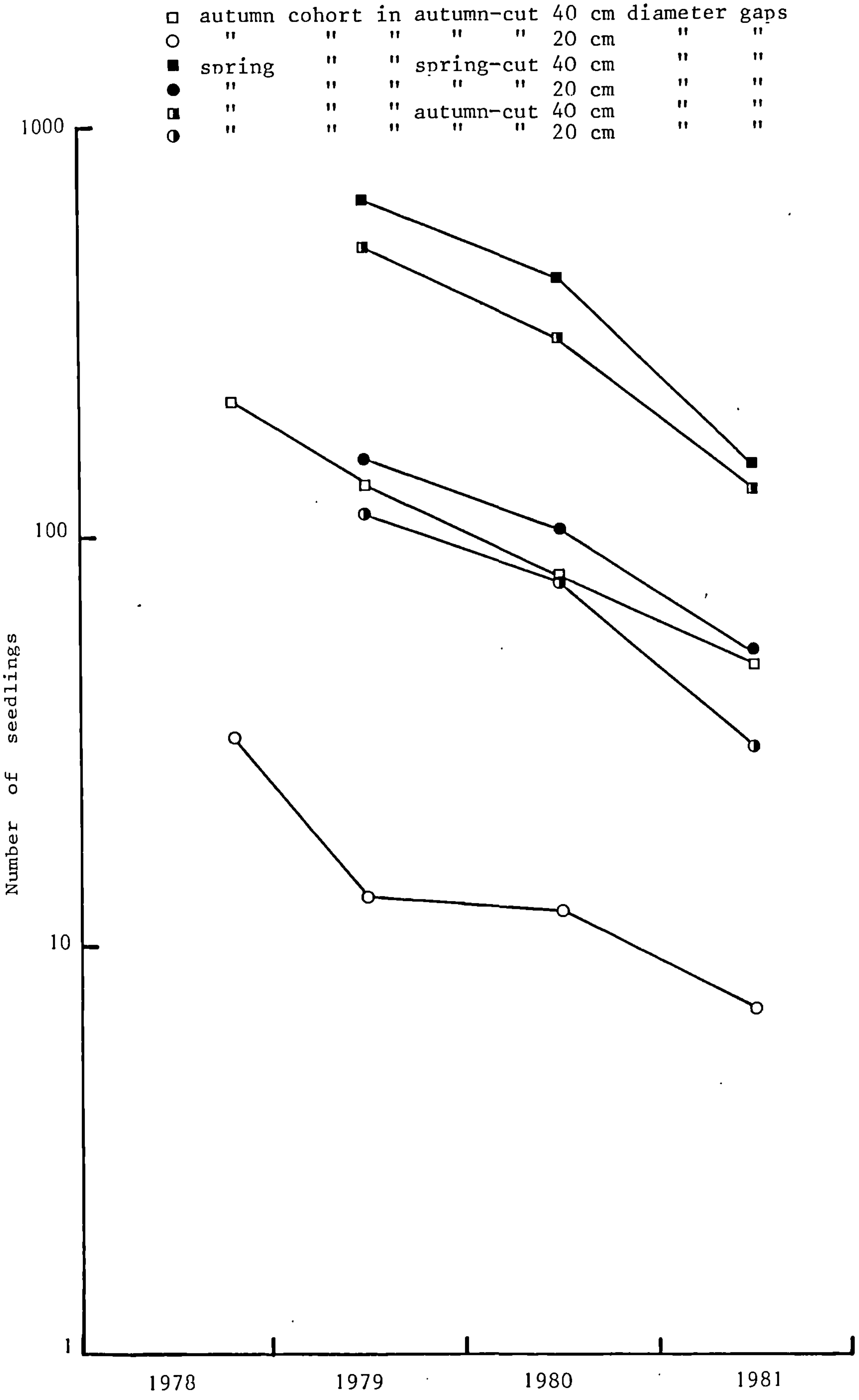
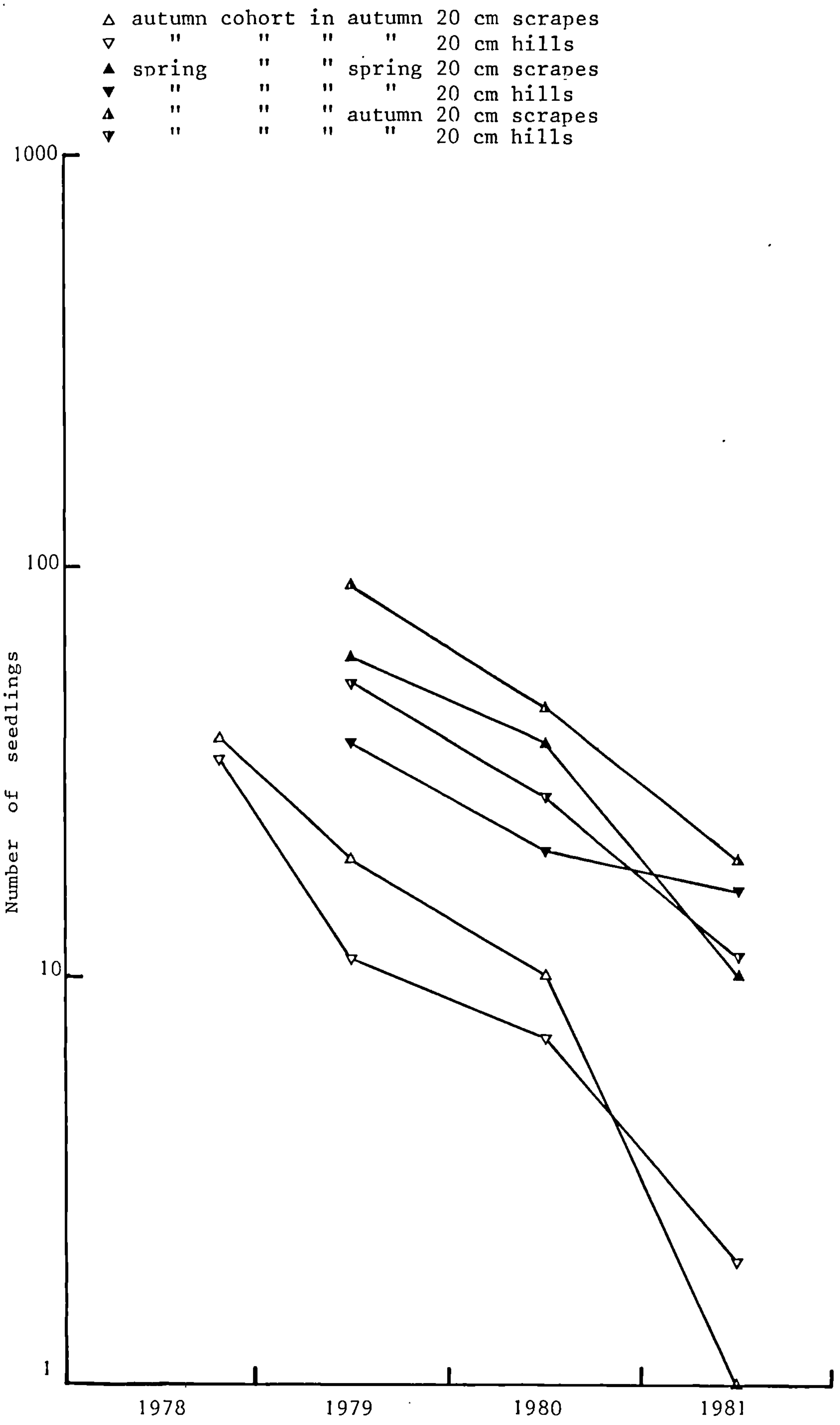


Figure 5.2 (contd.)



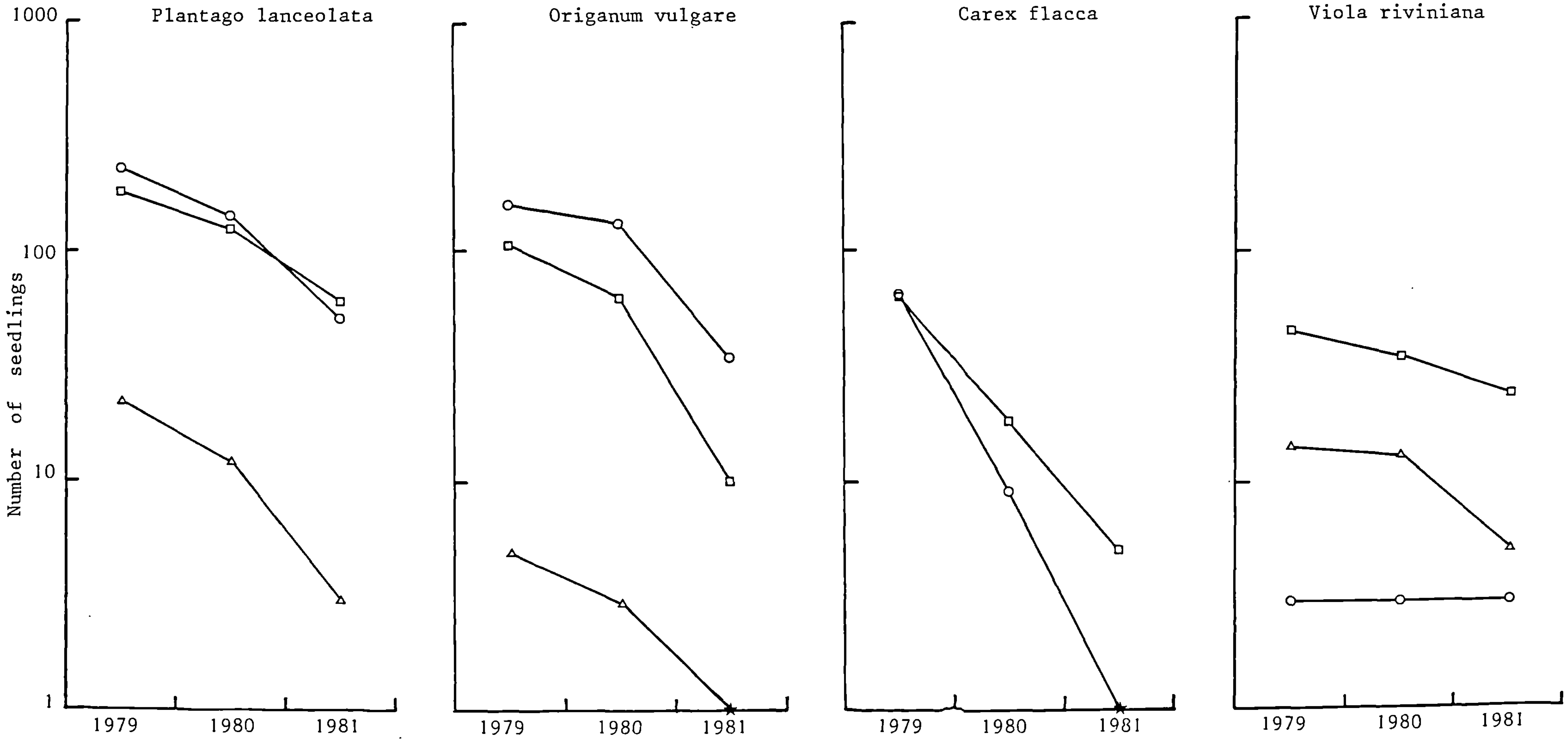
1979 to 1980. The survival curves for seedlings of Festuca ovina and Thymus praecox in gaps, are remarkably similar, as are those for Koeleria macrantha and Lotus corniculatus. Approximately 25% of the initial seedling total for the first three species and also C. rotundifolia, was surviving at the end of the experiment. Seedling totals of Lotus corniculatus were depleted most severely during the period 1979-1980 but over 40% survived to 1981. Pimpinella saxifraga seedlings suffered least mortalities and over 50% of the initial total survived in both spring- and autumn-cut gaps. Seedling losses of F. ovina and P. saxifraga in controls, mirrored closely the pattern for gaps, but survival of K. macrantha seedlings was slightly greater in controls where lower levels of mortality were experienced in the period 1979-1980.

On the north-facing slope, seedling mortality patterns differed in the eight species considered (Fig.5.3). There were differences in the percentage of initial total surviving, and also in the period during which heaviest losses occurred. With the exception of Carex flacca and Agrostis capillaris, rates of seedling loss were greater during the period 1980-1981 than 1979-1980. Seedlings of Origanum vulgare suffered particularly between 1980 and 1981, but the difference between years was less marked amongst seedlings of Plantago lanceolata, Campanula rotundifolia, Centaurea nigra and Viola riviniana. Mortality patterns were similar in autumn- and spring-cut gaps for seedlings of all species considered, with the exception of C. flacca and H. lanatus. In these latter species a slightly higher proportion survived in autumn-cut gaps. Even though seedling numbers in undisturbed vegetation were considerably lower than in gaps, patterns of mortality mirrored those observed in gaps.

Figure 5.3 Survival curves for seedlings of eight species occurring in 40 cm diameter gaps and controls on the north-facing slope.

□ autumn-cut gaps ○ spring-cut gaps △ controls (undisturbed vegetation)

* number of seedlings surviving = 0



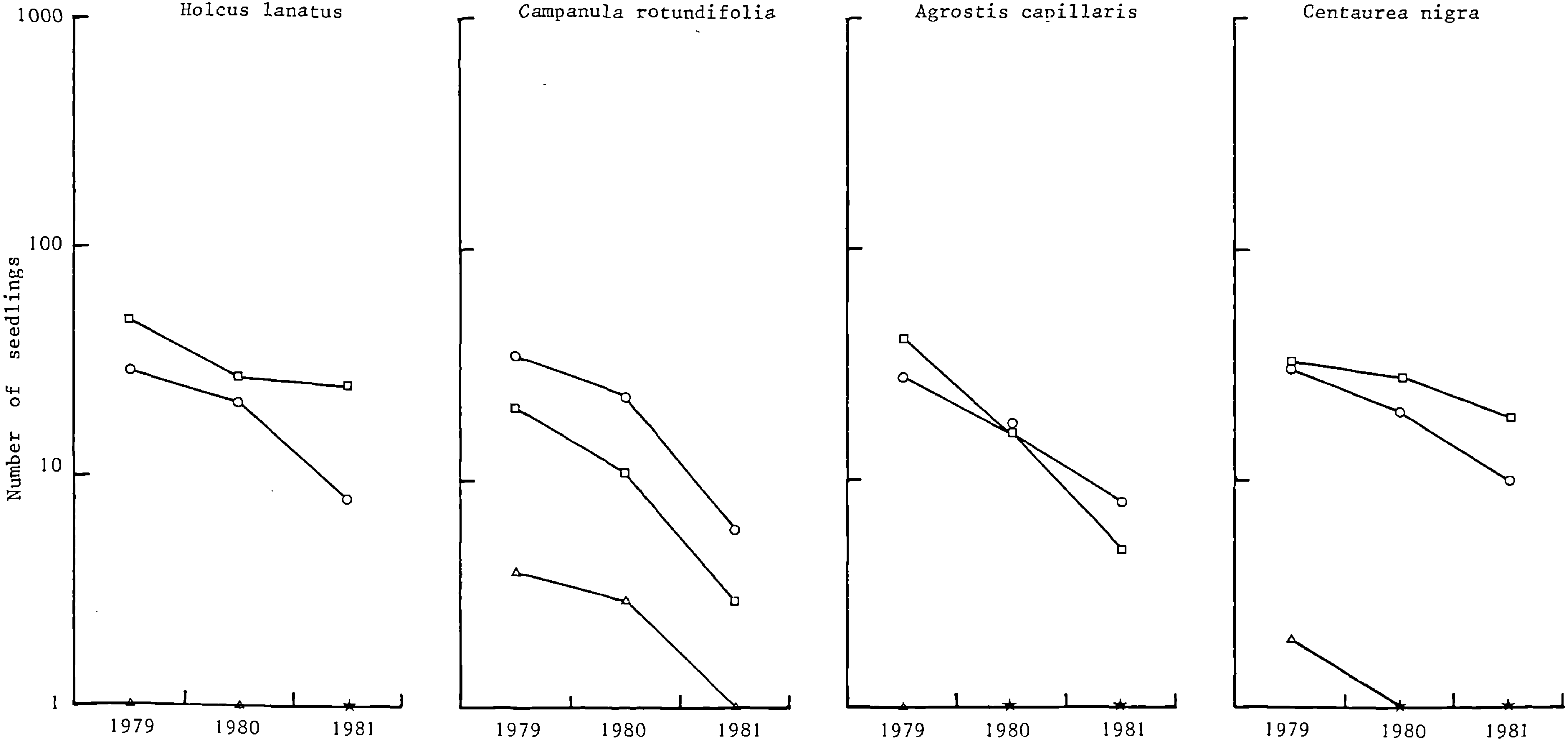


Figure 5.3 (contd.)

Figure 5.4 Survival curves for seedlings of six species occurring in 40 cm diameter gaps and controls on the south-facing slope

□ autumn-cut gaps ○ spring-cut gaps △ controls (undisturbed vegetation)

* number of seedlings surviving = 0

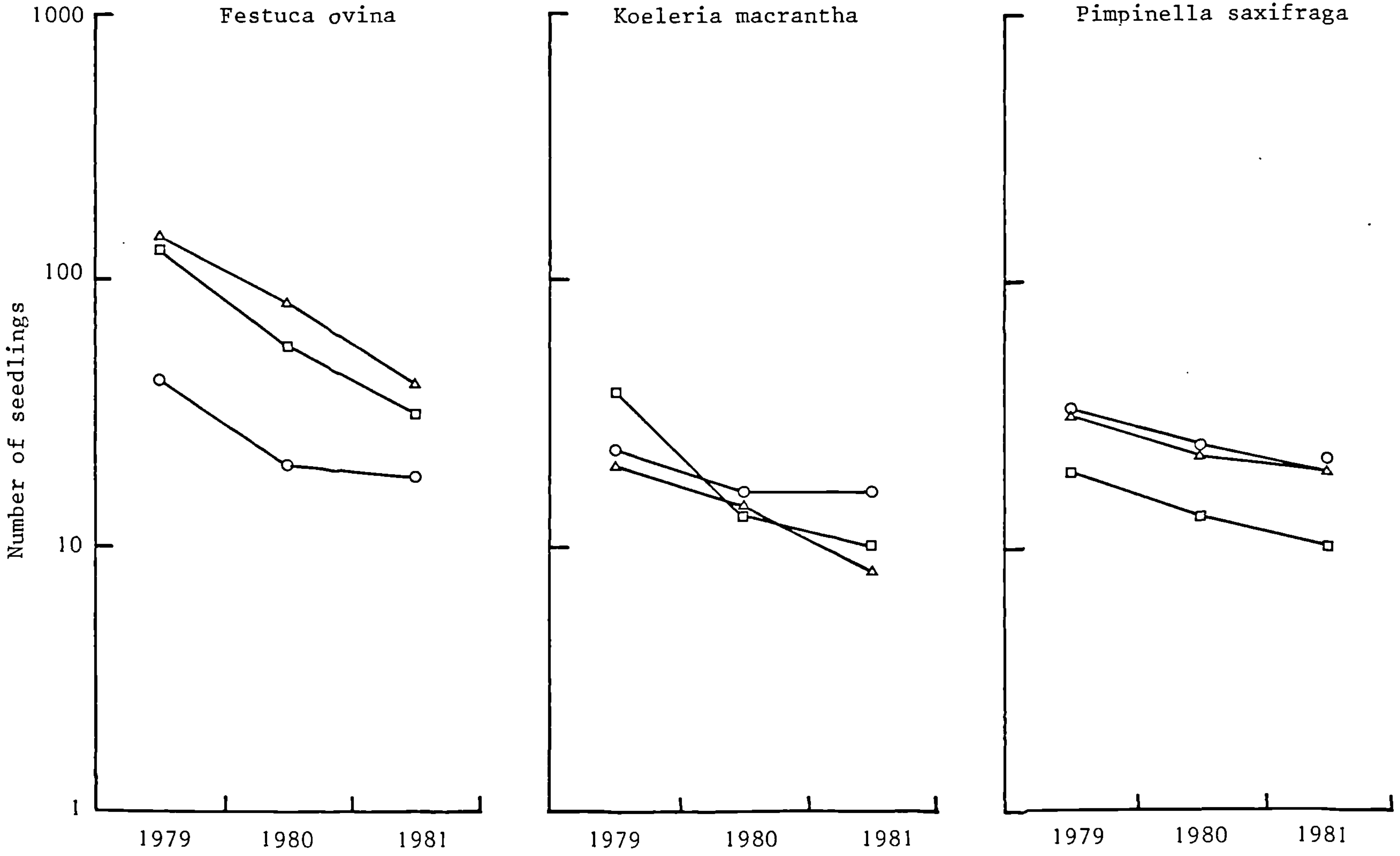


Figure 5.4 (contd.)

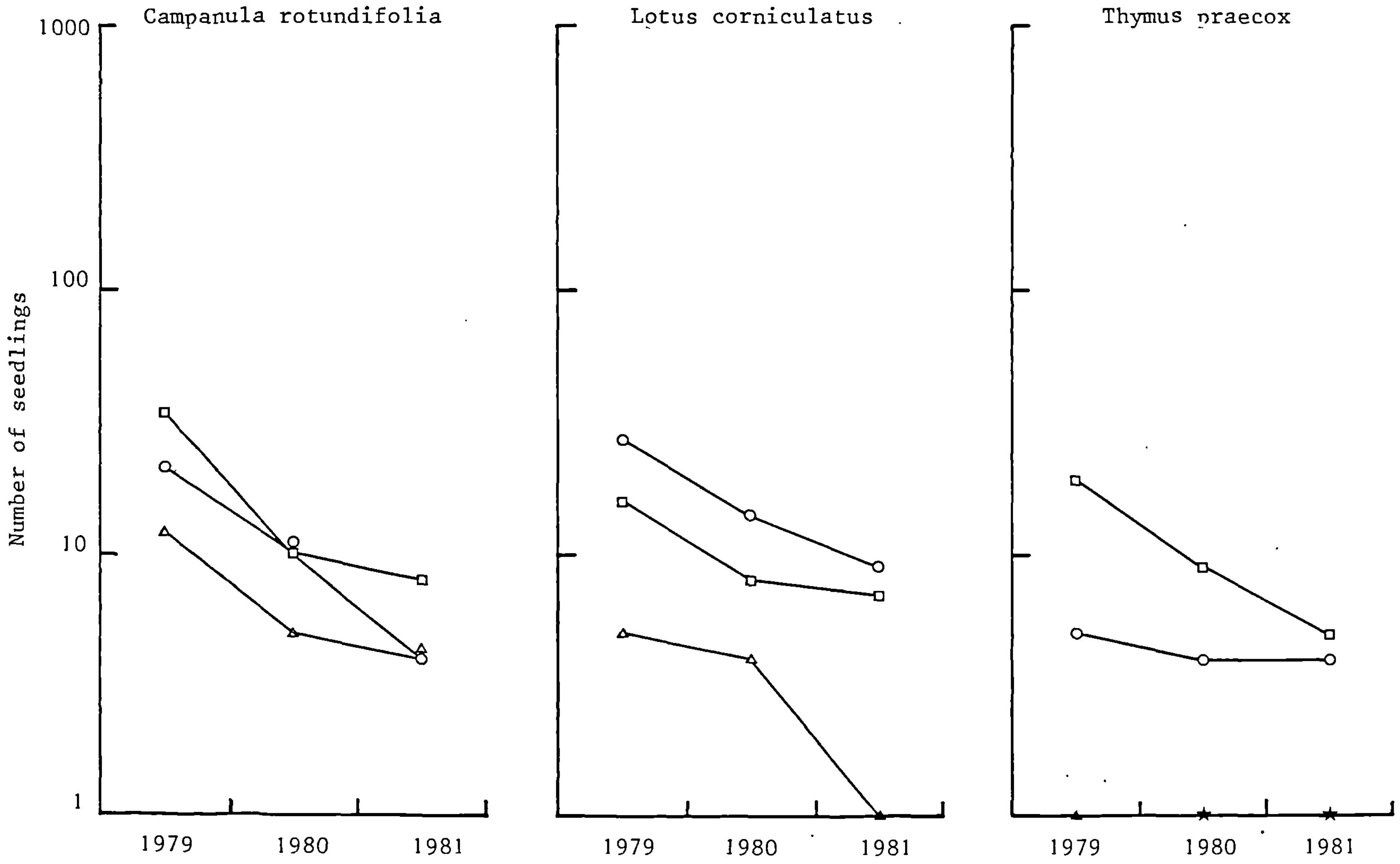
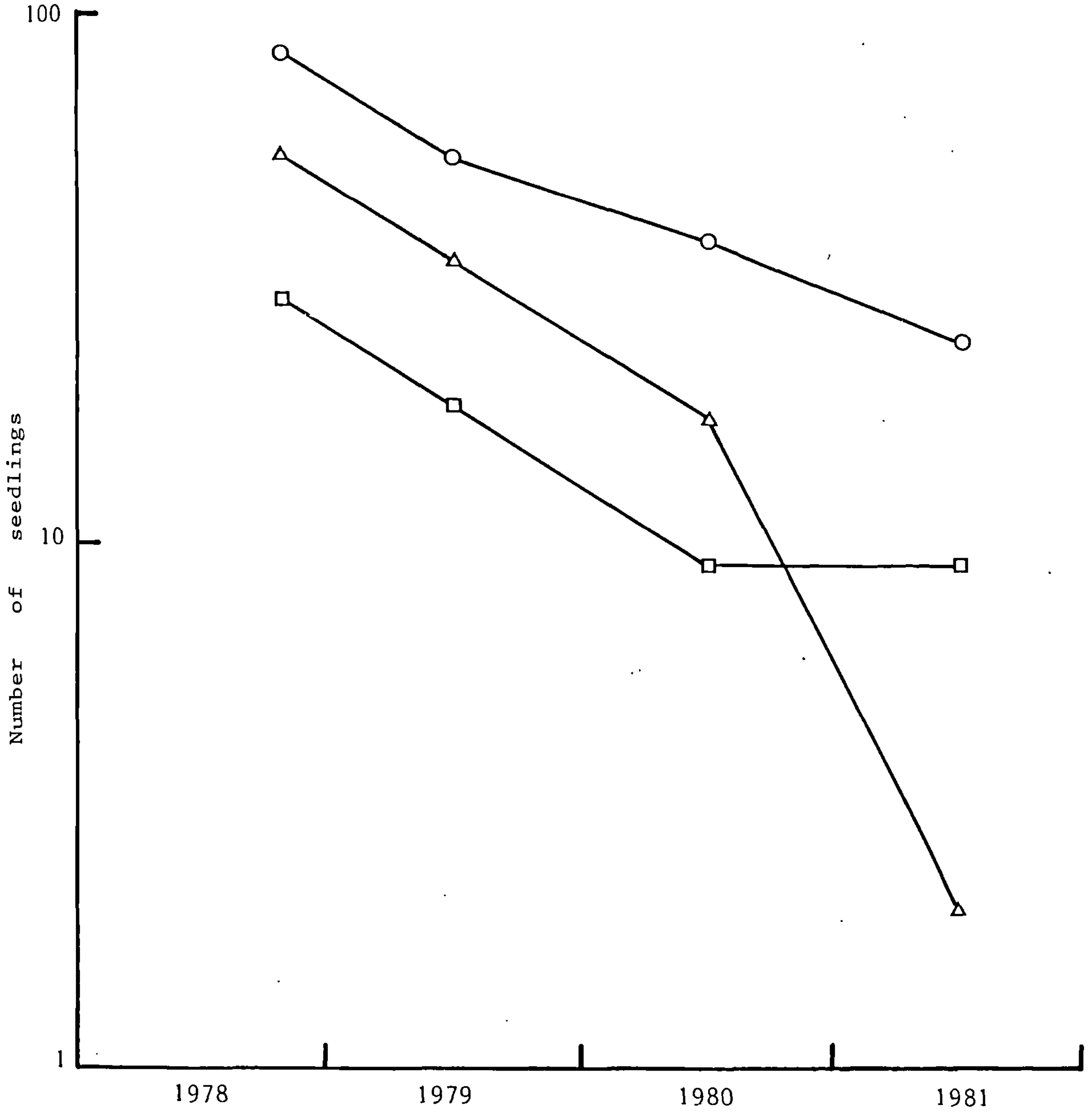


Figure 5.5 Survival curves for the autumn cohort of seedlings of three species occurring in autumn-cut gaps.

○ Plantago lanceolata

△ Origanum vulgare

□ Holcus lanatus



Survival curves for the autumn cohorts of Holcus lanatus, Origanum vulgare and Plantago lanceolata are plotted separately in Fig.5.5. A striking feature of these graphs is the similar patterns of mortality experienced by all three species over the first 18 months of the experiment. By 1981 losses of H. lanatus seedlings showed signs of stabilization in contrast to O. vulgare, which suffered greatly increased mortalities between 1980 and 1981. Over the period of the investigation, P. lanceolata was distinctive in the continuously low levels of mortality experienced by seedlings.

SEEDLING YIELD

The total dry weight of seedlings from the marked cohorts varied considerably from one replicate to another (Fig.5.6). On the north-facing slope, larger gaps and scrapes contained the greatest quantities per unit area of seedling material but on the south-facing slope relationships between gap size and total seedling shoot dry weight were less clear. The largest autumn-cut gaps supported more seedling material than smaller gap sizes and there was some indication of an inverse relationship between scrape size and seedling yield, but such trends were less easy to identify for spring-cut gaps.

Mean seedling dry weights calculated for a variety of gap types revealed considerable variability in the data (Table 5.6). This phenomenon was investigated further by consideration of the distribution of seedling dry weights in 40 cm diameter gaps and controls on both slopes. The results are presented graphically in Fig.5.7. Totals for autumn gaps and controls include seedlings surviving from

Fig. 5.6 Relationships between size of gap and quantities of seedling material.

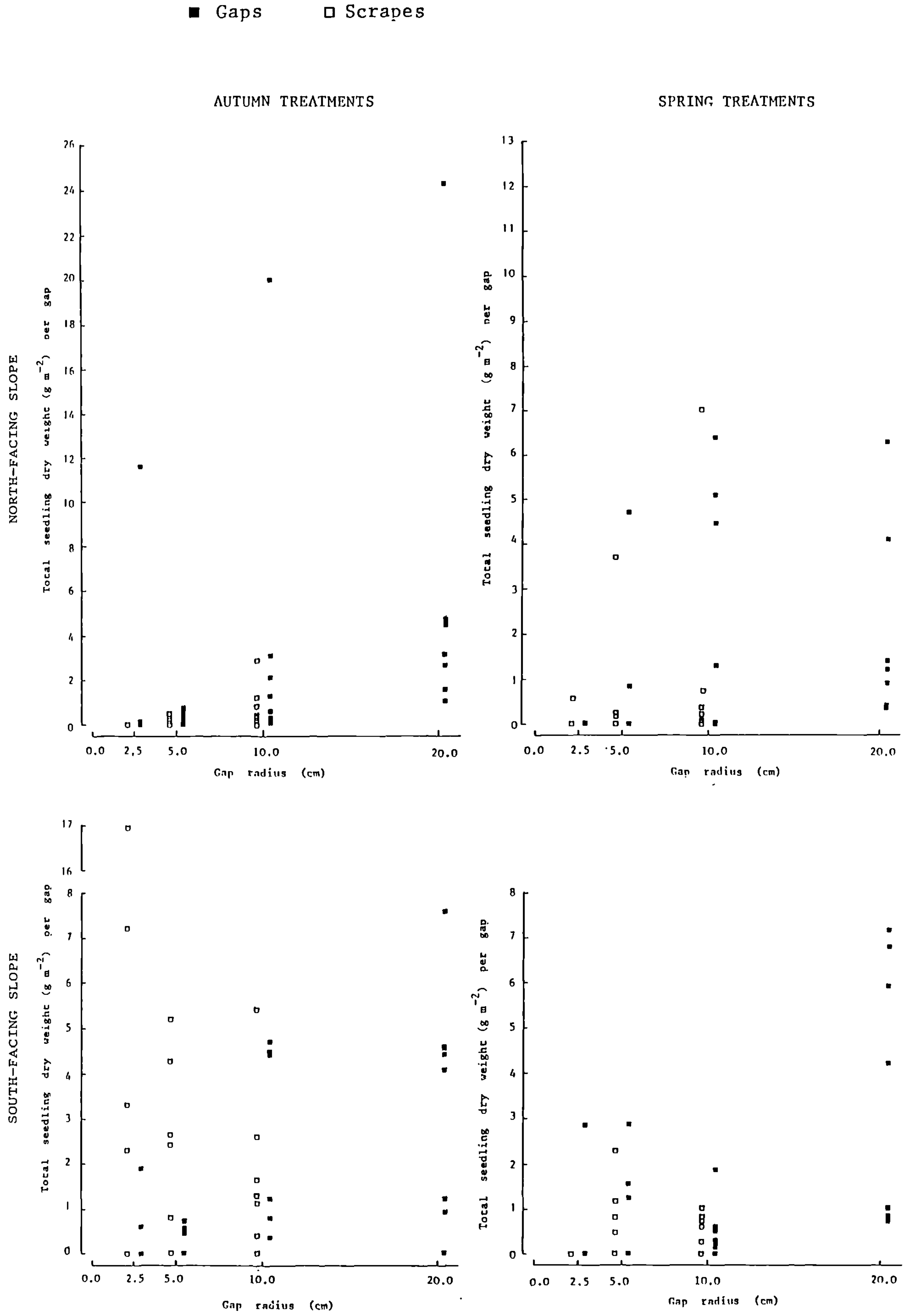


Table 5.6

Mean shoot dry weight (mg) of seedlings of all species in different gap types.

	Treatment*	C	A40G	A20G	A20H	A20S	S40G	S20G	S20H	S20S
	n	19	170	37	14	20	148	52	16	10
North-facing slope	mean dry weight	12.28	28.89	27.35	16.78	9.32	12.51	19.22	28.30	26.78
	95% confidence limits	6.87	8.46	16.81	15.74	3.62	3.59	6.30	20.28	49.06
	n	84	91	45	13	44	117	17	6	6
South-facing slope	mean dry weight	11.10	31.99	11.29	6.48	8.96	50.27	6.71	16.18	18.08
	95% confidence limits	3.24	13.94	5.60	3.57	6.35	9.21	3.30	10.87	8.69

* codes as in Table 2.1.

both the autumn and spring cohorts. The distribution of seedling dry weight in these two cohorts is shown separately in Fig.5.8 for autumn-cut 40 cm diameter gaps on the north-facing slope.

It is clear from these figures that on the north-facing slope, autumn-cut gaps contained the largest seedlings, while spring-cut gaps contained seedlings comparable in size with the few which survived in undisturbed turf. The greater seedling dry weights in autumn-cut gaps were not entirely attributable to survivors from the autumn cohort which were undoubtedly the largest seedlings overall on the north-facing slope (Fig. 5.8). The range of sizes attained by seedlings in the spring cohort in autumn-cut gaps was much greater than for seedlings of similar age in spring-cut gaps. In consequence, mean seedling dry weight for the former was almost exactly twice as large as that for the latter.

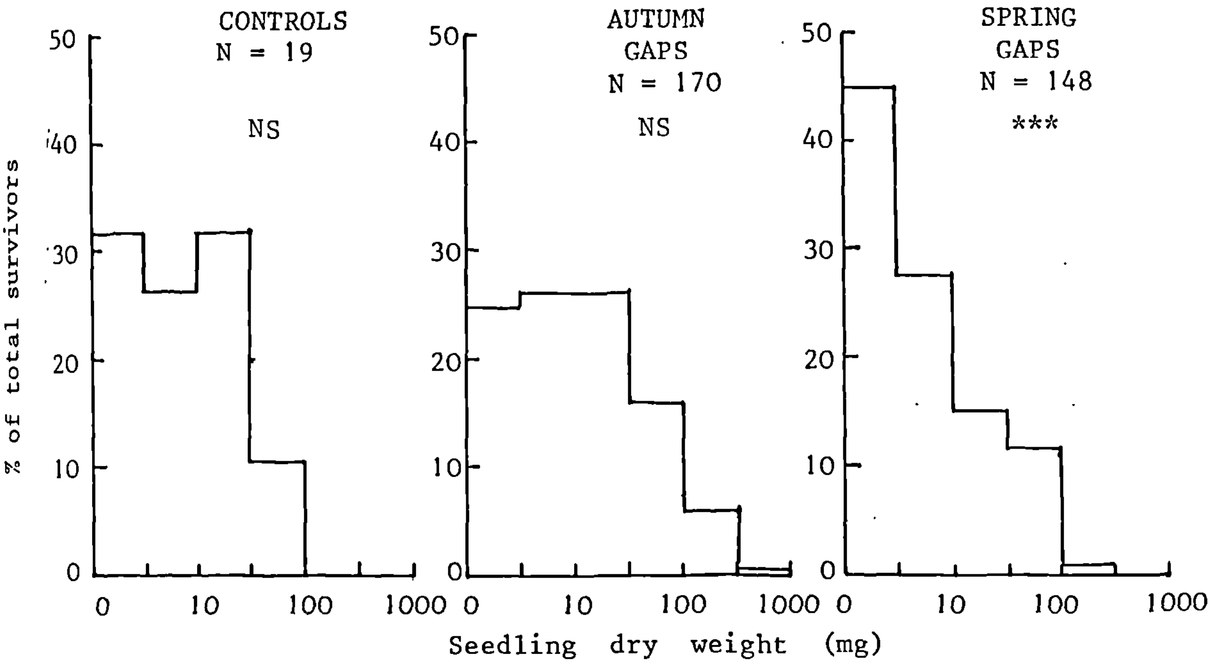
On the south-facing slope seedlings were also smaller in controls than in gaps. However, at this site there was little difference between autumn- and spring-cut gaps with respect to the dry weight of seedlings surviving in them.

The great range of seedling dry weights in these treatments was due in part to differences between species. However, the sizes attained by marked seedlings differed enormously within species also. Representative oven-dried specimens from both sites are shown in Plate 5 and the smallest and largest shoot dry weights recorded for a number of species are documented in Table 5.7.

Fig. 5.7 Frequency distributions of seedling dry weights in autumn- and spring-cut gaps of 40 cm diameter and controls on the north- and south-facing slopes.

Significance levels (Chi-square) refer to comparisons between number of seedlings <10 mg and number >10 mg. NS Not significant; *** significant P<0.001.

NORTH-FACING SLOPE



SOUTH-FACING SLOPE

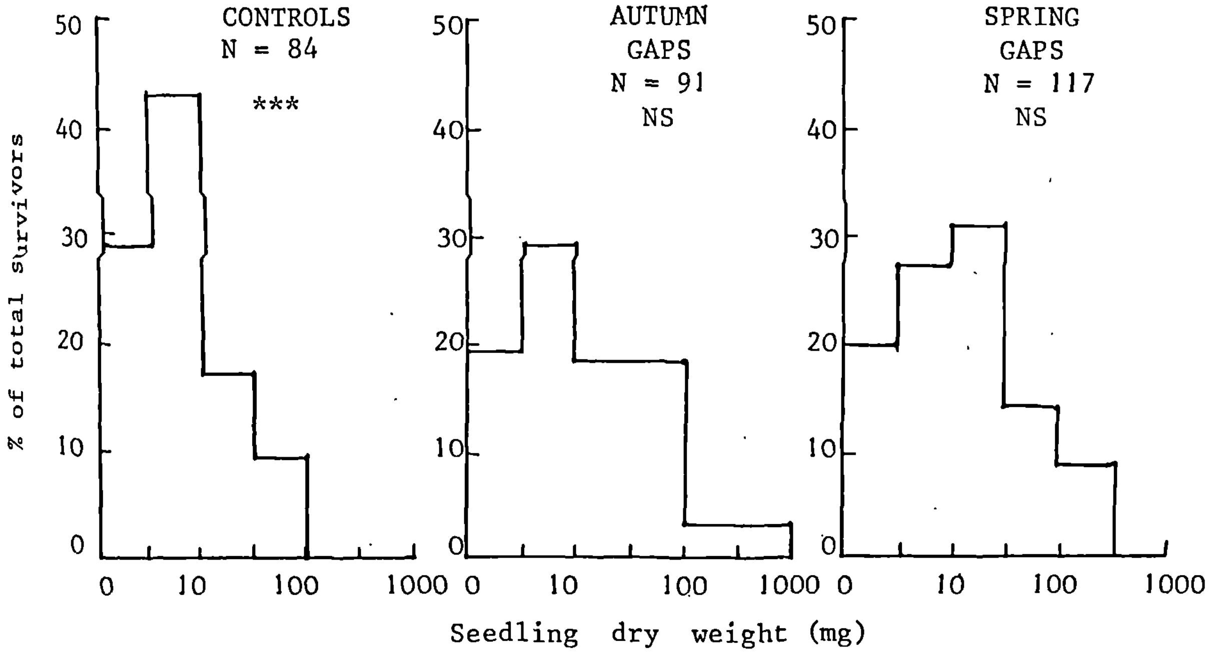


Fig. 5.8 Frequency distributions of seedling dry weights in the autumn and spring cohorts in autumn-cut 40 cm diameter gaps on the north-facing slope.

Significance levels (Chi-square) refer to comparisons between number of seedlings <10 mg and number >10 mg. NS Not significant; ** significant P<0.01.

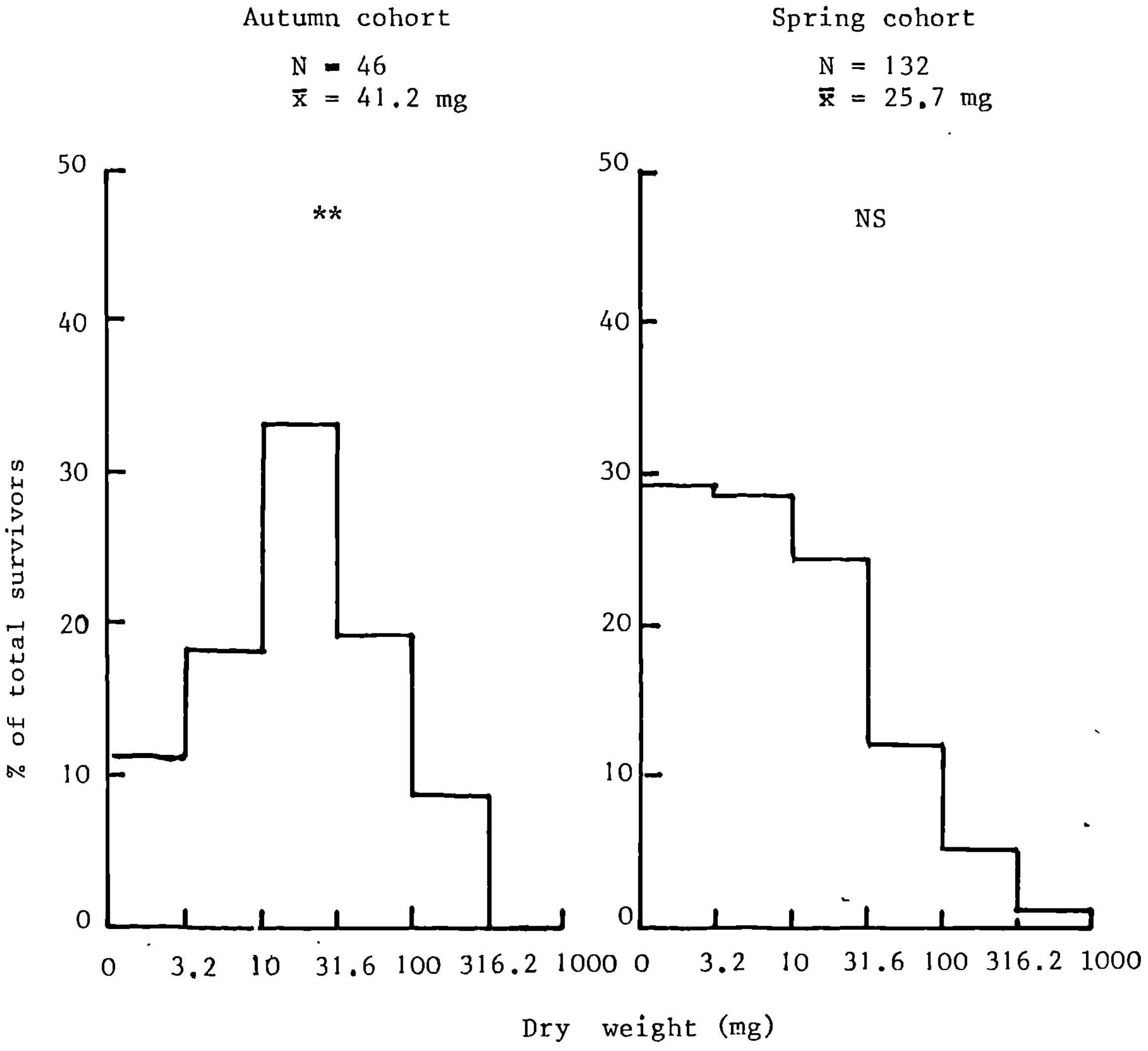


Table 5.7

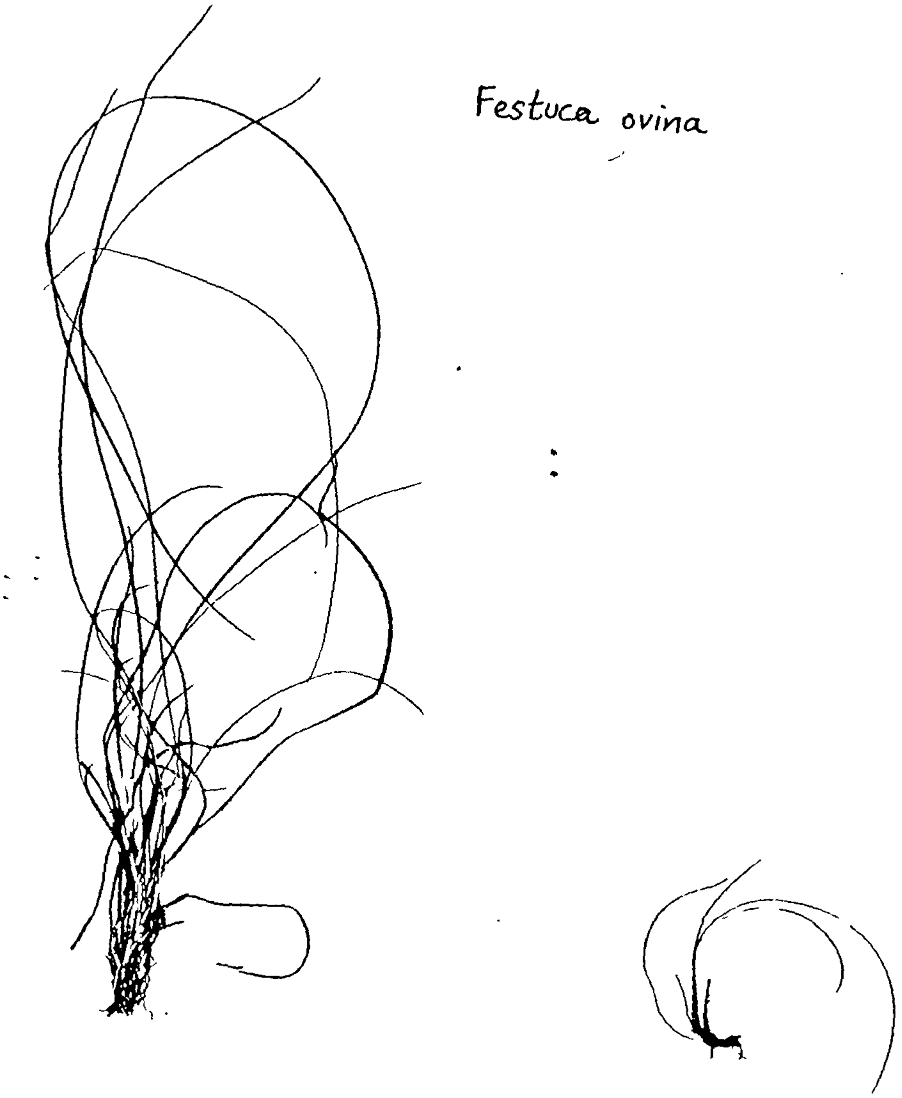
Smallest and largest shoot dry weights (mg) of seedlings of a variety of species harvested in 1981 from autumn-cut 40 cm diameter gaps.

	Shoot dry weight (mg)	
	smallest	largest
Holcus lanatus	1.1	455.5
Plantago lanceolata	1.9	235.7
Viola riviniana	1.6	28.8
Centaurea nigra	0.9	143.1
Festuca ovina	1.0	204.2
Koeleria macrantha	0.7	47.7
Pimpinella saxifraga	1.4	68.4
Lotus corniculatus	5.5	143.6

Plate 5 Representative oven-dried specimens of seedlings of *Holcus lanatus* and *Plantago lanceolata* harvested from spring 40 cm diameter gaps on the north-facing slope and *Festuca ovina* and *Pimpinella saxifraga* harvested from autumn and spring 40 cm diameter gaps respectively on the south-facing slope. All seedlings are comparable in age.

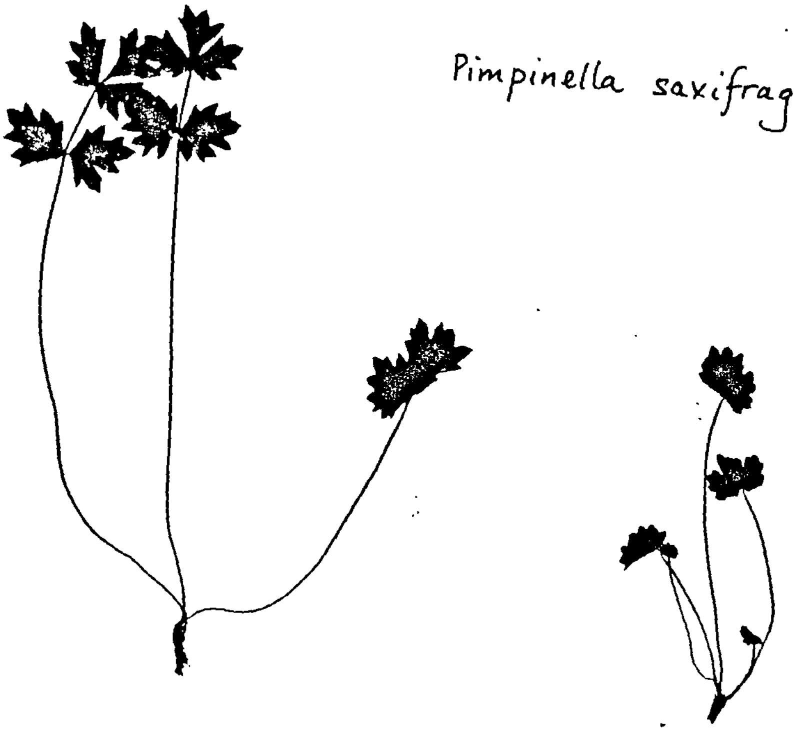
Holcus lanatus

Plantago lanceolata



Festuca ovina

1cm



Pimpinella saxifraga

RELATIONSHIPS BETWEEN PERCENTAGE SURVIVAL AND YIELD

There was no general relationship between the proportion of early colonists surviving in gaps of different character and their dry weight at the end of the experiment (Fig.5.9). Largest mean seedling dry weights tended to be associated with treatments in which large proportions of the seedlings survived on the north-facing slope but on the south-facing slope percentage survival and yield were not correlated.

POSITION IN GAP AS A DETERMINANT OF SURVIVAL

In Chapter 4 it was noted that the distribution of early seedling colonists in 40 cm diameter gaps showed a tendency to concentrate in the centre. Fig.5.10 shows the percentage survival of seedlings across these same gaps. Clearly seedlings survived in approximately equal proportions whatever their distance from the margin of large gaps, on both slopes.

Reference to Fig.5.11 reveals that the concentration of seedlings in downslope quadrants of gaps and scrapes and upslope quadrants of hills observed on the south-facing slope, was maintained over the period of the experiment. A greater proportion of the already larger number of seedlings in downslope quadrants of gaps and scrapes survived until 1981. It is difficult to assess the relative benefits of position on the rim or floor of scrapes, due to the small number of original colonists. On the north-facing slope there was a tendency for the floors of autumn scrapes and the rims of spring scrapes to be the most favourable positions (Fig. 5.12) while on the south-facing slope the reverse situation obtained.

Fig. 5.9 Comparison of seedling survival and mean yield in 40 cm and 20 cm diameter treatments on both slopes. 95% confidence limits for yield means are documented in Table 5.6.

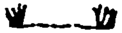
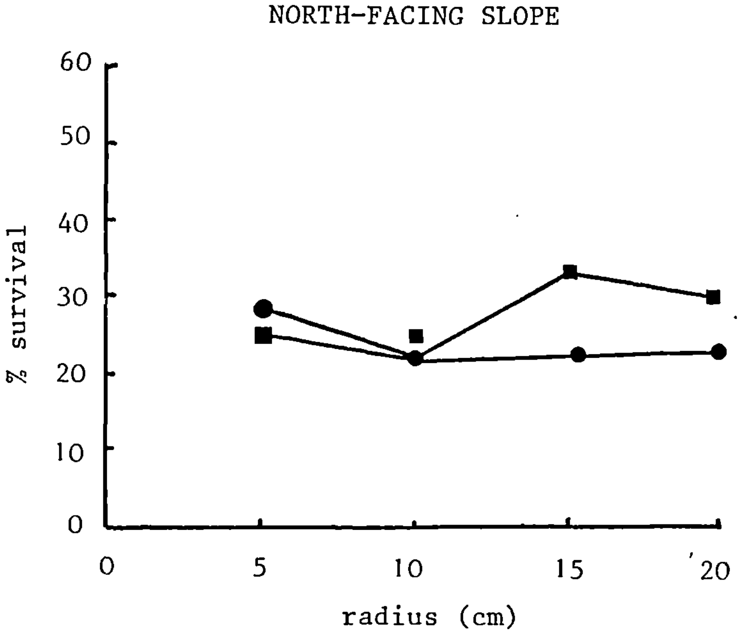
	Spr.	Aut.	Aut.	Spr.	Con.	Aut.	Aut.	Spr.	Spr.	
GAP TYPE										
% survival	13.7	18.3	21.0	21.9	24.3	28.3	29.6	33.3	43.2	North-facing slope
Yield (mg)	26.8	9.3	16.8	12.5	12.3	28.9	27.4	19.2	28.3	
% survival	37.5	36.9	40.6	47.4	33.1	27.1	36.4	25.0	66.7	South-facing slope
Yield (mg)	18.1	9.0	6.5	26.6	11.0	32.3	11.6	6.7	16.2	

Fig. 5.10 The proportion of initial seedling colonists surviving in different parts of autumn (■) and spring (●) 40 cm diameter gaps.



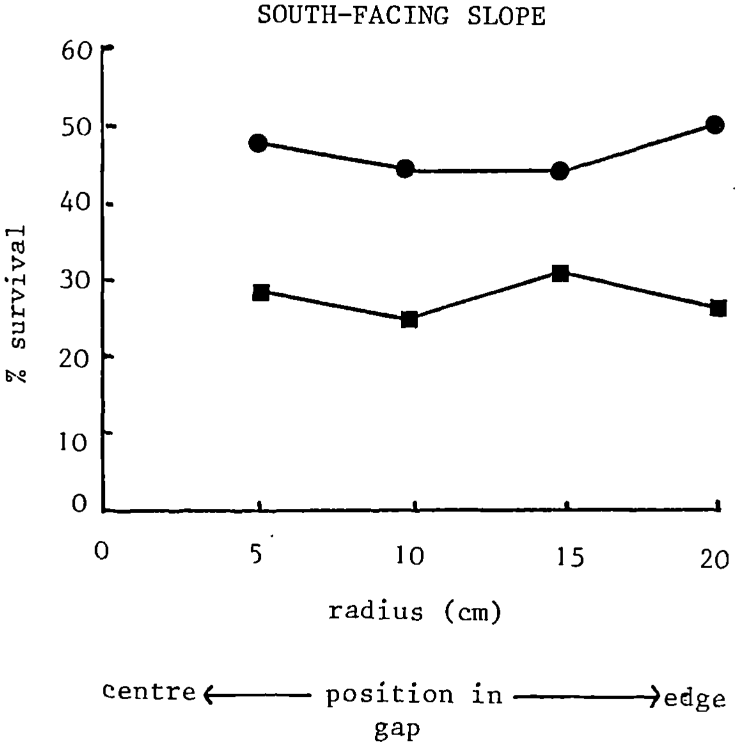


Fig. 5.11 Survival in upslope and downslope quadrants of 20 cm diameter gaps (20G), hills (20H) and scrapes (20S) on the south-facing slope.
The numbers in each quadrant show percentage survival of seedlings of perennial species in each location.

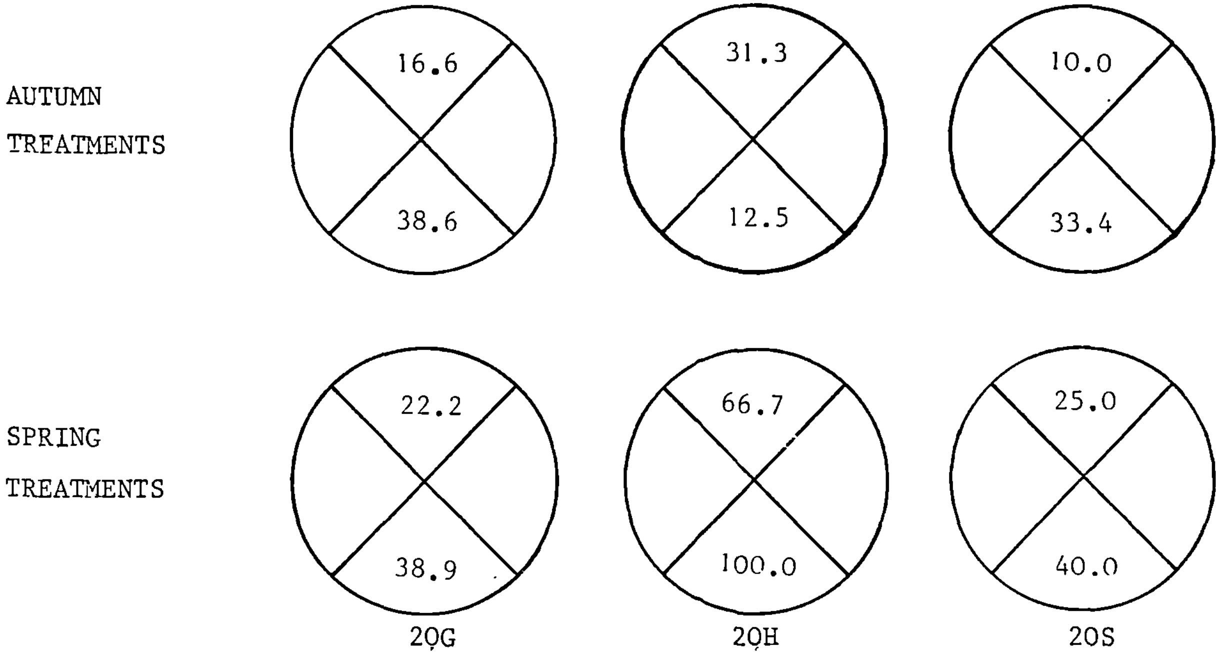
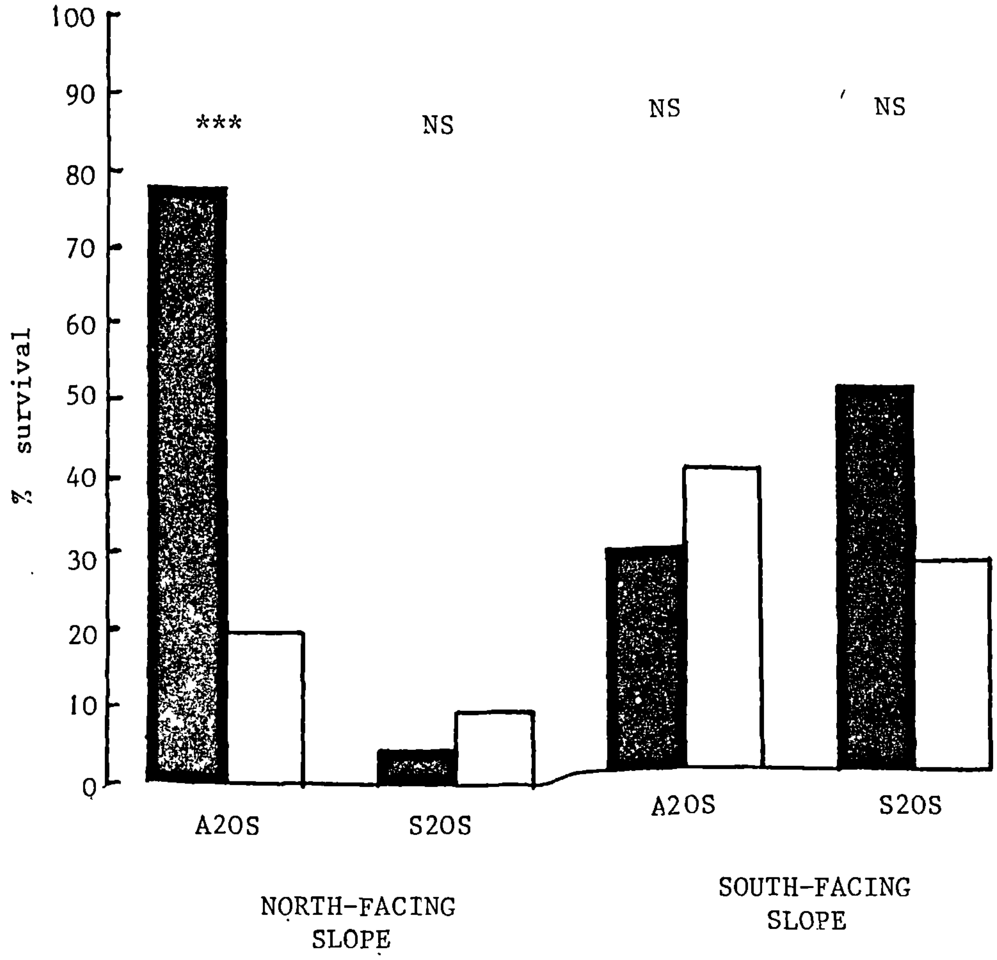


Fig. 5.12 Proportion of seedlings of perennial species surviving on floors and rims of 20 cm diameter scrapes.

■ indicates floor of scrape.

Significance levels (Chi-square) refer to comparisons between alive:dead ratios on floors and rims in each treatment.
NS Not significant; *** significant P<0.001.



PART II : RELATIONSHIPS BETWEEN THE CANOPY, SEEDLING SURVIVAL AND YIELD

PRELIMINARY ANALYSES

Early vegetative recolonization of gaps was recorded by means of photographs taken in 1979 on both slopes (Plate 3). When overlays of seedling colonization and survival were superimposed on these records, differing patterns were observed on each slope.

On the north-facing slope, surviving seedlings appeared to be concentrated in areas of the gap initially free from dense vegetative regrowth (Plate 6). On the south-facing slope, in contrast, initially less dense vegetation seemed to be associated with higher levels of seedling mortality, especially amongst annual forbs (Plate 7).

In order to investigate these patterns in more detail, tracings of early vegetative recolonization in autumn- and spring-cut 40 cm diameter gaps were made from colour slides projected through a photographic enlarger. Representative black and white line drawings produced by this technique for two autumn-cut gaps on the north-facing slope are presented in Figs. 5.13 and 5.14. Reference to the accompanying overlays showing the position of and yield attained by surviving seedlings in these gaps suggested that seedling yield was likely to be greater in gaps which were not rapidly recolonized early in the experiment.

There were thus two hypotheses worthy of further investigation:

(1) that seedling survival was negatively associated with the density of vegetative regrowth on the north-facing slope and positively associated on the south-facing slope;

Plate 6 Seedling positions relative to vegetative regrowth in a representative spring-cut 40 cm diameter gap on the north-facing slope. On the overlay yellow spots represent seedlings which died between 1979 and 1980. Red spots represent seedlings surviving in 1980 but dead by 1981. Green spots represent seedlings surviving in 1981.

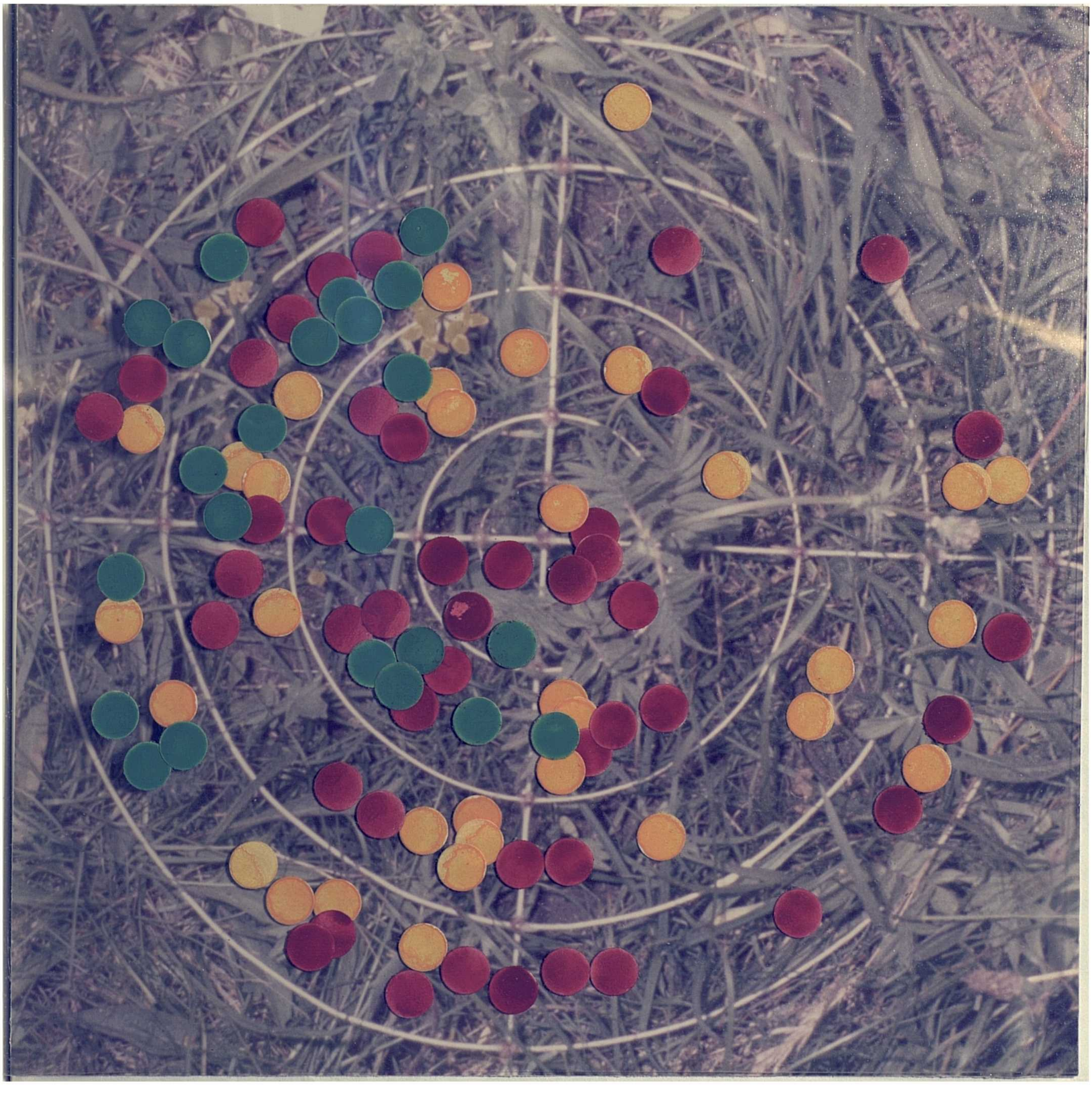
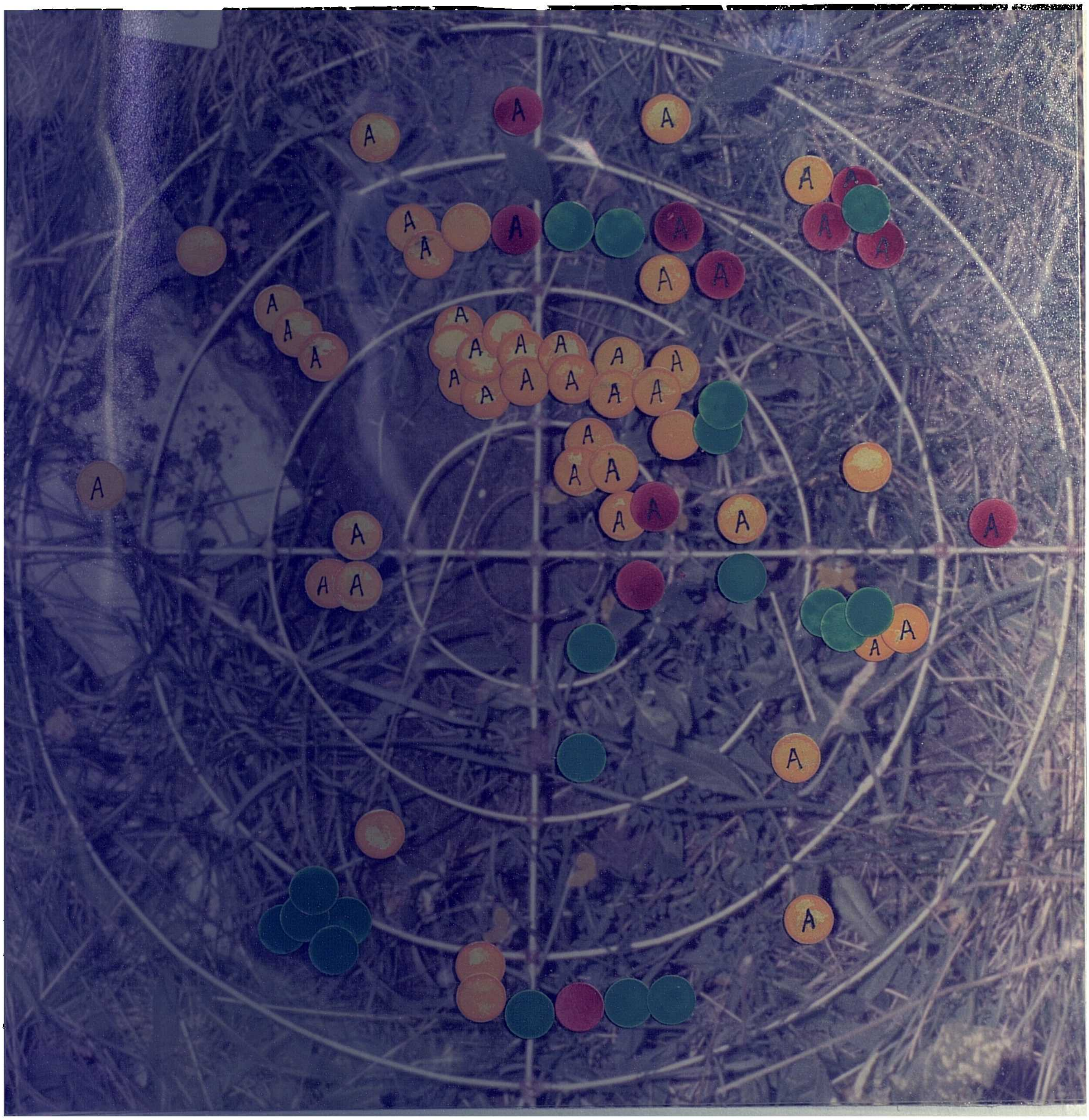


Plate 7 Seedling positions relative to vegetative regrowth in a representative spring-cut 40 cm diameter gap on the south-facing slope. On the overlay yellow spots represent seedlings which died between 1979 and 1980. Red spots represent seedlings surviving in 1980 but dead by 1981. Green spots represent seedlings surviving in 1981. Spots marked A represent the position of seedlings of annual/biennial species.



Figs.5.13 and 5.14 Line drawings produced by the method described on p.95 from colour photographs of early vegetative regrowth.

The overlays show position and yield of surviving seedlings (red spots) and the distribution of seedling mortality with respect to cover (blue crosses).

Key to seedling yield:

○	<1.00 mg
○	1.00 - 3.16 mg
○	3.16 - 10.00 mg
○	10.00 - 31.62 mg
○	31.62 - 100.00 mg
○	100.00 - 316.23 mg

Fig. 5.13

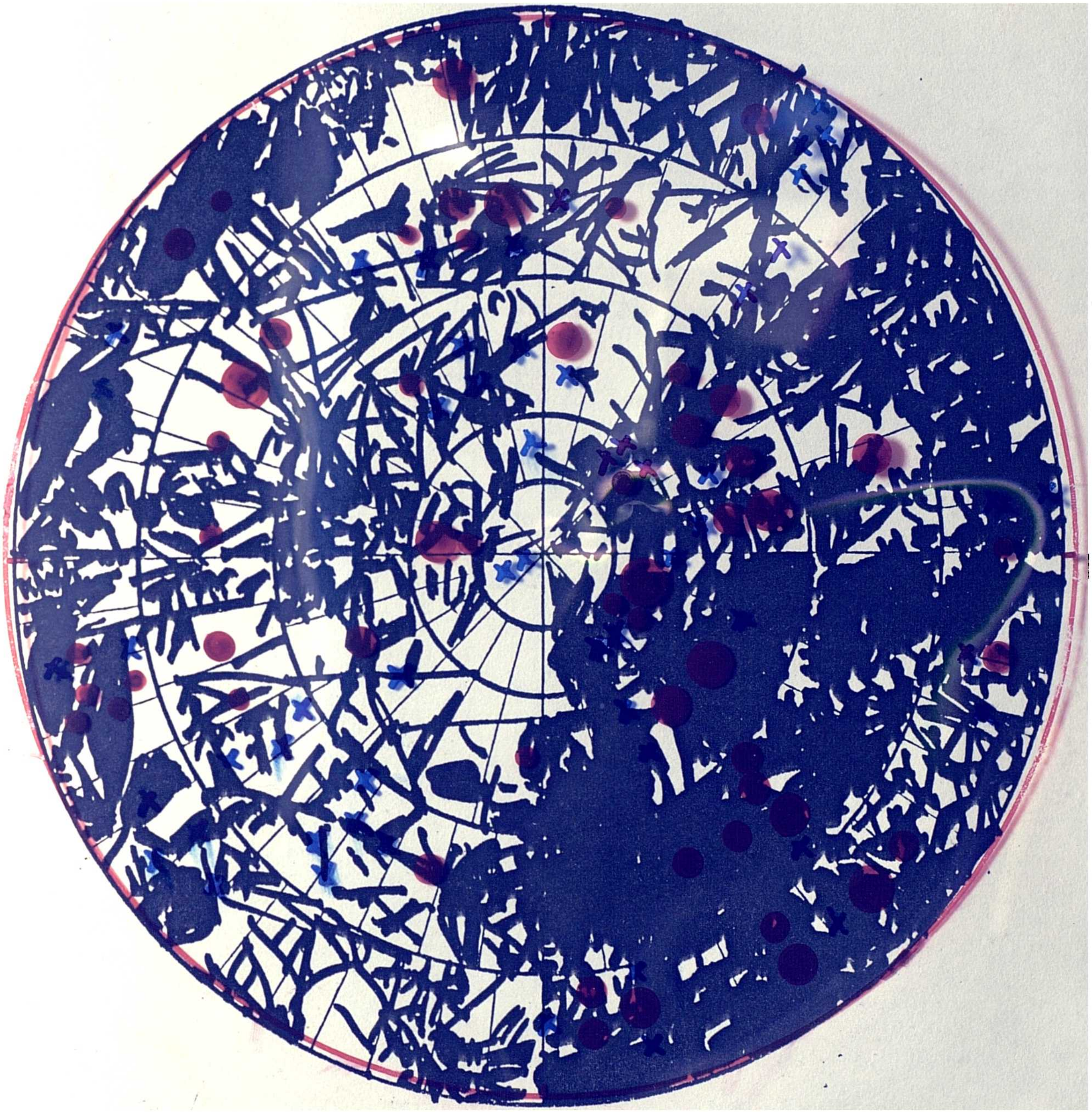
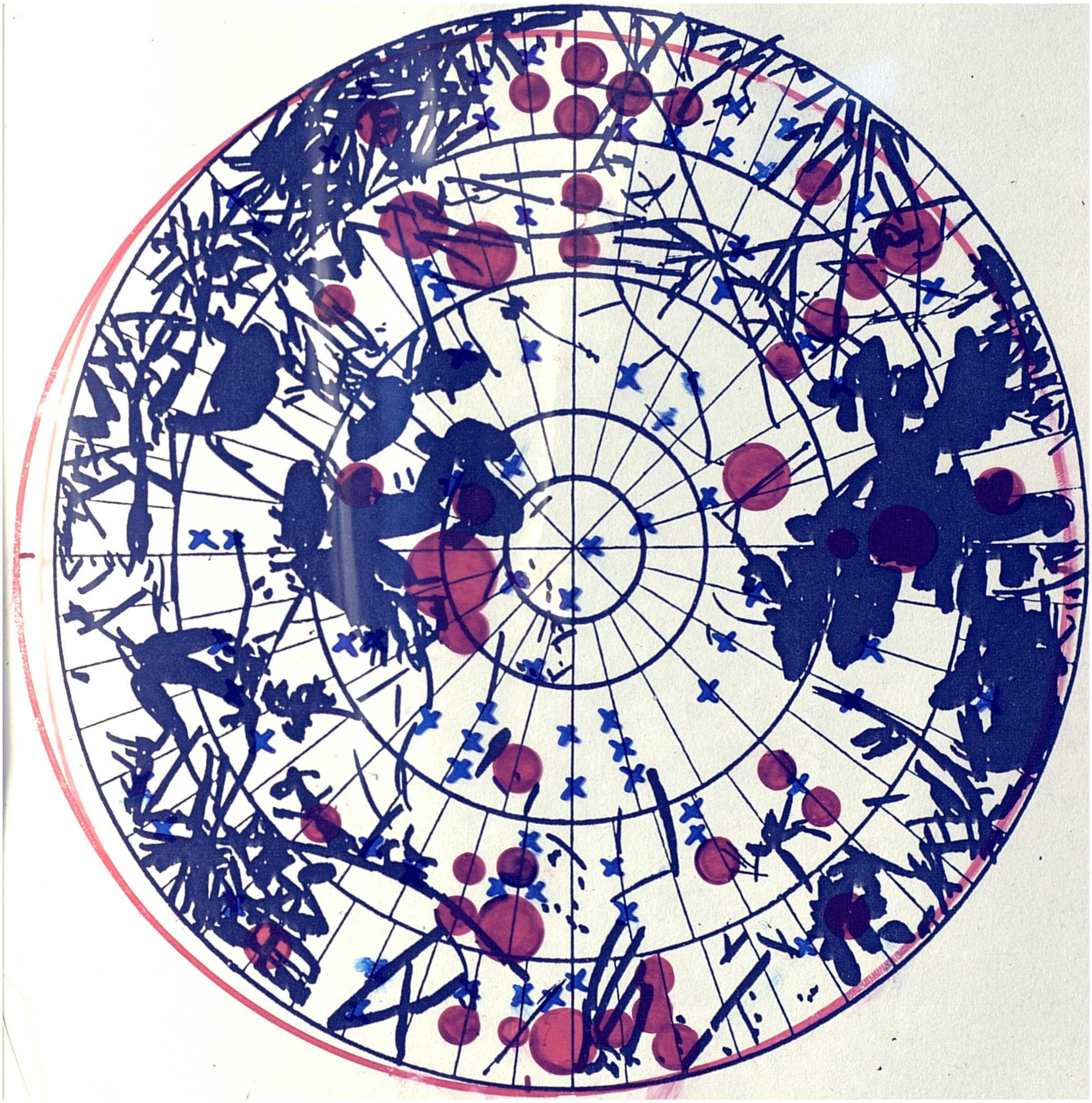


Fig. 5.14



(2) that larger seedling dry weights were attained in areas initially sparsely covered by vegetative regrowth.

These hypotheses were examined firstly in relation to early vegetative regrowth and then with respect to the distribution of dry matter in gaps as determined at the end of the experiment. The analysis was conducted on the 40 cm diameter gaps which provided the large area and numerous seedlings required for adequate statistical tests.

SEEDLING SURVIVAL AND YIELD IN RELATION TO EARLY VEGETATIVE REGROWTH

(a) Estimates of early cover using photographs

Percentage cover of initial vegetative regrowth in each 40 cm gap was assessed by means of point analysis, using the tracings derived from colour photographs in the manner previously described. A small circular cardboard frame was constructed with a central clear plastic area 2 cm in diameter. A regular grid consisting of 25 points 4 mm apart was imprinted into the plastic area using a dressmaker's pin. It was found that a tiny spot of yellow permanent ink applied to each hole greatly facilitated subsequent identification. The tracings were 0.4 times as large as the original gap, thus the 2 cm diameter quadrat corresponded to an 'on site' sampling area 5 cm in diameter.

The number of contacts between yellow spots and traced vegetation was recorded for each of one hundred random positions evenly distributed between the seven replicates of each treatment (see Fig.5.15). For each position, percentage cover was obtained by multiplying the number of contacts by four. From the frequency distribution of cover so obtained, the percentage occurrence of ten

Fig.5.15 Estimating cover using tracings from photographs of vegetative regrowth in gaps.

Tracing showing pattern of vegetative regrowth

Same tracing with circumrat in position

cover classes was obtained for each treatment. Results are shown graphically in Fig.5.16. The higher cover classes were more abundant in spring gaps than in autumn gaps on both slopes. This result was in close agreement with observations on vegetation density made earlier (Chapter 3, p.60) and strongly supported the validity of the technique.

(b) Patterns of germination and survival

In order to assess relationships between seedling position and early cover, the circumrat was used once again. For each subsection of the gap in which a seedling was located, the circumrat was placed with the subsection at its centre and percentage cover was estimated as before by counting contacts with vegetation and multiplying by four. In this way the cover in the area immediately surrounding each seedling was estimated, and frequencies of occurrence of seedlings in each cover class were obtained. Frequencies were then converted to seedling density in each cover class.

Relationships between germination, survival and percentage cover estimated in this way are shown in Fig.5.17. Seedling densities in all treatments are based on numbers present in June 1979. In autumn 40 cm diameter gaps on both slopes,and spring gaps on the north-facing slope, the density of seedlings was greater in the higher cover classes, i.e. seedling densities in 1979 were positively associated with increased cover. In spring gaps on the south-facing slope, although the lower cover classes occurred less frequently, seedling densities were significantly higher in these situations. Relationships between early cover values and eventual seedling survival were less clear. On the north-facing slope in spring gaps, the probability of survival was greater in less dense

Fig.5.16 The distribution of cover classes in autumn- and spring-cut 40 cm diameter gaps, as determined from photographic records of vegetative regrowth.

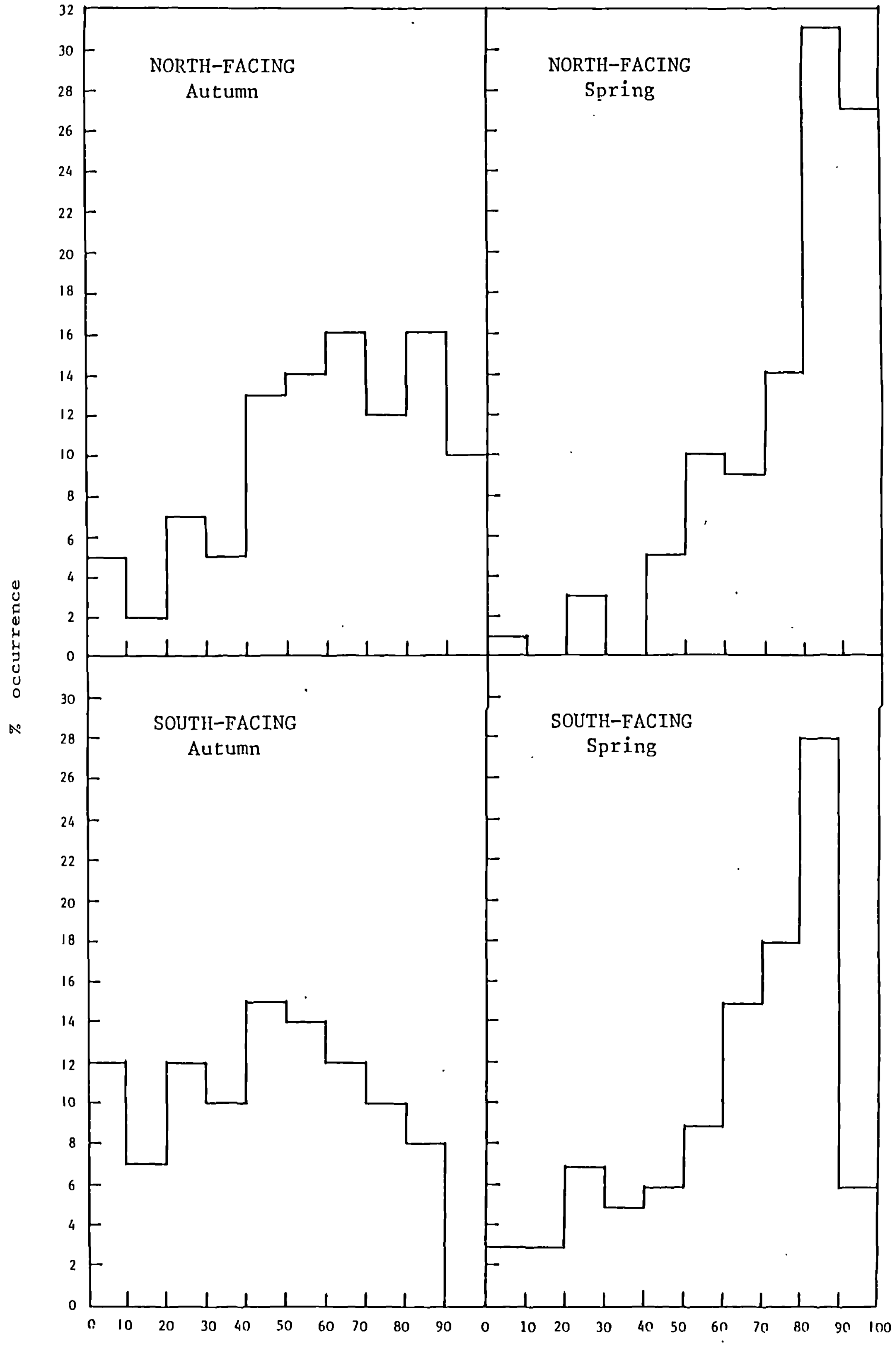
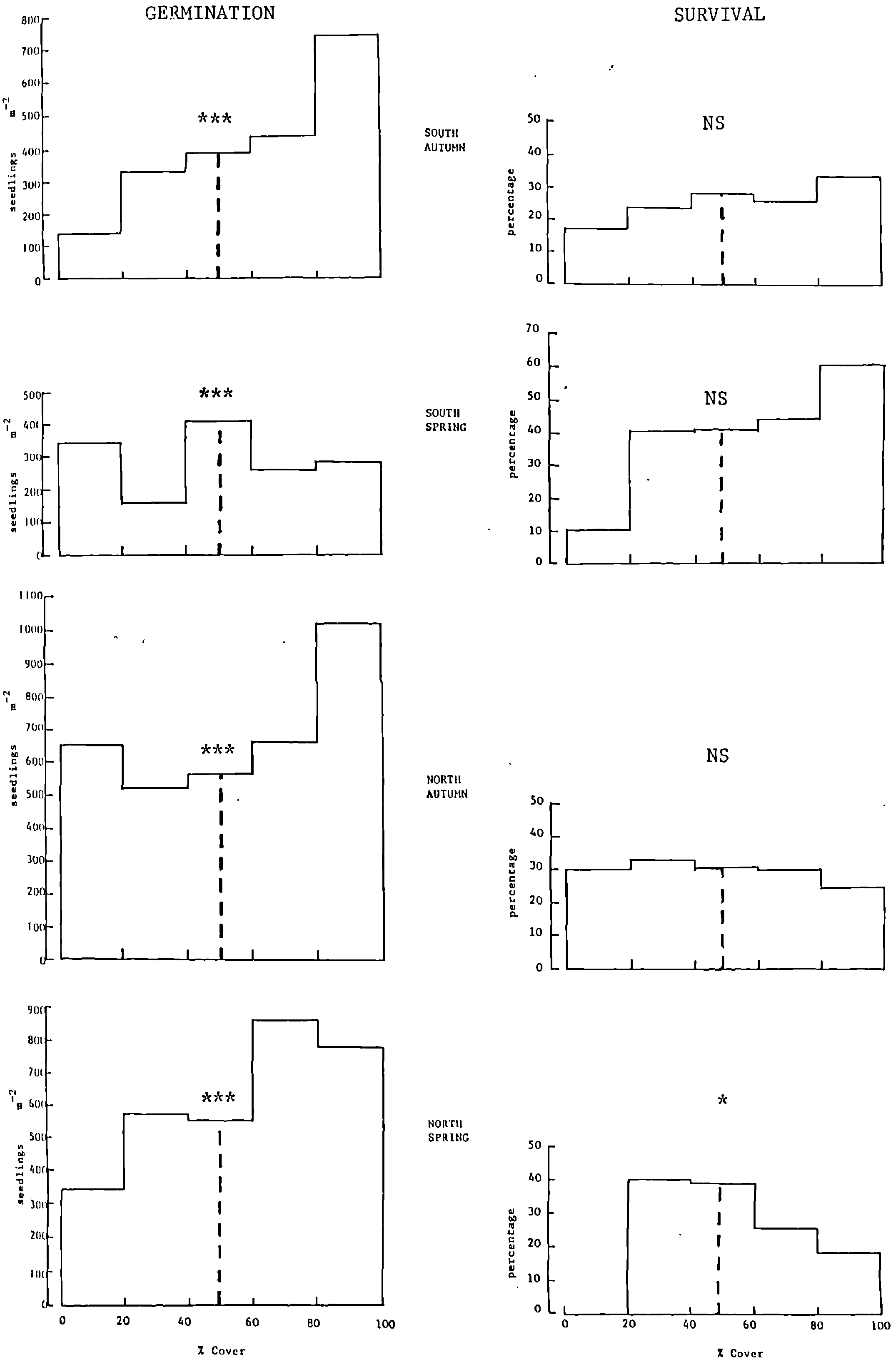


Figure 5.17 Distribution of initial seedling colonists and survivors in relation to early vegetative regrowth in 40 cm diameter gaps cut in the autumn and spring on both slopes. The significance of the differences in germination and the ratio survivors: mortalities, where cover was <50% and >50% are indicated as follows: NS = not significant; * = P<0.05; *** = P<0.001.



initial cover classes, but the density of vegetation in the early phases of gap recolonization appeared to have little impact on seedling survival in autumn gaps on both slopes, and spring gaps on the south-facing slope.

The distributions in relation to early regrowth of initial colonists and surviving seedlings of the perennial species *Plantago lanceolata*, *Origanum vulgare*, *Holcus lanatus* and *Viola riviniana* from the north-facing slope and *Koeleria macrantha*, *Festuca ovina*, *Campanula rotundifolia* and the biennial forb *Linum catharticum* from the south-facing slope are shown in Fig. 5.18. For all these species 1979 densities of seedlings increased as percentage cover increased as did survival on the south-facing slope. However, there are some interesting differences when associations between cover and patterns of survival are considered on the north-facing slope. *P. lanceolata* suffered higher levels of mortality in situations where early cover values were greatest. This was in marked contrast to the patterns observed in all species on the south-facing slope. *H. lanatus* and *V. riviniana* appeared to be positively associated with higher cover values while *O. vulgare* fell between these two extremes, suffering high levels of mortality in situations where early regrowth was either sparse or dense.

(c) Seedling yield

Mean dry weights of seedlings in relation to early vegetative regrowth are shown in Fig. 5.19. Log transformed values are included to take account of the great range in seedling size noted earlier (p. 93). In autumn gaps on both slopes, larger seedlings appeared to be associated with less dense vegetation. Seedling dry weights in spring gaps on the south-facing slope tended to be reduced at both

Fig. 5.18 Relationships between initial cover of resprouting vegetation, density of germinating seeds and eventual seedling survival in eight species.

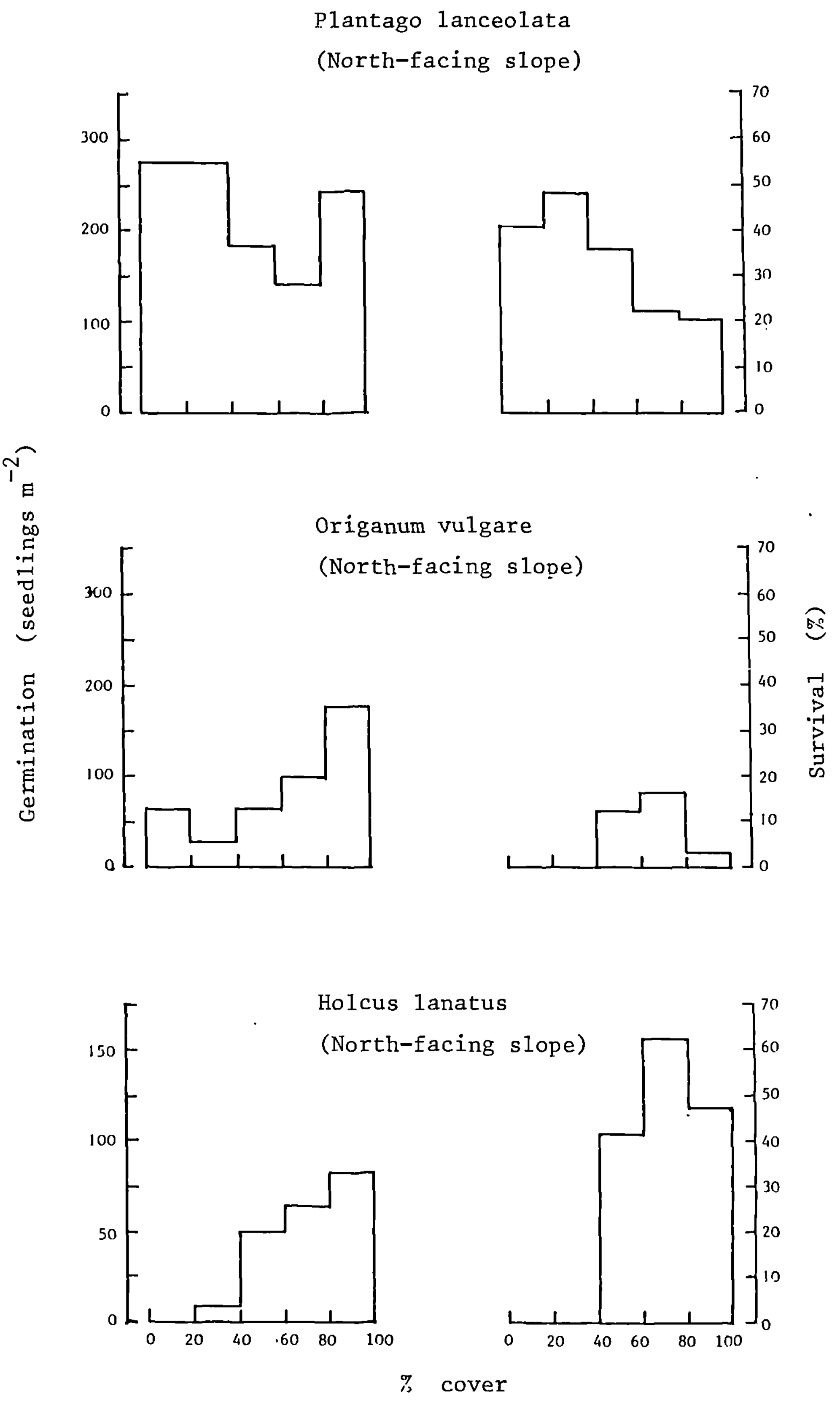
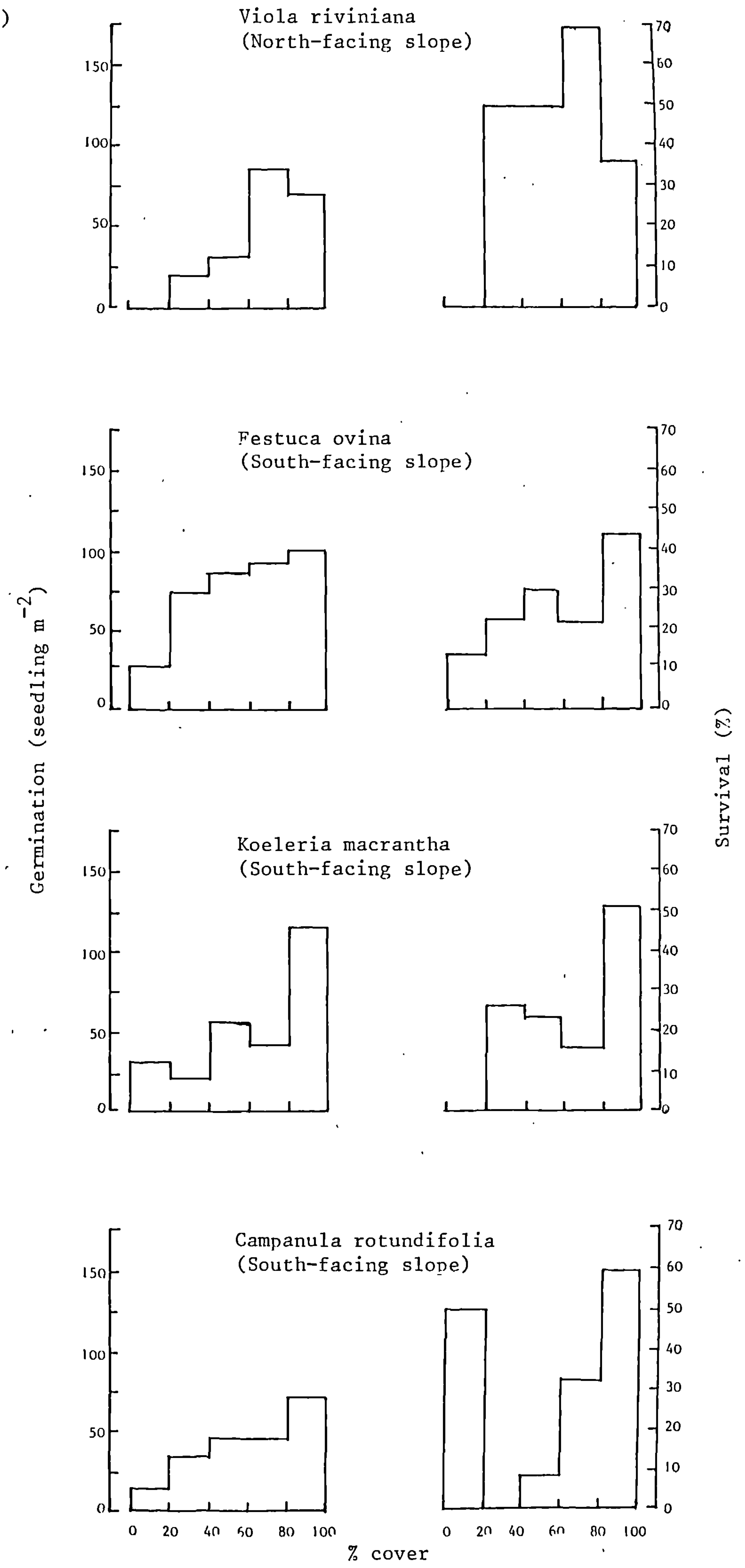


Fig. 5.18
(contd.)



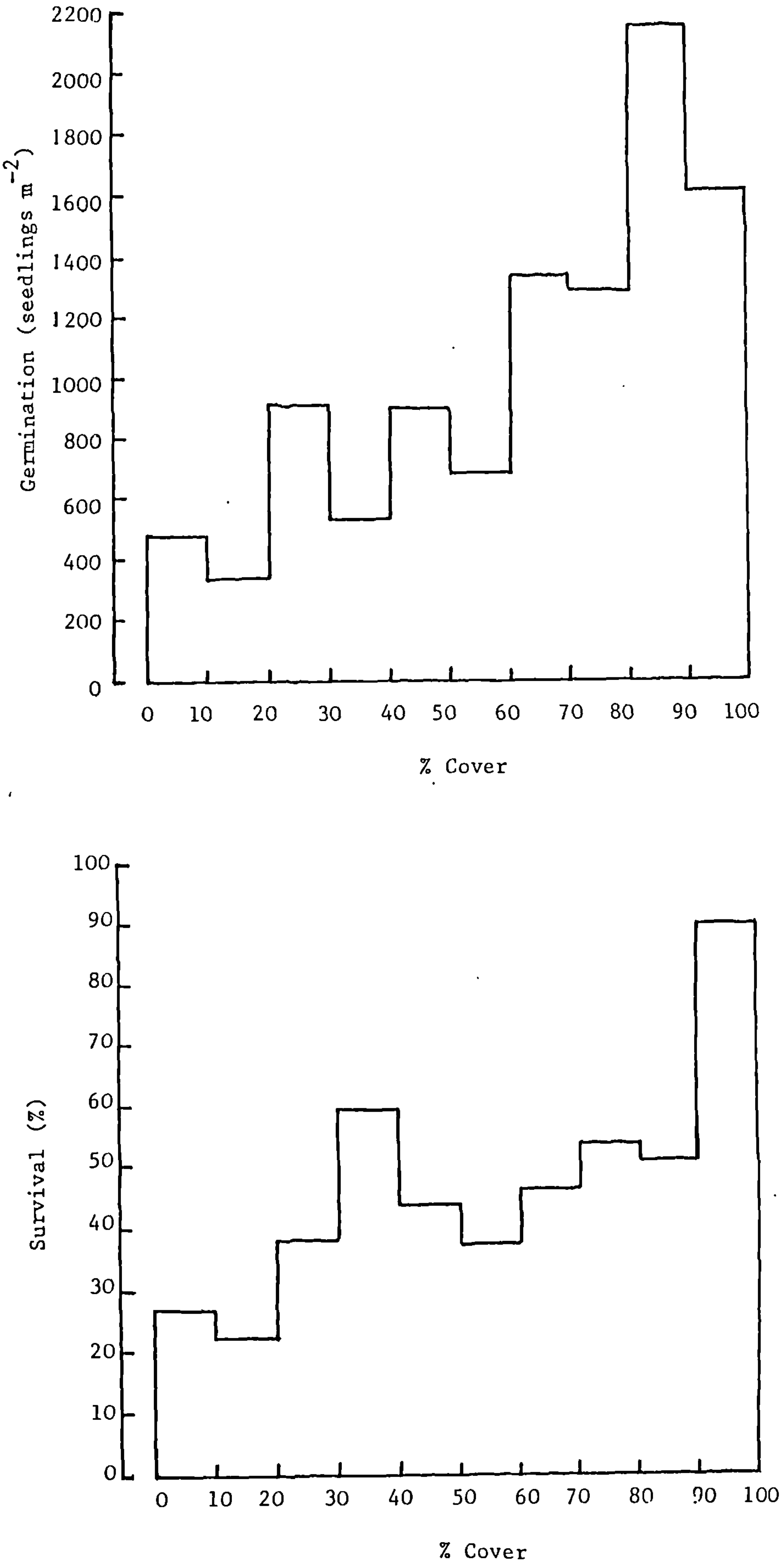
Viola riviniana
(North-facing slope)

Festuca ovina
(South-facing slope)

Koeleria macrantha
(South-facing slope)

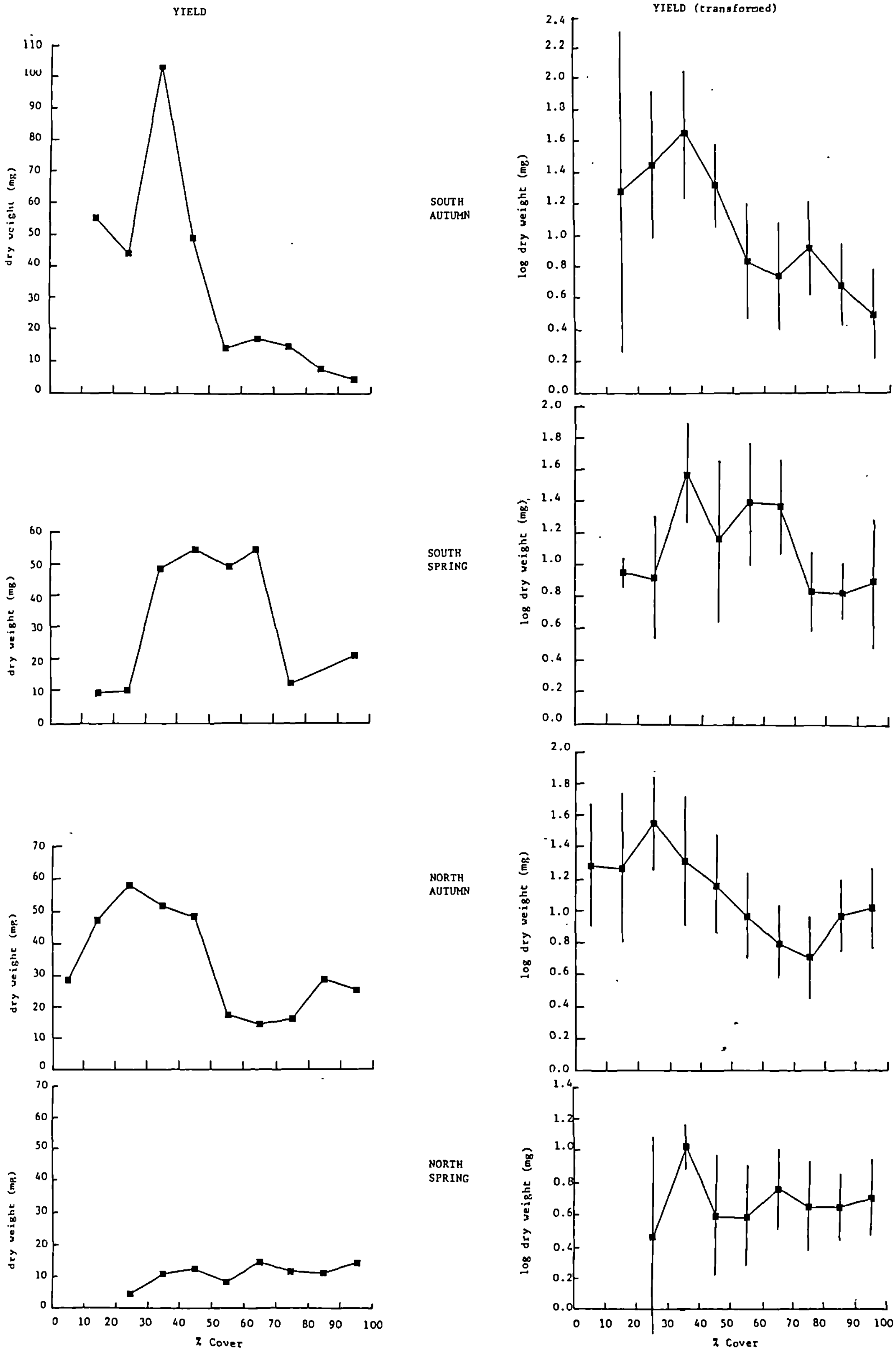
Campanula rotundifolia
(South-facing slope)

Fig. 5.18
(contd.)



Linum catharticum
(South-facing slope)

Fig.5.19 Distributions of seedling yield in relation to early vegetative regrowth in 40 cm diameter gaps cut in autumn and spring on both slopes.



extremes of cover while variations in cover had little impact on seedling size on the north-facing slope. In these gaps seedlings were uniformly small (p.93).

SEEDLING SURVIVAL AND YIELD IN RELATION TO DISTRIBUTIONS OF PLANT MATERIAL AT FINAL HARVEST

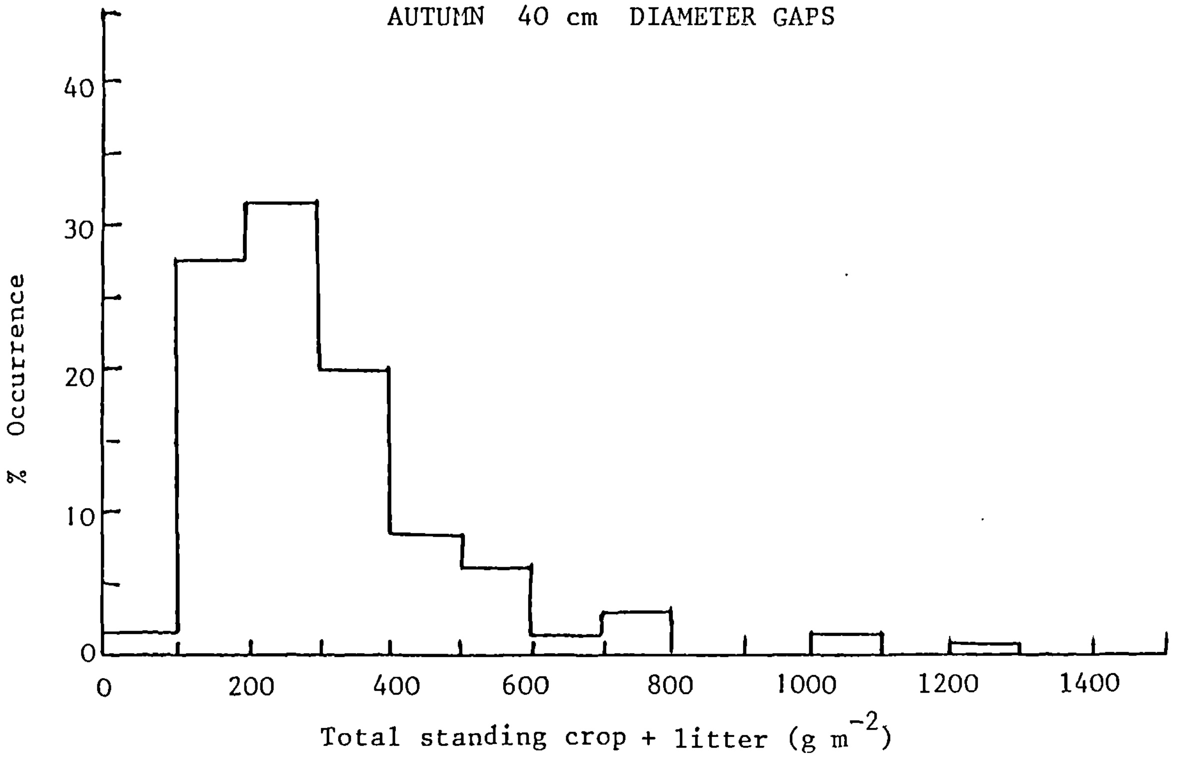
(a) <u>All species</u>

Subdivision of 40 cm diameter gaps at the final harvest in the manner described on p.37 and Fig.2.9 revealed that accumulated plant material (including litter and bryophytes) was not evenly distributed across gaps. Data from subsections in the two inner rings were amalgamated to give one value. In the adjoining ring, data from each pair of subsections in the four major quadrants, were amalgamated also, giving in total, 21 subdivisions of approximately equal area. The total standing crop (+ litter) was estimated in grammes per square metre for each subsection or fused group. In autumn gaps on both slopes it was found that a greater proportion of their area supported low accumulations of plant material (Figs. 5.20 and 5.21).

The number of seedlings located in each of the larger subsections used for the vegetative harvest was ascertained and their 1979 and 1981 densities with respect to the final distribution of plant material in gaps are plotted in Fig. 5.22. It is clear from this figure that the distribution of seedlings in 1981 differed from that in 1979. These differences were more apparent when percentage survival of seedlings in each class was examined (Fig. 5.23).

On the north-facing slope survival appeared to be negatively associated with quantity of plant material although this trend was much less marked in spring-cut gaps. On the south-facing slope it

Fig.5.20 Frequency distribution of total standing crop + litter in fused subsections (as described on p.99) in autumn- and spring-cut 40 cm diameter gaps on the north-facing slope.



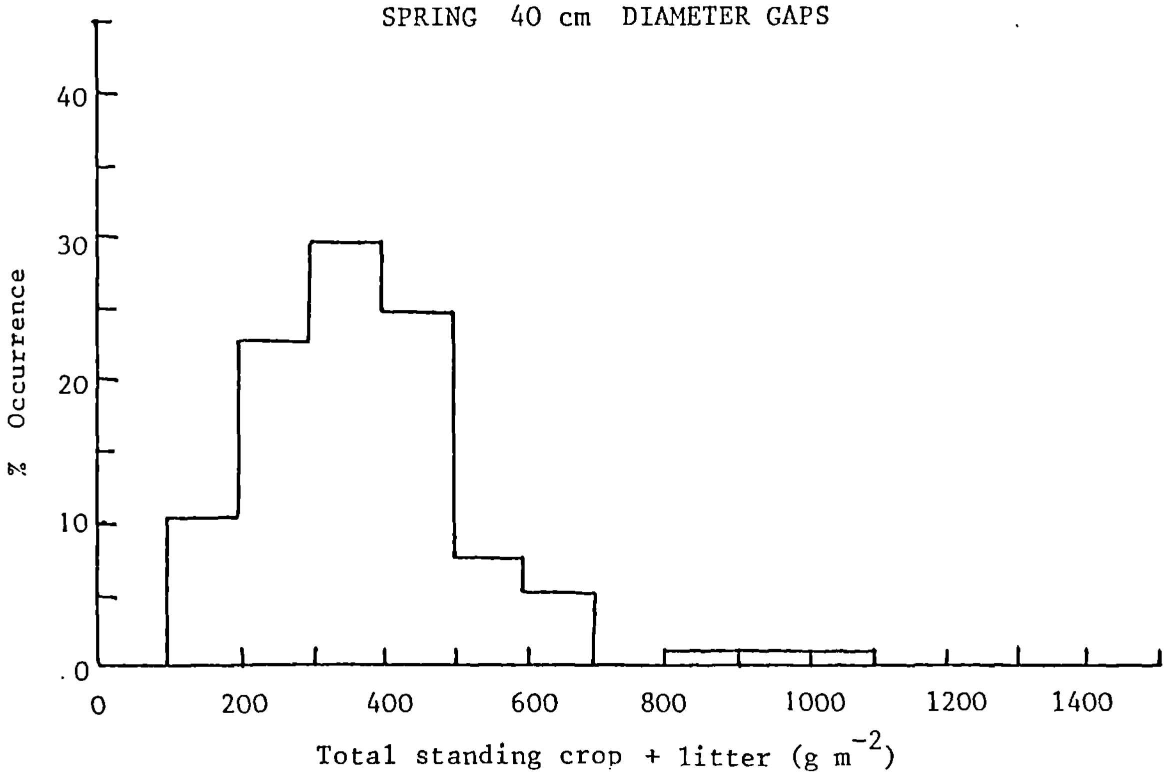


Fig. 5.21 Frequency distribution of total standing crop + litter in fused subsections (as described on p.99) in autumn- and spring-cut 40 cm diameter gaps on the south-facing slope.

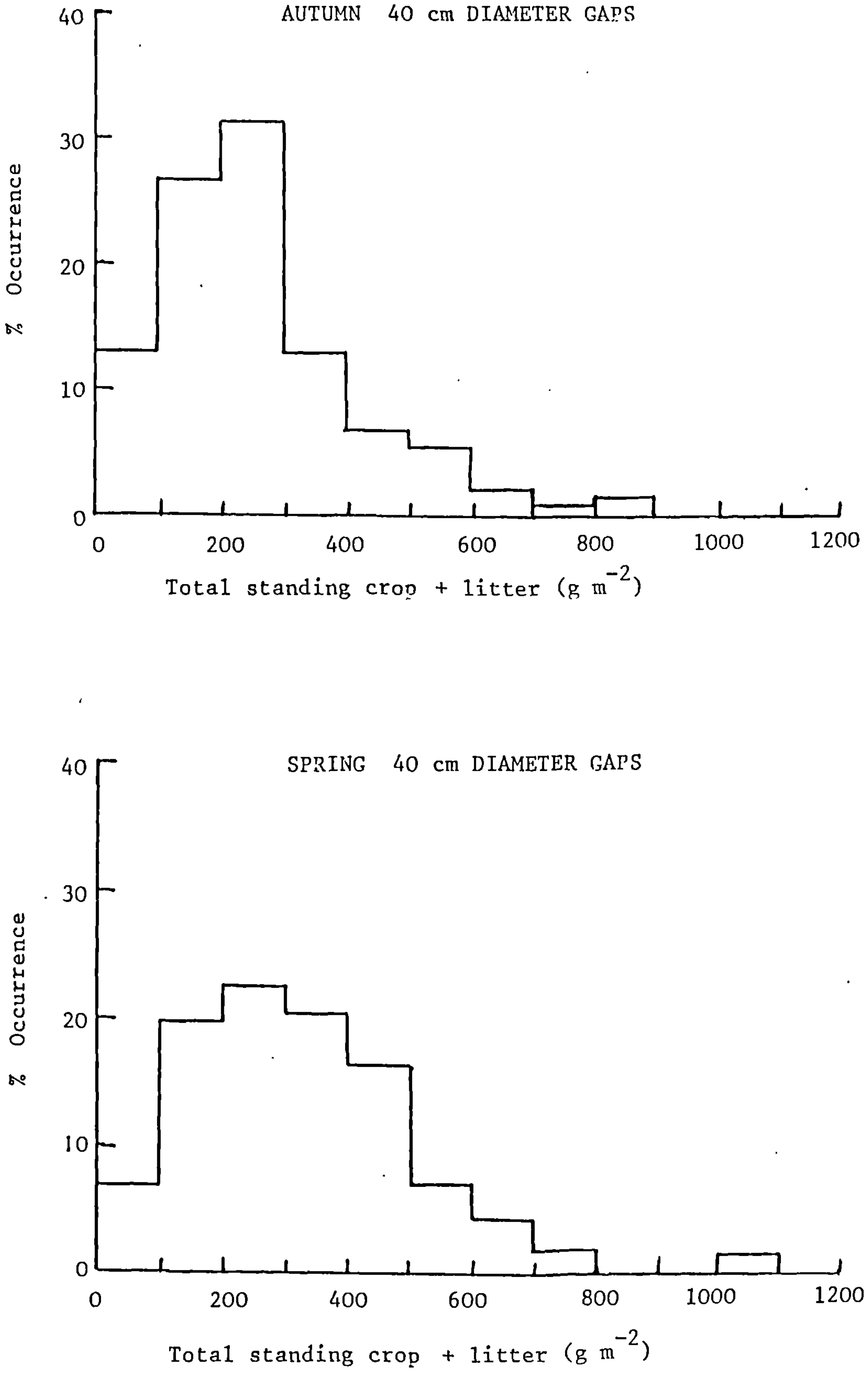


Fig. 5.22 The distribution with respect to final vegetation density, of seedlings in 1979 (unshaded bars) and 1981 (shaded bars) in autumn- and spring-cut 40 cm diameter gaps.

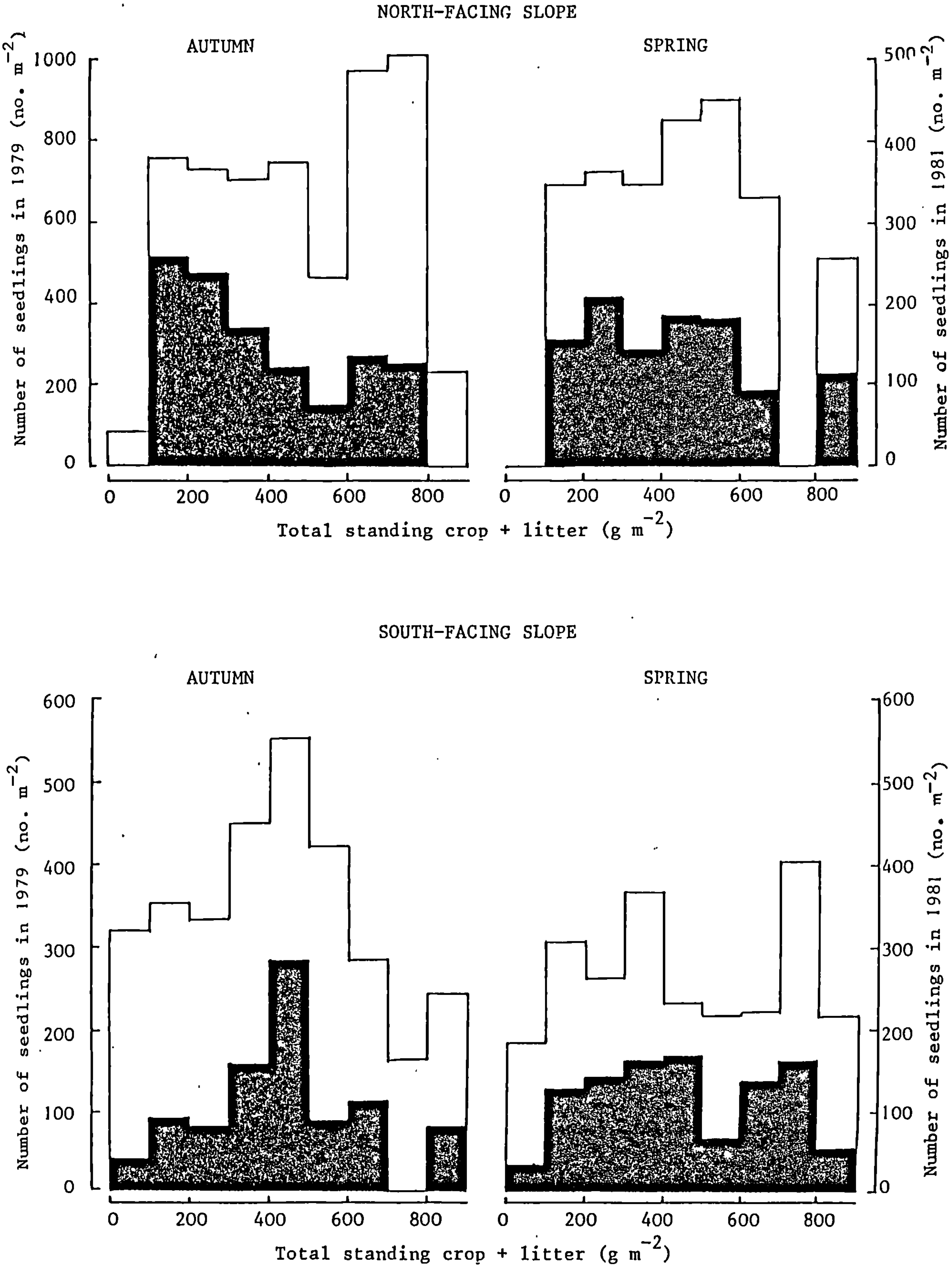
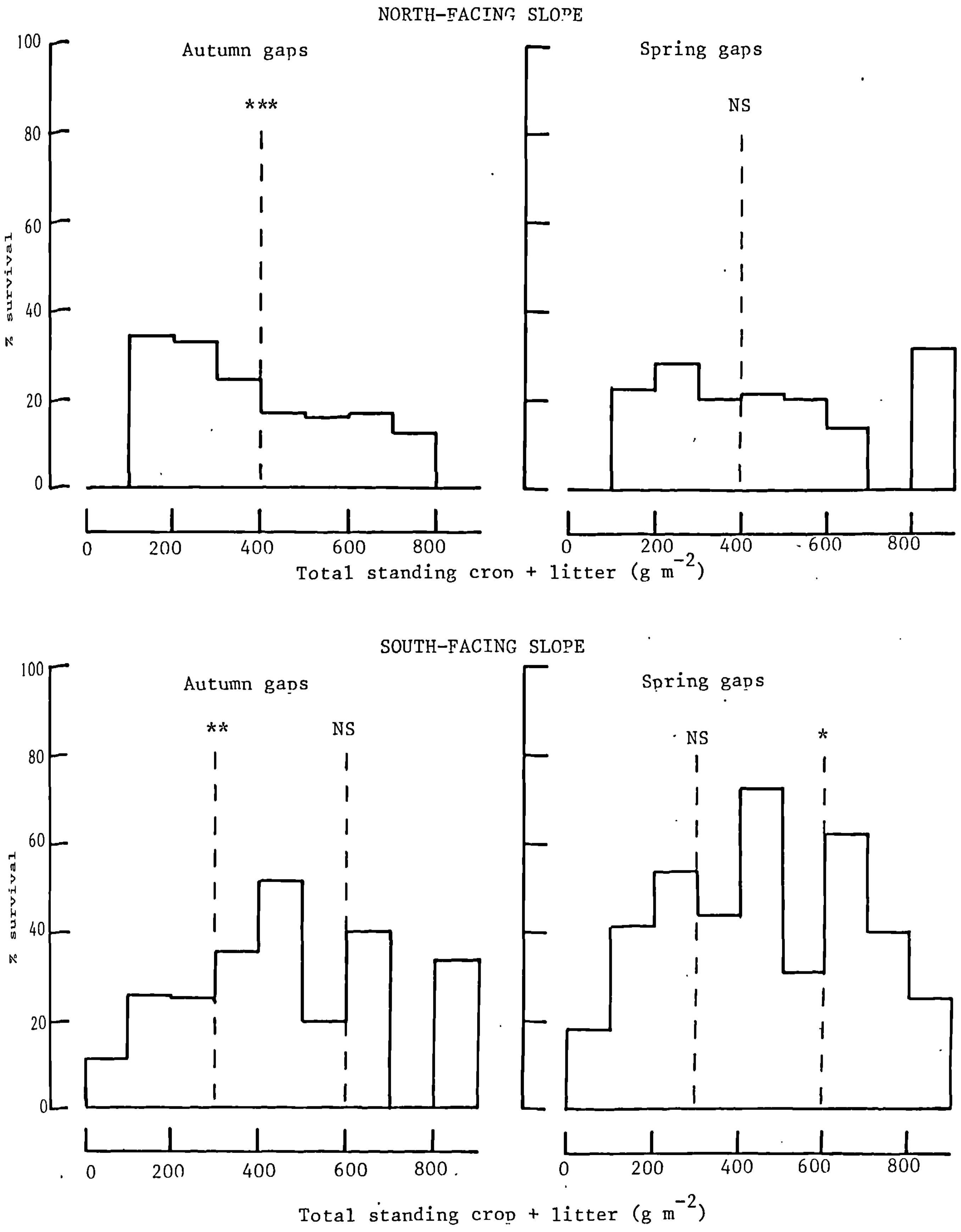


Figure 5.23 The relationship between final vegetation density and seedling survival in 40 cm diameter gaps. The significance of the difference in the ratio survivors;fatalities, in contigous classes (dashed lines) is denoted as follows; NS = not significant; * = P<0.05; ** = P<0.01; *** = P<0.001.



appeared that seedling survival was enhanced in situations where amounts of plant material were neither large nor small, a peak being reached where quantities were between 400-500 gm^{-2} in both autumn-and spring-cut gaps.

(b) Individual species

The identities and dry weights of individual seedlings surviving in each class are listed in Tables 5.8(a)-(d). It is clear from these tables that the largest seedlings were located where plant material accumulations were less dense. As noted earlier, seedlings varied greatly in size, both within and between species. Individuals with large dry weights did not always represent the most common species, e.g. only one seedling of Leontodon hispidus survived in autumn-cut 40 cm gaps on the south-facing slope and this weighed over 170 mg more than the largest Festuca ovina seedling in these gaps. In autumn-cut gaps seedlings from the autumn cohort were often but not always larger than spring germinating representatives of the same species.

Some species, e.g. Festuca ovina and Plantago lanceolata, were more abundant in certain classes while others which had been numerous in 1979 (Table 5.3), e.g. Holcus lanatus, Viola riviniana, Pimpinella saxifraga and in particular Origanum vulgare, were found in small quantities. The relationship between final accumulations of plant material, germination, survival and yield is explored separately for these species in Fig. 5.24.

The distributions of seedlings of Plantago lanceolata, Origanum vulgare, Viola riviniana and Holcus lanatus in 1979 relative to the density of vegetation at final harvest revealed marked differences between the four species. P. lanceolata seedlings were abundant

Table 5.8(a)

Distribution of seedling dry weights (mg) with respect to final cover in autumn-cut 40 cm diameter gaps on the north-facing slope.

	Total standing crop (including litter) g m^{-2}								
	0-99	100-199	200-299	300-399	400-499	500-599	600-699	700-799	800+
Achillea millefolium				2.4					
Agrostis capillaris		17.3*	1.6	4.9*					
		5.7		4.4*					
Anthoxanthum odoratum			5.1	31.7					
			6.8						
			2.0						
			18.3						
Arrhenatherum elatius			6.1		7.8*				
Avenula pubescens								2.4*	
Campanula rotundifolia			0.5						
			0.5						
			0.6						
Carex caryophyllea			3.4						
Carex flacca			25.3		5.0	4.7			
			4.2						
			4.6						
Centaurea nigra		4.2	9.2	22.4*			51.8*	20.5	
		9.8	0.9	39.1					
		5.0	0.9	143.1					
		4.3	10.7*	25.6					
		17.3	18.5	27.2					
		13.6							
		5.6							
Cirsium palustre			316.0						
Dactylis glomerata				9.2*					
Danthonia decumbens		13.2		13.7		11.8		27.6	
		59.1							
Festuca rubra		65.9*							
		7.1*							
Galium sterneri		15.6	5.5						
Holcus lanatus		7.5*	6.6	2.0	1.1*				
		4.0*	4.3	1.9					
		2.7	21.2	4.1*					
		4.1	64.8*	2.8					
		3.2	15.4	3.4					
		2.1	23.0	17.3*					
		455.5*	2.3	77.1					
		64.6*	43.4						
		19.2*							
Hypericum perforatum		6.5							
Origanum vulgare		5.5	2.1*	2.1	2.1				
		1.6*	2.3	9.8					
			6.5	2.6					
			0.8						
Plantago lanceolata		61.0	5.6	34.5	13.8	2.6	15.1*		
		11.2	74.6*	30.9	8.8				
		9.8	13.2*	51.3	2.4				
		13.0*	235.7*	11.7	20.2*				
		41.1*	67.6*	16.5	128.3				
		61.9*	161.5*	7.5					
		17.2*	190.8	57.8					
		51.7	41.0	182.7*					
		61.3*	17.2	13.1*					
		49.8*	14.6						
		22.9	18.9						
		18.3	52.2						
		130.0	1.9						
		24.4*	16.6*						
		20.0*	3.0*						
		75.5*	143.4*						
		199.6*							
		19.9*							
		18.6*							
		79.9							
		80.5*							
		79.9							
		18.0							
		38.4							
		149.6							
		49.6							
		3.1							
		1.5*							
Potentilla sterilis		21.2							
Scabiosa columbaria						24.7			
Senecio jacobaea		34.8							
Succisa pratensis			4.6						
Taraxacum spp.			1.9						
Viola riviniana		4.0	1.9	3.3					
		5.3	2.4	4.0					
		1.8	1.7						
		6.5	2.1						
		4.4	3.1						
		5.7	1.8						
		3.7	3.1						
		28.8	1.7						
			0.6						
			1.9						
			2.3						
			1.6						
			3.0						
			10.6						

* seedlings were survivors from the autumn cohort.

Table 5.8(b)

Distribution of seedling dry weights (mg) with respect to final cover in spring-cut 40 cm diameter gaps on the north-facing slope.

	Total standing crop (including litter) g m^{-2}								
	0-99	100-199	200-299	300-399	400-499	500-599	600-699	700-799	800+
Achillea millefolium		2.2							
Agrostis capillaris		1.1	1.8	4.3	5.6				
			0.6	13.2	2.9				
			2.0						
Anthoxanthum odoratum				31.8	9.1				
Avenula pubescens			2.4						
Campanula rotundifolia		1.2	0.4	0.5	0.2	0.9			
			0.6						
			0.1						
Carex caryophyllea		3.5	10.6	3.7	6.1				
			7.1	6.8	2.1				
				2.6					
Centaurea nigra			4.2	2.1	6.5		4.2		
			2.9	35.5	1.5		7.5		
				31.5					
				18.0					
Cirsium palustre					13.7				
					4.8				
Dactylis glomerata					13.4				5.9
Danthonia decumbens			25.0	77.3	13.8	5.9			
					43.3				
Festuca rubra				9.0					
Holcus lanatus			10.9		17.8	0.3			
			0.5		4.7	1.8			
					80.3				
					1.2				
Hypericum perforatum		7.7	9.6		2.3	10.3			
Origanum vulgare		2.1	1.8	8.2	1.0	0.6	3.2		
		1.4	2.5	10.8	2.6		2.0		
			1.6	1.3	1.0				
			1.0	0.8	0.5				
			0.3	2.1	1.9				
			1.0	1.5	2.3				
			4.0	1.9	1.8				
			4.0	1.1	2.3				
					7.6				
					1.2				
					1.4				
					2.2				
Plantago lanceolata		2.6	71.9	8.6	15.8	53.1			2.3
		2.5	1.5	88.6	62.5	11.3			
		1.2	1.7	5.0	39.5	53.6			
		5.3	3.2	22.9	130.5	4.0			
		81.9	2.0	5.1	1.8	97.2			
			2.7	2.5	7.1				
			7.7	1.0	1.8				
			8.3	8.8	1.5				
			75.2	8.2	20.1				
			11.0	3.8	2.0				
			8.9	4.3					
			1.4	79.2					
			14.0	3.8					
			11.1						
			9.3						
			38.9						
Succisa pratensis		21.6	13.0						
			6.4						
Viola riviniana		14.9		2.2	12.4				

Table 5.8(c)

Distribution of seedling dry weights (mg) with respect to final cover in autumn-cut 40 cm diameter gaps on the south-facing slope.

	Total standing crop (including litter) g m^{-2}								
	0-99	100-199	200-299	300-399	400-499	500-599	600-699	700-799	800+
Avenula pratensis		117.8			322.2	18.6			
Campanula rotundifolia	1.9	4.5	1.3		3.9		0.7		
			14.0		1.3		0.6		
Centaurea scabiosa				10.8					
Festuca ovina	4.3	2.7	3.4	16.3	3.6	7.0			
		52.9	24.9	8.6	4.4				
		8.0	2.1	1.1	7.6				
		204.2	4.1	1.3	4.7				
		42.3	2.4	5.7	1.1				
		59.5	22.1	7.6	67.5				
			9.7	8.5	12.9				
				17.8					
				9.7					
Helianthemum nummularium				2.2					
Hieracium pilosella		9.3	8.6	17.4					
		67.5							
		18.6							
Hieracium spp.			13.4						
Hypericum perforatum		4.1							
Koeleria macrantha		2.6	8.4	0.7	7.2				
		37.8		47.7	6.4				
		5.1			3.4				
					1.0				
Leontodon hispidus		376.6							
Lotus corniculatus	95.7		143.6		71.4				
	35.6		36.7		33.2				
			5.5						
Pimpinella saxifraga		14.9	2.5	6.1		68.4			1.4
		20.3	4.0	5.2					
		45.6	7.4						
Plantago lanceolata				22.0					
				75.9					
Poa pratensis			4.3						
Senecio jacobaea					3.2	18.1			
Thymus praecox		8.2	12.4						
		40.8	9.3						
			7.7						

Table 5.8(d)

Distribution of seedling dry weights (mg) with respect to final cover in spring-cut 40 cm diameter gaps on the south-facing slope.

	Total standing crop (including litter) g m^{-2}								
	0-99	100-199	200-299	300-399	400-499	500-599	600-699	700-799	800+
Arabis hirsuta				0.8	1.7				
Avenula pratensis		45.2	9.4	24.3					
Campanula rotundifolia			1.4	1.2					
			2.7	0.9					
Carex caryophyllea			17.6						
Centaurea scabiosa				21.0					
Dactylis glomerata				9.4		110.9			
Festuca arundinacea				4.1					
Festuca ovina	21.1	2.5	2.3	3.8	7.6		1.1		
		6.4	3.2	4.3	7.8				
		9.3		0.8	9.6				
		101.4		10.0	3.3				
		5.5			12.4				
Helianthemum nummularium		27.7	12.7	235.3	55.8			4.8	
				3.7					
Hieracium pilosella	47.6			26.6	8.5	33.3			
					16.7				
					12.7				
Hieracium spp.		32.3		14.3					
				15.5					
Hypericum perforatum		2.6	8.1						
Koeleria macrantha		37.3	3.6	8.2	6.3		2.5		
			7.5	1.1	10.7				
			9.6	1.3					
			14.2						
			10.8						
			112.6						
			16.8						
			10.8						
			5.2						
Leontodon hispidus		179.4	75.5			279.7			
		78.1							
Lotus corniculatus		3.4	65.5	25.4			122.6		25.2
		54.4	20.4	55.1					
		10.1							
Origanum vulgare			0.7		7.7				
			1.1						
Pimpinella saxifraga		14.3	3.6	4.3	75.8	1.3	18.8		
		4.8		11.8	9.6	14.5			
		11.9		14.7	6.5				
		14.9		41.2					
		18.3		10.6					
		4.8		14.4					
Plantago lanceolata			21.3		1.6				
			50.9		287.8				
					130.1				
					19.9				
					35.8				
					104.0				
Poa pratensis				4.2					
Scabiosa columbaria				79.6					
Senecio jacobaea			15.1						
Thymus praecox			21.2		0.6				
			2.2		0.7				
Trisetum flavescens		2.4							

Fig. 5.24 Relationships between final vegetation density, initial patterns of colonization (histogram) and survival (●) of seedlings of a variety of species in 40 cm diameter gaps on the north- and south-facing slopes.

—○— Data based on a small number of seedlings.

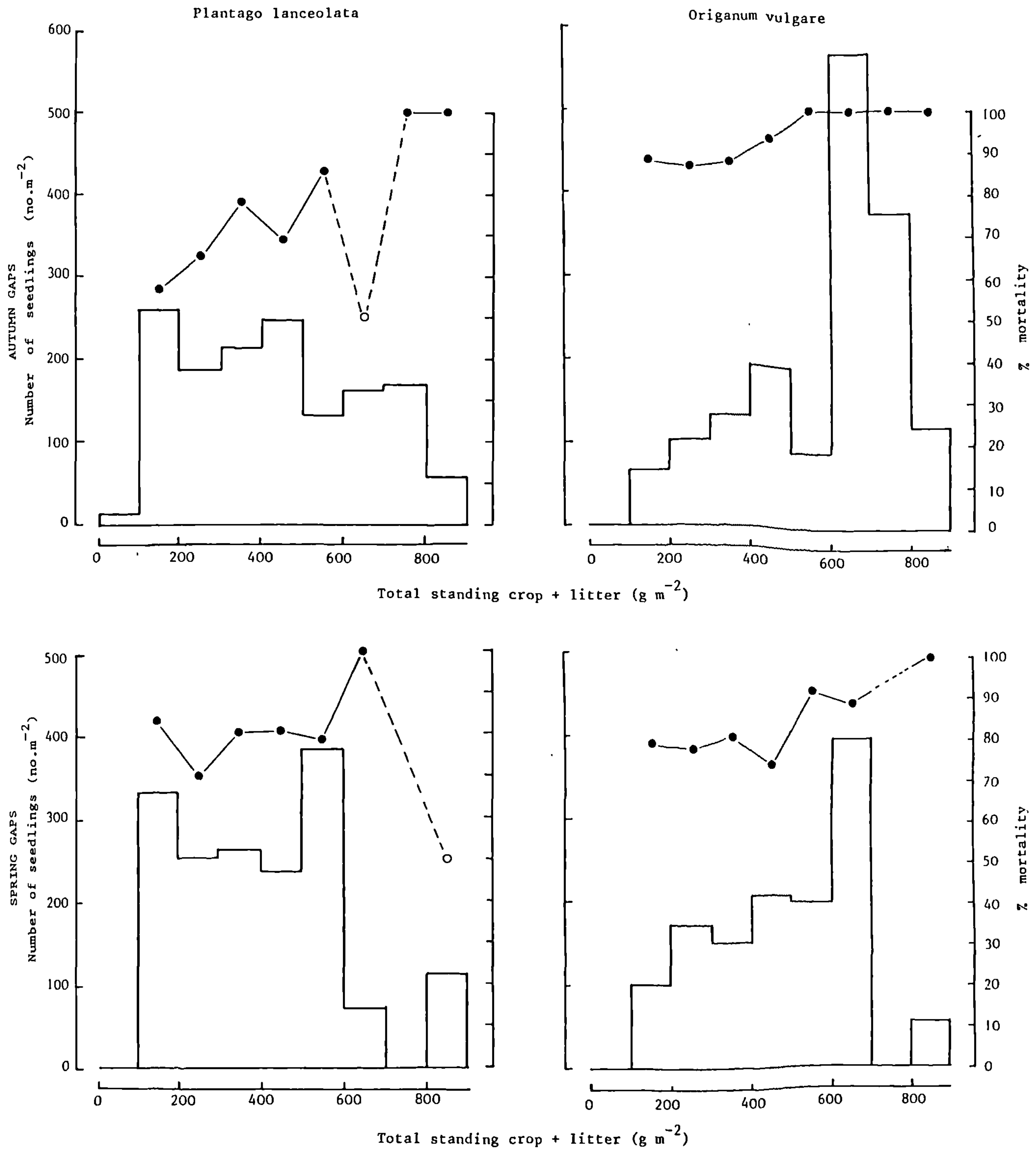
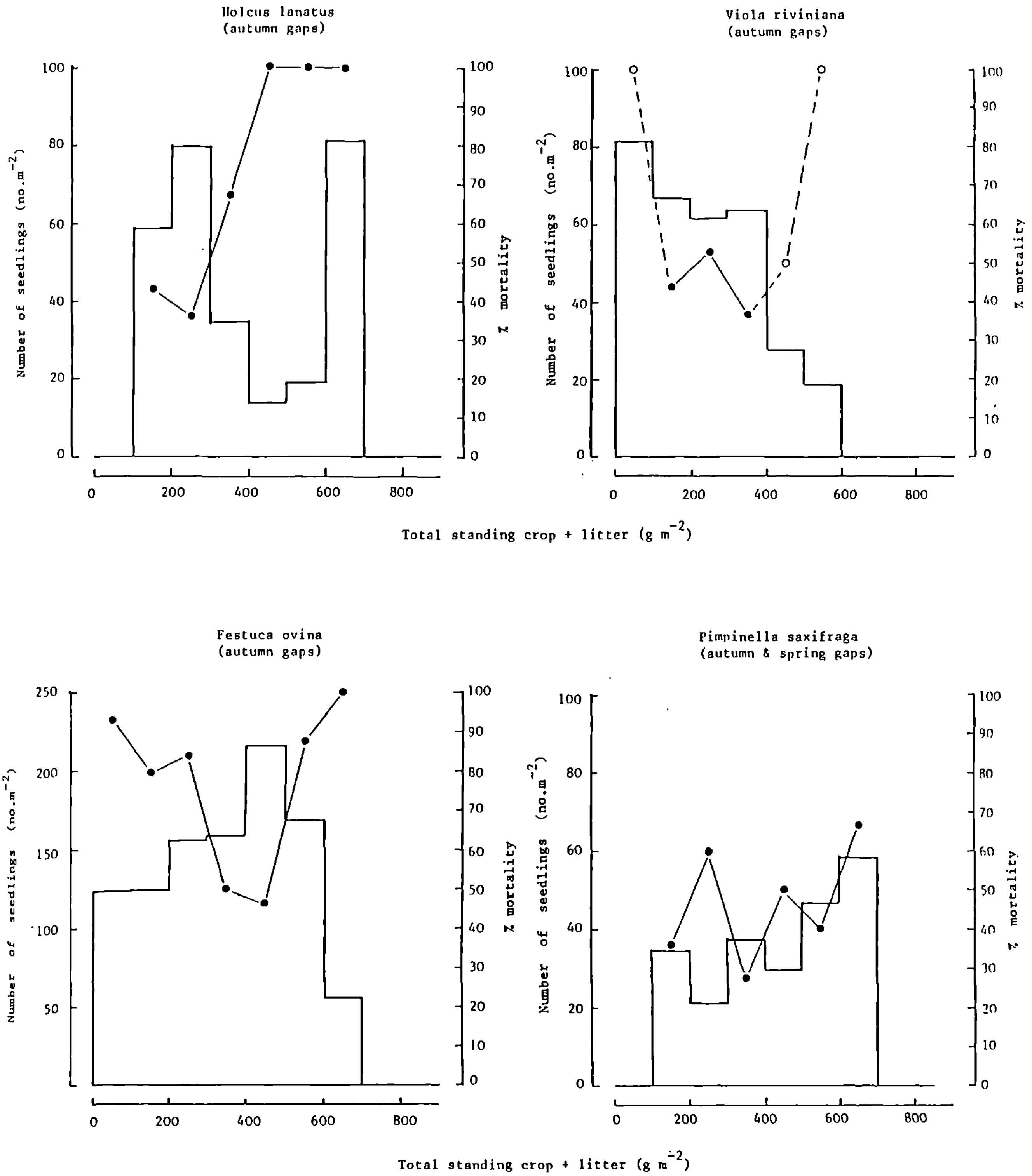


Fig. 5.24
(contd.)



across the whole range in autumn-cut gaps and were reduced in number only above 600 g m^{-2} in spring-cut gaps. Seedlings of O. vulgare were concentrated, in 1979, in situations which eventually yielded the highest quantities of plant material. In contrast, H. lanatus was strongly associated with more open situations as was V. riviniana, although a small number of seedlings of this species occurred at higher densities also.

All four species suffered lower levels of mortality where vegetation was less dense in autumn-cut gaps. This pattern was repeated for Origanum vulgare and Plantago lanceolata in spring-cut gaps. The occurrence of Holcus lanatus and Viola riviniana in spring-cut gaps was not investigated since seedlings were few in number in 1979.

Origanum vulgare suffered slightly lower levels of mortality in spring gaps than in autumn gaps, in contrast to Plantago lanceolata which survived better in autumn-cut gaps and in particular in situations where vegetation densities were low. In spring gaps, O. vulgare persisted at slightly greater vegetation densities than did P. lanceolata. Holcus lanatus and Viola riviniana both experienced lower levels of mortality in more open situations than either O. vulgare or P. lanceolata but neither species persisted at vegetation densities above 450 g m^{-2}.

On the south-facing slope Festuca ovina was the only species represented by numerous seedlings in June 1979. At this time, in autumn-cut gaps, seedling densities increased at higher vegetation density but decreased beyond 500 g m^{-2}. Seedlings of this species were less abundant in spring gaps and showed an irregular distribution with respect to final vegetation density. In autumn-cut gaps mortality in F. ovina seedlings was considerably reduced in the range 300-500 g m^{-2}. There was some indication of a similar pattern in spring-cut gaps.

Fifty-two seedlings of the spring germinating forb Pimpinella saxifraga appeared in 1979. Numbers were too low to permit separate analyses for autumn- and spring-cut gaps, and therefore data for both gap types were amalgamated. Germination in this species was positively associated with increasing quantities of vegetation. In contrast to Festuca ovina, mortality in P. saxifraga did not appear to be strongly dependent on vegetation density.

DISCUSSION

It is clear from Table 5.1 that a very large proportion of the seedlings recorded in gaps and controls on both slopes in November 1978 and June 1979 were no longer present at the end of the field investigation in 1981. The small number of individuals by which most species were represented soon after germination (Chapter 4) meant that for many it was difficult to assess survival in all but the broadest terms. At the time of first recording, it seemed reasonable to predict that species represented by such small numbers would soon be obliterated from the seedling flora. However, reference to Table 5.3 shows that this was not the case. Although even further depleted, many of the less common species were still represented in 1981. Some, e.g. Leontodon hispidus and Cirsium palustre, had attained dry weights in excess of those of the largest individuals of common species, e.g. Festuca ovina and Plantago lanceolata (Table 5.8).

Only two seedlings of perennial species achieved the status of flowering individuals during the course of the experiment, and as a result may be said to have truly 'established'. For all other seedlings it was necessary to define 'success' in terms of either percentage survival or seedling yield. It is clear from Fig. 5.9 that comparison between gap types is especially difficult using these determinants. Variations in survival and yield could be due to a preponderance of particular species or group of species in different gap types. This phenomenon is difficult to assess due to the small number of seedlings involved. As mentioned above, seedlings of many species less common in the initial seedling flora survived to the end of the experiment. It seems likely that chance played an important role in determining their presence in particular gap types.

Rates of loss of seedlings of perennial species from gaps, over the period of the experiment, differed at the two sites. During the period 1979-1980 it is suspected that the generally higher rates of mortality experienced on the south-facing slope are the result of exposure of very young seedlings to the hotter and drier weather conditions experienced over the summer months on slopes with this aspect. Between 1980 and 1981, seedlings were lost at a slightly higher rate than in the previous year on the north-facing slope, suggesting that seedling mortality was caused by some general influence, e.g. competition with established or re-establishing plants, operating at this site independently of gap character or season of origin. It is difficult to predict with certainty the final fate of seedlings surviving at the end of the experiment on this slope, but there was little or no indication of a deceleration in rates of loss and it seems unlikely that many seedlings would have been alive in 1982. In contrast, on the south-facing slope it seems that seedlings which survived through the earlier part of the investigation had a much better chance of survival over the period 1980-81. This situation could reflect some subtle changes in weather conditions between the two periods but it is tempting to suggest that strong selective pressures such as summer drought, over the earlier period, resulted in a situation in which only the most vigorous or most favourably-located seedlings survived.

These alternative explanations of differing mortality patterns on the two slopes are supported by closer investigation of surviving seedling locations in relation to the extent of vegetative recolonization in gaps. On the north-facing slope, there is no doubt that seedling survival was enhanced where both early and final accumulations of plant material were less dense (Plate 6, Figs.5.13, 5.14, 5.17, 5.23, 5.24). It is likely that competitive interactions would be least severe in these situations.

In contrast, on the south-facing slope risk of mortality was associated with open ground and by the time of final harvest, with situations in which large quantities of plant material had accumulated also (Plate 7, Figs.5.17, 5.23, 5.24). That intermediate levels of cover appeared to promote seedling survival is probably due to soil stabilization by roots of established plants. The mobility of seeds on the south-facing slope was noted earlier (Chapter 4, p.) and soil disturbance was cited by Davison as a major cause of seedling mortality at this same site (Davison 1964). This view is further supported by the differential survival rates experienced by seedlings in upslope and downslope quadrants of gaps, hills and scrapes (Fig.5.11). A 'shelter effect' such as this may explain the slightly higher levels of seedling survival found in spring-cut gaps. Although these gaps were six months younger, they were found to contain similar quantities of vegetation to autumn-cut gaps at the final harvest. Seedlings in older autumn-gaps were thus probably 'exposed' for longer periods of time. The possibility that *Linum catharticum* 'fits in' between established plants in exploiting small gaps was discussed by Grubb in relation to chalk grasslands (Grubb 1976). Data presented in this chapter showing positive associations of both germination and survival in this species with early canopy, would seem to support this hypothesis.

Micro-sites supporting the largest numbers of seedlings were not always those in which the largest seedlings were found, although on the north-facing slope this was generally the case and probably resulted once again from reduced competitive interactions. The generally smaller individuals in spring-cut gaps at this site may have been suppressed by the more rapid recolonization of these gaps as described in Chapter 3.

On the south-facing slope, some very large seedlings were located in situations otherwise apparently unfavourable for establishment (Table 5.8). The occurrence of such seedlings may be related to the characteristics of the species concerned. Some very large individuals of *Lotus corniculatus* were found in relatively open ground on the south-facing slope. This species rapidly extends a tap-root down into the soil soon after germination. In consequence seedlings are both anchored and likely to avoid desiccation due to surface droughting of soil in these more exposed locations; and are also less likely to suffer from the competitive effects of neighbours. Large seedlings of *Leontodon hispidus* were encountered in similar situations and probably attained their great size by similar means.

Seedlings of Festuca ovina and Koeleria macrantha tended to be larger in less dense vegetation. In fact seedlings of all species which survived in denser vegetation on both slopes were smaller on average than those in less dense vegetation. This was particularly the case in control areas of undisturbed vegetation where effects of root and shoot competition, and accumulations of litter and bryophytes were likely to be exerted most strongly. As a general rule, therefore, seedlings of large size were confined in large gaps.

On the north-facing slope where two cohorts of seedlings had been distinguished in autumn-cut gaps, the oldest seedlings, while larger as a group (Fig.5.8), were not always the largest representatives of particular species (Table 5.8(a)). Although amongst the earliest colonists of the gaps, members of this cohort were also exposed to the harsh winter weather conditions of late 1978 and early 1979, which may have retarded their growth to a certain extent. Seedling size, however, is not simply a function of age. Genetic variability between individuals may be an important determinant of differences in vigour and this may be compounded by the characteristics of the micro-site in which a seedling is located.

Micro-site as a controlling influence on the occurrence of seedlings of different species was investigated for a small number of the commonest species in 40 cm diameter gaps on both slopes. These species appeared to show subtle differences in distribution with respect to canopy either as young seedlings or as surviving individuals (Fig. 5.24). In 1979 on the north-facing slope Plantago lanceolata seedlings had been fairly evenly distributed with respect to cover in both autumn- and spring-cut gaps. In the latter, higher mortalities and generally lower seedling dry weights were observed and appeared to be due to suppression resulting from the more rapid vegetative recolonization which occurred in spring gaps. *Origanum vulgare*, in contrast, suffered generally higher levels of mortality in gaps cut at both seasons but despite this appeared to persist in slightly denser vegetation. Many of these seedlings were small and etiolated but otherwise appeared to be healthy. The greater densities of seedlings in 1979 in situations which eventually supported the largest quantities of material resultant from vegetative recolonization may be a reflection of previous depletion of buried seed reserves in more open situations.

The relatively smaller number of *Holcus lanatus* and *Viola riviniana* seedlings in 1979 causes difficulties in interpretation of their distributions with respect to canopy. Neither of these species appeared to have the capacity to persist in dense vegetation and seedlings of *V. riviniana* attained greater size away from dense canopy. Levels of mortality were lower in more open situations than for either of the two former species mentioned. There is also some evidence for the association of *H. lanatus* seedlings in 1979 with parts of the gaps which were not covered by dense vegetation at the end of the experiment. Such a distribution is in marked contrast to that observed in *O. vulgare* and may be the result of canopy-induced dormancy in surface-lying seeds.

On the south-facing slope it was possible to investigate two species only in this way, due to the small numbers of seedlings by which most species were represented in 1979. The enhanced survival of *Festuca ovina* seedlings in situations of intermediate vegetation density corresponds with the idea of a 'shelter effect' described earlier, and is supported by the fact that a number of seedlings of this species survived in undisturbed turf (Table 5.3(b)).

Seedlings of *Pimpinella saxifraga* in 1979 were more abundant than those of *Festuca ovina* in micro-sites eventually recolonized by dense vegetation. In contrast to the latter, however, *P. saxifraga* suffered lower rates of mortality at both higher and lower vegetation densities. This species has relatively large seeds and as a result seedlings are more robust in the early stages than those of *F. ovina*. It seems likely that this characteristic is linked with the ability of *P. saxifraga* to persist in denser vegetation. Seed reserves and early photosynthate are also incorporated into a tap-root. The value of this growth form for anchorage and avoidance of surface-droughting has been discussed previously.

CHAPTER 6

DISCUSSION

AN ASSESSMENT OF THE INVESTIGATIVE METHODS ADOPTED

In common usage, the word 'experiment' has come to imply a high degree of control on the part of the researcher, and generally involves a strong element of hypothesis testing. Any study concerned with naturally-occurring phenomena is, by its very nature, rather more 'open-ended' than this. Precision in the laboratory is exchanged for realism in the field, although results from either approach may have general relevance (Hunt & Doyle 1984). Relevance is not guaranteed in laboratory experiments, however. Subjects may be exposed to conditions so divorced from the real world that the resultant findings, although of interest, may have little bearing on naturally-occurring control mechanisms.

The work described in this thesis has characteristics of a controlled experiment in that gaps of known size and season of origin were created in a strictly standardized manner. However, beyond this, events were allowed to occur in as natural a fashion as possible. Hence recording activities and resultant disturbance of re-establishing vegetation was minimized in order to avoid serious interference with the recolonization process (Appendix 7). Human impact on the whole study area was also reduced as much as possible since the vegetation on both slopes, and especially on the south-facing slope, was vulnerable to trampling. Soil disturbance would have been very serious on such fragile systems if visits to the site, especially in the winter months, had been more frequent.

The consequences of this approach are that certain pieces of desirable information on the process of gap recolonization were not collected. It was not possible to study in detail the exact patterns of canopy expansion as gaps were recolonized vegetatively. Nor was a detailed analysis of timing of seedling mortality after germination attempted. In fact, data reported in Chapter 4 probably seriously underestimate the total number of seedlings which appeared in gaps in the period immediately after their creation.

Even though apparently homogeneous areas of vegetation were selected for study on both slopes, spatial heterogeneity in plant distributions occurred and there was no practicable method of assessing the presence, magnitude or variability of buried seed reserves in particular parts of the site. Replication thus became an important consideration in the experimental design. Seven replicates of each treatment provided a reasonable compromise between physical practicality and the prospect of repeatability in results.

For many analyses attempted, particularly at the species level, it soon became apparent that the 'hallmark' of this investigation was the individual nature of each replicate examined. This caused obvious difficulties in assessments of individual species responses either vegetatively or as seedlings, in gaps of particular characteristics. Particular difficulty was experienced in smaller gaps especially in relation to seedlings. The small surface area of these gaps relative to the larger ones may lead to a false picture of the importance of such gaps for seed regeneration. Increased replication of such treatments is essential if comparisons of naturally-occurring seedling phenomena are to be attempted between small and large gaps.

In view of the inadequate replication of small gaps, many of the analyses concerned with responses of individual species in these treatments have been regarded with caution. However, at levels above that of individual species, useful generalizations did emerge, e.g. the greater importance in small gaps of overhanging vegetation, the role of gaps in promoting seed regeneration on the north-facing slope, and the mobility of seeds of all species resulting from soil creep on the south-facing slope. In larger gaps where data were more reliable, differences between species in patterns of seedling establishment were detected also.

Many previous studies of seedling establishment of grassland plants in either field or garden plots have involved manual sowing of seeds, e.g. Charles (1961), Ross & Harper (1972), Kays & Harper (1974) and Silvertown & Wilkin (1983). In consequence large numbers of seedlings generally emerge and density dependent mortality may occur. Examination in the present study of natural regeneration phenomena in Millersdale, has revealed that at one site at least, seedling numbers are unlikely to be sufficiently large to lead to density dependent mortality.

Care must be exercised in extrapolations between controlled laboratory and field investigations and naturally-occurring phenomena. For example, Silvertown & Wilkin (1983) discovered by sowing 400 seeds each of Centaurea nigra and five other species into chalk grassland, that seedling emergence was closely related to degree of plant cover. In Millersdale the natural occurrence of C. nigra seedlings is unlikely to be dependent on such characteristics.

Fallen seed heads of this species were heavily predated by the vole population on the north-facing slope and very small numbers of seedlings of C. nigra occurred. Such very small populations are particularly vulnerable to unpredictable events such as predation by molluscs or upheaval by vole activity.

STUDY OF GAP RECOLONIZATION AS AN AID TO UNDERSTANDING THE VEGETATION OF NORTH- AND SOUTH-FACING SLOPES IN MILLERSDALE

There have been many previous studies of the vegetation developed on north- and south-facing slopes on calcareous substrata, (e.g. Pigott 1958, 1968; Perring 1959, 1960; Watson 1960; Ratcliffe 1961; Pope 1973; Sydes 1980). Particular attention has been paid to the factors controlling the restriction of certain species to north- or south-facing slopes, a feature which seems to be related to the wider geographical distribution of the species in question (Pigott 1958, 1968; Jarvis 1963). Differences in moisture relations between the two aspects are frequently cited as major determinants of species occurrence on such slopes, a view supported by the fact that many species of drier south-facing slopes exhibit classic xeromorphic adaptations. Pope (1973) has demonstrated experimentally, the poorer resistance of seedlings of species characteristic of north-facing slopes, e.g. Rumex acetosa, Potentilla erecta and Holcus lanatus to treatments simulating droughts of the intensity and duration of those experienced on south-facing slopes in Derbyshire.

Although the two sites in Millersdale selected for study and described in this thesis were located on a north- and a south-facing slope on the Carboniferous limestone in Derbyshire, the objective of the present investigation was not to identify major climatic or topographic influences on the vegetation, but rather to examine the dynamic structure of such contrasted communities by investigating species responses to the artificial creation of gaps in the turf. It was found that the recovery process occurred largely through the vegetative regrowth of damaged plants (Chapter 3). Regeneration from seed also occurred but the importance of gaps in facilitating this process differed considerably on the two slopes (Chapter 4). Seedling position relative to the position of vegetative regrowth appeared to be an important determinant of 'success' but the influence of proximal vegetation was quite different on the two slopes (Chapter 5).

(a) Vegetative recolonization

Analysis of initial patterns of recovery after autumn damage (Figs.3.4 and 3.5) revealed considerable differences in species responses. The phenological cycle and in particular the time of year at which species usually reach a peak of biomass production proved to be a good indicator of their recovery potential in autumn-cut gaps. The tendency of bryophyte species to grow well in cooler, moister weather conditions, greatly enhanced their likelihood of being early colonists of autumn gaps also. On the north-facing slope in Millersdale, where bryophytes are an important component of the turf, the prominence of faster-growing species such as Pseudoscleropodium purum (Furness 1980; Furness & Grime 1982) in gaps created late in the year is not surprising.

However, there were no consistent relationships with either potential growth rate or nuclear DNA content in differential species responses to damage. Recorded R_{max} values (Grime & Hunt 1975) are based on measurements made on seedlings under laboratory conditions and may not therefore be a strong indicator of growth potential in established plants. Large nuclear DNA contents appear to confer a particular advantage in the expansion of leaf photosynthetic area at the beginning of the growing season (Grime, Shacklock & Band 1984). However, differences between species tend to disappear as the season progresses, plants with small and large nuclear DNA contents growing equally well.

On both slopes the longer term effects of gap cutting appeared to be expressed as changes in the relative abundance of species. By the end of the experiment, on the north-facing slope certain species, particularly grasses, were much reduced in importance in gaps relative to undisturbed vegetation. On the south-facing slope changes in relative abundance were in general less marked than on the north-facing slope where the hierarchy of species established amongst resprouts soon after gap cutting bore little relation to that prevailing at the time of final harvest in 1981.

A previous investigation of the vegetation of the south-facing slope in Millersdale (Grime & Curtis 1976), suggests that species established at this site are strongly influenced by both drought and mineral nutrient stress. Under these conditions natural selection appears to have favoured slower-growing species with limited capacities for lateral spread. Such a combination of characteristics is unlikely to promote the rapid expansion of certain members of the community even taking into account the flush of nutrients which may have occurred as a result of damage inflicted during gap cutting. It is not surprising therefore, that little alteration in the relative abundance of species in gaps occurred over the period of the experiment.

In contrast, vegetation developed on the north-facing slope contains a mixture of species, many of which, e.g. Arrhenatherum elatius, Anthoxanthum odoratum, Holcus lanatus and Plantago lanceolata, are common components of other more productive grassland communities. The increased importance of these species in gaps suggests that damage to the turf may be involved in the mechanism allowing their co-existence with other longer-lived or more slowly-growing plants, e.g. Carex flacca and Succisa pratensis, in the vegetation at this site. Localized disturbances caused by vole activity or more widespread fire damage may be sufficient natural causes to maintain these species in the community over long periods. A similar dependence on disturbance was indicated for a number of minor components, e.g. Viola riviniana, which appeared to benefit from the relaxation of competitive dominance resulting from gap cutting.

The creation of artificial gaps and quantitative analysis of the recolonization process, has thus considerably aided our understanding of the interactions between species in these two contrasted limestone grassland communities. The effects of gap cutting in autumn and spring are summarized in Fig.6.1 which shows biomass attained by different species in the system, plotted according to the position occupied by each in a matrix, obtained by triangular ordination of common vegetation types of the Sheffield region using concepts based on Grime's model (Grime 1974). The ordination method is described in Appendix 8. Such diagrams clearly show the differences in composition of the vegetation of the two slopes and the shift in favour of more competitive and ruderal species (sensu Grime 1974) after gap cutting on the north-facing slope, contrasting with the relatively small changes experienced on the south-facing slope.

Fig. 6.1 The composition of the vegetation in 40 cm diameter controls and gaps on a north- and a south-facing slope in Millersdale.

KEY TO SPECIES BIOMASS

○	<1.00 g m^{-2}
○	1.00-3.16 g m^{-2}
○	3.16-10.00 g m^{-2}
○	10.00-31.62 g m^{-2}
○	31.62-100.00 g m^{-2}
○	100.00-316.23 g m^{-2}

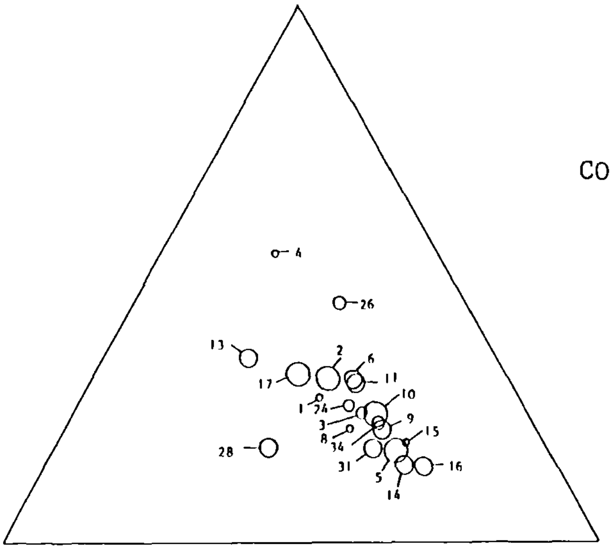
KEY TO SPECIES

1	Achillea millefolium
2	Agrostis capillaris
3	Anthoxanthum odoratum
4	Arrhenatherum elatius
5	Avenula pratensis
6	Avenula pubescens
7	Briza media
8	Campanula rotundifolia
9	Carex caryophyllea
10	Carex flacca
11	Centaurea nigra
12	Centaurea scabiosa
13	Dactylis glomerara
14	Danthonia decumbens
15	Galium sterneri
16	Festuca ovina
17	Festuca rubra
18	Helianthemum nummularium
19	Hieracium pilosella
20	Holcus lanatus
21	Koeleria macrantha
22	Leontodon hispidus
23	Linum catharticum
24	Lotus corniculatus
25	Luzula campestris
26	Origanum vulgare
27	Pimpinella saxifraga
28	Plantago lanceolata
29	Poa pratensis
30	Polygala vulgaris
31	Succisa pratensis
32	Thymus praecox
33	Trisetum flavescens
34	Viola riviniana

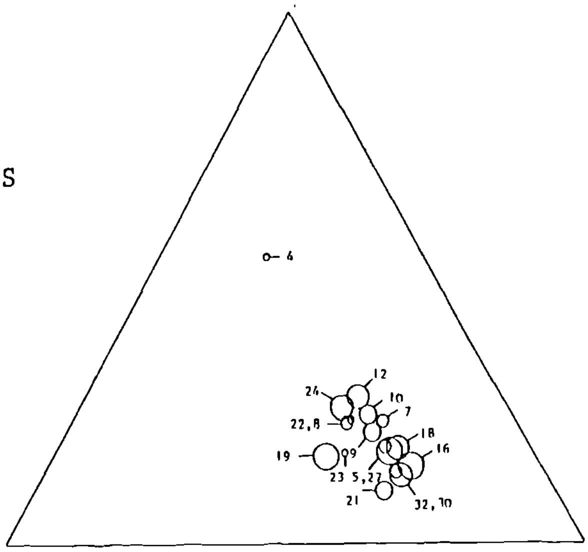
Fig. 6.1
(contd.)

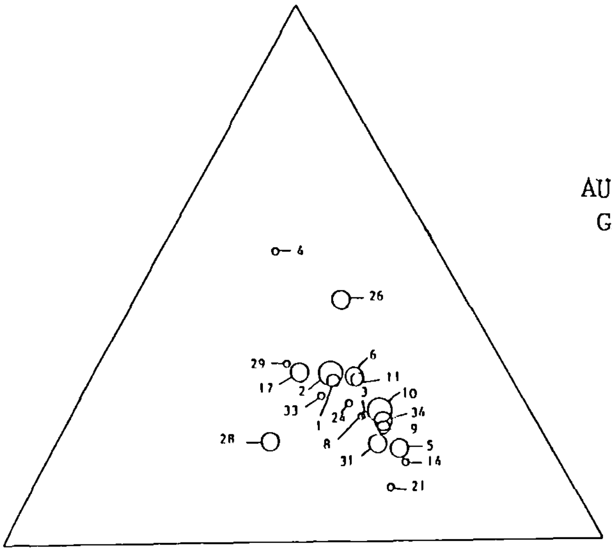
NORTH-FACING SLOPE

SOUTH-FACING SLOPE

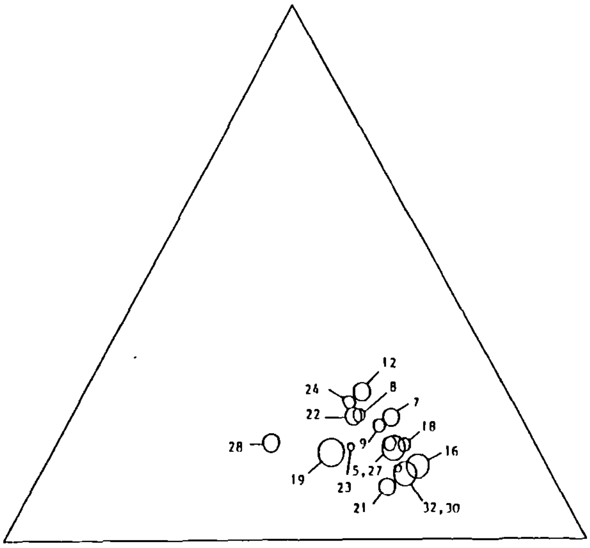


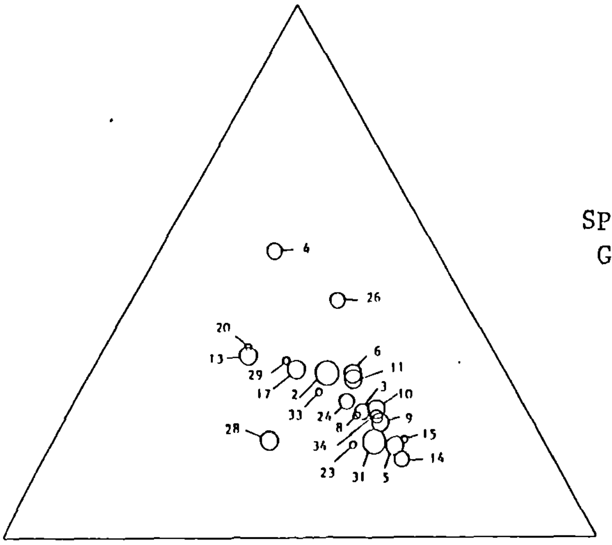
CONTROLS



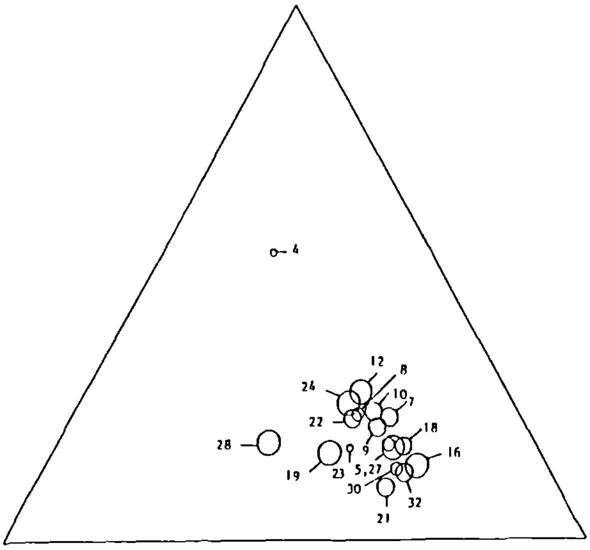


AUTUMN
GAPS





SPRING
GAPS



(b) Seedling colonization

Differences between the two slopes were apparent also in the contribution of seedlings to the gap recolonization process. Although varying in identity according to season, seedlings were a common component throughout the year, in the turf on the south-facing slope and creation of artificial gaps did not greatly increase their number. In contrast, regeneration from seed on the north-facing slope was strongly gap-dependent as manifested by the explosive increase in germination in gaps and enhanced survival of seedlings in less dense vegetation.

The seedling flora on both slopes bore some impact of season. Low levels of autumn germination on the north-facing slope contrasted markedly with the preponderance of perennial grass species which occurred as seedlings at this time on the south-facing slope. Here the more or less synchronous germination in moist autumn conditions of species such as *Festuca ovina*, *Koeleria macrantha* and *Avenula pratensis*, may facilitate the exploitation of bare ground created by summer drought damage. Seedlings of perennial forb species were abundant in the spring, especially on the north-facing slope.

More species were represented as seedlings in large gaps on both slopes but it was a notable feature of the seedling flora that the species most common in the established turf were not necessarily the most abundant as seedlings. This was particularly true on the north-facing slope where *Plantago lanceolata* and *Origanum vulgare*, both relatively minor components of the established community were prominent as gap colonists from seed. These two species appear to maintain large reserves of seed in the soil (Thompson 1977; Thompson

& Grime 1979) and in consequence, rapid colonization of unpredictable disturbances in response to altered light and temperature regimes is possible.

Few seedlings of Origanum vulgare survived the period of the experiment but many seedlings of Plantago lanceolata developed into large and robust individuals and one specimen flowered. It seems likely that this species although capable of some local vegetative expansion, is partially dependent for continued existence in the turf on regeneration from seed in local bare patches. Such dependence on opportunities for seed regeneration corresponds with patterns observed for other short-lived forbs in chalk grassland such as Scabiosa columbaria and Linum catharticum (Verkaar et al. 1983).

Of the species most abundant in the established turf Festuca ovina on the south-facing slope was the only one for which large numbers of both freshly-germinated and surviving seedlings were recorded. Grime & Curtis (1976) suggest that the spread of this small tussock species is strongly dependent on seedling establishment, although Watt (1981) also reports spread by rooting of peripheral shoots as ageing tussocks decay. Large viable seed collections of Avenula pratensis, Succisa pratensis, Helianthemum nummularium, Thymus praecox and many other common species on the two slopes were made by E. G. Cresswell for use in experiments described in Cresswell (1982). The paucity of seedlings of these species in gaps in Millersdale was apparently not related to either failure of seed production or poor viability.

Silvertown & Wilkin (1983) suggest that "cover dependent germination and mortality plays a significant role in the colonization of gaps but a lesser role in determining which species establish successfully." Studies of the position of seedlings in relation to cover from re-establishing plants in the Millersdale gaps (Chapter 5), suggest that cover dependent mortality is indeed an important determinant of establishment. Both positive and negative effects of cover were observed on south- and north-facing slopes respectively, and some differences were observed between species. Such interactions between seedlings and re-establishing vegetation are an important feature of the gap recolonization process and have received little detailed study in previous investigations.

In the less severe conditions associated with open soil on the north-facing slope, large numbers of seeds germinated and a greater proportion of seedlings survived and attained substantial dry weights in situations where cover remained sparse. However, seedlings of some species, notably Origanum vulgare, persisted in denser vegetation at this site, and on the south-facing slope association with established vegetation considerably enhanced survival. Many of the seedlings in these situations were relatively small but healthy at the time of final harvest. The fact that close proximity to established plants did not lead to increased risk of mortality conflicts with previously held ideas on the competitive exclusion of seedlings from turf composed of perennial species. Recent evidence from studies of mycorrhizal connections between plants of different species suggests that carbon may be transferred between unrelated plants through a common fungal mycelium. Further, it is postulated that transfer is strongly influenced by shading of 'receiver' plants (Francis & Read 1984). A mechanism of this kind may enable seedlings of a number of species to persist in close proximity to larger plants and may also be responsible for the continued existence of large numbers of seedlings in undisturbed turf on the south-facing slope.

Although not a full-scale demographic survey, the investigations of regeneration from seed in artificially-created gaps described in Chapters 4 and 5 have yielded considerable insights into the vegetation dynamics of the two study sites in Millersdale. It has been shown that although gap recolonization occurred largely as a result of vegetative regeneration, the importance of gaps for the successful sexual reproduction of species in the community, particularly on the north-facing slope, cannot be ignored. On the north-facing slope, it seems likely that a considerable proportion of the seedlings which appeared in gaps arose from persistent reserves of seed in the soil (Table 4.9). This situation provides field evidence in support of the role of seed bank models Type III and IV (as proposed by Thompson & Grime 1979) in the maintenance of diversity in systems suffering spatially and temporally unpredictable disturbance.

On the south-facing slope, species with seed reserves conforming to seed bank models Type I and II (Thompson & Grime 1979) were prominent in the community. More or less synchronous germination in these species in either autumn or spring appears to facilitate efficient exploitation of gaps which are a regular and recurring natural feature of the turf after summer drought and winter frost damage. At this site the creation of artificial gaps did not greatly increase seedling totals of perennial species, but the occurrence of vigorous seedlings, likely to be successful in establishment, was clearly associated with bared areas.

From a large number of previous studies it is established that newly emerged seedlings are extremely vulnerable and may be obliterated in a variety of ways, e.g. Miles (1973). Seedlings emerging in shade may be particularly vulnerable (e.g. Grime 1965;

Mahmoud & Grime 1974). Fungal attack (reviewed by Burdon 1982) is a common cause of seedling mortality, but unfavourable climatic conditions and predation may provide significant early checks on seedling growth. The gap studies reported in this thesis have shown that susceptibility to soil disturbance and later interactions with proximal established plants may be important determinants of germination, survival and subsequent establishment of seedlings in grasslands developed on north- and south-facing limestone slopes in Derbyshire.

EVIDENCE FOR THE EXISTENCE OF REGENERATION NICHES

Niche differentiation is a mechanism frequently invoked in attempts to explain co-existence in species-rich communities (e.g. Whittaker 1975; Grime 1979; Tilman 1982). The theoretical variety of niches available is expanded if Grubb's ideas on the existence of a 'regeneration niche' are accepted (Grubb 1977). In order that regeneration niches may contribute to the mechanisms maintaining co-existence at a site, it is necessary for species to differ from each other in one or more aspects of their reproductive biology.

Salisbury provides copious data on variations in seed production in common species (Salisbury 1942) while Ridley (1930) and Van der Pijl (1972) document the enormous range of dispersal mechanisms exhibited by plants. There is also abundant evidence that species vary in their abilities to germinate at different seasons of the year (Thompson & Grime 1979; Cresswell 1980, and this study).

The problem is to determine whether such variations between species are sufficient to allow continued co-existence. However, as postulated by Grubb (1977), differences in reproductive biology between co-existing species may cause critical differences in their abilities to exploit gaps of varying characteristics. The time of year at which such disturbances occur may also favour some species rather than others.

In the investigation described in this thesis, the variability in seedling numbers and identity between replicates previously discussed, precludes attempts to identify affinities between species and different gap types in the manner envisaged by Grubb (1976) for chalk grasslands and Denslow (1980) for tropical rainforests. Studies in which seeds are sown into gaps are likely to be more informative in this respect. There is no doubt, however, that the time of year at which a gap is formed may have important implications for seedling colonization. The seedling flora which appears is not only dependent on the ability of species to germinate in prevailing weather conditions, but is also governed in the longer term by the rate at which a gap is healed vegetatively. Evidence from this investigation suggests that autumn-cut gaps, due to their slower rate of infill, provide the greatest opportunities for a variety of species to establish.

However, if regeneration niches are to play a part in maintaining diversity in a community, species must differ from each other in a more precise manner than this. Analyses of seedling establishment in relation to vegetative recovery in gaps (Chapter 5) revealed that certain species did appear to differ in their regeneration characteristics beyond the stage of flowering, seed set and dispersal. On the north-facing slope Origanum vulgare and Holcus lanatus seemed to germinate in rather different micro-sites. Plantago lanceolata, while of more widespread occurrence as seedlings, appeared to be less tolerant of dense vegetation than O. vulgare and more tolerant than H. lanatus and Viola riviniana, both of which were strongly dependent on more open situations for survival and growth. Similarly, on the south-facing slope there was evidence that two co-existing species, Festuca ovina and Pimpinella saxifraga, both strongly dependent on seed regeneration due to limited capacities for lateral spread, exhibited rather different abilities to persist in a range of vegetation densities. Such subtle differences in germination and seedling survival may indicate the existence of distinct regeneration niches for such species.

CURRENT THEORIES ON THE MAINTENANCE OF SPECIES DIVERSITY

Popular theories on the maintenance of species diversity fall into two distinct groups; those which demand that the community is in equilibrium and those which do not. Equilibrium is generally accepted to involve a competitive balance between species and it is essential to equilibrium theories that impacts of environment and management should be relatively constant from year to year and over the area of vegetation studied. In such situations the maintenance of diversity is thought to require a high degree of niche differentiation (Whittaker 1975). An extensive theory of niche differentiation based on complementary mechanisms of resource capture and/or demand, has been proposed by Tilman (1982).

Non-equilibrium theories of species diversity have been formulated to deal with situations in which the attainment of competitive balance is prevented, usually as the result of localized or unpredictable disturbances, e.g. Connell (1972, 1978), Pickett (1980). The models of Grime (1973, 1979) and Huston (1979) also recognize the role of disturbance in controlling species diversity and as such may qualify as non-equilibrium models. However, Peet, Glenn-Lewin & Wolf (1983) contend that both these models are in fact equilibrium models since they describe a type of diversity maintained under relatively constant and predictable forms of disturbance.

Difficulties in applying such models to practical problems are further complicated by difficulties in the recognition of equilibrium communities in a field situation. The two sites in Millersdale contain many species, e.g. *Avenula pratensis*, *Koeleria macrantha*, and *Carex caryophyllea*, found by Wells *et al*. (1976) to be restricted to swards probably undisturbed for at least 130 years, and as such might indicate habitat and community continuity. However, it is known that management practices in the dale, particularly the grazing of sheep, have altered in recent times. The known history of periodic burning, formerly deliberate but more recently accidental (Lloyd 1968), also tends to suggest that external forces may be instrumental in defining the character of the established vegetation.

In Millersdale it is clear that disturbance in the form of artificially-created gaps does not lead to the introduction of species new to the systems either from a soil seed bank or even from wind-dispersed seed. On the south-facing slope, gaps are a natural and regularly occurring feature in the vegetation, being caused by summer drought and winter frost damage. It is likely that the variety of species occurring at this site is due in large measure to such vicissitudes of climate, interacting with mineral nutrient stress to prevent any individual species becoming dominant over large areas. Many of the species on this site are represented by discrete individuals with poor capacities for lateral spread. In this connection it is interesting to note that even the most abundant grass, *Festuca ovina*, appears to be strongly dependent on reproduction from seed and many species have transient seed banks and synchronous germination, a characteristic which has been linked with seasonally predictable disturbance (Thompson & Grime 1979).

On the north-facing slope, disturbance in the form of gaps, while greatly increasing opportunities for regeneration from seed, also had a marked impact on the composition of the sward as a whole. The tendency of Avenula pratensis and other grasses such as Dactylis glomerata and Festuca rubra, to grow large and shade out other members of the community was halted by the kind of damage suffered during and after gap creation. In consequence a number of species less able to tolerate the expansion of these potential dominants were found to occur in greater abundance. Intermittent disturbance thus appears to be an important factor in the maintenance of diversity among established plants at this site.

After analysis of events succeeding experimental interference it is proposed that the vegetation of the north-facing slope in Millersdale corresponds to a non-equilibrium community in which diversity may be explained by theories of micro-succession in gaps (Connell 1972; Picket 1980). In contrast, the diverse community established on the south-facing slope, only a few hundred yards away, appears to contain an assemblage of plants in concert with regular and predictable disturbances caused by seasonal variations in weather, and the continual mineral nutrient stress characteristic of limestone soils. Quantitative analyses of gap recolonization phenomena after artificial disturbances revealed little alteration in the relationships between species at this site, suggesting that the vegetation of the south-facing slope represents an equilibrium community.

IMPLICATIONS FOR MANAGEMENT

Equilibrium communities, by their very nature, are resilient, i.e. they return to equilibrium after disturbance (Pimm 1984). However, degree of resilience in slow-growing systems, such as that on the south-facing slope in Millersdale, depends on the magnitude of the perturbation experienced and it is conceivable that major disturbances may have such impact that return to equilibrium does not occur. In such circumstances a new community with differing characteristics might establish. Manual interference with vegetation structure in such communities therefore requires a certain amount of care; too little is unlikely to have any visible effects, too much may alter the characteristics of the community beyond immediate repair. In non-equilibrium systems such as the vegetation of the north-facing slope the task of the manager is more clear-cut since the character of the community will undoubtedly change unless disturbances occur from time to time.

In Millersdale it seems that diversity in the two grassland systems is being maintained by naturally occurring phenomena, i.e. climate and nutrient status on the south-facing slope and occasional fires and small-scale vole activity on the north-facing slope. However, at this latter site accidental fires are increasingly rare and the expansion of Avenula pratensis tussocks noted over the period of the investigation suggests that fire as a controlling mechanism on diversity is of less importance than formerly. In consequence, competitive exclusion of some of the more minor components is to be expected in the long term. Studies of the process of recolonization in artificially-created gaps, as reported in this thesis have revealed that the possibility exists for 'fine-tuning' of species composition and relative abundance, although, due to the character of the vegetation, there is less scope for manipulation on the south-facing slope.

It is clear that management for a forb-rich community must involve damage at both sites and particularly in the more productive vegetation of the north-facing slope. Here the effect of disturbance is to reduce the abundance and competitive influence of grasses, so allowing some of the 'understorey' species such as Viola riviniana and Plantago lanceolata and many other minor components to expand. It is likely that repeated clearances would be necessary to maintain these latter species in a position of prominence.

On the south-facing slope, where some differential species responses to damage at various times of the year occurred, the possibility exists for management designed to manipulate the abundance of individual species in a controlled way. Thus removing vegetation to ground level in the autumn could be used either to promote Thymus praecox or reduce Lotus corniculatus while creation of a shorter turf would allow the expansion of species such as Hieracium pilosella and Leontodon hispidus. Conversely, extensive damage should be avoided if Helianthemum nummularium is a desirable component of the turf.

In order to promote regeneration from seed and thus enhance genetic diversity in vegetation such as that developed on the north-facing slope the creation of gaps appears to be essential. However, the prevailing weather conditions at the time of year at which a gap is formed are likely to have a strong controlling influence on the seedling flora which appears. Since weather conditions are not predictable with season in Britain, considerable variations in flowering, seed set and timing and quantity of germination are to be expected from year to year. For these reasons gaps created at identical periods in successive years may result not only in differing seedling totals but also varied grass forb ratios and even substantial changes in species composition. Such was shown to be the case in Millersdale. For similar reasons it is not possible to predict seedling input from particular species. Seedlings of Thymus praecox, were considerably more numerous in gaps cut in the spring of 1980 than in the spring of 1979. This has important implications in a management context for although it may be possible to identify conditions favourable for a particular species, e.g. gaps of suitable character created at particular times of the year, there are no guarantees that desirable seedling numbers will appear.

The time of year at which gaps were created in this investigation may have had negative effects also. It seems very likely that seedlings of species capable of germinating early in the year. e.g. Linum catharticum, Viola riviniana and Succisa pratensis, were actually removed by spring gap cutting activities. For these species the timing of artificial gap creation is critical. Many more seedlings of these species were found in gaps cut the previous autumn.

By means of the study of the natural process of gap recolonization in Millersdale, it has been possible to characterize the vegetation of these north- and south-facing limestone slopes not only in terms of their species composition but also in terms of the dynamic relationships between species and the preponderance of sexual and asexual regeneration. Such information greatly increases the possibilities for effective management in these and similar situations.

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APPENDIX 1

North-facing slope: species composition of the established vegetation in the experimental area (October 1978).

Species	Total dry wt. ($g\ m^{-2}$)	% of total dry wt.
Agrostis canina	0.022	<0.01
Agrostis capillaris	1.949	0.19
Anthoxanthum odoratum	2.371	0.24
Arrhenatherum elatius	2.783	0.28
Avenula pratensis	7.403	0.74
Avenula pubescens	12.373	1.24
Dactylis glomerata	19.851	1.98
Danthonia decumbens	1.742	0.17
Festuca ovina	0.264	0.03
Festuca rubra	13.484	1.35
Holcus lanatus	1.195	0.12
Poa pratensis	0.636	0.06
Trisetum flavescens	0.422	0.04
TOTAL GRASSES	64.494	6.44
Carex caryophyllea	7.066	0.71
Carex flacca	25.546	2.55
Luzula campestris	0.121	0.01
TOTAL GRAMINOIDS	32.733	3.27
Achillea millefolium	3.377	0.34
Angelica sylvestris	1.186	0.12
Campanula rotundifolia	1.051	0.11
Centaurea nigra	12.749	1.27
Galium saxatile	0.011	<0.01
Galium sterneri	0.440	0.04
Galium verum	5.108	0.51
Hieracium sp.	0.040	<0.01
Hypericum perforatum	0.338	0.03
Leontodon hispidus	0.138	0.01
Lotus corniculatus	3.210	0.32
Origanum vulgare	6.834	0.68
Pimpinella major	0.844	0.08
Pimpinella saxifraga	0.254	0.03
Plantago lanceolata	6.986	0.70
Potentilla erecta	0.182	0.02
Rumex acetosa	0.004	<0.01
Serratula tinctoria	0.740	0.07
Succisa pratensis	31.311	3.12
Valeriana officinalis	3.120	0.31
Viola riviniana	2.071	0.21
Unidentified forbs	0.784	0.08
TOTAL FORBS	80.775	8.06

APPENDIX 1 (contd.)

Species	Total dry wt. (g m^{-2})	% of total dry wt.
TOTAL LIVING HIGHER PLANTS	178.003	17.76
HIGHER PLANT LITTER	320.502	31.98
TOTAL HIGHER PLANT MATERIAL	498.504	49.74
Bryum sp.	0.607	0.06
Bryum rubens	0.011	<0.01
Calliergon cuspidatum	5.280	0.53
Dicranum scoparium	16.476	1.64
Eurhynchium praelongum	41.836	4.17
Eurhynchium striatum	5.056	0.51
Fissidens taxifolius	0.407	0.04
Hypnum cupressiforme	24.115	2.41
Lophocolea bidentata	10.148	1.01
Mnium hornum	0.455	0.05
Plagiomnium undulatum	4.612	0.46
Pseudoscleropodium purum	51.949	5.18
Thuidium tamariscinum	0.916	0.09
Tortula ruralis	0.011	<0.01
Unidentified bryophytes	1.204	0.12
TOTAL LIVING BRYOPHYTES	163.083	16.27
BRYOPHYTE LITTER	340.662	33.99
TOTAL BRYOPHYTE MATERIAL	503.745	50.26
TOTAL STANDING CROP + LITTER	1002.249	

APPENDIX 2

South-facing slope: species composition of the established vegetation in the experimental area (October 1978).

Species	Total dry wt. (g m^{-2})	% of total dry wt.
Arrhenatherum elatius	0.309	0.04
Avenula pratensis	39.436	4.88
Avenula pubescens	0.084	0.01
Brachypodium sylvaticum	1.498	0.19
Briza media	3.047	0.38
Dactylis glomerata	5.767	0.71
Danthonia decumbens	1.516	0.19
Festuca ovina	18.604	2.30
Festuca rubra	2.520	0.31
Koeleria macrantha	13.607	1.69
Trisetum flavescens	0.007	<0.01
TOTAL GRASSES	86.396	10.70
Carex caryophyllea	1.520	0.19
Carex flacca	0.240	0.03
TOTAL GRAMINOIDS	1.760	0.22
Arabis hirsuta	0.956	0.12
Campanula rotundifolia	0.095	0.01
Centaurea nigra	0.236	0.03
Centaurea scabiosa	2.200	0.27
Galium sterneri	0.516	0.06
Hieracium sp.	0.298	0.04
Hieracium pilosella	19.611	2.43
Linum catharticum	0.298	0.04
Lotus corniculatus	1.971	0.25
Origanum vulgare	0.091	0.01
Pimpinella saxifraga	1.629	0.20
Plantago lanceolata	0.458	0.06
Polygala vulgaris	0.200	0.03
Succisa pratensis	0.091	0.01
Veronica officinalis	0.080	0.01
TOTAL FORBS	28.731	3.56
Helianthemum nummularium	10.626	1.32
Thymus praecox	21.029	2.60
TOTAL SHRUBS	31.655	3.92

APPENDIX 2 (contd.)

Species	Total dry wt. (g m^{-2})	% of total dry wt.
TOTAL LIVING HIGHER PLANTS	148.542	18.39
HIGHER PLANT LITTER	468.920	58.07
TOTAL HIGHER PLANT MATERIAL	617.462	76.46
TOTAL LIVING BRYOPHYTES	53.786	6.66
BRYOPHYTE LITTER	133.524	16.53
LICHENS	2.789	0.35
TOTAL LOWER PLANT MATERIAL	190.098	23.54
TOTAL STANDING CROP + LITTER	807.560	

APPENDIX 3

Summary of final harvest results from controls, gaps and scrapes on the north-facing slope.

Mean dry weight (g m^{-2})

	Controls*	Autumn 40 cm gaps	Spring 40 cm gaps	Autumn 20 cm gaps	Spring 20 cm gaps	Autumn 10 cm gaps	Spring 10 cm gaps	Autumn 20 cm scrapes	Spring 20 cm scrapes	Autumn 10 cm scrapes	Spring 10 cm scrapes
Grasses	61.3± 58.8	29.3± 16.0	49.4± 17.6	27.8± 17.9	20.4± 21.2	33.1± 58.1	23.6± 31.5	15.0± 13.7	8.7± 9.8	2.5± 2.2	10.5± 16.0
Graminoids	18.9± 8.3	16.7± 8.9	14.7± 7.1	10.8± 5.6	14.4± 9.5	16.5± 11.3	20.9± 17.6	11.6± 13.0	6.2± 6.6	10.3± 7.2	5.1± 7.9
Forbs	25.5± 13.3	30.1± 19.5	34.3± 13.7	32.4± 19.6	73.1± 69.9	7.4± 6.4	15.7± 13.2	12.7± 7.5	17.4± 10.5	4.5± 5.9	4.1± 4.1
Trees/shrubs	trace	-	-	-	trace	-	-	-	-	-	-
TOTAL: Rooted herbs	105.7± 71.0	76.1± 39.9	98.4± 18.1	71.0± 40.3	107.9± 83.6	57.0± 65.9	60.1± 51.7	39.3± 30.8	32.4± 15.9	17.3± 13.2	19.7± 21.6
Herb litter	222.9± 46.6	162.7± 37.0	205.1± 30.0	157.6± 53.2	147.4± 42.7	166.9±138.4	138.6± 74.1	113.5± 46.1	129.2± 28.8	117.8± 42.7	95.4± 42.3
Live bryophytes	57.3± 36.8	29.1± 24.5	27.2± 10.8	27.6± 20.1	35.6± 17.6	32.8± 10.4	62.1± 26.2	38.5± 11.9	46.2± 22.0	41.2± 28.2	46.8± 12.9
Bryophyte litter	248.5±163.3	47.2± 34.0	48.0± 25.7	100.5± 36.8	115.9± 85.7	79.1± 46.9	77.4± 47.3	93.5± 54.4	58.5± 26.5	138.4±113.7	63.4± 26.9
TOTAL: Bryophytes	305.7±195.8	76.4± 52.5	75.2± 34.8	128.1± 41.7	151.5± 96.9	111.9± 45.0	139.6± 48.7	132.0± 60.2	104.7± 46.7	179.6±116.0	110.1± 44.0
Annuals/ biennials	-	0.1± 0.1	trace	trace	-	-	-	trace	trace	-	-
Marked seedlings	0.3± 0.3	6.0± 7.6	2.1± 2.1	3.9± 6.6	4.4± 4.3	0.2± 0.3	0.8± 1.6	0.8± 0.9	1.2± 2.3	0.1± 0.3	0.7± 1.4
Unmarked seedlings	0.2± 0.1	0.5± 0.4	0.6± 1.1	0.5± 0.3	0.6± 0.5	0.3± 0.5	0.5± 0.9	0.5± 0.7	0.7± 1.0	0.6± 1.1	0.2± 0.5
TOTAL: Seedlings	0.5± 0.4	6.6± 7.4	2.7± 3.0	4.5± 6.7	5.1± 4.6	0.6± 0.6	1.3± 1.8	1.4± 1.2	2.2± 3.0	0.7± 1.1	0.9± 1.5
Overhanging vegetation	37.6± 36.0	29.0± 21.2	27.5± 9.2	84.9± 32.3	96.2± 56.7	171.6± 88.0	119.0± 29.1	73.3± 25.6	154.3±128.8	99.2± 28.6	230.5±194.8
TOTAL: Standing crop + litter	672.4±154.6	350.9± 70.9	408.9± 51.2	446.3± 86.7	508.1±128.3	508.0±158.1	451.4±115.6	359.4± 89.8	422.8±127.6	414.6±125.6	456.2±212.2

N.B. Data for spring 10 cm scrapes are based on six replicates.

* Controls were 40 cm in diameter.

APPENDIX 4

Summary of final harvest results from controls, gaps and scrapes on the south-facing slope.

Mean dry weight (g m^{-2})

	Controls*	Autumn 40 cm gaps	Spring 40 cm gaps	Autumn 20 cm gaps	Spring 20 cm gaps	Autumn 10 cm gaps	Spring 10 cm gaps	Autumn 20 cm scrapes	Spring 20 cm scrapes	Autumn 10 cm scrapes	Spring 10 cm scrapes
Grasses	89.4 ± 34.6	37.6 ± 11.9	49.7 ± 14.9	47.1 ± 27.6	55.9 ± 34.8	44.9 ± 48.9	82.2 ± 30.1	32.2 ± 26.7	25.3 ± 26.1	18.7 ± 14.9	6.0 ± 5.6
Graminoids	8.4 ± 7.6	6.0 ± 6.0	10.2 ± 3.9	19.2 ± 15.3	9.3 ± 8.6	9.2 ± 13.1	2.4 ± 4.4	15.3 ± 16.9	2.9 ± 3.9	-	7.0 ± 10.4
Forbs	74.0 ± 20.8	57.4 ± 24.6	86.8 ± 20.6	68.6 ± 29.1	78.8 ± 41.9	30.2 ± 21.9	52.0 ± 62.3	53.5 ± 30.7	49.5 ± 34.8	60.4 ± 60.2	50.6 ± 67.0
Trees/shrubs	37.4 ± 37.7	26.4 ± 33.9	9.3 ± 5.9	28.0 ± 38.3	12.4 ± 9.7	15.6 ± 22.5	15.6 ± 22.6	27.1 ± 25.9	22.3 ± 15.7	16.0 ± 17.3	9.9 ± 10.3
TOTAL: Rooted herbs	209.3 ± 33.4	127.5 ± 34.9	155.9 ± 27.4	162.9 ± 46.4	156.5 ± 52.6	99.8 ± 63.0	101.3 ± 44.4	128.2 ± 77.8	100.0 ± 48.2	95.1 ± 56.3	73.5 ± 69.6
Herb litter	299.5 ±125.5	122.5 ± 31.8	158.9 ± 28.3	152.2 ± 27.0	147.9 ± 42.5	152.6 ± 73.4	146.1 ± 79.4	150.3 ± 71.7	104.8 ± 55.7	112.9 ± 53.6	130.5 ± 54.5
Live bryophytes	42.7 ± 31.6	7.4 ± 2.9	10.5 ± 6.6	17.8 ± 10.5	9.1 ± 6.0	37.3 ± 18.8	22.1 ± 14.7	38.4 ± 27.0	15.2 ± 10.0	50.1 ± 55.6	77.8 ± 45.5
Bryophyte litter	60.4 ± 69.5	9.9 ± 5.8	10.7 ± 7.6	16.6 ± 12.1	5.2 ± 3.7	21.0 ± 15.4	10.9 ± 4.0	45.3 ± 42.8	9.9 ± 8.7	77.1 ±113.1	73.6 ± 67.1
TOTAL: Bryophytes	103.2 ±101.0	17.3 ± 8.6	21.2 ± 13.6	34.4 ± 24.2	14.2 ± 8.6	58.3 ± 34.6	33.0 ± 15.4	83.7 ± 69.2	25.0 ± 18.4	127.2 ±151.8	151.4 ±100.9
Annuals/ biennials	0.3 ± 0.3	1.0 ± 0.6	0.7 ± 0.4	1.0 ± 1.0.	0.7 ± 0.6	0.6 ± 0.9	0.5 ± 0.6	0.8 ± 0.9	0.9 ± 1.1	0.5 ± 0.7	0.2 ± 0.4
Marked seedlings	1.0 ± 0.7	3.3 ± 2.5	3.8 ± 2.7	2.7 ± 2.1	0.5 ± 0.6	0.3 ± 0.4	0.8 ± 1.1	1.8 ± 1.6	0.5 ± 0.4	2.6 ± 1.7	0.6 ± 0.9
Unmarked seedlings	1.2 ± 0.7	1.5 ± 1.0	2.7 ± 0.6	3.2 ± 1.4	2.8 ± 1.4	1.1 ± 1.4	2.1 ± 1.8	1.7 ± 0.7	3.2 ± 2.3	2.8 ± 2.6	1.1 ± 0.6
TOTAL: Seedlings	2.6 ± 1.2	5.8 ± 2.8	7.2 ± 2.7	6.9 ± 2.1	4.0 ± 2.2	1.9 ± 1.6	3.3 ± 2.6	4.3 ± 2.4	4.5 ± 2.8	5.9 ± 2.9	2.0 ± 1.4
Overhanging vegetation	28.2 ± 20.6	31.0 ± 28.0	21.4 ± 8.3	40.1 ± 27.0	49.6 ± 28.3	178.5 ±175.9	82.2 ± 30.1	64.8 ± 55.3	122.0 ±102.8	90.5 ± 55.2	112.0 ± 36.0
TOTAL: Standing crop + litter	638.7 ±156.1	304.1 ± 46.1	364.6 ± 59.0	396.5 ± 77.3	372.2 ± 76.7	491.1 ±105.2	366.0 ± 61.7	431.3 ±122.2	356.5 ±183.2	431.6 ±187.2	470.9 ±149.5

NB. Data for autumn-cut 20 cm and 10 cm diameter gaps are based on six replicates

* Controls were 40 cm in diameter.

APPENDIX 5

Total number of seedlings recorded in all replicates of each treatment on the north-facing slope.

Treatment codes:

C = controls
40G = 40 cm diameter gaps
20G = 20 cm " "
10G = 10 cm " "
5G = 5 cm " "
20S = 20 cm " scrapes
10S = 10 cm " "
5S = 5 cm " "
20H = 20 cm " hills
5H = 5 cm " "
10M = 10 cm " gaps, with clippings re-applied
10R = 10 cm " gaps, with roots removed

APPENDIX 5

(a) North-facing slope, autumn treatments recorded November 1978.

	C*	40G	20G	20H	20S	10G	10S	10M	10R	5G	5H	5S	TOTAL
GRASSES													
Agrostis capillaris		12		4	11	1			1				29
Anthoxanthum odoratum		1	1										2
Arrhenatherum elatius		4	1				1						6
Avenula pratensis		2				1							3
Avenula pubescens		2											2
Dactylis glomerata		3											3
Festuca rubra		2											2
Holcus lanatus		29		3	2		1	1					36
Koeleria macrantha		1											1
Unidentified grass							2						2
TOTAL GRASSES		56	2	7	13	2	4	1	1	0	0	0	86
FORBS[a]													
Achillea millefolium					1								1
Campanula rotundifolia		3											3
Carex flacca				1									1
Centaurea nigra		5	1	1		1	2						10
Epilobium spp.		1			1								2
Galium sterneri				1									1
Hypericum perforatum		2			1								3
Luzula campestris			1		1		1						3
Origanum vulgare		54	11	16	8	2	3		1				95
Plantago lanceolata		85	16	3	11	1	4	1	3			1	124
Rumex acetosa		1											1
Succisa pratensis				2									2
Taraxacum spp.					1								1
Valeriana officinalis			1				1						2
Unidentified forb		4	1	2	1								8
TOTAL FORBS		155	31	27	25	4	11	1	4	0	0	1	258
TOTAL SEEDLINGS	0	211	32	34	38	6	15	2	5	0	0	1	344

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* 549 cm^2 undisturbed turf.

[a] including the graminoids <u>Carex caryophyllea</u>, <u>Carex flacca</u> and <u>Luzula campestris</u>

(b) North-facing slope, autumn treatments recorded June 1979.
Figures in parentheses are numbers of seedlings surviving in the autumn cohort previously recorded (Appendix 5 (a))

	C*	40G	20G	20H	20S	10G	10S	10M	10R	5G	5H	5S	TOTAL+
GRASSES													
Agrostis capillaris	1	33 (8)	2	(1)	1 (5)	5 (1)		1		1			43 (15)
Anthoxanthum odoratum		10 (2)	3		2	1	3	1	1				21 (2)
Arrhenatherum elatius	1	(2)			2								2 (2)
Avenula pratensis		1	1			(1)	(1)	1					3 (2)
Avenula pubescens		1 (2)											1 (2)
Briza media					1								1
Dactylis glomerata	1	(3)					1		2				3 (3)
Danthonia decumbens	5	7	2							2			11
Festuca ovina	1												0
Festuca rubra	1	(2)											0 (2)
Holcus lanatus	1	30 (18)	6	1 (2)	7 (1)	(1)	1	1 (1)	1				47 (23)
Koeleria macrantha		(1)											0 (1)
TOTAL GRASSES	11	82 (38)	14 (0)	1 (3)	13 (6)	6 (2)	5 (1)	4 (1)	4 (0)	3 (0)	0 (0)	0 (0)	132+ (51)
FORBS[a]													
Achillea millefolium		3	1		1 (1)								5 (1)
Angelica sylvestris	1					1							1
Campanula rotundifolia	4	19 (2)	3	4	4	1	1					2	34 (2)
Carex caryophyllea		7	4										11
Carex flacca		62	10	3	10	3	2		3				93
Centaurea nigra	2	30 (3)	3	5	6	(1)	2 (2)	2					48 (6)
Cirsium palustre		1	1										2
Epilobium spp.	1	2 (1)			4 (1)	1	1	1					9 (2)
Galium sterneri		2											2
Hieracium spp.	2	1				1	4						6
Hypericum perforatum	1	9		1	1				1				12
Leontodon hispidus				2									2
Linum catharticum	2	24	4	1	5		2				1	1	38
Lotus corniculatus		3		2									5
Luzula campestris					(1)			1					1 (1)
Origanum vulgare	5	71 (34)	27 (7)	9 (5)	12 (6)	8 (2)	7 (1)	1	(1)	2		3	140 (56)
Pimpinella saxifraga		3	1	1	3	1	1	1			1		12
Plantago lanceolata	22	127 (53)	38 (6)	6	23 (4)	9	6 (1)	8	1	3	3	3 (1)	227 (65)
Potentilla sterilis		4	1										5
Primula veris				4		1							5
Scabiosa columbaria		1											1
Senecio jacobaea		2											2
Serratula tinctoria	1	1	2										3
Sonchus asper		1											1
Succisa pratensis	5	13	3	10 (2)	7	1	1		1	1		1	38 (2)
Taraxacum spp.	3	1	2		(1)								3 (1)
Valeriana officinalis	2	3		(1)									3 (1)
Viola riviniana	14	45	2	3	4		2	1	3				60
TOTAL FORBS	65	435 (93)	102 (13)	51 (8)	81 (14)	30 (3)	25 (4)	15 (0)	9 (1)	6 (0)	5 (0)	10 (1)	769+(137)
TOTAL SEEDLINGS	76	517(131)	116 (13)	52 (11)	94 (20)	36 (5)	30 (5)	19 (1)	13 (1)	9 (0)	5 (0)	10 (1)	901+(188)

N.B. Data for treatment 10M are based on six replicates.
* 8796.2 cm^2 undisturbed turf.
+ Totals in this column do not include seedlings present in controls.
a including the graminoids Carex caryophyllea, Carex flacca and Luzula campestris.

APPENDIX 5

(c) North-facing slope, spring treatments recorded June 1979.

	C*	40G	20G	20H	20S	10G	10S	10M	10R	5G	5H	5S	TOTAL+
GRASSES													
Agrostis capillaris	1	28	9		6	3		1	1	1		1	50
Anthoxanthum odoratum		9	6			2			1				18
Arrhenatherum elatius	1			1									1
Avenula pratensis		1			1			1					3
Avenula pubescens		2	1				1						4
Dactylis glomerata	1	5	1	1	1								8
Danthonia decumbens	5	11	6	1		1				1			20
Festuca ovina	1												0
Festuca rubra	1	1											1
Holcus lanatus	1	29	12		6	2	2			1			52
Koeleria macrantha		1											1
Trisetum flavescens								2					2
TOTAL GRASSES	11	87	35	3	14	8	3	4	2	3	0	1	160+
FORBS[a]													
Achillea millefolium		3	1		1						1		6
Angelica sylvestris	1												0
Campanula rotundifolia	4	35	9		2		2		1	1		1	51
Carex caryophyllea		15	1		2								18
Carex flacca		64	11		2	1		2	2		1		83
Centaurea nigra	2	30	6	2	9	3	3	1					54
Cirsium palustre		4	1	1	2	1							9
Epilobium spp.	1	2			1	2							5
Heracleum sphondylium									1				1
Hieracium spp.	2	1											1
Hypericum perforatum	1	9	3	1									12
Linum catharticum	2	6								1	3		10
Lotus corniculatus		1		1	1	1			1				5
Luzula campestris									1				1
Origanum vulgare	5	158	25	8	20	11	2	2	8	1	2	1	238
Pimpinella saxifraga		1						1					2
Plantago lanceolata	22	229	56	16	17	9	1	6	7	6	2		349
Primula veris		2											2
Rumex acetosa		4											4
Scabiosa columbaria		1	3										4
Serratula tinctoria	1												0
Sonchus asper		1											1
Succisa pratensis	5	6		4		2							12
Taraxacum spp.	3												0
Valeriana officinalis	2	3	1		1								5
Viola riviniana	14	3	1	1	1	1	1				2		10
Unidentified forb		1											1
TOTAL FORBS	65	579	118	34	59	31	9	12	21	9	11	2	885+
TOTAL SEEDLINGS	76	666	153	37	73	39	12	16	23	12	11	3	1045+

* 8796.2 cm^2 undisturbed turf.

\+ Totals in this column do not include seedlings present in controls.

a including the graminoids <u>Carex caryophyllea</u>, <u>Carex flacca</u> and <u>Luzula campestris</u>.

APPENDIX 6

Total number of seedlings recorded in all replicates of each treatment on the south-facing slope.

Treatment codes:

C = controls

40G = 40 cm diameter gaps

20G = 20 cm " "

10G = 10 cm " "

5G = 5 cm " "

20S = 20 cm " scrapes

10S = 10 cm " "

5S = 5 cm " "

20H = 20 cm " hills

5H = 5 cm " "

10M = 10 cm " gaps, with clippings re-applied

10R = 10 cm " gaps, with roots removed

APPENDIX 6

(a) South-facing slope, autumn treatments recorded November 1978.

	C*^{c}	40G	20G^{b}	20H^{c}	20S^{b}	10G^{b}	10S^{c}	10M^{c}	10R^{c}	5G^{c}	5H^{c}	5S^{b}	TOTAL^{+}
GRASSES													
Anthoxanthum odoratum		1					1						2
Arrhenatherum elatius		3	1		1	1		1					7
Avenula pratensis	1	30	6	1	3	2		1					43
Briza media	4	45	4	3	2	1	1			1	1	1	59
Festuca arundinacea			22			3	1						26
Festuca ovina	13	264	46	9	12	14	7	3	6	6		4	371
Festuca rubra		2											2
Koeleria macrantha	3	94	17	5	6	3	2	5	1	5	7	1	146
Poa pratensis			1										1
Unidentified grass		9	2			1		1					13
TOTAL GRASSES	21	448	99	18	24	25	12	11	7	12	8	6	670^{+}
FORBS^{a}													
Arabidopsis thaliana		1	1	1		43	6	1					53
Campanula rotundifolia		20	3	4				6	1	1			35
Galium sterneri							1						1
Gentianella amarella		51	155	14	10	5		3	1		1	1	241
Helianthemum nummularium		4	1	4									9
Hieracium pilosella		39	2		4	2			1				48
Hieracium spp.			1										1
Hypericum hirsutum			1										1
Leontodon hispidus			1										1
Linum catharticum		1											1
Lotus corniculatus			1		1								2
Origanum vulgare		4										6	10
Pimpinella saxifraga		1						1					2
Polygala vulgaris				4									4
Senecio jacobaea		1											1
Sonchus asper		16	4										20
Taraxacum spp.		1											1
Thymus praecox	1	36	3		3	1							43
Unidentified forb		26	5	1	4	5	1	2					44
TOTAL FORBS^{a}	1	201	178	28	22	56	8	13	3	1	1	7	518^{+}
TOTAL SEEDLINGS	22	649	277	46	46	81	20	24	10	13	9	13	1188^{+}

* 392.7 cm^{2} undisturbed turf.

\+ totals in this column do not include seedlings present in controls.

a including the sub-shrubs Helianthemum nummularium and Thymus praecox.

b data based on 6 replicates.

c data based on 5 replicates.

APPENDIX 6

(b) South-facing slope, autumn treatments recorded June 1979.

	C*	40G	20G	20H	20S	10G[b]	10S	10M	10R	5G[b]	5H	5S	TOTAL+
GRASSES													
Arrhenatherum elatius		1	1										2
Avenula pratensis	22	16	7		2	1	2	1		1		1	31
Brachypodium sylvaticum				1									1
Briza media	1	2	2						1				5
Dactylis glomerata	3		1		1	2						1	5
Festuca arundinacea			9		2								11
Festuca ovina	143	129	52	6	19	8	8	1	8	8	4	6	249
Koeleria macrantha	20	38	10	2	8	1	4	1	1			1	66
Poa pratensis		1	1										2
Trisetum flavescens		1											1
Unidentified grass	1		1										1
TOTAL GRASSES	190	188	84	9	30	14	14	3	10	9	4	9	374+
FORBS[a]													
Arabis hirsuta	1		1		1		1					1	4
Arenaria serpyllifolia		3		1		1							5
Betula pubescens		1											1
Campanula rotundifolia	12	34	8			2	4		1			1	50
Galium sterneri							1	1					2
Gentianella amarella	10	62	3			4	5	1	1				76
Helianthemum nummularium	4	5			1		1						7
Hieracium pilosella	3	6	1		2	1	1						11
Hieracium spp.	1	8	2	1	1				2				14
Hypericum perforatum		5			5								10
Leontodon hispidus	2	1	3			1				1			6
Linum catharticum	229	845	269	57	70	36	69	48	61	17	9	22	1053
Lotus corniculatus	5	16	1	2	5	3	3		1				31
Origanum vulgare		5			8							5	18
Pimpinella saxifraga	31	19	24	18	65	1	9	9			1	4	150
Plantago lanceolata		4			1								5
Polygala vulgaris	2	2	2	1	1	1							7
Senecio jacobaea		5									2		7
Silene nutans	2	6	3		2		1	1				1	14
Solidago virgaurea		2		1	4				1				8
Sonchus asper	6	5	3		1			1			1		11
Taraxacum spp.	1												
Thymus praecox	1	19	3		3		4	3	2				34
Viola hirta		1											1
Unidentified forb		1			1								2
TOTAL FORBS[a]	310	1055	323	81	171	50	99	64	69	18	13	34	1968+
TOTAL SEEDLINGS	500	1243	407	90	201	64	113	67	79	27	17	43	2351+

* 8796.2 cm^2 undisturbed turf.

\+ totals in this column do not include seedlings present in controls.

a including the trees/shrubs *Helianthemum nummularium* and *Thymus praecox* and *Betula pubescens*.

b data based on six replicates.

APPENDIX 6

(c) South-facing slope, spring treatments recorded June 1979.

	C*	40G	20G	20H	20S	10G	10S	10M	10R	5G	5H	5S	TOTAL+
GRASSES													
Arrhenatherum elatius			1										1
Avenula pratensis	22	7	3		3			1	1	2		1	18
Briza media	1	2	2										4
Dactylis glomerata	3	7											7
Festuca arundinacea		1				2							3
Festuca ovina	143	42	18		2	1	3	5	3	1	1		76
Koeleria macrantha	20	23	4		1	2						1	31
Poa pratensis		1				1							2
Trisetum flavescens		1				1							2
Unidentified grass	1												TOTAL
GRASSES	190	84	28	0	6	7	3	6	4	3	1	2	144+
FORBS^a													
Arabis hirsuta	1	3	1										4
Campanula rotundifolia	12	21	3	1		1		1	1	1			29
Carex caryophyllea		1											1
Centaurea scabiosa		1											1
Gentianella amarella	10					1							1
Helianthemum nummularium	4	16	2		2	1	1						22
Hieracium pilosella	3	7			1		1					1	1
Hieracium spp.	1	8	2	1	1					1			13
Hypericum perforatum		10	2										12
Leontodon hispidus	2	7											7
Linum catharticum	229	237	53	22	12	11	6	23	16	6	19	5	401
Lotus corniculatus	5	27	8	1	2	3	4	1	1			1	48
Origanum vulgare		3	1		1		1		1				7
Pimpinella saxifraga	31	33	14	5	1	4	4	4	1				66
Plantago lanceolata		11							1				12
Polygala vulgaris	2	3					2						5
Scabiosa columbaria		1											1
Senecio jacobaea		1							2				3
Silene nutans	2	2	1	1					1				5
Solidago virgaurea		1					1					1	3
Sonchus asper	6	5				2		1	1				9
Taraxacum spp.	1	1											1
Thymus praecox	1	5	4			3	1	1					14
Trifolium campestre			1		4								5
Ulmus glabra			2										2
Viola hirta							1						1
Unidentified forb		1			2		3		1				7
TOTAL FORBS^a	310	405	94	31	26	26	25	31	26	8	10	8	690+
TOTAL SEEDLINGS	500	489	122	31	32	33	28	37	30	11	11	10	834+

* 8796.2 cm^2 undisturbed turf.

+ totals in this column do not include seedlings present in controls.

a including the trees/shrubs Helianthemum nummularium and Thymus praecox and Ulmus glabra, and the graminoid Carex caryophylles.

APPENDIX 7

Laboratory studies of regeneration in gaps

12 matched turves from a productive roadside verge dominated by Elymus repens, Arrhenatherum elatius, Alopecurus pratensis and Dactylis glomerata were transferred to a controlled growth room. In each turf, four gaps (3, 6, 9 and 12 cm in diameter) were created by removing all vegetation within a circular template down to ground level, and a control area 12 cm in diameter was marked.

During the next 80 days, six cohorts of shoots and seedlings were marked with coloured rings in six of the turves but no marking took place in the other six turves. Mortality patterns in the marked cohorts in all 5 treatments were recorded for a period of 180 days after the gaps were first created. After 180 days the plant material which had recolonized gaps in both marked and unmarked turves was harvested destructively, shoot by shoot, each shoot then being identified to species, dried and weighed.

Growth-room studies of this kind have confirmed that the most successful of the shoots invading a vegetation gap are those which appear in the first stage of recolonization. This is illustrated in Fig.A7.1 from which it is apparent that, in Elymus repens, the highest density of survivors in a population of invading shoots occurred in the cohort appearing during the first ten days.

Comparisons between final harvest data obtained from turves which had been marked and those which had not, indicate that marking and recording activities undertaken with such regularity may have seriously affected the process of gap recolonization (Fig.A7.2, Tables A7.1, A7.2 and A7.3).

Fig. A7.1 Survivorship of successive cohorts of *Elymus repens* shoots invading 12 cm diameter gaps in a productive turf.
The cohort sequence is: □ , 1; ■ , 2; ○ , 3; ● , 4; △ , 5; ▲ , 6.

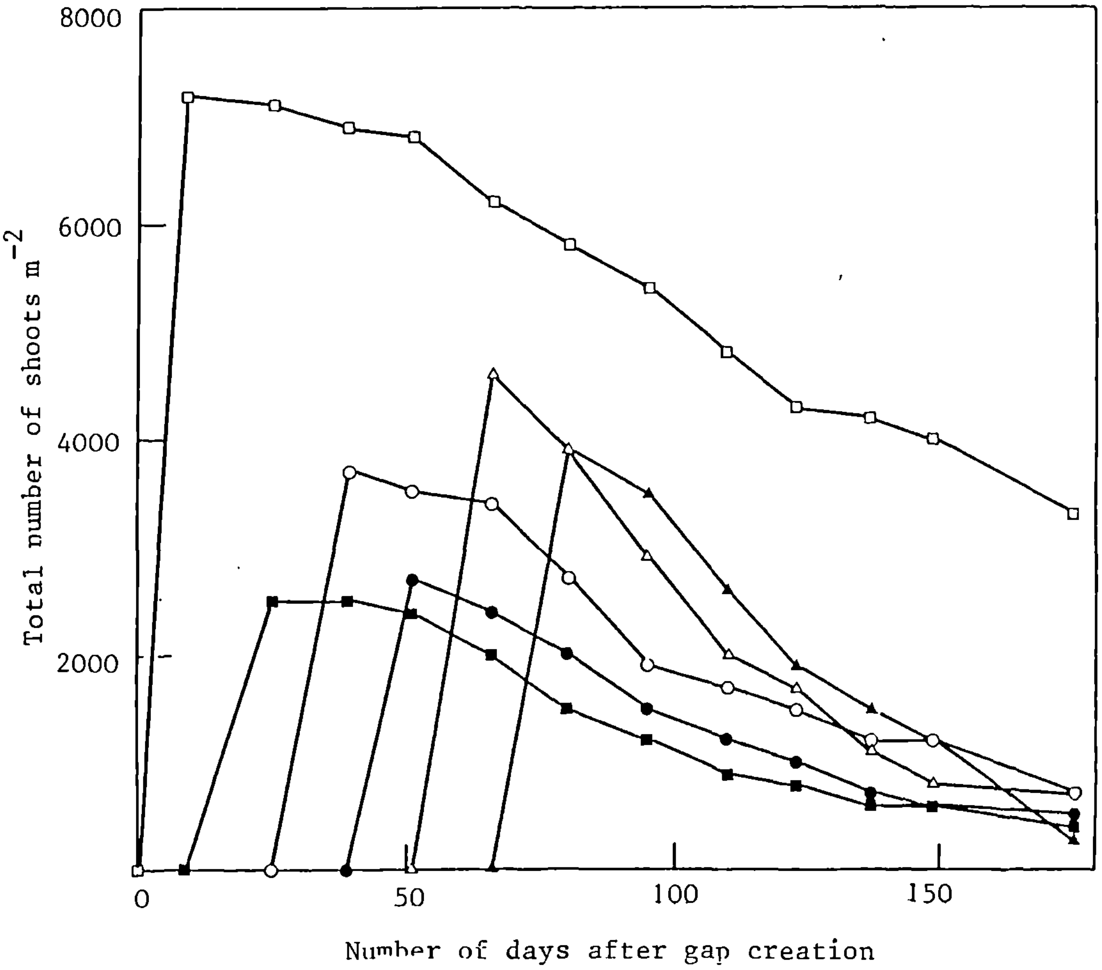

Fig. A7.2 Total standing crop in gaps of various sizes and in control turf.

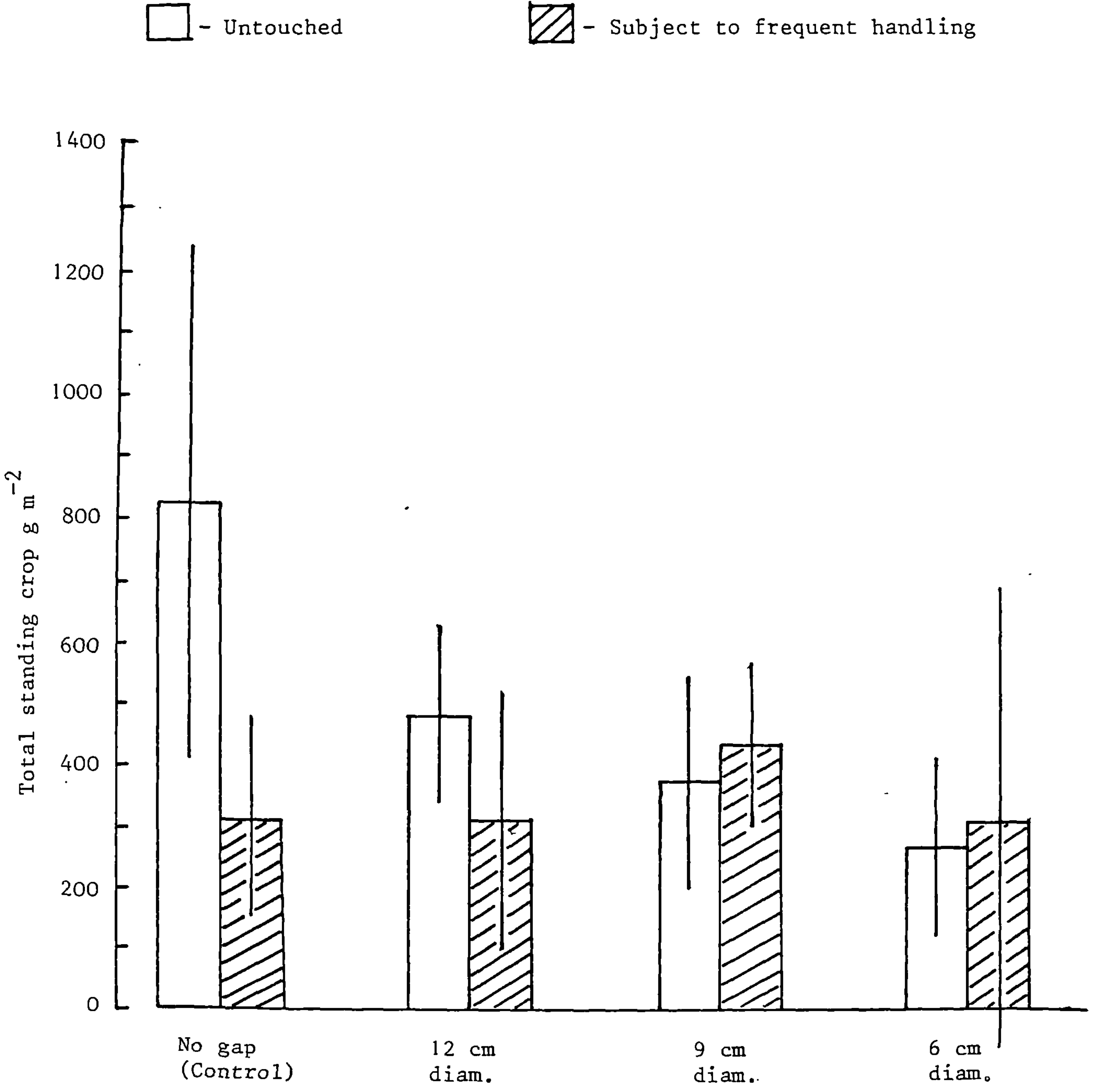

Table A7.1
Seedlings present in marked and unmarked turves after 180 days.

	Total number of seedlings in six replicates				
	C	12G	9G	6G	3G
unmarked turves	12	43	19	11	1
marked turves	8	13	11	1	1

Treatment codes:
C = control (12 cm diameter)
12G = 12 cm diameter gap
9G = 9 cm " "
6G = 6 cm " "
3G = 3 cm " "

Table A7.2
Biomass of Elymus repens in marked and unmarked turves.

	Mean dry weight (g m^{-2})				
	C	12G	9G	6G	3G
unmarked turves	269.5	237.2	239.6	117.0	120.9
marked turves	72.9	51.8	73.6	84.9	16.0

Treatment codes:
As for Table A7.1

Table A7.3
Numbers of shoots of Elymus repens in marked and unmarked turves.

	Total number of shoots in six replicates				
	C	12G	9G	6G	3G
unmarked turves	258	179	112	20	9
marked turves	107	102	45	38	2

Treatment codes:
As for Table A7.1

APPENDIX 8

Brief description of the triangular ordination procedure used in Figure 6.1 (from Grime 1984)

The initial step in the ordination was to attempt to classify with respect to strategy the herbaceous species of the Sheffield region. The method involved the use of a dichotomous key (Fig.A8.1) based upon characteristics of life-history, morphology and phenology and allowed species to be assigned to one of seven positions (Fig.A8.1 inset) corresponding to a characteristic pair of stress and disturbance coordinates and situated within a circular area of the triangular model conforming to the strategic range proposed for herbaceous plants (Grime, 1979, Fig.18, page 73). It should be emphasized that this was merely an approximate and provisional classification which could be applied with certainty to only a restricted number of species. No attempt was made to classify species for which critical data were lacking and species known to exhibit major genetic variation in life-history and morphology were also omitted. This procedure allowed the classification of 204 species (henceforward described as marker species) including many of the commoner herbaceous plants of the region.

The next step was to ordinate vegetation samples drawn from the range of habitats represented in the Sheffield region. Each 1 m^2 sample was located in the triangle by reference to the positions and frequencies of the component marker species. This was achieved by calculating mean stress and disturbance corordinates in which the contribution of each marker species was weighted according to its frequency in the vegetation sample. By this procedure, 2008 vegetation samples were ordinated and found to be distributed fairly evenly within the central circular area of the triangle. This allowed a calculation of the percentage occurrence of each species within each of 81 hexagonal zones of the circle and this in turn permitted contours to be drawn describing the distribution of each species.

Figure A8.1
Dichotomous key