

THE ROLE OF DISTURBANCE IN PERMANENT PASTURES

by

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## ABSTRACT

This thesis investigates how small disturbances influence community structure in three permanent pastures. Small disturbances play an important role in providing spatial heterogeneity that permits new recruits to enter populations in closed sward communities, thereby promoting diversity and species co-existence.

The thesis has four components: the first two are based on observation and measurement of the occurrence of small disturbances, molehills and dung pats, in three pastures. Within pasture seasonal changes in disturbance regime were related to changes in patterns of species abundance by multidimensional contingency table analysis. *Dactylis glomerata*, *Agropyron repens* and *Taraxacum officinale* increased in highly disturbed plots, whereas *Holcus lanatus* and *Trifolium repens* decreased. Invasion of molehills and dung pats was usually by rhizomes or stolons from surrounding plants. Seedling recruitment was rare: *Trifolium repens* was the only species dependent on small gaps for sexual regeneration. Patterns of species replacement on and around the disturbances were non-random.

The third part of the thesis investigated the effects of selective removal of *Lolium perenne*, *Holcus lanatus* and *Trifolium repens* from the oldest and youngest pastures. Strong responses to the removal of these species were found only in grasses in the youngest pasture. This is consistent with the hypothesis that competition decreases over time because of niche divergence, but may also reflect biological accommodation to grazing pressure.

The fourth part of the thesis investigated changes in species composition in simulated swards in response to different regimes of mowing, fertilizer and small gap creation. Species composition was strongly influenced by mowing and fertilization but was unresponsive to small gap creation.

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## 1. INTRODUCTION

Plant communities are characterized by heterogeneity in both space and time. They are non-uniform systems that continually change. Changes result from the death and regeneration of individual plants and their parts.

The view that vegetation is a dynamic system has had a long history. Aristotle imparted the principle of motion to all natural things but held that change was directed towards a goal. This view was maintained for nearly 2000 years. Although Galileo believed all motion to be circular, and hence, not directed towards goals, the observation of change was reiterated in the *Dialogue* "On earth I continually see herbs, plants, animals generating and decaying .... the appearance of the earth undergoing perpetual change".

The Aristotelian view of motion towards a goal was held by one of the most eminent early ecological theorists. Clements (1916) considered the plant community developing toward a climax vegetation state, analogous to an organism undergoing change and development. This view was upheld and promoted by many ecologists but not without opposition. One of the main challenges came from H.A. Gleason (1926) who argued that the botanical composition of an area resulted from the interaction of two 'fortuitous and fluctuating factors', immigration and environment.

The view of communities as structured, orderly entities, still persists even though Clements' organism viewpoint has been discredited with the shift in ecology, from

Aristotelian essentialism to more probabilistic thinking. Structure, i.e. order and organization, may be imposed either from within the community, by the plants themselves, or externally, through forces imposed upon the community. This distinction was originally applied by Tansley (1935) to successional communities. He distinguished autogenic succession in which "changes are brought about by the action of the plants themselves on the habitat" from allogenic succession in which "changes are brought about by external factors". Evidence of community structure, inferred from non-random patterns of species distribution in the community, has been used to challenge Gleason's hypothesis of random association of individual species. Ecologists, however, have taken an increasingly 'Gleasonian' approach as evidence accumulates that "every species of plant is a law unto itself, the distribution of which in space depends upon its peculiarities of migration and environmental requirements. Its disseminules migrate everywhere, and grow wherever they find favourable conditions" (Gleason 1926). Structure is believed to result from feedback from established individuals, controlling species composition and abundance of seedlings, and from interactions between these recruits (Harper 1977). Thus, although species have distinct life histories that lead to an individualistic response, pattern in their association suggests rules of assembly rather than random events.

Disturbances are a natural component of all communities. Recently, the influence of disturbance regimes on community structure and function has become the focus of much research effort. This interest arose from two impetuses. First, a body of evidence accumulated against classical Clementsian succession and showed that communities were continually reset to earlier successional stages by disturbances.

This led to an hypothesis that community composition could be controlled by the rate and intensity of disturbance (cf. Connell 1978). Second, the application of Gause's hypothesis of competitive exclusion of species occupying the same niches led to an examination of niche requirements of plant species. The argument has been advanced by Harper (1969) that "the essentially similar requirements of all green plants - solar radiation, water, carbon dioxide, and a basic set of mineral nutrients - provide little opportunity for diversification in relation to food supply. This is in strong contrast with organisms at higher trophic levels where the food net is focused less conspicuously on a few environmental supply factors, and much of the diversity of fauna can be interpreted in terms of differences in food or feeding habit." Grubb (1977), who repeated and expanded this notion, contends that our lack of understanding of plant co-existence is due in part to a failure to take into account the phenomenon of regeneration in plant communities. Furthermore, disturbance could provide a source of temporally and spatially heterogeneous sites for vegetation regeneration that would permit niche separation and species co-existence.

A recent definition of disturbance (Sousa 1984a) focuses on gaps providing sites for regeneration. Sousa defines disturbance as "a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established". Disturbance can result from both physical processes, *e.g.*, fires, floods, drought, storms, and from biological processes *e.g.*, predation, grazing, diggings of mammals and insects. The impact of both physical and biological sources of disturbance appears similar, removing organisms or their parts and

creating opportunities for recruitment (Sousa 1984a).

Two additional definitions de-emphasize recruitment as a characteristic response to disturbance and emphasize the discrete onset of disturbance and change of resource availability. Bazzaz (1983) defined disturbance as "a sudden change in the resource base of a unit of the landscape that is expressed as a readily detectable change in population response". White and Pickett (1985) defined disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment". Harper (1977) distinguishes between disasters, and catastrophic disturbances. Disasters happen sufficiently frequently in the life span of populations that they exert a selective pressure whereas catastrophies occur so infrequently that populations would lose their "genetic memory" of it by the next time it recurred (Begon *et al.* 1986) and therefore exert no selective force. In this context the eruption of Mount St Helens is termed catastrophic whereas the eruptions of Kila Laua would be disasterous.

Disturbance regimes are characterized by various descriptors. White and Pickett (1985) list: spatial distribution; frequency and return cycle; rotation period or turnover rate, which refers to the time needed to disturb a given area; predictability; size or area of disturbance; magnitude intensity which refers to the force of the disturbance event; severity of the impact on the organism or community; and, synergism, the effect on the subsequent occurrence of other disturbances. Not all of these descriptors are applicable to every type of disturbance. For example, it would be unprofitable to measure the magnitude

intensity of animal mounds whereas this is an important descriptor of avalanches where the force required to snap tree stems is of interest.

Natural disturbances occur in most communities (see reviews by Sousa 1984a; Pickett and White 1985) including, for example, coniferous and deciduous forests (e.g. Henry and Swan 1974; Oliver and Stephens 1977; Runkle 1981, 1982), shrubland (e.g. Christensen 1985), grassland (e.g. Loucks *et al.* 1985) and intertidal areas (e.g. Dayton 1971; Levin and Paine 1974; Sousa 1979). Disturbance affects various levels of organization: the impact on individual growth, architecture, and dispersal (e.g. Watt 1925; Sousa 1979; Canham and Marks 1985) may result in changes in population genetic structure (Jain 1983; Thompson 1985), age (Tande 1979), size (Veblen 1985) and in community composition, richness (Denslow 1980, 1985), dominance and structure (Brokaw 1985).

While the prevalence of disturbance has been documented, there exists a lack of cogent theory concerning the processes and effects of disturbance. Two hypotheses on the effects of disturbance on communities are current: the intermediate disturbance hypothesis (Connell 1978) and the "rate of competitive displacement" hypothesis (Huston 1979). Both are interrelated and suffer from imprecision. The intermediate disturbance hypothesis argues that species richness will be higher in communities experiencing some intermediate level of disturbance frequency, intensity and size, and lower in those experiencing both much lower and much higher frequencies of disturbance. Problems arise in quantifying intermediacy and its relationship to the system under investigation. Other problems arise on

subdividing disturbance into components such as magnitude, frequency and size in which intermediacy in each may have different impacts on the community (Pickett and White 1985). The underlying assumptions of the intermediate disturbance hypothesis are based on a successional sequence undergoing directional change toward a climax steady-state. Disturbance resets the successional sequence to an earlier stage, increases within community heterogeneity and, over larger geographic areas, establishes a dynamic equilibrium (Connell 1978).

Huston's (1979) "rate of competitive displacement" hypothesis may be viewed as an extension of the intermediate disturbance hypothesis (Connell 1978), although it owes an academic debt to both Grime (1973, see Peet *et al.* 1983) and to theories of predator-mediated co-existence (Caswell 1978). In these theories, disturbance (or management, or predation and herbivory) delays the competitive exclusion of one species by another by periodic reductions in population size. The prolonging of the period to exclusion promotes species co-existence and maintains diversity. Competitive exclusion is accelerated by increased growth rate of the dominant species and diversity is increased by any condition that reduces the rate of growth, including disturbance. For example, low levels of essential nutrients would reduce growth rates and result in higher diversity than in a similar situation with higher nutrient availability (Huston 1979), though, of course, very low nutrient levels restrict the number of species able to establish leading also to low diversity (Grime 1973, 1979). Huston's model, like the predator-mediated co-existence model, focuses on the role of individual or population reduction in promoting species co-existence but fails to take account of changes in resource availability initiated by disturbance. For example, disturbance



may alter nutrient availability (Bazzaz 1983; Vitousek 1985) or create sites suitable for seedling or other propagule establishment (Grubb 1977; Sousa 1979).

There is a rich literature on the impact of disturbance on forest and intertidal communities (Sousa 1984a). Studies of disturbance in grassland communities have mainly neglected pastures (but see Jones 1933a,b,c,d) and have been in rangeland (see White 1985) and prairie systems. For example, in tall grass prairie, Platt (1975) studied the role of badger mounds on species associations. Badger mounds increased spatial heterogeneity, led to temporal partitioning in biomass production, and enhanced species co-existence by providing a site for colonization and establishment of a guild of fugitive species that were restricted to these small-scale disturbances. Unlike Platt's study, Loucks *et al.*'s (1985) investigation of the response to fire, gopher mounds and small-scale erosion sites in the Wisconsin sand prairies found preferential colonization that led to changes in species abundance rather than specialist colonization of disturbances. They concluded that sand prairie grassland community composition is closely linked to the multiple-scale disturbance regimes.

My thesis examines the role of disturbance in a common grassland community, the permanent pasture. Pastures are widespread throughout temperate climates and contain a mix of sown and native species. They persist in many areas only because of periodic disturbance from either mowing or grazing without which they would be rapidly invaded by shrubs and trees. In addition, pastures are subject to numerous small-scale disturbances from small mammals and insects as well as scrapings and droppings from grazers.

The thesis has four components: the first two are based on observations of the occurrence of small-scale disturbances and species abundance in three pastures. In the third and fourth parts, species abundance was manipulated in field experiments. Field observations were used to study spatial and temporal heterogeneity in pastures. First, within-pasture seasonal changes in disturbance regimes were related to changes in pattern of species abundance. Second, colonization of small gaps recorded at monthly intervals was used to determine the temporal patterns of species establishment. In the third part, the effects of selective removal of dominant grasses and white clover on the abundance of the remaining species was investigated to determine the extent of the contribution of dominants to community structure and species co-existence. The final component of the study involved the setting up of an experiment to investigate species' response to the interaction of larger-scale disturbance, mowing, with small-scale gap formation under different nutrient regimes.

### 1.1. STUDY AREA

The study area comprises three contiguous pastures located at 25704 Fraser Highway, Aldergrove, British Columbia (SW 1/4 sec. 25, Twp. 10) on a farm owned by William and Mary Chard. The farm is situated at 49° 03' 45" N. Lat. and 122° 30' 45" W Long. in the Coastal Douglas fir biogeoclimatic zone (Krajina 1965). The elevation of the pastures varies from 110m to 122m above sea level. Two of the pastures are generally flat and slightly sloping, whereas the third is gently rolling (see contour maps in Aarssen and Turkington 1985a).

The pastures lie on a parent material of Pleistocene glaciomarine deposits. The soils are Luvisolic Humo-Ferric Podzols and Orthic Humic Gleysols (Canada Soil Survey Committee 1978). They are moderate- to fine-textured clay loams which are moderately to poorly drained. The average top soil depth (A + B horizons) is from 80-100cm. The pH is moderately acid, ranging from 5.2 - 5.9. Results of detailed soil analysis for the pastures can be found in Aarssen and Turkington (1985a).

The area has a relatively mild, wet winter and a warm, drier summer. Environment Canada climatic data recorded at Aldergrove, 2.4km east of the farm, provided monthly mean temperatures for the 21 year period from 1960 to 1980 (Figure 1-1). During the study period (1982-1985), winters have been generally milder than average: monthly mean minimum temperatures were somewhat higher than normal whereas monthly mean maximum temperatures were near normal (Figure 1-2). December 1983, however, was a particularly cold month in which precipitation was also lower than normal. Mean annual rainfall for the period 1964-1980 was 1652.3mm (S.D. 232.8), most of which fell in the winter (Figure 1-3). May 1984 was exceptionally wet (265.7mm) but this was well below a seasonal peak of 347.4mm in November 1983.

The area was first cleared for farming around 1900 and periodic clearing continued over the next forty years to encompass all of the present three pastures. These were last ploughed and seeded in 1939, 1958 and 1977 respectively, and prior to reseeding, all had been pastures. All pastures were originally sown with a seed mixture, comprising by volume, 5-10% *Trifolium*

Figure 1-1. Monthly mean temperatures at Aldergrove, B.C. summarized for the period from January 1982 to December 1984 compared with the 21-year average of monthly mean temperatures.

- △ 1982
- 1983
- 1984
- 21-year average

## MONTHLY MEAN TEMPERATURE

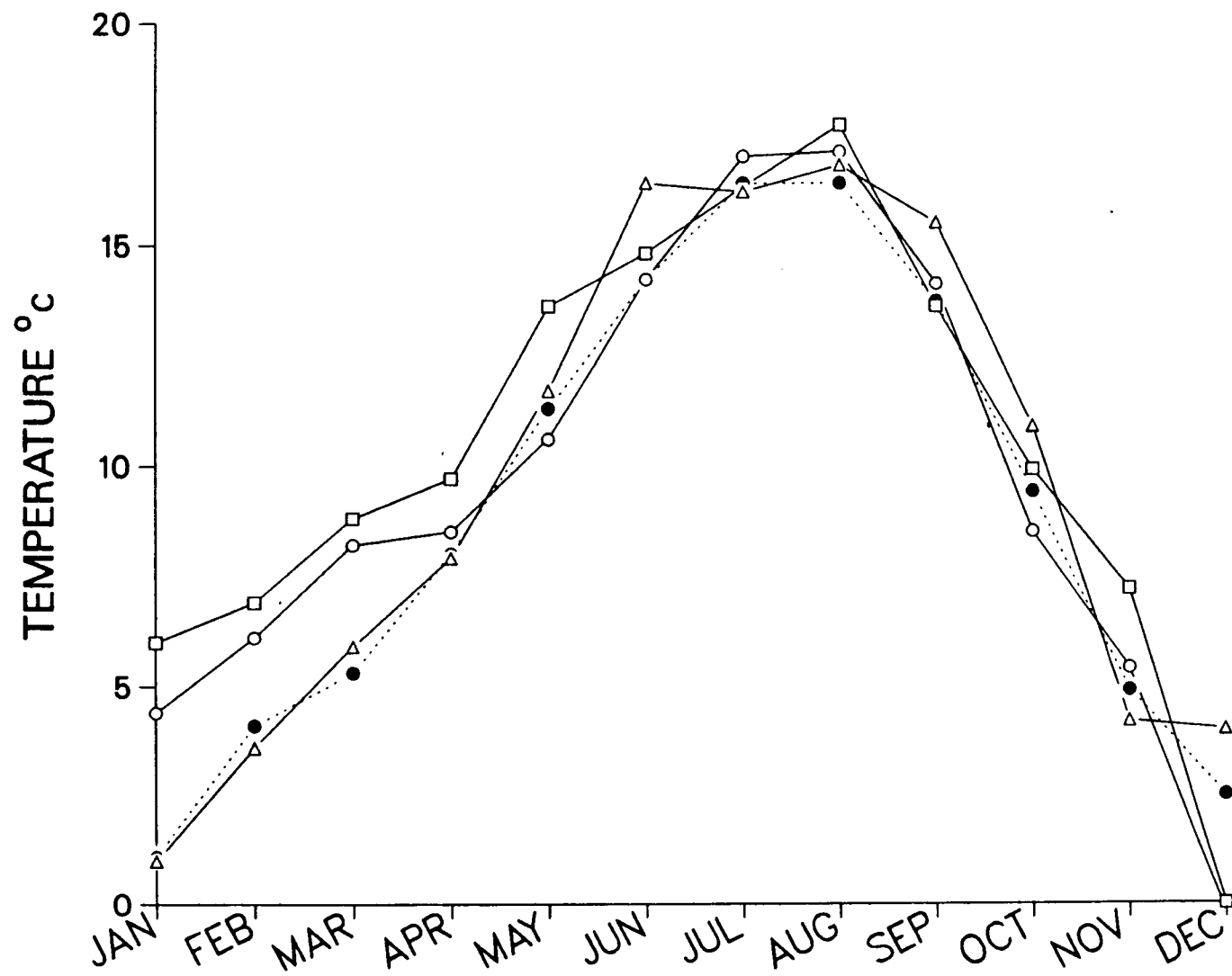


Figure 1-2. Monthly mean maximum and minimum temperatures at Aldergrove, B.C. summarized for the period from January 1982 to December 1984 compared with the 21-year averages.

△ 1982

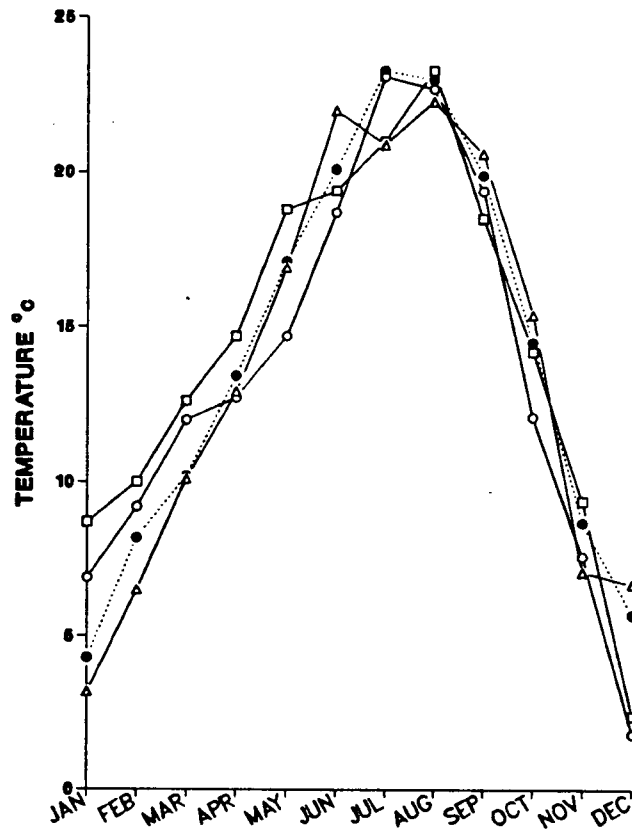
□ 1983

○ 1984

● 21-year average

## MONTHLY MEAN MAXIMUM TEMPERATURE

13



## MONTHLY MEAN MINIMUM TEMPERATURE

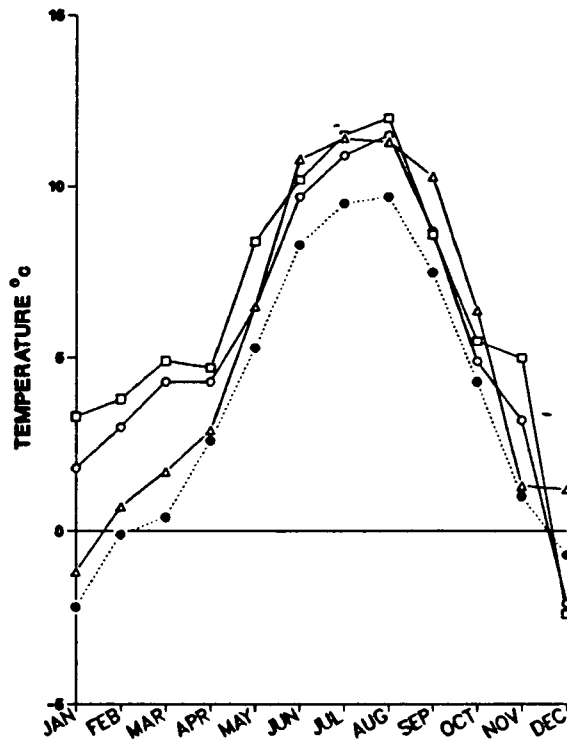


Figure 1-3. Monthly mean precipitation at Aldergrove, B.C. summarized for the period from January 1982 to December 1984 compared with the 17-year average of monthly mean precipitation.

△ 1982

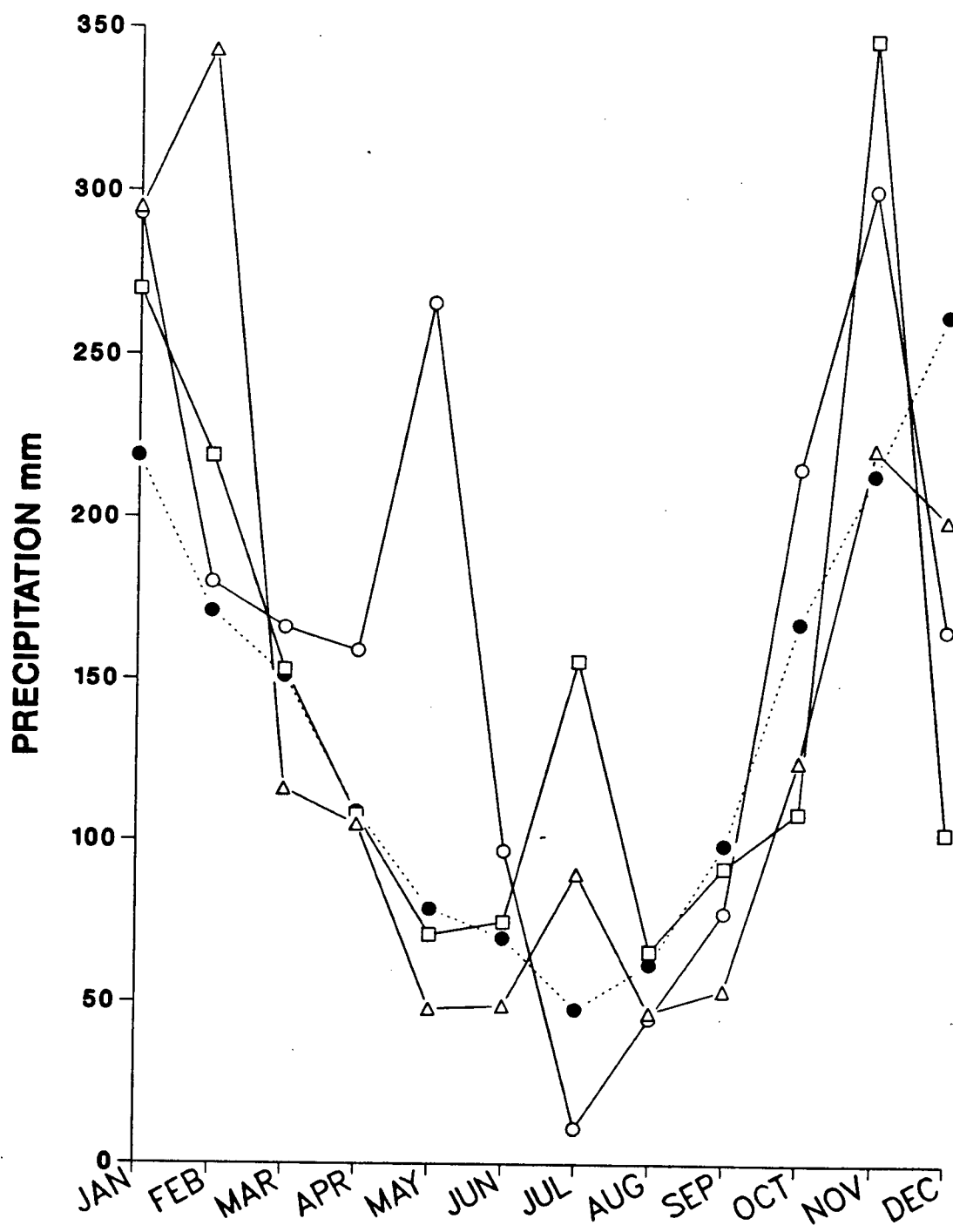
□ 1983

○ 1984

● 17-year average



# MONTHLY MEAN PRECIPITATION



*repens*, 15-20% *Dactylis glomerata* and 70-80% of a mixture known locally as Buckerfields Highland mix. The species proportions in the mix varied and the exact composition seeded is known only for the 1977 pasture (Table 1-1). The mix used in 1977 differed from that used in 1939 and 1958 by the addition of tetraploid *L. perenne* and the large 'Ladino' *T. repens*. Various other species not in the original sowing mix have become established in the pastures (Table 1-2).

Table 1-1. Species composition of 'Highland Mix' with sowing proportions used in 1977 pasture.

Species	Percent composition
<i>Dactylis glomerata</i> L.	45
<i>Trifolium pratense</i> L.	20
<i>Lolium perenne</i> L.	15
<i>Lolium multiflorum</i> Lam.	10
<i>Phleum pratense</i> L.	5
<i>Trifolium repens</i> L.	2
<i>Trifolium repens</i> var. Ladino	3

Table 1-2. Species list for the three pastures in 1985.

	1939	1958	1977
<b>Grasses</b>			
<i>Agropyron repens</i> (L.) Beauv.	x	x	x
<i>Agrostis alba</i> L.	x	x	x
<i>Alopecurus geniculatus</i> L.	x	x	x
<i>Alopecurus pratensis</i> L.			x
<i>Anthoxanthum odoratum</i> L.	x	x	x
<i>Dactylis glomerata</i> L.	x	x	x
<i>Festuca pratensis</i> Huds.			x
<i>Festuca rubra</i> L.	x	x	x
<i>Glyceria declinata</i> Breb.	x		
<i>Holcus lanatus</i> L.	x	x	x
<i>Lolium multiflorum</i> Lam.			x
<i>Lolium perenne</i> L.	x	x	x
<i>Lolium multiflorum</i> x <i>Lolium perenne</i>	x	x	x
<i>Phleum pratense</i> L.	x	x	x
<i>Poa compressa</i> L.	x	x	x
<i>Poa trivialis</i> L.	x	x	x
<b>Non-grasses</b>			
<i>Achillea millefolium</i> L.	x	x	x
<i>Capsella bursa-pastoris</i> L.	x	x	x
<i>Carex</i> sp.	x	x	x
<i>Cerastium vulgatum</i> L.	x	x	x
<i>Cirsium arvense</i> (L.) Scop.	x		x
<i>Gnaphalium uliginosum</i> L.	x		
<i>Hypochoeris radicata</i> L.	x	x	x
<i>Juncus</i> sp.	x	x	
<i>Medicago lupulina</i> L.	x	x	x
<i>Plantago lanceolata</i> L.	x	x	x
<i>Plantago major</i> L.	x	x	x
<i>Ranunculus acris</i> L.	x	x	x
<i>Rumex acetosella</i> L.	x	x	x
<i>Rumex crispus</i> L.		x	
<i>Rumex obtusifolius</i> L.	x	x	x
<i>Stellaria media</i> (L.) Vill.	x	x	x
<i>Taraxacum officinale</i> Weber	x	x	x
<i>Trifolium pratense</i> L.	x	x	x
<i>Trifolium repens</i> L.	x	x	x

x - denotes species present in pasture

A strict management regime is not followed. The farm was managed for dairy production until 1983 and subsequently switched to beef production; however, no changes in management practices in the pastures ensued. The cattle may graze in the pastures between May and November, though frequently, grazing is delayed until after the pastures are cut for hay. In recent years, the pastures have been cut in late June or early July and then strip-grazed by 20-30 cattle once sufficient regrowth has occurred. After a pasture has been strip grazed, the cattle roam freely until the end of the grazing season, usually in November. The pastures have never been treated with chemical pesticides, herbicides or fertilizer, other than barnyard manure which is spread sporadically to maintain soil fertility.

## 2. PATTERNS OF DISTURBANCE AND THEIR INFLUENCE ON BOTANICAL COMPOSITION

### 2.1. INTRODUCTION

Pastures are regarded as biotic plagio-climax vegetation (Tansley 1939), i.e. vegetation maintained by grazing and mowing. This management regime retains the pasture in a relatively stable state but there is nonetheless wide spatial and temporal variation in botanical composition of pastures (e.g., Spedding 1971; Watkin and Clements 1978; Vickery 1981; Thorhallsdottir 1984; Snaydon 1985). The management regime is also one of the most important ecological features of the pasture because grazing animals not only defoliate, but also create many small-scale disturbances within the pasture - hoof marks, urine patches and dung pats. These disturbances, and additional activities of small mammals and insects, create openings or gaps within the otherwise continuous sward. The rate and manner of colonization of these gaps may have an important impact on the species composition of the pasture, species diversity and population flux.

Dung and urine have been found to affect pastures (e.g. Norman and Green 1958; During and McNaught 1961). Urine provides nutrients, mainly nitrogen and potassium, to the sward which may stimulate yield and depress the abundance of clovers (During and McNaught 1961; Mundy 1961). Norman and Green (1958) found that a single application of urine had a negligible effect on species composition, but around dung patches, *Dactylis glomerata*, *Trifolium repens* and *Festuca rubra* all increased in both cover and yield. MacDiarmid and Watkin

Patterns of disturbance and their influence on botanical composition / 20 (1971) showed that grasses (mainly *Lolium* spp.) increased in relative abundance around dung patches while clovers (mainly *T. repens*) did not. They also found that plants underneath dung decayed rapidly and regrowth was minimal although Hutchinson (1979) noted that a number of species (e.g. *Poa trivialis*, *Agrostis stolonifera*, *Lolium* spp.) were able to penetrate the patch and survive. *T. repens* was one of the first invaders of areas left bare by decaying dung (Weeda 1967).

On average a cow produces about 9kg of urine and 28kg (fresh weight) of dung daily, defecating 11-15 times per day (MacLusky 1960; Marsh and Campling 1970). In the 150 day grazing season typical of the Aldergrove pastures, even if cows were penned at night and only 50% of dung were deposited while grazing, that would amount to about 2100kg of dung per animal and 63,000kg for a small dairy herd of 30 cows. The area covered by a single dung pat ranges from  $0.05\text{m}^2$  to  $0.12\text{m}^2$  (Petersen *et al.* 1956) and the total area affected by dung is estimated to be about six times the actual area covered (Norman and Green 1958; MacLusky 1960). Therefore from 7425 to  $17,820\text{m}^2$  (20-50% of the three pastures) could be affected by dung in a 150 day grazing season.

Harper (1977) summarized the possible effects of dung in pastures: (i) smothering and exclusion of light from plants; (ii) a local change of nutrient relations; (iii) a local change in the pattern of grazing because animals tend to avoid fouled areas; and (iv) creation of an area for colonization by new or existing individuals.

Another source of spatial variation in many pastures is from molehills. Molehills

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in the Fraser Valley are produced by the coast mole (*Scapinius orarius* True). These moles eat arthropods, annelids and molluscs exclusively. A mole can consume more than 100 worms per day. A study on moles in the Fraser Valley found that the number ranged from 2 - 10 per hectare and was correlated to the number of earthworms (Glendenning 1957). Moles are least active in the summer months. In search of food, a single mole may create 200 to 400 hills between October and March, excavating up to 500m of tunnels usually from 15 to 20cm below the soil surface (Glendenning 1957).

Tansley and Adamson (1925) noted that molehills in dune slacks had a characteristic flora differing from the surrounding vegetation. A study of buried seed in molehills in pastures (Jalloq 1975) showed a different buried seed population on molehills than in the sward. Rothwell (1977) investigated the colonization of molehills in Welsh pastures and noted that *Holcus lanatus*, *Agrostis capillaris* (syn. *A. tenuis*) and *Anthoxanthum odoratum* had significantly lower abundance on molehills than in the adjacent sward, whereas *Ranunculus repens* increased on molehills. In contrast, also in Welsh pastures, Davies (1966) found molehills to be colonized mainly by *A. capillaris* and implicated molehills in the degeneration of productive pasture to that dominated by weedy species. Molehills have effects in common with dung in that (i) plants are smothered and excluded from light and (ii) bare areas are created for plant colonization.

Temporal variation in plant abundance in pastures may be related to variation in the environment such as seasonal changes, grazing management, or fertilizer application (Snaydon 1985). Temporal variation may also reflect the lifespan of

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plants or parts of plants (Thorhallsdottir 1984) in which the genotype of the  
plant interacts with abiotic and biotic factors.

This chapter examines the influence of two small-scale disturbances, dung and  
molehills, on the distribution and relative abundance of species in a series of  
adjacent pastures. The approach taken was to describe and correlate patterns of  
vegetation and patterns of disturbance within pastures. Three objectives were  
pursued: (i) to assess temporal variation in species abundance; (ii) to measure the  
intensity of disturbance caused by cow dung and molehills; and, (iii) to relate the  
pattern of disturbance to the pattern of distribution of species abundance.

## **2.2. METHODS**

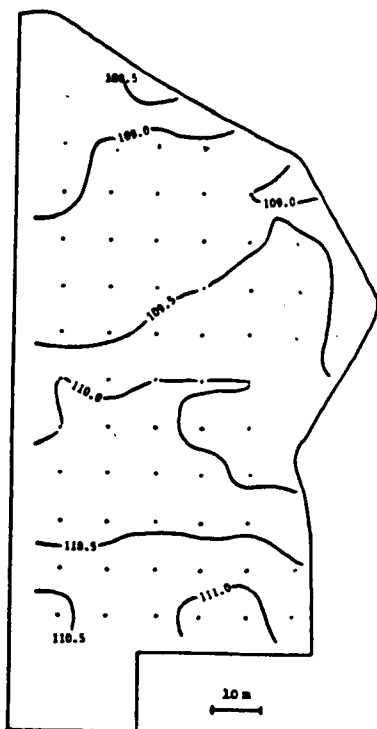
### **2.2.1. Field methods**

To measure vegetation patterns and disturbance regimes in the three Aldergrove  
pastures, each pasture was subdivided into 5 x 5m plots. In order to facilitate  
comparison with data previously collected from these pastures (Aarssen 1983),  
plots were systematically located at 10m intervals along established transect lines  
that were approximately 10m apart. Buffer zones of 10m - 20m from the  
pastures' boundaries were used in all pastures to avoid edge effects and  
obviously swampy areas. There were 48 plots in the 1977 pasture, 50 in the  
1958 pasture and 47 in the 1939 pasture (Figure 2-1).

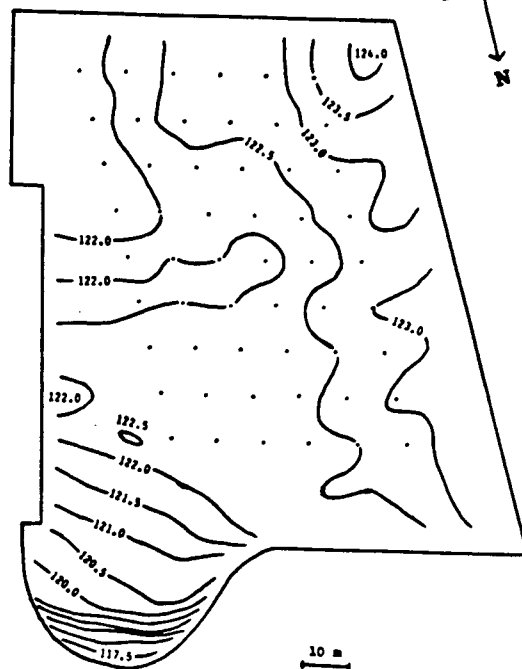
The plots were surveyed on eight occasions; each spring, summer and fall, from



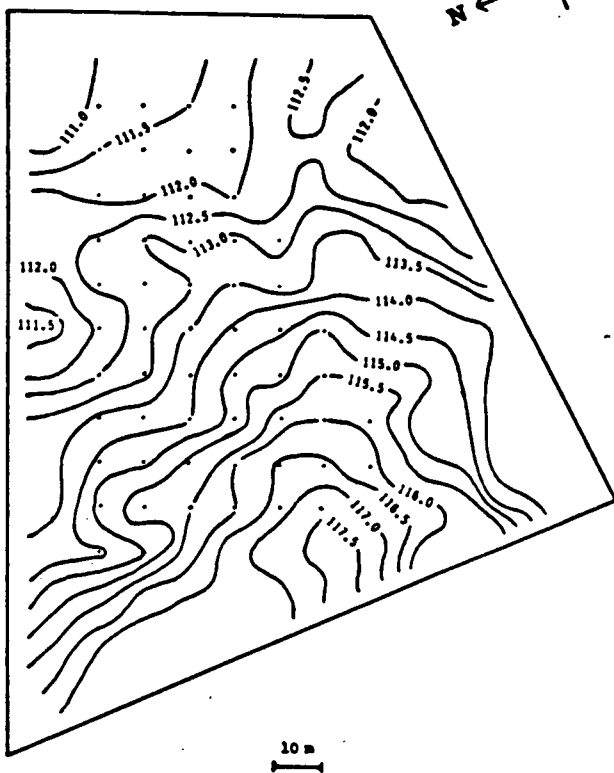
Figure 2-1. Location of the plots on contour maps of the three pastures.  
Elevation in metres.



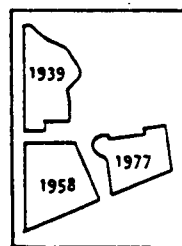
1939 PASTURE



1977 PASTURE



1958 PASTURE



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July 1982 to October 1984. At each survey, the position and diameter of all molehills and all dung pats were plotted. Vegetation was surveyed using four .5 x .5m quadrats per plot placed at 2m intervals along one of the plot diagonals. Each quadrat was subdivided into a grid of 25 points. The species rooted at each point, or bare ground, was recorded. This method was preferred over that used by Aarssen (1983) in these pastures because it is less subject to bias toward larger species and error from variability in wind speed and grass length.

### **2.2.2. Analytical methods**

Vegetation data were analysed by reciprocal averaging of the total mean rooted cover for each pasture, using an algorithm outlined by Orloci (1978). Species cover for each sampling period was compared between pastures to detect similar patterns and trends, using the Michigan Interactive Data Analysis System (MIDAS) (Fox and Guire 1976) version of profile analysis.

Multidimensional contingency table analysis was used to analyse patterns of disturbance and patterns of species abundance. Contingency table analysis describes the structural relationship between variables (Fienberg 1980) and is especially useful when variables are not independent. Its application to ecological data is discussed by Fienberg (1970) who recommends its use if observations have unequal variances and if the underlying distribution is not normal.

Variables are cross-classified into discrete categories referred to as cells. The

expected value of a cell ( $e_{ij}$ ) is calculated by multiplying the row total ( $n_{i+}$ ) by the column total ( $n_{+j}$ ) and dividing by the total number of observations (N):

$$e_{ij} = \frac{n_{i+} \cdot n_{+j}}{N} \quad (1-1)$$

Equation (1-1) may be expressed as a log-linear model of the form

$$\log e_{ij} = \log n_{i+} + \log n_{+j} - \log N \quad (1-2)$$

This model can be reformulated in terms analogous to analysis of variance (Fienberg 1970, 1980)

$$\log e_{ij} = u + u_{1(i)} + u_{2(j)} \quad (1-3)$$

where:

$u$  - grand mean of logarithm of expected cell frequency

$u_{1(i)}$  - deviation from grand mean of expected counts in cell of level  $i$  of variable 1

$u_{2(j)}$  - deviation from grand mean of expected counts in cell of level  $j$  of variable 2

The model assumes that the variables are independent and if this is not so, an interaction effect must be incorporated such that

$$\log e_{ij} = u + u_{1(i)} + u_{2(j)} + u_{12(ij)} \quad (1-4)$$

In this form, a greater number of variables may be incorporated but the number

of possible models rapidly rises as the number of variables increases. For example, in the case of two variables, only two models are possible, with three variables there are 8 different models and with four variables 113 different models (Fienberg 1980). It is possible that a large number of these models will fit the data and the saturated model with all possible interaction terms always produces expected values equal to the observed values. The statistic used to test goodness of fit of the models is the likelihood ratio chi-square:

$$\chi^2 = 2 \sum (\text{observed}) \log (\text{observed/expected}) \quad (1-5)$$

This statistic may be partitioned into several additive parts and was used in this study to test for the presence of an interaction effect.

To examine whether disturbance regime has any relationship to species abundance, a four-way classification was used. This consisted of one response variable, species abundance, and three explanatory variables, disturbance regime, season and year. Species abundance was categorized as high, medium or low for species with greater than 10% cover, and into presence or absence for those with less than 10% cover. Disturbance regime of a plot was categorized as high, medium or low. Season (spring, summer or fall) and year of the survey were included to account for differences in abundance associated with the timing of vegetative growth and flowering, and the various aspects of climate and management that vary from year to year. The selected model assumed interactions existed between disturbance, year and season, and between abundance, year and season. To test for a relationship between disturbance and abundance,

the interaction term of abundance and disturbance was added to the model. The difference between the likelihood ratios for the two models was tested against a chi-square distribution to determine if the addition of the interaction term significantly improves the fit of the model. The more specific test for a three-way interaction between abundance, disturbance and season, or between abundance, disturbance and year was accomplished by the subtraction of the likelihood ratio of each model containing one three-way term from the model containing both terms. The two-way interaction of disturbance and abundance is a simpler but more specific case of three-way interaction (Fienberg 1980). The choice of models may be termed the maximal choice in that the model contains as many terms as possible. Effects may be missed in this approach but any significant improvement has no other explanation in terms of the full model used.

One potential problem in this type of analysis is the formation of categories from discrete data. There is no best way to accomplish the groupings although the choice of cut-off points for categories does influence the size of the interaction observed (Fienberg 1970). Cut-off points to group disturbances regimes were kept constant over the three pastures. If a total of three or fewer molehills or dung pats per season were found in a plot, that plot was arbitrarily considered to have a low disturbance rate, similarly between three and fifteen was considered an intermediate rate and more than fifteen, a high rate. Cut-off points for each species were varied because of the probability that the carrying capacity of each field differs for some species. A number of cut-off points were tried for each species.

## 2.3. RESULTS

### 2.3.1. Vegetation

The species composition of the three pastures differed in mean percent cover (Table 2-1). Percent cover of the ten most abundant species in each pasture at each of the eight surveys is shown in Figure 2-2. Profile analysis revealed no significant parallel trends in the abundance of any species in the three pastures, even though some changes in species cover appeared to be strikingly consistent; e.g. *Poa compressa* abundance from summer 1983 to fall 1984 in all three pastures; *Lolium perenne* from fall 1982 to fall 1984; and, *Trifolium repens* throughout the study period in the 1939 and 1977 pastures. One trend found in Aarssen's (1983) cover data, collected from 1979 to 1981, that continued through 1982 to spring 1984, was the decline in abundance of *Dactylis glomerata* in the 1977 pasture. There were other major shifts in species abundance; an increase in abundance of *T. repens* in the 1977 and 1939 pastures, and an increase in *L. perenne* in the 1939 pasture, but these did not follow from any pattern observed in the previous three years. The abundance of *Festuca rubra* in the 1958 pasture is related to topographic features. The short-lived, grazing-sensitive *Trifolium pratense*, present in the Aarssen (1983) study of these pastures, had declined to less than 1% of the cover and consequently has been grouped with 'other species'.

The results of reciprocal averaging ordination of species abundances from all eight sampling periods combined (Figure 2-3) showed the 1939 and 1977 pastures, the

Table 2-1. Mean species cover in the three pastures averaged over eight surveys from July 1982 to October 1984.

Species	1977	1958	1939
<i>Lolium perenne</i>	17.87	10.18	23.05
<i>Holcus lanatus</i>	13.79	13.39	12.98
<i>Dactylis glomerata</i>	9.51	15.11	4.98
<i>Agropyron repens</i>	5.76	8.06	2.76
<i>Phleum pratense</i>	2.18	6.11	0.91
<i>Poa compressa</i>	13.36	16.13	20.78
<i>Trifolium repens</i>	17.92	7.08	17.37
<i>Taraxacum officinale</i>	9.04	6.03	7.09
<i>Ranunculus acris</i>	1.77	1.05	2.33
<i>Plantago lanceolata</i>	1.08	1.60	0.21
<i>Festuca rubra</i>	0.02	6.58	0.28
<i>Agrostis alba</i>	1.02	0.55	1.34
<i>Anthoxanthum odoratum</i>	0.93	0.58	0.51
<i>Cerastium vulgatum</i>	0.03	0.13	0.08
<i>Juncus</i> spp.	0.06	0.20	0.00
Bryophytes	2.01	1.49	0.66
Bare ground	2.34	4.42	2.03
Dung	0.59	0.80	1.31
Other	0.69	0.46	0.97



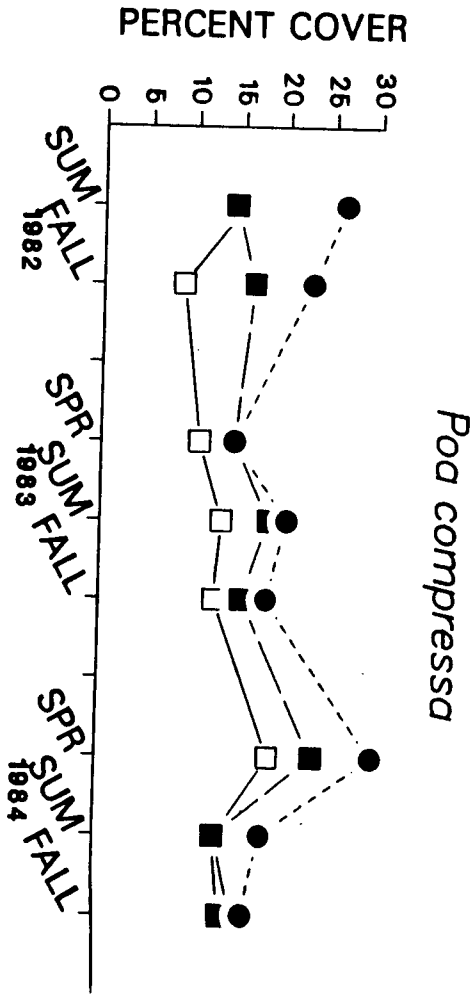
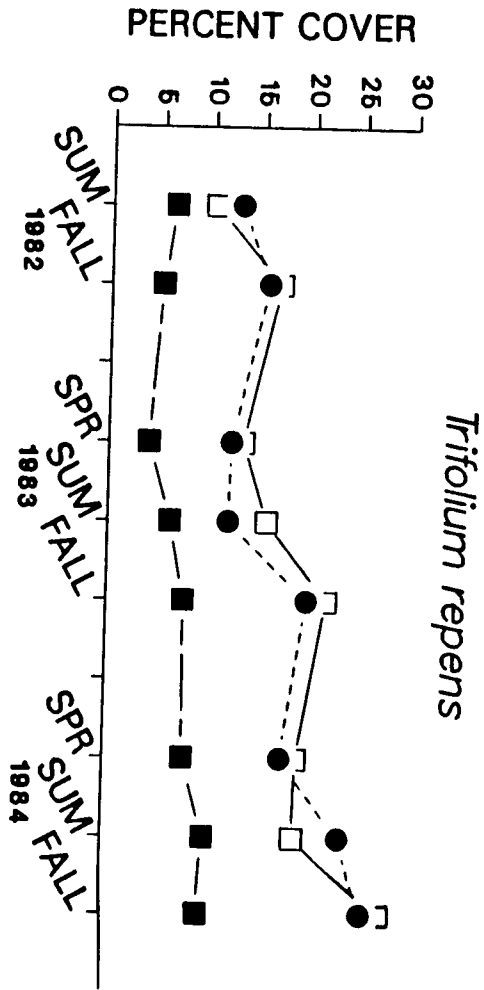
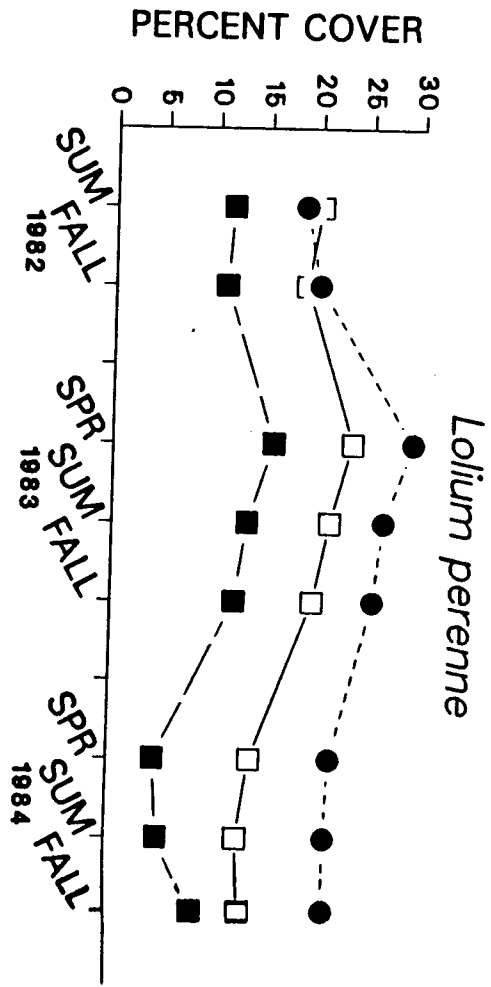
Figure 2-2. The percentage cover of the 10 most common species in the three pastures over the study period from summer 1982 to fall 1984.

SPR - spring, SUM - summer

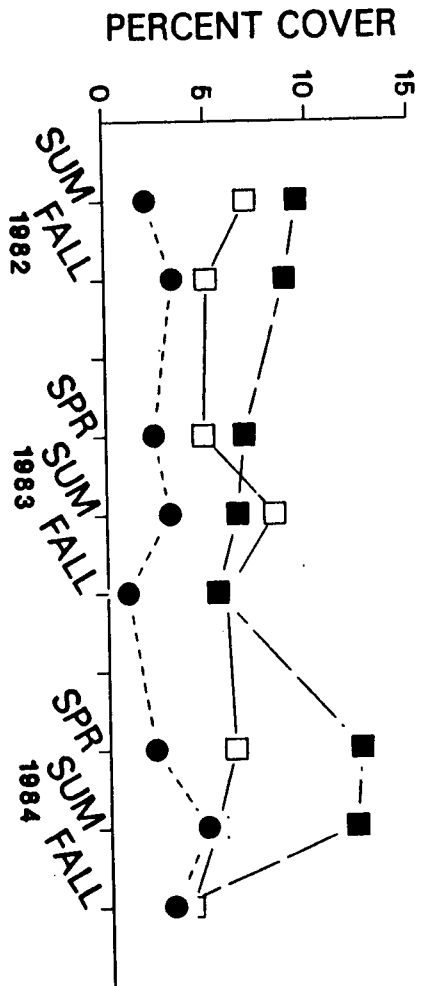
□ 1977 pasture

■ 1958 pasture

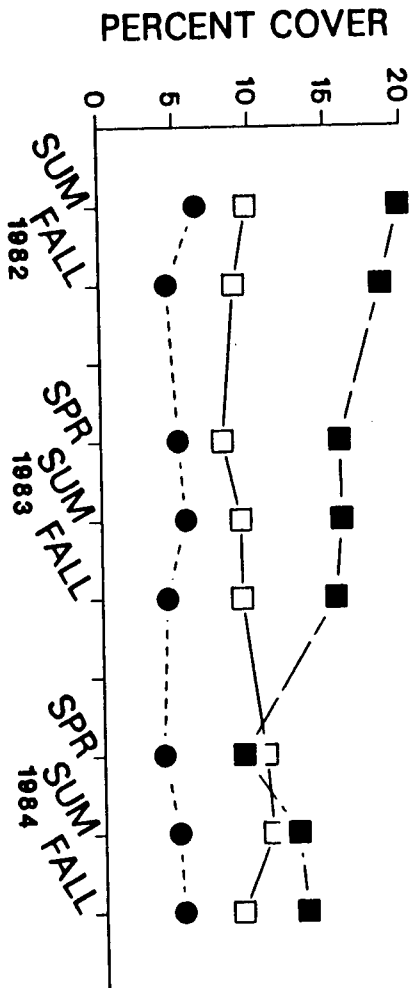
● 1939 pasture



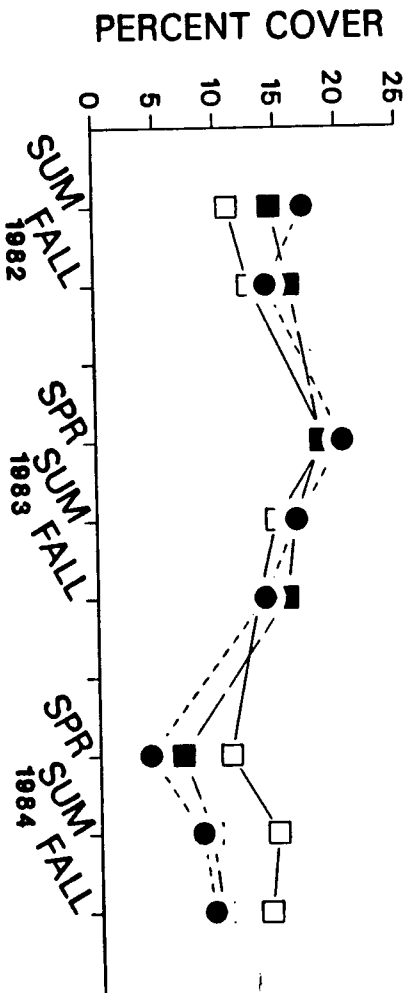
*Agropyron repens*



*Dactylis glomerata*



*Holcus lanatus*



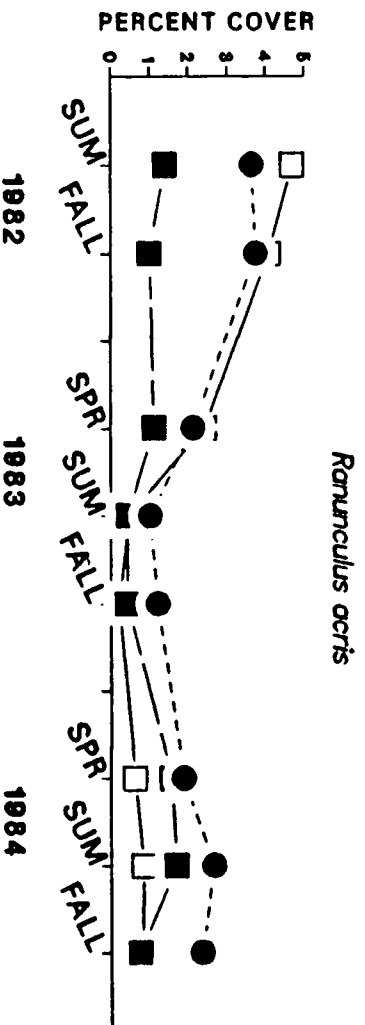
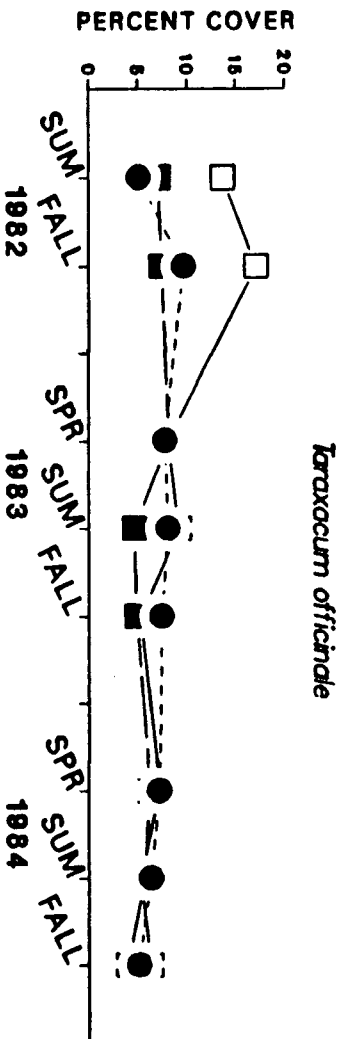
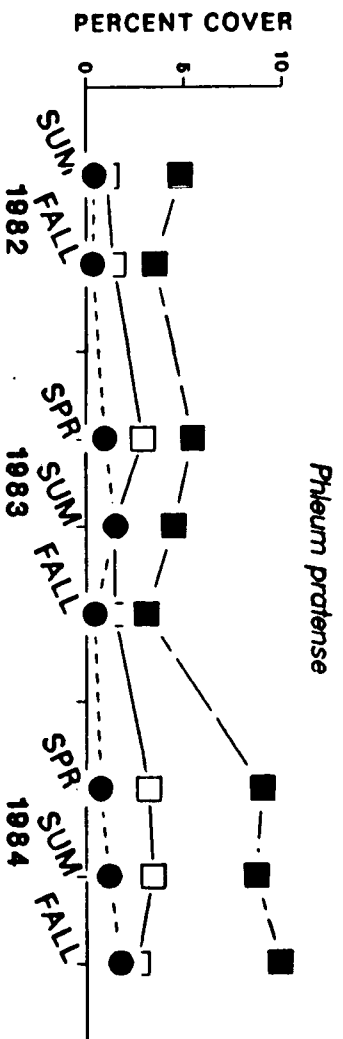
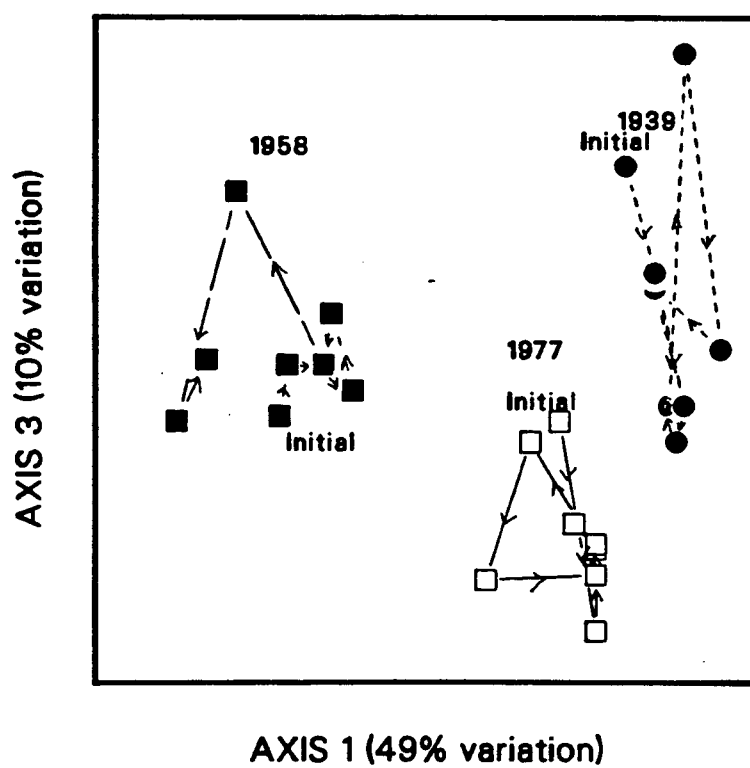
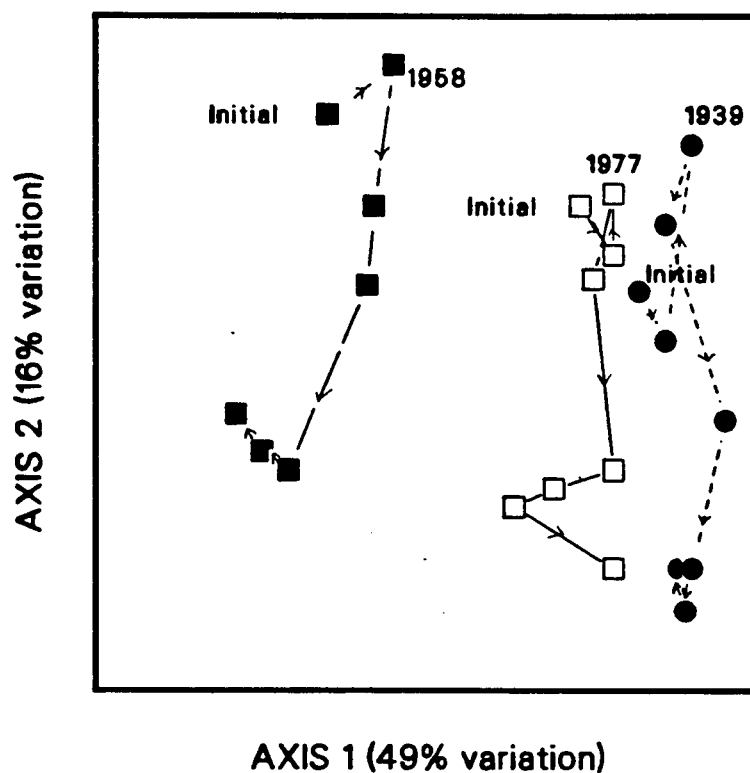


Figure 2-3. Reciprocal averaging ordination of the abundance of all species found in the three pastures in eight surveys from July 1982 to October 1984.

INITIAL - indicates the first survey in July 1982.



oldest and youngest pastures respectively, grouped near each other on the first axis, distant from the mid-aged 1958 pasture. The first axis represents a gradient based on the average abundance of each species and the second axis reflects the change in abundance of species located on the extremes of underlying physical gradients (Hill 1973). On the second axis, all pastures displayed approximately the same range of variation, although at slightly different positions along the axis. When points were joined sequentially to form a time-line between surveys, species composition in all pastures followed the same direction along the second axis. On the third axis, species composition appeared to oscillate in the 1977 and 1939 pastures.

### **2.3.2. Disturbance**

Molehill and dung counts in each plot were summed to form a disturbance measure. The three pastures show different disturbance regimes (Table 2-2). Means for each pasture were tested by using SNK on square root transformed data. The mean number of disturbances in the 1939 and 1958 pastures was not significantly different but dung formed the major component in the 1939 pasture and molehills in the 1958 pasture. The 1977 pasture had a significantly lower number of disturbances than the other two pastures ( $p < 0.05$ ) although there were a larger number of molehills than in the 1939 pasture. The 1977 and 1958 had similar average amounts of dung. The amount of dung and the number of molehills varied both seasonally and yearly in each field.

To determine if the distributions of molehills, dung and disturbances were

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random, these were tested against the Poisson distribution, or against the negative binomial distribution if the variance- mean ratio indicated contagion (i.e.  $>1$ ). The overall disturbance pattern fitted either the Poisson (11 out of 24) or the negative binomial (11 of 24) distributions and the remaining two were contagious distributions that did not fit any of the simple unimodal distributions (Table 2-2). Dung deposition usually fitted a Poisson distribution (19 out of 24), whereas molehill distribution fitted a negative binomial in 16 of 24 cases. Complex contagious bimodal distributions were not tested because of the computational difficulties surrounding them.

The number of disturbances in a plot was examined to determine whether certain areas of the pastures had consistent patterns of disturbance. Categories of disturbance regimes previously defined for contingency table analysis were used to group plots. All three pastures had plots that had consistently high, intermediate and low disturbance rates (Figure 2-4). There were also a number of plots that varied greatly in the amount of disturbance from one sampling period to the next. In the 1977 and 1958 pastures, the consistently low disturbance plots were associated with a lack of molehills. The 1939 pasture also had areas of low mole activity but the higher dung levels in this pasture made no plot consistently low in disturbance. Molehill distribution has been similarly mapped (Figure 2-5). Because dung deposition was almost always random, the amount in each plot varied at each survey although there was a slight tendency for more to be located at the narrow entrance to the 1939 pasture.

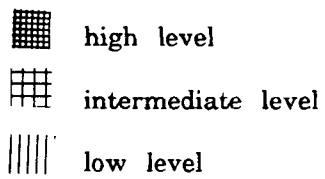


Table 2-2. Mean number of disturbances, molehills and dung per 5x5m plot in the three pastures at each survey period. The data fitted a Poisson distribution except those indicated by (\*) fitted a negative binomial distribution or (#) fitted no simple distribution.

	Disturbance			Molehill			Dung		
	1939	1958	1977	1939	1958	1977	1939	1958	1977
Summer 1982	6.00	1.98	7.23	1.87*	1.84*	3.77*	4.13	0.14#	3.46
Fall 1982	9.26	13.24*	7.75*	4.62#	9.06#	3.96*	4.64	4.18	3.79
Spring 1983	6.68*	9.80#	4.92*	1.02#	6.22*	3.73*	5.66	3.58	1.19
Summer 1983	7.26	7.22	3.58	1.83*	4.18*	3.58	5.43#	3.04	0.0
Fall 1983	13.73	17.92*	13.56	1.98*	11.46#	6.33*	11.75	6.46	7.23
Spring 1984	18.63	15.50*	12.19*	4.40#	12.64#	6.04*	14.23#	2.86	6.15*
Summer 1984	2.21*	5.30*	4.42#	2.21*	5.30*	4.42#	0.0	0.0	0.0
Fall 1984	11.45*	12.02*	9.73	4.34*	7.92*	4.96*	7.11	4.10	4.77
Mean	9.40 <sup>a</sup>	10.37 <sup>a</sup>	7.92 <sup>b</sup>	2.78 <sup>a</sup>	7.33 <sup>b</sup>	4.60 <sup>c</sup>	6.62 <sup>a</sup>	3.05 <sup>b</sup>	3.32 <sup>b</sup>

Means of Disturbance, Molehill, or Dung that do not share a common code (a,b,c) are significantly different ( $p < 0.05$ ).

Figure 2-4. Maps of the three pastures showing plots with consistently high, intermediate and low levels of total disturbance. Plots left blank varied in the amount of disturbance from one survey period to the next.



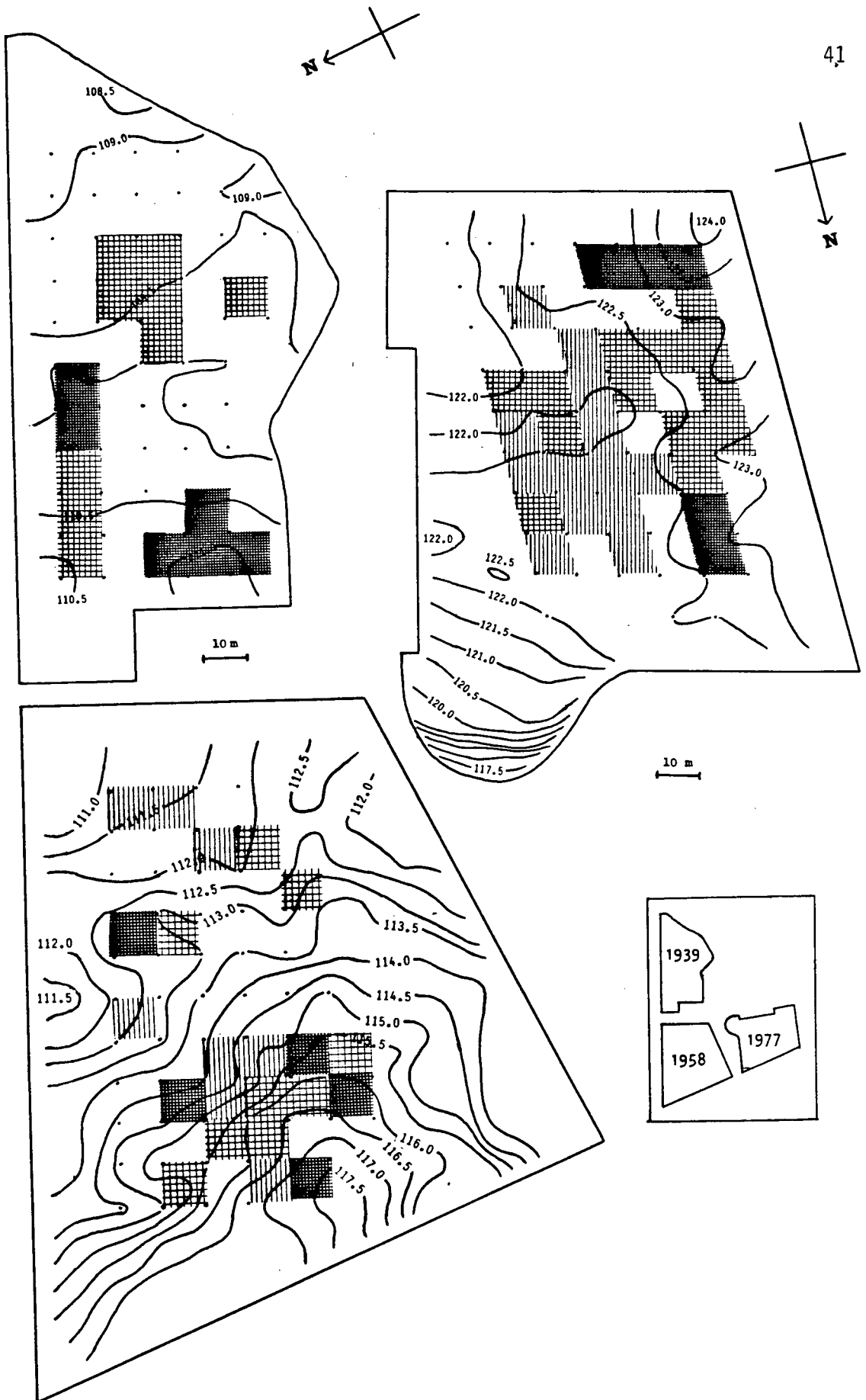
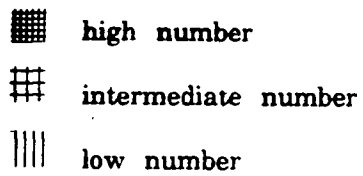
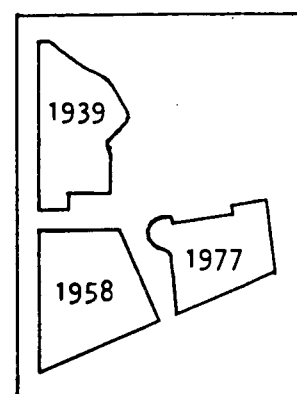
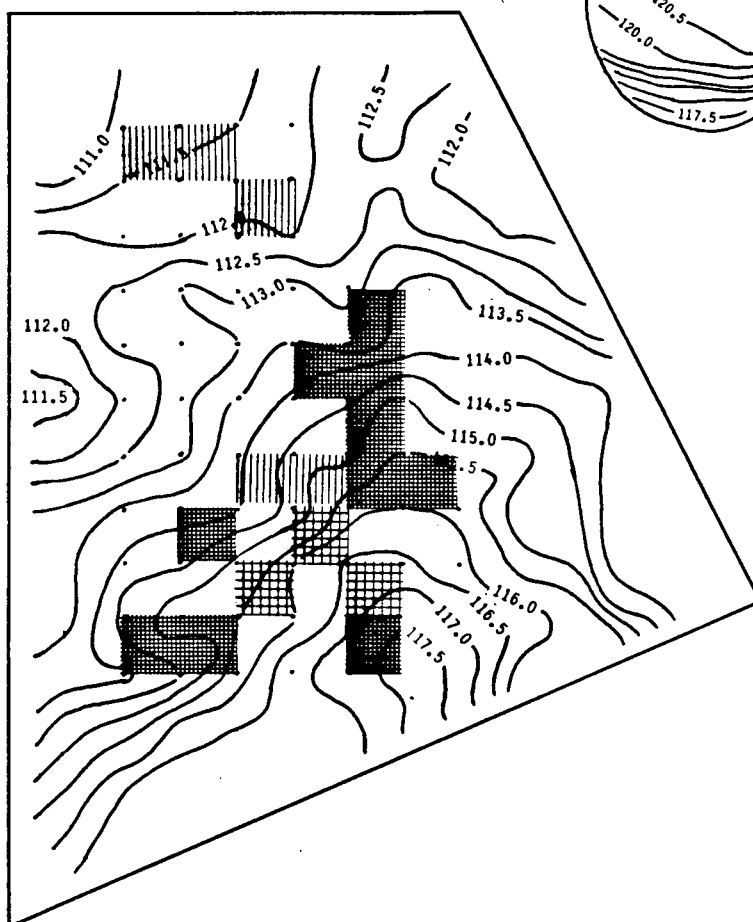
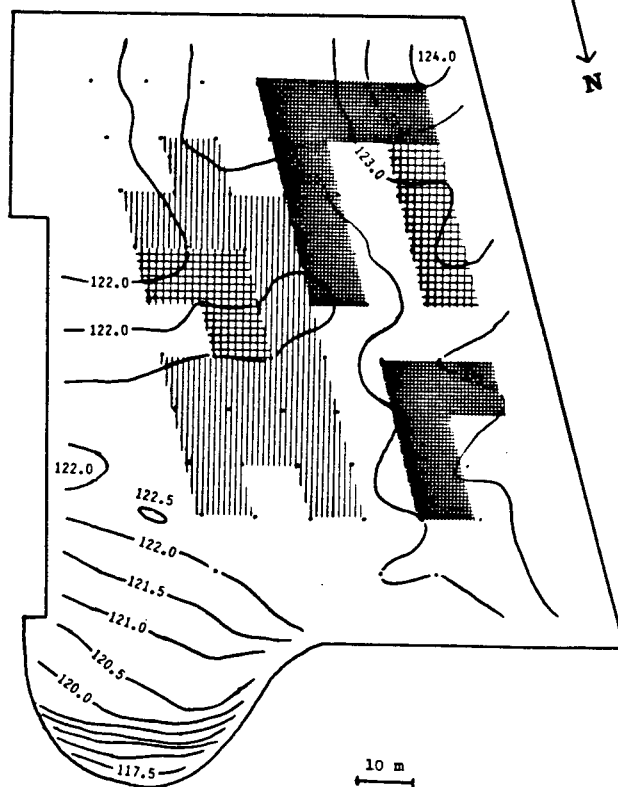
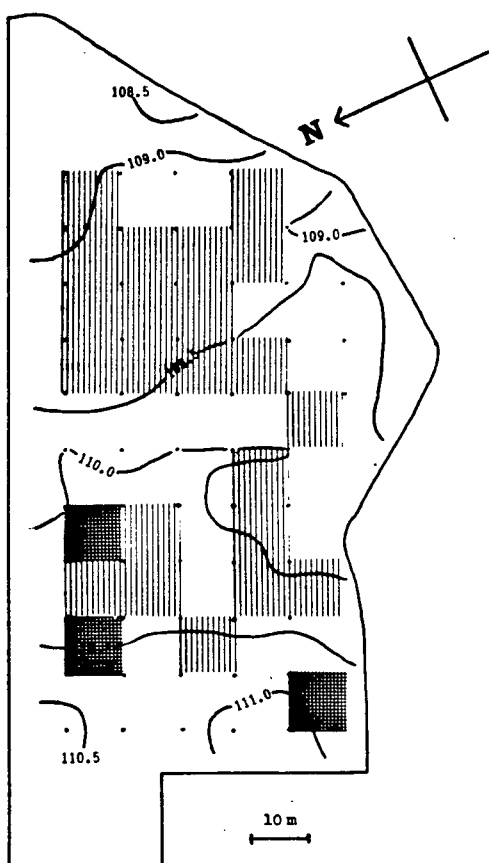


Figure 2-5. Maps of the three pastures showing plots with consistently high, intermediate and low numbers of molehills. Plots left blank varied in the number of molehills from one survey period to the next.





### 2.3.3. Interaction of vegetation and disturbance

The interaction of species abundance and the disturbance regime was first determined for two possible response sequences: (i) an immediate response to the current disturbance regime and (ii) a delayed response to the disturbance regime of the previous season. These two sequences were then decomposed into the components of disturbance, molehill distribution and dung distribution. Component interaction with abundance was also determined. Significant interactions between disturbance patterns and the abundance of the nine most common species are shown in Table 2-3. Each species showed an individualistic response pattern: some increased, some decreased and some interacted with season or year, increasing or decreasing over certain time periods.

*Lolium perenne* had no change in abundance associated with the disturbance regime of the current survey. There was, however, a significant ( $p < 0.05$ ) increase in abundance in the next survey in highly disturbed plots in the 1939 and 1977 pastures. The response of abundance to disturbance in the 1939 pasture was dependent on year, that is, management practices and climatic regimes. Although *L. perenne* increased in two pastures, it should not be assumed that the species always increases; in the 1958 pasture, there was a non-significant negative interaction between abundance and disturbance ( $0.5 > p > 0.1$ ).

*Holcus lanatus* had approximately the same abundance in all pastures (about 15%) and the same cut-off points were used in all analyses. *H. lanatus*

Table 2-3. Significant interaction of species abundance with current and previous (1) disturbance regime, (2) molehills, and (3) dung distributions: (+) indicates increased abundance and (-) indicates decreased abundance at high disturbance rates.  
 \* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; \*\*\* -  $p < 0.001$ ; s - seasonally dependent interaction; y - yearly dependent interaction.

Species	Pasture	Current season disturbance			Previous season disturbance		
		(1)	(2)	(3)	(1)	(2)	(3)
<i>Lolium perenne</i>	1977				+		+
	1958						
	1939				y		
<i>Holcus lanatus</i>	1977	s*	s*		-***	-***	
	1958	-**	-***		-*	-**	s*
	1939	-*					
<i>Trifolium repens</i>	1977	-***	-***	+*	-***	-***	
	1958	-*		s***	y*	-**	
	1939						
<i>Dactylis glomerata</i>	1977	+***	y**		+***	+***	+
	1958	+*	+**		s/y*	+***	
	1939	y*	+	+**		+***	
<i>Agropyron repens</i>	1977	+***	+***		+	+**	
	1958	+**	+**		y*		
	1939	+			y	+	+
<i>Taraxacum officinale</i>	1977	+***	y**		+***	s**	
	1958	s*	s*	y*	+	y*	y*
	1939	+	+		+	+	
<i>Poa compressa</i>	1977				y*		
	1958	s*			s		y*
	1939	+	s				+
<i>Phleum pratense</i>	1977	+*	+		+***	+	
	1958	-*	s/y*				s*
	1939			-*			
<i>Ranunculus acris</i>	1977					-*	-*
	1958						
	1939		-*				

abundance decreased in all pastures in response to disturbance in the current season. In the 1977 pasture, however, the response was dependent on season ( $p < 0.05$ ): a decrease in abundance occurred in the summer and fall but there was a slight increase in disturbed areas in the spring. *H. lanatus* appeared to decrease primarily with increasing number of molehills in the 1977 ( $p < 0.05$ ) and 1958 pastures ( $p < 0.05$ ). This may be because molehills rather than dung made the major contribution to the disturbance regime in these pastures. There was also a significant decrease in plots disturbed in the previous season in the 1977 and 1958 pastures ( $p < 0.001$  and  $p < 0.05$ , respectively). In the 1958 pasture, *H. lanatus* showed a seasonal response to dung deposited in the previous season ( $p < 0.05$ ). The interaction was negative in the spring and summer but positive by the fall.

*Trifolium repens* decreased in response to current disturbance in the two pastures in which significant interactions were found ( $p < 0.001$  and  $p < 0.05$  in the 1977 and 1958 pastures respectively). The overall decrease is suggested to be due to molehills because *T. repens* increased in abundance with increasing dung deposition in the 1977 pasture ( $p < 0.05$ ) although the increase was restricted to summer in the 1958 pasture ( $p < 0.001$ ). The overall decrease in abundance was still significant in the survey in the following season ( $p < 0.01$  and  $p < 0.05$  in the 1977 and 1958 pastures respectively), and this decrease was associated with molehills.

Three species, *Dactylis glomerata*, *Agropyron repens* and *Taraxacum officinale* showed significantly increased abundance in highly disturbed plots in all three



pastures. In addition, all three species increased significantly with molehills suggesting that it was that component of disturbance which most affected abundance. There were some exceptions to the overall pattern (Table 2-3). *T. officinale*, in particular, had a strong seasonal and yearly component to its interaction with disturbances.

The response of *Poa compressa* to disturbance was highly variable. In the 1958 pasture, *P. compressa* showed a seasonal interaction with current disturbance ( $p < 0.05$ ), increasing in the summer and fall but decreasing in the spring. The interaction with the previous disturbances was also seasonal but only increased in the fall, that is, the decrease in spring persisted into the summer and the summer increase into the fall, but the fall increase in abundance did not carryover into spring. In the 1939 pasture, *P. compressa* abundance interacted with disturbance ( $p < 0.05$ ) and was most abundant at medium disturbance rates. There was a seasonal component to the interaction with molehills in which *P. compressa* only increased in the summer ( $p < 0.01$ ).

*Phleum pratense* was also inconsistent in its response to disturbance. In the 1977 pasture, *P. pratense* increased in highly disturbed plots ( $p < 0.05$ ). *P. pratense* showed an overall decrease with disturbance in the 1958 pasture ( $p < 0.05$ ) and dung in the 1939 pasture ( $p < 0.05$ ) and showed seasonal and yearly variations in its interaction with molehills. *P. pratense* was absent from molehill sites formed in the spring but present on them in the summer and fall. Because *P. pratense* generally had peak abundance in the spring (Figure 2-2) and declined in relative abundance over the growing season, the overall effect of disturbance was to

decrease abundance. *P. pratense* responded seasonally to the dung previously deposited ( $p < 0.05$ ): presence in spring was positively related to dung of the previous fall and, to lesser extent, summer abundance to spring dung but fall abundance was negatively related to dung deposited in the summer.

No overall significant response to disturbance was recorded for *Ranunculus acris*. This species showed decreased abundance ( $p < 0.05$ ) at high molehill densities in the 1939 pasture. In the 1977 pasture, there was no response to current disturbance, although decreases in abundance were associated with previous disturbances. *R. acris* was absent from plots with many molehills but it was present in medium density dung sites. These interactions led to no overall significant response to disturbance.

## 2.4. DISCUSSION

### 2.4.1. Vegetation

Species abundance in the three pastures is characterized by spatial and temporal heterogeneity. Fluctuations in abundance from year to year have been documented in other grassland communities (e.g. Rabotnov 1966, 1974; Kletter 1968; Snaydon 1985) although the chalk grasslands studied by Grubb *et al.* (1982) changed remarkably little over a 12 - 15 year period. Undoubtedly, some temporal variation is associated with seasonal growth patterns such as the spring increase in *Phleum pratense* abundance and the fall increase of *Trifolium repens* (Figure 2-2). Whether gains represent vegetative expansion or recruitment into the

population, or declines result from death of entire plants or from their parts, is unknown. This presents a problem, however, only for demographers interested in the fate of individuals.

Despite the lack of significant parallel changes in species abundance among pastures, reciprocal averaging ordination indicated trends in botanical composition followed the same direction in all pastures. The absence of trends associated with pasture age differs from the findings of Aarssen (1983) in these pastures. He found a strong directional trend in community composition and high variability in species composition in the 1977 pasture. Since Aarssen's survey, the 1977 and 1939 pastures have become more similar in species composition. It is possible that topographical variation evident in the 1958 pasture differentiates its botanical composition from the other two relatively flat pastures. The method of data collection may have contributed to differences in results. Rooted cover is a two-dimensional method and as such is less variable than Aarssen's method which allows for a three-dimensional estimate. Information from the vertical dimension is sacrificed in rooted cover estimates for less bias and greater repeatability.

Aarssen (1983) attributed differences in the variability in species composition in the 1977 compared to 1939 pasture to the time available for biotic interactions, and hence, for selective forces to accumulate and generate biological accommodation. Biological accommodation between individual plants led to increased stability in the old pasture. Results from this study, however, suggest that accommodation takes place within the first five years after seeding and establishment. This accommodation may be in response to both biotic and abiotic

factors and involve both genetic change (Snaydon 1978) and acclimation (Berry and Bjorkman 1980; Bradshaw 1965). Subsequently, community composition stabilizes and oscillates in response to such factors as management, grazing and fertilization (e.g. Jones 1933a,b,c,d), and climate (Garwood and Tyson 1979; Kleter 1968).

#### 2.4.2. Disturbance

Because the distribution of dung in the pastures is random, usually fitting a Poisson distribution, all the plants have an equal chance of being affected by dung. Molehills, on the other hand, generally fitted a negative binomial distribution. This distribution can arise from a number of models and the consequences to plants growing near molehills are quite different under these models. The distribution may result from a mixture of several Poisson distributions, each having a different mean, such that the means are a continuous variate with a  $X^2$  distribution (Bliss and Fisher 1953). The negative binomial distribution is also related to the Poisson such that, in some cases, data fit a Poisson at low population densities and a negative binomial at higher densities. This is not simply the case with the dung and molehill densities seen in Table 2-2 because some higher densities fit the Poisson and some lower densities fit the negative binomial.

A negative binomial distribution may also arise from non-random contagion. If a distribution is unimodal and the "presence of one individual in a division increases the chance of other individuals falling into that division, a negative

binomial will fit best" (Student 1919, in Bliss and Fisher 1953). A negative binomial can result then from a mixed or compound Poisson distribution without contagion, or from contagion which changes the probability of the following events (Bliss and Fisher 1953). If the distribution results from a compound Poisson, then the chances of being killed are approximately the same throughout the pasture but if it results from contagion, plants growing near molehills are more likely to be killed than those growing further away.

#### **2.4.3. Interaction of vegetation and disturbance**

Each species responded differently to the disturbance pattern. Species may be roughly divided into three groups: increasers, decreasers and indifferent, although there are exceptions within groups. The response of some species (e.g. *Taraxacum officinale*, *Poa compressa*) to disturbance was to increase but only in certain years, or seasons, or parts of the growth cycle and to decrease in others. External factors such as climate (e.g., a wet spring or summer), or management (e.g., intense grazing in summer or fall) influence species response. Patterns of response have been described but the mechanisms generating the response are still to be investigated.

The pattern of response had no correlation to morphology. A robust tillering grass (*Dactylis glomerata*), a rhizomatous grass which usually exists as single tillers (*Agropyron repens*), and a clonal dicot that spreads by apomictic seed (*Taraxacum officinale*) were all found to increase with disturbance. Similarly, *Holcus lanatus*, a closely tillering, clumped grass which only occasionally spreads

by stolons and, *Trifolium repens* a clonal, stoloniferous and capable of rapid expansion and independent existence of ramets were both found to decrease with disturbance.

The nature of the disturbance also varies. Dung is not only an agent of mortality but also acts to fertilize, releasing nutrients to surrounding plants. It also affords protection, because cows rarely graze within 30cm of fouled areas (Norman and Green 1958). Many seeds can survive passage through the cow and subsequently germinate (Hutchinson 1979). Dung may serve to disperse seed over long distances from plants both within and outside a pasture.

Molehills have a less complex interaction: during formation plants are uprooted and smothered. In addition to freeing areas for colonization, the process of molehill building also brings up a seed source different from that of the surrounding sward (Jalloq 1975). Many of these seeds have been buried and come from a temporally distant source so that not only are different species represented but also different genotypes, containing an "evolutionary memory" (Harper 1977) of the genetic make-up of the pasture.

The foregoing discussion of the results has inferred a dynamic response from static patterns, i.e. increased abundance was achieved through colonization or invasion of open space. This is not necessarily the only mechanism. For example, *Taraxacum officinale* can invade only by seed but its seedlings rarely survive on molehills (R. Parish, unpublished data), however, its long tap root frequently survives burial so that it persists while other species are removed.

Static pattern need not have a dynamic corollary. There may exist a group of correlated patterns of which only two have been related. For example, *Holcus lanatus* proliferates in areas where water is abundant and is often found where water tables are high (Beddows 1961; Watt and Haggard 1980; R. Parish, pers. obs.). In winter, if the water table in these areas is sufficiently high to exclude moles during their very active period, October to March, high abundance associated with lack of disturbance may not represent exclusion from disturbance sites but a correlation with a third factor, high water levels. Rothwell's (1977) data, however, argues against this interpretation. He found that when *H. lanatus* was present in the sward it was significantly lower in abundance on adjacent molehills which suggests that it was unable to colonize these disturbances.

There are a number of limitations to studies using correlation of patterns. The coincidence of patterns is not sufficient to imply causation. Patterns may be linked by other correlated factors leading to dangers in inferring mechanisms or processes based on changes in patterns. Some of these problems could have been circumvented by an experimental or manipulative approach. One approach would have been to disturb repeatedly certain areas of the pasture. Experimental work such as that of Sousa (1979) in the intertidal showed that perennial species were eliminated by high disturbance rates and ephemerals came to dominate. Another approach would be to remove moles and thereby eliminate a source of disturbance in order to compare which species dominated in their presence or absence. If it had been feasible to create artificial disturbances throughout the pastures and manipulate density, the analysis of subsequent vegetation response would have been unlinked to correlations with groups of other factors. In the

following chapter, I examine invasion of molehills and dung pats in an effort to resolve some of these issues.



### 3. INVASION OF DISTURBANCES

#### 3.1. INTRODUCTION

Pastures are subject to a variety of disturbances of various magnitudes such as drought, erosion, animal mounds, grazing, scrapings and droppings. Such disturbances create spatial heterogeneity and thus influence species and genetic diversity in the community. Disturbance is currently viewed as providing a dynamic mosaic of small to large, short-lived patches that can be utilized by opportunistic invaders (Platt 1975; Loucks *et al.* 1985) or be recolonized in a more or less predicable pattern of succession (Begon *et al.* 1986). Disturbance may then result in an increase in species diversity by permitting the establishment of opportunistic species that cannot compete in the closed sward and increase genetic diversity by providing 'safe sites' for seed germination and establishment of both colonizing and established species. Grubb (1977) has suggested that the formation of gaps may be essential to the maintenance of species richness in communities.

Plants are generally considered to be immobile organisms but the growth form of many pasture species allows movement through space both vertically and horizontally. This mobility permits the individual to sample a spatially variable environment and allows colonization of gaps within the sward. The relative contribution of new individuals compared to the expansion of old individuals will alter spatial heterogeneity and affect community composition. If species differ in their ability to colonize disturbances, the community will reflect those differences.

The pasture environment provides different challenges to component species. Typically, pasture species are perennials which have the ability to persist and expand within the sward. Superimposed upon this are numerous gaps which provide an environment where the ability of a species to colonize and multiply rapidly is a more important element of success.

In this study, the colonization of individual gaps created by molehills and dung pats was monitored along with associated changes in the botanical composition of the surrounding sward. The objectives were (i) to determine patterns of species invasion of disturbance; (ii) to determine patterns of species persistence and replacement; and, (iii) to compare the abilities of species to invade both open space and closed sward.

### **3.2. METHODS**

#### **3.2.1. Field Methods**

The plots described in Chapter 2 were used in this study. Ten plots were randomly chosen in each pasture for each of two survey periods (August 1983 to May 1984, and August 1984 to May 1985). Within each plot, one recently formed molehill and one recently deposited dung pat were selected. A .5 x .5m quadrat, subdivided into 100 systematically arranged points was centered on the molehill or dung pat and the plant species rooted directly under the 100 points (crosswires on the quadrat) were recorded. Depending on the availability of the pasture, surveys could begin in August to October and were repeated monthly

until the molehill or dung pat was completely covered with vegetation or until May when the grass was too long to record accurately by this method.

The method required repeated measurements in accurately relocatable quadrats. Because there were cattle and mowing equipment in the pastures, permanent stakes could not be used to mark quadrats. Instead, acrylic paint was applied to the ground at the four corners of the quadrat and this allowed relocation of the quadrat in subsequent surveys to be accurate within a few millimeters.

### 3.2.2. Analytical methods

Transition probabilities were calculated, using the CROSSTABS procedure of SPSS.x, from the monthly record of species at each point in the quadrat. Data were pooled over the 10 molehills and 10 dung pats per pasture and analysed separately by pasture and by year.

A model developed by de Jong and Greig (1984) was used to determine if species replacement over the study period deviated from random. The model describes the behaviour of first-order Markov chains where transitions in which the identity of a species at any one point remained the same (self-transitions) were excluded from the analysis. The removal of self-transitions obviated distinguishing between individuals of the same species occupying the same space at different times. To test the overall pattern of species replacement, a program was written by J. Emmanuel (University of British Columbia, pers. comm.) based on a maximum likelihood fitting algorithm developed by de Jong *et al.* (1983). A

second program written by K. Pollson (pers. comm.), based on algorithms developed by de Jong and Greig (1985), tested for randomness in pattern of replacement of each species pair. Rare species, less than 2% cover, were eliminated from the analysis because a minimum expected value of 3 was specified for the calculation of chi-square values.

### 3.3. RESULTS

#### 3.3.1. Species persistence: self-transition

Species vary in their ability to hold onto, or persist in, a given space. Persistence, defined as the percentage of a given species, present in the initial survey, that occupied the same point in the sward throughout each nine month survey period, ranged from 0 to 100% (Table 3-1). The variability of a species' ability to persist was large; for example, *Ranunculus acris*, encompassed the entire range within the same field and year. Species persistence within a pasture, disturbance type and year was ranked and Friedman rank correlation was calculated to determine if average ranks were the same. The pattern of species persistence differed in different years, among pastures, and whether around molehills or dung pats ( $p < 0.001$ ). The resultant groupings from multiple range tests of the rankings suggested that persistence was generally higher in 1984 than 1983, i.e., fewer plant parts died and were replaced by different species in 1984. When the percentage of species persisting were pooled over disturbance, pasture or year, only differences in rankings between years emerged significant ( $p < 0.001$ ) and ability of species to persist showed no significant

Table 3-1. Percentage of species that persist throughout the nine month study period in the sward around molehills and dung pats. Included is the percentage of the molehill and dung pat that remains uncolonized.

Species	1977 pasture				1958 pasture				1939 pasture			
	molehill		dung		molehill		dung		molehill		dung	
	1983	1984	1983	1984	1983	1984	1983	1984	1983	1984	1983	1984
<i>Dactylis glomerata</i>	51.8	40.3	68.6	58.1	35.7	48.8	70.9	78.0	33.3	76.7	31.6	83.0
<i>Holcus lanatus</i>	42.5	66.1	44.4	70.9	9.3	26.2	32.2	29.8	16.8	40.4	5.1	51.3
<i>Lolium perenne</i>	31.7	47.7	41.5	54.8	3.9	32.3	33.9	20.0	33.6	36.8	25.6	60.5
<i>Phleum pratense</i>	64.3	11.1	60.0	50.0	31.3	52.3	72.0	55.6	-	-	0.0	60.0
<i>Poa compressa</i>	34.0	29.0	47.2	37.1	9.3	22.0	53.5	36.8	27.7	41.7	14.4	53.7
<i>Agropyron repens</i>	2.7	7.7	2.4	6.7	9.8	4.8	41.0	21.6	0.0	30.0	4.3	30.8
<i>Trifolium repens</i>	29.1	48.1	45.2	49.6	21.4	61.9	52.6	55.0	40.7	46.6	19.8	55.2
<i>Taraxacum officinale</i>	33.3	48.9	45.8	55.6	15.6	48.3	81.3	51.9	37.7	55.2	34.8	54.5
<i>Ranunculus acris</i>	45.1	60.0	0.0	57.1	0.0	30.0	60.0	50.0	100	42.9	0.0	71.4
Moss	15.0	5.4	11.4	11.6	-	12.8	45.8	15.9	7.7	13.3	0.0	15.4
Molehill	21.6	27.5	4.5	0.0	30.9	44.8	15.4	23.6	26.8	27.2	5.7	4.8
Dung	0.0	0.0	16.4	5.8	0.0	0.0	26.5	22.5	4.0	0.0	11.4	4.3
Rank	4	7	5	8.5	2	6	11	10	3	8.5	1	12

Friedman Test Statistic = 49.31,  $p < 0.0001$

Multiple range test of ranks

12=11=10=8.5=7  $\neq$  1

12=11  $\neq$  2

12  $\neq$  3

differences between pastures nor disturbance types.

### 3.3.2. Patterns of species replacement

#### 3.3.2.1. Monthly transition probabilities

Tables of species transitions were generated (using the CROSSTABS program) from one monthly survey to the following one, and from the initial to the final survey (see Appendix 1). Each observed value was expressed as a percentage of the total row count so that the tables sum to 100% along the rows. Each percentage value can be considered to be the probability of the replacement of the row species by the column species. Of the 22 species found on or around disturbances, not all were sufficiently abundant to be consistently involved in replacement. The values generated were used to calculate the average monthly probability of transition for each species (see Table 3-2 for representative examples). The diagonals are the probability that the same species remains in the same location from one survey period to the next (self-transition) and the off-diagonals are the probability of its replacement by another species. The probability of persisting from one survey to the next was very high for most species, but this probability is dependent on the time interval between surveys. For example, in 1983, *Dactylis glomerata*, in the sward around molehills in the 1977 pasture, had a 87.9% (Table 3-2) probability of persisting from one month to the next but a 51.8% (Table 3-1) probability of persisting over the nine month survey period. This analysis also estimated monthly colonization rates on disturbances, for example, because dung in 1983 in the 1977 pasture had a

Table 3-2. (a)Average monthly transition probability of a row species being replaced by a column species for eight common species on and around molehills, and the average monthly probability of molehill colonization by column species in the 1977 pasture during 1983-1984 survey period.

	Molehill	<i>Dactylis</i> <i>glomerata</i>	<i>Holcus</i> <i>lanatus</i>	<i>Lolium</i> <i>perenne</i>	<i>Phleum</i> <i>pratense</i>	<i>Poa</i> <i>compressa</i>	<i>Agropyron</i> <i>repens</i>	<i>Trifolium</i> <i>repens</i>	<i>Taraxacum</i> <i>officinale</i>
Molehill	<b>70.6</b>	1.5	1.0	6.9	1.3	6.1	3.1	3.6	2.6
<i>Dactylis glomerata</i>	3.7	<b>87.9</b>	0.8	2.0	0.6	2.3	0.4	0.8	0.4
<i>Holcus lanatus</i>	3.0	0.5	<b>83.1</b>	2.5	0.3	4.4	1.0	3.2	0.3
<i>Lolium perenne</i>	5.3	1.8	1.8	<b>76.9</b>	0.4	7.5	1.4	2.6	0.8
<i>Phleum pratense</i>	5.6	0.0	0.0	0.0	<b>89.9</b>	0.5	0.0	2.5	0.5
<i>Poa compressa</i>	3.3	2.2	0.8	3.9	0.4	<b>82.4</b>	2.1	2.0	1.4
<i>Agropyron repens</i>	5.9	3.4	2.0	8.3	0.0	7.4	<b>67.2</b>	2.5	0.5
<i>Trifolium repens</i>	6.3	1.1	1.1	2.7	0.8	4.6	0.8	<b>79.1</b>	0.9
<i>Taraxacum officinale</i>	3.7	1.6	0.0	2.5	0.6	2.2	0.6	1.6	<b>84.8</b>

(b)Average monthly transition probability of a row species being replaced by a column species for eight common species on and around dung pats, and the average monthly probability of dung colonization by column species in the 1977 pasture during 1983-1984 survey period.

	Dung	<i>Dactylis</i> <i>glomerata</i>	<i>Holcus</i> <i>lanatus</i>	<i>Lolium</i> <i>perenne</i>	<i>Phleum</i> <i>pratense</i>	<i>Poa</i> <i>compressa</i>	<i>Agropyron</i> <i>repens</i>	<i>Trifolium</i> <i>repens</i>	<i>Taraxacum</i> <i>officinale</i>
Dung	<b>75.4</b>	1.1	2.0	4.7	0.4	3.2	2.4	7.6	2.0
<i>Dactylis glomerata</i>	1.9	<b>90.8</b>	1.5	1.5	0.0	1.2	0.0	1.5	0.4
<i>Holcus lanatus</i>	1.5	0.3	<b>85.3</b>	1.7	0.5	4.2	0.5	3.5	0.7
<i>Lolium perenne</i>	1.9	1.0	1.5	<b>82.8</b>	0.1	5.8	0.9	2.9	1.0
<i>Phleum pratense</i>	0.0	0.0	4.9	0.0	<b>92.7</b>	0.0	0.0	2.4	0.0
<i>Poa compressa</i>	0.8	1.1	1.9	3.6	0.2	<b>85.6</b>	0.9	2.0	0.9
<i>Agropyron repens</i>	2.5	0.6	3.8	6.3	0.0	5.6	<b>58.8</b>	9.4	2.5
<i>Trifolium repens</i>	1.8	0.3	2.5	2.2	0.1	3.8	0.3	<b>86.0</b>	0.8
<i>Taraxacum officinale</i>	1.4	0.5	0.0	2.4	0.0	0.5	0.0	4.8	<b>89.5</b>

75.4% probability of remaining as dung, about 24.6% of dung was colonized each month.

### 3.3.2.2. *Transition probabilities over the survey period*

Values from the transition probability matrices (Appendix 1) were used to estimate the probability of replacement of one species by another over the survey period from fall to spring in a given year. Tests for randomness of the pattern of replacement showed that on both disturbance types in all three pastures, in both years, species replacement was not random ( $p < 0.0001$ ) and there was a strong pattern to the replacement process (Table 3-3). Test for randomness in the replacement pattern of each pair of species, e.g. the replacement of *Lolium perenne* by *Trifolium repens*, or the replacement of *Holcus lanatus* by *Agropyron repens*, showed that in almost all cases the pattern was non-random.

To determine if the pattern of replacement of one species by other species at each survey was constant over time, contingency table analysis of the monthly pattern of replacement was used. Results from analyses including self-transition and excluding self-transitions are shown in Tables 3-4 and 3-5 respectively. Colonization patterns on molehills and dung pats changed over time throughout the study period. In the sward around disturbances, some species, such as *Poa compressa*, were replaced by different species at different times of the year whereas others, such as *Dactylis glomerata*, had the same pattern of replacement each month. In fact, some species, *D. glomerata*, *Taraxacum officinale* and *Ranunculus acris*, in particular, had such strong patterns of persistence that they



Table 3-3. Deviations from random of replacement patterns of common species, growing on and around molehills and dung pats in the three pastures.

Year	Disturbance	$X^2$	Significance
<u>1977 Pasture</u>			
1983	Molehill	214.5	$p < 0.0001$
	Dung	366.3	$p < 0.0001$
1984	Molehill	211.5	$p < 0.0001$
	Dung	203.8	$p < 0.0001$
<u>1958 Pasture</u>			
1983	Molehill	285.9	$p < 0.0001$
	Dung	346.2	$p < 0.0001$
1984	Molehill	179.7	$p < 0.0001$
	Dung	237.4	$p < 0.0001$
<u>1939 Pasture</u>			
1983	Molehill	207.9	$p < 0.0001$
	Dung	390.7	$p < 0.0001$
1984	Molehill	271.1	$p < 0.0001$
	Dung	471.5	$p < 0.0001$

Table 3-4. Species showing differences in the monthly pattern of replacement when self-transitions are included: \* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; \*\*\* -  $p < 0.001$ ;  
- insufficient replacements for analysis.

Species	1977 pasture				1958 pasture				1939 pasture			
	molehill		dung		molehill		dung		molehill		dung	
	1983	1984	1983	1984	1983	1984	1983	1984	1983	1984	1983	1984
<i>Dactylis glomerata</i>				**	***	*			**			
<i>Holcus lanatus</i>	**	**	*	***	***		*		***		***	
<i>Lolium perenne</i>	***	***							***	**	***	
<i>Phleum pratense</i>		***		*	*	**			-	-		
<i>Poa compressa</i>	***	*	***	***	***	**		**	***	***	***	*
<i>Agropyron repens</i>	*	-			***							
<i>Trifolium repens</i>	***	**	***	*	***				***	***	***	*
<i>Taraxacum officinale</i>			***		***	**			*		***	
<i>Ranunculus acris</i>	-		*		-							
Moss		**	***			***		***		**	***	***
Molehill	***	***			***	*			***			
Dung	-		***	***	*		***	***		**	***	***

Table 3-5. Species showing significant differences in the monthly pattern of replacement when self-transitions are excluded: \* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; \*\*\* -  $p < 0.001$ ; - insufficient replacements for analysis.

Species	1977 pasture				1958 pasture				1939 pasture			
	molehill		dung		molehill		dung		molehill		dung	
	1983	1984	1983	1984	1983	1984	1983	1984	1983	1984	1983	1984
<i>Dactylis glomerata</i>	-	-	-	-	**		-	-		-	-	
<i>Holcus lanatus</i>	**			***	**				**	-	**	
<i>Lolium perenne</i>	***	-		-				-	***	**	***	
<i>Poa compressa</i>	***		**	**	***	**		**	***	**	***	
<i>Agropyron repens</i>	***	-		-			-	-	-	-	-	
<i>Trifolium repens</i>	*				-		-	-		**	*	
Moss	-	**	**		-		-		-	-	-	
Molehill	***	*		-	***	***			***	***		
Dung	-			***	-	***		***	-		***	*

had an insufficient number of replacements by other species to allow analysis.

### 3.3.3. Colonization of disturbances

In general, about 12 species invaded disturbed sites and the number of species was not significantly different between dung and molehills, pastures nor year of survey.

#### 3.3.3.1. Seedling recruitment

Very few seedlings were recorded on disturbed sites throughout the year and even fewer became established (Table 3-6). *Trifolium repens* seedlings were found only in late April and May on molehills and decayed dung pats. Seedling have not been observed in the sward in the Aldergrove pastures. Seedlings of *T. repens* were marked and their survival followed over the summer through mowing and later grazing. Survivorship from germination in spring to the following August ranged from 2% to 45%. In 1984, both a greater number of seeds germinated and seedlings survived (Figure 3-1).

#### 3.3.3.2. Colonization patterns

To compare the ability of different species to invade disturbed sites, a ratio was calculated of the final percentage on the disturbed site divided by the initial percentage abundance around it (Figure 3-2). Percentage abundance was used in this ratio to standardize differences in size between area disturbed and that

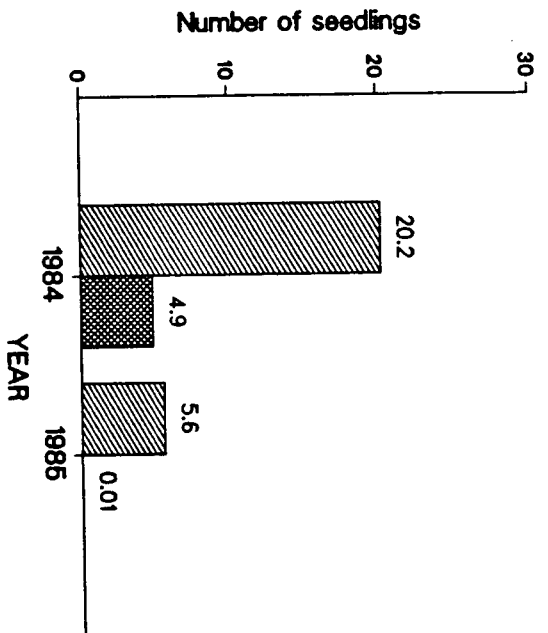
Table 3-6. Number of seedlings per square metre found on disturbances (molehills and dung pats) in the three pastures.

Species	1939 pasture		1958 pasture		1977 pasture	
	1983	1984	1983	1984	1983	1984
<i>Lolium perenne</i>		3.80			7.92	1.16
<i>Poa compressa</i>			1.32		0.92	0.56
<i>Holcus lanatus</i>			10.0		0.92	
<i>Alopecurus pratensis</i>			0.68			0.56
<i>Agrostis alba</i>						1.16
<i>Taraxacum officinale</i>			1.32			0.56
<i>Ranunculus acris</i>		3.8	2.68	1.08		
<i>Rumex acetosella</i>			2.0		0.98	
<i>Plantago lanceolata</i>			1.32		0.48	
<i>Cerastium vulgatum</i>		1.92	0.68			
<i>Medicago lupulina</i>	1.60		2.0			

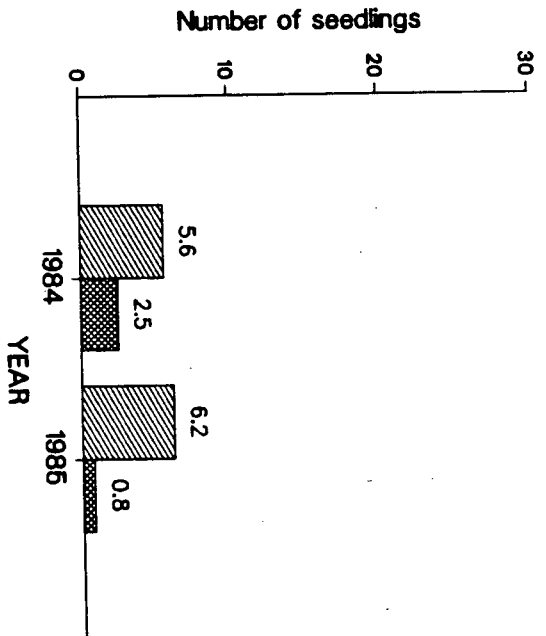
Figure 3-1. Average number of *Trifolium repens* seedlings per molehill or dung pat germinating in April and surviving until August in each pasture for two consecutive years.

- /// initial number per disturbance in April
- final number per disturbance in August

1939 pasture



1958 pasture



1977 pasture

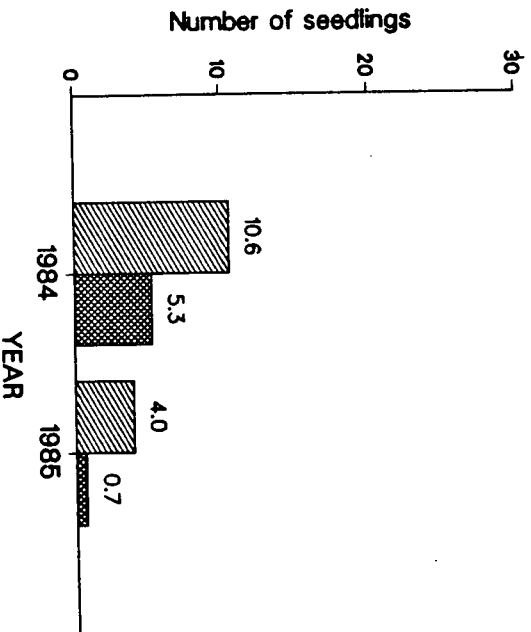
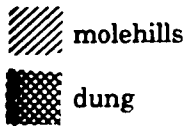
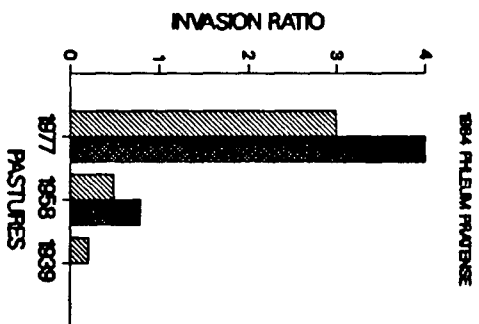
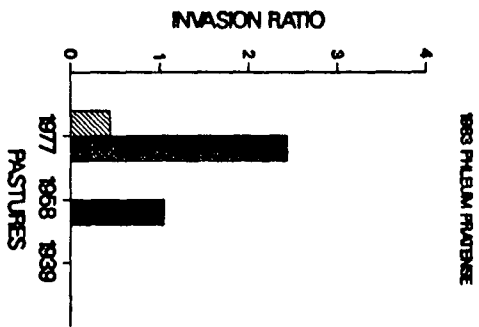
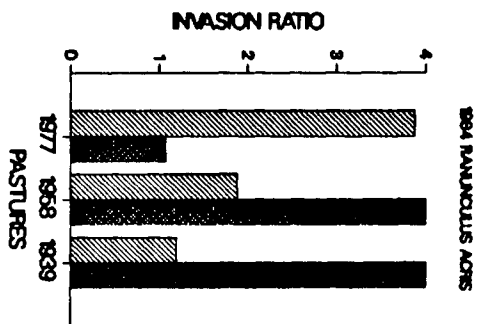
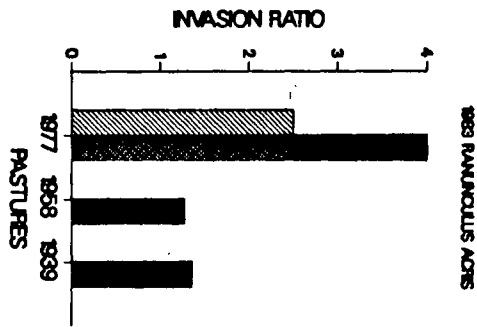
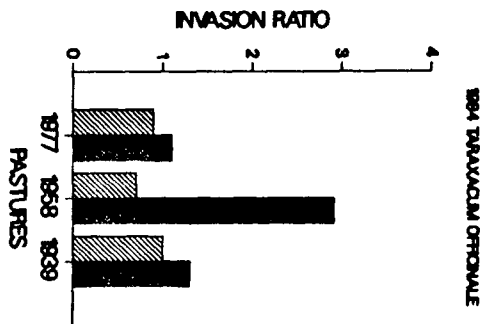
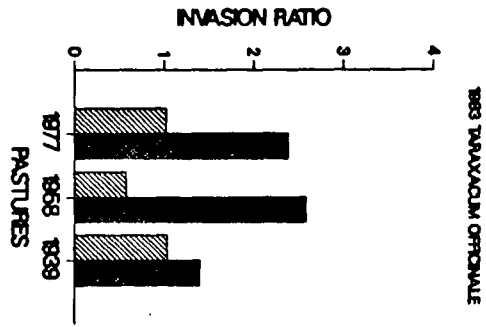


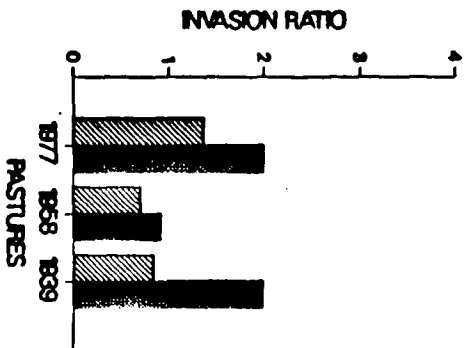
Figure 3-2. Invasion ratio of species final percentage abundance on disturbed sites divided by initial percentage abundance around the disturbance. If the ratio is  $>1$ , species are more abundant on the disturbed site than around it; if the ratio is  $<1$ , species are less abundant than in the surrounding sward.



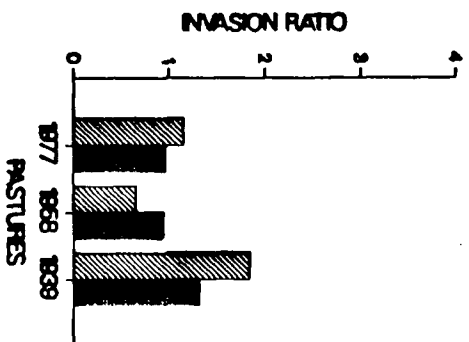




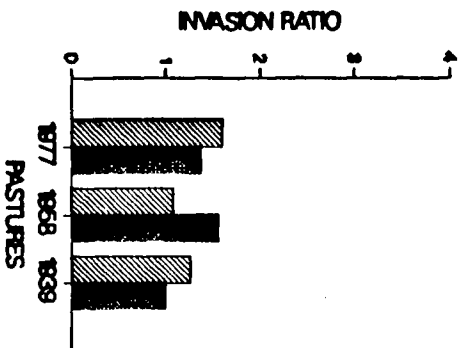
1983 POA COMPLESSA



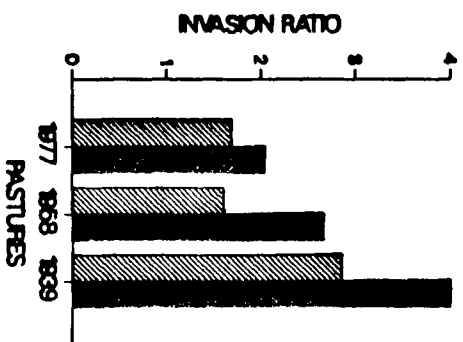
1984 POA COMPLESSA



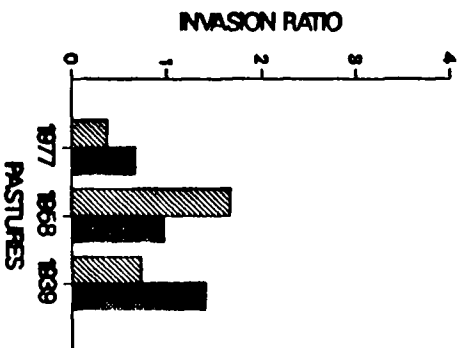
1983 AGROPTON NERBUS



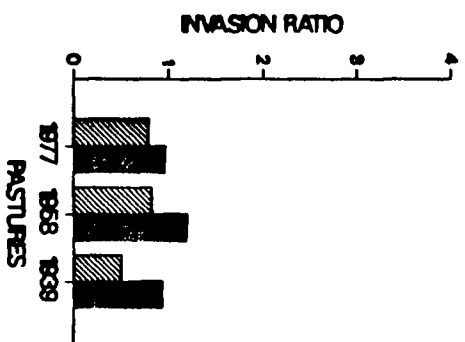
1984 AGROPTON NERBUS

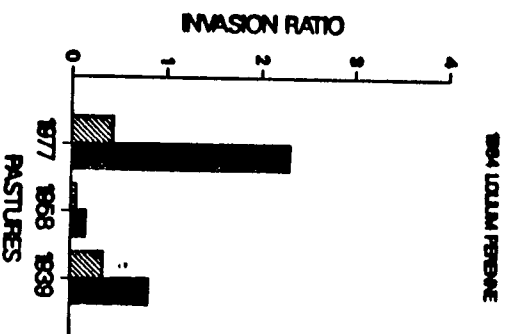
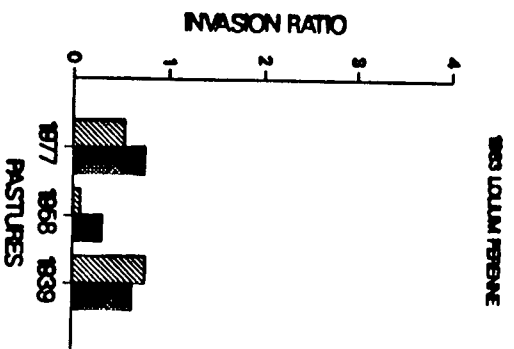
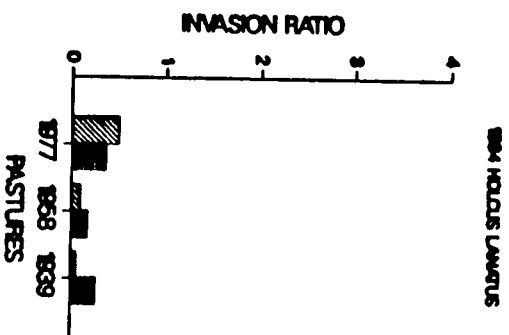
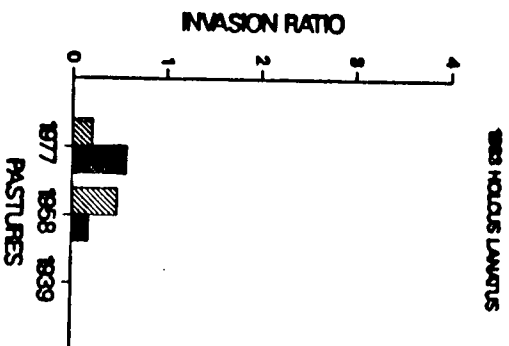
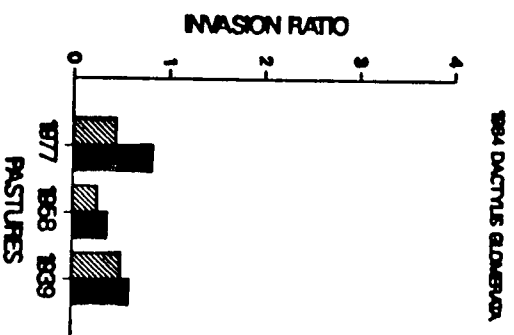
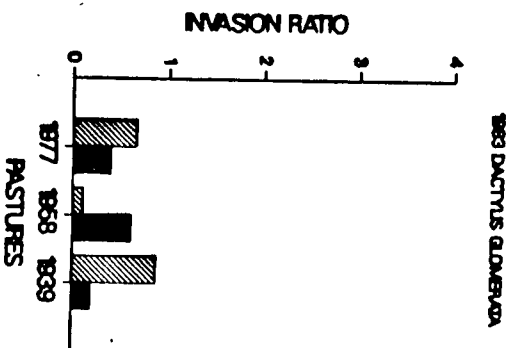


1983 TRIFOLIUM NERBUS



1984 TRIFOLIUM NERBUS



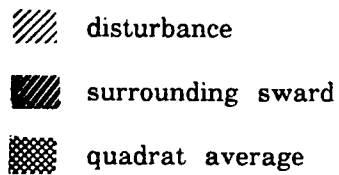


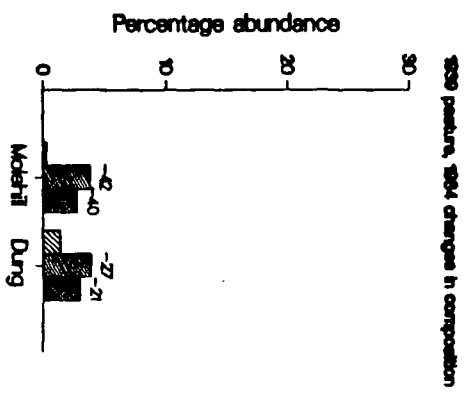
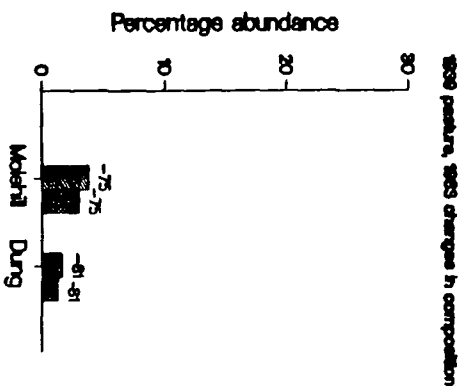
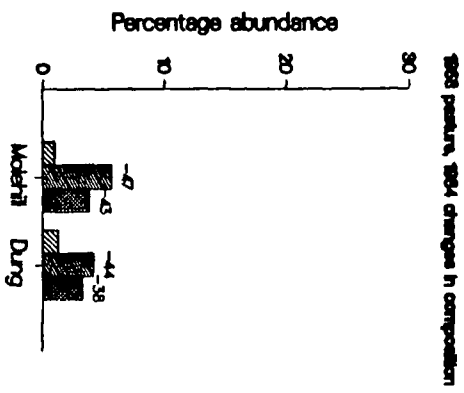
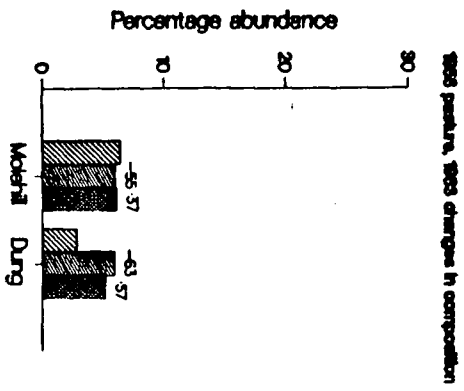
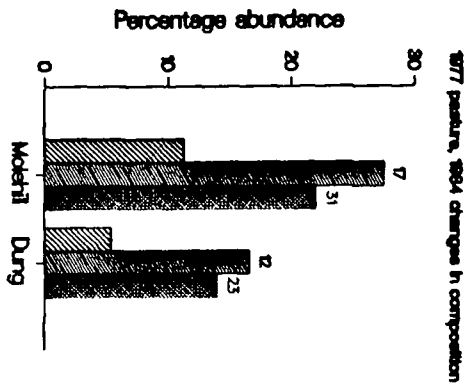
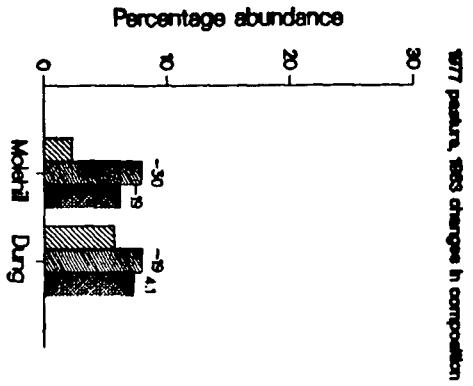
remaining around the disturbance. If the ratio was  $>1$ , the species was more abundant on disturbed areas than in the surrounding sward (e.g. *Agropyron repens*, *Poa compressa*); if the ratio was  $<1$ , the species was less abundant on disturbed sites than in the surrounding sward (e.g. *Dactylis glomerata*, *Holcus lanatus*).

#### 3.3.4. Changes in botanical composition

The pastures are characterized by changes in species abundance over time: some species decreased whereas others increased. The change in abundance of a species in this survey was governed by its behaviour in the surrounding sward plus its ability to colonize disturbed areas. Figure 3-3 shows, by pasture and disturbance type, percentage abundance of a species in the final survey on the disturbed area, in the sward around the disturbance and in both, i.e. the area covered by the sampling quadrat. The change in percentage abundance from the initial to final survey has been calculated from the change in number of rooted individuals or tillers for both the area around the disturbance and the entire area sampled (disturbed site plus surrounding sward). Obviously percentage change on disturbed areas was always 100% increase over initial abundance. For some species, such as *Trifolium repens* and *Agropyron repens*, if there were a decline in abundance in the sward, an overall increase could still occur because of proportionally higher invasion onto the disturbed site.

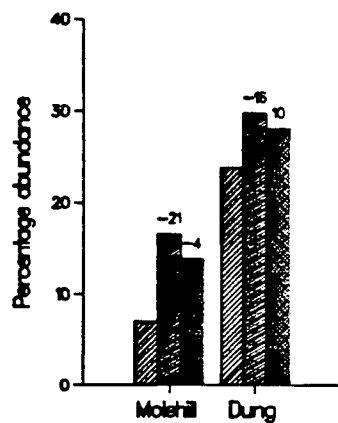
Figure 3-3. Percentage abundance of species at the final survey on molehills and dung pats, in the surrounding sward, and over the entire 0.25m<sup>2</sup> quadrat. The percentage change in composition from initial to final survey has been calculated for the surrounding sward and the entire quadrat area. The percentage change in species abundance on the disturbed area is either zero (no invasion) or 100%.



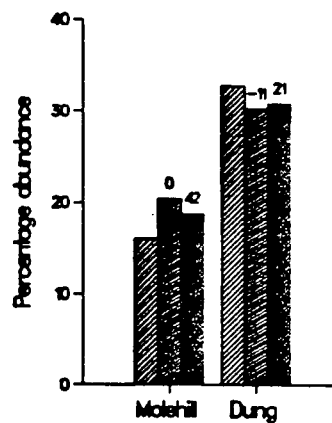


*Holcus lanatus*

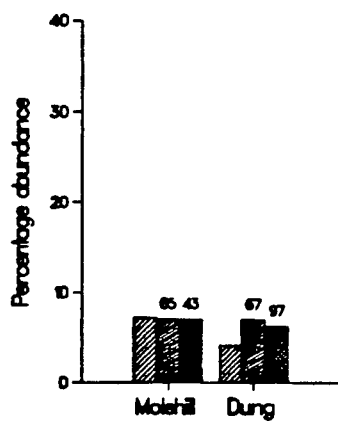
1977 pasture, 1963 changes in composition



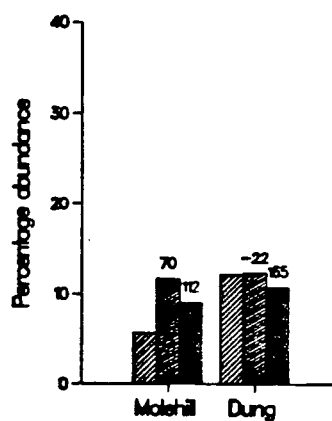
1977 pasture, 1964 changes in composition



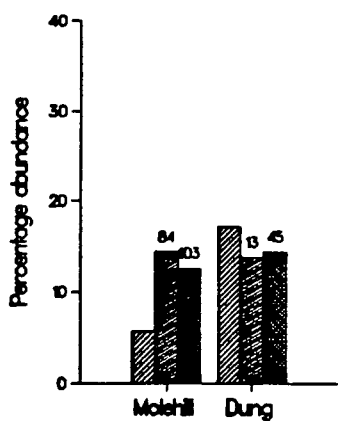
1968 pasture, 1963 changes in composition



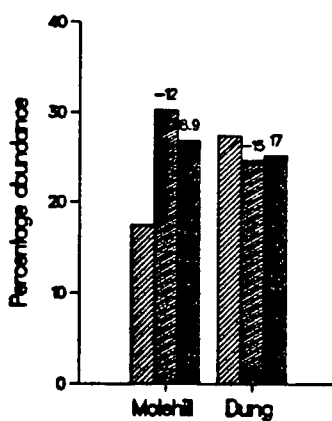
1968 pasture, 1964 changes in composition



1969 pasture, 1963 changes in composition

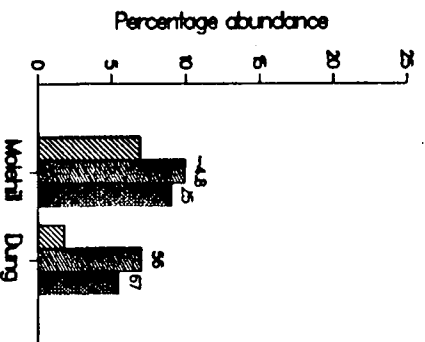


1969 pasture, 1964 changes in composition

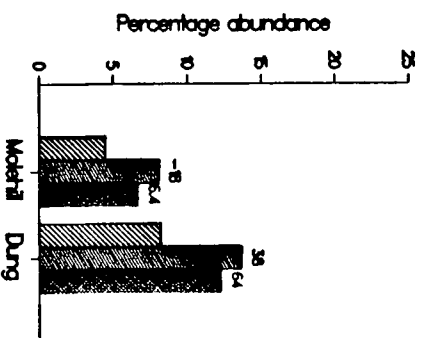


Trifolium repens

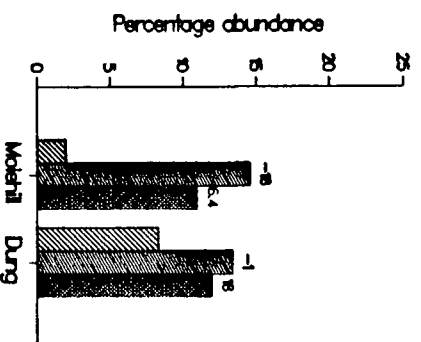
1977 pasture, 1983 changes in composition



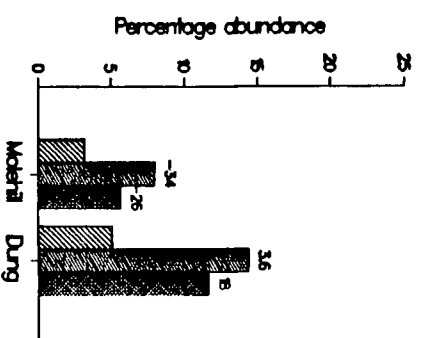
1977 pasture, 1984 changes in composition



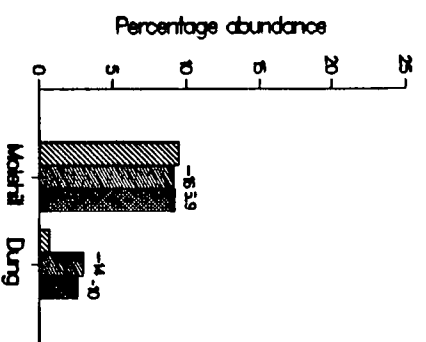
1986 pasture, 1983 changes in composition



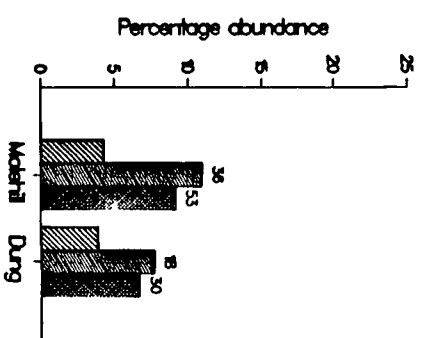
1986 pasture, 1984 changes in composition



1989 pasture, 1983 changes in composition



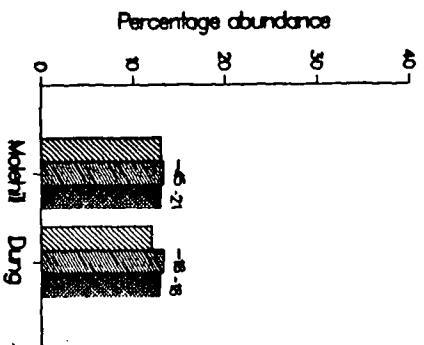
1989 pasture, 1984 changes in composition



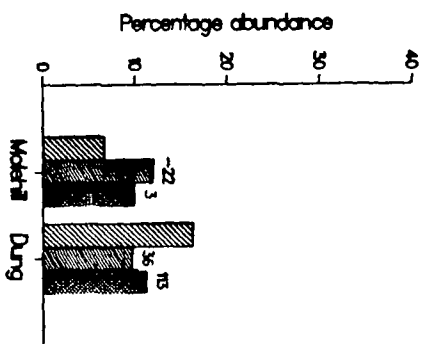
Dactylis glomerata



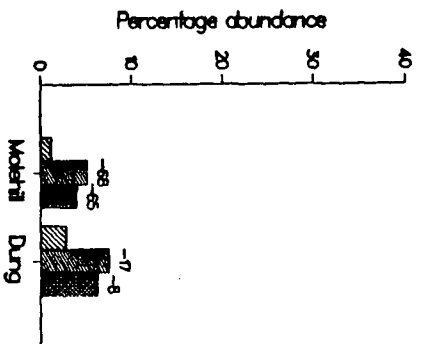
1977 pasture, 1983 changes in composition



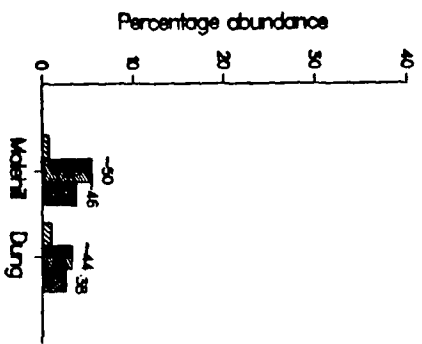
1977 pasture, 1984 changes in composition



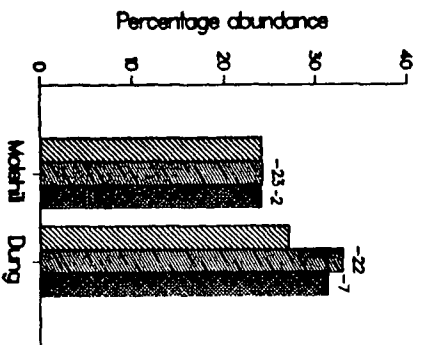
1983 pasture, 1983 changes in composition



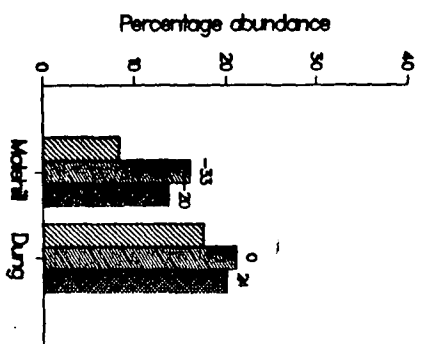
1983 pasture, 1984 changes in composition



1989 pasture, 1983 changes in composition

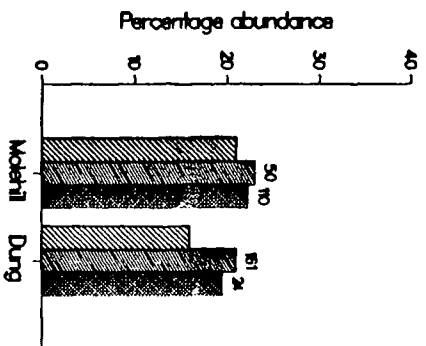


1989 pasture, 1984 changes in composition

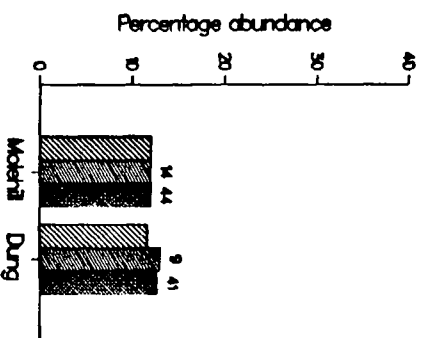


Lolium perenne

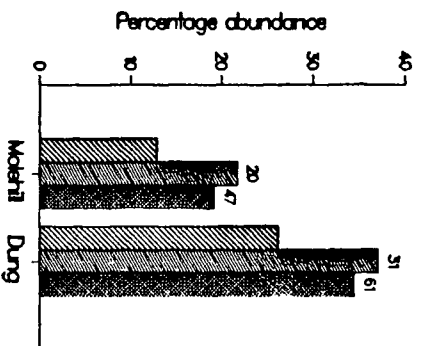
1977 pasture, 1983 changes in composition



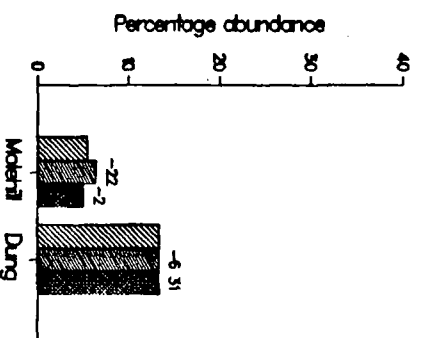
1977 pasture, 1984 changes in composition



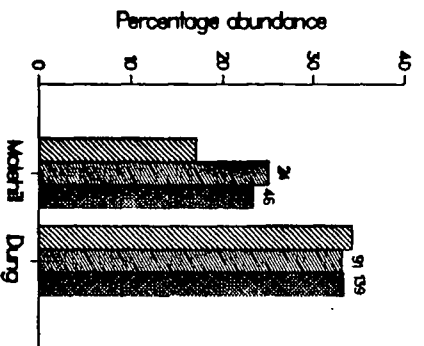
1983 pasture, 1983 changes in composition



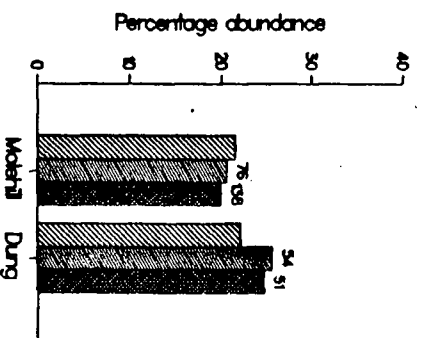
1983 pasture, 1984 changes in composition



1983 pasture, 1983 changes in composition

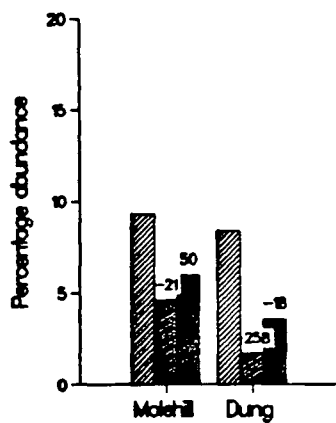


1983 pasture, 1984 changes in composition

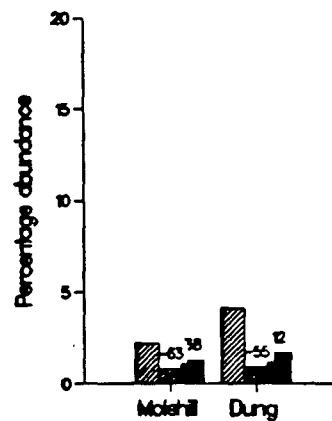


Poa compressa

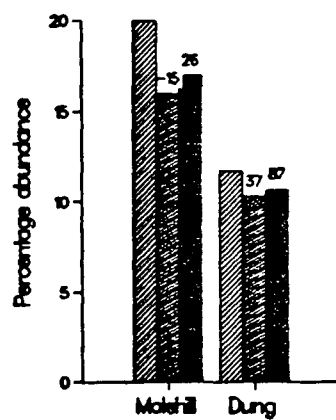
1977 pasture, 1983 changes in composition



1977 pasture, 1984 changes in composition



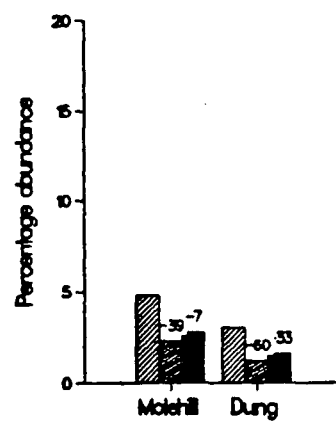
1988 pasture, 1983 changes in composition



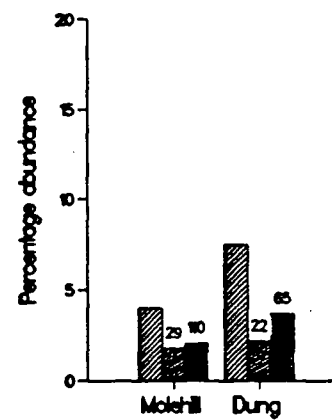
1988 pasture, 1984 changes in composition



1989 pasture, 1983 changes in composition

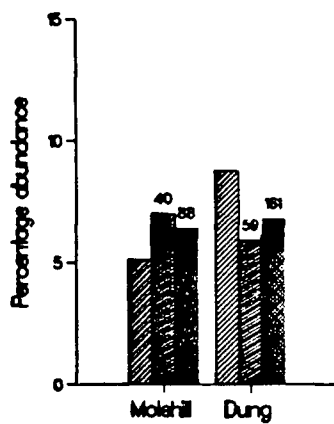


1989 pasture, 1984 changes in composition

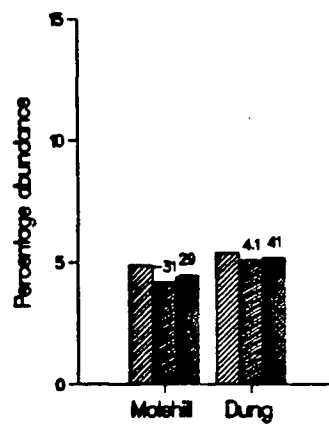


*Agropyron repens*

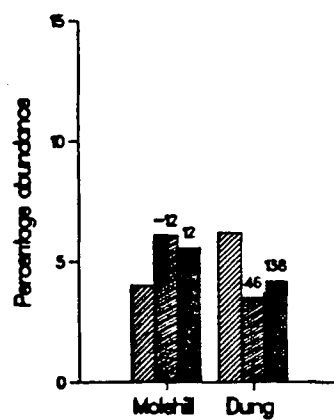
1977 pasture, 1983 changes in composition



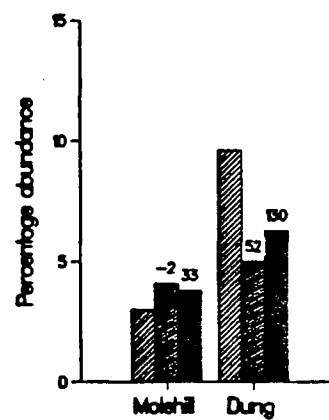
1977 pasture, 1984 changes in composition



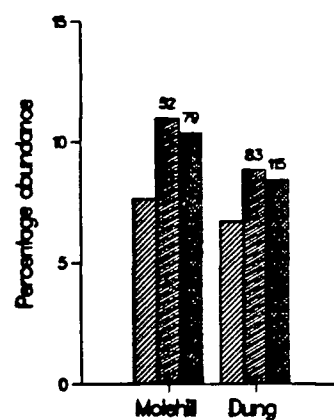
1988 pasture, 1983 changes in composition



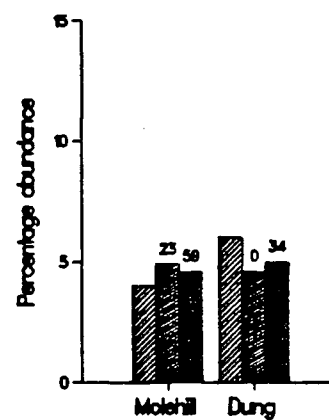
1988 pasture, 1984 changes in composition



1989 pasture, 1983 changes in composition



1989 pasture, 1984 changes in composition



Taraxacum officinale

### 3.4. DISCUSSION

#### 3.4.1. Species persistence

In general, the probability that a species would be found at the same point over the nine month study period was low (Table 3.1), suggesting that temporal heterogeneity was high. Persistence serves as an estimate of genet survivorship for species such as *Ranunculus acris* and of ramet survivorship for clonal species such as *Taraxacum officinale* which grow as independent individuals. For other species (i.e., tillering grasses, *Trifolium repens* and *Poa compressa*), the relationship between persistence and survivorship is obscured. This was not only because release of space may result from death of parts, not individuals, but also because of difficulties distinguishing between different individual plants of the same species occupying the same space in successive time periods.

The greatest death risk to established plants appears to occur during the period of most active growth (Sagar 1970; Sarukhan and Harper 1973). The timing of this period varies with the species under consideration: most grasses grow faster in the spring, April to May, at a temperature optimum between 13 and 18°C, whereas *Trifolium repens* grows faster later in the season at a temperature optimum around 24°C (Spedding 1971). The estimates of persistence reflect the intense growth/death phase for both *T. repens* and grasses, because the survey usually ran from August, when *T. repens* was growing rapidly, to April, when the grasses were growing vigorously.

### 3.4.2. Species replacement and invasion

Potentially, any species could be replaced by any of the species in the pasture but only the most abundant were consistently involved in the replacement processes. Replacements were not random, i.e., space capture by a species was not proportional to the abundance of that species in the pastures. The tests for non-randomness were based on a first order Markovian model. This assumes that the system has no memory, i.e., that the current state is determined only by the previous one. Over the study period, the sample size was inadequate to include sufficient multiple transitions to test for higher order effects in which the probability of a species replacement would depend on states prior to the previous one. Higher order processes would not be improbable if some species had temporary seasonal advantages and pre-empted space that was subsequently relinquished to the prior occupant.

Thorhallsdottir (1984), using a Markovian model to describe species replacements in a pasture in Wales, found that between-season replacements were non-random but between-year replacements were proportional to species abundance in the pasture. She concluded that temporal heterogeneity was very fine-grained but species became thoroughly mixed over longer periods. In addition, she suggested that the majority of non-random interactions took place during periods of rapid growth and expansion.

The considerable variation among the ability of species to invade disturbed areas appeared to be linked to morphological form. This finding differs from the

conclusion of the previous chapter. Pattern detected at one scale of observation ( $0.25\text{m}^2$ ), was lost at another scale ( $25\text{m}^2$ ). In general, rhizomatous (*Agropyron repens* and *Poa compressa*) and stoloniferous (*Trifolium repens*) species invaded disturbed sites in proportionally higher abundance than they had in the surrounding sward. Tillering grasses (*Dactylis glomerata*, *Holcus lanatus* and *Lolium perenne*) were less abundant on disturbed sites than in the surrounding sward. There were exceptions to this: *Phleum pratense*, a tillering grass, invaded dung although it was a poor invader of molehills.

The inability of *Phleum pratense* to invade disturbed sites in the 1939 pasture, but its ability to invade in the 1977 pasture appears to be based on a genetic difference in the *P. pratense* seeded in the pastures. Prior to approximately the 1960's in the Fraser Valley, an old land race of *P. pratense* was sown in pastures but this practice was discontinued. The more robust variety 'Climax' used in the mix after the early 1960's (Richardson Seed Co., pers. comm.) has the ability to invade disturbed areas.

The apparent ability of *Taraxacum officinale* to invade disturbed sites is an artefact because no new individuals established, rather, mature plants emerged from under the disturbance. Emergence was often as long as three months after the disturbance had occurred. This agrees with Rothwell's (1977) findings that *T. officinale* could survive burial. The high abundance of *T. officinale* associated with disturbance is due to root regeneration on sites on which species less tolerant of burial are removed.

The invasion of disturbed areas is a non-competitive process whereas performance in the sward involves both non-competitive and competitive interactions. Because of the closed nature of the sward in order for an individual to expand horizontally, another must relinquish space. Release of space may be due to density independent forces such as frost or trampling. The non-randomness of replacements, however, suggests that replacement was governed by species interactions not merely proximity. Performance on disturbed sites has been related to species mobility and investment in horizontal growth. There is no *a priori* reason to expect these characters to be linked to performance in the sward. But some species show similar performances in both situations, *e.g.*, *Poa compressa* increased in both whereas *Holcus lanatus* and *Lolium perenne*, which usually failed to establish well on disturbed areas, also decreased in the sward.

In contrast, some species had divergent responses. *Phleum pratense* increased in the sward but invaded dung only, suggesting that a response to nutrient enrichment facilitated lateral growth, a finding consistent with the fertilizer treatment in Chapter 5. Its lack of response on molehills may have been due to lower moisture availability (M. Pitt, pers. comm.). *Dactylis glomerata* also increased around dung but it was still a poor invader of disturbed sites.

*Agropyron repens* was the only species showing an ability to invade disturbed sites but generally decreasing in the surrounding closed sward. This suggests that disturbance may provide a refuge serving as the primary agent in determining the pattern of abundance of *A. repens* in the pastures.



### 3.4.3. Recruitment and colonization

The role of dung and molehills in providing an entry into the community for new species, or even for sexually produced progeny of established species, was negligible. Colonization by seed occurred consistently only in two species, *Ranunculus acris* and *Trifolium repens*. *R. acris* germinated both on disturbed sites and in the sward but *T. repens* was restricted to disturbed areas. Similarly, Turkington *et al.* (1979) observed *T. repens* seedlings on molehills but not in the sward, and seed sown into the sward failed to establish (0.89% germination) whereas on cleared plots, seed germinated (39% germination). It appears that sexual propagation of *T. repens* in pastures is obligately linked to disturbances.

In contrast to these findings, Platt (1975) described a guild of fugitive species specialized to exploit badger mounds in tall-grass prairie. Other North American grassland studies have confirmed a role for disturbance in providing suitable sites for germination and survival of annuals (Allen and Knight 1984), or taxa differing from the surrounding area (Polley and Collins 1984; Loucks *et al.* 1985). Differences between these studies in native prairies and in the Aldergrove pastures could be used to support an argument for evolution of specialists based on native systems being of sufficient longevity to foster such niche differentiation. Additional support for this interpretation can be derived from Belsky's (1986) observations in the old and relatively pristine Serengeti ecosystem (Whyte 1974) that colonization of disturbed sites was dominated by seedlings and not by vegetative expansion. Disturbances often present different micro-environments which provide opportunities for differential regeneration of species in the community

(Grubb 1977). Badger mounds (Platt 1975) and buffalo wallows (Polley and Collins 1984) retain higher soil moisture than surrounding areas. Although physical characteristics of molehills were not measured in this study, it is assumed that they have a characteristic pattern of higher soil temperatures and lower moisture typical of mounds in northern latitudes (cf. Spittlehouse 1985). The presence of species that can exploit this heterogeneity probably depends on the frequency of disturbance in addition to the time dimension. Time could be either of evolutionary or ecological length. Evolutionary time would permit the development of mechanisms to exploit heterogeneity and differentiate species, and an ecological time scale would allow influx of species with limited dispersal mechanisms to reach, for example, previously glaciated or formerly non-agricultural sites.

One factor tends to obscure comparisons between this study and most on native grasslands. Molehills and dung pats average about  $0.07\text{m}^2$  in area whereas most of the previous studies were of larger disturbances ( $0.2 - 2.0\text{m}^2$ ). Size of opening can strongly influence patterns of germination and survival (Davis and Cantlon 1969; Miles 1974; Goldberg and Werner 1983). Miles (1974) found an inverse relationship between germination and survival in gaps of different sizes; proportionally more seeds germinated in  $25\text{cm}^2$  gaps but survivorship was highest in  $2500\text{cm}^2$  gaps. Rapp and Rabinowitz (1985) using artificial disturbances of about  $27\text{cm}^2$  found no difference in seedling survival in disturbed versus control areas. In addition, a plethora of evidence exists to support differentiation among species in pre-germination requirements and conditions for survival and growth. Although Grubb (1977) has argued that these differences in regeneration

requirements maintain species richness in communities, it appears that heterogeneity provided by molehills and dung pats is relatively unimportant to species richness in these pastures.

The finding that space made available by disturbances (molehills and dung pats) is generally filled by the expansion of existing individuals is in accord with Sousa's (1984b) observations. Sousa observed that small patches were colonized rapidly by encroachment of adults along the edges and attributed the high rate of closure to the larger perimeter to area ratio of small disturbances. Rapid closure, i.e., within a year, of small disturbances may restrict colonization by species without persistent seed or long distance dispersal mechanisms. Because of the restriction of recruitment of new individuals these disturbances act primarily as agents of mortality removing individuals but providing limited opportunities for new individuals to enter the population. Individuals of a species are eliminated at random but replacement is by individuals (species) with specific characteristics.

## 4. INFLUENCE OF SPECIES REMOVAL ON INTERSPECIFIC INTERACTION

### 4.1. INTRODUCTION

Over the past twenty-five years, perturbation experiments have been used increasingly to determine relationships between species and analyse the structure of communities, (e.g., Sagar and Harper 1961; Pinder 1975; Gross 1980; Fowler 1981; Hils and Vankat 1982). One type of perturbation experiment involves selective removal of one or more species from the community and measurement of the magnitude of the response by the remaining associated species.

Early removal experiments measured the response of target species to the mass removal of associated groups of species. For example, Sagar and Harper (1961) found that vegetative expansion and seedling establishment of *Plantago* spp., and Putwain and Harper (1970) for *Rumex* spp., was restricted by grasses rather than by other dicotyledenous species. Later studies aggregated the target species to examine community structure. For example, Pinder (1975) removed dominant grasses in old-fields and detected a diffuse response of increasing biomass in the remaining subordinate species. Also in old-fields, Allen and Forman (1976) found removal of tall species caused the greatest changes in the response of remaining species. The response of species to removal was non-reciprocal; for example, few species could invade patches from which *Potentilla simplex* had been removed but *P. simplex* was able to invade areas made vacant by the removal of other species.

Removal experiments were used to determine pairwise interspecific interactions by Fowler (1981) in grasslands and by Silander and Antonovics (1982) in coastal marsh-dune communities. Species interaction in both these communities were rarely reciprocal and could be specific or diffuse. In addition, interactions varied seasonally and changed when the same species pairs interacted in different environments (Silander and Antonovics 1982).

The ability of removal experiments to determine competitive interaction between species has been challenged by Bender *et al.* (1984). They argued that except in a two-species community, the presence of a net gain in one species following the removal of another is not a sufficient or necessary condition to demonstrate competition. The gain reaction may actually result from interaction with a third species. Similarly, the absence of response to removal may not necessarily demonstrate absence of competition. Because of a network of interactions, response to removal may be weak or non-existent. To avoid this ambiguity, Bender *et al.* (1984) suggest the separate removal of each species in the community to create a complete interaction matrix. This approach is conceded to be impractical in most multispecies communities, not to mention prohibitively expensive in time and cost.

Another consideration raised by Bender *et al.* (1984) is that of overlooked species. In defining a community such as a pasture in terms of botanical composition, some obvious and some inconspicuous members of the community are overlooked. Pastures, by definition, always include grazing species, whose effect on the pasture is enormous. Even if the effects of the overlooked species on target

species are very large, the interaction is negligible if the effects of the target species on the ignored species are very small (Bender *et al.* 1984). It is reasonable to assume that in pastures, although the cumulative effect of all herbaceous species on grazers is very large, the effect of each component species on the grazer is very small. Thus, the interaction between plant species can be validly studied in isolation from the consumer effect.

Ecological theory argues that coexisting plants diverge in their use of resources and thereby reduce or avoid competition; Harper (1967) called this "ecological combining ability". Likewise, Fowler (1981), working in an 30-year-old grassland in North Carolina stated that "this is a community characterized by relatively weak and approximately equal competitive relationships among all of its component species " (p. 851). Aarssen (1983), however, suggests an alternative possibility: he argues for strong competitive interactions between individual species that become more equal over time. Furthermore, he argues that if competition is an organizing force in determining community structure, there should be strong, unequal interaction in recent pastures and strong, equal interactions in older ones. The predictions of both viewpoints are the same - strong interactions will be found in recently established communities. In older communities, interactions should be detectable if they are strong but not if they are weak or reduced through niche divergence. Unfortunately, it is beyond the scope of removal experiments to differentiate between the mechanisms that lead to equality in interactions among species over time.

The physical proximity and similar sowing and management histories of the

Aldergrove pastures make them suitable to test for changes in species interactions over time. This chapter describes a removal experiment carried out using three of the common species: *Lolium perenne*, one of the originally seeded grasses, *Trifolium repens* a seeded legume, and the weedy grass *Holcus lanatus*. The design allowed an examination of the species interactions with each other and with associated species and the effects of their combined removal. If one of the three dominant species is removed, the remaining dominant species could control the resultant interactions. Moreover, removal of species combinations as well as single species allows any substructuring of the community to be observed.

## 4.2. METHODS

### 4.2.1. Field methods

Four sites were selected in the 1939 and 1977 pastures. The sites were chosen to conform to the following criteria: (i) absence of any mole activity; (ii) no visually obvious discontinuities in vegetation; (iii) slopes of less than 5%; and (iv) absence of any evidence of waterlogging. The 1958 pasture was excluded from the study because of the difficulty in finding sufficient sites which met these criteria.

The sites were staked into 2.8 x 6m blocks and further subdivided into eight one metre square plots. Around each plot was a 10cm boundary from which all vegetation was removed, and an uncleared zone 20cm wide was left between

plots. Plots within each site were assigned randomly to one of eight removal treatments shown in Table 4-1.

The four sites in each pasture were initially surveyed in July 1983. Rooted frequency in each plot was measured by placing a 50 point, 0.5x0.5m square grid, four times, to give a total 200 points per  $1\text{m}^2$  plot.

Although the sites selected for the experiment were visually uniform, considerable variation existed in rooted frequency of the three removal species and consequently, in the amount of bare ground exposed after removal (Table 4-2). Removal of the grasses and clover began in late July and continued throughout August and September. All plots were cleared of regrowth in September and October. A screwdriver or large iron nail was used to dig out the grasses and lift the *Trifolium repens* stolon and roots. Care was taken to avoid disturbing the remaining vegetation and loosened soil was pressed back into place. As far as possible, plots were kept dung-free during the duration of the experiment by removing any depositions.

In July 1984, one year after the initial survey, the plots were re-surveyed in the same manner as in 1983. Subsequently, the plots were cleared of regrowth of all three species through fall 1984 and again in spring 1985. The final survey was made in July 1985. In an effort to minimize seasonal and management-induced variations, each survey was made as soon as possible after haymaking, although a timelag was necessary to allow regrowth of species to an identifiable size.



Table 4-1. Species removed from eight plots in the 1939 and 1977 pastures.

Treatment	Species removed
C	control plot, no species removed
T	<i>Trifolium repens</i> removed
H	<i>Holcus lanatus</i> removed
HT	<i>Holcus lanatus</i> and <i>Trifolium repens</i> removed
L	<i>Lolium perenne</i> removed
LT	<i>Lolium perenne</i> and <i>Trifolium repens</i> removed
LH	<i>Lolium perenne</i> and <i>Holcus lanatus</i> removed
LHT	<i>Lolium perenne</i> , <i>Holcus lanatus</i> and <i>Trifolium repens</i> removed

Table 4-2. Percentage cover of removed species in four replicates in July 1983.

Treatment	Percentage cover removed				
<u>1939 pasture</u>					
	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>mean</u>
<i>T</i>	6.5	12	9.5	11	9.8
<i>H</i>	9	14	23	29	18.8
<i>HT</i>	16	17	43	31	26.8
<i>L</i>	26	25	24.5	18	23.4
<i>LT</i>	54	41	32.5	38.5	41.5
<i>LH</i>	47	41	54.5	54.5	49.3
<i>LHT</i>	48.5	47.5	70	70.5	59.1
<u>1977 pasture</u>					
<i>T</i>	15.5	8.5	6.5	19	12.4
<i>H</i>	11	8	18.5	27.5	16.3
<i>HT</i>	30	26	38	59	38.5
<i>L</i>	9.5	14.5	28	34	21.5
<i>LT</i>	35	28.5	39	45.5	37.0
<i>LH</i>	26	22.5	32.5	54.5	33.9
<i>LHT</i>	37	46	43.5	75	50.4

#### 4.2.2. Analytical methods

To determine the effects of *Lolium perenne*, *Holcus lanatus* and *Trifolium repens* removal on the abundance of remaining species, the difference in rooted frequency between the initial 1983 and final 1985 survey was used. The model chosen is univariate, that is, effects of all removals were tested on one respondent species at a time. Some species, for example *Rumex acetosella* and *Alopecurus geniculatus*, occurred too infrequently for statistical analysis. Analysis of variance computer program 2V of BMDP (Dixon 1983), analysis with three fully crossed factors and no groupings, was used. The identification of three factors, removal of *L. perenne*, *H. lanatus* and *T. repens* from each relevant treatment whether as single species or combination examined the effects of single removals as well as the two- and three-way interactions.

Because the removed species and the respondent species have different initial abundances, an expansion rate, ( $R_{ij}$ ) was calculated to standardize the response of species *i* to removal of species *j*.  $R_{ij}$  is measured by using the change in rooted frequency of species *i* from 1983 to 1985, divided by the original 1983 frequency, i.e.

$$R_{ij} = (N_{ij} - N_i) / N_i \quad (4-1)$$

where

$N_i$  - original abundance of species *i* (in 1983)

$N_{ij}$  - abundance of species *i* (in 1985) when removed

species *j* is zero

If the original abundance of a species in a plot was zero, the expansion rate

was not calculated for that treatment plot to avoid division by zero. Expansion rate ( $R_{ij}$ ) was examined in response to the abundance of the removed species and as a response to amount of area available for colonization.

### 4.3. RESULTS

#### 4.3.1. 1939 pasture

There was considerable regeneration of *Lolium perenne* after initial removal but little of *Holcus lanatus* and *Trifolium repens* in July 1984; however, in August and September, *T. repens* invaded the removal plots by stolon extension from adjacent areas. In July 1985, regeneration of removed species was essentially zero. In the 1939 pasture, differences between controls and treatment plots were not significant (i.e.  $p > 0.05$ ) in most cases (Tables 4-3 and 4-4) despite the removal of large amounts of cover and the opening up of bare ground for colonization. Bare ground increased overall in the experimental sites but was significantly less in those from which *H. lanatus* had been removed. It does not necessarily follow that *H. lanatus* removal sites were more readily colonized. Rather, species had an extra growing season to invade bare ground created in 1983 because *H. lanatus* did not regenerate after removal and did not colonize from seed in 1984, so that little further treatment was required and no new bare spots were made in the second season.

Neither *Lolium perenne* nor *Holcus lanatus* responded to the removal of the other nor to the removal of *Trifolium repens*. *T. repens* showed a significant increase

Table 4-3. Mean difference (n=4) in species percentage cover in the 1939 pasture from 1983 to 1984. Year effect indicates differences in abundance averaged over all treatments. Removal effect indicates differences in abundance attributed to different treatments. \* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; \*\*\* -  $p < 0.001$ .

Species	control	T	H	HT	L	LT	LH	LHT	year effect	removal effect
<i>Agropyron repens</i>	2.3	-2.0	4.8	-0.5	-3.3	4.8	1.5	-0.2	0.59	
<i>Dactylis glomerata</i>	-10.2	0.4	4.8	6.7	0.0	-0.5	0.9	6.9	0.59	
<i>Holcus lanatus</i>	-26.1	-26.4	-	-	-28.0	2.8	-	-	0.01**	
<i>Lolium perenne</i>	-7.4	5.3	-4.6	2.8		-	-	-	0.31	
<i>Poa compressa</i>	-1.9	19.3	-5.3	13.8	-5.3	18.5	9.7	23.7	0.34	
<i>Phleum pratense</i>	0.3	1.8	0.3	3.6	-1.5	0.0	1.3	-0.4	0.22	
<i>Anthoxanthum odoratum</i>	1.8	2.2	1.3	1.8	3.8	4.0	2.4	1.8	0.05	
<i>Agrostis alba</i>	0.0	-3.8	-1.3	0.0	-2.5	0.0	0.5	5.0	0.73	$H^*, LT^*$
<i>Trifolium repens</i>	39.2	-	23.7	-	30.8	-	39.9	-	0.30	
<i>Ranunculus acris</i>	0.3	2.9	1.8	2.9	7.8	3.0	0.8	5.3	0.02*	$LTH^{**}$
<i>Taraxacum officinale</i>	-1.8	-2.9	-5.3	-2.4	0.0	-5.8	-11.2	1.0	0.02*	

Table 4-4. Mean difference (n=4) in species percentage cover in the 1939 pasture from 1983 to 1985. Year effect indicates differences in abundance averaged over all treatments. Removal effect indicates differences in abundance attributed to different treatments. \* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; \*\*\* -  $p < 0.001$ .

Species	control	T	H	HT	L	LT	LH	LHT	year effect	removal effect
<i>Agropyron repens</i>	12.3	-1.5	16.5	3.0	5.8	13.0	14.5	1.8	0.23	
<i>Dactylis glomerata</i>	-6.0	2.5	4.3	10.8	3.5	5.5	5.8	15.5	0.24	
<i>Holcus lanatus</i>	-18.0	-17.5	-	-	-19.5	5.0	-	-	0.06	
<i>Lolium perenne</i>	-18.3	-3.5	-7.5	-4.8	-	-	-	-	0.38	
<i>Poa compressa</i>	6.3	22.3	-1.3	24.0	10.3	30.5	18.5	47.8	0.07	HT*
<i>Phleum pratense</i>	0.8	0.0	1.8	4.5	0.0	9.3	3.3	3.0	0.04*	
<i>Anthoxanthum odoratum</i>	2.3	4.8	1.0	7.5	1.5	4.5	1.5	8.0	0.19	
<i>Agrostis alba</i>	0.0	-3.8	-4.5	-1.0	-2.8	0.0	0.0	6.0	0.25	
<i>Trifolium repens</i>	23.8	-	23.5	-	32.5	-	48.8	-	0.02*	
<i>Ranunculus acris</i>	2.3	4.0	6.0	5.0	11.0	9.5	7.5	10.3	0.04*	
<i>Taraxacum officinale</i>	-4.5	-4.0	-9.8	-6.3	-3.8	-5.3	-13.5	2.8	0.01**	HT*

( $p=0.017$ ) in abundance in the two year period but did not expand preferentially in either the *L. perenne* or *H. lanatus* removal plots.

Both *Poa compressa* and *Taraxacum officinale* responded to the joint removal of *Trifolium repens* and *Holcus lanatus* ( $p<0.05$ ); but whereas, *P. compressa* abundance increased under this treatment, the decline of *T. officinale* was accelerated. Abundance of *T. officinale* in the 1939 field declined gradually over the experimental period ( $p=0.006$ , see also Table 4-4). *Ranunculus acris* abundance increased ( $p=0.036$ ) although it was not significantly increased by any treatment.

#### 4.3.2. 1977 pasture

In July 1984, there was little regeneration of the removed species in three of the four replicates in the 1977 pasture, although *Trifolium repens* invaded the removal plots in August and September. The fourth replicate was recleared and, along with the other recleared replicates, showed little regeneration of removed species by July 1985. Several grasses responded to the removal of *Trifolium repens* and the combined removal of *T. repens* and *Holcus lanatus* (Tables 4-5 and 4-6). *Dactylis glomerata* increased with the removal of *T. repens* ( $p<0.01$ ), *H. lanatus* ( $p<0.05$ ) and with the LHT removal ( $p<0.01$ ), and *Phleum pratense* increased with the combined removal of *T. repens* and *H. lanatus* ( $p<0.05$ ). Both *Poa compressa* and *Anthoxanthum odoratum* increased in overall abundance during the experimental period ( $p=0.020$  and  $p=0.004$  respectively): both increased significantly with *T. repens* removal ( $p<0.01$  and  $p<0.001$  respectively) and,

Table 4-5. Mean difference (n=3) in species percentage cover in the 1977 pasture from 1983 to 1984. Year effect indicates differences in abundance averaged over all treatments. Removal effect indicates differences in abundance attributed to different treatments. \* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; \*\*\* -  $p < 0.001$ .

Species	control	T	H	HT	L	LT	LH	LHT	year effect	removal effect
<i>Agropyron repens</i>	-16.3	-0.7	1.6	6.7	-1.0	12.0	-0.7	7.7	0.65	
<i>Dactylis glomerata</i>	-2.3	4.7	0.0	10.0	0.7	5.3	8.3	2.3	0.24	
<i>Holcus lanatus</i>	-5.0	0.3	-	-	5.0	13.0	-	-	0.13	
<i>Lolium perenne</i>	-10.3	-21.3	-13.3	-9.3	-	-	-	-	0.07	
<i>Poa compressa</i>	-3.3	10.0	2.7	5.3	3.3	7.0	0.7	39.7	0.07	T*, LHT*
<i>Phleum pratense</i>	2.7	-1.3	2.7	3.3	1.3	2.7	0.0	-1.7	0.53	T**
<i>Agrostis alba</i>	7.7	0.7	1.3	2.7	0.7	0.7	1.7	2.3	0.40	
<i>Trifolium repens</i>	27.3	-	28.7	-	24.3	-	26.3	-	0.89	
<i>Ranunculus acris</i>	0.7	-0.3	-1.7	3.3	1.7	1.7	1.3	2.0	0.30	
<i>Taraxacum officinale</i>	-8.3	2.3	-7.3	-0.7	-8.7	-1.33	-8.0	-8.33	0.03*	

Table 4-6. Mean difference (n=4) in species percentage cover in the 1977 pasture from 1983 to 1985. Year effect indicates differences in abundance averaged over all treatments. Removal effect indicates differences in abundance attributed to different treatments. \* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; \*\*\* -  $p < 0.001$ .

Species	control	T	H	HT	L	LT	LH	LHT	year effect	removal effect
<i>Agropyron repens</i>	-10.8	-21.5	-15.5	-9.0	-10.8	-9.8	-16.0	-8.5	0.10	
<i>Dactylis glomerata</i>	3.8	14.5	10.3	26.0	5.3	18.3	17.0	16.5	0.07	H*, T** LHT**
<i>Holcus lanatus</i>	13.0	10.8	-	-	18.3	21.8	-	-	0.06	
<i>Lolium perenne</i>	-25.0	-20.0	-14.0	-4.5		-	-	-	0.12	H*
<i>Poa compressa</i>	-8.3	17.3	15.8	22.5	4.8	17.3	8.3	42.5	0.02*	T**
<i>Phleum pratense</i>	4.3	0.3	1.0	5.5	1.5	2.8	1.3	0.8	0.14	HT*
<i>Anthoxanthum odoratum</i>	2.5	14.3	5.3	5.5	5.8	10.3	8.5	13.8	0.004*	T***, HT*
<i>Agrostis alba</i>	3.5	0.0	0.3	0.8	-3.0	0.3	1.0	0.5	0.45	
<i>Trifolium repens</i>	17.3	-	31.0	-	24.0	-	39.5	-	0.0004*	
<i>Ranunculus acris</i>	3.5	3.0	0.3	6.3	3.5	1.75	3.75	7.5	0.094	
<i>Taraxacum officinale</i>	-10.5	-7.75	-8.25	-4.25	-12.0	-9.75	-7.0	-11.25	0.09	



additionally, *A. odoratum* responded to the combined removal of *T. repens* and *H. lanatus* ( $p < 0.05$ ).

Of the removed species, only *Lolium perenne* showed a significant ( $p < 0.05$ ) response to the removal of another species: *L. perenne* declined in abundance over the experimental period but its decline was less where *Holcus lanatus* had been removed. This relationship was not reciprocal: the removal of *L. perenne* did not affect the abundance of *H. lanatus*.

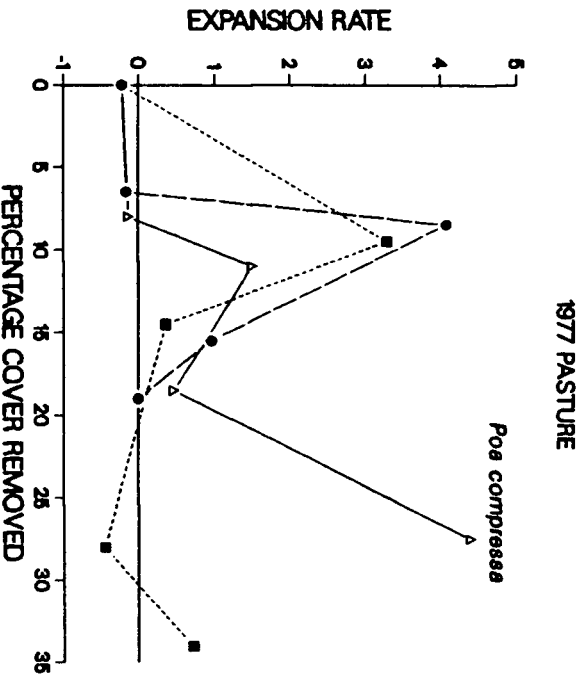
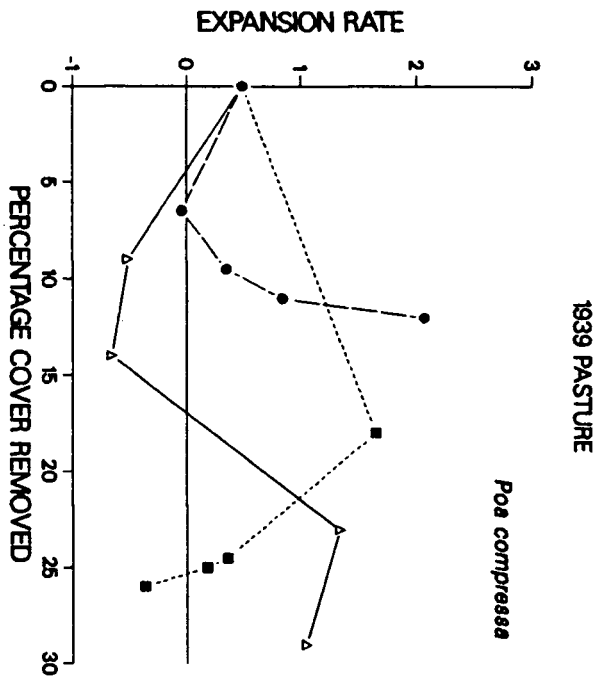
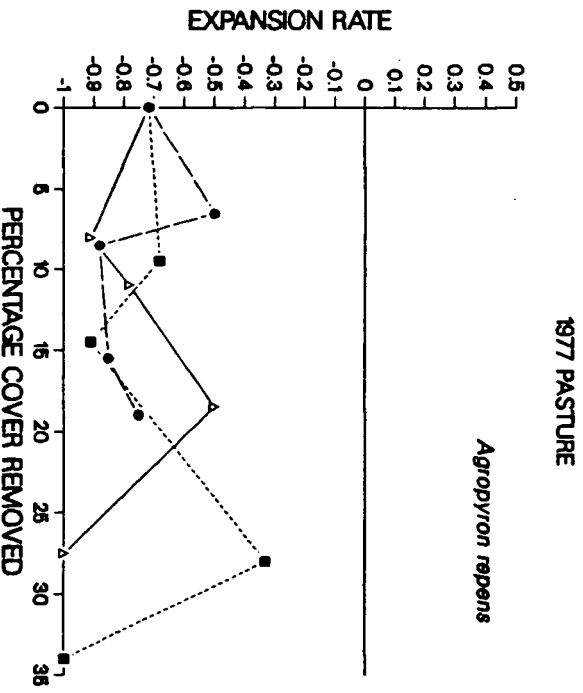
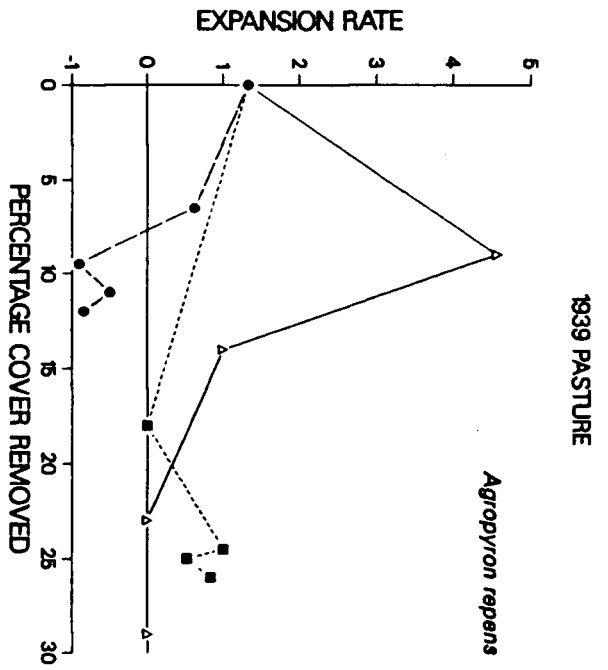
Among the dicots, the trend of declining *Taraxacum officinale* and increasing *Trifolium repens* and *Ranunculus acris* abundances was the same as in the 1939 field (see also Table 4-6). No dicot responded significantly to any of the removal treatments.

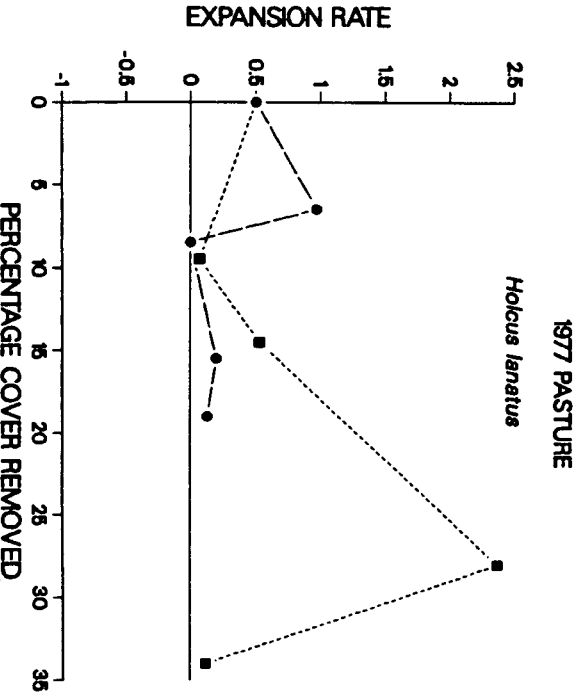
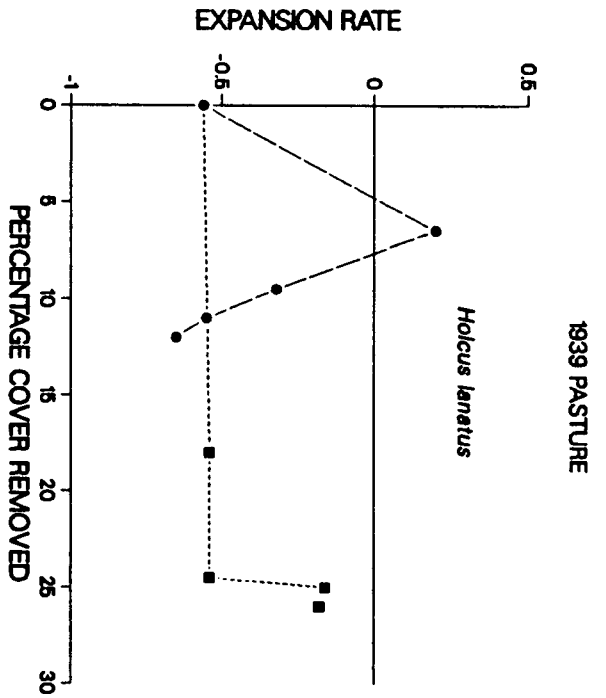
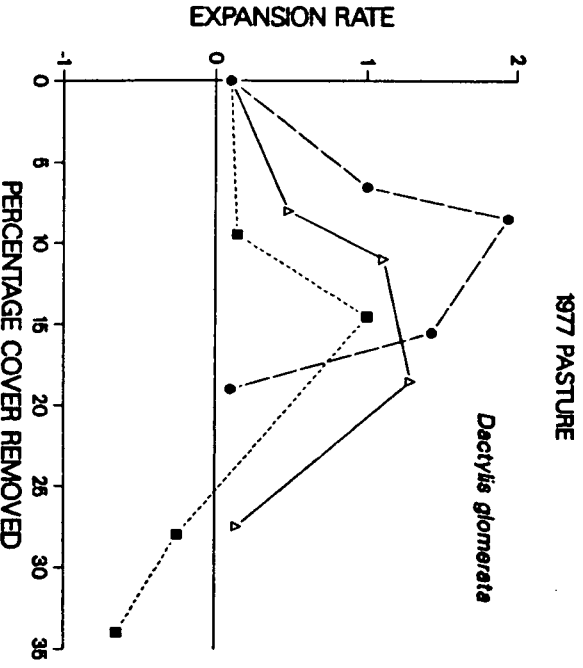
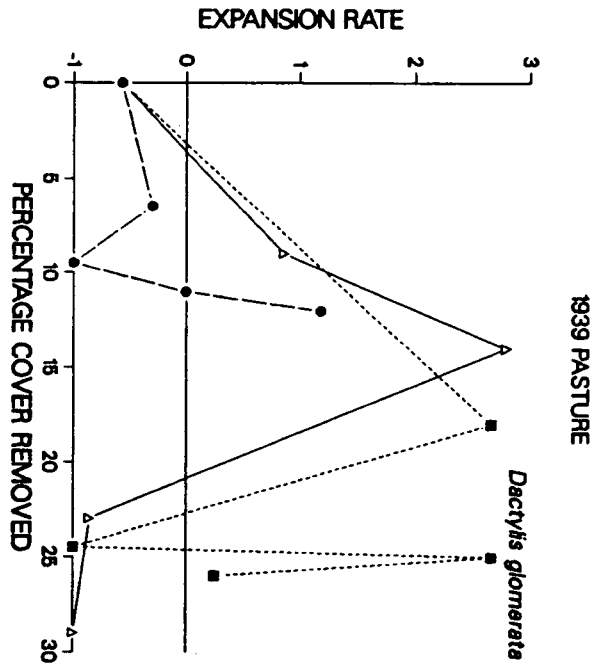
#### 4.3.3. Expansion rate

Expansion rate ( $R_{ij}$ ) was calculated using equation 4-1 and plotted as a function of the amount of *Lolium perenne*, *Holcus lanatus* and *Trifolium repens* removed (Figure 4-1). The response of  $R_{ij}$  to the amount of each species removed used only single species removals to avoid the complication of differing or synergistic responses to two or more species removals. Figure 4-2 illustrates the relationship between expansion rate and the area available for colonization and uses cover removed from all four replications of all removal treatments as the independent variable. Expansion rate of a species was normalized using a Box-Cox transformation. The coefficient of determination of the regression of normalized

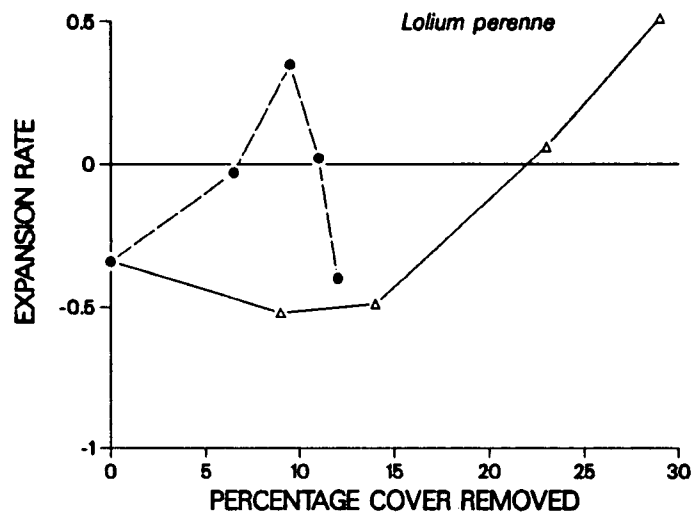
Figure 4-1. Expansion rate from 1983 - 1985 of species remaining in each of the four replicates after the removal of *Lolium perenne*, *Holcus lanatus* and *Trifolium repens*. Expansion rate at 0% cover removed is the average change in cover in the control plots.

- *Lolium perenne* removed
- △ *Holcus lanatus* removed
- *Trifolium repens* removed

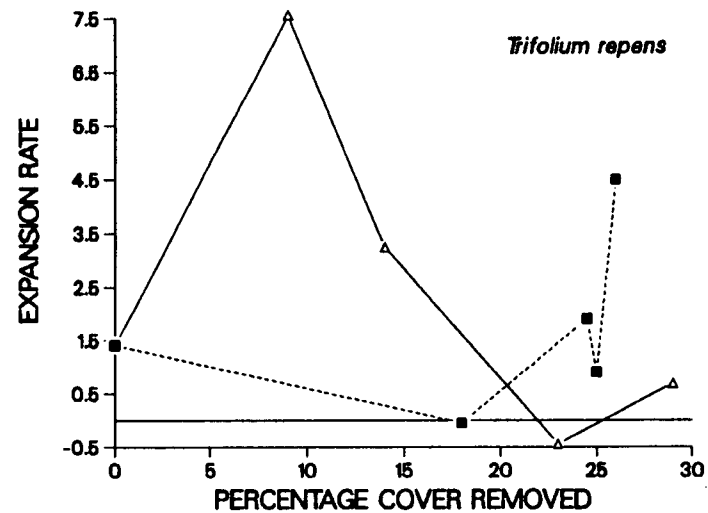




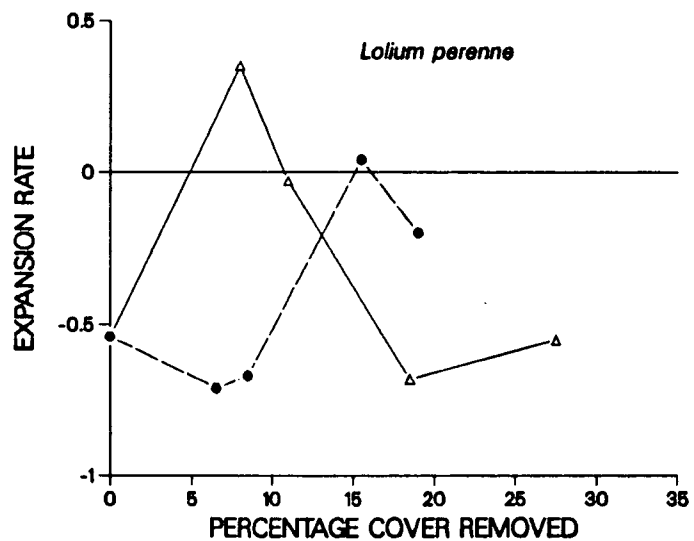
1939 PASTURE



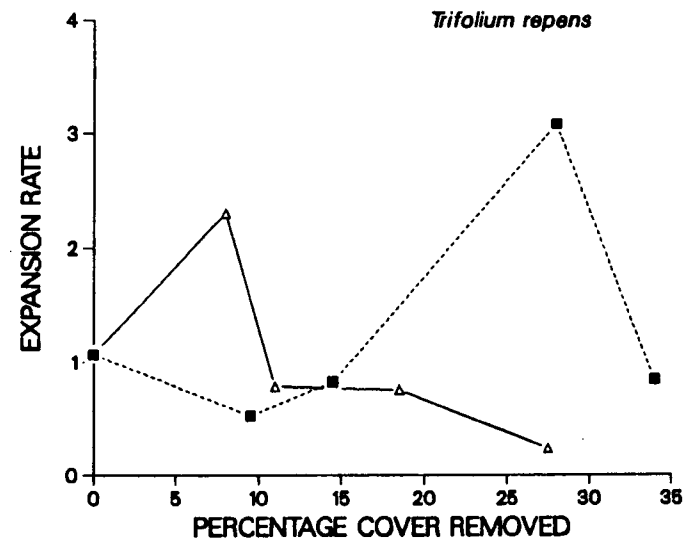
1939 PASTURE



1977 PASTURE



1977 PASTURE



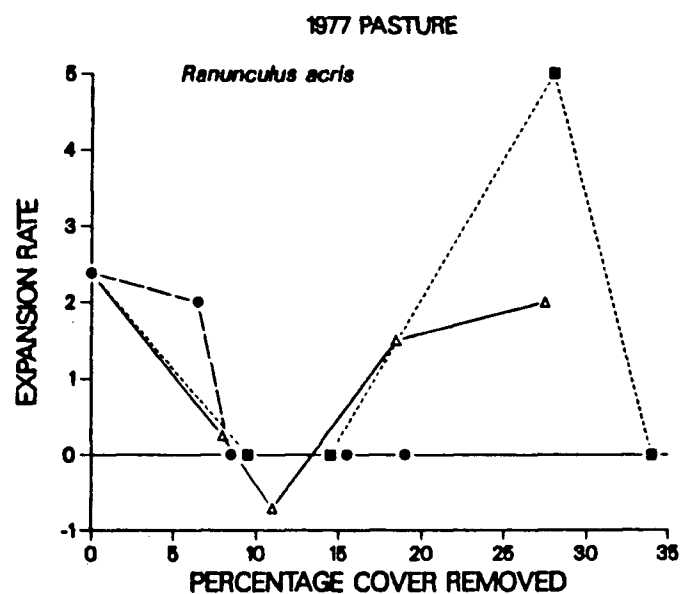
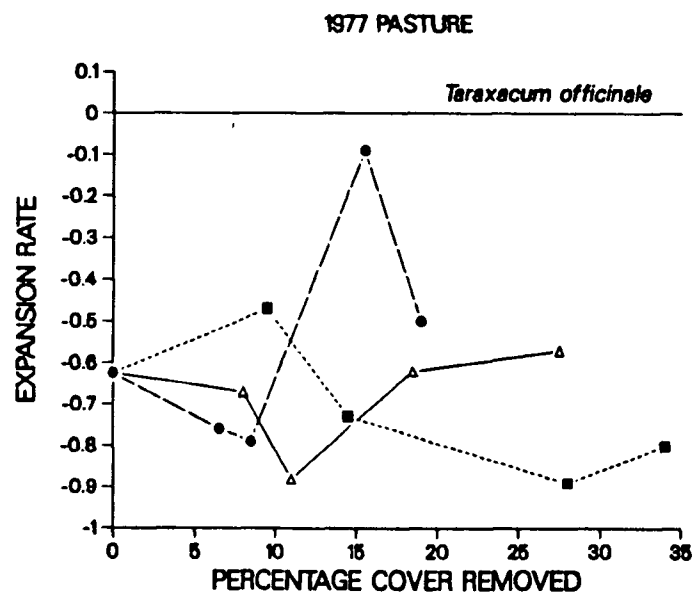
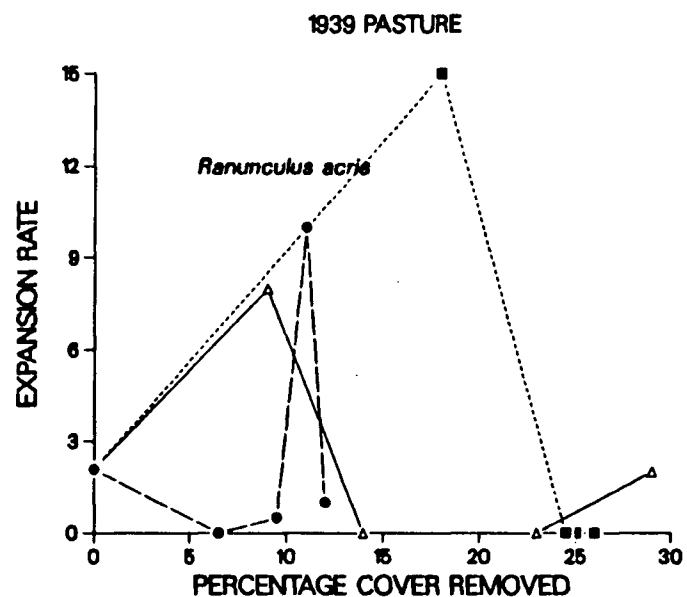
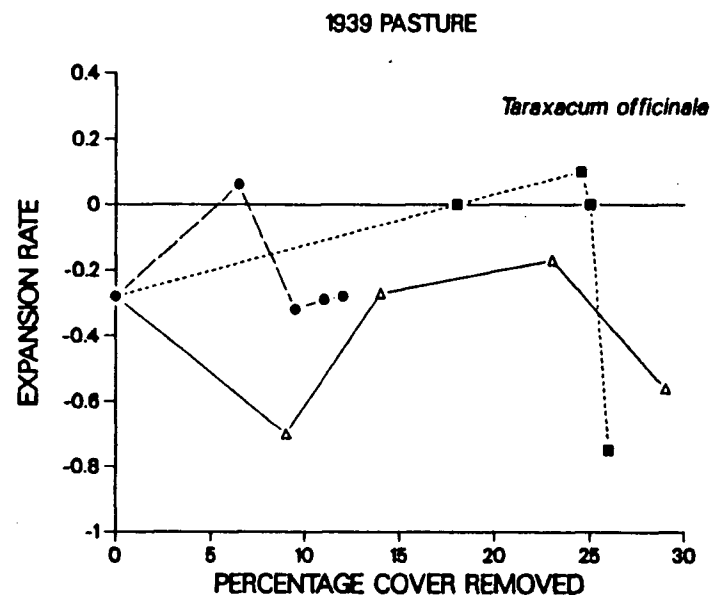
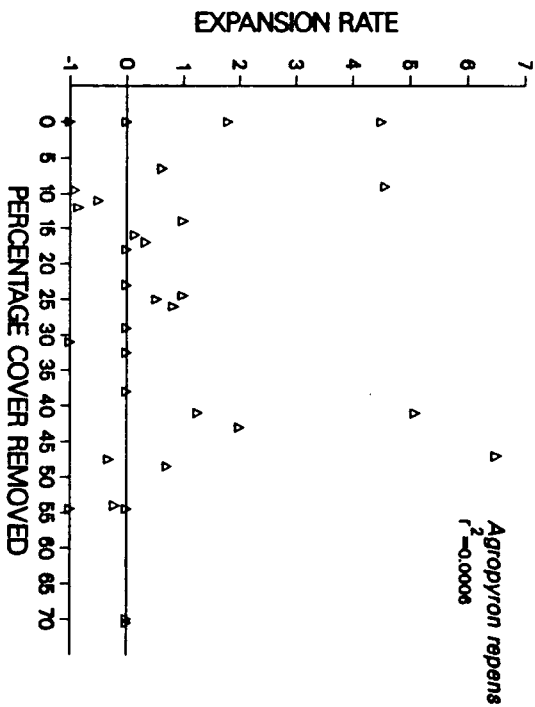
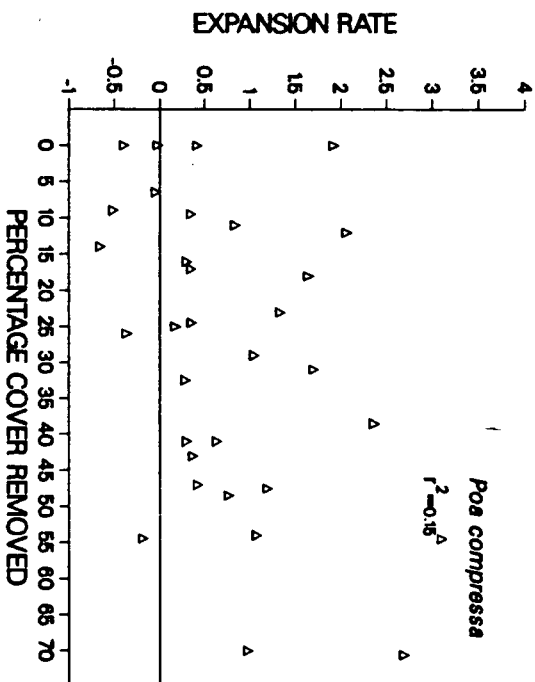


Figure 4-2. Expansion rate from 1983 - 1985 of species remaining after removal treatments against the percentage cover removed in each of four replicates of eight treatments (n=32). Coefficient of determination and significance of the regression were calculated from normalized values of the expansion rate.

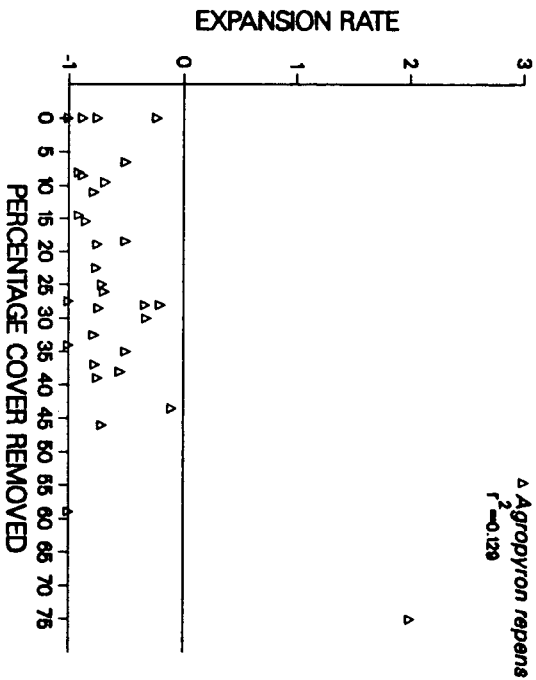
# 1939 PASTURE



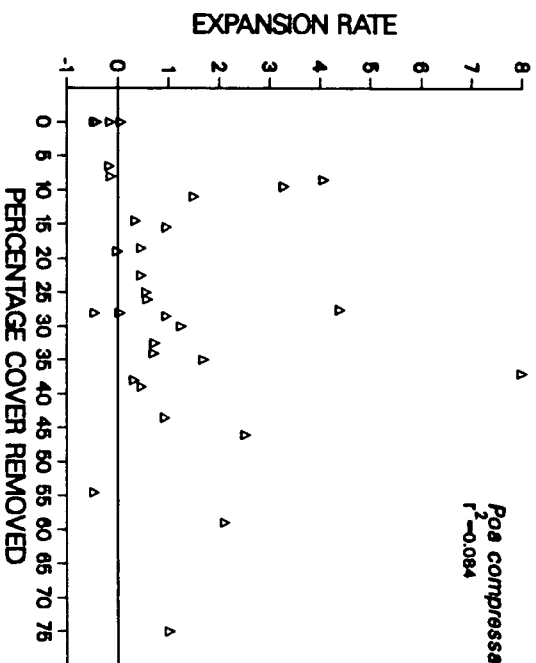
# 1939 PASTURE



# 1977 PASTURE

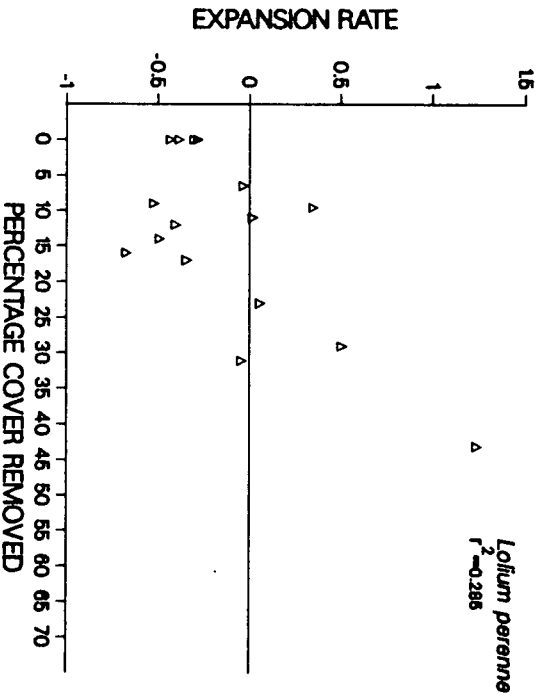


# 1977 PASTURE

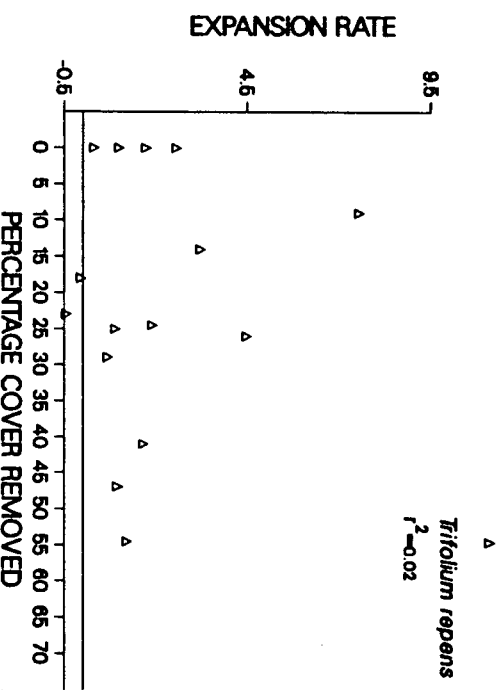




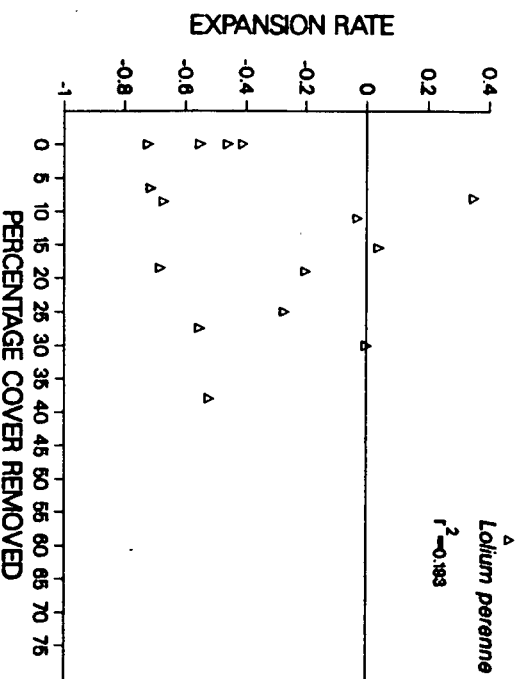
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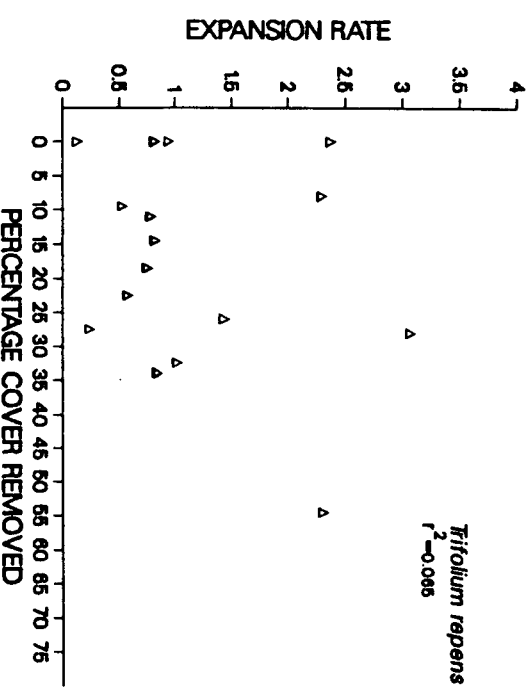
# 1939 PASTURE



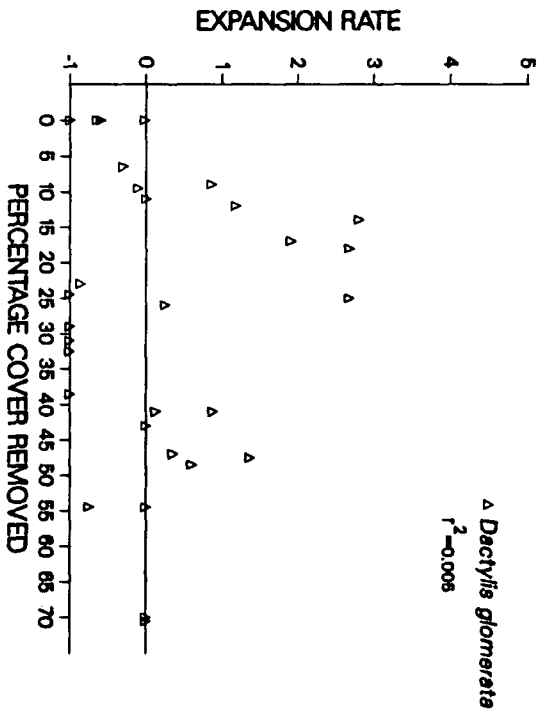
# 1977 PASTURE



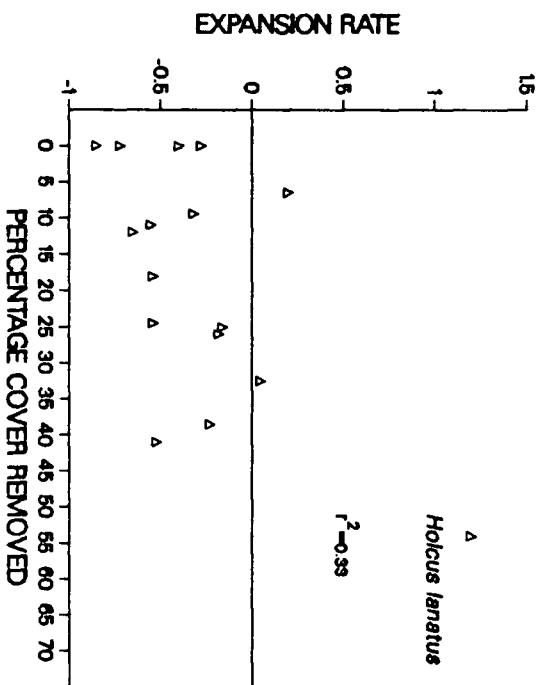
# 1977 PASTURE



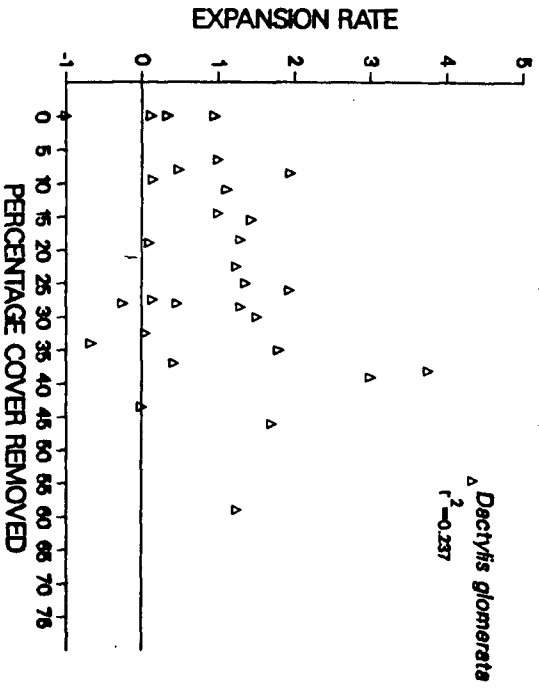
1939 PASTURE



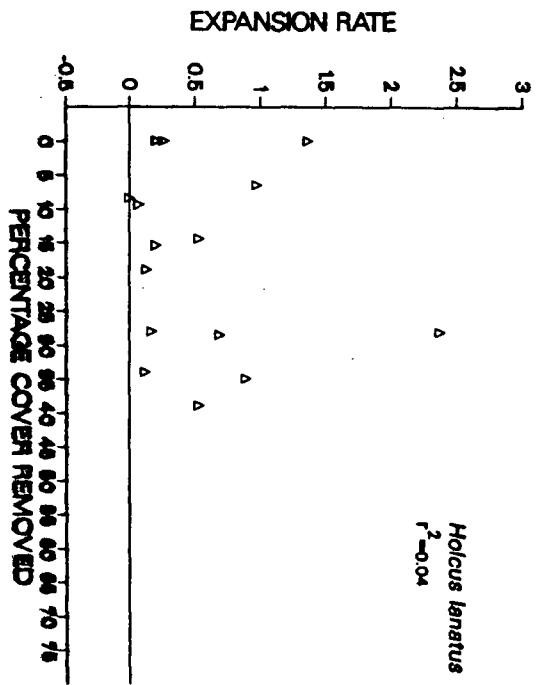
1939 PASTURE



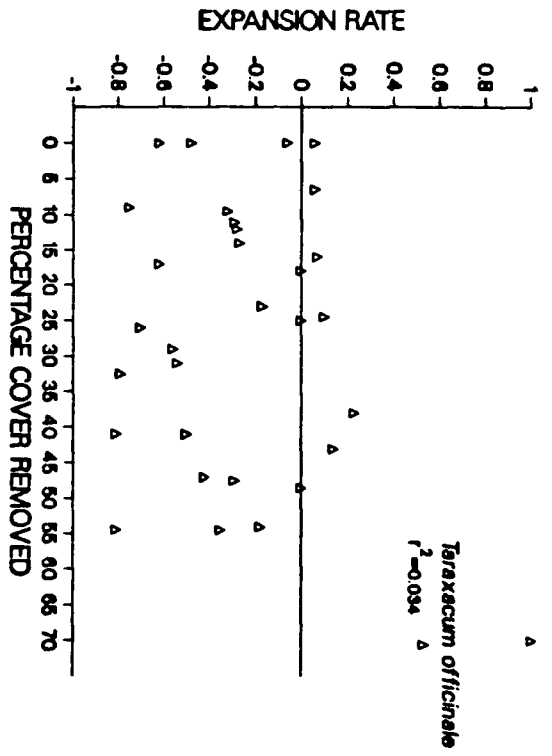
1977 PASTURE



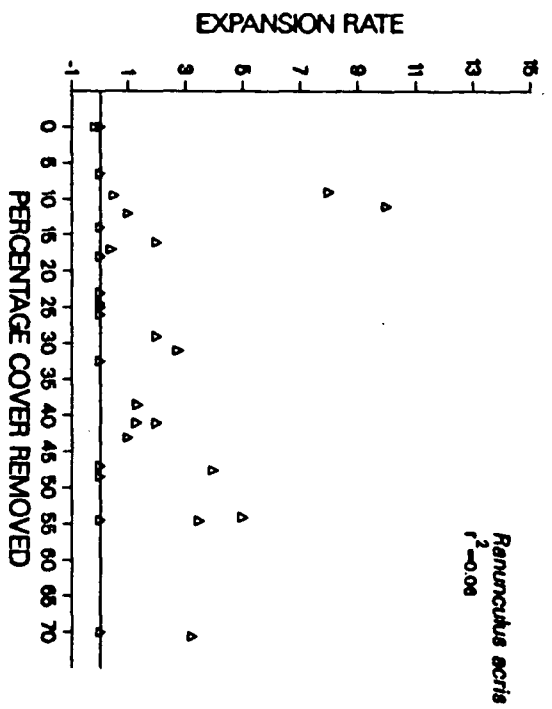
1977 PASTURE



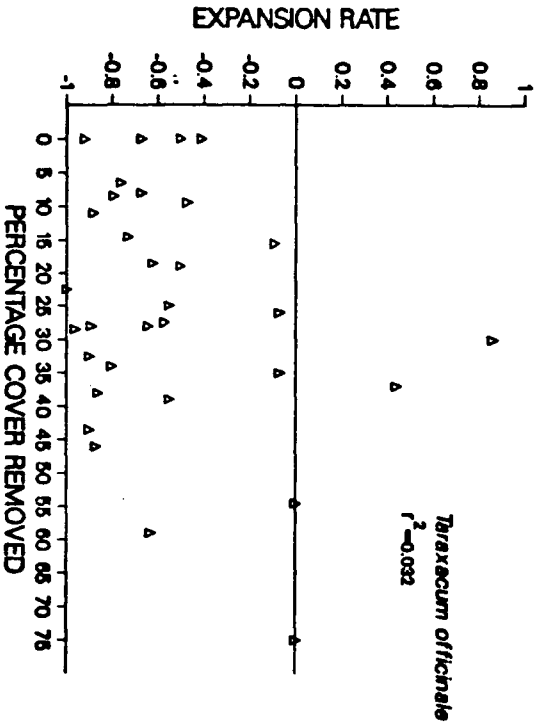
1939 PASTURE



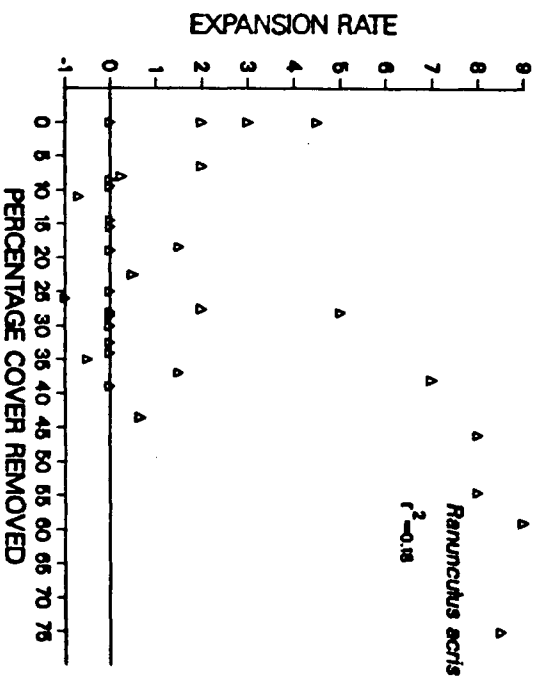
1939 PASTURE



1977 PASTURE



1977 PASTURE



scores on percentage cover removed is included in Figure 4-2.

*Poa compressa* which showed a significant response to *Trifolium repens* removal in the 1977 pasture and to HT treatment in the 1939 pasture (Tables 4-6 and 4-4), showed a concomitant increased expansion rate with increased *Holcus lanatus* removal in both pastures. Moreover, expansion rate increased with increased *T. repens* removal in the 1939 pasture but fell off sharply when large amounts of *T. repens* were removed in the 1977 pasture (Figure 4-1).

Expansion rates of *Dactylis glomerata* and *Lolium perenne* showed no consistent pattern of response to removal (Figure 4-1); however, both *D. glomerata* and *L. perenne* were able to take advantage of open space and respond with increased expansion rate (Figure 4-2). *Ranunculus acris* appeared to have a high expansion rate; this is anomalous because it changed from zero presence in some plots. Both the rate of *R. acris* expansion and the rate of *T. officinale* decline were independent of treatment.

Expansion rates of species were averaged over replications of each single species removal and over the change in abundance in the controls for 1983 - 1985 period (Table 4-7). Values are only for those species originally present in three or more of the four replicates. Expansion rates in controls were very similar to those in removal treatments. Some species, such as *Trifolium repens* showed consistently high expansion rates while others, such as *Dactylis glomerata* and *Agropyron repens*, showed rapid spread only on occasion. Analysis of variance on Box-Cox transformed expansion rates and a non-parametric test (Kruskal-Wallis)

Table 4-7. Mean expansion rate for the period 1983-1985 for species found initially in at least three of four replicates.  $R_{ic}$  is the response in control plots,  $R_{ih}$  in *Holcus lanatus* removal plots,  $R_{il}$  in *Lolium perenne* removal plots and  $R_{it}$  in *Trifolium repens* removal plots.

Species	Expansion rate	1939	1977
<i>Agropyron repens</i>	$R_{ic}$	1.767	-0.715
	$R_{it}$	-0.410	-0.745
	$R_{ih}$	x	-0.797
	$R_{il}$	0.783	-0.730
<i>Dactylis glomerata</i>	$R_{ic}$	-0.567	0.100
	$R_{it}$	-0.040	1.117
	$R_{ih}$	0.450	0.755
	$R_{il}$	1.148	0.055
<i>Holcus lanatus</i>	$R_{ic}$	-0.562	0.507
	$R_{it}$	-0.330	0.325
	$R_{il}$	-0.355	0.772
<i>Lolium perenne</i>	$R_{ic}$	-0.347	-0.535
	$R_{it}$	-0.015	-0.385
	$R_{ih}$	-0.110	-0.227
<i>Poa compressa</i>	$R_{ic}$	0.485	-0.227
	$R_{it}$	0.805	1.220
	$R_{ih}$	0.307	1.560
	$R_{il}$	0.457	0.980
<i>Trifolium repens</i>	$R_{ic}$	1.412	1.070
	$R_{ih}$	2.767	1.022
	$R_{il}$	1.815	1.322
<i>Taraxacum officinale</i>	$R_{ic}$	-0.275	-0.625
	$R_{it}$	-0.207	-0.535
	$R_{ih}$	-0.437	-0.685
	$R_{il}$	-0.150	-0.722

x- species present in less than three of four replicates in 1983.

on untransformed scores showed the rates were not significantly associated with treatment, and consequently, significant responses to removal discussed in the previous section cannot be explained by differential expansion rates of the responding species.

#### 4.4. DISCUSSION

Grass species had a greater number of significant responses to removal in the 1977 pasture than in the older 1939 pasture. Other authors have found that removal experiments in old fields and pastures demonstrate weak or diffuse interspecific interactions. For example, Fowler (1981) found no evidence of differences in magnitude of response of one species to the removal of others and concluded that relationships among species were relatively weak and diffuse. Veresoglou (1983) found that removal of subdominants, both in an old pasture and under more controlled glasshouse conditions, had little impact on remaining species.

That members of the same species showed a significant response to removal in the newer but not in the older pasture supports the hypothesis that competition between neighbouring species abates over time, either through niche divergence (Harper 1964), or by increased equality of resource acquisition (Aarssen 1983). Support, however, depends on acceptance of the 1977 and 1939 pastures representing a chronosequence. Like all chronosequences based on spatial arrangements of differing ages, this can be challenged. There is no doubt that the genetic composition of the sown species differs from 1939 to 1977. *Lolium*

*perenne* is the diploid variety in the 1939 pasture and tetraploid in the 1977 pasture. Nevertheless, *L. perenne* collected from both pastures, despite initial phenotypic differences, had complete overlap of morphological characters after growing for two years in a common garden (R. Turkington, unpubl. data). Similar results were observed for *Trifolium repens* and *Holcus lanatus*. Abiotic factors are unlikely to be substantially different in the two pastures because of close proximity and similar topography. Although soil differences exist between the two pastures (Aarssen and Turkington 1985a), many of these difference may be due to soil development over time, i.e. the multiplicity of processes triggered by plant growth and decay. This is not to say that the 1977 pasture will mirror the present condition of the 1939 pasture 38 years in the future because past history influences further development. Rather, it suggests that relationships between species will follow a similar course of development.

If strong competitive interactions occur in the newer pasture, what species compete? The increased abundance of the grasses, *Dactylis glomerata*, *Poa compressa* and *Anthoxanthum odoratum*, upon removal of *Trifolium repens*, may have resulted from their release from suppression by *T. repens*, although this seems unlikely. An alternative and testable hypothesis is that the removal of *T. repens* provides a source of nitrogen for which other species compete. Nitrogen products left behind by decaying *T. repens* roots and nodules can facilitate growth and expansion. If the grasses are able to take advantage of this nitrogen source, competition is not between *T. repens* and the grasses but among grasses for the nitrogen made available by *T. repens* decay.

That the increased abundance of grasses on *Holcus lanatus* removal is because of release from competitive suppression is supported by other studies. Evidence of competition was found in replacement series studies (Aarssen 1983; Turkington and Aarssen 1984) and pairwise competition studies (Aarssen and Turkington 1985b), in which *H. lanatus* demonstrated a strong competitive advantage over *Lolium perenne* which, however, decreased with pasture age. In *Dactylis glomerata* - *H. lanatus* interactions, *D. glomerata* had a competitive advantage, but demonstrated a similar trend of increasing equality of yield with increasing pasture age (Aarssen and Turkington 1985b). These trends were postulated to result from two different mechanisms: niche differentiation between *D. glomerata* and *H. lanatus*, and balancing of the competitive abilities of *L. perenne* and *H. lanatus*. Thus, *H. lanatus* may act to control the expansion of other grasses in the initial stages of community formation.

In removal experiments, it is possible that species respond directly to the presence of open space. *Dactylis glomerata* in the 1977 pasture showed a trend of increased expansion rate in response to increased available space and increased significantly in the *LHT* combined removal which always left large amounts of open area. A lack of response to *L. perenne* removal, however, indicates that space alone is not the only consideration. The presentation or geometry of that space may be involved. Jayasingam (1985) found that the removal of densely rhizomatous, clumped plants had a greater impact on the abundance of remaining species than removal of loosely rhizomatous species. In removing the various species, we observed that clearing *Holcus lanatus*, a densely tillering, clumped species, left larger, more discrete gaps than the other removals. These



observations do not explain the differences in response of the same species to the same treatment in two different pastures.

The applicability and utility of removal experiments to study community structure and determine competitive interactions has already been challenged (Bender *et al.* 1984). Additional limitations of the approach became evident during the study I conducted. Removal experiments in pastures may inadvertently mimic grazing, albeit selective grazing, and therefore, may not represent a novel perturbation. Indeed, at the end of the grazing season, it was visually impossible to distinguish removed from grazed areas. Grazing, however, leaves roots and rhizomes that later regenerate.

Grazing provides an intermittent but directional pressure to which plants in the older pasture have been subject for a longer time period. I have argued previously (Chapter 2) that biological accommodation seems to take place rapidly, i.e. within five years from initial establishment, and will show in Chapter 5 that species composition responds rapidly to management practices. In this chapter, the experiment may be uncovering fine-scale accommodation that continues for many subsequent years. Some portion of the measured response may be attributed to diminution of competition but some also reflects convergence in response to grazing pressure.

## 5. INFLUENCE OF MOWING, FERTILIZATION AND DISTURBANCE REGIMES

### 5.1. INTRODUCTION

Pastures are maintained by grazing or mowing. These activities remove biomass, eliminate individual plants and influence the distribution, abundance and competitive balance between species. Darwin (1859) recognized that grazing and mowing prevented vigorous species from eliminating the less vigorous in a lawn experiment. It has long been recognized that grazing management of pastures has a profound influence on botanical composition (e.g., Jones 1933a,b,c; Baker 1937; Milton 1940). Evidence from both grazing trials and manipulations of cutting frequency and intensity indicate that species' response to changes in the management regime can be quite rapid, taking place in a time frame of within a few months to a year or more (Jones 1933d; Gervais 1960). In addition, the experimental exclosure of grazers such as rabbits (Tansley and Adamson 1925; Watt 1957) and sheep (Welch and Rawes 1964) have demonstrated a decrease in the number of plant species and, the addition of grazers in biological control experiments (Dodd 1940 in Harper 1969; Huffaker and Kennet 1959) has shown an increase in species diversity. The results of these latter additive experiments are unfortunately confounded by disruption of the existing vegetation prior to experimental manipulation (Harper 1969).

Grime (1973) has proposed that forms of management such as grazing or mowing prevent competitive species from attaining maximum size, thereby

reducing their competitive edge and increasing species diversity. Caswell (1978) viewed the grazer as a predator, and argued that grazed species are maintained through a form of predator-mediated co-existence which delays competitive exclusion. In the absence of grazing, competitive exclusion dominates; at high grazing densities, grazers would be non-selective and exert a uniformly high predation pressure resulting in a decrease in species co-existence; and, at low grazing densities, grazers would be selective and exert an intermediate, patchy pressure resulting in an increase in co-existence (Caswell 1978).

Low nutrient levels constrain the rate of dry matter production of vegetation (Grime 1973, 1977) while fertilization usually increases size and growth rate (Spedding 1971). In pure stands, accelerated growth rate increases the rate of mortality (Sukatschew 1928, in Harper 1977) and in mixtures, can alter the competitive outcome (Stern and Donald 1962a,b). Mahmoud and Grime (1976) found no change in the hierarchy of dominance when fertilizer was added to grass mixtures. *Arrhenatherum elatius* remained the dominant grass in all mixtures and completely eliminated the subdominant grass, *Festuca ovina*, at higher fertilizer levels. The addition of fertilizer to nutrient-deficient vegetation usually causes large-statured species to expand and reduces the number of species in a given area (Grime 1979).

Ecological and agronomic studies confirm the importance of grazing and nutrient levels in determining plant abundance and influencing species co-existence but little attention has been given to their interaction with the small gaps that are inherent in animal grazing e.g., rabbit scrapings and cattle hoof skids. These

small gaps may function to provide micro-sites for seed germination and seedling establishment (Silvertown 1981), serve as a refuge for non-aggressive species, or facilitate vegetative expansion of existing plants. Both Grubb (1977) and Grime (1979) have stressed the importance of gaps in facilitating the ingress of, and maintaining, species in the community.

To properly understand the influence of grazing and fertilization on pasture composition requires controlled field experiments. This facility was not available at the Aldergrove pastures so that to estimate this, a pasture-like area was seeded at the University of British Columbia South Campus Field Station. An experiment was designed to measure the effects on pasture species of the simultaneous manipulation of levels of mowing, fertilization and removal of small divots to create small gaps and simulate discrete disturbances. Although mowing differs from grazing in many ways (e.g. it is homogeneous, lacks the biting and pulling action of the grazer, and is non-selective) it is a best approximation of grazing in a field station facility.

## 5.2. METHODS

Preparation for the experiment commenced in May 1982 in a section of the South Campus Field Station. Seed was sown at a rate of  $4\text{g/m}^2$ ; the seed mix (Table 5-1) approximated the proportions of Buckerfields Highland Mix over the past few years. This is the same mix used in the youngest pasture at Aldergrove in 1977. It was fertilized in June 1982 with half normal dilution of 20-20-20 fertilizer and weeded as required. By May 1983, the sown species

dominated the plots and no further weeding was necessary.

The experimental procedure began in May 1983. The seeded area was subdivided into 8 blocks. Four of the blocks received  $150\text{g/m}^2$  of 4-12-8 dry fertilizer every 3 weeks and the remaining four received no fertilizer. Each pair of fertilized - unfertilized blocks were further subdivided into 4 mowing treatments: every week, once every 3 weeks, once every 6 weeks and no mowing. Within each of the eight combinations of mowing and fertilizer treatments were four  $1\text{m}^2$  plots. From these  $1\text{m}^2$  plots, different 'disturbance regimes' were imposed by removing circular divots 10cm in diameter. Originally I had planned four small gap intensities: no divots, 1 divot every week, 2 divots every 2 weeks and 4 divots every 2 weeks but this proved to be too intense. Subsequent to July 1983, the regime was modified to: no divots, 1 divot every 2 weeks, 2 divots every 4 weeks and 4 divots every 4 weeks. The divots were made by randomly locating the appropriate number of spots and pounding a metal plug into the ground to remove the upper 1-2cm of soil and rooted material. The treatments ran from May to October of each year from 1983 to 1985 and are planned to continue beyond this date to assess longer-term effects.

All plots were surveyed in September 1985, using four  $.5 \times .5\text{m}$  quadrats per  $1\text{m}^2$  plot. Each quadrat was subdivided into a grid of 25 points and the rooted cover at each point was recorded (100 points per plot). *Lolium perenne* and *L. multiflorum* were not distinguished because of difficulties in differentiating them in the vegetative state.

Table 5-1. Percentage composition of the original seed mix.

Species	Percentage
<i>Dactylis glomerata</i>	46
<i>Lolium perenne</i>	12
<i>Lolium multiflorum</i>	8
<i>Phleum pratense</i>	4
<i>Trifolium pratense</i>	15
<i>Trifolium repens</i>	15

### 5.3. RESULTS

In September 1985, all of the seeded species plus several volunteers were present in the plots (Table 5-2). The origin of *Festuca pratensis* is uncertain although it can occur in commercial seed sources of *Lolium* spp. Of the seeded species, only *Dactylis glomerata* was found in all treatments and its mean abundance was similar to the input frequency of 46%. The abundance of ryegrasses (*Lolium* spp.) and clovers (*Trifolium repens* and *T. pratense*) was considerably lower than had originally been seeded.

Analysis of the abundance data was univariate by species using a BMDP (Dixon 1983) fully crossed factorial analysis of variance. Only the nine most common species (>2% cover) plus bare ground were analysed. Mowing had a highly significant effect on the percentage cover of all species except *Phleum pratense*; fertilization had a significant effect on six species; but, divot removal had a significant effect only on *Dactylis glomerata* ( $p=0.0509$ ) (Table 5-3).

Table 5-2. Mean and standard deviation of the percentage cover of species and bare ground on South Campus treatment plots in September 1985.

Species	Mean	S.D.
<i>Dactylis glomerata</i>	45.5	16.4
<i>Lolium</i> spp.	8.89	7.01
<i>Agrostis</i> sp.	6.73	12.1
<i>Hypochoeris radicata</i>	5.04	5.83
<i>Festuca pratensis</i>	4.91	4.60
<i>Trifolium repens</i>	4.48	6.20
<i>Rumex acetosella</i>	3.44	5.21
<i>Trifolium pratense</i>	2.89	4.58
<i>Phleum pratense</i>	2.34	2.51
<i>Poa</i> sp.	0.43	1.63
<i>Holcus lanatus</i>	0.23	1.12
<i>Taraxacum officinale</i>	0.21	0.77
<i>Cirsium arvense</i>	0.20	0.62
<i>Plantago major</i>	0.13	0.61
<i>Medicago lupulina</i>	0.13	0.69
<i>Cerastium vulgatum</i>	0.07	0.36
<i>Plantago lanceolata</i>	0.05	0.21
<i>Alopecurus pratensis</i>	0.02	0.12
<i>Agropyron repens</i>	0.02	0.12
Moss	0.03	0.17
Bare ground	14.3	11.9

Because divot removal rarely had a significant effect, these treatments were combined to show species response to fertilization and mowing (Figure 5-1). The percentage cover of *Dactylis glomerata* was reduced by frequent mowing but other species responded positively to some frequency of cutting. The fine weedy grass, *Agrostis* sp., was abundant only in the frequently mown blocks, whereas *Lolium* spp. and *Festuca pratensis* were more abundant at intermediate mowing frequencies. *Trifolium repens* was reduced less by more frequent mowing than the taller, more upright *T. pratense*. Weedy dicots, *Rumex acetosella* and *Hypochoeris radicata* were most abundant at intermediate mowing frequencies.

Table 5-3. Percentage variation in abundance of common species and bare ground explained by different mowing (m), fertilization (f) and divot removal (d) regimes. \*\*\* -  $p < 0.001$ ; \*\* -  $p < 0.01$ ; \* -  $p < 0.05$ .

Species	m	f	m-f	d	m-d	f-d	mfd
	***	**	***	*			
# <i>Dactylis glomerata</i>	31	37	8.2	1.7	1.2	0.4	3.1
	***	*	**				*
# <i>Lolium</i> spp.	60	7.1	5.5	1.2	1.9	0.9	3.9
		*					
# <i>Phleum pratense</i>	3.0	44	1.6	3.4	4.5	1.4	3.2
	***	**	***			*	
# <i>Trifolium repens</i>	30	32	18	1.3	1.5	1.9	1.9
	***	**	***				
# <i>Trifolium pratense</i>	23	31	16	0.3	4.6	0.2	4.1
	***				**		
<i>Festuca pratensis</i>	20	0.4	2.7	4.9	12	1.0	7.2
	***		***				
<i>Agrostis</i> sp.	53	1.2	6.2	0.4	1.8	0.2	1.5
	**	**	***				
<i>Hypochoeris radicata</i>	24	27	11	1.3	2.6	0.6	2.1
	**						
<i>Rumex acetosella</i>	28	2.0	9.8	2.5	3.5	0.3	1.8
	***		**		*		
bare ground	66	2.1	6.2	2.0	2.4	0.9	2.1

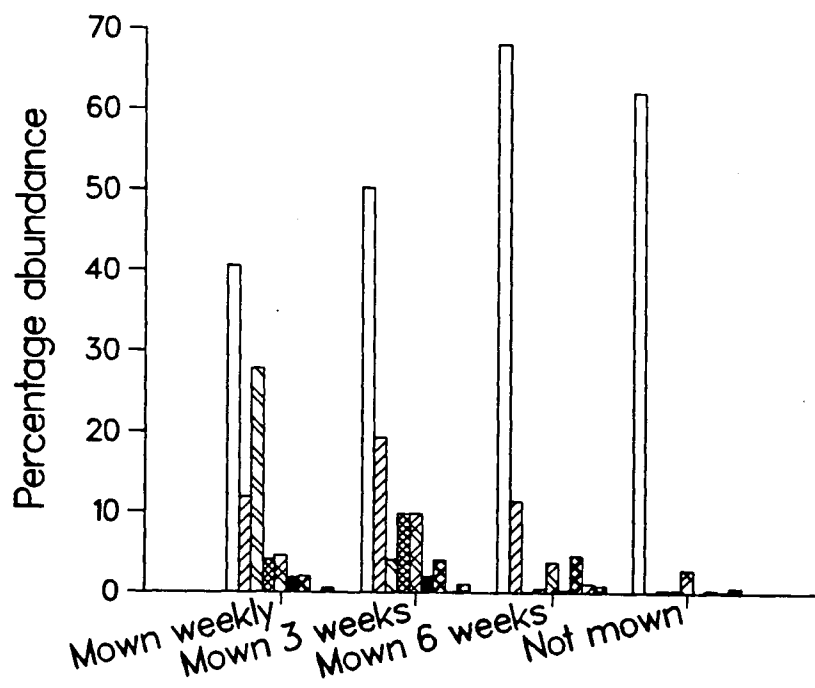
Species labelled with an # were constituents of the original seed mix.



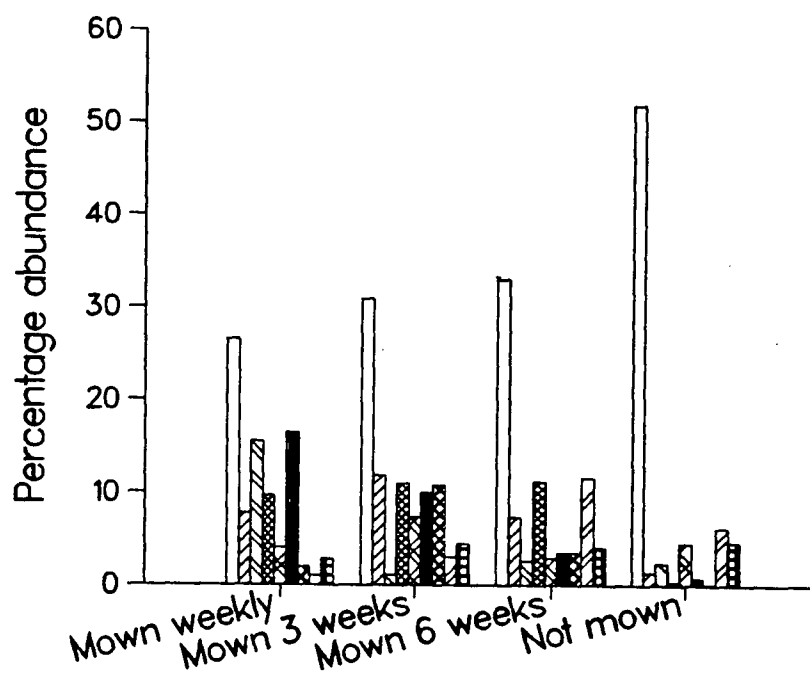
Figure 5-1. Percentage abundance of nine species on fertilized and unfertilized plots subject to different mowing regimes.

- ☐ *Dactylis glomerata*
- ☒ *Lolium perenne*
- ☐ *Agrostis* sp.
- ☒ *Hypochoeris radicata*
- ☒ *Festuca pratensis*
- ☒ *Trifolium repens*
- ☒ *Rumex acetosella*
- ☒ *Trifolium pratense*
- ☒ *Phleum pratense*

## Fertilized plots



## Unfertilized plots



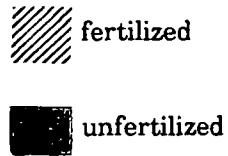
Fertilization increased the abundance of all the responding grasses and decreased the abundance of clovers, a result typical of grass-clover mixtures (Herriott and Wells 1960; Stern and Donald 1962a,b; Dennis and Woledge 1985).

Many species showed a strong interaction effect between fertilization and mowing and some species responded to an interaction with divot removal. Mowing and low intensity gap formation increased the abundance of *Festuca pratensis* whereas lack of fertilizer and medium intensity gaps increased the abundance of *Trifolium repens*.

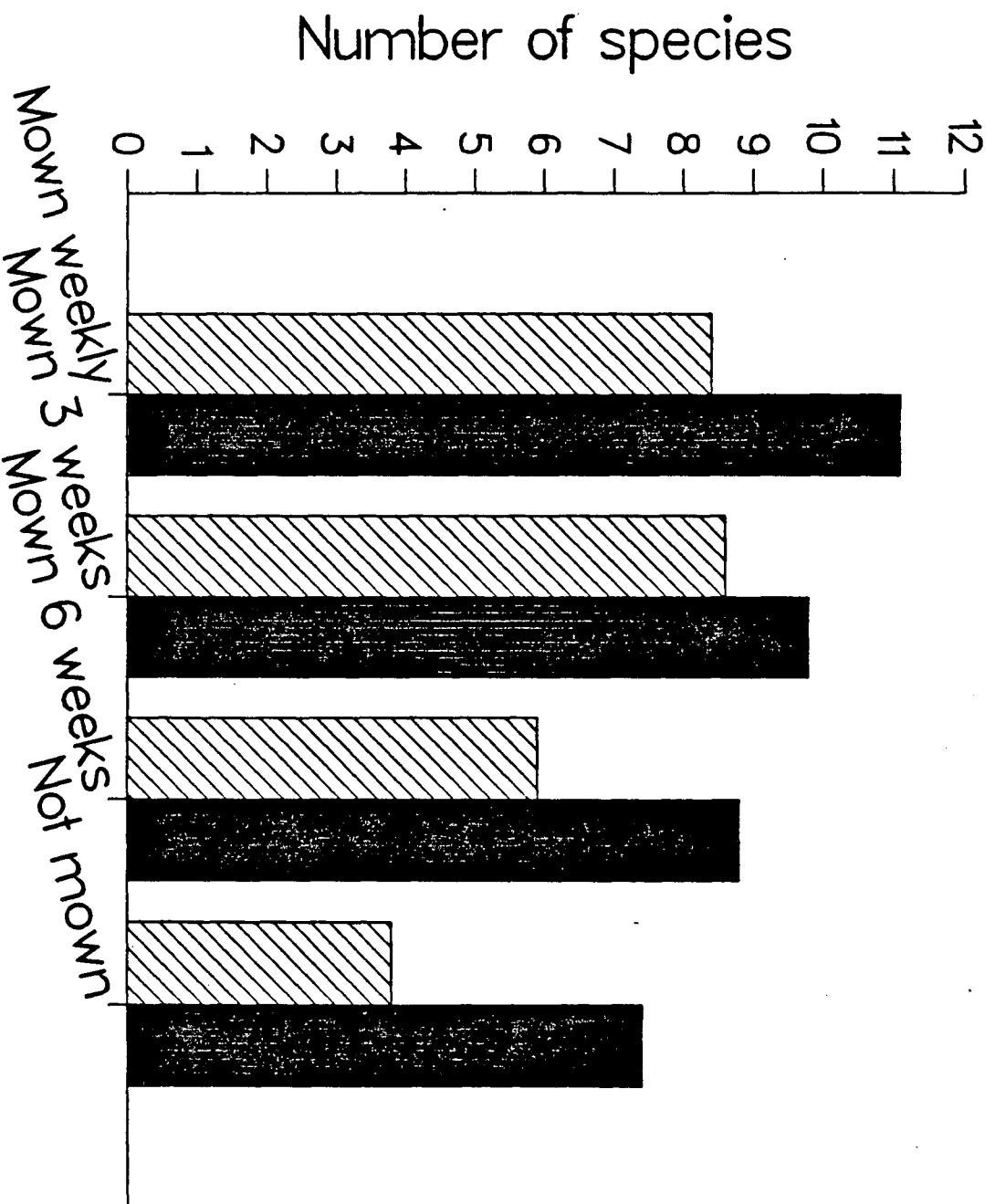
The amount of bare ground decreased with the addition of fertilizer and with increased mowing frequency. At the highest mowing frequency, however, there was a greater proportion of bare ground in the most intense divot removal treatment leading to an interaction effect.

The number of species per  $1\text{m}^2$  plot ranged from 2 - 14, averaging eight species per plot. The lowest number of species was associated with fertilized, least frequently mowed plots and the greatest number with unfertilized, most frequently mowed plots (Figure 5-2). The distribution of the variance of number of species per plot was unknown, and therefore, analysis of variance was not strictly applicable to test for treatment effects. Nonetheless, factorial analysis of variance was used in an exploratory manner, because the large number of treatment cells constrained the use of alternate non-parametric techniques. Results were similar for both untransformed and square-root transformed values: highly significant mowing and fertilizer effects ( $p < 0.001$ ) and strong interaction effects

Figure 5-2. Number of species per square metre on fertilized and unfertilized plots subject to different mowing regimes.



# Number of species per plot



( $p < 0.05$ ) but no effect from divot removal on the number of species in the plot.

#### 5.4. DISCUSSION

Mowing and fertilizing were found to strongly influence species abundance and plot composition. The response of species abundance to mowing and fertilizer regimes has been associated with tolerance of shading and many large-statured species such as *Dactylis glomerata*, responding primarily to nitrogen, shade smaller-statured species (Stern and Donald 1962a,b; Snaydon 1971; Rhodes and Stern 1978). Shading is further exacerbated by infrequent cutting. Fertilization of grasses frequently suppresses low growing clovers, because grasses are able to grow taller in response to nitrogen application. Mowing can also provide nitrogen to grasses, because cutting clovers causes leaf and nodule drop, thereby increasing the amount of nitrogen transferred to grasses and favouring their growth (Bland 1967). Unlike fertilization alone, the repeated cutting of grasses and clover prevents shading, thereby ameliorating suppression of clover.

The cultivars used in this experiment are typical of those sown in pastures. Most cultivars sown in pastures are selected for herbage production, i.e., rapid, upright growth and to a lesser extent, seed production (Snaydon 1984). These cultivars require a nutrient-rich environment to maintain them as the dominant species (Grime 1979). Grime relates the reduction in species density over the past thirty years in European meadows and pastures to increased "competitive dominance brought about by stimulating the yield of more robust and productive species and genotypes through application of high rates of mineral fertilizer" (p.

125). In the absence of continued fertilizer input, however, botanical composition of pastures changes to a mixture of sown, naturalized and weedy species. In addition, grazing selects against many of the characters for which cultivars are bred so that naturalized pasture populations are more likely to contain more low growing and laterally spreading forms than the original seed source. Snaydon (1984) also points out that the traits of cultivars may well carry the penalty of poorer persistence so that established pastures will contain a greater range of variation in plant populations as well as higher species density.

In pastures, grazing removes biomass that would shade and suppress the growth of less vigorous or small-statured species, thereby delaying competitive exclusion of these species. Competition for light, water and nutrients interacts with grazer - predator frequency, intensity and selectivity to determine botanical composition and species co-existence. Grime's (1973) proposed model, in which maximum potential species density is found at intermediate levels of nutrient availability, predicts that maximum species density occurs in relatively infertile pastures. In infertile pastures, the interaction of the five processes (Grime 1979) that control species density are such that (i) dominance of large species is reduced; (ii) nutrient "stress" and (iii) disturbance are increased which promotes (iv) ingress of suitable species and (v) niche differentiation. Accordingly, the continued decline in abundance of *Dactylis glomerata* in the Aldergrove pastures, could be attributed to failure to maintain high fertility levels coupled with reduction because of its sensitivity to grazing.

The experiment in this chapter confirms that mowing and fertilization influences

species composition and co-existence but negates a role for small disturbances. The created gaps appear to neither facilitate nor impede species abundance and spread, and to have no effect on species richness. These gaps provide no additional opportunities for new species to establish in the plots. These results agree with the observations of Rapp and Rabinowitz (1985) who created disturbances of about  $27\text{cm}^2$  in tall grass prairie and found that seedling survival was no greater on disturbances than in undisturbed controls. This is probably related to a number of factors. First, constituent species of the community may have either no need for gaps or require a larger area to trigger germination (Grime 1979; see Hilton *et al.* 1984 for variation within a species). A second factor is the influence of surrounding plants on survival and growth of seedlings. In general, more space leads to higher seedling survival and growth (Gross 1980; Snaydon and Howe 1986) although intolerance of heat and desiccation may limit establishment of some species in very large openings (Harper 1977). A third consideration is that even if gaps were favourable for seedling establishment, the amount of divot removal was inadequate and did not significantly increase the amount of bare areas available. Rather, the results indicated that plant spacing in response to cutting and fertilizer treatment had a greater effect on creating bare ground than actual divot removal.

The results of this experiment invoke a comment on certain experimental practices to determine competitive outcome on interactions between species. It is apparent that the outcome of species interactions can be manipulated, to a greater or lesser extent, by the cutting and fertilization regime. Numerous examples exist such as the increased production of *Lolium perenne* relative to



*Dactylis glomerata* with increased frequency of cutting or earliness of defoliation (England 1968) or the reduction in suppression of *Agrostis capillaris* (syn. *A. tenuis*) by *L. perenne* with severe defoliation (Harris and Thomas 1972). Replacement series, additive, and Nelder designs used to test competitive interactions, all require management regimes which often include fertilization and clipping for biomass estimation. Such management can strongly influence the outcome of species interactions and the results of such experiments can be generalized only with extreme caution.

## 6. GENERAL DISCUSSION

The sun rises and the sun sets

and hurries back to where it rises.

The wind blows to the south and turns to the north

round and round it goes, ever returning on its course.

All streams flow to the sea, yet the sea is never full.

To the place the streams come from, there they return again.

**Ecclesiastes, Chapter 1, vs 5-7**

The chapters of this thesis focus on aspects of the role of disturbance in a pasture community. Disturbance by grazing or mowing is intrinsic to the maintenance of pastures in non-grassland climates. In addition, on a local scale "grazing animals frequently sit, lie, scratch and paw on the pasture in addition to walking, running and jumping on it" (Spedding 1971) and they also deposit dung and urine. Add to these activities, mounds of small animals, insect grazing and mechanical disturbance from haymaking and harrowing and the view of pastures as dynamic and disrupted is confirmed.

It is not surprising that one feature of the Aldergrove pastures is the variability associated with plant abundance because fluctuations in abundance in grasslands and pastures are well documented (e.g. Rabotnov 1966, 1974; Spedding 1971; Vickery 1981; Thorhallsdottir 1984; Snaydon 1985). They are characteristically reversible, and associated with variations in meteorological and (or) hydrological conditions on a seasonal, yearly or short-term (e.g. 1-3, 5-10 years) basis

(Rabotnov 1974). Biotic interactions, such as the nitrogen-mediated feedback loop that is posited for *Lolium/Trifolium* fluctuations (Blaser and Brady 1950), also lead to changes in relative abundance. Moreover, management decisions on timing and extent of mowing, grazing and fertilizing, effect species composition and abundance.

Yet, despite the flux of species composition, the botanical composition of the pastures is remarkably stable. Over the eight years that records have been kept for these pastures, only the 1977 field showed directional change in species composition and abundance and this ceased 4-5 years subsequent to ploughing and seeding. No species present in the initial seed mix has been completely eliminated from these pastures although the abundance of *Trifolium pratense* is severely reduced. Rather, it appears that the initial species composition determined the subsequent composition although proportions have changed (cf. Egler 1954). Ingress of weedy species occurs rapidly - witness the abundance of *Holcus lanatus*, *Taraxacum officinale*, *Agropyron repens* and *Ranunculus acris*. The composition of the pastures appears, nevertheless, to be constrained by the major biomass/abundance contributors which vary in relative proportions from year to year. Less abundant species are interspersed in various patterns which apparently have little impact on the total dynamics. One can imagine visiting the pastures in future years and seeing the same species maintaining various proportions and distributions of abundance within some set of limits for which neither boundary conditions nor rules of assembly are yet defined or understood.

Maintenance of the limits and rules appears to be dependent on the continuation

of the management practices in the pastures. Holling (1973) notes that in 'real world examples' systems may persist indefinitely until a novel introduction changes the driving variables and flips the system outside the boundary conditions. For example, permanent or long term removal of herbivores or repeated harvesting for maximum yield are likely to strain the resilience of the system and push it beyond current boundaries. But, within the current management practices, the pastures appear to exhibit considerable variation within stable limits.

The three pastures are not entirely closed communities, existing as they do within a matrix of semi-rural copses, roads and rights-of-way that constrains species and gene influx. Both plant and animals are able, however, to disperse to a limited extent between the pastures. Observations suggest that the continued presence of *Trifolium pratense* in the older pastures is derived from recruitment from adjacent right-of-ways whereas the occasional local outbreak of *Gnathaliium uliginosum* is from a persistent seed bank. These species are minor constituents of the community, but major constituents, such as *Holcus lanatus*, have dispersed into the pastures, not only from adjacent areas but also, via a seed bank accumulated over time (see Grime 1979).

Small disturbances such as molehills and dung pats have been shown to play little or no role in providing access for weedy species to establish neither in the Aldergrove pastures nor on South Campus. In order for seedlings to grow, however, a space of some size must be available. The size required will be dependent on species (e.g. Denslow 1980) or genotype (Hilton *et al.* 1984). Many

species have a requirement for light, or high or fluctuating temperatures in order to germinate. Hilton *et al.* (1984) found that *Poa trivialis* seed from plants growing in closed grassland swards germinated under low red:far-red ratios similar to dense shade conditions whereas those from open, arable land required higher red:far red ratios. Other studies have shown that the rate of seedling emergence is lower when vegetative cover is high (e.g. Fenner 1978; Silvertown 1981; Gross 1984) and growth and survival is typically reduced (Ross & Harper 1972).

On average, between 1.2% (in the 1939 pasture) and 3.4% (in the 1958 pasture) was bare from various causes during the study period. Grazing and associated activities removed considerable biomass and left numerous small gaps because plants, some more readily than others (e.g. *Dactylis glomerata*) were more readily uprooted. Very small gaps may be sufficiently large for many pastures species to regenerate. Indeed, root death after loss of shoot mass may even provide, after complex cycling through soil fauna, an enriched nutrient environment for seedling establishment (Newbery 1979). Several authors (e.g. King 1971; Snaydon & Howe 1986) have shown that nutrient limitation by established plants is a major deterrent of seedling establishment although the extent to which this affects survival is species dependent.

In the pastures, molehills and dung pats provided sites for establishment of *Trifolium repens*, and to a lesser extent, *Ranunculus acris* seedlings. Neither species required these gaps to maintain their presence in the community. *Ranunculus acris* was found to germinate and survive in a variety of gap sizes

whereas *T. repens* spread by stolons throughout the pastures. Cahn and Harper (1976) suggested that frequent inputs of new genotypes of clonal species is essential to avoid local dominance by a few either competitively dominant or long-lived clones. Occasional seedling establishment (3% of the ramet population per year) is sufficient to maintain considerable genet variation within a population (Soane and Watkinson 1979). In good seed years, e.g. 1984, seedling establishment of this magnitude was calculated to occur in the pastures (R. Parish, unpublished) but the frequency of 'good' seed years has yet to be established.

The variability in seed germination recorded for *Trifolium repens*, cautions against generalizations that molehills and dung pats never have a role in sexual regeneration of pasture species. In the fall of 1982, a large flush of monocot seedlings was observed in the three pastures both on and off molehills. It is a pity that no crystal ball or seer provided the foresight to measure seedling survivorship that first year because no other monocot flush was observed in subsequent years. It appears that seed germination is highly episodic in these pastures.

Gaps such as molehills and dung pats did provide opportunities for vegetative expansion. These gaps appeared to function in a manner similar to small gaps in forests (Runkle 1982) allowing competitive release of neighbouring individuals. Pasture species that are able to take advantage of these openings are usually those capable of rapid lateral spread either by rhizomes (e.g. *Agropyron repens*, *Poa compressa*) or stolons (e.g. *Trifolium repens*).

Formation of molehills and dung pats killed most plants that were buried under them although those capable of regeneration from fleshy roots (e.g. *Taraxacum officinale*) survived temporary burial. In general, the probability of death for a genet depends on its size. The contribution of small disturbance to the removal of genets of such species as *Trifolium repens* and *Poa compressa*, in which ramets may be spread over large areas was probably minimal, but genet death could result for closely tillering grasses such as *Holcus lanatus* and *Lolium perenne*. McNeilly & Roose (1984) found that the number of genotypes of *L. perenne* per unit area of an old pasture was considerably lower than in younger pastures. The loss of genotypes during sward establishment has been related to the loss of smallest individuals, often resulting from small differences in timing of seedling emergence (Ross & Harper 1972). Subsequent losses have been attributed to competitive dominance of a few superior genotypes which are adapted to sward management practices (McNeilly & Roose 1984). Strong competitive interactions have yet to be demonstrated in pastures (Strong 1983) despite generally accepted statements that they do exist (Donald 1963; Snaydon 1978). Small disturbances serve to randomly remove individuals yet provide no consistent opportunity for new recruits to enter. Depletion of genotypes may, in part, result from random removal without replacement, rather than selective processes.

Species respond differently to disturbance of various sizes. *Trifolium repens* could utilize molehills and dung pats for both sexual propagation and vegetative colonization. *Dactylis glomerata* was frequently found to occupy the same point from fall to spring. In addition, *D. glomerata* generally increased in the sward around dung but not around molehills, proliferated when fertilizer was added to

artificial swards, and responded positively when *T. repens* was removed. These observations suggest that *D. glomerata* was able to take advantage of nutrient release, either by pre-empting nitrates released by decaying nodules or by capturing nutrients leached from dung. *D. glomerata* had, however, little ability to invade molehills and dung pats.

The response of *Lolium perenne* was very variable. In general, it did not invade small disturbances. In a year of declining abundance, *L. perenne* declined less in areas from which *Holcus lanatus* had been removed. Removal of *H. lanatus* led to increases in several species although *H. lanatus* did not increase with removal of other species nor could it readily invade molehills and dung. These findings agree with those of Thorhallsdottir (1984) who found *H. lanatus* effectively held space against invasion by other species but showed little tendency to pre-empt gaps in the sward.

The response pattern of individual species to molehills and dung pats recorded at 0.25 m<sup>2</sup> scale of observation was not evident at 25 m<sup>2</sup>. The direction of association of species and disturbance, in general, was not predictable from one scale of observation to the other. There were exceptions: *Agropyron repens* readily invaded small disturbances and its abundance increased in areas of high disturbance and *Holcus lanatus*, unable to exploit disturbances, was not abundant in disturbed areas. For other species, invasion pattern was not a factor significantly influencing distribution of abundance within the pasture at anything beyond the local scale. From these discrepancies, I must conclude that despite significant interaction between pattern of species abundance and disturbance,



disturbances *per se* have little organizing or causal force. The most obvious explanation of the pattern within the pastures is that because most significant interactions were associated with molehills, plant species were tracking resources linked to those that moles were also exploiting. Because moles predominantly consume earthworms, species positively associated with increased density of molehills may be those exploiting areas of increased soil fertility.

Aarssen (1983) and Aarssen and Turkington (1985a) have proposed a model of community processes derived from observations and experiments on species from these pastures. They suggested that the community evolved over time as less fit genotypes were eliminated by competition and grazing. The resultant community is characterized by strongly competitive individuals that co-exist because of a competitive stalemate in which none can achieve an advantage. Recruits are filtered through interactions with existing individuals so that only those of equivalent abilities in that time and location persist.

Evidence to support or refute this model was not collected in this study in the same pastures. Yet, a discussion of some of the ideas seems appropriate. In order to have selection, there must be genetic variation, which is generated by mutation and/or recombination. In higher plant populations, genetic variation is usually achieved by sexually produced seeds. This study of the Aldergrove pastures provided little information on rates of recruitment for most species but because of the focus on small disturbance, some idea of the 'life history' of *Trifolium repens* has emerged. Seed germination is apparently highly episodic. Probably it is restricted to gaps of  $500\text{cm}^2$  or greater; none were observed in

any of the smaller gaps. Seedling density varied and mortality was generally high. However, early mortality resulted from, in the main, such density-independent factors as grazing by slugs and small mammals, burial by re-opening of mole tunnels, or up-rooting by haymaking. Initial interactions with other individual plants were most certainly intraspecific but occurred after the plant became established on the disturbance. Without specific demographic studies following the fates of these survivors as other species spread into the gaps, it is impossible to refute Aarssen's hypothesis of competitive combining ability. I will suggest, however, the following scheme: once established in the relatively competition-free environment of the molehill, *T. repens* begins to spread laterally into the sward. In areas where conditions are favourable, internodes are short and individual plants concentrate biomass in these areas but where conditions are unfavourable, internodes are long and individuals do not establish abundantly (Solangaarachchi 1985). What constitutes a 'favourable' site? Axiomatically, it is adequate resource levels. This can result from numerous factors; (1) resources may not be limiting, i.e. abundant beyond the capability of the plant to deplete in the time frame available; (2) resources may be available because of partitioning by niche differentiation (ecological combining ability); (3) resources may be available because ability to exploit is equivalent (competitive combining ability). The relative importance of these factors was not tested but the role of selection appears to be much less than previously postulated: recruits are rare, random events predominate, yet the pastures remain stable..

If pastures are characterized by random event, it does not follow that they are also characterized by random processes. Events may trigger an orderly series of

processes. The replacement of one species by another is not random. The complex, interweaving of scale and pattern observed in the pasture suggests a combination of process and forces whose interaction await further study.

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## **8. APPENDIX 1**

Transition probability of row species being replaced by a column species, on and around molehills in the 1939 pasture for the period from September 1984 to April 1985.

	Molehill	<i>Dactylis glomerata</i>	<i>Holcus lanatus</i>	<i>Lolium perenne</i>	<i>Phleum pratense</i>	<i>Poa compressa</i>	<i>Agropyron repens</i>	<i>Trifolium repens</i>	<i>Taraxacum officinale</i>	<i>Ranunculus acris</i>
Molehill	33.9	3.5	0.4	8.1	0.4	18.4	2.8	18.4	3.9	1.4
<i>Dactylis glomerata</i>	0.0	91.7	0.0	0.0	0.0	5.0	1.7	1.7	0.0	0.0
<i>Holcus lanatus</i>	0.0	8.5	42.6	12.8	0.0	19.1	0.0	10.6	2.1	0.0
<i>Lolium perenne</i>	4.1	2.9	1.2	43.9	0.6	17.5	0.6	19.9	2.9	2.3
<i>Phleum pratense</i>	0.0	10.0	10.0	10.0	0.0	0.0	0.0	40.0	10.0	0.0
<i>Poa compressa</i>	1.2	2.4	2.4	6.0	0.0	59.5	1.2	16.7	3.6	3.6
<i>Agropyron repens</i>	10.0	10.0	0.0	10.0	0.0	10.0	30.0	10.0	0.0	0.0
<i>Trifolium repens</i>	4.5	4.9	0.4	6.9	0.8	15.8	2.4	57.1	1.6	1.2
<i>Taraxacum officinale</i>	3.4	0.0	3.4	6.9	0.0	13.8	0.0	3.4	62.1	6.9
<i>Ranunculus acris</i>	0.0	0.0	0.0	0.0	0.0	0.0	14.3	14.3	0.0	71.4

Transition probability of row species being replaced by a column species, on and around molehills in the 1958 pasture for the period from August 1983 to April 1984.

	Molehill	<i>Dactylis glomerata</i>	<i>Holcus lanatus</i>	<i>Lolium perenne</i>	<i>Phleum pratense</i>	<i>Poa compressa</i>	<i>Agropyron repens</i>	<i>Trifolium repens</i>	<i>Taraxacum officinale</i>	<i>Ranunculus acris</i>
Molehill	37.8	2.0	6.4	1.2	0.0	12.9	20.5	7.2	4.0	0.0
<i>Dactylis glomerata</i>	5.2	56.5	1.7	3.5	5.2	15.7	6.1	2.6	0.9	0.0
<i>Holcus lanatus</i>	8.1	2.3	25.6	4.7	5.8	19.8	10.5	5.8	9.3	1.2
<i>Lolium perenne</i>	10.8	10.8	2.0	9.8	8.8	22.5	12.7	8.8	2.9	4.9
<i>Phleum pratense</i>	12.5	12.5	0.0	0.0	50.0	12.5	0.0	0.0	6.3	0.0
<i>Poa compressa</i>	14.4	4.2	3.4	4.2	5.1	33.9	12.7	7.6	7.6	0.0
<i>Agropyron repens</i>	10.6	5.7	3.3	3.3	3.3	23.6	38.2	1.6	2.4	1.6
<i>Trifolium repens</i>	0.0	7.1	10.4	3.6	0.0	10.7	0.0	46.4	7.1	0.0
<i>Taraxacum officinale</i>	13.3	2.2	4.4	4.4	2.2	15.6	22.2	6.7	26.7	0.0
<i>Ranunculus acris</i>	0.0	0.0	0.0	50.0	0.0	0.0	25.0	0.0	25.0	0.0

Transition probability of row species being replaced by a column species, on and around molehills in the 1977 pasture for the period from August 1984 to April 1985.

	Molehill	<i>Dactylis</i> <i>glomerata</i>	<i>Holcus</i> <i>lanatus</i>	<i>Lolium</i> <i>perenne</i>	<i>Phleum</i> <i>pratense</i>	<i>Poa</i> <i>compressa</i>	<i>Agropyron</i> <i>repens</i>	<i>Trifolium</i> <i>repens</i>	<i>Taraxacum</i> <i>officinale</i>	<i>Ranunculus</i> <i>acris</i>
Molehill	27.5	4.1	11.9	6.9	5.5	11.9	2.3	15.1	5.0	3.3
<i>Dactylis glomerata</i>	0.0	44.7	7.9	5.3	13.2	13.2	0.0	5.3	5.3	0.0
<i>Holcus lanatus</i>	0.0	4.4	77.8	4.4	0.0	4.4	0.0	6.7	0.0	0.0
<i>Lolium perenne</i>	3.4	1.7	19.0	41.4	3.4	13.8	0.0	6.9	1.7	0.0
<i>Phleum pratense</i>	0.0	14.3	0.0	57.1	28.6	0.0	0.0	0.0	0.0	0.0
<i>Poa compressa</i>	5.0	10.0	10.0	5.0	2.5	40.0	2.5	7.5	7.5	0.0
<i>Agropyron repens</i>	20.0	0.0	0.0	20.0	0.0	20.0	0.0	40.0	0.0	0.0
<i>Trifolium repens</i>	0.0	3.9	9.0	1.3	2.6	5.1	1.3	69.2	1.3	1.3
<i>Taraxacum officinale</i>	14.3	4.8	0.0	4.8	9.5	19.0	0.0	4.8	42.9	0.0
<i>Ranunculus acris</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0

Transition probability of row species being replaced by a column species, on and around dung in the 1939 pasture for the period from August 1983 to April 1984.

	<i>Dactylis</i>	<i>Holcus</i>	<i>Lolium</i>	<i>Phleum</i>	<i>Poa</i>	<i>Agropyron</i>	<i>Trifolium</i>	<i>Taraxacum</i>	<i>Ranunculus</i>	Dung
	<i>glomerata</i>	<i>lanatus</i>	<i>perenne</i>	<i>pratense</i>	<i>compressa</i>	<i>repens</i>	<i>repens</i>	<i>officinale</i>	<i>acris</i>	
<i>Dactylis glomerata</i>	35.0	0.0	15.0	0.0	25.0	0.0	10.0	5.0	10.0	0.0
<i>Holcus lanatus</i>	2.1	12.8	14.9	2.1	36.2	0.0	21.3	6.4	4.3	0.0
<i>Lolium perenne</i>	1.7	0.8	40.9	0.0	34.6	0.4	10.1	8.4	1.3	0.0
<i>Phleum pratense</i>	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Poa compressa</i>	2.0	1.0	30.6	0.0	35.7	2.0	14.3	4.1	4.1	0.0
<i>Agropyron repens</i>	0.0	0.0	35.3	0.0	29.4	11.8	5.9	11.8	5.9	0.0
<i>Trifolium repens</i>	1.4	0.0	23.2	0.0	33.3	1.4	30.4	4.3	2.9	0.0
<i>Taraxacum officinale</i>	0.0	0.0	22.2	0.0	25.9	0.0	3.7	44.4	0.0	0.0
<i>Ranunculus acris</i>	16.7	0.0	50.0	0.0	33.3	0.0	0.0	0.0	0.0	0.0
Dung	0.7	0.0	26.9	0.0	34.3	3.0	17.2	6.7	1.5	8.2

Transition probability of row species being replaced by a column species, on and around dung in the 1958 pasture for the period from September 1983 to April 1984.

	<i>Dactylis</i>	<i>Holcus</i>	<i>Lolium</i>	<i>Phleum</i>	<i>Poa</i>	<i>Agropyron</i>	<i>Trifolium</i>	<i>Taraxacum</i>	<i>Ranunculus</i>	Dung
	<i>glomerata</i>	<i>lanatus</i>	<i>perenne</i>	<i>pratense</i>	<i>compressa</i>	<i>repens</i>	<i>repens</i>	<i>officinale</i>	<i>acris</i>	
<i>Dactylis glomerata</i>	75.8	0.0	1.6	0.0	12.9	1.6	3.2	1.6	0.0	0.0
<i>Holcus lanatus</i>	1.4	32.9	1.4	1.4	43.8	4.1	8.2	1.4	0.0	0.0
<i>Lolium perenne</i>	4.9	2.4	41.5	2.4	34.1	7.3	4.9	0.0	0.0	0.0
<i>Phleum pratense</i>	0.0	0.0	0.0	88.9	0.0	0.0	11.1	0.0	0.0	0.0
<i>Poa compressa</i>	3.1	0.0	5.4	4.7	68.2	10.1	3.1	2.3	0.0	0.0
<i>Agropyron repens</i>	5.9	2.9	5.9	8.8	14.7	52.9	0.0	0.0	0.0	0.0
<i>Trifolium repens</i>	0.0	0.0	5.3	0.0	21.1	5.3	63.2	0.0	0.0	0.0
<i>Taraxacum officinale</i>	0.0	0.0	9.1	0.0	0.0	0.0	9.1	81.8	0.0	0.0
<i>Ranunculus acris</i>	0.0	0.0	0.0	0.0	0.0	0.0	20.0	0.0	60.0	0.0
Dung	8.3	2.8	2.8	2.1	26.2	11.7	4.1	6.2	1.4	32.4

Transition probability of row species being replaced by a column species, on and around dung in the 1977 pasture for the period from September 1984 to April 1985.

	<i>Dactylis</i>	<i>Holcus</i>	<i>Lolium</i>	<i>Phleum</i>	<i>Poa</i>	<i>Agropyron</i>	<i>Trifolium</i>	<i>Taraxacum</i>	<i>Ranunculus</i>	Dung
	<i>glomerata</i>	<i>lanatus</i>	<i>perenne</i>	<i>pratense</i>	<i>compressa</i>	<i>repens</i>	<i>repens</i>	<i>officinale</i>	<i>acris</i>	
<i>Dactylis glomerata</i>	75.6	0.0	4.4	2.2	4.4	2.2	6.7	2.2	0.0	2.2
<i>Holcus lanatus</i>	7.5	73.1	1.5	1.5	3.0	1.5	10.2	0.0	0.0	0.0
<i>Lolium perenne</i>	3.1	12.5	53.1	0.0	6.3	0.0	21.9	3.1	0.0	0.0
<i>Phleum pratense</i>	16.7	0.0	0.0	50.0	0.0	0.0	16.7	0.0	0.0	0.0
<i>Poa compressa</i>	1.9	5.6	13.0	0.0	42.6	0.0	20.4	3.7	0.0	1.9
<i>Agropyron repens</i>	0.0	0.0	22.2	22.2	0.0	11.1	22.2	0.0	11.1	0.0
<i>Trifolium repens</i>	9.8	9.8	5.2	3.3	11.8	0.7	54.9	2.6	0.7	0.7
<i>Taraxacum officinale</i>	4.5	0.0	9.1	4.5	9.1	0.0	13.6	54.5	4.5	0.0
<i>Ranunculus acris</i>	0.0	0.0	0.0	0.0	0.0	0.0	33.3	16.7	50.0	0.0
Dung	8.2	5.4	16.3	6.1	11.6	4.1	32.7	5.4	1.4	3.4



Transition probability of row species being replaced by a column species, on and around dung in the 1939 pasture for the period from September 1983 to October 1983.

	<i>Dactylis</i> <i>glomerata</i>	<i>Holcus</i> <i>lanatus</i>	<i>Lolium</i> <i>perenne</i>	<i>Phleum</i> <i>pratense</i>	<i>Poa</i> <i>compressa</i>	<i>Agropyron</i> <i>repens</i>	<i>Trifolium</i> <i>repens</i>	<i>Taraxacum</i> <i>officinale</i>	<i>Ranunculus</i> <i>acris</i>	Dung
<i>Dactylis glomerata</i>	97.9	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Holcus lanatus</i>	0.0	87.2	2.6	0.0	5.1	0.0	2.6	0.0	0.0	2.6
<i>Lolium perenne</i>	0.0	0.7	90.1	0.0	4.6	0.7	2.0	0.0	0.7	0.7
<i>Phleum pratense</i>	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Poa compressa</i>	0.0	1.7	5.0	0.8	85.1	2.5	1.7	0.0	0.8	0.8
<i>Agropyron repens</i>	0.0	15.4	15.4	0.0	0.0	69.2	0.0	0.0	0.0	0.0
<i>Trifolium repens</i>	0.0	0.0	1.9	0.0	1.4	0.0	94.3	0.0	1.0	0.0
<i>Taraxacum officinale</i>	3.0	0.0	0.0	0.0	0.0	0.0	3.0	90.9	0.0	0.0
<i>Ranunculus acris</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0
Dung	0.7	0.0	10.9	0.4	10.9	2.5	7.6	2.9	1.4	60.5

Transition probability of row species being replaced by a column species, on and around molehills in the 1939 pasture for the period from September 1983 to October 1983.

	Molehill	<i>Dactylis</i> <i>glomerata</i>	<i>Holcus</i> <i>lanatus</i>	<i>Lolium</i> <i>perenne</i>	<i>Phleum</i> <i>pratense</i>	<i>Poa</i> <i>compressa</i>	<i>Agropyron</i> <i>repens</i>	<i>Trifolium</i> <i>repens</i>	<i>Taraxacum</i> <i>officinale</i>	<i>Ranunculus</i> <i>acris</i>
Molehill	75.6	0.7	0.0	5.3	0.0	8.1	0.4	5.3	1.8	0.0
<i>Dactylis glomerata</i>	5.0	95.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Holcus lanatus</i>	4.3	2.1	70.2	10.6	0.0	6.4	0.0	2.1	0.0	0.0
<i>Lolium perenne</i>	10.5	0.0	0.6	79.5	0.6	4.1	0.6	2.9	1.2	0.0
<i>Phleum pratense</i>	10.0	0.0	0.0	0.0	60.0	20.0	0.0	0.0	0.0	0.0
<i>Poa compressa</i>	8.3	0.0	0.0	3.6	0.0	76.2	4.8	4.8	0.0	0.0
<i>Agropyron repens</i>	0.0	10.0	0.0	0.0	0.0	0.0	70.0	1.0	0.0	0.0
<i>Trifolium repens</i>	9.3	0.4	0.4	2.0	0.0	2.4	0.4	84.2	0.0	0.4
<i>Taraxacum officinale</i>	6.9	0.0	0.0	3.4	0.0	6.9	0.0	3.4	79.3	0.0
<i>Ranunculus acris</i>	14.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	85.7