

ABSTRACT

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ABSTRACT

Mounds built in pastures by the subterranean ant Lasius flavus often have a vegetation which differs markedly from their surroundings. I set out to compare the relative abundances of plant species on and off ant-hills in some grasslands in southern Britain, and to define those characteristics of species which mainly determine their success or failure on the mounds.

Large ant-hills and the surrounding grassland were sampled in detail at five acid grassland sites in the Gower peninsula, Glamorgan, and thirteen chalk grassland and chalk heath sites in southern Britain. Mounds were often dominated by perennials which could grow up through heaped soil, like Polytrichum piliferum P. juniperinum on the Gower and Thymus drucei and Helianthemum chamaecistus on the chalk. Annuals such as Aira praecox and Arenaria serpyllifolia were frequently confined to ant-hills. However, many species, especially rosette or semi-rosette hemicryptophytes, were consistently uncommon on ant-hills, including Luzula campestris, Cirsium acaule, Poterium sanguisorba and Filipendula vulgaris. The pleurocarpous mosses Pleurozium schreberi and Pseudo-scleropodium purum were more abundant on north-facing than south-facing aspects of the mounds.

Two main factors influenced plant patterns. Firstly, the heaping of soil over the plants by the ants often caused considerable seedling mortality. Secondly, species differed in their ability to disperse 'seed' onto the mounds. When I compared the viable 'seed' 'banks' present in equal weights and surface areas of ant-hill and pasture soils, by keeping the samples moist and counting the emergent seedlings, the 'seeds' of those species uncommon on ant-hills were much less frequent in ant-hill than pasture soil. Most seedlings on the mounds probably

result from 'seed' dispersal onto the mound surfaces.

Soil analyses show no large and consistent differences in nutrient concentrations between ant-hill and pasture soils and thus it seems unlikely that nutrient levels greatly influence the striking distributions of many species.

The vegetation on and off two hundred and six mounds of a wide range of size and activity was recorded in detail on a 1.2ha plot at Aston Rowant N.N.R., Oxon. Mapping showed that species rarely occurred on ant-hills when they were absent from the sward nearby. From scatter diagrams of the abundance of each species in relation to ant-hill volume and ant activity on a mound, it was possible to deduce how succession of some species on ant-hills might occur, if ant-hill volume were proportional to ant-hill age. The following hypothesis is consistent with the evidence.

'Young' mounds are heaps of soil which smother existing vegetation. They are invaded in particular by Festuca rubra, Lotus corniculatus, Carex flacca, Leontodon hispidus and Helianthemum chamaecistus (if in the sward nearby). Thymus drucei invades the mounds vegetatively as they expand in basal area, and gradually becomes a more important component of the vegetation. Carex flacca and Hieracium pilosella rosettes become restricted to the edges of ant-hills because the continual heaping of soil onto the tops of the mounds causes their burial and death there. However, Leontodon hispidus and Plantago lanceolata, often present inside the margins of medium and large mounds, set abundant seed there and their seedlings sometimes become established on the bare soil on top.

By this time, the summits of ant-hills tend to be occupied by Helianthemum chamaecistus and Thymus drucei, which can grow up through the heaped soil.

Small mounds are often deserted by the ant colony. Their vegetation

becomes closed and the relative abundances of species approach those of the surrounding sward more closely than on active ant-hills of the same volume. In the absence of burial, Carex flacca, Leontodon hispidus, Plantago lanceolata and Hieracium pilosella become established over the whole surface; H. pilosella rosettes are far more dense on abandoned mounds than active ones of the same size. When mounds are abandoned the chambers and channels disappear, organic matter accumulates, an A_0 horizon is formed and the previously structureless soil becomes aggregated into peds.

The life cycles of the species with the most marked patterns in relation to ant-hills were studied more fully in field and laboratory experiments. The species characteristic of ant-hills usually have either vigorous vegetative growth when smothered, the ability to flower on the mounds in the year after germination or both. For instance, established plants of Helianthemum chamaecistus and Thymus drucei, woody chamaephytes which often dominate ant-hills, can grow up through 3-4cm of suddenly-heaped soil. Yet they rarely establish themselves from seed on the mounds. In Arenaria serpyllifolia, Veronica arvensis and other winter annuals, the flowers are predominantly self-pollinated, seed-set is high, the seeds are light (60 - 270 ug) and inhibited from germinating under only 5mm of soil, a high proportion (40 %) of those released onto the mounds germinate each year, and the seedlings rapidly decline in number. For instance, a cohort of 2078 seedlings of Arenaria serpyllifolia followed from August 1971 to July 1972 had a half-life of 0.14 years, the seedlings dying from rabbit-scraping, soil heaping, self-thinning, fungal infection, rainwash and so on. Nevertheless, almost every surviving seedling flowered in the late spring of the first year. The minute seed weights of these species are insufficient to allow them to become established in closed vegetation. Their seeds may be inhibited from germinating under swards by the higher ratio of far red to red light there; Arenaria serpyllifolia, Veronica arvensis and Myosotis

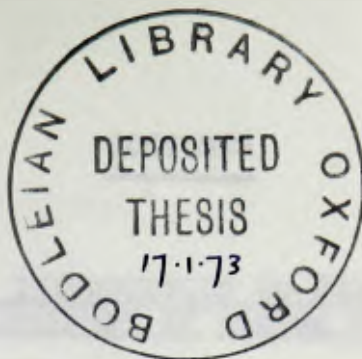
ramosissima seeds did not germinate under two layers of Tilia leaves in a laboratory experiment. Cerastium holosteoides resembles Thymus and Helianthemum in being a perennial chamaephyte able to grow up through newly-heaped soil to some extent, and resembles the winter annuals in flowering the year after germination and producing abundant small (180 ug) seeds which hardly germinate under two layers of Tilia leaves.

The species with roughly equal abundances on and off ant-hills are frequently stoloniferous and able to grow up through heaped soil to some degree (e.g. Agrostis stolonifera, Festuca rubra, Campanula rotundifolia, Galium verum) or short-lived and able to flower on the mounds (e.g. Euphrasia officinalis agg., Gentianella amarella, Linum catharticum and Medicago lupulina).

All the species which are considerably more abundant in the sward than on the mounds are perennials, with very slow vegetative reproduction. Thus they depend on invasion by seed to become established on ant-hills. Only a small proportion of the rosettes in the sward flower each year, the flowers are cross-pollinated, the fruits are comparatively heavy (600 - 4000 ug), the seedlings are susceptible to burial, their development on the mounds is slow and they do not flower within the first two years. Their seedlings are robust enough to establish themselves in swards. Nevertheless, within this framework, the factors affecting their abundances on the mounds differ from species to species. For instance, in Cirsium acule the number of fruits produced is reduced to 10-14 per capitulum per year by the weather, predation and parasitism. Their dispersal is hindered by the high frequency of pappi lost before dispersal, the heavy achenes and the weather. The production of vigorous seedlings on the mounds may be affected by fungal parasitism, and their survival is probably poor because they are susceptible to burial. Seedling development is slow on ant-hills and no flowering plants were seen there. In Leontodon hispidus, however, dispersal of achenes onto the mounds is efficient, and 5-9 of achenes germinate on ant-hills, so that seedlings are frequent on

the mounds in autumn. Seedlings develop slowly, remain small, and are susceptible to burial, but mature rosettes inside the perimeter of active ant-hills often flower profusely and reproduce vegetatively. Thus Leontodon maintains larger populations on ant-hills than Poterium sanguisorba and Cirsium acaule. On the other hand, Carex flacca maintains high densities of rosettes around the edges of 'active' ant-hills because of vigorous vegetative reproduction; reproduction from seed is negligible. Poterium sanguisorba and Plantago lanceolata were also investigated.

Thus the ant-hill environment acts as a sieve, letting through those species which can flower early on or grow up through heaped soil, and excluding those which cannot flower on the mounds, with poor dispersal and slow seedling development. The flora of 'active' ant-hills is maintained at a lower stage of succession than the surrounding vegetation by the constant addition of soil to the surface. The vegetation resembles that of fixed calcareous dunes and of Breckland grass-heath before myxomatosis, two communities in which sand movements also provide an element of environmental 'unpredictability'. Those species which invest a high proportion of their total net assimilation in reproduction are pre-adapted to colonise and maintain themselves on ant-hills. Those species selected for efficiency in maintaining themselves in a closed community, with heavy fruits and an inability to flower early in life, cannot maintain themselves at a high density in a community of an earlier successional stage.



THE PLANT ECOLOGY

OF

ANT-HILLS IN GRASSLAND

A thesis submitted for the
Degree of Doctor of Philosophy
in the University of Oxford

by

T.J. KING, B.A.

September,
1972

Pembroke College,
Oxford.

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Appendix references.

PREFACE

(i) In describing ant-hills, I have made many apparently unsubstantiated statements of fact. All these are backed up by field notes, but to give details would have interrupted the flow of the text and made it impossibly long. Data not included in the thesis are available on application.

(ii) Sources for the nomenclature of plants are as follows:

Angiosperms & Pteridophytes ; Clapham et al. (1962), modified by Dandy (1969).

Mosses ; Warburg (1963).

Liverworts ; Paton (1965).

Lichens ; James (1965).

(iii) Most of the statistical procedures used in the thesis are described in Sokal & Rohlf (1969).

ACKNOWLEDGEMENTS

I am most grateful to my long-suffering wife, Heather, for her support and encouragement throughout the work described here.

I should also like to thank the following:

Dr. S.H.J. Woodell, my supervisor, for first stimulating my interest in ecology and ant-hills, and for help and guidance over the last seven years in ways too numerous to mention. The Regional Staff

of the Nature Conservancy, for their consistently helpful attitude.

Richard Jennings and Alasdair Barclay, successively wardens of Aston Rowant N.N.R., for their practical help and friendly interest.

Mr. Ken Hicks, for constructing the topograph and helping in numerous other ways. Mr. Peter Turner, for photographic help.

Dr. M.G. Bulmer, Dr. H.C. Dawkins, Dr. P. Grubb, P.T.J. Hawes, Dr. M.G. Morris, A.R. Perry, F.B. Thompson and Dr. E.M. Wedsworth for helpful discussions. G.D. Darlington, F.R.S., and F.R. Whatley, successively

Professors of Botany, for providing research facilities in the Oxford Botany School. The Natural Environment Research Council (Research

Studentship) and the Nuffield Foundation (Biological Scholarship) for financial support. My father, for transporting bulky equipment,

and financial help. Mrs. F.J. Templeton for typing the text,

Mrs. Jan Bolongaro for typing the appendices, Mrs. Anne-Marie Gray for typing the large table, Mr. Brian Purvis for drawing some of the diagrams and Mr. B. Archer for photographing and printing them.

CHAPTER 1

GENERAL INTRODUCTION TO THE VEGETATION AND ENVIRONMENTOF *Lasius flavus* MOUNDS.1.1. INTRODUCTION

Ant-hills built by *Lasius flavus* F. (Hymenoptera, Formicidae) are frequent in British pastures (Collingwood 1957), but the distinct differences in plant species composition and abundance between the mounds and the grassland surrounding them have never been satisfactorily described or explained. I therefore set out to quantify the relative abundances of species on and off ant-hills in some grasslands in southern Britain, and to identify the main factors which influence the population sizes on the mounds of species with consistent patterns in relation to ant-hills.

In this chapter, I use data from the scattered literature and my own work to describe the mounds, their vegetation, and the environmental differences between the ant-hills and the pasture which might affect plant growth and distribution. At the end, I briefly discuss the relationships between vegetation and environment on mole-hills.

1.2. MOUNDS, ANTS AND VEGETATION

Each mound begins as a heap of bare soil which smothers short vegetation or covers the stem-bases of grasses in tall vegetation. These 'incipient' mounds ultimately give rise to the 'mature' ant-hills which frequently occur in old pastures in regularly-distributed groups (Fig. 1).



Fig.1. A group of 'mature' ant-hills on the S.W. side of my plot at Beacon Hill, Aston Rowant N.N.R., Oxon., May 1969.



Fig.2. Ant-hill on my plot with the following typical features: abundant Helianthemum chamaecistus and Thymus drucei (some of which has the gall caused by Eriophyes thomasi); Rabbit droppings on the summit; patches of soil heaped up by the ants; rosette species (e.g. Plantago lanceolata, Leontodon hispidus) present at the base but less frequent on top; short vegetation. 13 August 1971.

Every mound is (or was) the breeding centre of a L. flavus colony containing up to 24,500 workers (Pickles 1940b, Odum & Pontin 1961, Waloff & Blackith 1962) which has a subterranean territory extending up to 1.5 m or so from the centre of the ant-hill. The workers forage underground (Pontin 1955, 1957 etc.), living mainly on the excretions of root-living aphids and by eating aphids and coccids (Pontin 1958, 1961a), many of which may be obligate myrmecophiles (e.g. Nixon 1951, Pontin 1960a). The ants only appear above ground during the nuptial flight and when soil is being heaped onto the surface. Soil-heaping usually occurs at night, after rain (Pickles 1936, Pontin 1955), in summer. In southern England, L. flavus individuals are torpid from about early November to early March, when little soil-heaping occurs. The rate at which soil brought up from below is added to the mound surface varies from mound to mound and from place to place. Because newly-heaped soil is only colonised slowly, the plant cover on 'hills occupied by L. flavus colonies is usually discontinuous. Other frequent features of 'active' ant-hills, (Fig. 2), are rabbit scrapes and dunging patches, vegetation which is shorter than that surrounding the mounds, and a greater percentage cover of Thymus drucei than in the sward, at least in calcareous grassland.

Grubb et al. (1969) list three 'notable floristic features' of ant-hill vegetation on 'chalk heath' at Lullington Heath N.N.R., Sussex:

- (1) The relative abundance of annuals (e.g. Euphrasia officinalis agg.) and short-lived perennials (e.g. Medicago lupulina) where the rate of smothering is not too great.

(ii) The relative rarity of long-lived rosette-type perennial dicotyledons (e.g. Filipendula vulgaris), and tussock-type grasses.

(iii) The abundance of long-lived perennials of relatively low stature able to grow through the smothering soil, e.g. Thymus drucei, T. pulegioides, Helianthemum chamaecistus, Asperula cynanchica, Galium verum, G. mollugo, Veronica officinalis, Agrostis stolonifera, Festuca rubra, Holcus lanatus. These impressions are confirmed in subsequent chapters by my quantitative data.

Other accounts of the vegetation on L. flavus mounds are in Pfeiffer (1933), Haarlov (1960), Waloff & Blackith (1962), Thomas (1962), Jennings (1965), Lambley (1967), Aitcheson et al. (1967), Voronov (1968), and Griffiths (1968), but their sampling techniques are usually too imprecise and their sample sizes too small to yield worthwhile results. The differences in species abundances between the ant-hills and the surrounding vegetation which I regard as quantitatively proven are given in Table 1. These data confirm the impressions of Grubb et al. (1969) which were listed earlier.

Voronov (1968), working in Russia, marked ant-hills derived from the invasion of mole-hills in 1947 and followed plant succession on them. The freshly-dug mole-hills remained almost bare in the first year. They were invaded by Marchantia polymorpha and Brachythecium salebrosum, then by Urtica urens, Stellaria holostea and other herbs, and finally by Festuca rubra and other grasses. The process may take decades.

Vegetation sometimes differs on the north and south sides of mounds. On the Hermitage Plain, Jaegersborg Park, Denmark,

Table 1. Quantitative evidence of differences in plant species abundance between ant-hills and the surrounding sward

Jennings (1965). Aston Rowant N.N.R., Oxon. 35 transects laid, each across the summit of an ant-hill but including the surrounding pasture. Species presence recorded in successive 15 cm lengths of transect (377 AH, 280 SV).

More frequent on ant-hills: Thymus drucei** Myosotis ramosissima*

More frequent in pasture: Achillea millefolium**
Fragaria vesca**
Leontodon hispidus**
Plantago lanceolata**
Crepis capillaris**
Dactylis glomerata*
Cirsium acaule**
Hieracium pilosella**
Lotus corniculatus**
Viola hirta**
Carex flacca**

Dominant species recorded in successive 15 cm lengths of transect:

More dominant on ant-hills: Thymus drucei**
Helianthemum chamaecistus*

Lambley (1967). Amberley, Arundel, Sussex (TQ 014102). 30 ant-hills and 30 pasture quadrats samples and presence recorded.

More frequent in pasture: Carex flacca**
Poterium sanguisorba**

Griffiths (1968). Downs above Willingdon, Sussex. Frequency of species on and off mounds using point quadrats.

More frequent on ant-hills: Thymus drucei**

(*, $0.05 > P > 0.01$; **, $P < 0.01$) 2×2 contingency tables were constructed and a χ^2 test or a two-tailed Fisher's exact test used, as appropriate.

the north sides of the ant-hills bore a closed turf of Festuca ovina, but the open, poorly-developed plant cover on the south sides was characterised by Cladonia spp., Ceratodon purpureus and a dwarf, non-flowering form of Achillea millefolium (Haarlov 1960). Festuca species often grow more luxuriantly on north-facing than on south-facing aspects of L. flavus mounds in British grasslands (see chapter 3). Thomas (1962) mentions that pleurocarpous mosses like Pseudoscleropodium purum may be more abundant on north than south sides of ant-hills in chalk grassland.

Colonies of L. flavus may die out for no apparent reason, but are often killed when their mounds are invaded by other ant species, e.g. Myrmica rubra or M. scabrinodis at Silwood Park, Ascot, Berks. (Waloff & Blackith 1962). Newly-formed L. flavus colonies are likely to be exterminated by existing ones (Pontin 1963). Grubb et al. (1969) compared the frequencies of plant species on mounds abandoned by the ants, and those still occupied, at Lullington Heath N.E.R., Sussex. I applied two-tailed Fisher's exact tests to their data. In 'tall chalk heath', Agrostis stolonifera, Erica cinerea, and Asperula cynanchica were significantly ($P < 0.05$) more frequent on deserted than active mounds, but Thymus drucei 'preferred' occupied ones. In short 'secondary grassland', Hieracium pilosella, Medicago lupulina and Plantago lanceolata were significantly ($P < 0.05$) more frequent on active than unoccupied mounds.

After myxomatosis in 1953-4/^{had} virtually eradicated the rabbit population, many Lasius flavus colonies were killed by the encroaching scrub (Potts 1970), or tall grasses like Brachypodium pinnatum (Pontin 1963). The dense shading of the soil surface

also prevents the foundation of new colonies (Pontin 1955, 1960b). However, the mounds are slow to disappear; Grubb et al. (1969) state that old mounds can still be seen at Madingley Wood, Cambs., sixty-five years after woodland invasion.

The data mentioned in this section indicate that some species may have distinct patterns in relation to L. flavus ant-hills. These patterns might be affected by the size and age of a mound, aspect, and the level of ant activity. It may be possible to explain some of these patterns in terms of some of the environmental factors discussed in the next section.

1.3. COMPARISON BETWEEN ANT-HILL AND PASTURE ENVIRONMENTS

1.3.1. General

I explain here why, in subsequent chapters, certain environmental factors are ignored whilst the influence of others on the vegetation is described in detail. I discuss in turn the effects of the ants on the soil, their direct influences on vegetation, the impact of other organisms on both soil and vegetation, and the microclimates of the mounds.

1.3.2. The effects of L. flavus on the soil

The workers take soil particles or aggregates to the surface in their mandibles, or sometimes pull up aggregates with their legs. Hearlov (1960) investigated the sizes of the soil particles heaped up by the ants by placing equal numbers of workers in five connected chambers, each containing soil sieved to a different particle size. The ants did not channel in sections with particles 3-0.75 mm and preferred the smaller dimensions without discrimination. The maximum span of the mandibles of L. flavus workers is 0.65 mm. Particles 1.2-0.75 mm

(up to 0.17 g) were only moved one at a time, those 0.75-0.385 mm one or two at a time, and those 0.385-0.1 mm several at a time. Haarlov suggested that the particles in an aggregate were held together by moisture rather than by salivary secretions of the ants, because they were water-unstable.

The heaping of soil particles onto the surface can occur at a considerable rate. Waloff & Blackith (1962) followed the growth of eighteen mounds at Silwood Park, Ascot, Berks. for seven years and estimated by an overall regression that they increased in height by 2.28 cm per year and in maximum diameter by 7.03 cm a year. The yearly increments in volume of the seven ant-hills which were occupied the longest are given in Table 2.

Table 2. Yearly increments in volume of seven of the ant-hills whose heights and diameters were measured by Waloff & Blackith (1962) over seven years

Volumes were calculated from their data using the formula given in Appendix 3.

Yearly increments (cm³)

<u>Ant-hill number</u>	1953-54	1954-55	1955-56	1956-57	1957-58
1	3037	4350	2565	6907	222
2	502	7858	970	7516	772
3	2345	985	1583	-1647	1263
4	772	765	-66	1253	0
6	3510	3163	8700	-1221	3725
9	2715	9193	141	259	362
10	948	1651	179	1279	20241
continued	1958-59	1959-60			
1	-1227	7268			
2	-388	7449			
3	63	1851			
4	721	-1468			
6	0	4949			
9	Abandoned				
10	22531	5986			

Some mounds grew much faster than others, and all grew at a rate which fluctuated appreciably from year to year. I measured the volumes of newly-heaped soil on the same twenty ant-hills at Aston Rowant N.N.R., Oxon in two successive years (Appendix 25), and found that whilst some mounds did not increase in size, others had up to $1,600 \text{ cm}^3$ of soil added to the surface per 'year' (by 17 August). However, I obtained a correlation coefficient of $r = 0.71$ ($P < 0.001$ from zero) between the volumes of soil heaped onto the same mound in both years.

Thus ant-hills of the same age may differ markedly in size, and vice versa. Nevertheless the mean age of the large mounds in a population probably exceeds that of the small mounds. Haarlov (1960) calculated that if the ants heaped up 10 gm of soil per working day and worked a 150-day year, a conical mound 30 cm high and a metre in diameter would have taken 80-90 years to build. Yet in Waloff & Blackith's (1962) study, mound no.10 increased in volume by $22,531 \text{ cm}^3$ between October 1958 and September 1959; at this rate, a mound of Haarlov's size could be anything ~~from~~ ^{over} four ~~to infinity~~ years old.

Plants growing on the ant-hills or next to them are often covered by soil heaped onto the surface (Fig. 3) and may die if

Fig. 3. Burial of the bases of rosettes of Carex flacca and Leontodon hispidus by newly-heaped soil on a mound at Aston Rowant N.N.R., Oxon., 2 September 1971.



they cannot grow up through it. The probable importance of soil heaped up by the ants in eliminating seedlings is only obvious when the same mound is examined closely over several months. Active mounds may have a vegetation cover of 5-20% in summer, but when newly-heaped soil is removed, vegetation with a cover of 80% or more may be found underneath. By autumn, most bare soil has been re-invaded by the species which can grow up through heaped soil. At the small proportion of sites where ants build mainly on the south sides of the mounds, there may be aspect patterns in the plant species (Chapter 3). Burial may also impose dormancy on seeds (Chapter 5).

The soil aggregates heaped onto the surface of an active ant-hill may have the same mechanical composition as pasture soil (Haarlov 1960, Voronov 1968, Griffiths 1968) but their structure is markedly different. The peds in newly-heaped ant-hill soil are much smaller than those under pasture vegetation; the aggregates are exposed to the elements (e.g. to comminution by raindrops) and low in organic matter, forming an immature, structureless soil which crusts easily when dry and often seems water-repellent.

The ratio of space to solid in soil profiles is greater in 'active' ant-hills than in soil under the surrounding vegetation, because of the greater density there of chambers and channels excavated by the ants. By displacing air from soil samples, Griffiths (1968) estimated that the pore-space was 12% higher in ant-hill than pasture soils. The bulk density of ant-hill soil from my plot at Beacon Hill, Oxon, was 0.8 times that of surrounding vegetation soil (Table 3).

Table 3. Comparison of bulk densities of ant-hill and surrounding soils (16 August 1970)

Method. Two ant-hills were chosen at random from those with each of eight 100 m² sampling plots arranged randomly over my Beacon Hill plot at Aston Rowant N.N.R. 16 pairs of soil samples were collected, one of each pair from the top of an ant-hill, and the other from the pasture soil 30 cm away from the mound. A heavy steel soil corer was used; samples were taken from about the top 5 cm of soil, but the precise depth of the hole made by the corer was measured after it had been withdrawn. The mean diameter of 16 cores was used in the calculation of the volume of each core. The samples were dried for 48 hours at 105°C at the laboratory and weighed.

Sources of error. Occasionally the ant-hill soils did not cohere well. Deep roots, e.g. those of *Helianthemum*, often caused trouble. In the surrounding soil samples, deep roots and stones often caused difficulty.

Mean Bulk density (g/cm ³)	Ant-hills	Pasture
	0.45±0.010	0.56±0.024

$t = 4.118$, $P < 0.001$ by the 'method of paired comparisons'.
[15]

Measurements of the water content of soil samples taken from the northern and southern sides of the same five mounds and the pasture nearby are given in Table 4. The analysis of variance shows that over all dates the water content is significantly lower in mound soils than surrounding soils,¹ and on southerly than northerly aspects of ant-hills. Crusted soils have even lower moisture levels (Table 5). The difference in water content between mound and pasture soils would be even greater if expressed on a unit volume, rather than a unit dry weight, basis. However, I have not yet compared the curves of water potential against soil water content for ant-hill and

¹Voronov (1968) showed (his Table 6) that the water content of ant-hill soil at several sites was 0.5-0.33 (at least) that of pasture soil. Pickles (1936) states that the superstructure of the mound is drier than the surrounding soil, Griffiths (1968) claimed that ant-hill soils were 'generally drier' and Grubb et al. (1969) state that 'drought is more intense'; these authors give no evidence.

Table 4. Comparison of water contents of ant-hill and surrounding soils.

Method One ant-hill was chosen at random from those within each of five 100m² sampling plots arranged randomly over my Beacon Hill plot at Aston Rowant N.N.R., Oxon. Selection was restricted to large mounds. The same five mounds were sampled on each occasion.

One sample was collected from the south side (S) of each ant-hill, another from the north side (N) and a third from the pasture soil (P) 30cm away from the mound in a random direction. The top 5cm of soil only was collected. Organic debris and stones were picked out of the samples in the field. The samples were taken to the laboratory in sealed containers, weighed in situ, dried for 48 hours at 105°C and reweighed.

Results		% water contents (by dry weight)			
S1	25.1	32.2	29.8	62.8	18.0
N1	31.4	38.0	48.7	72.9	45.1
P1	43.4	54.3	53.5	74.5	45.9
S2	26.2	43.0	36.7	68.0	28.0
N2	37.1	53.5	50.0	71.3	44.5
P2	50.9	47.8	67.7	75.4	47.7
S3	28.9	38.0	27.0	68.7	26.4
N3	31.2	39.0	42.4	70.6	35.4
P3	52.5	52.7	63.2	69.0	40.8
S4	24.9	42.3	28.4	72.7	30.8
N4	35.0	43.6	33.8	74.4	29.9
P4	47.3	55.8	53.6	82.6	48.1
S5	37.7	48.5	45.3	66.5	47.6
N5	38.2	51.3	47.2	87.7	59.6
P5	47.7	47.9	46.8	75.1	44.9

Analysis of variance on untransformed data.

Source	d.f	M.S.	Fs	The following aspect differences were significant ($P < 0.05$) by Gabriel's (1964) sum of squares simultaneous test procedure: N/S** N/P** N&S/P*** S/P***. (., $P < 0.05$; .., $0.01 > P > 0.001$, ..., $P < 0.001$) >0.01
Aspect(A)	2	1487.28	13.98**	
Date(B)	4	3127.09	89.01***	
Ant-Hills(C)	4	163.50		
A x B	8	84.15	4.09*	
A x C	8	106.35		
B x C	16	35.13		
A x B x C	32	20.57		
	74			

Table 5. % water contents (by dry weight) of crusted soils collected from 3 ant-hills on my plot on 14 September 1971, after a 10-day drought.

Depth	AH1	AH2	AH3
0-1cm	17.2	16.3	16.0
1-2cm	23.3	27.4	24.1
2-5cm	40.4	32.4	30.1

pasture soils. The greater susceptibility to drought of ant-hill soils may partly be due to the large exposure to solar radiation and wind of bare soil and soil covered by short vegetation, the large surface area of ant-hills in relation to their volume and the low organic matter content of the soils of 'active' mounds.

Droughts on ant-hills in summer and autumn may contribute towards seedling deaths (e.g. in Arenaria serpyllifolia, Chapter 5), and lower the 'microsite density' for seed germination. Some circumstantial evidence suggests that low water availability may limit the growth of Festuca species on the mounds. In both 1969 and 1970 (Fig. 4) Festuca rubra died off on the tops of mounds at Aston Rowant N.N.R., Oxon., after long summer droughts, even in areas fenced against sheep and rabbits,

Fig. 4. Parched Festuca rubra on ant-hills on the north side of Beacon Hill, Aston Rowant N.N.R., Oxon. on 29 June 1970. There had been a complete drought from 12 May to 15 June.



and on ant-hills with no evidence of rabbit grazing, scratching or defaecation. I also noticed this phenomenon at Cefn Bryn, Gower, Glamorgan after a five-week drought (Appendix 6). Elton (1959) noted that after two rainless months at Wytham Woods, Berks., 'the grass growing on large L. flavus mounds is blasted brown with drought'. Festuca rubra on ant-hills tends to be more luxuriant on northerly than southerly aspects and around the edge than on top. It is shallow-rooted; the maximum root depth ranged from 5.7-11.6 cm and the depth of the main feeding roots from 2-10 cm in 11 samples from ant-hills at Aston Rowant (10 October 1971). Festuca rubra on the mounds is often much shorter than in the sward, both in short ungrazed vegetation, like the secondary grassland at Lullington Heath, and in plots which have been fenced against sheep and rabbits for five years at Aston Rowant N.N.R. Paired ant-hill and pasture samples of F. rubra were taken from Aston Rowant on 11 December 1969 and grown up for eight months on J.I. compost in a cold frame. In this time ant-hill Festuca increased in mean height from 4.62 to 37.16 cm; this increment in growth did not differ significantly ($P > 0.05$) from those recorded in the pasture samples and in pasture samples cut to 'ant-hill height'. Thus there is no genotypic difference in height between ant-hill and pasture Festuca rubra. Its growth on ant-hills is probably limited by water or nutrient availability, and the evidence below suggests that nutrients are much less likely than water to be limiting there.

The analyses of ant-hill and surrounding soils given in the literature are summarised in Table 6, together with my own

Table 6. Soil analyses of *L. flavus* mounds from the literature!

pH	Site	Mean in ant-hill soil	Mean in Pasture soil	Sig. of difference
Lambley(1967)	Amberley, Sussex.	7.73 $\pm$ 0.115(8)	7.51 $\pm$ 0.07(6)	N.S.
	Ifield Wood, Sussex.	5.32 $\pm$ 0.085(6)	4.88 $\pm$ 0.13(6)	*
Haarlov(1960)	Jaegersborg Park, 0-2cm	5.57(4)	5.45(2)	N.S.
	Copenhagen, Denmark.			
	3-5 cm	5.6(4)	5.0(2)	N.S.
	8-10 cm	5.62(4)	5.25(2)	N.S.
Griffiths(1968)	Willingdon, Sussex	7.88 $\pm$ 0.06(20)	7.47 $\pm$ 0.13(20)	**
Thomas(1962)	Aston Rowant N.N.R.	8.6(1)	7.1(1)	
	Kingley Vale N.N.R.			
	plateau	6.5(1)	7.9(1)	
	valley	8.6(1)	7.7(1)	
Czerwinski et al				
(1971)	Strzeleckie water meadows, Poland KCI	6.87(2)	6.35(1)	
		6.6(2)	5.9(1)	
Pickles(1940a)	Thornhill, Yorks	5.04(21)	4.36(21)	**
King	Rhossili Down, Glamorgan.	4.31(20)	4.19(16)	N.S.
	Aston Rowant N.N.R.	7.31(25)	7.26(25)	N.S.
Grubb et al(1969)	Lullington Heath NNR.	6.0-7.9(10)	4.5-6.4(47)	
		7.0-8.4(20)	5.0-6.9(25)	
Exchangeable H ⁺ (m eq./100g)				
King	Rhossili Down	4.2(20)	4.91(16)	N.S.
Exchangeable Ca ⁺⁺ (m eq./100g)				
Czerwinski et al(1971)		17.81(2)	12.17(1)	
Lambley(1967)	Amberley	30.64 $\pm$ 1.063(8)	30.48 $\pm$ 0.933(5)	N.S.
	Ifield Wood	2.7 $\pm$ 0.41(6)	1.62 $\pm$ 0.41(6)	***
Exchangeable Ca ⁺⁺ (p.p.m)				
Thomas(1962)	Aston Rowant	1310(1)	980(1)	
	Kingley Vale plateau	780(1)	790(1)	
	Kingley Vale valley	1680(1)	980(1)	
CaCO ₃ (%)				
Lambley(1967)	Amberley	65 $\pm$ 0.53(6)	66.3 $\pm$ 0.76(6)	N.S.
King		13.1(19)	14.25(19)	N.S.
Ca(total%)				
Thomas(1962)	Aston Rowant	1.34(1)	0.77(1)	
	Kingley Vale plateau	0.55(1)	0.79(1)	
	Kingley Vale valley	2.00(1)	1.15(1)	
Exchangeable Mg ⁺⁺ (m eq./100g)				
Czerwinski et al(1971)		1.34(2)	0.38(1)	
Exchangeable Mg ⁺⁺ (p.p.m)				
Thomas(1962)	Aston Rowant	28(1)	43(1)	
	Kingley Vale plateau	93(1)	73(1)	
	Kingley Vale valley	23(1)	35(1)	
Mg(total%)				
Thomas(1962)	Aston Rowant	0.40	0.36	
	Kingley Vale plateau	0.31(1)	0.27(1)	
	Kingley Vale valley	0.37(1)	0.32(1)	

1. Figures in brackets are sample sizes. N.S., $P > 0.05$; *, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$; ***, $P < 0.001$.

<u>Exchangeable K⁺ (m eq./100g)</u>		AM	SV	
Czerwinski et al (1971)		0.18(2)	0.07(1)	
Lambley (1967)	Amberley	2.28 [±] 0.250(5)	1.72 [±] 0.38(5)	
	Ifield Wood	4.99 [±] 0.53(6)	2.42 [±] 0.20	
<u>Exchangeable K⁺ (pp.m.)</u>				
Thomas (1962)	Aston Rowant	73(1)	24(1)	
	Kingley Vale plateau	80(1)	15(1)	
	Kingley Vale valley	33(1)	10(1)	
<u>Total K (%)</u>				
Thomas (1962)	Aston Rowant	0.72(1)	0.62(1)	
	Kingley Vale plateau	0.49(1)	0.42(1)	
	Kingley Vale valley	1.10(1)	1.00(1)	
<u>Total K₂O (mg/100g soil)</u>				
Czerwinski et al (1971)		5.3(1)	1.3(1)	
<u>Exchangeable Na⁺ (m equiv./100g)</u>				
Lambley (1967)	Amberley	3.51 [±] 0.126(5)	3.26 [±] 0.128(5)	N.S.
	Ifield Wood	3.18 [±] 0.226(6)	3.35 [±] 0.076(5)	N.S.
<u>Total exchangeable bases (m.eq./100g)</u>				
King	Rhossili Down	2.62(20)	2.32(16)	
Czerwinski et al (1971)		19.72(2)	12.82(1)	..
<u>Organic matter (%)</u>				
Czerwinski et al (1971)		8.58(2)	6.52(1)	
Thomas (1962)	Aston Rowant	19.7(1)	20.0(1)	
	Kingley Vale plateau	18.7(1)	22.6(1)	
	Kingley Vale valley	19.2(1)	22.8(1)	
Lambley (1967)	Amberley	4.18 [±] 0.458(6)	4.20 [±] 0.678(6)	N.S.
	Ifield Wood	1.98 [±] 0.515(6)	3.44 [±] 0.500	.

results from Aston Rowant N.N.R. and the north end of Rhossili Down, Gower, Glamorgan. My methods of sampling and analysis are described in Appendix 1. The pH, total exchangeable bases, exchangeable potassium and calcium, and extractable phosphorus all tend to be slightly higher in ant-hill than pasture soils, but total nitrogen is about the same and the percentage of organic matter tends to be lower in the mounds. However, since the bulk density of ant-hill soils is lower than pasture soils many of these nutrient concentrations might be relatively lower in ant-hill soil if expressed on a unit volume, rather than a unit dry weight, basis.

When the results of analyses of ant-hill soils are given in the literature the sampling depths, the ages of the mounds and their levels of ant activity are usually not recorded. Yet all these factors may influence the results. For instance, pH (Appendix 8) and organic carbon content (Haarlov 1960) may change with depth. Voronov (1968) found that the organic carbon content changed with the age of the mound, and Grubb et al. (1969) showed that in tall chalk heath at Lullington Heath, 'active' ant-hills had pHs of 6.0-7.9 (10 samples) whilst abandoned mounds had pHs of 4.5-7.4 (10). The differences in soil properties of mounds of different ages and 'building activities' are discussed further in Chapter 4.

I grew oats var Proctor in a cold frame, on ant-hill and pasture soil taken from my plot at Aston Rowant N.N.R.; growth was similar on both soils, and no nutrient deficiency symptoms appeared. Griffiths (1968) grew Thymus drucei, wheat and radishes on both soil types but germination and seedling growth

in each species was similar on mound and pasture soil. I doubt if nutrient concentrations influence the striking distributions of many species in relation to ant-hills since the analyses show no large and consistent differences in nutrient concentration between mound and pasture soil.

1.3.3. The direct effects of *L. flavus* on the vegetation

Pontin (1968, pers. comm.) thinks it unlikely that *L. flavus* workers selectively eliminate plant species by biting their roots. Like other Formicidae, *L. flavus* probably cannot break down cellulose. Nevertheless, the workers must encounter plant roots whilst channelling, they can gnaw through paper and polythene bags, and Pickles (1936) found some chewing a rhizome of *Pteridium aquilinum*. Unfortunately one cannot ascribe any root damage seen in *L. flavus* mounds to *L. flavus*, and if the species attacked plant roots under laboratory conditions this would not suggest that it did so in the field.

There are no reports of *L. flavus* carrying seeds or fruits. *L. flavus* forages underground and must encounter seeds less often than species which forage over the surface (e.g. *L. niger*). 'Seeds are very rarely found in the brood chambers of *L. flavus*' (Pontin 1968, pers. comm.). Seed carrying is unlikely to be seen if it occurs, but since workers can move soil particles up to 0.17 g in weight (Haarlov 1960), they could move the seeds or fruits of any grassland species. It is possible that some seeds are not distinguished from soil particles and are heaped onto the surface in the same way. Seeds placed on the surfaces of ant-hills or in nests developed under pieces of wood are apparently ignored. I have assumed in subsequent chapters that the only

seeds present in the soil of the mounds result from seed-dispersal onto the initially seed-sterile soil, and that ants do not selectively eat seeds of particular species.

L. flavus releases formic acid, especially when disturbed or attacked. However, formic acid is a normal constituent of soils as a breakdown product of humus (Stevenson 1964). On acid soil active mounds are rarely more acid than the soils surrounding them, and in calcareous soils the acid would be quickly neutralised. Short chain organic acids are rapidly broken down in soils by microbial activity; I doubt if formate has any selective toxicity effect on plant species.

1.3.4. The effects of other animals on ant-hill soil and vegetation

Here, after briefly mentioning the aphids, I discuss damage to ant-hills caused by mammals and birds, and the effects of rabbit dunging and rabbit and sheep grazing.

Aphids may reach high densities in grassland soils (Salt et al. 1948), but as they have their own parasites (Pontin 1959) and may make up a substantial proportion of the ants' diet, population explosions of aphids are probably rare. There is no evidence that aphids are more abundant on the roots of plants growing on ant-hills than on plants growing in the pasture, or that they can selectively eliminate plant species.

Seedlings (Chapter 5) and mature plants are often killed when the mounds are damaged by animals or birds. Rabbit scraping and burrowing is much more frequent on ant-hills than around them, but rabbits rarely demolish mounds completely. There is sometimes poaching by badgers (Griffiths 1968), by cattle, or by sheep sleeping on the mounds at night. In winter a high

proportion of the diet of the green woodpecker (Pontin 1961b), and of grey partridge (Perdix perdix) chicks (Potts 1970) may consist of L. flavus, and conical holes 5 cm deep and 1.5-3 cm in diameter at the surface, made by green woodpeckers, are frequent in L. flavus mounds in autumn and winter. Pheasants damage and sometimes destroy mounds by dust-bathing (Pontin 1963 and pers. obs.).

Rabbits preferentially use ant-hills as latrines (e.g. Thomas 1962, Elton 1966). Their pellets, which occasionally kill small seedlings by shading them (Chapter 5), often become incorporated in mounds as they are covered by newly-heaped soil. This might increase the organic matter content, water-holding capacity (Salisbury 1952), and phosphorus (Pigott & Taylor 1964) and nitrogen contents of ant-hill soil. Harper (1969) implies

Fig. 5. The effects of rabbits on an ant-hill at Beacon Hill, Aston Rowant N.N.R. (2 September 1971). There are numerous rabbit droppings on the soil surface, the vegetation on top is closely grazed, a hollow has been dug near the summit and rabbit scraping and trampling may have contributed to the death of vegetation on top of the mound.



that a 'specialised flora' develops on rabbit latrines on ant-hills because of the higher phosphorus and nitrogen levels there, but I have yet to find such a flora on L. flavus mounds.

Rabbit (Pigott 1955, Griffiths 1968) and sheep (Hawes 1971, pers. comm.) grazing is often more intense on ant-hills than in the surrounding vegetation.¹ What are the effects of this concentration of grazing on the relative abundance of plant species on the mounds?

In short chalk grassland, the species composition and height of the vegetation on ant-hills seems identical in ungrazed, sheep-grazed and rabbit-grazed areas. The plant cover is invariably short and often dominated by Festuca rubra and Thymus drucei. The balance of species seems unaffected by grazing, although grazing is concentrated on the grasses rather than on unpalatable herbs like Thymus and Helianthemum chamaecistus. This is because the growth of Festuca on mounds in ungrazed areas is very slow anyway, probably being limited by low water or nutrient availability. The situation is like that in Breckland 'grass heath' before myxomatosis (Farrow 1925), where rabbits reduced the luxuriance of the vegetation but its growth rate was mainly limited by soil water levels.

In tall chalk grasslands, rabbit grazing is often concentrated on the ant-hills (Griffiths 1968 and pers. obs.), and may allow low-growing species like Thymus drucei to persist on the mounds and the ant colonies to survive. In the absence of grazing, mounds in tall grasslands may ultimately bear a dense tall growth of coarse grasses (Lerna erecta, Arrhenatherum elatius, Festuca rubra, Brachypodium pinnatum etc.), which shades/ out

¹ Some evidence for this is given on p. 53.

low-growing species and may kill the ant colony. Thus the species composition of the ant-hill flora can be greatly affected by grazing in tall grasslands.

Grazing on the mounds and in the sward often greatly affects viable seed production there, and hence the rate at which some species invade ant-hills from the surrounding vegetation (Chapter 5), or the rate at which a species spreads by seed once it has colonised a mound. On the other hand, rabbits, sheep and cattle may disperse viable seeds in their coats or guts.

1.3.5. The microclimate of the mounds

Two general points require emphasis. Firstly, because microclimatic factors vary between the bottom and top, between bare and vegetation-covered soil and on different aspects, a mound is usually more heterogeneous in microenvironment than an equal surface area of the surrounding pasture. Fluctuations of temperature, humidity and evaporation on ant-hills are probably much greater than in the sward, where they are 'damped' by the tall, complete vegetation cover. Secondly, although many of the statements in this section are based on discontinuous measurements of environmental factors at Aston Rowant N.W.R. in 1971, I have not quantified the microclimates of the mounds thoroughly. Plants are the best integrators of environment, and the appropriate time for investigating particular factors in detail would be after field experiments (like those described in Chapter 5) had suggested that they might be important in influencing plant patterns.

Seasonal and diurnal temperature fluctuations in ant-hill soil are greater on southern than northern aspects,¹ and decrease with depth. Temperatures over 40°C frequently occur beneath bare soil on the south side of the mounds on summer days when the air temperature exceeds 21°C. Since the temperature of the bare soil must often fall below air temperature at night in summer, shallow-rooted plants may gain some water by condensation in the surface soil from the atmosphere, as in dune soils (Salisbury 1952). However, the amplitude of temperature fluctuations is reduced under vegetation. For instance, on 16 September 1971, a warm day on which the air temperature reached 24.5°C, the soil temperature 1 cm deep on the south side of an ant-hill reached 36.3°C, but 2-3 cm away, under Festuca rubra or Leontodon hispidus, the highest temperature recorded at the same depth was 26-27°C. The march of temperature under vegetation on the south side of the mound resembled that under soil on the north side. Haarlov (1960) found that temperature fluctuations under soil on the north sides of ant-hills were similar to those in pasture soil at the same depth.

Most radiant energy from the sun which reaches soil and its plant cover is used in evaporating water. I have already shown that the mounds are usually drier than the surrounding soil and that their south sides are often drier than their north slopes.

¹ Haarlov (1960) used maximum and minimum thermometers to measure temperature fluctuations at 2 cm depth in ant-hill and pasture soil at Jaegersborg Park, Denmark from 1 June 1942 to 31 August 1943. The amplitude of seasonal and diurnal temperature fluctuations was greater on south aspects of mounds (where the temperature once reached 44°C) than on the north. Temperature measurements made on ant-hills at the Bowling Alley, Wytham Woods, Berks., using a continuous Grant recorder with thermistor probes, confirm his results (Dr. S.R.J. Woodell, pers. comm.).

Dew, frost and snow lie longer on the northern than the southern sides. Plants on south-facing aspects of ant-hills are under much greater evaporative stress in summer than those on the north. For instance, I measured evaporation from all aspects of a mound, with Piche-type evaporimeters, every twenty minutes from 0955-1655 hrs on 10 September 1971, a typical summer's day with both overcast and sunny periods on which the air temperatures reached 22°C. The integrated evaporation from the middle of the south side of the ant-hill was 2.74 times that from the north. Changes in evaporation rate closely reflected fluctuations in the temperature, which reached 40.5°C under 0.5 cm of soil on the southerly slope but only 23°C on the northerly one.

Wind speed over an ant-hill's surface depends on the height of vegetation in the wind's travel before it reaches the mound (measurements at Aston Rowant N.N.R., e.g. 16 August 1971). When the height of the surrounding sward is well below that of the summit of the 'hill, much of the mound's surface, and its plant cover, may be exposed even to slight breezes, with a consequent increase in evaporation. Yet when the vegetation around the mound is almost as tall as its summit, wind movement across its surface can only be detected with anemometers in very windy conditions. Thus the microclimate of an ant-hill is ameliorated when it is surrounded by tall grasses.

Most plant species grow equally well and are equally abundant on all aspects of ant-hills. However, Festuca rubra often grows more luxuriantly on north-facing than south-facing aspects, as mentioned in section 1.3.2. This may reinforce the microclimatic differences between north and south slopes which

already existed, and might sometimes impose patterns on other plant species (Chapter 3). *Pleurocarpous* mosses, like *Pleurozium schreberi* at Rhossili Down (Chapter 2) and *Pseudoscleropodium purum* at Aston Rowant (Chapter 3) may be significantly ($P < 0.05$) more abundant on northern than southern aspects of ant-hills. Desiccation and/or high soil temperatures might contribute to seedling deaths on the south sides of the mounds but I only have evidence of this for seedlings of *Arenaria serpyllifolia* (Chapter 5).

1.4. COMPARISON OF *L. flavus* ANT HILLS WITH OTHER ANIMAL ARTEFACTS, ESPECIALLY MOLE-HILLS

There are numerous reports in the literature that the vegetation on mounds built by other species of ants, rodents (e.g. Ross et al. 1969), termites (reviewed by Lee and Wood 1971) or moles may sometimes differ from that surrounding them. However, even in the occasional cases in which the relationship between vegetation and environment on an animal artefact has been investigated more fully (e.g. Goodland 1965 and pers. comm.), the results shed little light on the relationship between vegetation and environment on *L. flavus* ant-hills. Other mounds differ from *L. flavus* 'hills in shape and size and have been built in different vegetation and environments by animals with different population sizes, food preferences, foraging habits, effects on the soil, abilities to heap it up and so on. Nevertheless, the relationships between vegetation and environment on mole-hills are worth discussing here, because mole-hills often bear a different flora to ant-hills, even in the same pasture.

The differences between ant-hills and mole-hills in chalk grassland at Aston Rowant N.N.R. are summarised in Table 7. The mole-hills are invaded by species like Poterium sanguisorba, Carex flacca, Cirsium acaule, Leontodon hispidus and Plantago lanceolata, which are abundant in the surrounding vegetation but strikingly less so on ant-hills. The main reasons why these species flourish on mole-hills but not on ant-hills are probably the presence of their rootstock bases, rhizome fragments and seeds in mole-hill soils, and the absence there of recurrent soil heaping onto the surface. My observations on the colonisation of mole-hills in chalk grasslands (Appendix 2) complement those of Urbain & Marty (1920), Davies (1966), Voronov (1968) and Watt (1971). These authors describe plant successions on mole-hills which last 2-4 years. By this time, the mole-hill is swamped by invading species, and eroded or trampled to the level of the surrounding soil. Ant-hills are not susceptible to much trampling damage when 'mature' because they are held together by the dense root mat often present in the upper layers of the soil, which is sometimes reinforced by a network of deep woody stems of the dwarf shrubs Helianthemum chamaecistus and/or Thymus drucei.

L. flavus colonies may begin in mole-hills (Gould 1747, Haarlov 1960, Voronov 1968); Pontin's (1960b) results show that newly-fertilized L. flavus queens preferentially burrow into bare soil. This may be why ant-hills and mole-hills are sometimes confused. For example, Fansley & Adamson's (1925) 'mole-heaps' were probably ant-hills, and Mellanby (1971, p.144) illustrates ant-hills at Parsonage Down, Wilts, and calls them mole-hills.

Table 7. Differences between ant-hills and mole-hills at
Aston Rowant N.F.R.

PROPERTY	ANT-HILLS (AH)	MOLE-HILLS
Life-span	Indefinite? Usually far exceeds 2-4 years.	2-4 years.
Growth	Gradual, until abandoned.	Sudden and rapid, then slow decrease in volume.
Erosion	Slow, once plant cover established.	Much faster erosion, by rain and trampling, back to level of surrounding soil.
Basal area	Increases in height and basal area until much taller and larger than mole-hills.	Slow decrease in height as eroded. Basal area constant.
Soil	Structureless, stoneless, organic matter content usually lower than surrounding soil.	Structured, stony, organic matter content equal to that of surrounding soil.
Soil heaping	Some heaped up each year, until abandoned.	Larger volume heaped up suddenly. No further heaping.
Smothering of plants by heaped soil	Occurs each year.	Occurs when mole-hill built, but not subsequently.
Seeds and other propagules in heaped soil	Hardly any.	Viable seed 'bank' in soil probably equivalent to that in surrounding soil. Root fragments, rhizomes and stolons, able to regenerate, occur in heaped soil.
Viable seed 'rain' onto soil surface	Lower density. <u>Density</u> decreases towards summit. (More selection of 'well-dispersed' seeds?)	Higher density.
Vegetation height	Usually shorter than SV*	Similar to SV*
Characteristic Vegetation	Differs from SV. Species asterisked less abundant on AH than in SV. <u>Thymus drucei</u> , <u>Helianthemum chamaecistus</u> , annuals, small acrocarps, <u>Cerastium holosteoides</u> etc. more abundant than in SV.	Similar to SV. <u>Poterium sanguisorba</u> ,* <u>Carex flacca</u> ,* <u>Cirsium acaule</u> ,* <u>Leontodon hispidus</u> ,* <u>Plantago lanceolata</u> ,* <u>Festuca rubra</u> , <u>Galium verum</u> , <u>Lotus corniculatus</u> all frequent.

* SV = surrounding vegetation.

1.5. SUMMARY

I review previous work on the ecology of the ant Lasius flavus and the mounds which it builds in British grasslands. The short, incomplete vegetation cover on 'active' ant-hills often has a different species composition to the surrounding sward. Plant species patterns may be affected by the size or age of a mound, aspect, or the level of ant activity. The main factors which influence the occurrence or abundance of particular species on the ant-hills are probably the heaping of soil over the surfaces of plants by the ants, the greater susceptibility to drought of ant-hill than pasture soils, and in tall vegetation, rabbit-grazing.

CHAPTER 2

THE VEGETATION OF ANT-HILLS IN ACIDIC *Agrostis tenuis*/*Festuca ovina* GRASSLANDS ON THE GOWER PENINSULA, SOUTH WALES

2.1. INTRODUCTION

I set out first to quantify the differences between the vegetation on the mounds and in the pasture at several sites in acidic (this chapter) and calcareous (Chapter 3) grasslands. I began by sampling acidic grasslands because patterns of species in relation to ant-hills might be more obvious in species-poor than species-rich vegetation. Detailed experiments could not be carried out at the Gower sites because of their distance from Oxford and their exposure to humans and grazing animals. Yet the descriptive results provided a useful check on my conclusions from chalk grasslands (Chapter 3 onwards) and often helped me to suggest general properties of ant-hills (Chapter 6).

In the Gower peninsula several Old Red Sandstone (Conglomerate) hills (George 1940) dominate the surrounding plain. Most of these hills have been common land for centuries, grazed mainly by horses and sheep, and those areas which have not been invaded by *Pteridium aquilinum* are grassy and often bear dense populations of *L. flavus* mounds. The heavily grazed swards are typically 2-5 cm high and have a species composition typical of *Agrostis tenuis*/*Festuca ovina* grasslands in the western uplands of Britain (Tansley 1939), with these two species forming a dense matrix in which *Galium saxatile*, *Rumex acetosella*, *Anthoxanthum odoratum* and *Luzula campestris* are frequent and *Nardus stricta* and *Sieglingia decumbens* sometimes occur. This vegetation

covers shallow (10-20 cm deep) heavily podsolised acidic (pH 3.5-4.8 in top 5 cm) nutrient-poor sandy soils in which quartz and jasper pebbles increase with depth. The sites I sampled were all within 4 km of the sea and very exposed to sea gales and sea mist. The mean total annual rainfall is about 1105 mm.

I shall describe the patterns of species in relation to large ant-hills at five sites. I sampled four of them (Harding's Down, Cefn Bryn, Llanmadoc Down and the south end of Rhossili Down) by subjectively estimating the percentage covers of all species on ant-hills and in quadrats placed in the sward (section 2.2.). The vegetation on and off the mounds at the north end of Rhossili Down was sampled intensively by a complex point quadrat technique (section 2.3). Site details and results are given in Appendices 4-9.

2.2. COMPARISONS OF ANT-HILL AND SURROUNDING VEGETATION AT HARDING'S DOWN, CEFN BRYN, LLANMADOC DOWN AND SOUTH END OF RHOSSILI DOWN

2.2.1. Methods

The sampled sites were homogeneous areas with the highest ant-hill densities. Sampling sites were not selected because they had distinctive ant-hill vegetation. Methods used in the recording of site details and ant-hill characteristics are given in Appendix 3.

At each place I paced out two co-ordinates at right angles to one another to form a rectangle which enclosed over sixty mounds. I found random points by pacing; at each point, I selected the nearest mound for sampling. Since *L. flavus* mounds are usually regularly-distributed (Appendix 3) I was selecting

a more or less random sample. Only ant-hills at least 15 cm high and 30 cm in mean basal diameter were sampled, so that in a small sample, successional effects on smaller mounds would not obscure differences in species abundance on and off large mounds.

The edge of the mound was defined with a piece of string as the place where the slope of the mound made an angle with the slope of the soil around it. The margin could usually be determined precisely but sometimes had to be defined arbitrarily. The percentage cover of every species (Angiosperms, Bryophytes, Lichens) rooted in the mound was estimated on a percentage scale. All species with a cover of less than 1.5% were recorded as having a cover of 1%. The height and diameter of the mound, the vegetation height, the percentage cover of bare soil and the volume of newly-heaped soil were estimated (Appendix 3). Animal grazing, droppings or damage was recorded.

After each ant-hill had been sampled, a 0.5 x 0.5 m quadrat was placed in the surrounding vegetation with the centre of one of its sides 0.3 m from the edge of the mound in a random direction. The percentage covers of all species, vegetation height etc. were assessed as for the ant-hill. The surrounding vegetation quadrat was associated with each mound because the resulting paired comparisons design (randomised blocks with two treatments per block) provided a more efficient significance test than the completely randomised design appropriate if all the surrounding vegetation quadrats had been arranged randomly over the sampled site. By using a paired comparisons design, the effect of local variations in the percentage cover of a species was subtracted from the error variance. Eight ant-hill/pasture

quadrat pairs were sampled at each site (ten at Cefn Bryn). In the significance tests (Appendix 3) the blocks from which a species was absent were ignored.

2.2.2. Results

Site details and full results are given in Appendices 4-7. The results from all four sites are combined and summarised in Fig. 6, for all the species which occurred in ten or more blocks altogether. The histograms suggest that Aira praecox, Dicranum scoparium and Polytrichum juniperinum have a marked preference for ant-hills, and that Agrostis tenuis, Anthoxanthum odoratum, Luzula campestris, Rhynchospora squarrosa, Sieglingia decumbens and possibly Festuca ovina and Hypnum cupressiforme are much more abundant in the sward than on the mounds. These impressions are confirmed by the results of significance tests on the raw data (Table 8), but discussion of these distributions is deferred until section 2.4.

2.3. COMPARISON OF VEGETATION ON AND OFF ANT-HILLS AT THE NORTH END OF RHOSILI DOWN

2.3.1. Introduction

At the northern end of Rhossili Down, along the path from Hillend to the Beacon, a concave grassy area sloping 7° to the north and locally known as 'Bessie's meadow' supports a dense population of L. flavus mounds (Fig. 7). Details of the site and its environment are given in Appendix 8. In vegetation, soil, geology, climate, history and grazing regime 'Bessie's meadow' was very similar to the other Gower sites, but the ant-hills there were sampled in detail, using a point quadrat technique.

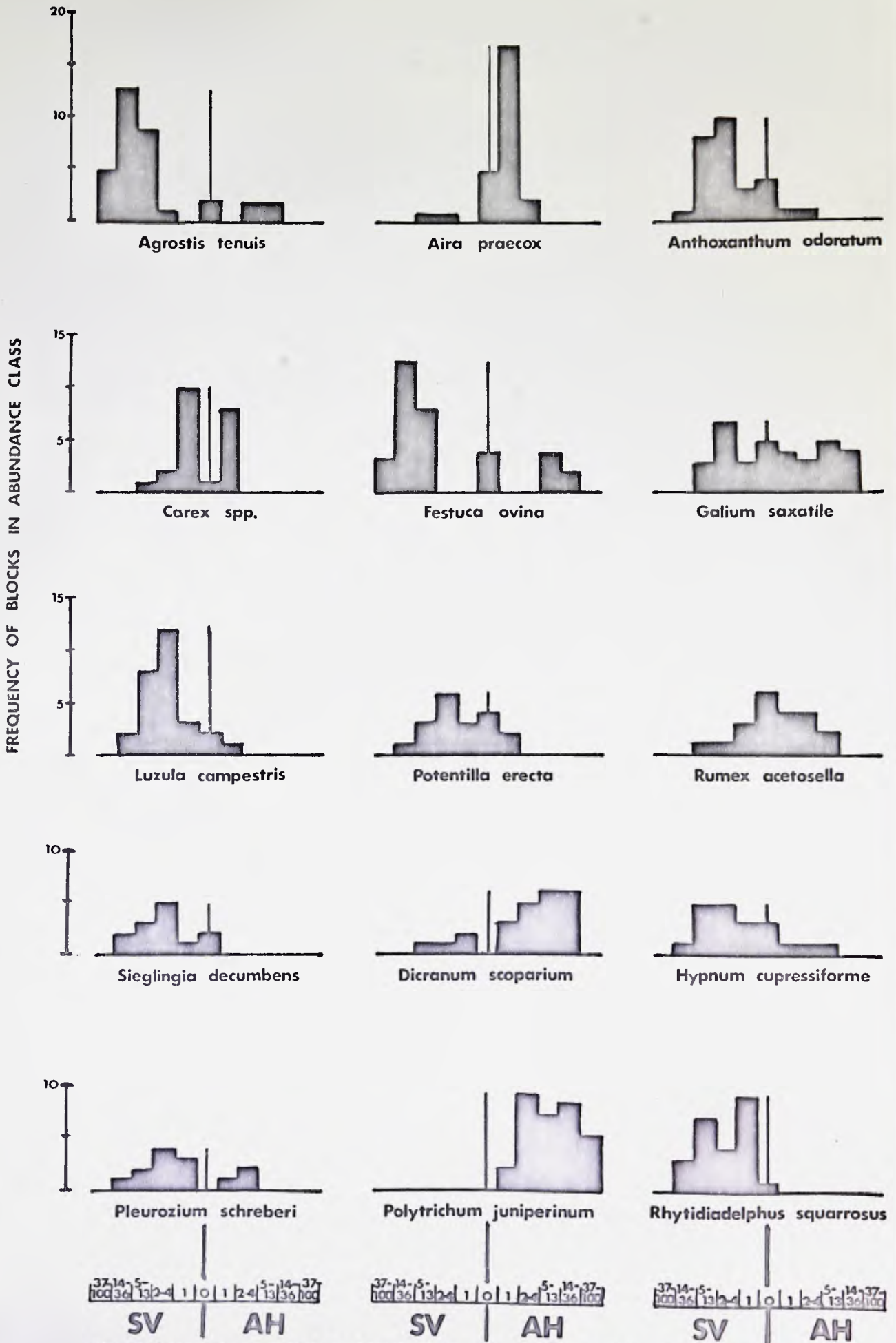
Fig. 6. Histograms of the relative abundances of species on and off ant-hills at four sites in the Gower peninsula

The difference between the estimated percentage covers of the species on the mound and in its associated surrounding vegetation quadrat was calculated for each 'block' in which the species had been recorded. These differences were grouped together to produce a frequency distribution for each species. The classes, from left to right, are as follows:

1. 100-37% more cover in the surrounding vegetation than on ant-hills.
2. 36-14% "
3. 13-5% "
4. 4-2% "
5. 1% "
6. 0% equal cover on and off the mounds.
7. 1% more cover on ant-hills than in the surrounding vegetation.
8. 2-4% "
9. 5-13% "
10. 14-36% "
11. 37-100% "

The scale was calculated by dividing $\log_{10} 100$ by 5, and intended to be log-normal (Williams 1964). Because of a calculation error the scale is only approximately log-normal, but the visual effect is similar. Those species with the 'centre of gravity' of their histograms well to the left of the central vertical line are mainly confined to the pasture, whilst those more frequent to the right of the line usually have a greater percentage cover on ant-hills than in the sward.

Fig.6



DIFFERENCES IN PERCENTAGE COVER BETWEEN EACH ANTHILL AND ITS ASSOCIATED SURROUNDING VEGETATION QUADRAT, GROUPED IN ABUNDANCE CLASSES. ONLY THOSE IN WHICH THE SPECIES OCCURRED WERE INCLUDED.

Table 8. Species significantly ($P < 0.05$) more abundant either on ant-hills or in the surrounding vegetation in at least one of the four acid grassland sites sampled

The first figure represents the number of sites at which the species was significantly more abundant in one area than the other, and the figure in brackets is the number of sites at which the species occurred.

<u>Ant-hills</u>	<u>Surrounding vegetation</u>
<u>Polytrichum juniperinum</u> 4(4)	<u>Agrostis tenuis</u> 3(4)
<u>Aira praecox</u> 2(4)	<u>Luzula campestris</u> 3(4)
<u>Dicranum scoparium</u> 2(4)	<u>Rhytidiadelphus squarrosus</u> 3(4)
<u>Polytrichum piliferum</u> 1(4)	<u>Anthoxanthum odoratum</u> 2(4)
<u>Frequent species with apparently no preferences include:</u>	<u>Festuca ovina</u> 2(4)
<u>Galium saxatile</u>	<u>Pteridium aquilinum</u> 1(1)
<u>Rumex acetosella</u>	<u>Hieracium pilosella</u> 1(1)
<u>Carex spp.</u>	<u>Hypochoeris radicata</u> 1(2)
<u>Hypnum cupressiforme</u>	<u>Nardus stricta</u> 1(3)
<u>Pleurozium schreberi</u>	<u>Potentilla erecta</u> 1(3)
	<u>Pseudoscleropodium purum</u> 1(3)
	<u>Sieglingia decumbens</u> 1(3)

Fig. 7. View over the site sampled at the north end of Rhossili Down (May 1968).

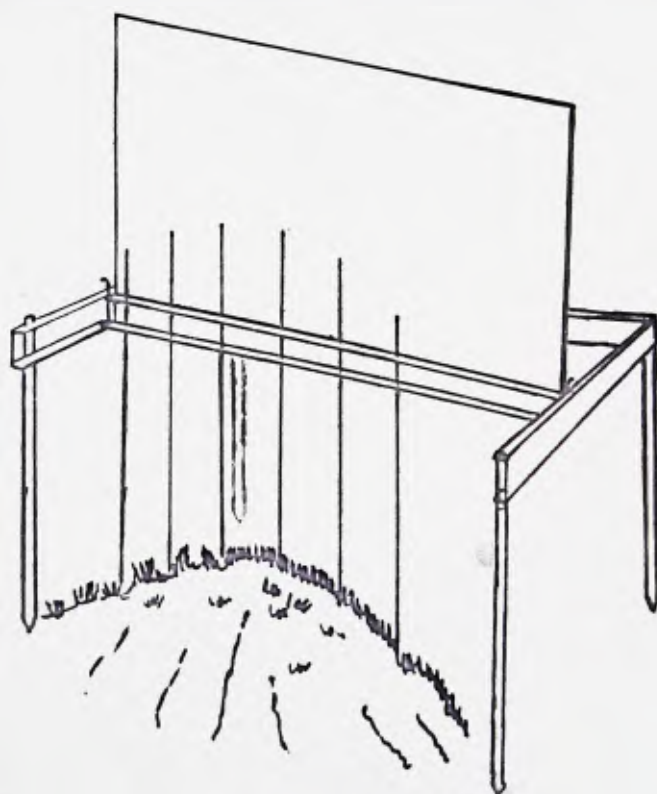


2.3.2. Methods

2.3.2.1. Sampling. A homogeneous sampling area 25 x 40 m was marked out. The 497 mature mounds in it were numbered and twenty random 'hills', each at least 15 cm high and 30 cm in mean basal diameter, were selected for sampling. Quite independently, 16 random 1 m² quadrats were positioned in the surrounding vegetation.

I had designed a portable 'three-dimensional topograph' for point quadrat sampling (Fig. 8). An aluminium frame just over a metre square is supported by an adjustable aluminium leg at each corner and can be levelled with a spirit level. Within the frame, supported by two sides of it, runs a vertical board 85 cm high bearing waterproofed graph paper. In front of the graph paper, at the base of the board, is a conventional point quadrat frame carrying a hundred sharpened steel pins, of identical length, at 1 cm intervals. The board can be located

Fig. 8. The 'three-dimensional topograph'.



precisely along the frame by holes bored in the frame 1 cm apart. Thus for any given position of the frame, 10,000 possible points can be sampled, and the relative micro-topographic heights of each point can be measured by reading off the height of the top of each pin against the graph paper on the board.¹

Each ant-hill was sampled in the following manner. The topograph was set up over the mound with one axis due North/South, and levelled. By inspection, lowering the pins at intervals, etc., the positions of the summit and margins of the ant-hill were recorded in terms of two co-ordinates, the distance along the frame and the distance across the board. The topograph was removed but the positions of its legs were marked. In the laboratory a vertical projection of the ant-hill was drawn on graph paper and its area divided into octants radiating from the summit. Within each octant was a number of possible sampling points, each defined by an intersection of lines on the graph paper. Fifteen random sampling points were defined in each octant with tables of random numbers. The co-ordinates of each point were transferred to standardised recording sheets, the topograph was re-erected in the field in an identical position, and the one-hundred and twenty selected points sampled. At each sampling point the species touched by the sharpened tip of the pin as it was lowered through the vegetation were recorded, and the height of the pin against the graph paper was noted.

Since the topograph was horizontal but the experimental site sloped, the vertical microtopographic height of each sampled point had to be corrected to its perpendicular height above a sloping plane (or two intersecting planes) if the

¹ This idea came from Boorman & Woodell (1966).

heights of different points on the same ant-hill were to be meaningfully compared. This sloping basal plane was defined by dropping eight points just off the mound at each of the SW, SE, NW and NE corners and noting their vertical microtopographic heights. Each group of eight measurements was averaged, and since the mean positions of the four resulting points in the co-ordinate frame were known, the exact position(s) and slope(s) of the basal plane(s) could be defined, and the vertical microtopographic heights converted to heights perpendicularly above this plane by simple geometry.

Each pasture quadrat was sampled by 120 points arranged in a 12 x 10 systematic grid, but topographic heights were not determined.

The advantages and disadvantages of point quadrat sampling compared with subjective estimation are discussed in section 4.2.1.

2.3.2.2. Map Production. In the selection of the random sampling points on ant-hills, maps had been drawn of the positions of each sampled point on vertical projections of the twenty sampled mounds. Each of the 2,400 sampled points can be defined on these maps by (i) its distance from the summit, as a percentage of the distance from the summit to the margin through the point, and (ii) the radial angle of the point from the summit. This is necessary since the mounds differ greatly in size and shape. If all these points were plotted on the same circular diagram with the summit at the centre, the density of points over the circle would be homogeneous since the sampling points were selected at random. If only the points which hit a particular species are plotted, in the same way, on a similar diagram,

they should be distributed randomly if the species is. The species maps which are illustrated are not polarographs like those, e.g. of Perring (1959). On my dot-diagrams, two points at the same distance from the summit may have been sampled from parts of ant-hills with completely different slopes.

2.3.3. Results

The full results appear in Appendix 9 and are summarised in Table 9. As at some of the other Gower sites, Dicranum scoparium, Polytrichum juniperinum and P. piliferum¹ are much

Table 9. Mean percentage covers (calculated on untransformed data) of the most abundant species on and off ant-hills at the North end of Rhossili Down, March-April 1968

*, $0.05 > P > 0.01$; **, $P < 0.01$; N.S., not significant, by a χ^2 test for independence between the point quadrat frequency of the species and the area sampled.

SPECIES	ANT-HILL	PASTURE
<u>Agrostis tenuis</u>	50.4 $\pm$ 4.05	69.9 $\pm$ 3.09**
<u>Anthoxanthum odoratum</u>	2.3 $\pm$ 0.72	13.0 $\pm$ 2.44**
<u>Festuca ovina</u>	37.2 $\pm$ 3.45	36.0 $\pm$ 3.37N.S.
<u>Galium saxatile</u>	11.0 $\pm$ 1.73	10.1 $\pm$ 1.87N.S.
<u>Luzula campestris</u>	0.3 $\pm$ 0.12	7.1 $\pm$ 1.84**
<u>Potentilla erecta</u>	0	1.2 $\pm$ 0.51**
<u>Rumex acetosella</u>	2.5 $\pm$ 0.90*	1.3 $\pm$ 0.34
<u>Dicranum scoparium</u>	4.2 $\pm$ 2.05**	0.6 $\pm$ 0.32
<u>Hypnum cupressiforme</u>	1.4 $\pm$ 0.36**	0.5 $\pm$ 0.18
<u>Pleurozium schreberi</u>	12.9 $\pm$ 3.17**	10.3 $\pm$ 3.33
<u>Polytrichum juniperinum</u>	20.4 $\pm$ 4.05**	0.3 $\pm$ 0.22
<u>P. piliferum</u>	14.9 $\pm$ 2.55**	0.1 $\pm$ 0.13
<u>Pohlia nutans</u>	0.4 $\pm$ 0.17**	0
<u>Rhytidiadelphus squarrosus</u>	4.9 $\pm$ 1.98**	2.7 $\pm$ 0.43

more abundant on the mounds than in the surrounding vegetation but Anthoxanthum odoratum, Luzula campestris and Potentilla erecta have a marked 'preference for' the surrounding sward.

¹Smith (1964) notes that Polytrichum juniperinum and P. piliferum are both common on ant-hills in Glamorgan.

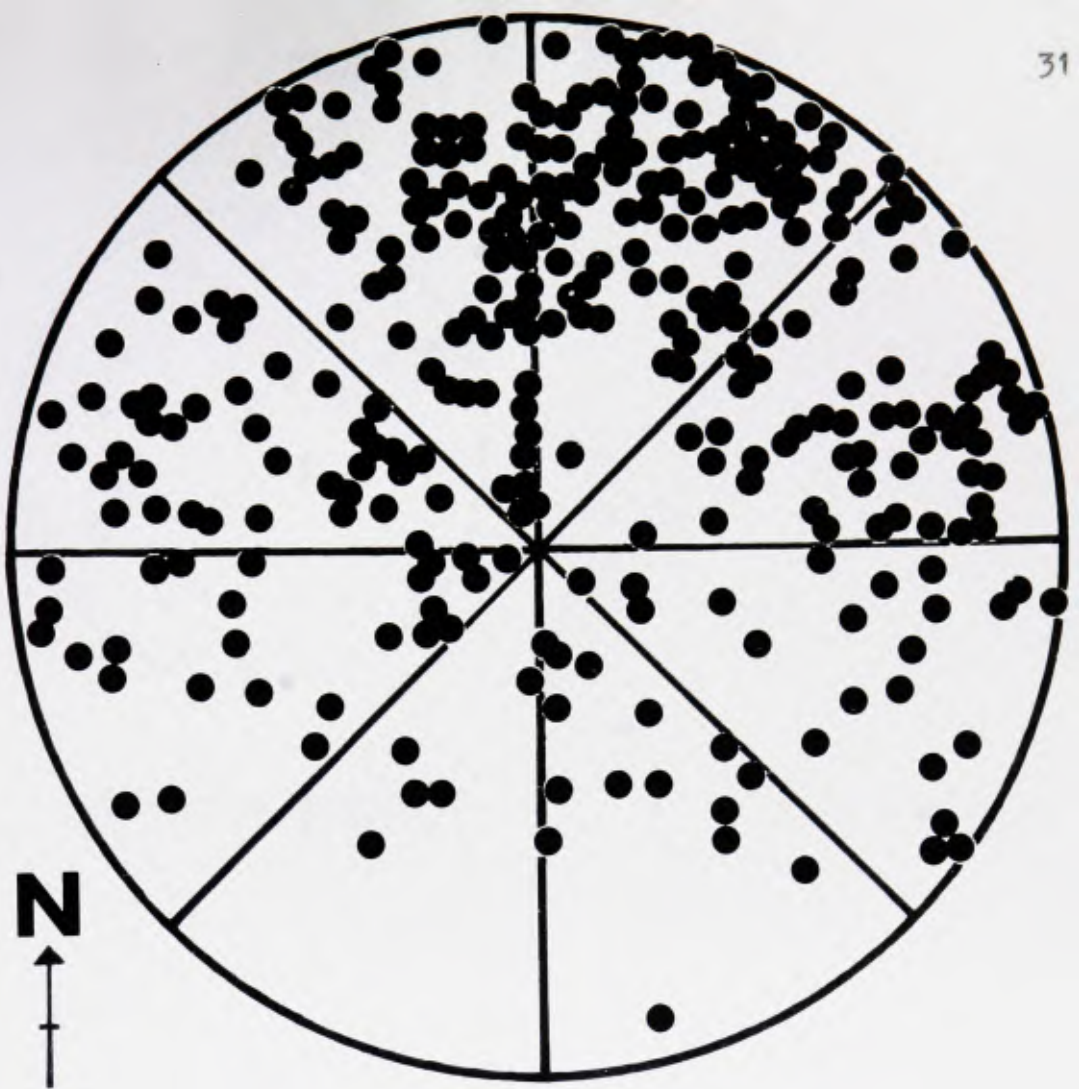


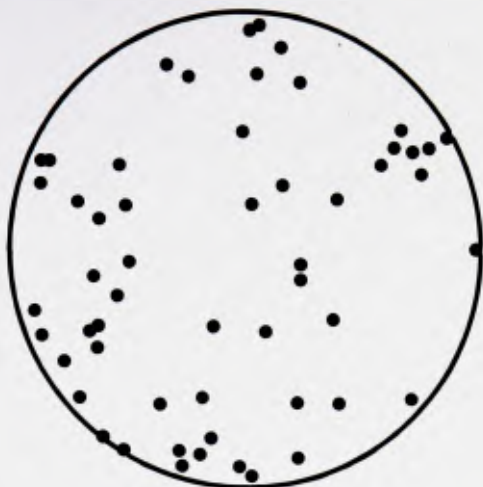
Fig. 9. Total pattern of the pleurocarpous moss Pleurozium schreberi on 20 mounds at the north end of Rhossili Down, March-April 1968.

The diagram was constructed by the method outlined in section 2.3.2.2. When species frequency on north and south aspects was compared in a 2x2 contingency table, there was a highly significant lack of independence between aspect and the abundance of Pleurozium. ($\chi^2_{[1]} = 117.2$, $P < 0.005$)

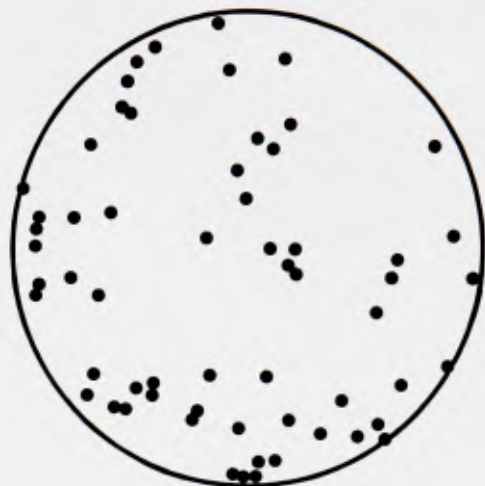
Of species not recorded in the survey, Aira praecox (frequent), Thymus drucei and Sedum anglicum seemed to be confined to ant-hills but Nardus stricta was abundant between them.

Five species had significantly ($P < 0.05$) non-random patterns on ant-hills when the points hitting them were mapped (Figs. 9 & 10). Pleurozium schreberi is far more frequent on northern than southern aspects, Anthoxanthum odoratum and Rumex acetosella are more abundant around the margin than in the centre,

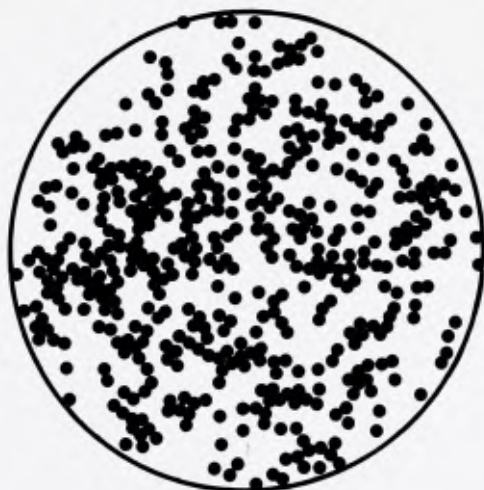
Fig.10.



Anthoxanthum odoratum
When frequency in the central half of the area was tested against that in the outer half by a $\chi^2_{[1]}$ test, $\chi^2_{[1]} = 6.16$ ($0.05 > P > 0.01$); thus more frequent around margin.

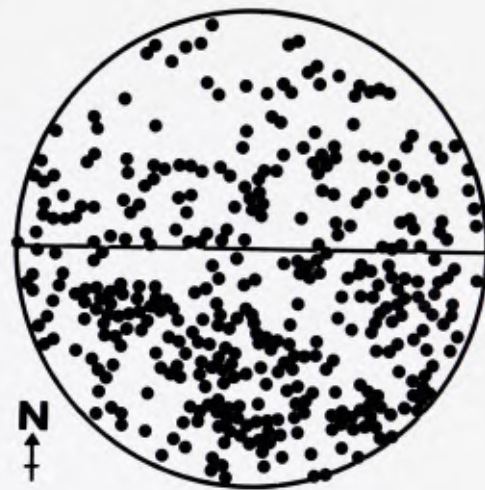


Rumex acetosella
For central/outer half, $\chi^2_{[1]} = 10.97$ ($P < 0.001$); thus more frequent around margin.



Polytrichum juniperinum
For central/outer half, $\chi^2_{[1]} = 47.36$ ($P < 0.001$); thus more frequent on top

Frequency in octants from W-NE was tested against that in the other five (2 x 2 table). $\chi^2_{[1]} = 9.25$ ($P < 0.01$); thus more frequent on south than north.



Polytrichum piliferum
For central/outer half, $\chi^2_{[1]} = 5.61$ ($0.05 > P > 0.01$); thus more frequent on top.

For NW-E/other 5 octants, $\chi^2_{[1]} = 21.15$ ($P < 0.001$); thus more frequent on south than north.

Polytrichum juniperinum has a much higher cover at the summit than near the edge (and a slight tendency towards the south side) and P. piliferum is commoner on northerly than southerly aspects with a slight 'preference for' the tops.

Some of these patterns are confirmed by the distributions of species with perpendicular height (Table 10). Agrostis tenuis, Galium saxatile and Pleurozium schreberi are more abundant near the bases than on the tops of the mounds but Polytrichum juniperinum is most frequent at the summits, and P. piliferum is commonest just below the top.

The twenty mounds in the sample were ranked in order of increasing 'ant activity' on the basis of the density of ants in soil samples taken from the mounds, and the volume of soil heaped onto the surface. Anthoxanthum odoratum, with a Kendall's coefficient of rank correlation of $T = 2.204$ ($0.05 > P > 0.01$), became less abundant as the 'ant activity' increased, but no other species yielded a significant correlation.

2.4. DISCUSSION

Some species 'prefer' or 'avoid' ant-hills at more than one of the five sites, Aira praecox, Dicranum scoparium, Polytrichum juniperinum and P. piliferum are in the former category and Agrostis tenuis, Anthoxanthum odoratum, Festuca ovina, Luzula campestris and Potentilla erecta in the latter. What causes these marked differences in species patterns?

The four species which are more abundant on ant-hills than in the pasture are all characteristic colonisers of bare acid soil on over-grazed pastures, inland sandy regions, screes

Table 10. Distribution of species with perpendicular height on ant-hills at the north end of Rhossili Down

Method. The perpendicular height of each sampled point above the basal plane(s) was calculated, and expressed as a percentage of the height of the highest sampled point on the ant-hill. The data for all twenty mounds were combined, and are summarised below, with the percentages grouped in classes of 10%; i.e., class 1 contains all points within < 10.1% of the total ant-hill height, class 2 points within 10.1-20% and so on.

% frequency of each species amongst the points in each height class.

CLASS	<u>Arrhizis</u> <u>tenuis</u>	<u>Anthoxanthum</u> <u>odoratum</u>	<u>Festuca</u> <u>ovina</u>	<u>Galium</u> <u>saxatile</u>	<u>Rumex</u> <u>acetosella</u>	<u>Pleurozium</u> <u>schreberi</u>	<u>Polytrichum</u> <u>juniperinum</u>	<u>Polytrichum</u> <u>piliferum</u>
1 (base)	57.3**	3.3	41.2	9.4	3.3	18.4	17.3	9.1***
2	51.8	4.2	44.0	12.5	4.8	15.5	14.3*	10.1*
3	53.6	2.6	37.8	16.4**	1.5	16.0	16.3	15.3
4	50.3	2.5	43.1	14.7	2.0	13.2	19.3	13.7
5	59.4**	1.6	34.9	9.2	4.0	14.5	17.7	14.1
6	43.1*	0.4**	36.2	17.1*	2.4	6.5***	22.4	19.9
7	48.1	1.8	31.1*	8.8	2.7	11.4	18.8	23.8***
8	45.4	2.4	32.0	10.3	1.0%	13.7	19.6	20.3
9	39.2**	0.4**	40.1	7.2*	2.5	11.4	28.7**	13.1
10 (top)	46.2	4.9	37.8	7.0*	0.7%	7.0**	23.1	15.4

*, 0.05 > P > 0.01; **, 0.01 > P > 0.001; ***, P < 0.001.

The t-test suggested by Bailey (1959) for comparing an observed proportion with a standard was used throughout, except in those cases marked with a %, in which the t-test based on the angular transformation, given on p.607 of Sokal & Rohlf (1969), was used.

and burnt heathland. They are more frequent on the summits of mounds than elsewhere and this pattern seems to reflect the distribution of bare soil heaped up by the ants. The winter annual Aira praecox flowers profusely on ant-hills, and its caryopses may be efficiently wind-dispersed, since they only weigh 142 µg. Aira would probably survive any periods of intense burial as a 'seed' (May to August), although of course burial might impose seed dormancy. The Polytrichum species can regenerate from spores via protonemata or from vegetative fragments. Once established, they may persist for some time; apparently separate P. juniperinum shoots which I excavated were often attached underground to the decaying, much-branched remains of the same plant, which extended up to 15 cm into the mound. Presumably the moss has grown up through heaped soil over many years. Leach (1931) showed by experiment and observation that P. piliferum reacted to burial by increasing its branching, growing up through the soil and producing abundant rhizoids. Dicranum scoparium might also have this ability.

Polytrichum juniperinum occurs most frequently on the very tops of ant-hills at Rhossili Down, whilst P. piliferum is most abundant just below it, on the south sides of the summits. I cannot explain this difference in their distribution, but it might be worth comparing their water relations.¹

The five species which have higher percentage covers in the pasture than on ant-hills are all perennials characteristic

¹Dixon (1924) wrote that P. piliferum is a plant of 'dry heaths' but P. juniperinum of 'heaths'. Suominen (1969) p.199 found that P. piliferum was indifferent to aspect on Finnish railway embankments but P. juniperinum was more frequent on northerly than southerly aspects.

of short, closed, acid grassland. Their lower density on the mounds than off them might be due to a lower birth rate on the mounds than in the swards (e.g. due to inefficient dispersal, poorer germination or seedling survival, or slower vegetative reproduction), a higher death rate (e.g. because of lower tolerance to some microclimatic factor, or susceptibility to death by burial), or both. I have no information about death-rates, although the negative correlation between the frequency of Anthoxanthum odoratum and 'ant activity' might be due to smothering of the species by newly-heaped soil. However, the birth-rates of species on ant-hills may be largely limited by the rate at which seeds and fruits can arrive there, since of the five species only Luzula and Agrostis have efficient vegetative reproduction, which is a slow means of dispersal even under conditions of low competitive stress. All these species fruit abundantly in the swards, but the tops of ant-hills are often above the level of the fruiting inflorescences, and the fruits may be heavy (e.g. Luzula campestris, 660 μ g, Anthoxanthum odoratum 567 μ g, Festuca ovina 684 μ g). Thus the fruit 'rain' onto the tops of mounds is probably of low intensity. The 'banks' of viable seed in ant-hill and pasture soils were compared in an experiment described in detail in Appendix 23 and summarised in Table 11. The 'seeds' of Agrostis tenuis, Festuca ovina, Anthoxanthum odoratum, Luzula campestris, Potentilla erecta and Sieglingia decumbens are all more abundant in pasture soils than those taken from the tops of ant-hills. These results indicate that the ability of certain species in the sward to disperse their propagules onto the mounds should be borne in mind when their patterns are explained.

Table 11. Total estimated viable seed contents of roughly equal weights of ant-hill and surrounding soil taken from the northern end of Rhossili Down in December 1968.

Paired soil samples of the same surface area were taken from each of 25 random mounds and the pasture nearby, and kept in a cold frame at Oxford for nearly nineteen months. They were kept moist, and at intervals they were churned up and the seedlings which had emerged were identified and removed. All the species with significantly ($P < 0.05$) unequal numbers of seedlings emerging from ant-hill and pasture soils are listed below, together with Galium saxatile, Luzula campestris and Rumex acetosella. Experimental details, sources of error and results are given in Appendix 23.

	AH	SV	Sig†
<u>Agrostis tenuis</u>	93	513	**
<u>Aira praecox</u>	613	83	**
<u>Anthoxanthum odoratum</u>	6	45	**
<u>Festuca ovina</u>	29	176	**
<u>Galium saxatile</u>	145	219	N.S.
<u>Luzula campestris</u>	0	7	N.S.
<u>Potentilla erecta</u>	5	48	*
<u>Rumex acetosella</u>	28	244	N.S.
<u>Sieglingia decumbens</u>	0	18	*

† Two-tailed Wilcoxon signed-ranks tests for matched pairs were used.

N.S., $P > 0.05$; *, $0.05 > P > 0.01$; **, $P < 0.01$

The greater abundance of Pleurozium schreberi on the northern than the southern sides of ant-hills¹ could be due to death by desiccation on the south sides of mounds, or to the inability of the moss to photosynthesise on the southern aspects for long enough to exceed compensation point. These possibilities are discussed further in Chapter 5 with reference to the similar pattern of Pseudoscleropodium purum on mounds at Aston Rowant N.N.R.

¹ Suominen (1969) found that Pleurozium schreberi was confined to north-facing railway embankments in Finland.

2.5. SUMMARY

In Chapter 2 I compare the vegetation on and off L. flavus ant-hills at five sites in the Gower peninsula, South Wales. Aira praecox, Dicranum scoparium, Polytrichum juniperinum and P. piliferum are more frequent on the mounds than in the sward, but Agrostis tenuis, Anthoxanthum odoratum, Festuca ovina, Luzula campestris and Potentilla erecta have the reverse pattern. Galium saxatile showed no 'preference'. The distributions of some species on the mounds were mapped at the north end of Rhossili Down. Anthoxanthum and Rumex acetosella were commoner around the margins than on the tops, Polytrichum juniperinum was more frequent on the summits than elsewhere, Pleurozium schreberi was far more abundant on north than south slopes and Polytrichum piliferum was densest on the south side just below the top. I discuss some of the factors which could influence these patterns and show that the density of viable seed of species less abundant on ant-hills is lower in mound than pasture soil.

CHAPTER 3

THE VEGETATION OF ANT-HILLS IN SOME CALCAREOUS GRASSLANDS AND
CHALK HEATHS IN SOUTHERN ENGLAND

3.1. INTRODUCTION

I compared ant-hill and pasture vegetation at thirteen sites. Six of these were in Wiltshire, four at Aston Rowant N.N.R., Oxon. and three at Lullington Heath, Sussex. The results enabled me to select species with consistent patterns in relation to ant-hills for further investigation.

3.2. METHODS

I used the same sampling technique as for the first four Gower sites (section 2.2.1). In this, eight 'blocks' were sampled at each site, each consisting of one random ant-hill and one 0.25 m^2 quadrat placed 30 cm away from the mound in the surrounding vegetation. The percentage cover of every species in each sample was estimated subjectively on a percentage scale, and several 'environmental variables' were recorded (Appendix 3).

3.3. RESULTS

Details of the sites, and full results, are given in Appendices 10-22. Site 13 is the short vegetation to the north of the control in the centre of my Beacon Hill plot at Aston Rowant N.N.R. (see map, Appendix 29). Some details of this site appear in Chapter 4, and the results are those for ant-hills 148, 168, 170, 176, 184, 190, 192 & 198 and surrounding vegetation quadrats 74, 84, 85, 89, 92, 95, 96 & 99 in the survey results in Appendix 28.

The results from all thirteen sites were combined and are summarised in Figs. 11-15. The diagrams suggest that Arenaria spp., Cerastium holosteoides, Helianthemum chamaecistus, Thymus drucei, Frisetum flavescens, Veronica arvensis and Bryum spp. 'prefer' ant-hills and that Carex flacca, Cirsium acaule, Cynosurus cristatus, Dactylis glomerata, Filipendula vulgaris, Heliototrichon pratense, Hypochoeris radicata, Leontodon hispidus, Plantago lanceolata, P. media, Poterium sanguisorba, Ranunculus spp., Succisa pratensis and Trifolium pratense 'avoid' them.

Most of these impressions are confirmed by the results of the significance tests (Table 12). Whilst only five species had a significantly ($P < 0.05$) greater percentage cover on the mounds than off them at at least one site, thirty-three showed at least one distinct preference for the surrounding vegetation. Several abundant species are equally common on ant-hills and in the sward, e.g. Agrostis stolonifera, Festuca spp., Koeleria cristata, Galium verum and Lotus corniculatus.

I noticed several dramatic aspect distributions whilst sampling in calcareous grasslands. For instance, at Aston Rowant N.N.R. sites 1 & 2, Pseudoscleropodium purum seemed more frequent on north than south aspects of the mounds. Its total pattern on 280 ant-hills in my Beacon Hill plot is summarised in Fig. 16, in which its greater luxuriance on northerly slopes is obvious.¹ In contrast, Thymus drucei and Helianthemum chamaecistus were more abundant on south-facing than north-facing

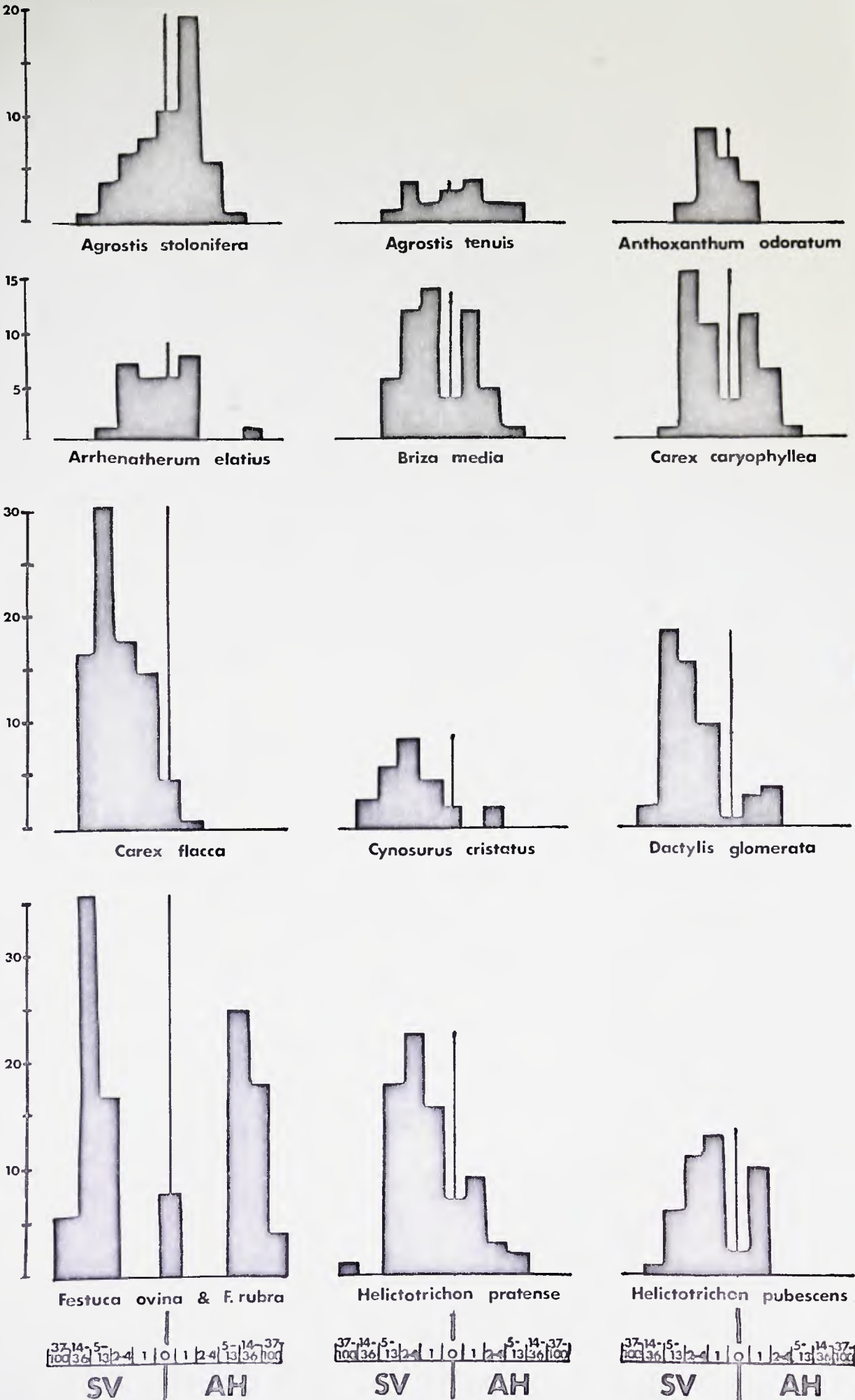
¹ The same pattern has been found in four (1969-72) University first year practicals at site P at Aston Rowant (see map, Appendix 29). It is discussed in Chapter 5.

Figs. 11-15. Histograms of the relative abundances of species on and off ant-hills at thirteen calcareous grassland and chalk heath sites in southern England.

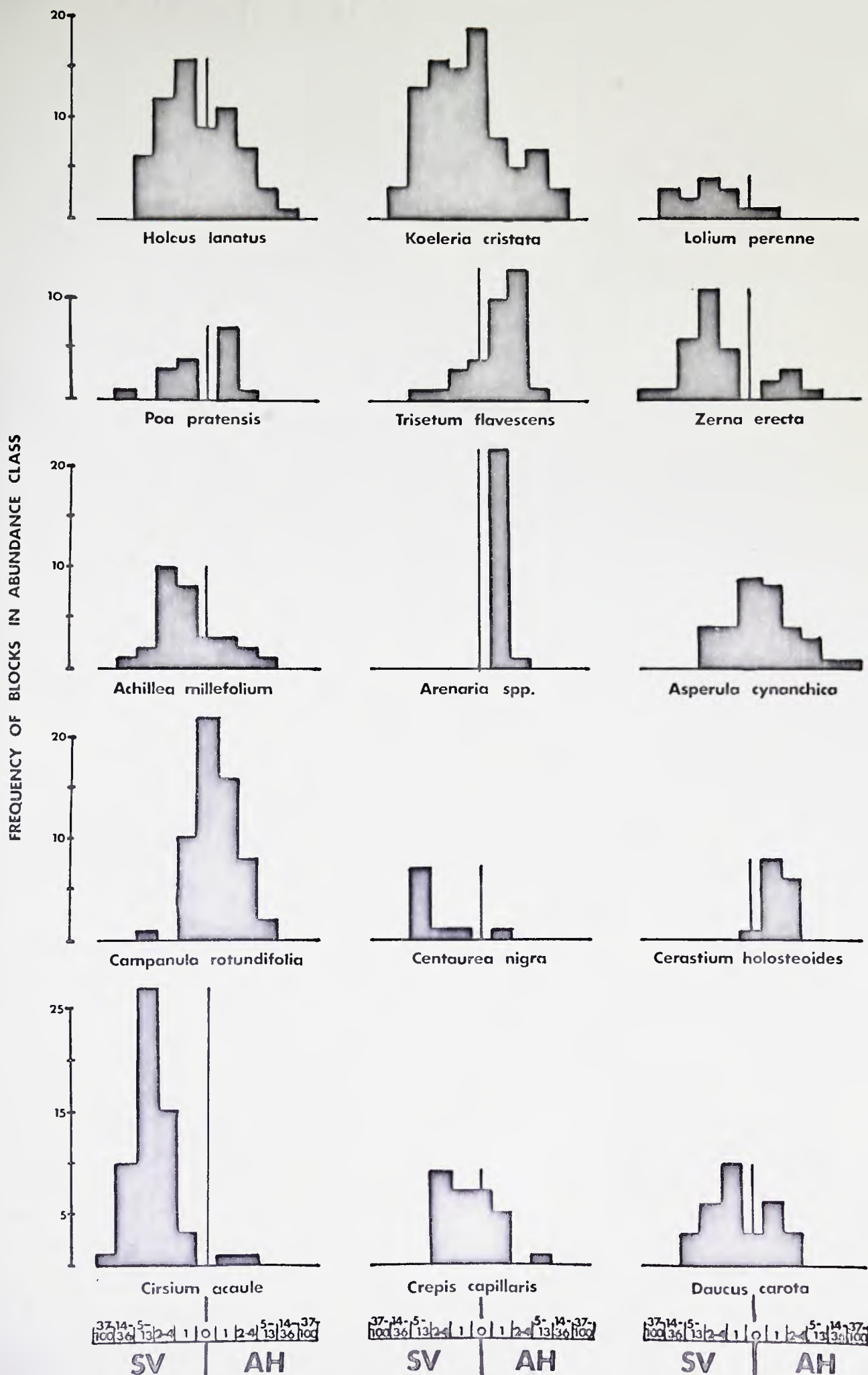
The production and meaning of the histograms is discussed in the caption to Fig.6, p.26. All species which occurred in ten or more blocks are included. All the species of Ranunculus, and of Bryum, in the sample, had similar patterns on the histograms and have been grouped together.

Fig.11

FREQUENCY OF BLOCKS IN ABUNDANCE CLASS



DIFFERENCES IN PERCENTAGE COVER BETWEEN EACH ANTHILL AND ITS ASSOCIATED SURROUNDING VEGETATION QUADRAT, GROUPED IN ABUNDANCE CLASSES. ONLY THOSE IN WHICH THE SPECIES OCCURRED WERE INCLUDED.

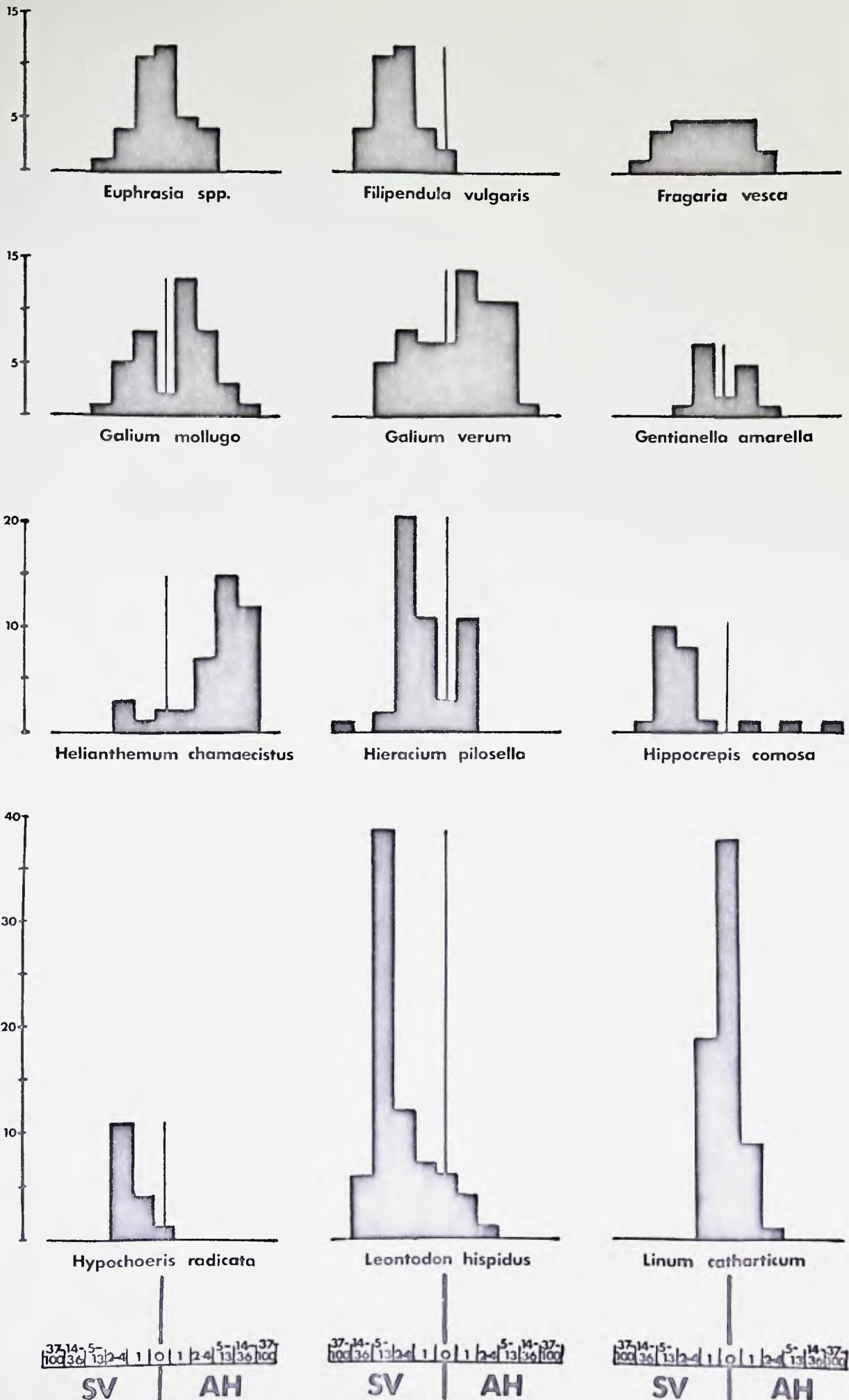


DIFFERENCES IN PERCENTAGE COVER BETWEEN EACH ANTHILL AND ITS ASSOCIATED SURROUNDING VEGETATION QUADRAT, GROUPED IN ABUNDANCE CLASSES. ONLY THOSE BLOCKS IN WHICH THE SPECIES OCCURRED WERE INCLUDED.

DICOTS.

Fig.13

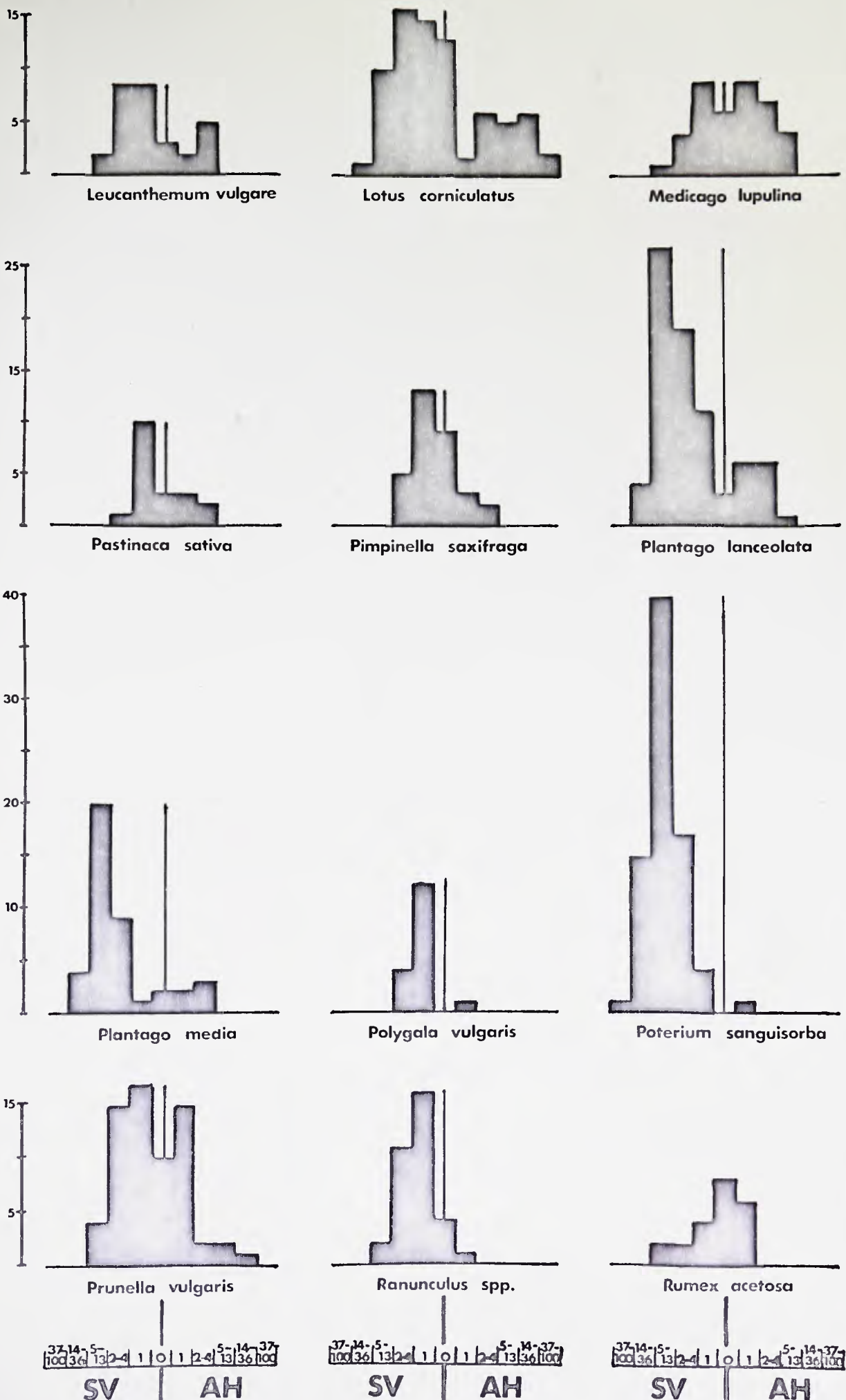
FREQUENCY OF BLOCKS, IN ABUNDANCE CLASS



DIFFERENCES IN PERCENTAGE COVER BETWEEN EACH ANTHILL AND ITS ASSOCIATED SURROUNDING VEGETATION QUADRAT, GROUPED IN ABUNDANCE CLASSES. ONLY THOSE BLOCKS IN WHICH THE SPECIES OCCURRED WERE INCLUDED.

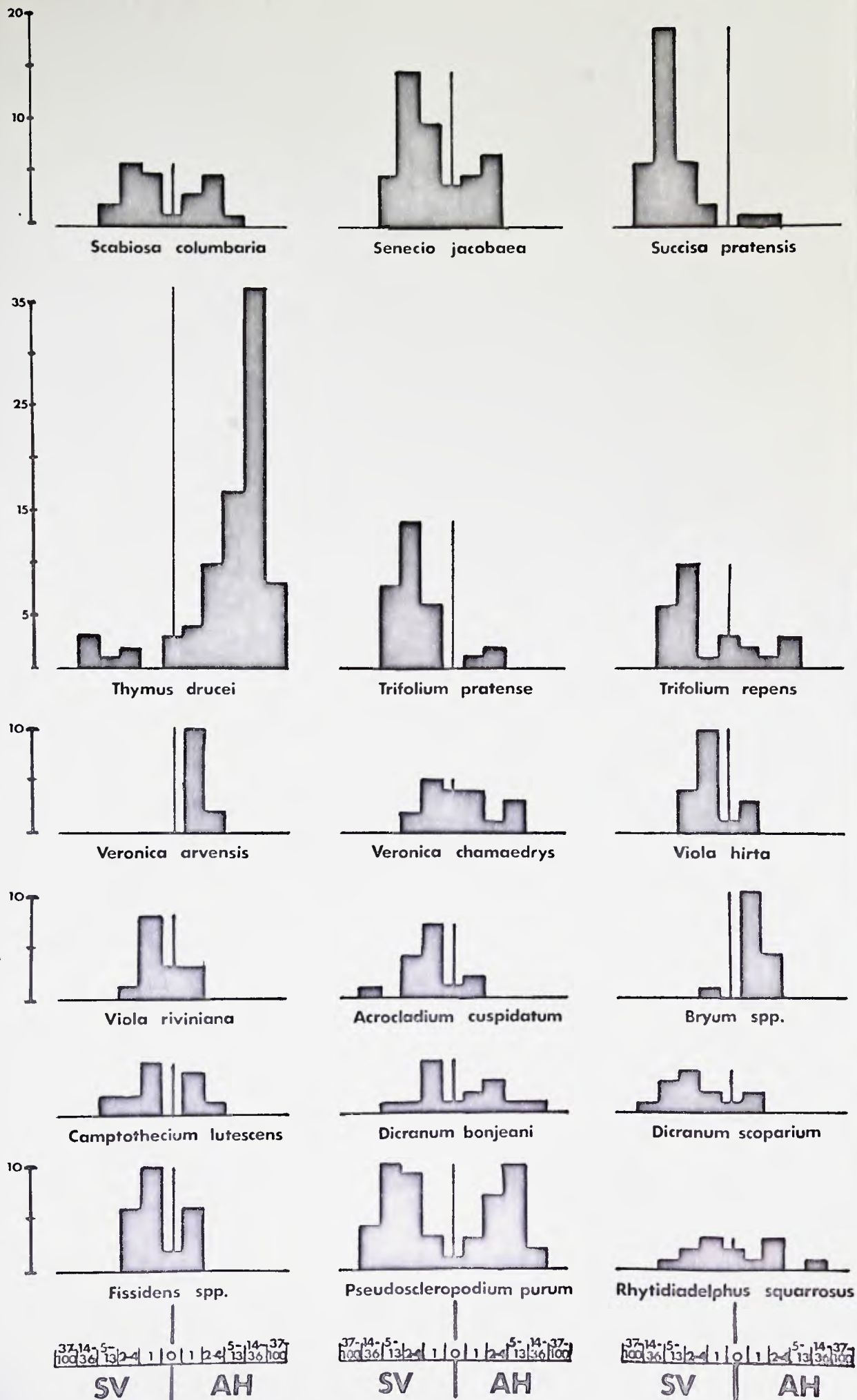
Fig.14

FREQUENCY OF BLOCKS IN ABUNDANCE CLASS



DIFFERENCES IN PERCENTAGE COVER BETWEEN EACH ANTHILL AND ITS ASSOCIATED SURROUNDING VEGETATION QUADRAT, GROUPED IN ABUNDANCE CLASSES. ONLY THOSE BLOCKS IN WHICH THE SPECIES OCCURRED WERE INCLUDED.

FREQUENCY OF BLOCKS IN ABUNDANCE CLASS



DIFFERENCES IN PERCENTAGE COVER BETWEEN EACH ANTHILL AND ITS ASSOCIATED SURROUNDING VEGETATION QUADRAT, GROUPED IN ABUNDANCE CLASSES. ONLY THOSE BLOCKS IN WHICH THE SPECIES OCCURRED WERE INCLUDED.

Table 12. Species significantly ($P < 0.05$) more abundant either on ant-hills or in the surrounding vegetation in at least one of the 13 calcareous grassland sites sampled

The first figure represents the number of sites at which the species was significantly more abundant in one area than the other, and the figure in brackets is the number of sites at which the species occurred.

Ant-hills

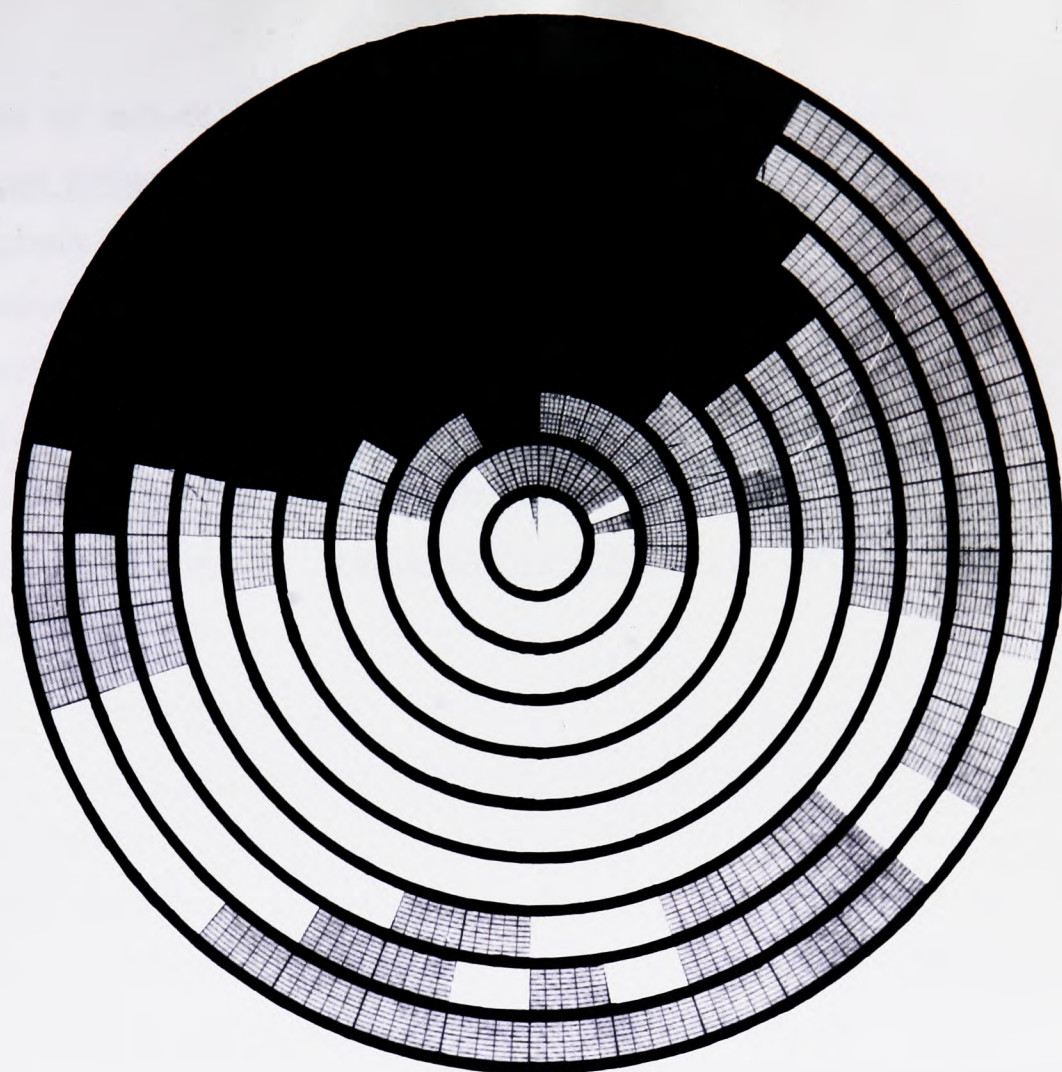
Thymus drucei 8(13)
Helianthemum chamaecistus 3(9)
Cerastium holosteoides 1(6)
Trisetum flavescens 1(8)
Arenaria serpyllifolia 1(9)

Frequent species with no 'preferences'

Agrostis stolonifera (13)
Festuca spp. (13)
Voelera cristata (12)
Lotus corniculatus (12)
Galium verum (12)
Senecio jacobaea (11)
Campanula rotundifolia (10)
Helictotrichon pubescens (9)
Linum catharticum (9)
Medicago lupulina (9)
Scabiosa columbaria (9)
Galium mollugo (9)
Pseudoscleropodium purum (9)
Asperula cynanchica (8)
Euphrasia spp. (8)
Leucanthemum vulgare (7)
Gentianella amarella (7)
Pimpinella saxifraga (7)

Surrounding vegetation

Poterium sanguisorba 10(12)
Carex flacca 10(13)
Leontodon hispidus 8(12)
Cirsium acaule 6(10)
Plantago lanceolata 5(12)
Helictotrichon pratense 5(13)
Plantago media 4(6)
Filipendula vulgaris 4(6)
Trifolium pratense 3(5)
Serna erecta 3(7)
Succisa pratensis 3(7)
Hieracium pilosella 3(10)
Dactylis glomerata 3(11)
Hippocrepis comosa 2(5)
Ranunculus acris 2(5)
Cynosurus cristatus 2(5)
Trifolium repens 2(7)
Holcus lanatus 2(12)
Prunella vulgaris 2(12)
Serratula tinctoria 1(1)
Carex humilis 1(1)
Hylocomium splendens 1(1)
Dicranum scoparium 1(3)
Centaurea nigra 1(3)
Hypochoeris radicata 1(4)
Lolium perenne 1(5)
Polygala serpyllifolia 1(5)
Fragaria vesca 1(7)
Pissidens adianthoides 1(7)
Daucus carota 1(8)
Crepis capillaris 1(9)
Briza media 1(11)
Carex caryophylla 1(12)



N
↑ **□ 0-9** **▨ 10-19** **■ 20-34** **■ >34**

Fig.16. Frequency of Pseudoscleropodium purum over the surface of 280 mounds in my Beacon Hill plot (1969).

Every fifth mound was examined. If P.purum was present, an outline of the margin of the ant-hill was drawn to scale on a cyclostyled sheet, as if the surface of the mound were a plane. Areas covered by P.purum were marked in.

In the laboratory, I placed a circular sheet of tracing paper, with lines 10° apart radiating from the centre, over each field map, with its centre over the summit. Whenever the moss occurred within a particular 10° sector, its presence within sub-areas of 0-10%, 10-20%, 20-30% etc. of the distance from the summit to the edge was noted. The presences for each mound were transferred to the same diagram, on polar co-ordinate graph paper, which finally (above) showed the number of times that P.purum was present in each of the 360 sub-areas.

Since these sub-areas increase in area from the centre outwards, comparisons between frequencies are only valid within each annulus.

sides of ant-hills at several sites. The total pattern of Thymus drucei on twenty mounds at Yarnbury Castle, Wilts is given in Fig. 17, and Fig. 18 illustrates the greater abundance of Helianthemum chamaecistus on southern than northern aspects of ant-hills at Aston Rowant N.N.R. Site 2. There, Helianthemum's distribution reflects that of bare soil but is negatively correlated with the cover of Festuca rubra, Leontodon hispidus, Pseudoscleropodium purum and possibly Fragaria vesca.

3.4. DISCUSSION

Thymus drucei and Helianthemum chamaecistus are strikingly more abundant on ant-hills than in the surrounding vegetation in the calcareous grasslands I sampled. Both species are woody xeromorphic chamaephytes which on ant-hills have deep root systems penetrating the underlying chalk, and a complex system of rooted woody shoots ramifying throughout the mounds. All the shoots of Thymus or Helianthemum emerging from the surface of an ant-hill frequently belong to the same plant. Shoots of both species can withstand intense burial by soil heaped up by the ants; when Thymus or Helianthemum is commoner on south-facing than north-facing sides of mounds (Figs. 17 & 18) it is usually at a site where soil-heaping by the ants is concentrated on southern aspects.

Arenaria serpyllifolia, Cerastium holosteoides and Trisetum flavescens were all significantly ($P < 0.05$) more frequent on ant-hills than off them at a single site. Annuals like Arenaria are often confined to ant-hills in certain areas (Table 13). Apart from Arenaria the most characteristic ant-

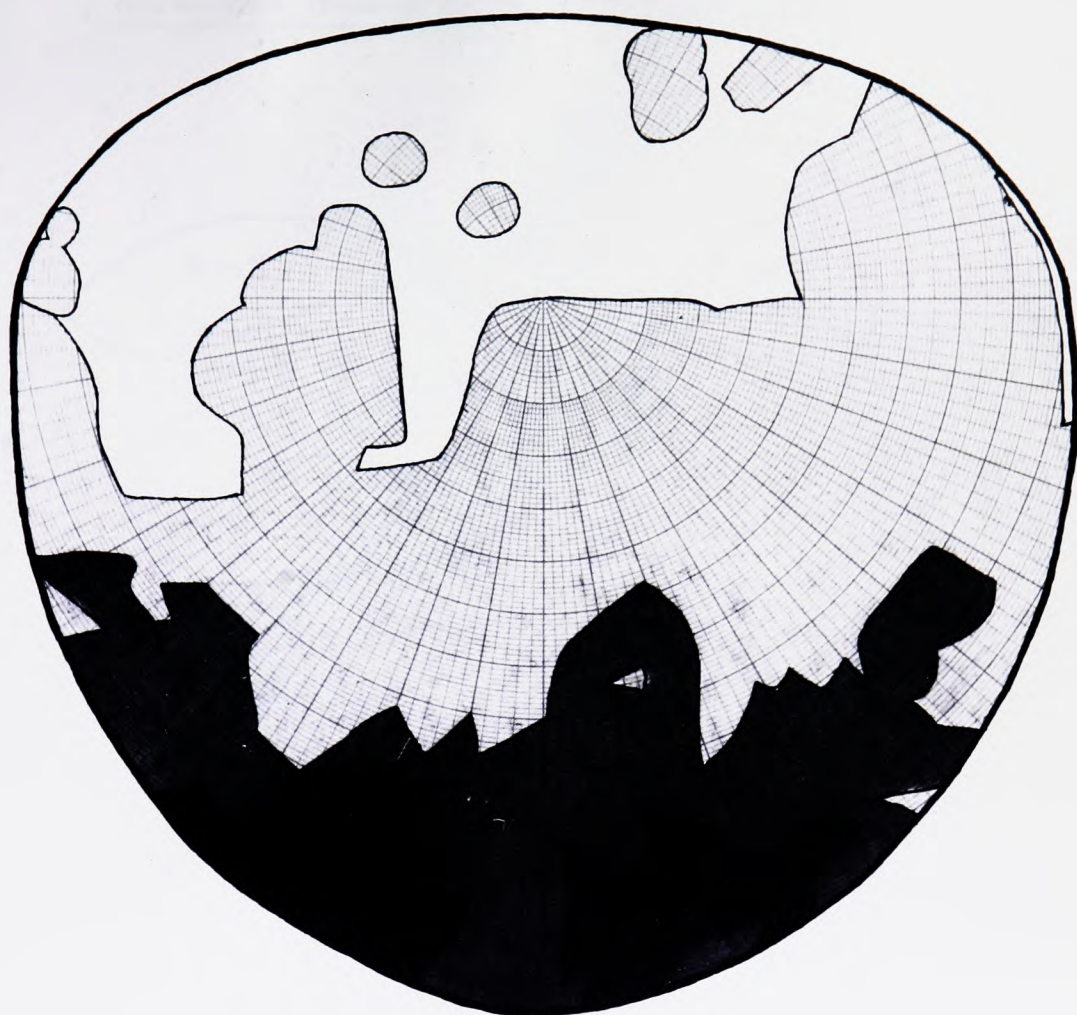
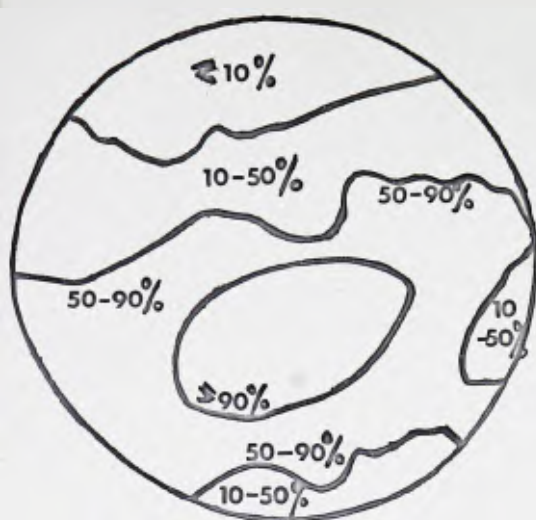


Fig.17. Frequency of Thymus drucei over the surfaces of 20 mounds at Yarnbury Castle, Wilts. (SU 035403), on 13 July 1969.

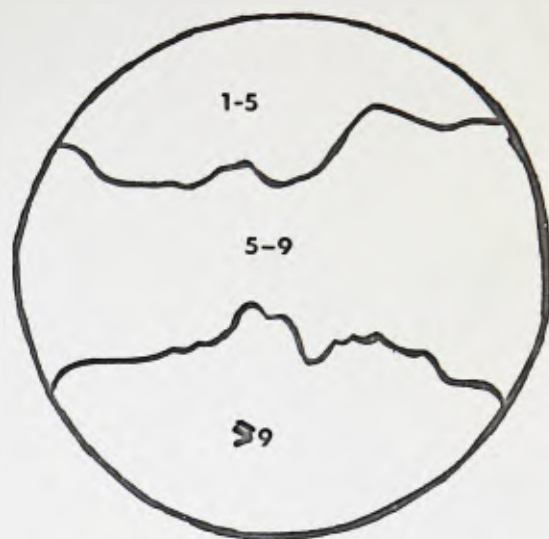
20 mounds in a population on a south-facing earthwork were selected at random. The surface of each ant-hill was mapped to scale on a cyclostyled sheet as if it were plane. Areas of Thymus were drawn in.

In the laboratory, zones of Thymus presence on each field map were defined by their radial angles from the centre and their percentage distances from the summit to the edge. They were transferred to the same diagram, which finally showed (above) the pattern of frequency of Thymus over the mound surface. The mean shape of the mounds was asymmetrical.

Fig.18. Mean aspect distributions of soil heaping and three species on ten random mounds at Beacon Hill, site 2, in 1971.



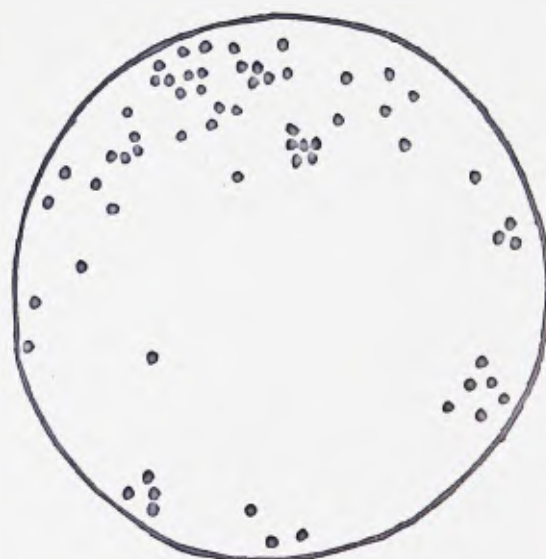
Heaped soil
% Frequency



Helianthemum chamaecistus
Frequency



Festuca rubra
Frequency



Leontodon hispidus
Total distribution

Table 13. Annuals apparently confined to ant-hills in certain areas.

- Aira carvophylla Worm's Head, Gower, Glam. (June 1970)
- Aira praecox Worm's Head, Cefn Bryn, and Llanmadoc Down, all in Gower, Glam. (June 1970); Silwood Park, Ascot Berks. (Waloff & Blackith 1962).
- Antennaria arvensis Site H, my plot, Beacon Hill, Oxon (1968); Earl's Hill, Salop (June 1972); Bowling Alley, Wytham Woods, Oxon. (May 1972).
- Arenaria serpyllifolia West Hill, Scratchbury and Cotley Hills, and White Sheet Downs, all Wilts (July 1969); Lullington Heath, Sussex, Sites 1, 2 and 3, near tumulus (see map, Appx. 16) (October 1971); Beacon Hill, Oxon on site 1, site 3, my plot, and sites M and N on the map in appendix 29.
- Bromus ferrugineus Worm's Head, Gower, Glam. (June 1970).
- Cardamine hirsuta Site C (map, Appx 29) Beacon Hill, Oxon (September 1971)
- Catanodium rigidum my plot, Beacon Hill, Oxon (August to October 1969)
- Cerastium holosteoideum West Hill, Scratchbury and Cotley Hills, Camp Down, White Sheet Downs, and site near Brixton Deverill, all Wilts. (July 1969); Winspit Bay, Dorset (April 1970); Worm's Head, Gower, Glam. (June 1970); Lullington Heath, Sussex, site 1 (October 1971); My Lady's Seat, and Bowling Alley, Wytham Woods, Berks (May 1972); my plot, and N. slope, Beacon Hill, Oxon (1969); Pfeiffer (1955).
- Cerastium semidecandrum Site 1 (see Map, Appx. 29) Beacon Hill, Oxon (June 1970)
- Cochlearia danica Winspit Bay, Dorset (April 1970)
- Errophila verna Worm's Head, Gower, Glam. (June 1970); Bald Hill, Oxon (June 1971); my plot, Beacon Hill, Oxon (June 1968); Messenger (1971), in Rutland.
- Filago minima Earl's Hill, Salop (August 1969)
- Myosotis arvensis around site 1, Beacon Hill, Oxon (June 1970)
- Myosotis discolor Earl's Hill, Salop (June 1972)
- Myosotis ramosissima my plot, sites 1 and 3, Beacon Hill, Oxon (1969-71); Grose (1957) in Wilts; Messenger (1971) in Rutland
- Nardus maritima Bald Hill, Oxon (M. J. L. Percival, T. C. E. Wells, pers. comm.)
- Oenothera peruviana Silwood Park, Ascot, Berks. (Waloff & Blackith 1962)
- Polygonum rufivagum (conf. B. T. Styles) Beacon Hill, Oxon (1969)
- Ranunculus parviflorus Bowling Alley, Wytham Woods, Berks. (S. R. J. Woodell pers. c.)
- Sagina apetala Worm's Head, Gower, Glam (June 1970)
- Sagina procumbens Harding's down, Gower, Glam. (June 1970)
- Senecio vulgaris my plot, Beacon Hill, Oxon (September 1971)
- Sherardia arvensis Bowling alley, Wytham Woods, Berks. (S. R. J. Woodell pers. comm.)
- Stellaria media Site C (see map, Appx. 29) Beacon Hill, Oxon (1971-2)
- Teesdalia radicans Earl's Hill, Salop (June 1972)
- Trifolium dubium Worm's Head, Gower, Glam. (June 1970); Winspit Bay, Dorset (April 1970); my plot, Beacon Hill, Oxon (1969); Sunday's Hill, Wytham Woods, Berks (August 1967)
- Veronica arvensis West Hill, Stockton Down, White Sheet Downs, all Wilts. (1969); my plot, north side, and site 1, Beacon Hill, Oxon (1969-70); Messenger (1971) in Rutland.
- Veronica serpyllifolia Cunnor Hurst, Berks. (May 1972)
- Vicia hirsuta near railway, Chipping Norton, Oxon (July 1968)

*extent of "annual races" unknown.

hill annuals in calcareous grasslands are Myosotis ramosissima, Trifolium dubium and Veronica arvensis. Cerastium holosteoides, a (usually) perennial chamaephyte, often only occurs on ant-hills. A survey of the north side of Beacon Hill, Aston Rowant N.N.R. confirmed these distributions (Table 14). It also

Table 14. The frequency of several species on 287 ant-hills and 287 associated 0.25 m² pasture quadrats on the north side of Beacon Hill, Aston Rowant N.N.R., June-August 1968

Six random points were selected in the vegetation either side of the footpath which runs down the north side of Beacon Hill. Every ant-hill within 20 m of each of these points was sampled. A quadrat was placed 0.3 m away from each ant-hill in a random direction, and carefully searched.

	<u>% Frequency</u>	
	<u>Ant-hills</u>	<u>Surrounding pasture</u>
<u>Arenaria serpyllifolia</u>	11.8	
<u>Catapodium rigidum</u>	3.5	
<u>Myosotis ramosissima</u>	14.9	
<u>Veronica arvensis</u>	13.6	0.4
<u>Euphrasia officinalis</u> agg.	13.2	14.9
<u>Linum catharticum</u>	49.8	44.6
<u>Medicago lupulina</u>	34.3	30.5

Erophila verna, Iberis amara, Polygonum rurivagum and Trifolium dubium all occurred on one ant-hill.

showed that the annual Euphrasia officinalis agg. (E. nemorosa and E. pseudokernerii), the (usually) biennial Linum catharticum and the (short-lived) perennial Medicago lupulina were equally abundant on and off the mounds. Gentianella amarella (Table 12) is in the same category. All four of these species must reproduce by seed in short chalk grassland, but if they can do so, why cannot Arenaria, Myosotis, Veronica and Cerastium? Two factors may be important. Firstly, the seeds of all the

ant-hill confined species germinate mainly in autumn, when the vegetation surrounding the mounds is at its most luxuriant and the rosette hemicryptophytes are in full leaf. On the other hand, the seeds of all the ant-hill indifferent species germinate mainly in spring. For example, Linum catharticum embryos have a chilling requirement of at least six weeks at 5°C (pers. obs.). This chilling requirement is usually satisfied by December in the field but germination is prevented until spring by low soil temperatures (S.C. Clark, 1969, pers. comm.). In spring, short chalk grassland swards often have exposed soil, partly because the leaves of rosette hemicryptophytes which died in autumn have not been replaced; seedlings can easily establish themselves in this non-competitive situation. Secondly, in contrast to the ant-hill confined group, the ant-hill indifferent group may have independent sources of nutrient supply, which could help them to withstand competition from nearby perennials. Medicago lupulina has nitrogen-fixing bacteria in root nodules and a seed which weighs 1220 µg, about seven times that of Cerastium (177 µg). Euphrasia spp. are hemiparasitic and in their nutrition are likely to resemble Odontites (Yeo, 1969, pers. comm.) which, as Govier et al. (1967,68) showed, can take up inorganic ions, water, amides, amino acids etc. from its host. Gentianella amarella is mycorrhizal and there is a report (Salisbury, 1970, pers. comm.) of mycorrhizae in Linum catharticum; mycorrhizae might improve the mineral nutrition of these species.

Carex flacca, Cirsium acaule, Filipendula vulgaris, Helictotrichon pratense, Leontodon hispidus, Plantago lanceolata, P. media and Poterium sanguisorba are the species which most

consistently maintain lower population densities on the mounds than in the pasture. Plants of Cirsium, Poterium and Filipendula are particularly uncommon on ant-hills, and one factor contributing to their absence there could be the inability of plants flowering in the sward to disperse their heavy fruits onto the surface of the mounds. Evidence given in Chapter 5 suggests that many of the species above depend on their fruits to colonise ant-hills. The 'banks' of viable seed in mound and pasture soils were compared in an experiment described in detail in Appendix 24 and summarised in Table 15. The seeds of Carex flacca and

Table 15. Total estimated viable seed contents of roughly equal weights of ant-hill and surrounding soil taken from my Beacon Hill plot at Aston Rowant N.N.S., Oxon in April 1969.

Paired soil samples of the same surface area were taken from each of 25 random mounds and the pasture nearby, and kept moist in a cold frame at Oxford for nearly nineteen months. They were churned up at intervals, and the seedlings which had emerged were identified and removed. All the species which had more than 20 emerging seedlings are listed below. The experimental details and results are in Appendix 24.

	AH	SV	SIG.† LEVEL
<i>Arenaria serpyllifolia</i>	143	1	**
<i>Carex flacca</i>	0	70	**
<i>Crepis capillaris</i>	5	23	N.S.
<i>Fragaria vesca</i>	28	127	N.S.
<i>Helianthemum chamaecistus</i>	38	123	N.S.
<i>Holcus lanatus</i>	26	275	**
<i>Linum catharticum</i>	84	52	*
<i>Plantago lanceolata</i>	9	14	N.S.
<i>Prunella vulgaris</i>	24	37	N.S.
<i>Ranunculus repens</i>	1	46	N.S.
<i>Rubus fruticosus</i>	6	14	N.S.
<i>Thymus drucei</i>	28	8	N.S.
<i>Veronica chamaedrys</i>	177	171	N.S.
<i>Viola hirta</i>	1	92	**

† Two-tailed Wilcoxon signed-ranks tests for matched pairs were used. N.S., $P > 0.05$; *, $0.05 > P > 0.01$; **, $P < 0.01$.

Viola hirta, both heavy seeded species never seen to fruit on ant-hills, were practically confined to pasture soil. Another factor which could lower the population sizes of these species on ant-hills is burial of their seedlings by ant-heaped soil; all seven dicotyledons listed above have a rosette habit.¹ Burial of Leontodon seedlings on the south sides of the mounds in Fig. 18 could account for its greater frequency on northerly aspects.

Grubb et al. (1969)'s work on the Lullington Heath ant-hills is discussed in Appendix 16 in the light of my own observations.

3.5. SUMMARY

I compare the vegetation on and off L. flavus ant-hills at thirteen calcareous grassland and chalk heath sites in southern England. Thymus drucei, Helianthemum chamaecistus and Cerastium holosteoides and annuals, like Arenaria serpyllifolia, are more abundant on the mounds than in the sward, but many species are consistently uncommon on ant-hills, including Carex flacca, Cirsium acaule, Filipendula vulgaris, Helictotrichon pratense, Leontodon hispidus, Plantago lanceolata, P. media, and Poterium sanguisorba. Pseudoscleropodium purum is sometimes far more abundant on northern than southern aspects, and Thymus and Helianthemum may occur mainly on the south sides of mounds, especially when soil heaping by the ants is concentrated there. I discuss some of the factors which might influence these patterns.

¹Burial of seedlings of these species is shown to be important, in Chapter 5.

CHAPTER 4

THE DISTRIBUTION OF SPECIES ON ANT-HILLS OF A WIDE RANGE OF SIZEAND ACTIVITY AT ASTON ROWANT N.N.R., OXON.4.1. INTRODUCTION

In chapters 2 and 3, I showed that the dramatic patterns of some species in relation to large mounds at a moment in time may be repeated at more than one site. These consistent patterns are likely to be due to an interaction between the basic biology of each species and the special properties of ant-hills. This interaction must be dynamic, continuing whilst a mound exists; thus to fully explain the pattern of a species, one should follow its immigration, fluctuations in population size and extinction on a mound from the time when the first heaped soil is seen. However, few useful data would be gained by following the large scale natural changes in vegetation on the same ant-hill over two or three years (e.g. by mapping the positions of mature rosettes, the distribution of Thymus drucei and Helianthemum chamaecistus) since these changes occur slowly and some ant-hills are at least tens, if not hundreds, of years old. Since I wished to gain an insight into the relative abundances of some species on mounds of different sizes and ant activities before investigating their population biology in detail (Chapter 5), I surveyed the vegetation on and off 206 mounds in a plot at Beacon Hill, Aston Rowant N.N.R., and tried to deduce dynamic changes in the composition of the ant-hill flora from a static sample.

I designed the survey to answer three main questions:

- (i) Is there a correlation between the presence or abundance of a species on ant-hills and its occurrence or abundance in the grassland nearby?
- (ii) Is there a 'succession' of species on mounds of increasing size (which may reflect increasing age)? If not, do the abundances of some species vary with the volume or ant-activity of the mounds on which they occur?
- (iii) How are rosettes of Carex flacca, Leontodon hispidus, Poterium sanguisorba etc. distributed on mounds of different sizes and soil-heaping activity?

Aston Rowant N.N.R., Oxon. (O.S. Grid reference SU727972) is situated on the western scarp of the Chilterns. The mean annual air temperature at the top of the scarp at this point is about 10°C, with a mean annual maximum of 14°C and minimum of 5.5°C. The total annual rainfall there is about 827 mm, compared with 635 mm on the plain below. The reserve falls within the region of Britain with the highest saturation deficit in the summer (Hemsley & Woodman 1960); Green (1959) estimated that in an average year, 'potential evaporation will begin to exceed rainfall towards the end of April and will continue to do so until the end of September. The total average water deficit (making no allowance for soil moisture storage etc.) would be about 164 mm.'

Beacon Hill projects from the scarp in a north-westerly direction and has smooth contours with a flat top reaching 244 m, about 122 m above the Aylesbury plain. The hill is mainly composed of Upper Chalk (Cretaceous), but a Clay-with-Flints

deposit of irregular shape and depth overlies the plateau in places. I used a 0.4 ha plot on the top of Beacon Hill (see folding-out map, Appendix 29) for ant-hill research, including this survey. All parts of 'my plot' were probably ploughed at least once between 1880 and 1920, but the short, closely rabbit-nibbled chalk grassland sward which developed has been slowly invaded by scrub since 1954 because of the lower grazing intensity since myxomatosis.¹ Sheep grazed the plot occasionally between 1966 and 1970; rabbit grazing is slight, mainly confined to the mounds, and most intense in the north-eastern half and the southern corner. Much of the plot is covered by a short, species-rich sward growing on shallow mull rendzinas 10-30 cm deep derived from the Upper Chalk, but there are large patches of taller, less diverse vegetation with a higher cover of coarse grasses (e.g. Dactylis glomerata, Brachypodium sylvaticum, Helictotrichon spp., Arrhenatherum elatius) on soils (often >40 cm deep) derived from fingers of Clay-with-Flints. The Clay-with-Flints was mainly formed from Eocene Reading Beds, but may contain some loessic material (Beckett 1960); the soils derived from it are reddish-brown, have a lower pH than those without Clay-with-Flints influence (about 5.0-6.0 against 6.7-7.3, in samples taken from the top 5 cm of mineral soil, pH measured in 0.01M CaCl₂), a heavy texture, no chalk fragments and a predominance of flints. In April 1968 the plot contained 1947 ant-hills of a wide range of size and 'activity'. It contained most of the species which, at the other chalk grassland sites surveyed, had been most abundant and had had the most

¹ The history of vegetation on my plot is described more fully in Appendix 21.

interesting patterns in relation to ant-hills. It could be visited frequently, the 'small boy' factor was absent, and a weather station, read daily, was situated 50 m away. A 40 x 40 m control area, containing 178 ant-hills, 68 of which were large, was fenced in 1968 to prevent interference with experiments by grazing animals. However, voles, birds and deer still slightly affected the ant-hill vegetation there.

4.2. METHODS

4.2.1. Vegetation sampling

Since there were sometimes great differences in the composition of ant-hill vegetation, even between nearby mounds of the same size, shape and 'activity', a large sample size was necessary to separate correlations of species patterns and environment from the 'random noise'. I took a systematic sample¹ of 206 ant-hills in the north-eastern half of my plot.² A random sample would have had to be taken by the time-consuming process of numbering each mound and re-locating those selected for sampling, since they were not evenly-distributed over the area. Parts of the plot where ant-hills were sparse might not have been represented in a random sample, but would be in a systematic one, and I was interested in trends in species abundance over the whole area. I placed strings 10 m apart from SE-NW across the sampled site and walked in zig-zag fashion between each adjacent pair of strings, sampling every fifth mound I found. A 0.25 m² surrounding vegetation quadrat, placed

¹The data were collected from August to November 1969.

²The sampled site included about 5 m of the north-eastern edge of the control area.

TABLE 16.

Comparison of vegetation-sampling by point quadrats and
subjective estimation

(i) General.

<u>PROPERTY</u>	<u>POINT QUADRATS (P.Q.)</u>	<u>SUBJECTIVE ESTIMATION</u>
Randomisation and pin positioning.	Takes time	Not needed
Precision/unit time	Probably less (Appendix 26)	Probably greater (Appendix 26)
Accuracy	Overestimation, possible, even with sharpened pins, since axis of pin has finite diameter (Goodall 1952)	Impossible to assess.
Unconscious bias	Sometimes possible in deciding what a pin has touched	Species which are straggly, or which have divided leaves, or which are in flower may be over-estimated. This possibility is the most serious disadvantage of the method.
Species	Not only rare but also fairly abundant species may be missed (Watson 1960)	Rare species often missed (Appendix 26) but census more complete than with P.Q..
Understanding of vegetation structure	Less: time spent following pins, noting results.	More: vegetation examined thoroughly.
Tall vegetation	Difficult to follow point of pin, even when pin inclined. Rest of vegetation must be disturbed. Pin itself pushes vegetation aside as it is lowered and alters the "true" cover.	Disturbance necessary, but cover easily assessed. Disturbance might change cover (e.g. of rosette species with upright leaves growing in tall swards).
Wind	Recording impossible in tall vegetation.	Recording little affected.
Time per sample	Longer if 20-60 random points used	Shorter.

(ii) Ant-hills

*AH = ant-hill

*SV = surrounding vegetation.

<u>PROPERTY</u>	<u>POINT QUADRATS</u>	<u>SUBJECTIVE ESTIMATION</u>
Randomisation time	Takes longer than in SV* quadrats as exact positions of AH* summit and perimeter must be known before randomisation	Not needed.
Randomisation	(i) Random points determined as if AH surface horizontal, and vertical pins used, as at Rhossili Down. Then a) points not random, as density higher on flat tops than on sloping sides of a mound b) species on sides of mounds might be underestimated and the comparison with sward invalidated. (ii) Pins placed at various angles <u>perpendicular</u> to AH surface. Randomisation over 5-dimensional surface by computer model. But this, and the siting of the random points on the AH surface, would have been impossibly time-consuming	This method unnecessary; AH surface was not regarded as horizontal. % cover regarded as proportion of AH surface covered by perpendicular, not vertical projection onto it of aerial parts of species.

Table 16 (continued)

<u>PROPERTY</u>	<u>POINT QUADRATS</u>	<u>SUBJECTIVE ESTIMATION</u>
Adjustment of estimates to account for AHs of different size	Taken care of in randomisation	AH size varied greatly. My concept of % cover had to be changed from one AH to the next.

30 cm away from the mound in a random direction, was associated with every alternate mound I sampled. I recorded the positions on the plot of all the sampled ant-hills and pasture quadrats (see distribution maps, Appendix 27).

I estimated the percentage covers¹ of all species on ant-hills subjectively, instead of using the point-quadrating technique which I had used to describe the vegetation on and off the mounds at the north end of Rhossili Down (Section 2.3). The two methods are compared in Table 16, where I also mention some special difficulties encountered in using point-quadrats on ant-hills. When I subjectively sampled two quadrats and an ant-hill on my plot five times each, the precision was high (Appendix 26), so that considerable credence can be attached to comparisons between my subjective estimates of percentage cover. Greig-Smith (1964) and Hershaw (1964) wrongly equate the errors in the subjective estimation of percentage cover in quadrats with those inherent in the $d = \text{dominant}$ to $r = \text{rare}$ method of subjective frequency estimation used by Tansley and his colleagues.

Frequency in Tansley's sense is a nebulous concept, usually used

¹Any biological variable should be measured on at least a 30-point scale if possible (e.g. the rule of thumb of Sokal & Rohlf, 1969, p.15) to minimise the errors if a variate is placed in the wrong class and to minimise the variance between several estimates of the same parameter, thus allowing more efficient significance tests. Percentage cover estimates can be converted into the Domin or Braun-Blanquet scales if needs be, but these scales are arbitrarily asymmetrical and have too few classes to be useful for statistical analysis.

to describe large areas, but the percentage cover of a species in a small gridded quadrat has an absolute value. A high degree of accuracy and precision can be achieved by an experienced worker estimating the percentage covers of all species in a small gridded quadrat.

When each ant-hill had been sampled, I put the 'spiders-web' (Fig. 19) over the mound with its centre on the summit. I drew the outline of the ant-hill's surface to scale on a cyclostyled plan of the 'spider's-web', and mapped every rosette of Cirsium acaule, Poterium sanguisorba, Hieracium pilosella, Leontodon hispidus, Plantago lanceolata, Carex flacca and Fragaria vesca. I noted the number of partially buried rosettes of each of these species on each ant-hill. I recorded each mound's mean height and diameter, vegetation height, the volume of newly-heaped soil, the % cover of bare soil and evidence of animal activity as described in Appendix 3, where the formula for calculating ant-hill volume is given. The accuracy of my estimates of the volume of newly-heaped soil is discussed in Appendix 25.

4.2.2. Data analysis

I devised a pencil-and-paper method for analysing my results, in which each species was dealt with independently, and absences from ant-hills apparently due to the absence of the species from the sward nearby were allowed for. Each sampled mound was represented by a point on a two-dimensional scatter diagram in which the axes are (i) 'Ant-hill burial activity', the percentage of the total volume of the ant-hill composed of newly-heaped soil, and (ii) the cubed root of the volume of the

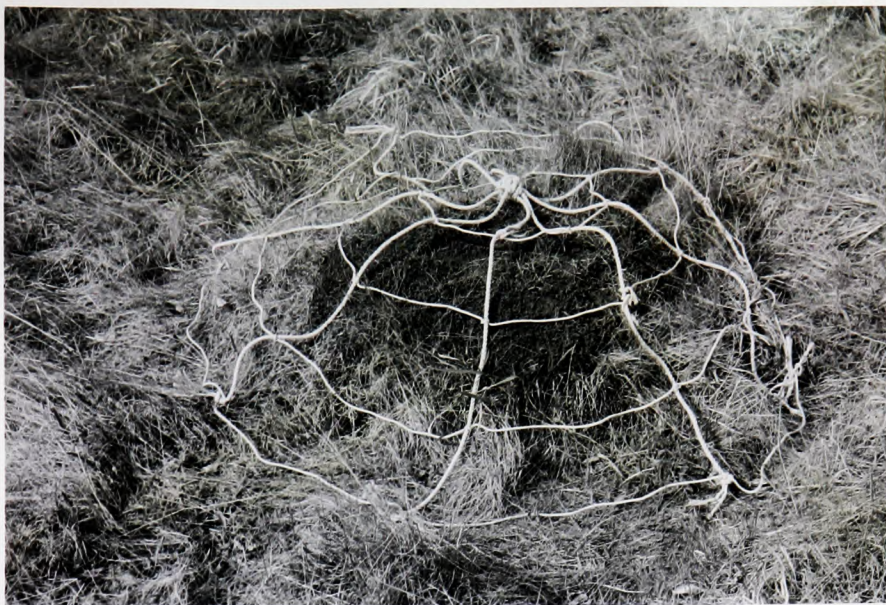


Fig. 19. The 'spider's-web'.

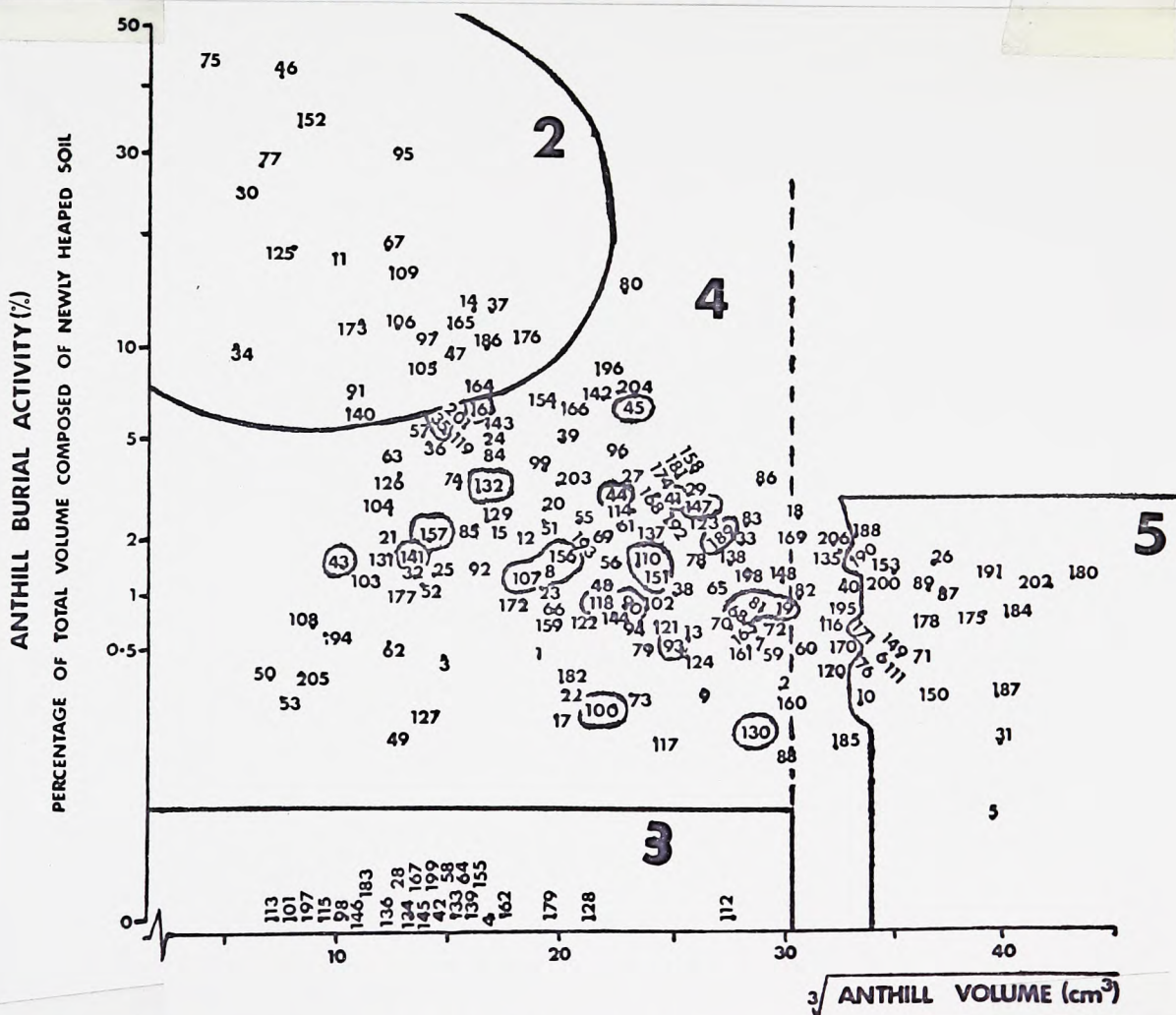


Fig. 20. The positions of the 206 sampled ant-hills on the scatter diagram of ant-hill burial activity against $3\sqrt{\text{ant-hill volume}}$. Groups 2, 3 and 5 were small and active, abandoned, and large and active, respectively. Group 4 was selected at random from those mounds, to the left of the vertical dotted line, which were not in any of the other groups. All 24 mounds in group 4 are ringed.

mound in cm^3 (Fig. 20). I made both axes non-linear to spread the points over the diagram. The scale of the vertical axis is the square root of the angularly-transformed 'ant-hill burial activity'. The two axes are functions of one another and 'ant-hill burial activity' and 'ant-hill volume' are negatively correlated to some extent. Large mounds cannot have a high proportion of their volume composed of newly-heaped soil, because an ant colony can only heap up a small volume of soil a year (maximum found at Aston Rowant in 1970 and 1971, 1600 cm^3).¹

A measure of the abundance of species X on each ant-hill was placed over each dot on its scatter diagram. The measure used was:

$$A_x = \frac{C_x}{\sum_{x=1}^z C_x}$$

where C_x was the estimated percentage cover of species X on the ant-hill and z = total number of species recorded on the mound. This ratio estimates the 'importance' of a species as a component of the vegetation on a mound, and compensates for the fact that total percentage covers often differ greatly between mounds merely because of different degrees of recent burial by soil heaped up by the ants.

On the scatter diagram of species X there remained dots to which no measure of abundance had been added, which represented ant-hills on which species X did not occur. Such mounds might

¹ The importance of this in ant-hill ecology is discussed in Chapter 5.

have had species X growing nearby; on the other hand, if the species were absent from the vicinity, the probability of its propagules reaching the mound would be vanishingly small. I wished to distinguish these two cases, so that the relationship between the abundance of species X and the axes would not be obscured by those absences from ant-hills which were due to its absence from the nearby pasture. Thus, on a map of the distribution of species X over the plot in the pasture quadrats, I defined zones of species presence and absence by drawing lines round all the groups of points at which the species had been found. Then, using a map of the distribution of species X over ant-hills in the plot, I concentrated on each ant-hill on which the species did not occur. If it fell within a zone of species presence in the sward, a zero was added to its dot on the scatter diagram. If it fell within a zone of species absence, its dot was deleted. Correlations between the presence or abundance of species X and ant-hill 'activity' or 'volume' were revealed when trends across the resulting graph were examined.

This method is similar to Whittaker's (e.g. 1967, 1970) 'gradient analysis'. Its main shortcoming¹ is that I have decided subjectively that 'ant-hill burial activity' and 'ant-hill volume', or factors highly correlated with them, account for more of the variation in species abundance on ant-hills in my plot than other 'environmental' variables.

¹The positions of abandoned mounds on the diagram are only correct if the volumes of ant-hills do not decrease after the *L. flavus* colony has died. Baxter and Hole (1967) found one *Formica cinerea montana* mound which declined in height from 30 cm to 8 cm when abandoned.

4.2.3. 'Mean Affinity Indices'

For each species in my sample, I calculated an 'Affinity Index' (AI) for ant-hills, from the raw data, as follows:

$$AI_x = \frac{10^3 \sum_{206AH} C_x}{\sum_{206AH} C_x + \sum_{103SV} K_x \left(\frac{\sum_y \sum_{206AH} C_x}{\sum_y \sum_{103SV} K_x} \right)},$$

where C_x is the estimated percentage cover of species x on an ant-hill (AH), K_x is the estimated percentage cover of the same species in a surrounding vegetation (SV) quadrat), and y is the total number of species recorded in the survey. The index ranged from 1000 for species confined to ant-hills (Arenaria serpyllifolia, Cerastium holosteoides, Trifolium dubium) to 0 for species absent from the mounds (Otenidium molluscum, Frullania tamarisci, Lophocolea bidentata). Festuca's AI was 483. I calculated a 'Mean affinity index' ($\overline{AI}_s$), indicating the relative proportions of 'ant-hill and pasture species' in an ant-hill or pasture sample (S), as the weighted average of the 'Affinity Indices' for all the species present in the sample; thus:

$$\overline{AI}_s = \frac{\sum_z \left(\frac{C_x}{\sum_z C_x} \cdot AI_x \right)}{\sum_z C_x},$$

where z is the total number of species in the sample.

4.3. RESULTS

Full results are given in Appendix 28.

The vegetation on the mounds is shorter than that in the

surrounding pasture (Fig. 21). Signs of grazing were seen on 168 mounds out of 206, but only in 4 of the 103 surrounding vegetation quadrats.¹ Rabbit grazing might have contributed towards the lower plant cover on ant-hills, as discussed in section 1.3.4. Rabbit droppings occurred on 153 of the mounds. Grazing and defaecation were not confined to particular areas of the plot, nor were they more frequent on ant-hills of certain sizes or activities.

There is a rough correlation between the number of species on a mound and the number of species in the pasture nearby (Fig. 22). The areas of the plot with fewest species, both on and off ant-hills, tend to be those with the tallest surrounding vegetation.²

When I mapped the presence of each species separately for sampled pasture quadrats and sampled ant-hills there was a marked similarity in the pattern of most species on and off the mounds in my plot.³ For instance, Helianthemum chamaecistus (Fig. 23) and Hieracium pilosella (Fig. 24) were both absent from the tall vegetation in the easterly corner, but did not occur in the ant-hills there.⁴ Three species were selected at random from the

¹ Observations on marked Festuca plants which had been recently grazed showed that in late summer and autumn signs of grazing persisted for about 2 months.

² When the data for the thirteen calcareous grassland and chalk heath sites (described in Chapter 3) were combined, there was a highly significant positive correlation between the number of species on a large ant-hill and the number of species in its associated surrounding vegetation quadrat ($r = 0.525$, $n = 104$, $P < 0.01$ from $\rho = 0$).

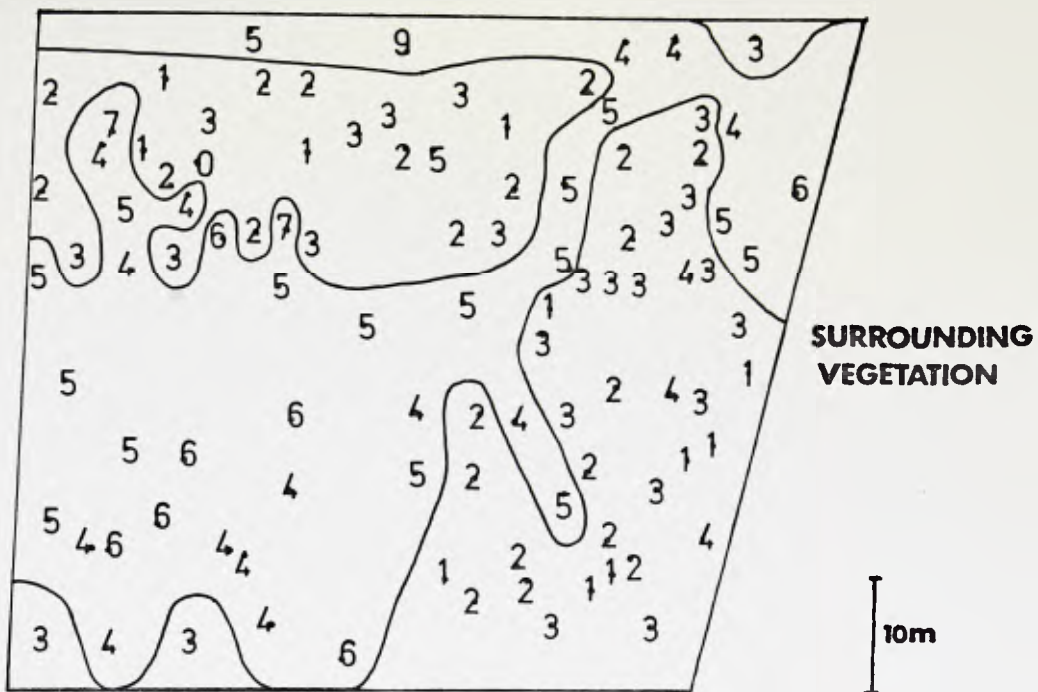
³ Only the 27 species which each occurred on more than 10 of the 206 ant-hills sampled were mapped.

⁴ Asperula cynanchica, Carex caryophyllaea, Dicranum bonjeanii, D. scoparium, and Medicago lupulina had exactly similar distributions.

Vegetation Height**SAMPLED PATTERN AT N.E. END OF MY BEACON HILL PLOT**

Key :

0, 0 - 2cm;	5, 15-17;
1, 2 - 4;	6, 18-20;
2, 5 - 8;	7, 21-23;
3, 9 - 11;	8, 24-26;
4, 12 - 14;	9, 27-29.



The lines separate samples with vegetation shorter than 12cm from the rest.

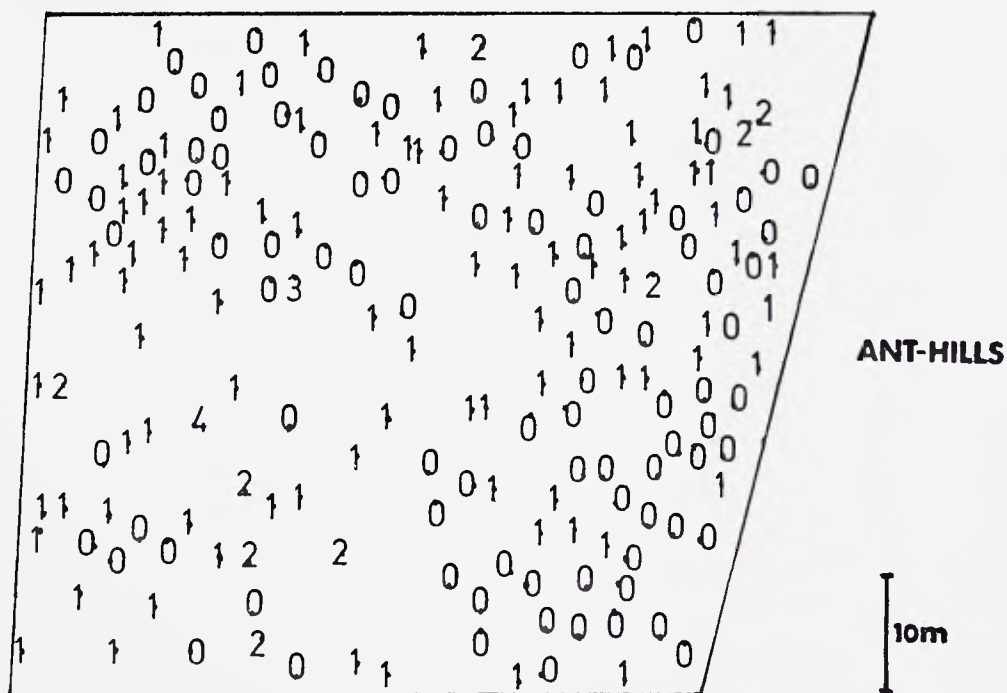
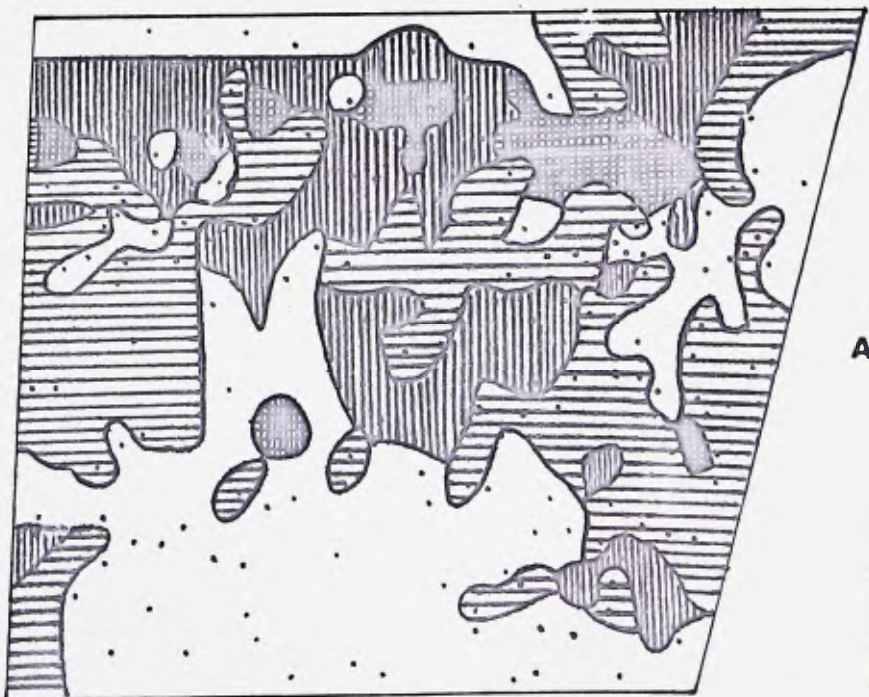
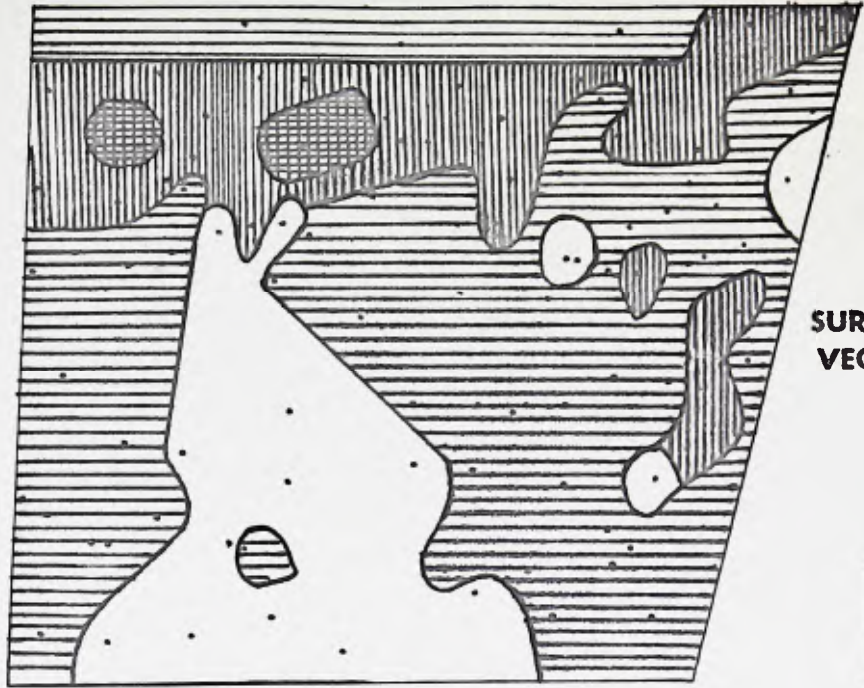


Fig.22

Total number of species per sample (AH or SV)

SAMPLED PATTERN AT N.E. END OF MY BEACON HILL PLOT



Total numbers of species on ant-hills were corrected for ant-hill area by an analysis of co-variance.

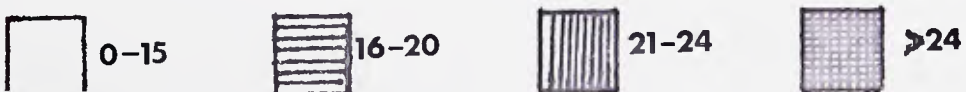


Fig.23

Helianthemum chamaecistus

SAMPLED PATTERN AT N.E. END OF MY BEACON HILL PLOT

Key: 1, 1%; 5, 17-24; 9, >54.
 2, 2-4; 6, 25-33;
 3, 5-9; 7, 34-43;
 4, 10-16; 8, 44-54;

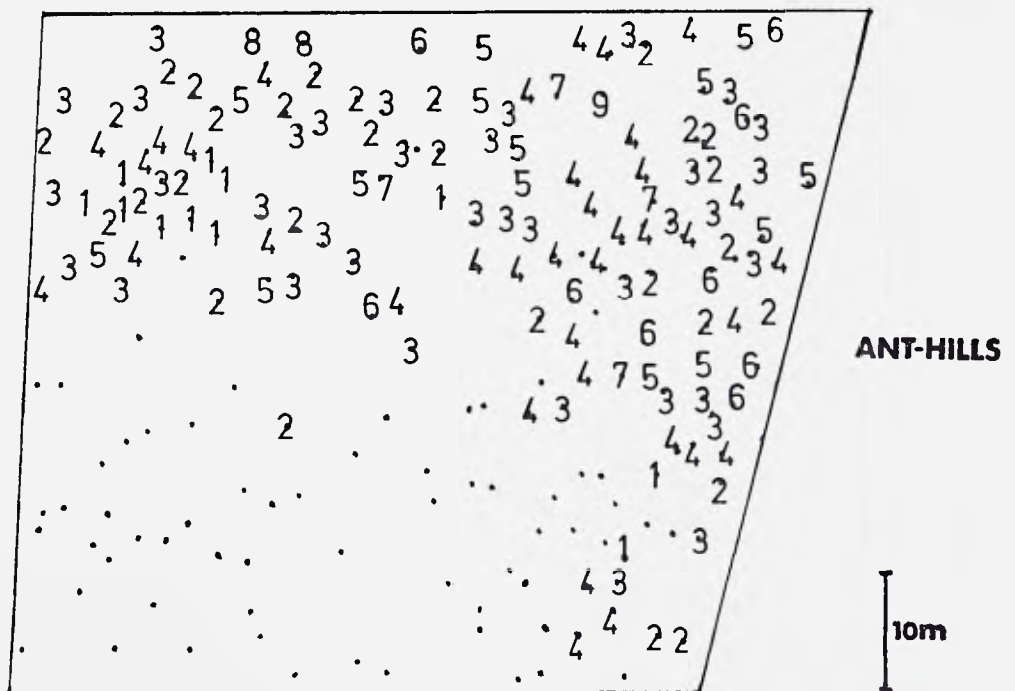
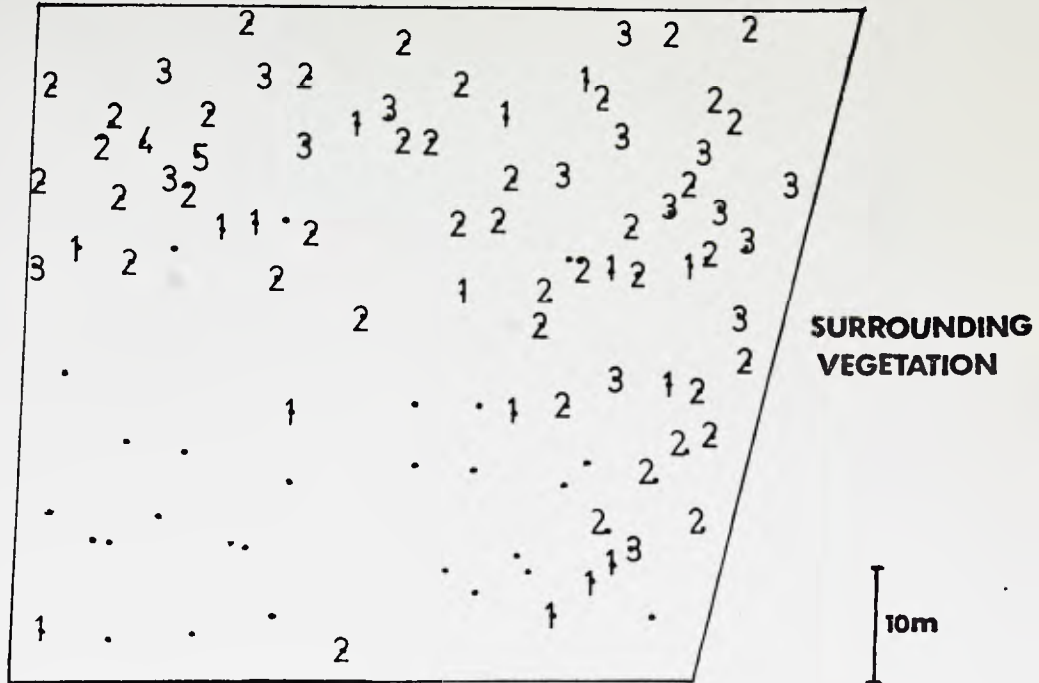
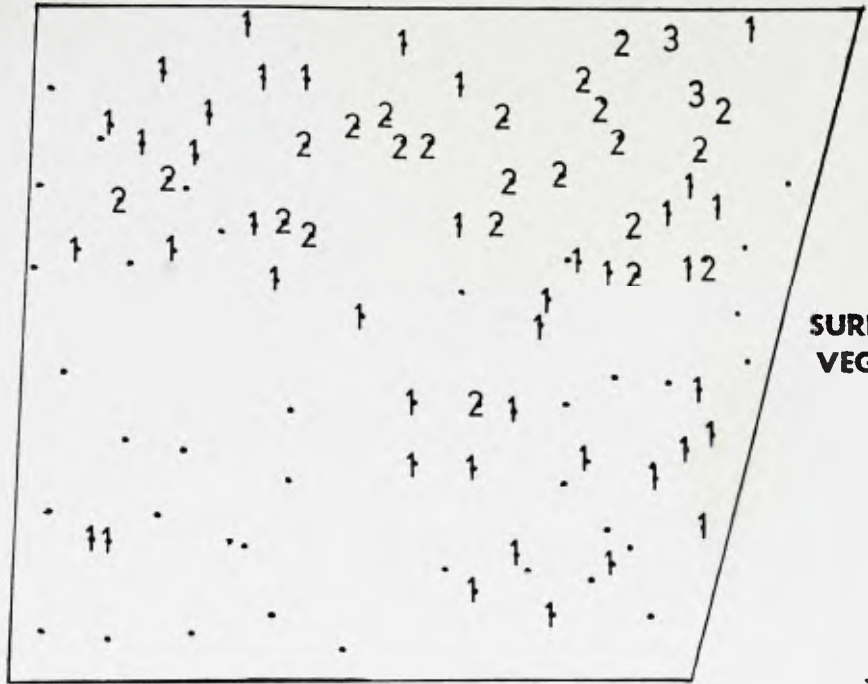


Fig. 24

Hieracium pilosella

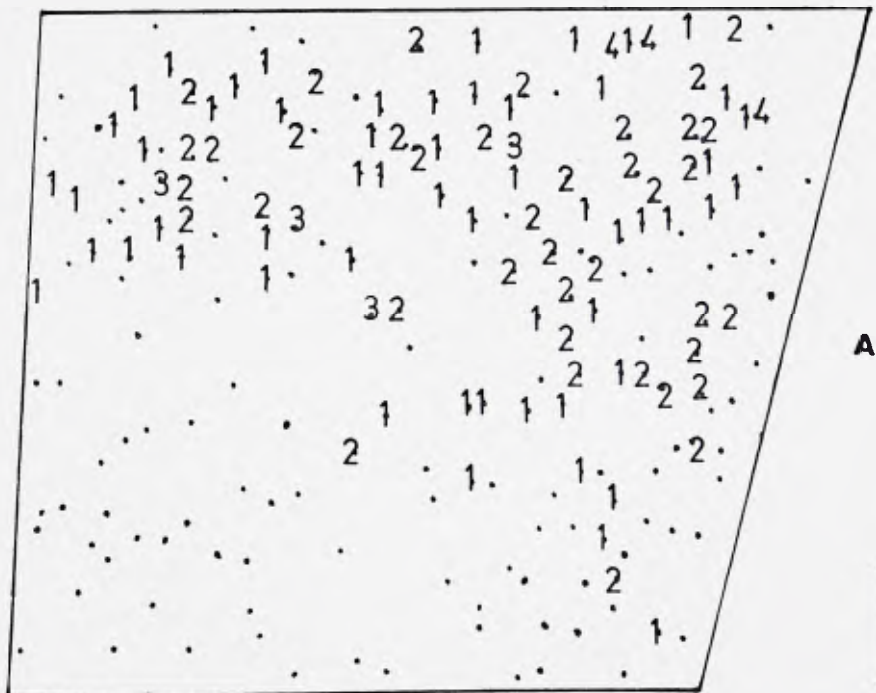
SAMPLED PATTERN AT N.E. END OF MY BEACON HILL PLOT

Key 1, 1% 3, 7 - 13;
 2, 2 - 6; 4, 14 - 23.



SURROUNDING
VEGETATION

10m



ANT-HILLS

10m

remaining twenty-five and their patterns over my plot are also illustrated; Brachypodium sylvaticum (Fig. 25), Briza media (Fig. 26) and Prunella vulgaris (Fig. 27). There is general agreement between ant-hill and pasture maps. Nevertheless, there was no correlation for any species between its abundance (% of total plant cover) on and off the mounds.

The species with significantly different percentage covers on and off 38 large ant-hills in the sample are listed in Table 17.

Table 17. Species with significantly ($P < 0.05$) different absolute percentage covers on and off large ant-hills on the north-eastern side of my Beacon Hill plot

Methods. Attention was confined to the 103 mounds associated with a surrounding vegetation quadrat. 38 of these mounds, marked by an asterisk in the table in Appendix 28, exceeded the arbitrary criterion of being > 15 cm high and > 30 cm in diameter, which was used in Chapters 2 and 3. Significance tests were applied, in the manner described in Appendix 3, to all species with at least 4 presences in either ant-hill or surrounding vegetation.

Ant-hills

Carex caryophylla *M
Helianthemum chamaecistus **W
Medicago lupulina **W
Thymus drucei **N.T.

*, $0.05 > P > 0.01$;

**, $P < 0.01$;

N.T., not tested;

M, McNemar test (Sokal & Rohlf, 1969, pp.614-5);

W, Wilcoxon two-tailed test for matched pairs.

Surrounding vegetation

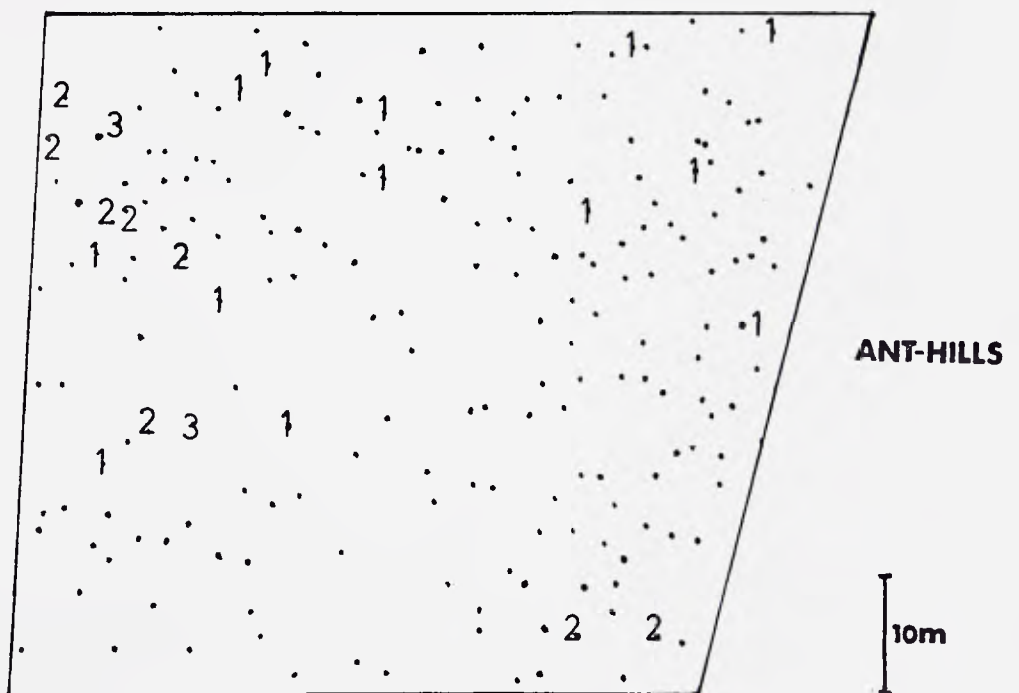
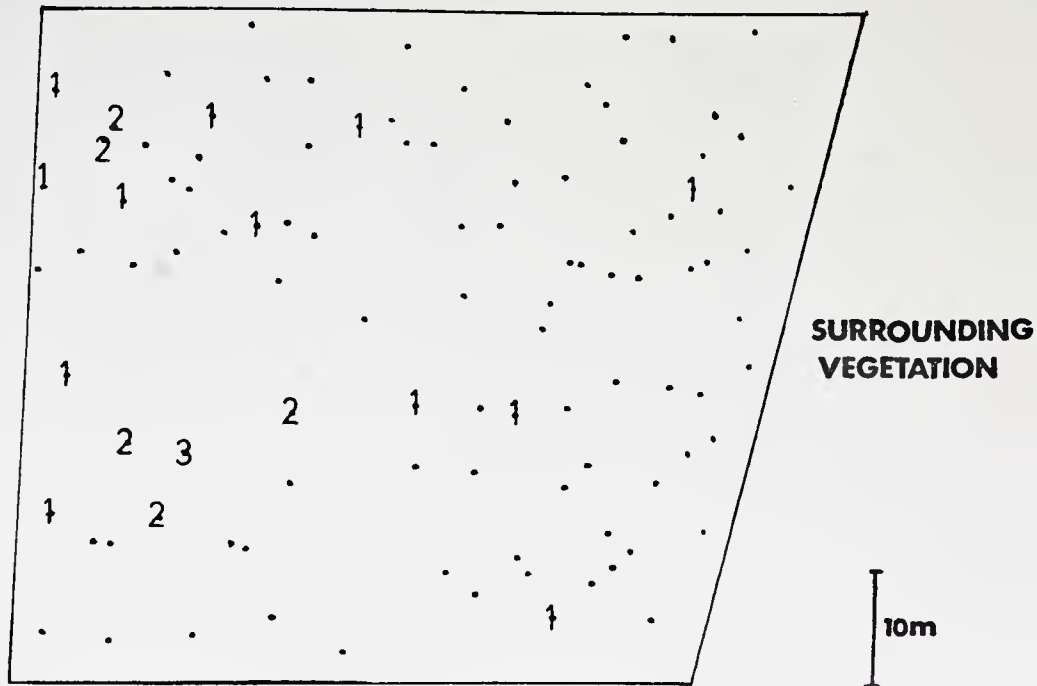
Carex flacca **N.T.
Cirsium acaule **N.T.
Dactylis glomerata *W
Festuca spp. **N.T.
Fissidens spp. **W
Fragaria vesca **W
Helictotrichon pratense **W
H. pubescens **W
Hieracium pilosella **W
Molcus lanatus *W
Hypochoeris radicata **W
Leontodon hispidus **W
Plantago lanceolata **W
Viola hirta **W
V. riviniana **M

Fig.25

Brachypodium sylvaticum

SAMPLED PATTERN AT N.E. END OF MY BEACON HILL PLOT

Key 1, 1%; 3, 7 - 15.
 2, 2 - 6;



Briza media

Key: 1,1%; 4,10 - 17;
 2,2-4; 5,18 - 26.
 3,5-9;

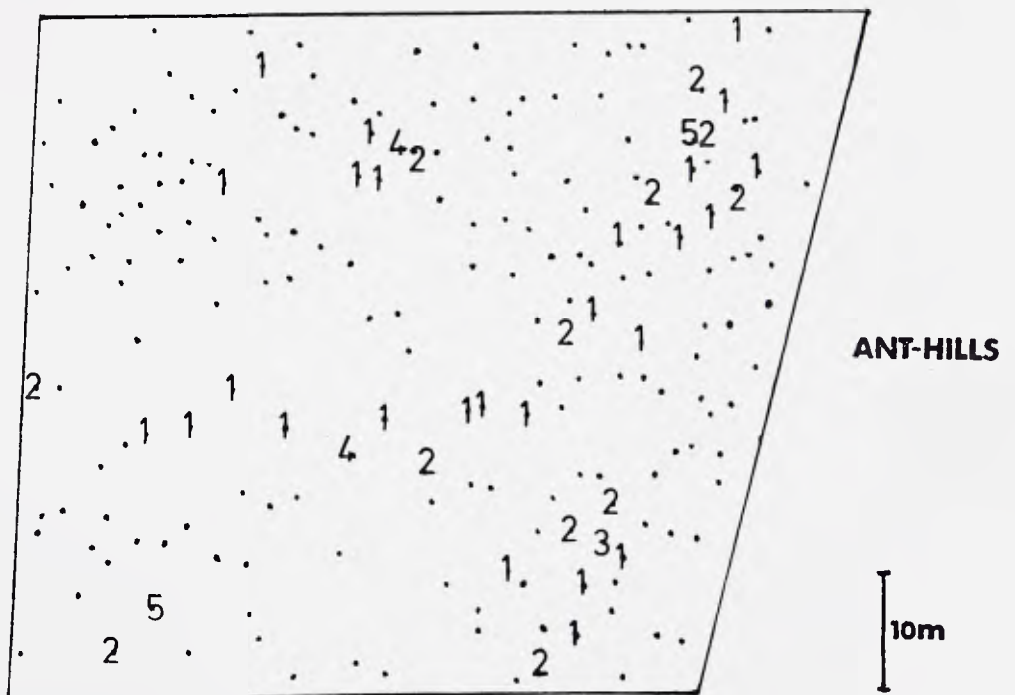
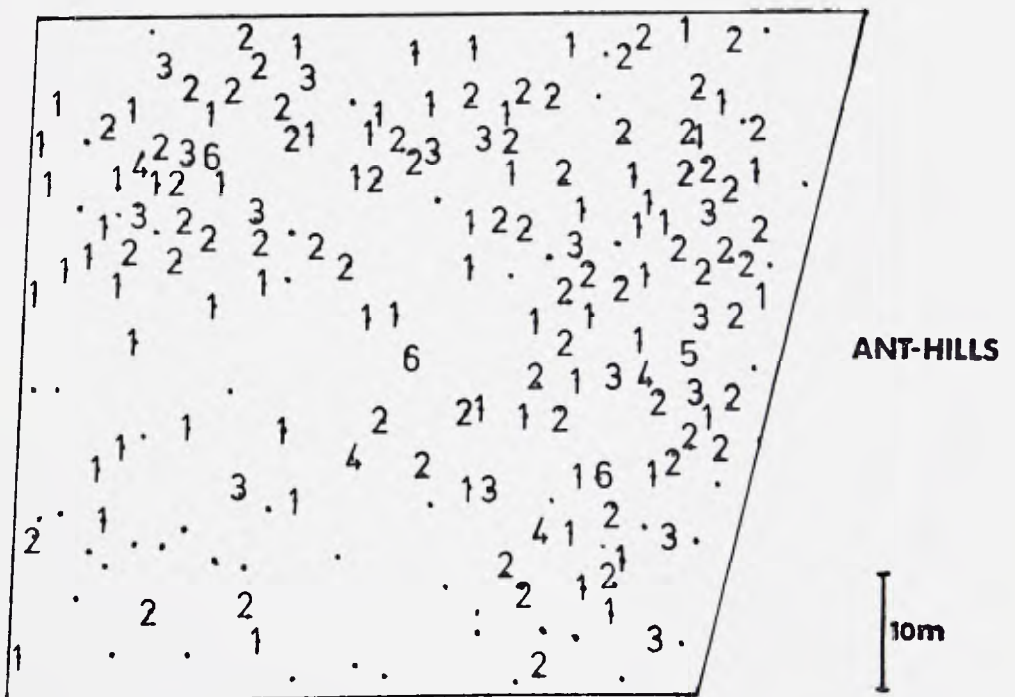
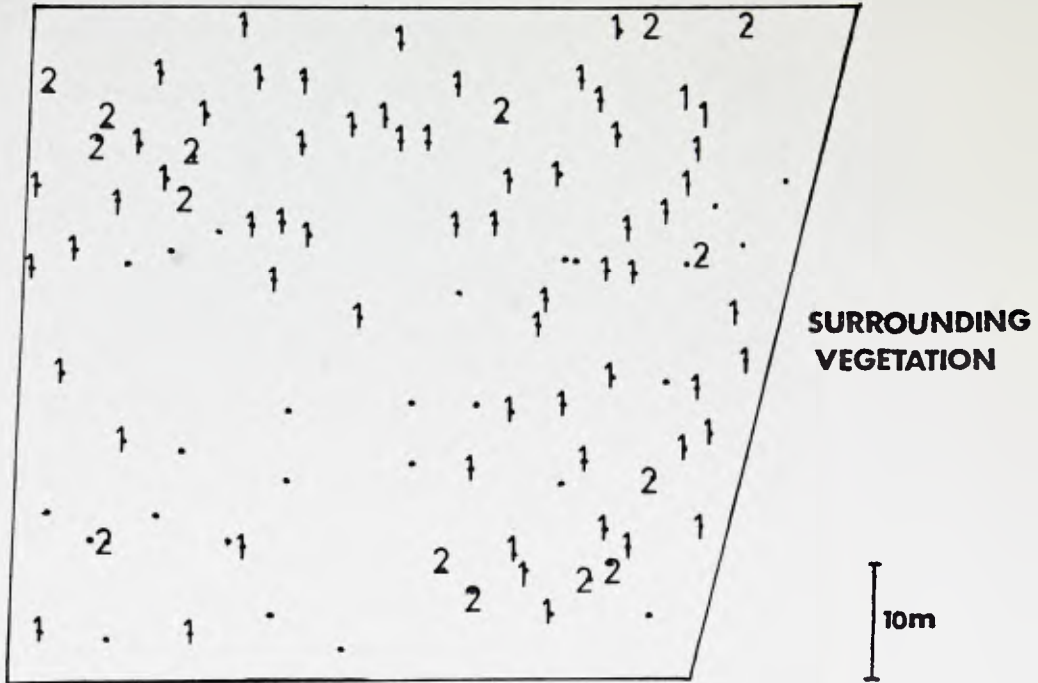


Fig.27

Prunella vulgaris

SAMPLED PATTERN AT N.E. END OF MY BEACON HILL PLOT

Key: 1, 1%; 4, 11 - 17;
 2, 2-4; 5, 18 - 26;
 3, 5-10; 6, 27 - 36.



Scatter diagrams of 'ant-hill burial activity' against the cubed root of ant-hill volume in cm^3 , constructed as described in section 4.2.2., were plotted for the twenty-seven species most frequent on ant-hills. Most species occurred sporadically on small mounds. The graphs of many of these species exhibited no vertical or horizontal patterns. I only illustrate here the species with unequivocal trends in frequency or abundance over the scatter diagram. I have assumed throughout that the abundance of a species on the scatter diagram is not confounded with the positions of certain ant-hills on my plot, because on the maps in Fig. 28 there is no obvious correlation between the volume or 'burial activity' of ant-hills and their position.

Thymus drucei and Helianthemum chamaecistus (Fig. 29) are both present on most small mounds, but whilst Helianthemum shows no marked trend over the scatter diagram, the proportion of mounds with a high Thymus component increases with ant-hill volume.

Arenaria serpyllifolia, Veronica arvensis and Cerastium holosteoides, all confined to ant-hills, occur only on active mounds (Fig. 30a).

Galium verum (Fig. 30b) and Agrostis stolonifera (Fig. 31b) are more abundant on the most active ant-hills of a given volume.¹ Agrostis is almost absent from small, active mounds, in contrast to Lotus corniculatus (Fig. 31a) which is one of the few species (with Festuca rubra, Helianthemum chamaecistus, Leontodon hispidus & Carex flacca) to consistently invade them.

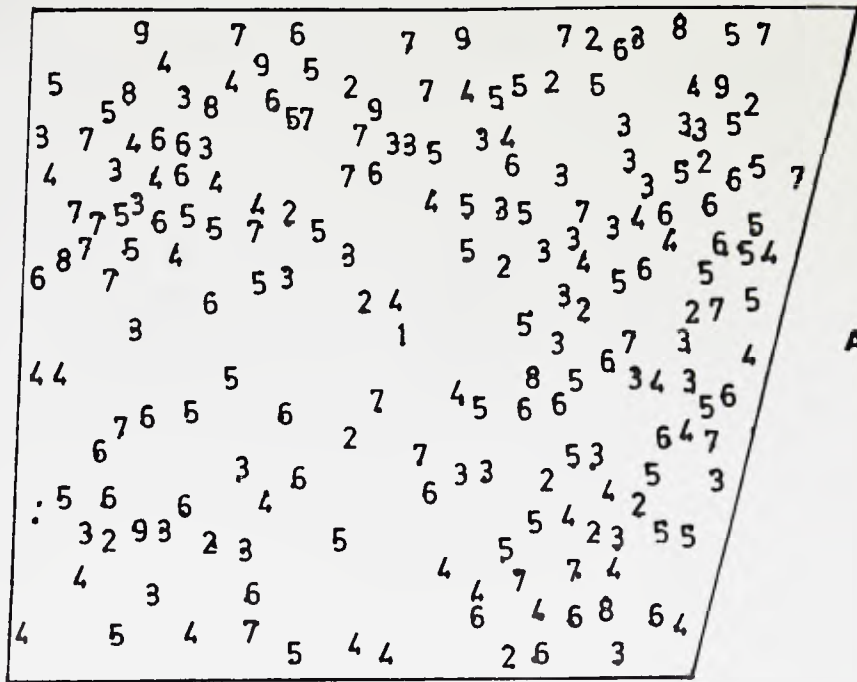
¹Grubb et al. (1969) mention that Agrostis stolonifera, Galium verum (and Holcus lanatus) are particularly characteristic of active mounds at Lullington Heath.

Fig.28

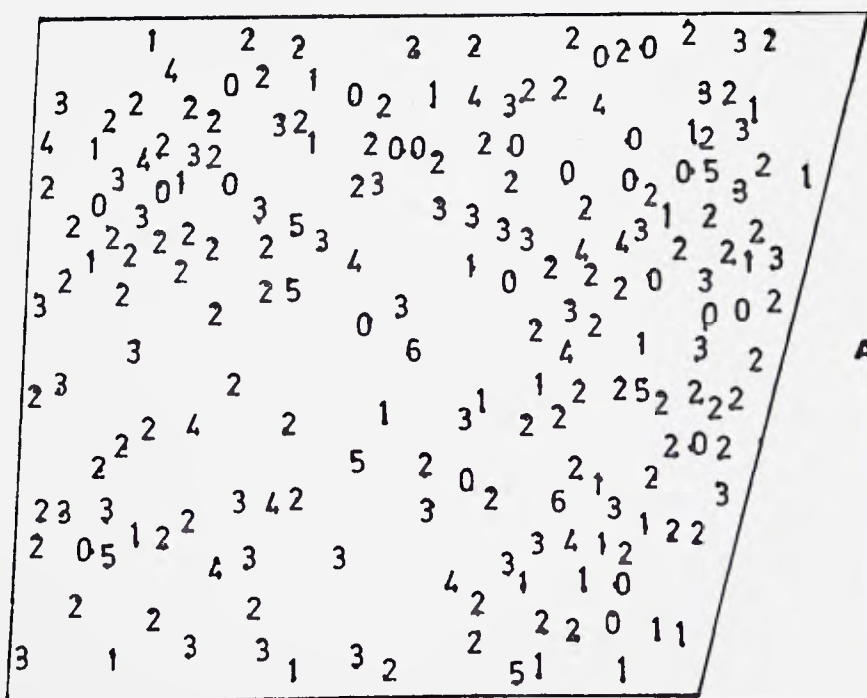
Ant-hill volume

Scale: units of $\sqrt[3]{\text{Ant-hill volume in cm}^3}$

- | | |
|----------------|----------|
| 1; 0 - 5 units | 6; 26-30 |
| 2; 6 - 10 | 7; 31-35 |
| 3; 11 - 15 | 8; 36-40 |
| 4; 16 - 20 | 9; 41-45 |
| 5; 21 - 25 | |

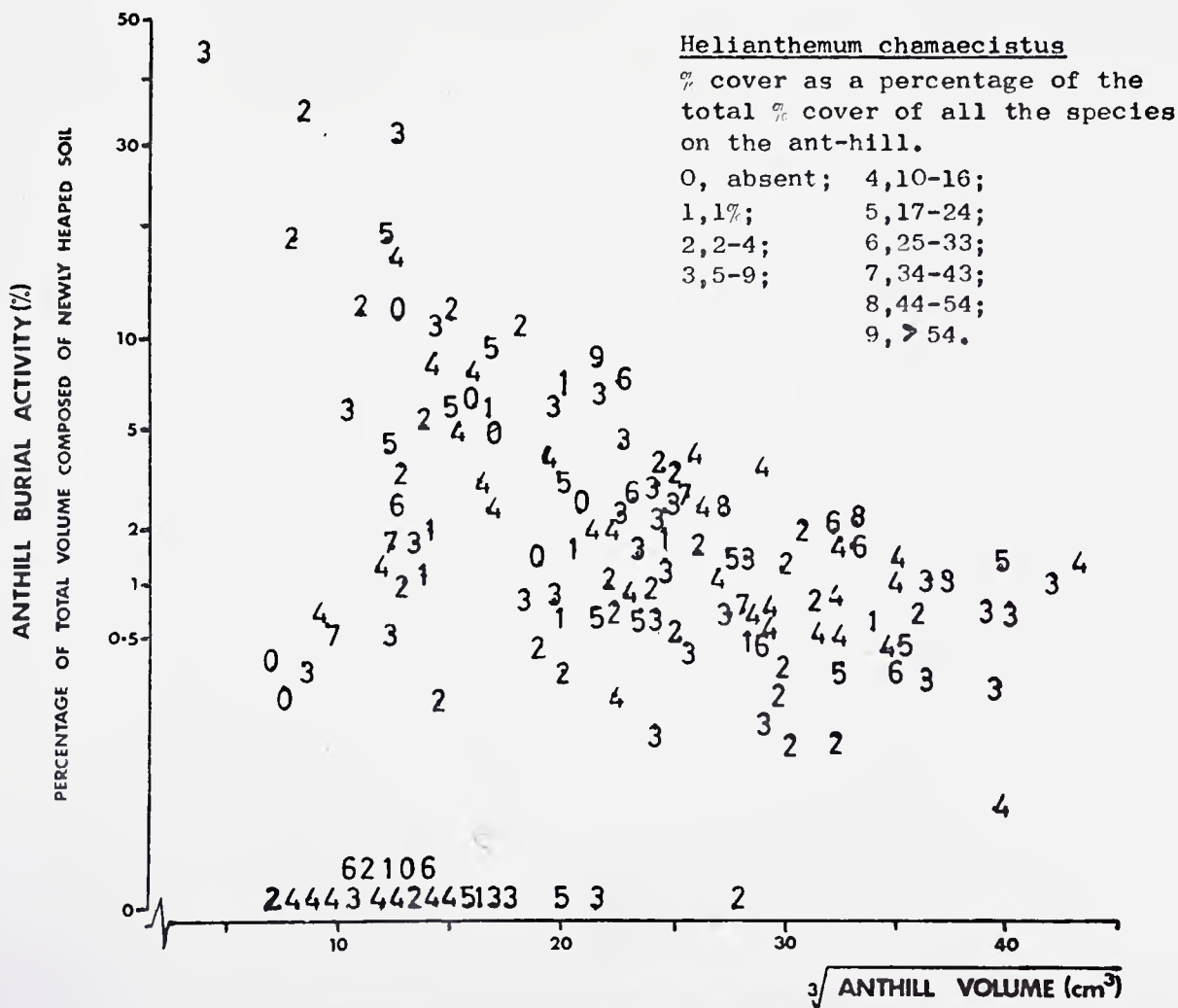
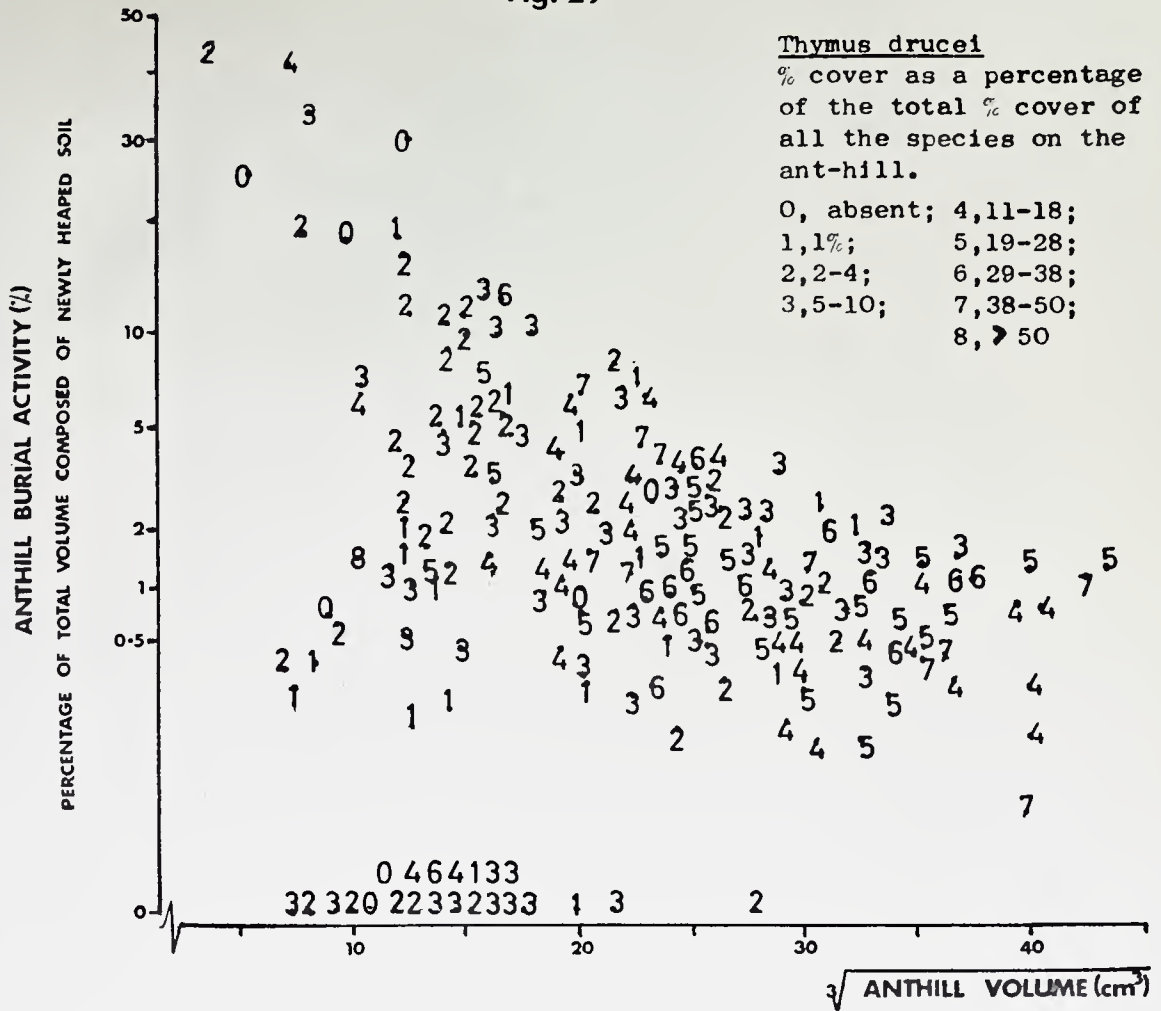


Ant-hill 'activity'



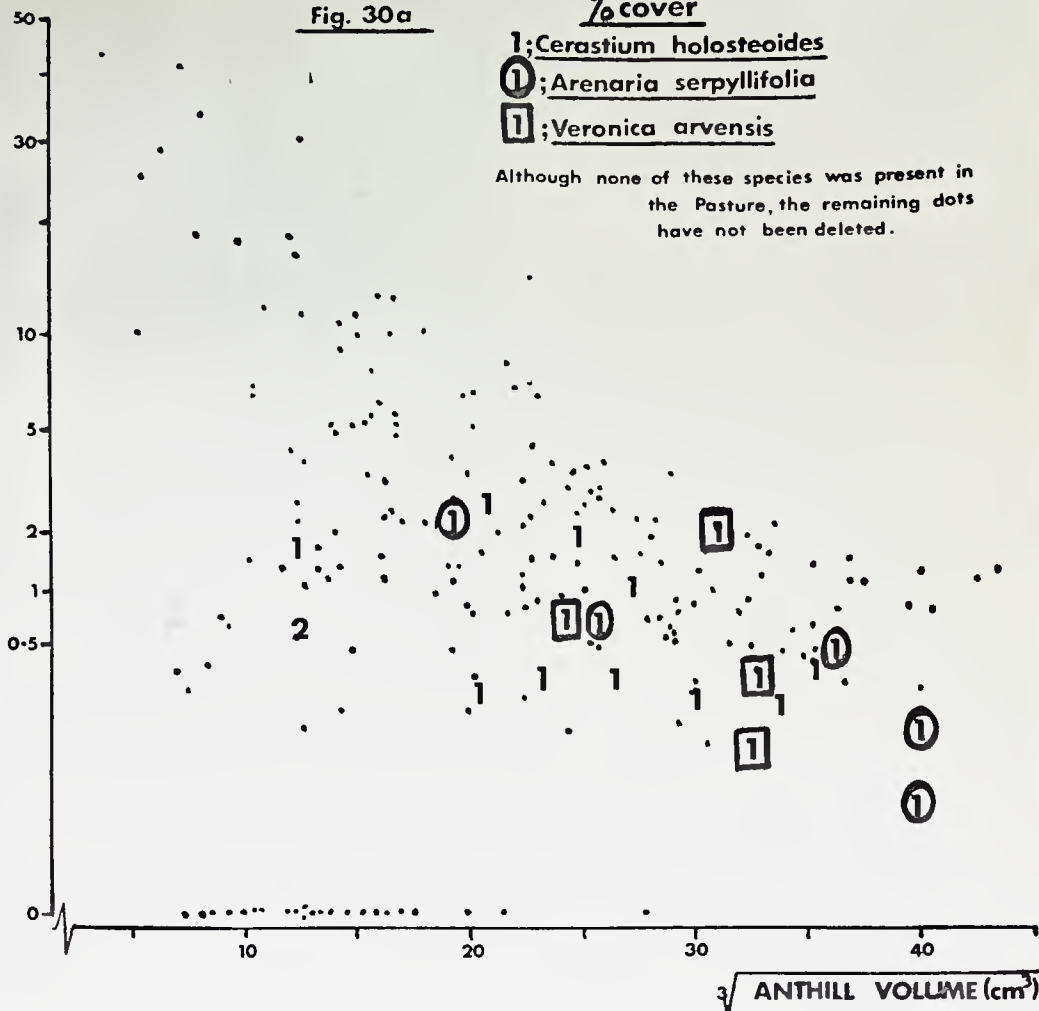
Arbitrary scale from 0 (no heaping) to 6.

Fig. 29



ANTHILL BURIAL ACTIVITY (%)

PERCENTAGE OF TOTAL VOLUME COMPOSED OF NEWLY HEAPED SOIL



ANTHILL BURIAL ACTIVITY (%)

PERCENTAGE OF TOTAL VOLUME COMPOSED OF NEWLY HEAPED SOIL

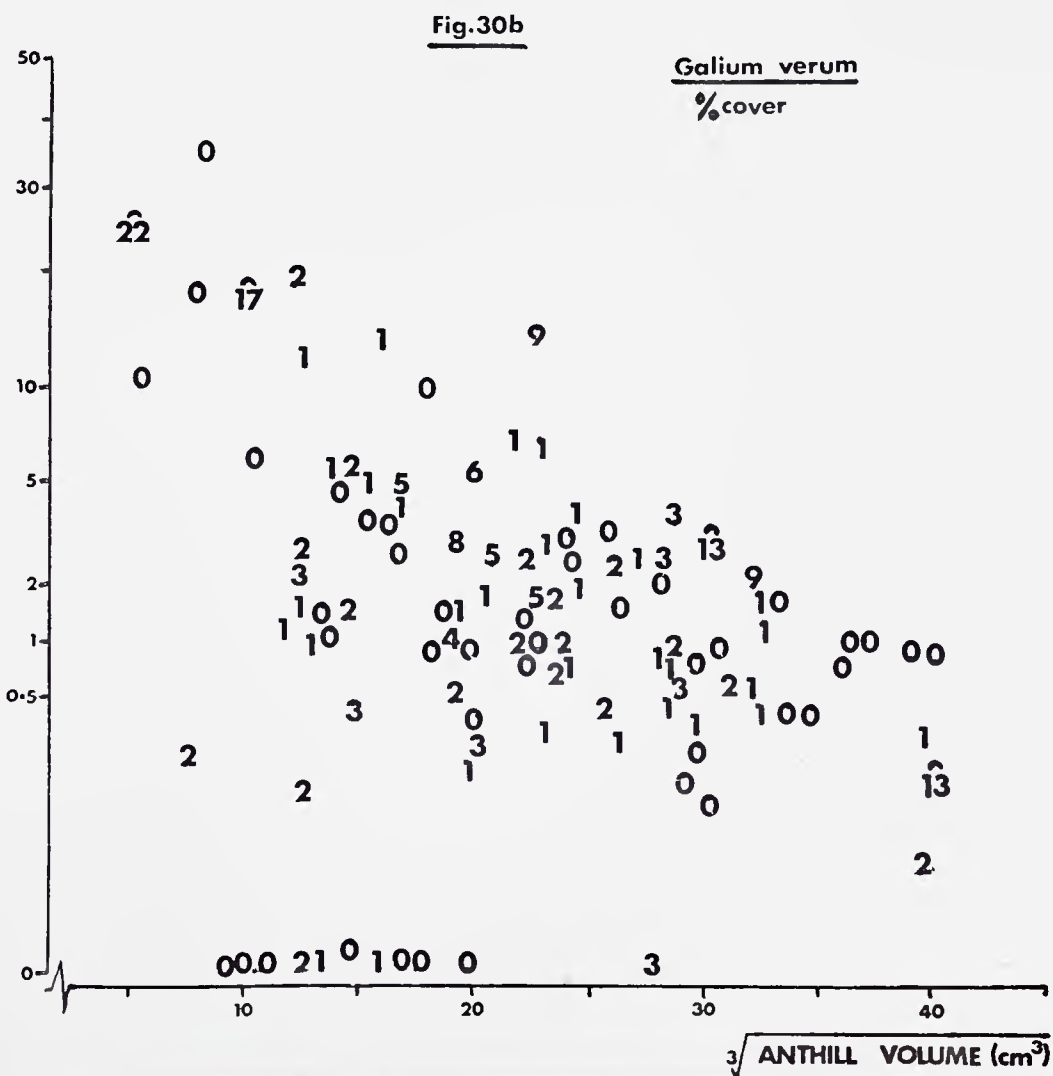


Fig.31a

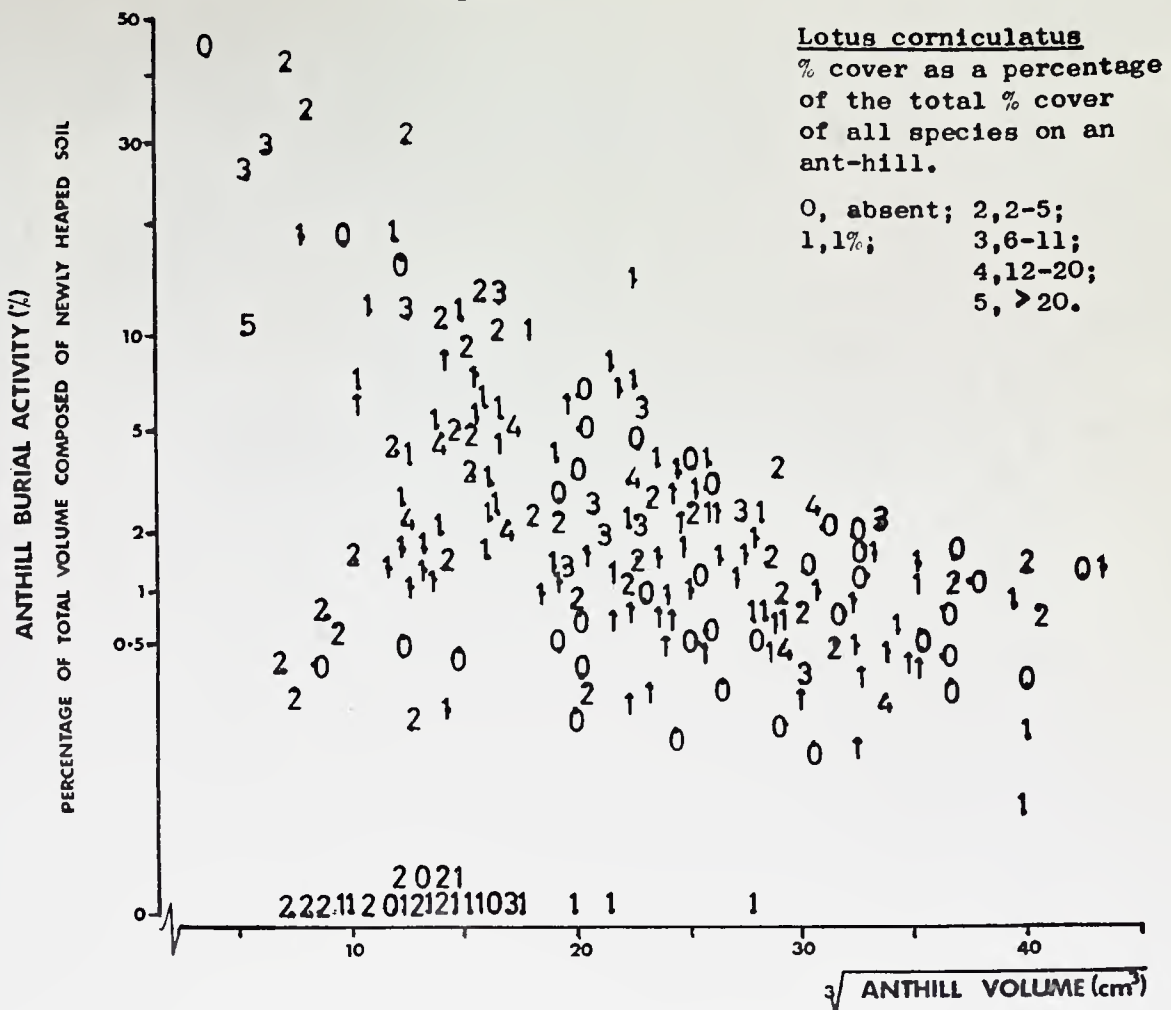
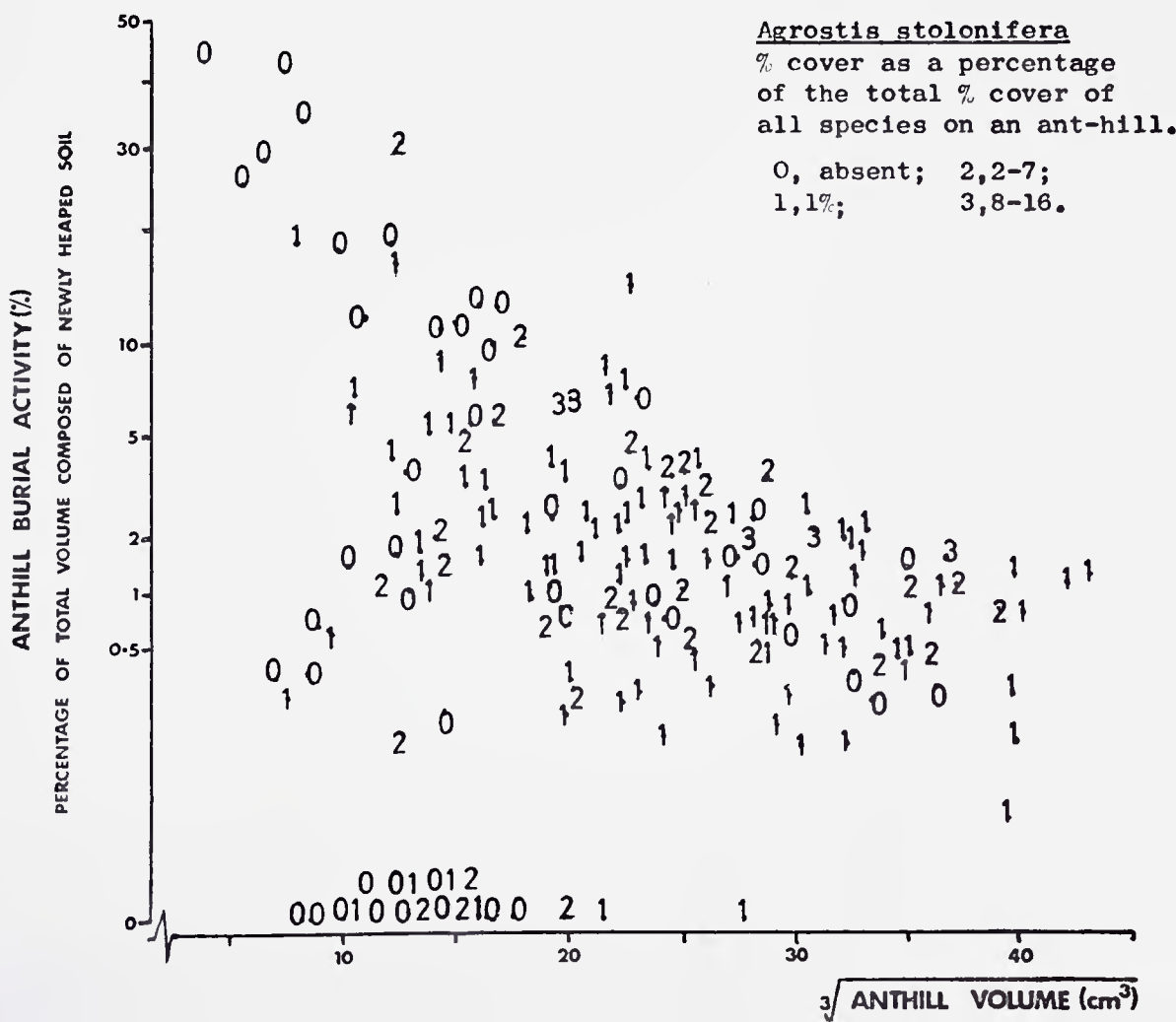


Fig.31b



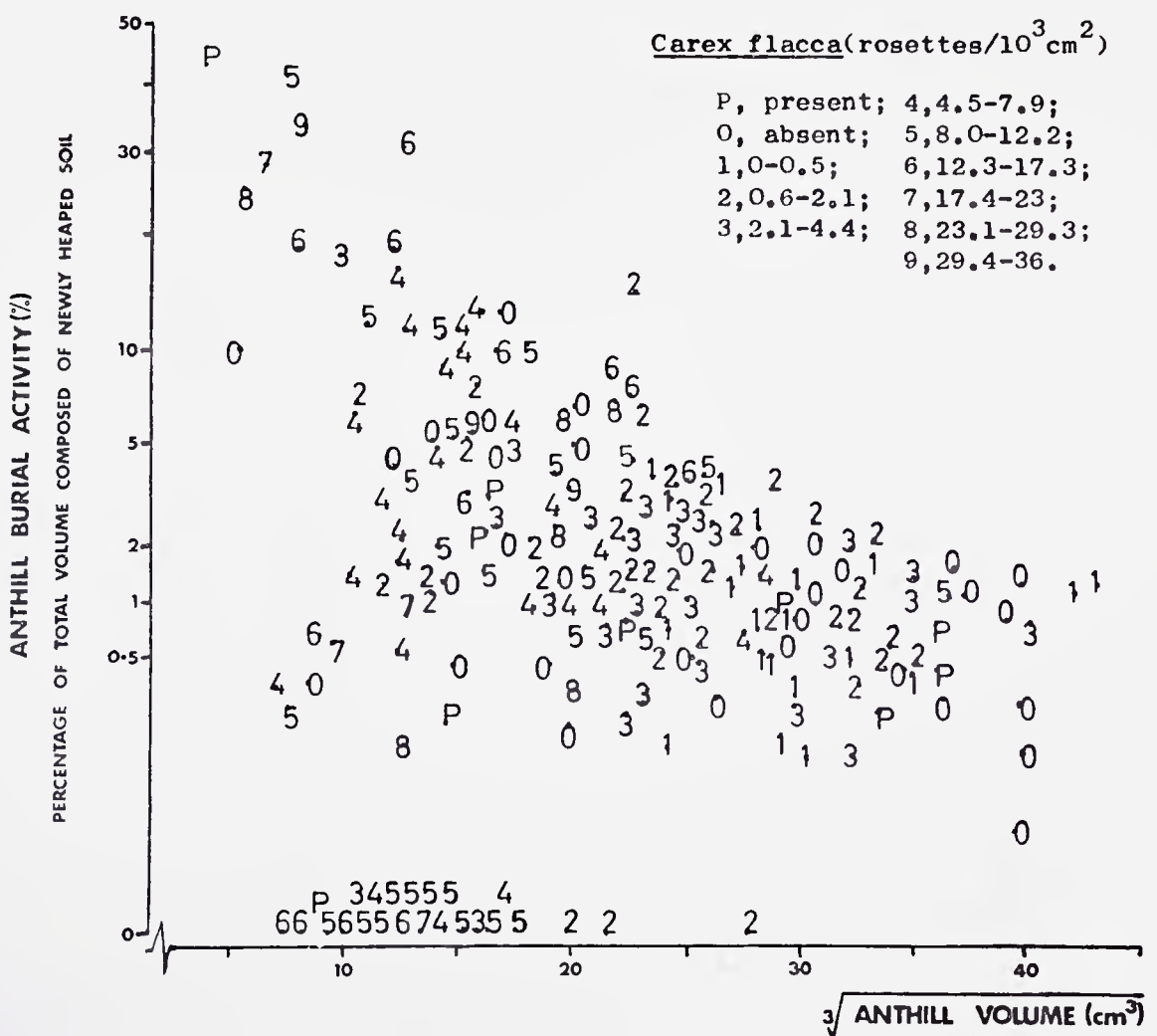
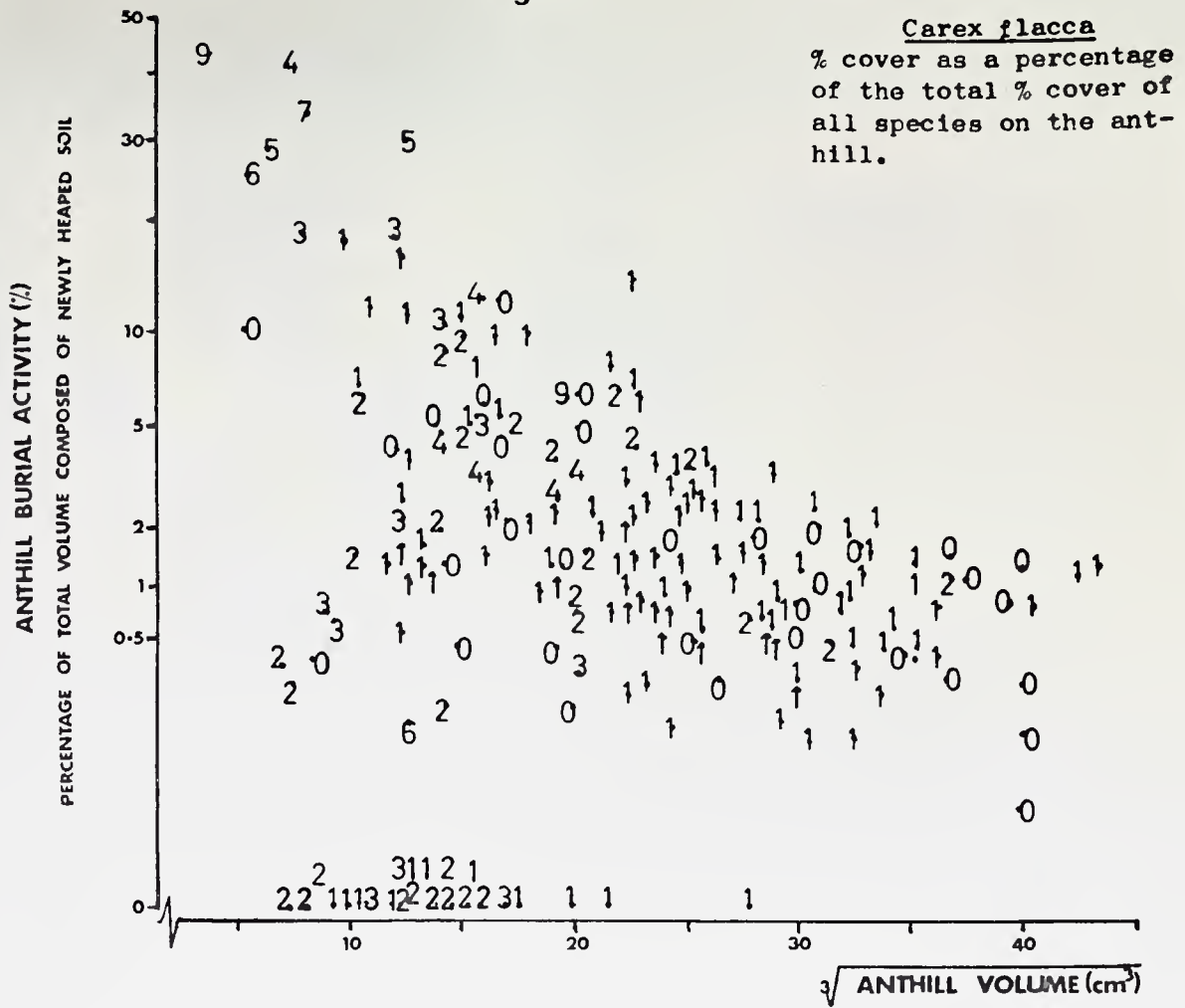
Although Carex flacca makes up a high proportion of the total plant cover on small, active mounds, both its importance and its density decline with increasing mound volume (Fig. 32). On small active ant-hills, and abandoned mounds, Carex rosettes are distributed randomly over the ant-hill surface (Figs. 33a & 33c), but on active mounds of about the same volume as the abandoned ones, Carex rosettes are significantly ($P < 0.01$) confined to the edge of the mound (Fig. 33d). On large active mounds the restriction of Carex to the periphery is even more marked (Fig. 33b). Carex rosettes often die once partly buried (Chapter 5); of the 1400 Carex rosettes found on the 206 mounds, 274 (19.5%) were at least partly covered by heaped soil. Fig. 36a shows that the proportion of Carex rosettes which are buried on an ant-hill declines with decreasing 'burial activity' and increasing ant-hill volume.

When Poterium sanguisorba rosettes (Fig. 34b) occurred on 'active' mounds, some of them were usually partly buried.

Hieracium pilosella, like Carex, appeared to invade ant-hills vegetatively more often than by seed. Its scatter diagrams (Fig. 35) show that both its proportion of the total plant cover, and its density, are greater on abandoned mounds than on active ones. This impression is confirmed by the density of its rosettes in Fig. 36c. Like those of Carex flacca, Hieracium rosettes are randomly distributed on small, active mounds (Fig. 36a) but confined to the edges of large, active mounds (Fig. 36b). On active (Fig. 36d) and abandoned (Fig. 36c) medium-sized ant-hills its rosettes have an intermediate pattern.

Leontodon hispidus (Fig. 37) is just as important on small mounds as large ones, and the density of its rosettes does not

Fig.32



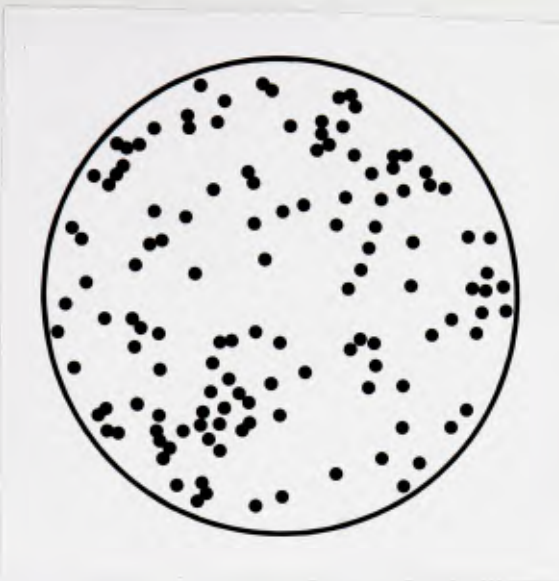


Fig.33a. Small, active ant-hills. When the frequency in the central half of the area was tested against that in the outer half, $\chi^2_{[1]} = 0.79$, N.S.

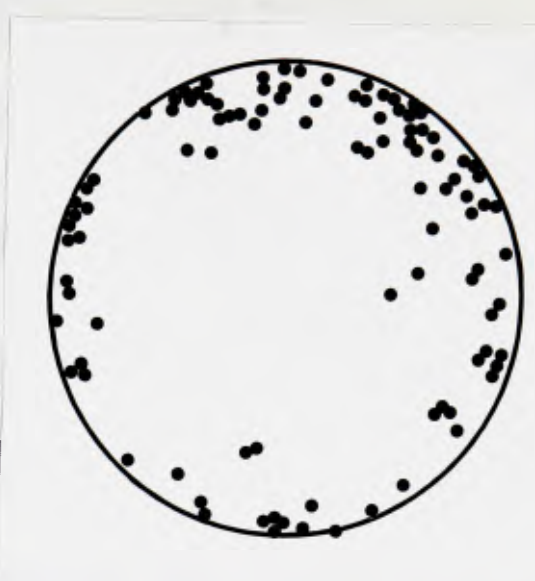


Fig.33b. Large, active ant-hills. For central/outer half, $\chi^2_{[1]} = 77.92^{***}$; thus much more frequent around margin.

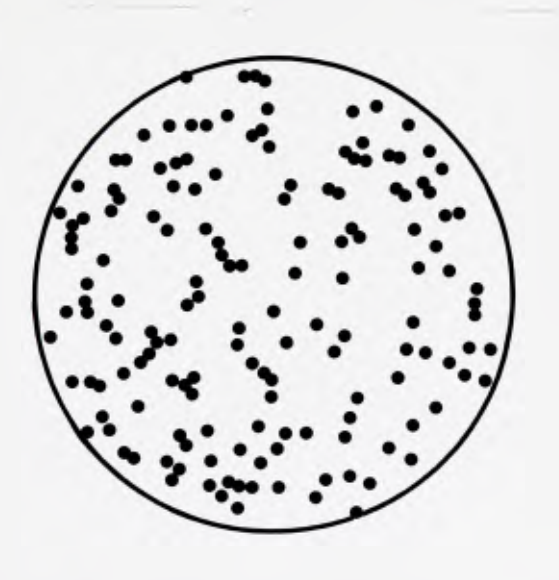


Fig.33c. Abandoned mounds. For central/outer half, $\chi^2_{[1]} = 0.33$ N.S.

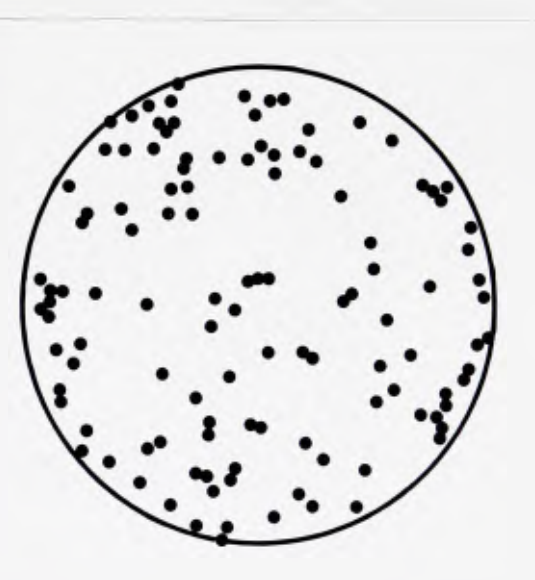


Fig.33d. Medium, 'active' mounds. For central/outer half, $\chi^2_{[1]} = 7.31^{**}$; thus more frequent around margin.

(N.S., $P > 0.05$; **, $0.01 > P > 0.001$; ***, $P < 0.001$)

1. Each diagram shows all the rosettes mapped on the 24 ant-hills in a group. The groups are defined in Fig.20, p.49-50. The maps were produced by the method described in section 2.3.2.2(p.29); however, these maps represent the surfaces of mounds, not vertical projections of sampled points on to a plane.

Fig.34a

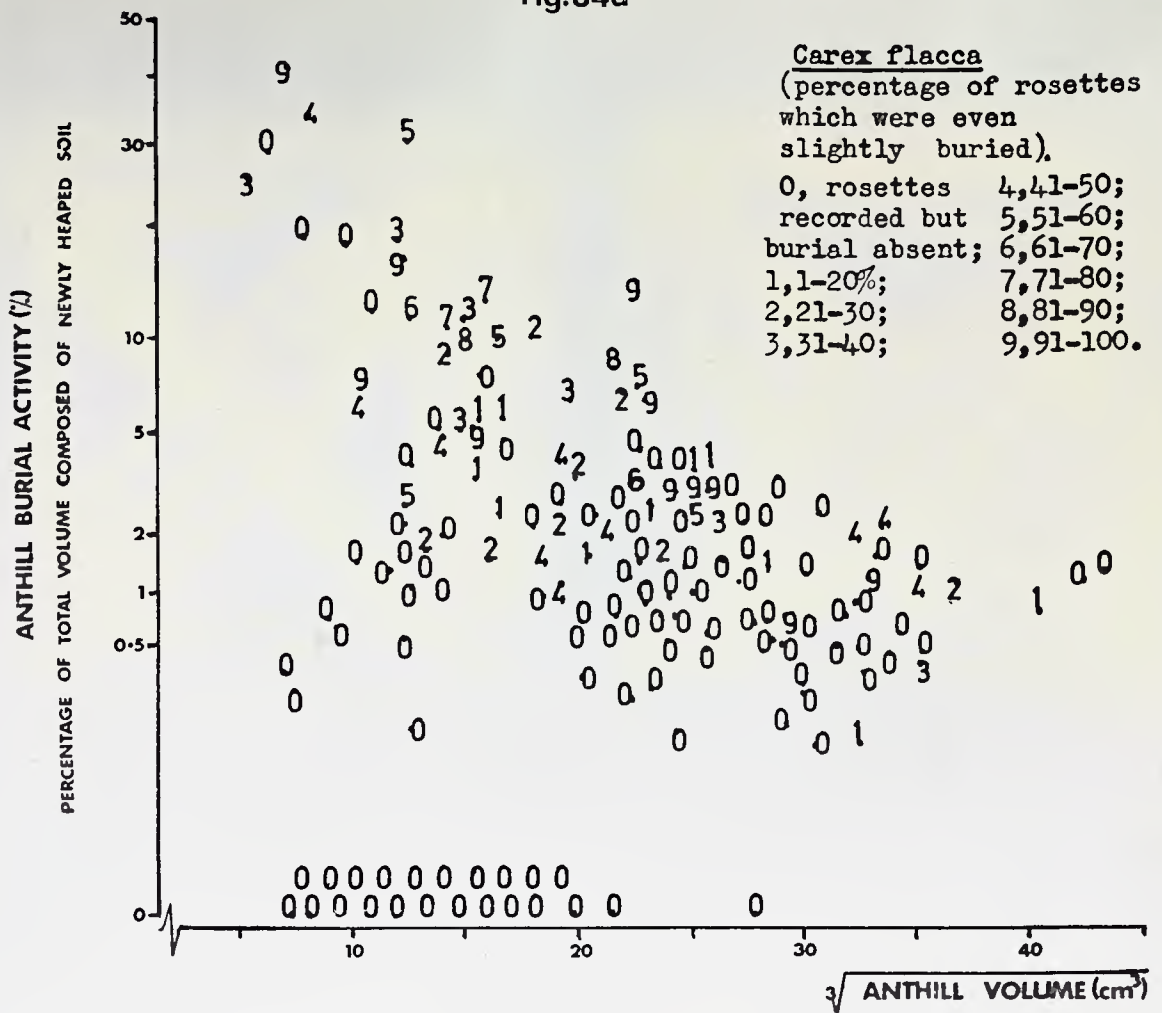


Fig.34b

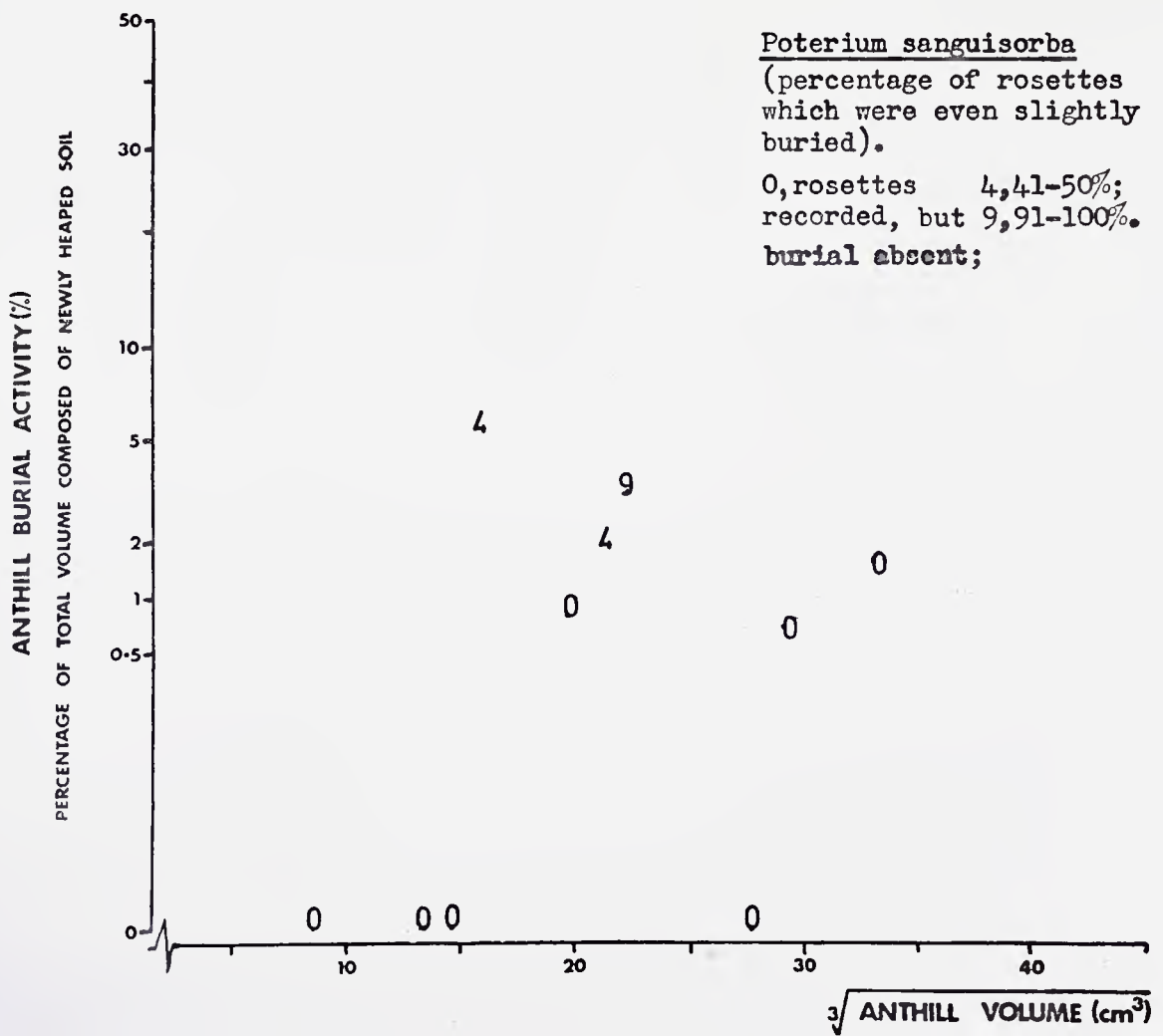
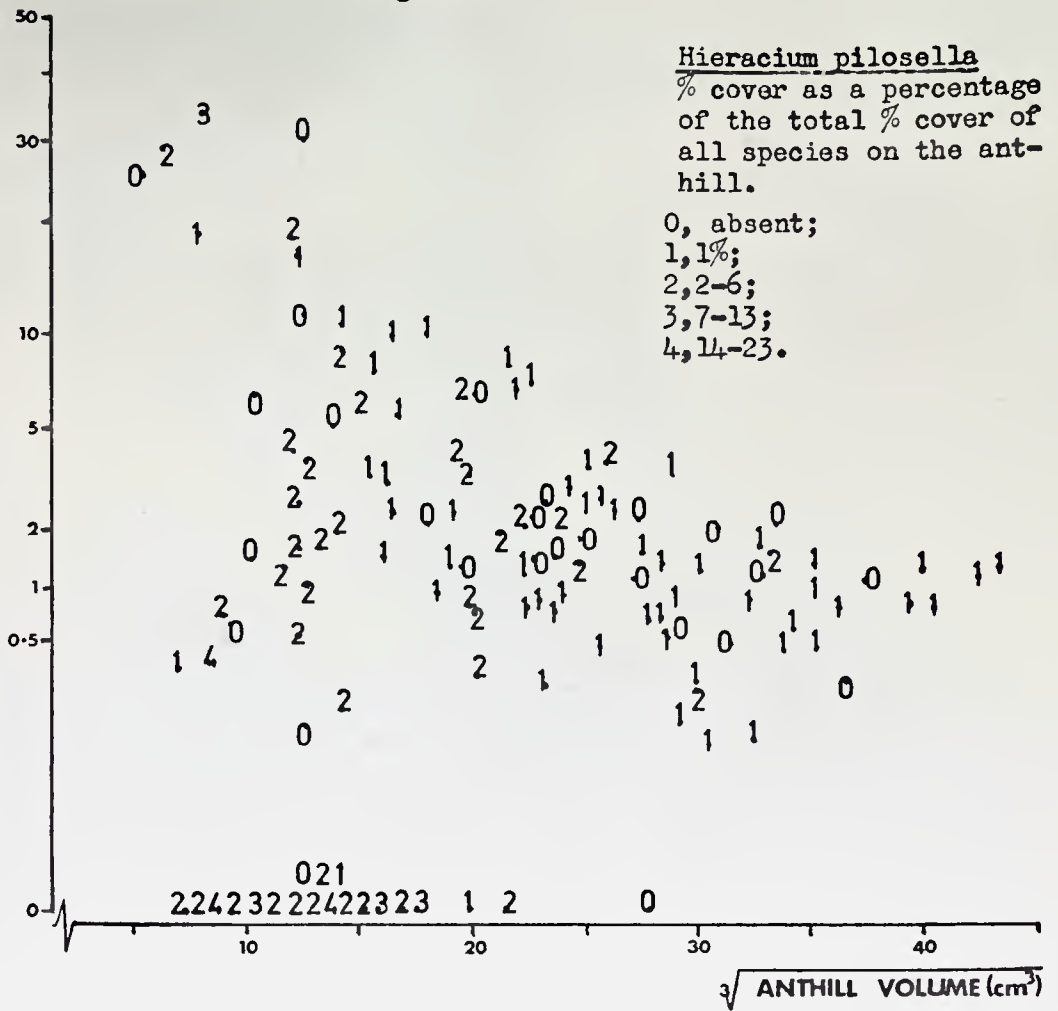


Fig.35

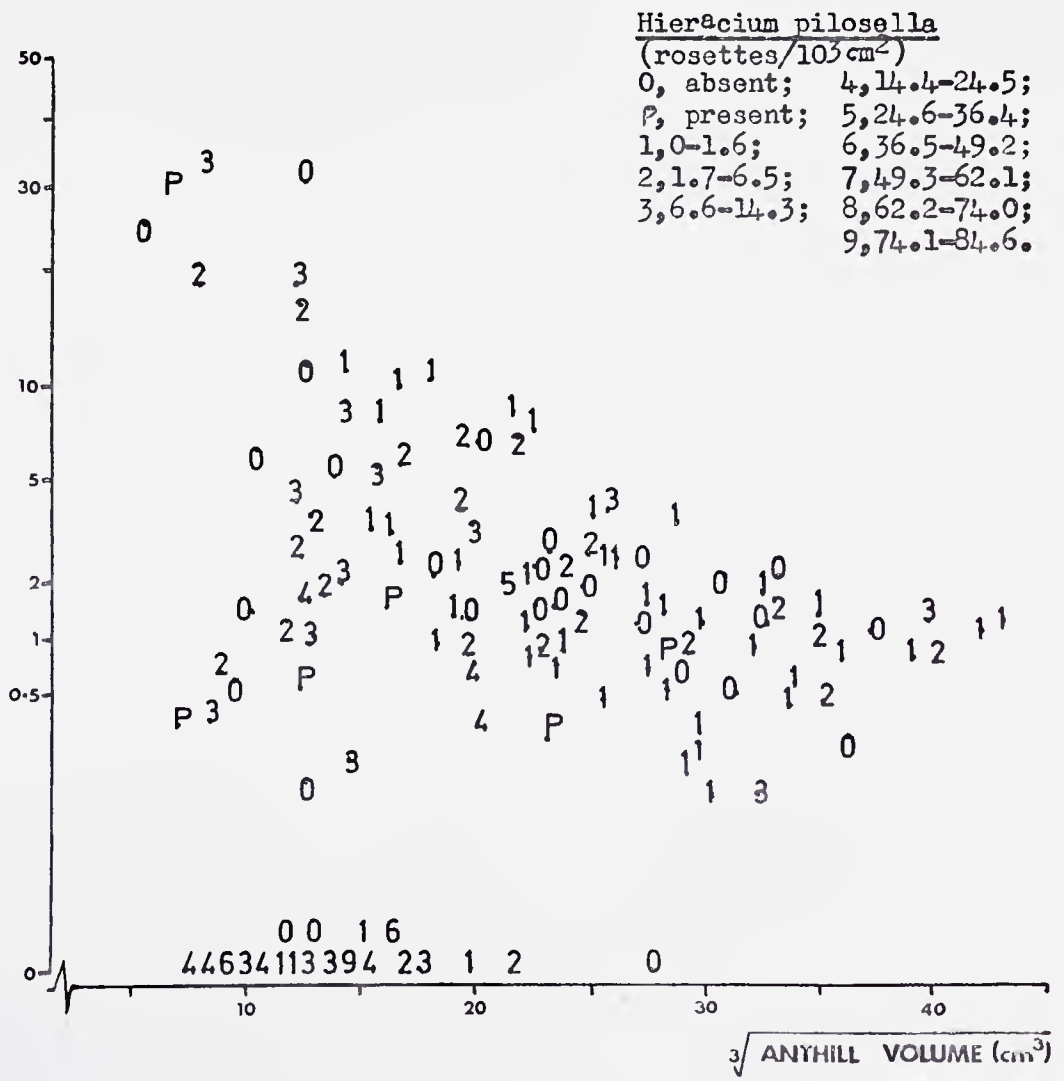
ANTHILL BURIAL ACTIVITY (%)

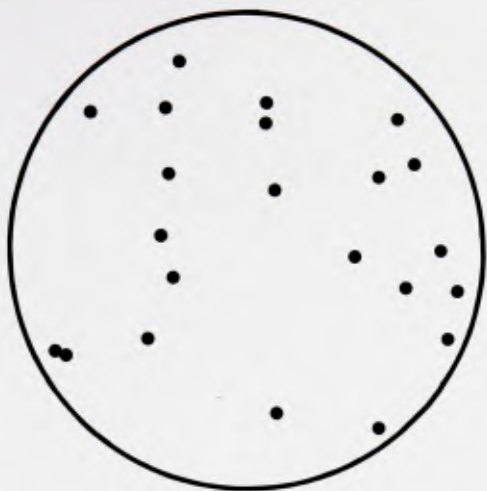
PERCENTAGE OF TOTAL VOLUME COMPOSED OF NEWLY HEAPED SOIL



ANTHILL BURIAL ACTIVITY (%)

PERCENTAGE OF TOTAL VOLUME COMPOSED OF NEWLY HEAPED SOIL

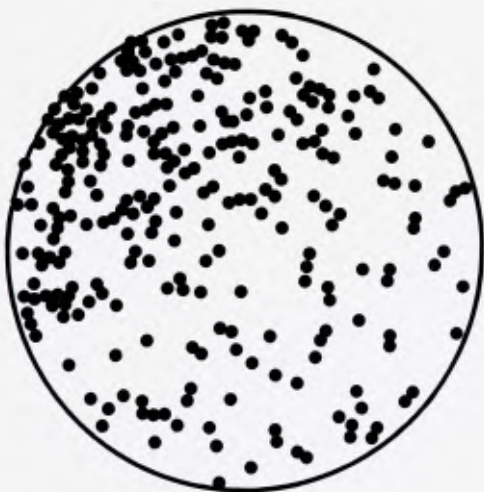


Fig.36a. Small, active ant-hills.

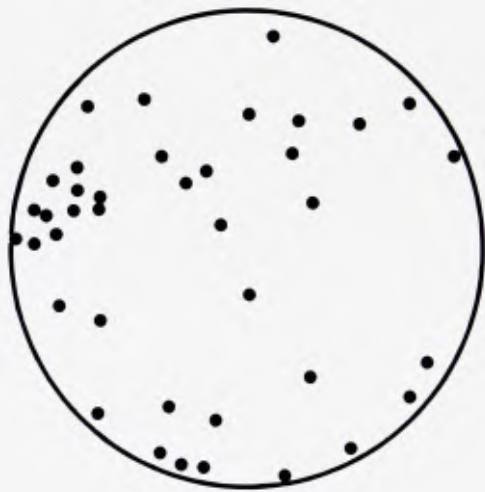
When the frequency in the central half of the area was tested against that in the outer half, $\chi^2_{[1]} = 0.18$, N.S.

Fig.36b. Large, active ant-hills.

For central/outer half, $\chi^2_{[1]} = 60.96^{***}$; thus much more frequent around margin.

Fig.36c. Abandoned mounds.

For central/outer half, $\chi^2_{[1]} = 4.22^*$; thus more frequent around margin.

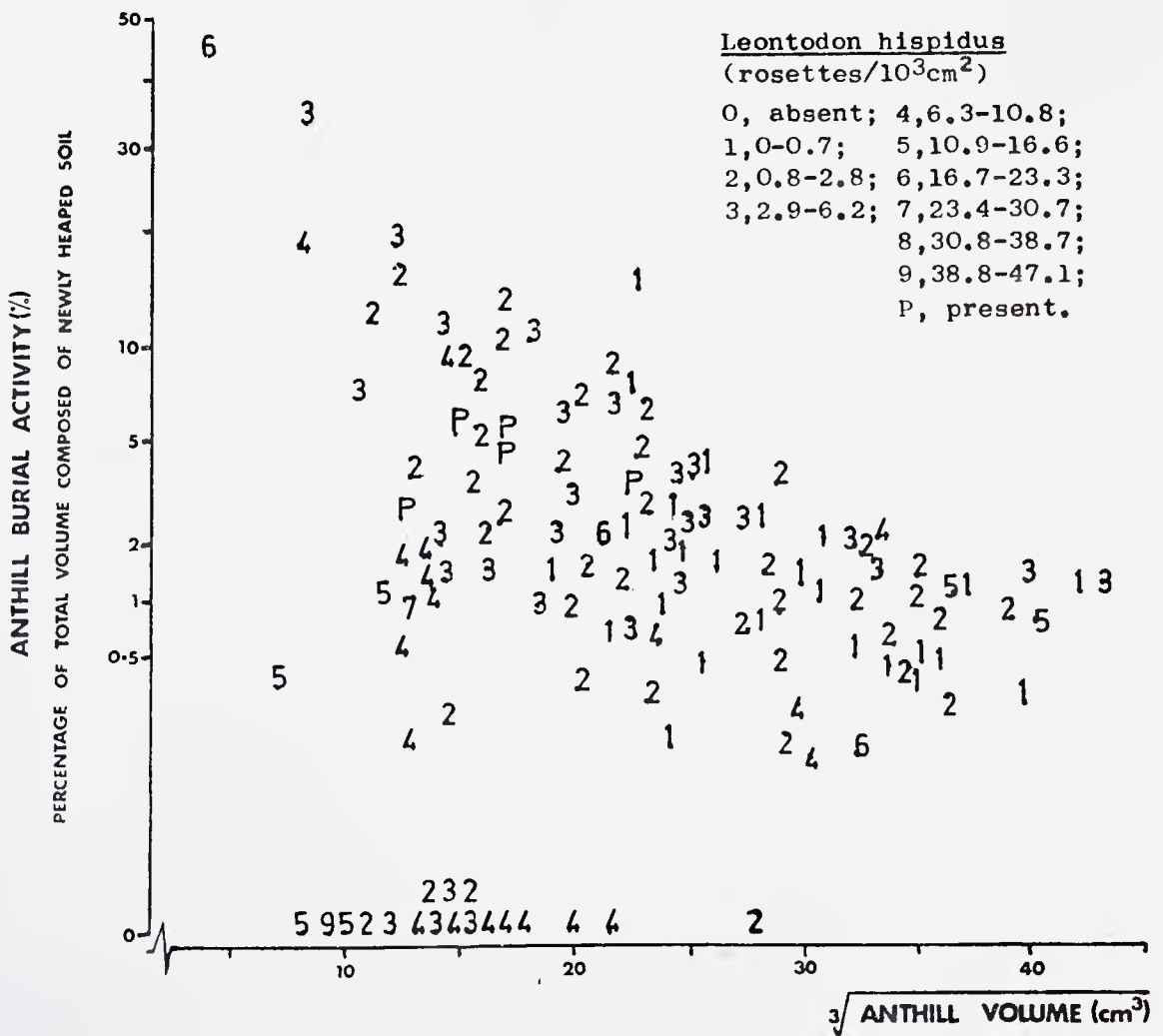
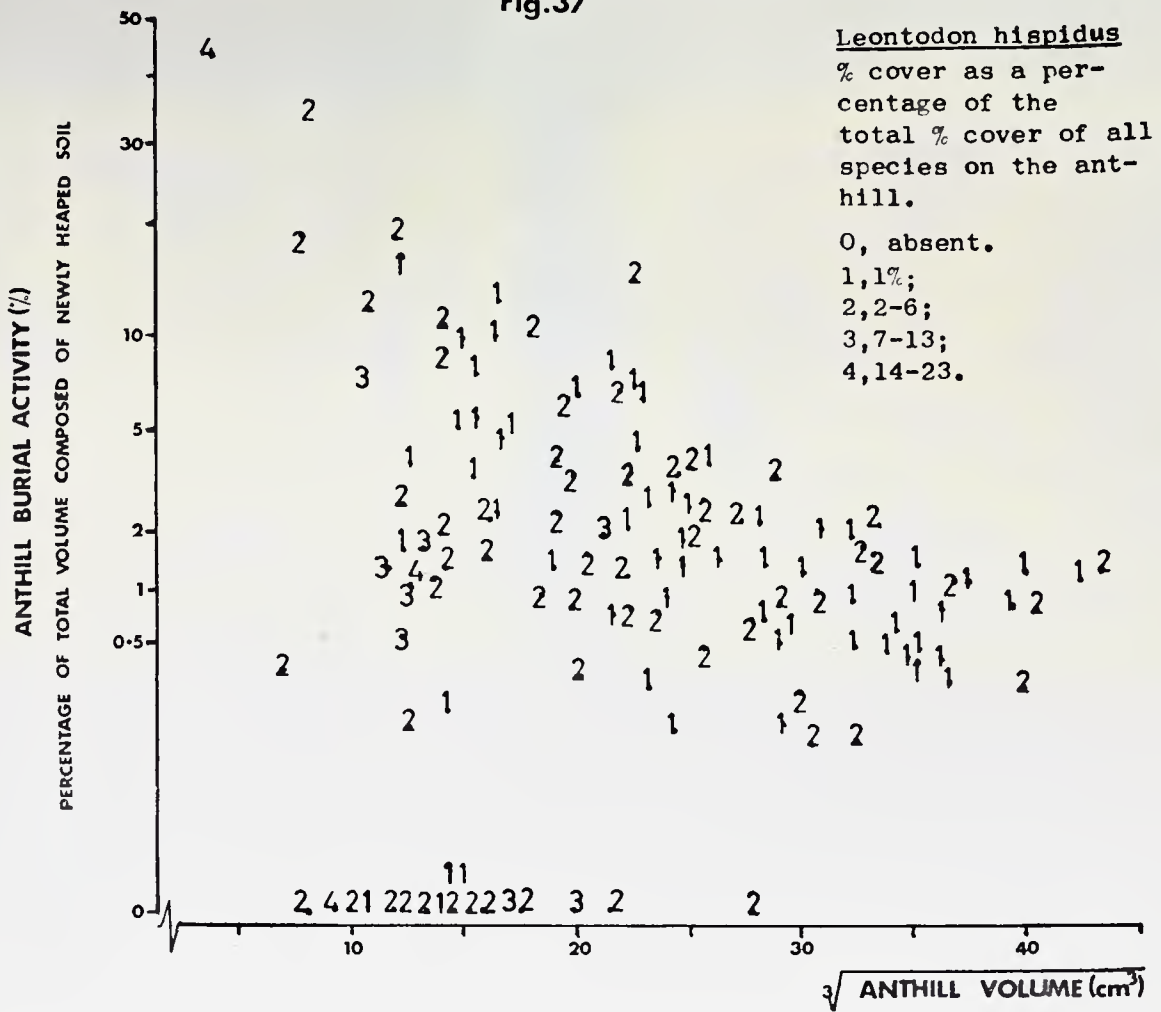
Fig.36d. Medium 'active' mounds.

For central/outer half, $\chi^2_{[1]} = 4.9^*$; thus more frequent around margin.

(N.S., $P > 0.05$; *, $0.05 > P > 0.01$; ***, $P < 0.001$)

1. Each diagram shows all the rosettes mapped on the 24 ant-hills in a group. The groups are defined in Fig.20, p.49-50. The maps were produced by the method described in section 2.3.2.2(p.29); however, these maps represent the surfaces of the mounds, not vertical projections of sampled points onto a plane.

Fig.37



differ much from left to right across the scatter diagram. The maps of Leontodon rosettes over the ant-hill surface (Figs. 38a & 38b) show that on large active mounds at least, a higher proportion of rosettes occur in the central half of the ant-hill area than in Carex flacca or Hieracium pilosella.

The patterns of Plantago lanceolata are similar to those of Leontodon, both on the scatter diagrams (Fig. 39) and the dot maps (Figs. 38c & 38d).¹

The average 'Mean affinity indices' for surrounding vegetation samples and for four groups of ant-hills of different volumes and activities (Table 18), suggest that ant-hill vegetation differs more from that of the sward as the mounds become larger. Much of the increase in average 'Mean affinity index' with ant-hill size is due to the increasing proportion of Thymus drucei in the vegetation.

Some of the differences between active and abandoned mounds in species abundance might be partly the result of (or indeed the cause of) changes in soil properties after the mounds have been deserted. Unfortunately the few, large, abandoned ant-hills on my plot mainly occur at the south-western end and were not represented in the survey. When the soil profiles of two of these large, abandoned mounds were compared with those of two large, active mounds nearby (at site H on the map in Appendix 29),

¹ Flowering rosettes of both Plantago and Leontodon were sometimes seen on sampled ant-hills, but Hieracium and Carex did not flower on the mounds.

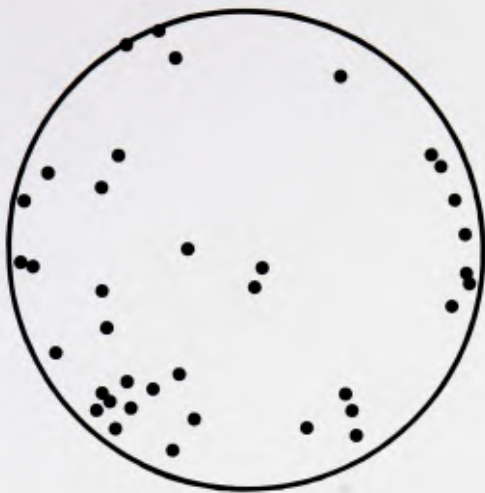


Fig.38a. *Leontodon hispidus*
Small, 'active' mounds



Fig.38b. *Leontodon hispidus*
Large, 'active' mounds.

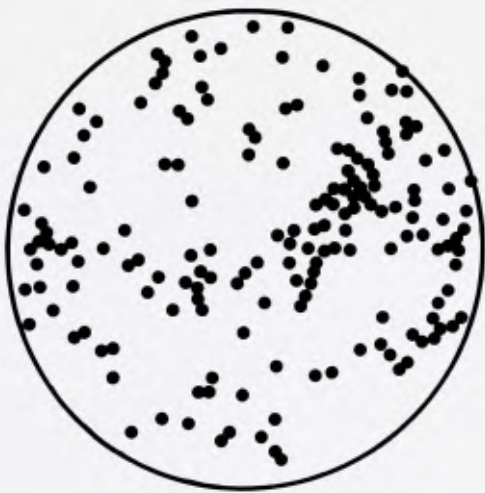


Fig.38c. *Plantago lanceolata*
Small, 'active' mounds

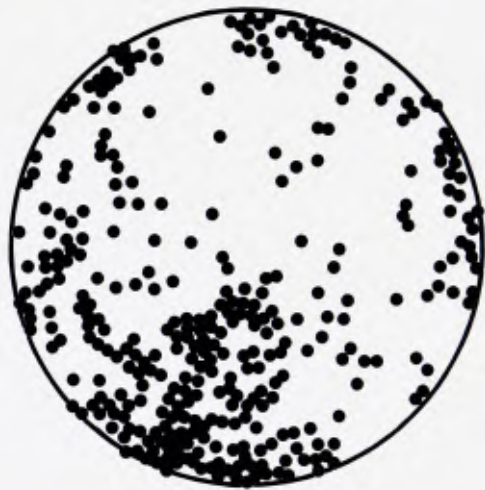


Fig.38d. *Plantago lanceolata*.
Large, 'active' mounds.

1. Each diagram shows all the rosettes mapped on the 24 ant-hills in a group. The groups are defined in Fig.20, p.49-50. The maps were produced by the method described in section 2.3.2.2.(p.29); however, these maps represent the surfaces of the mounds, not vertical projections of sampled points onto a plane.

Fig.39

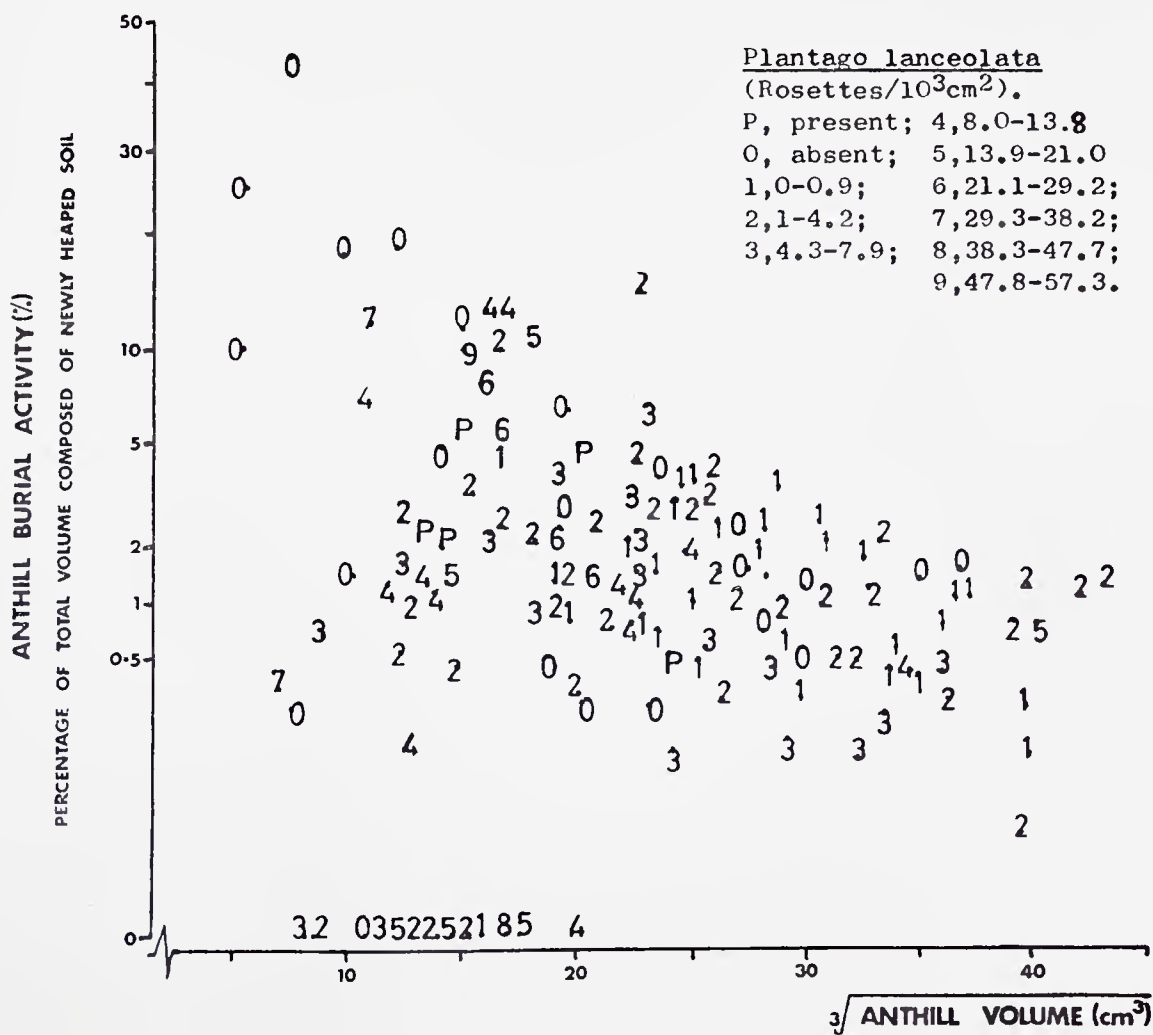
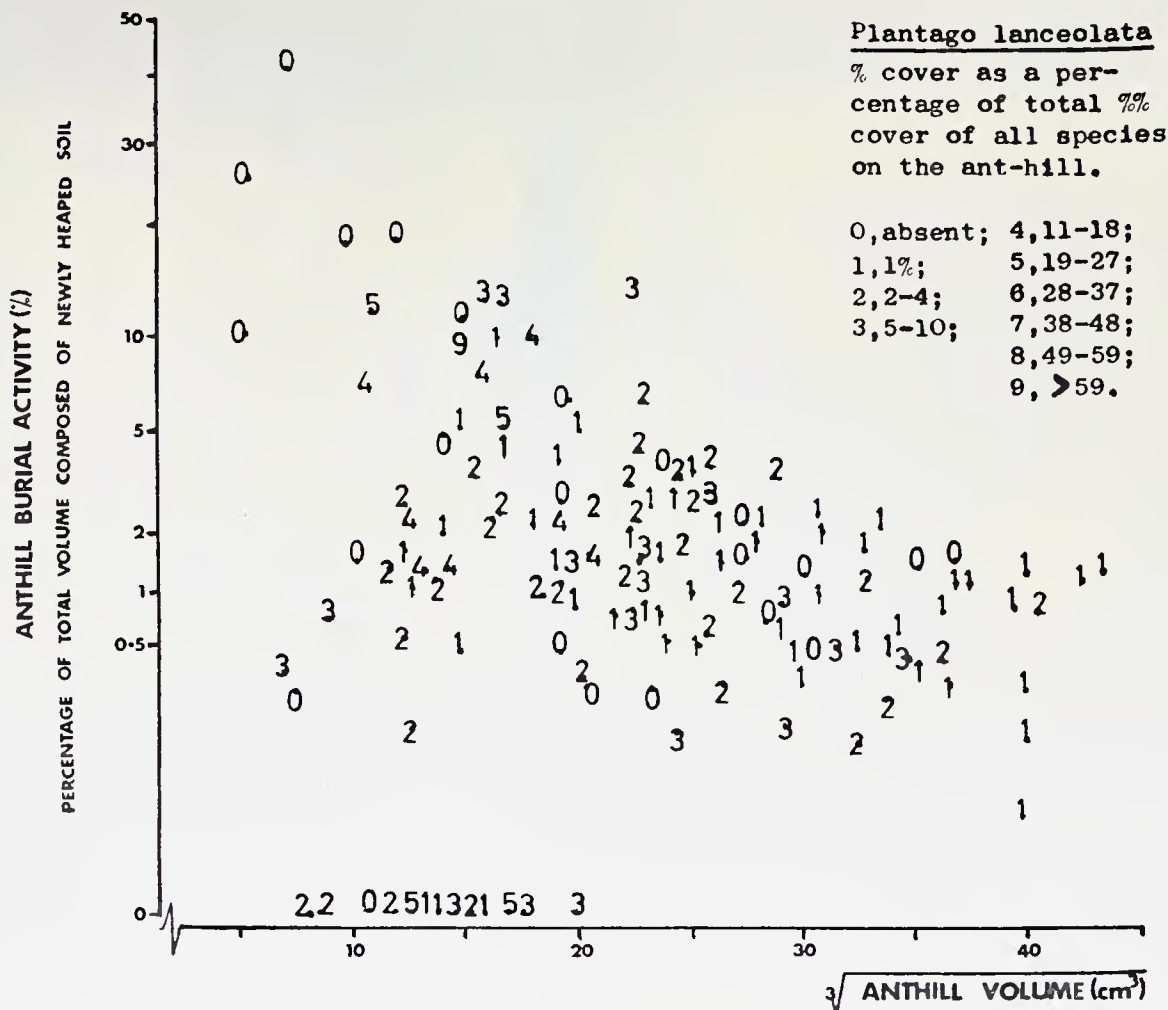


Table 18. Average 'Mean affinity indices' ($\overline{AI}_s$), for surrounding vegetation samples, and four groups of ant-hills of different sizes and activities

†Group:	1	2	3	4	5
Samples from:	Surrounding vegetation.	Small, very active ant-hills.	Small & medium abandoned ant-hills.	Small & medium active ant-hills.	Large active ant-hills.
Mean $\overline{AI}_s$:	448.5	518.5	521.2	571.8	608.45
Standard error of mean:	± 6.29	± 10.35	± 6.86	± 12.06	± 10.86

† 24 samples per group. Ant-hill groups as defined in Fig. 20. Surrounding vegetation quadrats selected at random from the 103 sampled.

Analysis of variance on untransformed data

Source	d.f.	N.S.	F _s
Among groups	4	88089.3	40.09***
Within groups	115	2192.0	
	119		

The following differences between groups were tested by Gabriel's (1964) sum of squares simultaneous test procedure:

Group 1/group 2***	2/3 N.S.	
1/3***	2/4**	3/4*
1/4***	2/5***	3/5**
1/5***	2/45***	4/5 N.S.
1/2/3/4/5***		1/2/3/4/5***

(N.S., $P > 0.05$; *, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$; ***, $P < 0.001$).

Similarities between groups. On the basis of the results of significance tests, group 1, groups 2&3, and groups 4&5 (bracketed above) form homogeneous sets, between which there are highly significant differences in 'Mean affinity indices'.

the active mounds had ant channels and chambers, no A_o horizon and a structureless soil, but the abandoned 'hills had no ant chambers or channels, some accumulation of humus to form A_o horizons, and soil particles associated into small peds. The soils of abandoned mounds have a higher organic matter and total nitrogen content¹ than active ant-hills of the same size (Fig.40). Leaching from the surfaces of abandoned mounds may lower their pH (Rhossili Down ant-hill profile, Appendix 8, and Grubb et al. 1969). This leaching is presumably counteracted on active mounds by the continual heaping of soil collected from below into the surface.²

4.4. DISCUSSION

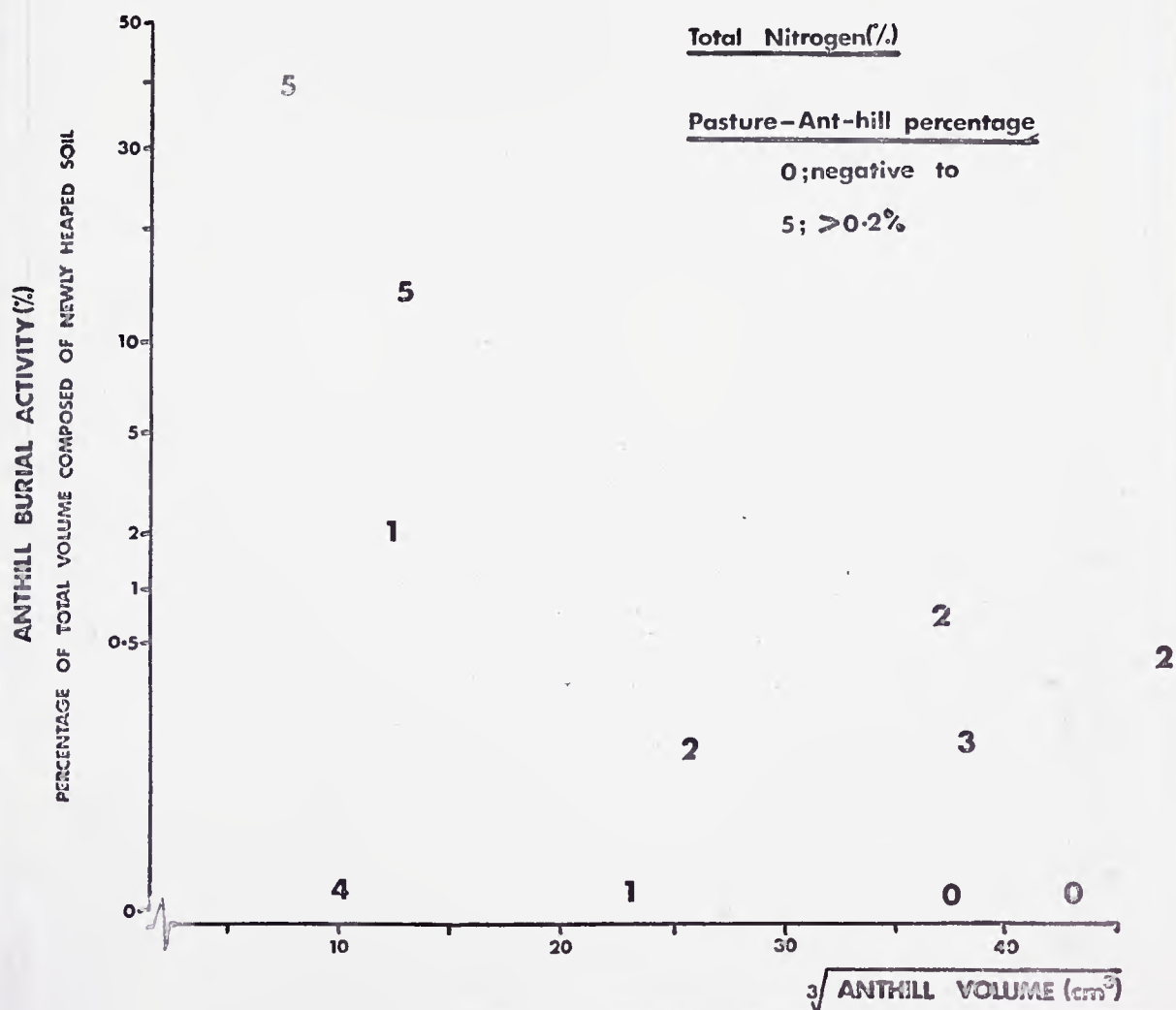
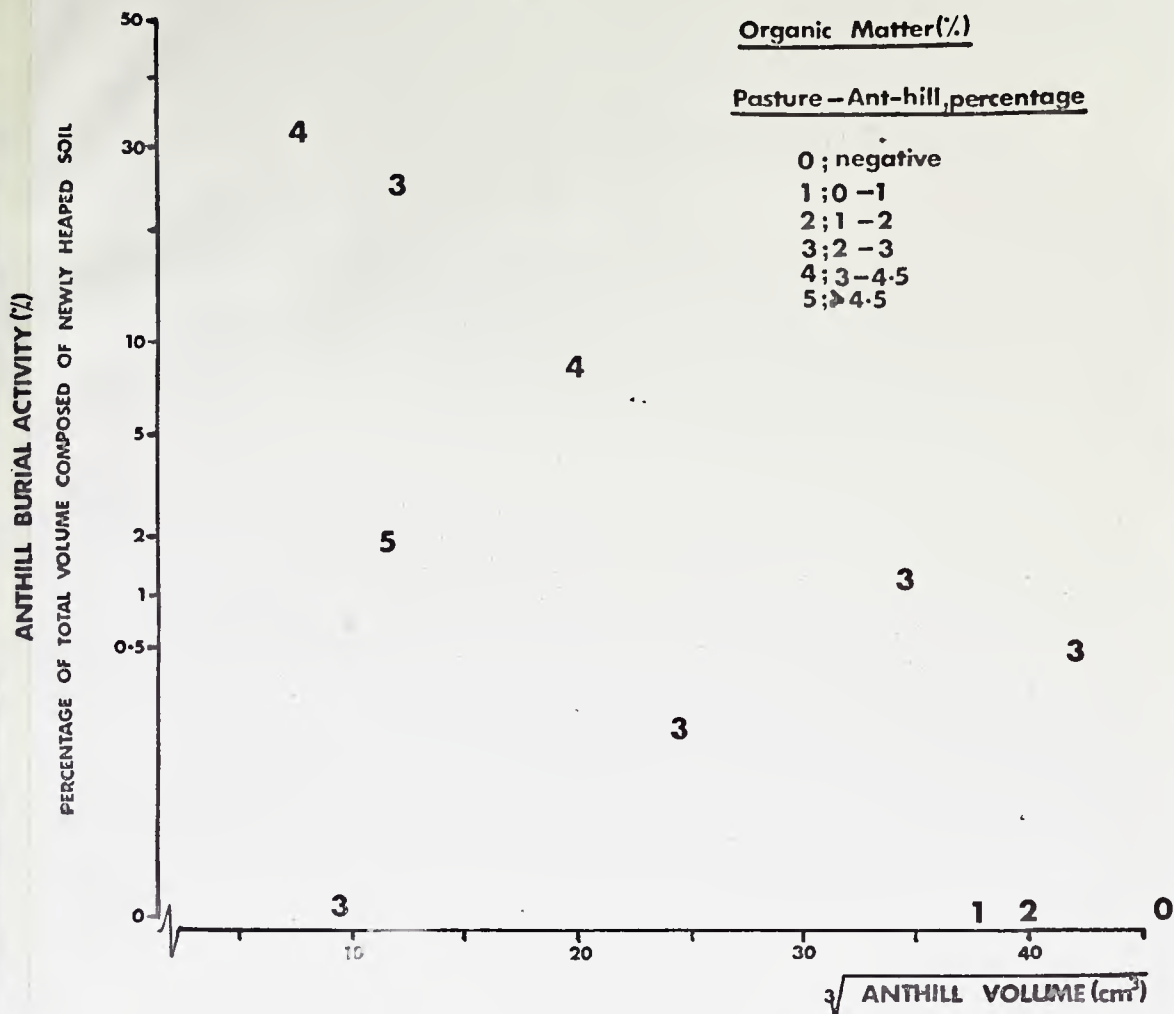
I gained four important insights into ant-hill ecology from the survey, apart from the data.

Firstly, a very high proportion of the species growing on an ant-hill occur in the vegetation immediately surrounding the mound. This is suggested by (i) the high correlation between the total number of species on and off ant-hills, both on my plot, and over all the calcareous grassland sites; and (ii) the correspondence between the presence of a species in the sward and its presence on mounds nearby, for all the species investigated in my plot. Even Helianthemum chamaecistus, with a great

¹Methods of soil analysis are explained in Appendix 1.

²I was unable to show that soil heaped up by the ants had a higher pH than that of the established ant-hill surface, under vegetation. On 16 May 1970 paired soil samples were taken from the first 12 ant-hills seen with newly-heaped soil on them, in my plot. The top 1 cm of established soil had a mean pH of 7.38, but the heaped soil had a mean pH of 7.40 (measured in 0.01M CaCl₂). The difference was non-significant at the 5% level by a t-test using the method of paired comparisons ($t_{[11]} = 0.405$).

Fig.40



affinity for ant-hills, does not occur on mounds in my plot when it is absent from the adjacent sward (Fig. 23).

Helianthemum chamaecistus and Thymus drucei, which can both grow up through heaped soil (Chapter 5), probably colonise ant-hills vegetatively when they are smothered as mounds increase in basal area. Yet there is also a marked similarity in ant-hill and pasture patterns for species like Brachypodium sylvaticum (Fig. 25) and Briza media (Fig. 26) which invade ant-hills entirely by seed. Thus the possible species composition of an ant-hill's vegetation is mainly limited to the species which occur nearby. Which of these species can invade the mound and maintain populations there depends partly on the 'dispersability' of their fruits or seeds and the efficiency of their vegetative reproduction, and partly on their reaction to the special environmental features of ant-hills, like droughting and burial.

Secondly, burial is probably an important factor in regulating the population sizes of some species on active mounds. Table 19 shows that at a moment in time, 19.5% of Carex flacca rosettes and 8.8% of Plantago lanceolata rosettes were at least partly buried. A high proportion of Carex rosettes is buried because of their high density on small, active mounds. I have no estimates of the proportion of Carex or Plantago rosettes which dies each year on a mound because of burial, nor do I know how many buried rosettes die, or how many dying buried rosettes are dying through causes other than burial. Yet I gained the impression that the elimination of mature rosettes through burial was important enough to cause (1) the restriction of Carex flacca rosettes to the edge of medium-sized active mounds (Fig. 33d) as compared with their random distribution over

Table 19. Frequency of burial of mature plants of some dicotyledonous species encountered on ant-hills in the survey

Species	Total no. rosettes recorded	Slightly buried	Half leaf area buried	†Buried and dying
<u>Carex flacca</u>	1400	160	82	32
<u>Cirsium acaule</u>	46	2	3	3
<u>Crepis capillaris</u>	384	13	1	0
<u>Fragaria vesca</u>	400	9	4	13
<u>Hieracium pilosella</u>	753	30	17	1
<u>Leontodon hispidus</u>	1014	27	7	6
<u>Plantago lanceolata</u>	1180	40	37	28
<u>Poterium sanguisorba</u>	24		3	2
<u>Viola hirta</u>	4	1	0	3

† This category includes all rosettes which were dead or dying and partly covered by soil, however much of their leaf areas were buried. 'Dying' rosettes were those which had more than a quarter of the area of every leaf browned at the tip.

abandoned ant-hills (Fig. 33c) and (ii) the greater densities of rosettes of Hieracium pilosella and Carex flacca on abandoned mounds than active ones of the same size.¹ Table 19 underemphasizes the importance of burial in eliminating plants on ant-hills, for two reasons. Firstly, seedlings are probably more susceptible to burial than mature plants (as shown in Chapter 5), but few seedlings were seen in the survey, buried seedlings might easily have been completely covered by heaped soil, and dead seedlings might decay and disappear more rapidly than dead mature plants. Secondly, the volume of soil (Table 2) heaped onto the surface of a mound may fluctuate markedly from year to year, and since only a small proportion of the ant-hills which I sampled were probably in a peak building year, my static picture would underestimate the importance of burial over several years in eliminating the rosettes of species. The absence of a species from a mound now might be due to the

¹ However, abandoned mounds probably have a much greater mean age than active ones of the same volume.

heaping of a considerable amount of soil onto its surface five or ten years ago.

The third insight into ant-hill ecology which I gained from the survey was that the species with the most interesting distributions on the scatter diagrams and over the dot maps fell into several natural groups governed by their responses to ant-hills: Arenaria serpyllifolia, Veronica arvensis and Cerastium holosteoides; Thymus drucei and Helianthemum chamaecistus; Cirsium acaule and Poterium sanguisorba; Leontodon hispidus and Plantago lanceolata; Carex flacca and Hieracium pilosella. The ecology of all these species, except H. pilosella, is described in detail in Chapter 5.

Fourthly, the survey suggests to me a 'successional' sequence for species on ant-hills in my plot, if I can regard the ant-hill volume (horizontal) axis as an age axis. This assumption is justified, since I have only considered general trends in species abundance across the scatter diagrams; but it is often dangerous to deduce a dynamic situation from a static one.¹ The following hypothesis is consistent with the evidence. Some ant-hills at various stages in this 'succession' are illustrated in Fig. 41.

Young ant-hills are heaps of soil which smother existing vegetation. They are invaded especially by Festuca rubra, Lotus corniculatus, Helianthemum chamaecistus (if in the sward nearby), Carex flacca (all vegetatively)² and Leontodon hispidus (mainly by seed).² Other species present near a mound may colonise it too.³

¹For instance, if Thymus had a higher percentage cover over the plot before myxomatosis than at present, its greater abundance on larger mounds now might not be due to its vegetative expansion as the ant-hills became bigger, but to the present low density of Thymus in the sward and the consequent less frequent invasion of the mounds.

²Excavation evidence.

³Species which first invade a mound may persist for some time; they may have a competitive advantage over later invaders.

Fig. 41. Some ant-hills at various stages of my hypothetical 'successional' scheme.



1. 'Incipient' ant-hill smothering the stem bases of grasses, with Prunella vulgaris, Lotus corniculatus, Veronica officinalis, and Leontodon hispidus (partly buried) present.



4. Large active mound, from above, with abundant Thymus drucei and Helianthemum chamaecistus, and a little Veronica officinalis. Leontodon hispidus is present in a circular band inside and outside the margin.



2. Abandoned mound, from the side, with Lecntodon hispidus, Lotus corniculatus and Plantago lanceolata.



3. 'Medium active' ant-hill from above, with Helianthemum chamaecistus growing up through heaped soil, partially buried rosettes of Plantago lanceolata, and dead and dying rosettes of Carex flacca on top.

Thymus drucei invades the ant-hill as it expands in basal area, and over the years, as the mound grows, becomes a more important component of the vegetation. The continual heaping of soil onto the top of the mound results in the burial and death of any Carex flacca and Hieracium pilosella there, and their restriction to the edge of the ant-hill. However, Leontodon hispidus and Plantago lanceolata, usually present around the margins of medium and large active mounds, set abundant seed there, and their seedlings sometimes become established on the bare soil on top. By this time, the summits of ant-hills tend to be occupied by Thymus drucei and Helianthemum chamaecistus, which can grow up through the heaped soil; rosette species are most frequent in a circular band around the basal slopes of the mounds.

The distribution of ant-hills on the scatter diagram shows that many small mounds are rapidly abandoned. Furthermore, all twelve 'incipient mounds' marked on my plot during the survey were apparently deserted, and covered by dense vegetation, by October 1971. On abandoned mounds, the vegetation becomes closed, and the relative abundances of species approach those of the surrounding sward more closely than on active ant-hills of the same volume. In the absence of burial rosettes of Carex flacca, Hieracium pilosella, Leontodon hispidus and Plantago lanceolata become established over the whole surface; the density of Hieracium ^{rosettes} exceeds that on active mounds of the same size. Thymus and Helianthemum, established whilst the mound was growing, may hold their own by putting more of their net assimilation into axillary than apical growth.¹ As the organic matter accumulates

¹This was a general impression gained from the survey.

in the soil, forming an A₀ horizon, the total nitrogen concentration of the soil, and probably its water holding capacity and total exchangeable bases, also increases. The mineral soil becomes structured into small peds and the soil begins to resemble that surrounding the mound.

Grubb et al. (1969) proposed a tentative scheme for succession on ant-hills at Lullington Heath, but when I examined over three hundred mounds at Lullington with their hypothesis in mind, I could find no evidence for it. In their scheme, Grubb et al. did not allow for the abrupt change from an open species-rich sward to a closed Festuca-dominated turf on deep loessic soils since myxomatosis, and they underestimated the effect which the species composition of the surrounding flora has on that of the ant-hill.

The surveys described in Chapters 2-4 enabled me to pinpoint those species with patterns in relation to ant-hills which were worth investigating further. The life-cycles of these species were then investigated in more detail at Aston Rowant N.N.R. (Chapter 5) in order to define the main factors influencing their population sizes on the mounds.

4.5. SUMMARY

The vegetation on 206 ant-hills of a wide range of size and ant-heaping activity on my plot at Beacon Hill, Aston Rowant N.N.R., Oxon. was described in detail. A surrounding vegetation quadrat was associated with every alternate mound.

There was a rough correlation between the total number of species on an ant-hill and the number of species in nearby surrounding vegetation quadrats. Species rarely occurred on

ant-hills when they did not grow in the sward nearby. Festuca rubra, Lotus corniculatus, Helianthemum chamaecistus, Carex flacca and Leontodon hispidus are the most abundant species on small, active mounds. Rosettes of Hieracium pilosella and Carex flacca are often more abundant on abandoned mounds than active 'hills' of the same size. Thymus drucei becomes an increasing component of the vegetation with larger mound volume. Agrostis stolonifera and Galium verum are most abundant on very active mounds.

The probable importance of burial in killing rosettes of dicotyledonous herbs is stressed. 19.5% of all Carex flacca rosettes on the mounds were at least partly buried; smothering of Carex probably causes its restriction to the edges of medium active mounds, whilst on medium abandoned mounds its rosettes are distributed randomly. Rosettes of Carex, Hieracium pilosella, Leontodon hispidus and Plantago lanceolata on large, active ant-hills occur mainly around the margins. When mounds are deserted by the ants, the chambers and channels disappear, organic matter accumulates, an A₀ horizon is formed, the previously structureless soil becomes aggregated into peds and its total nitrogen content increases.

A hypothesis is advanced to explain the probable course of 'succession' on both active and abandoned mounds on my plot.

CHAPTER 5

FACTORS AFFECTING THE PATTERNS OF CERTAIN SPECIES IN RELATIONTO ANT-HILLS AT ASTON ROWANT N.W.R.5.1. INTRODUCTION

In this chapter, I describe observations and experiments made on eleven species, mainly at Aston Rowant N.W.R., in 1969/72. I wished to define the factors affecting the patterns of these species, as a prelude to quantifying their life-cycles on ant-hills in detail. I studied Arenaria serpyllifolia, Cirsium acaule, Poterium sanguisorba and Leontodon hispidus more fully than the other seven species. Many of my data are elementary, because very little has been published on the basic biology of most common British grassland plants, I discuss in turn: Arenaria serpyllifolia, Veronica arvensis and other winter annuals, Cerastium holosteoides, Thymus drucei, Helianthemum chamaecistus, Cirsium acaule, Poterium sanguisorba, Leontodon hispidus, Plantago lanceolata, Carex flacca and Pseudoscleropodium purum.

5.2. METHODS

The experiments which only involved one species are described under the species concerned, but several methods were applied to more than one species and are listed below.

1. Standard germination conditions. Seeds were counted out onto two thicknesses of Whatman's no.3 filter paper in 9 cm petri-dishes kept on a laboratory bench.¹ The papers were kept moist

¹ Between 6 October and 6 December 1969 air temperature on the bench fluctuated mainly from 18-22°C, with a minimum of 16°C and a maximum of 23°C.

with distilled water; the dishes had lids but were not sealed.

2. Experiment A. Pilot experiment to investigate the effects of an increased ratio of far red to red light, such as might occur under a sward, on seed germination

For each species, the design¹ was 4 treatments x 2 replicates x 50 seeds. On 20 October 1969 50 seeds were placed on 2 thicknesses of Whatman's no.3 filter paper in each of 8 9 cm petri-dishes. Two dishes were kept on a laboratory bench in the light, and the other six were placed on a concrete roof under conditions of natural daylight. Two of these dishes remained in the light, two were surrounded by a double layer of aluminium foil, and the other two were completely surrounded by two layers of large Tilia europaea leaves, held on by elastic bands. The absorption spectrum of two Tilia leaves is illustrated by Black (1969), who used them for the same purpose. The filter paper was moistened with distilled water every 3-4 days if needed; the water was added to the dark and Tilia treatments under a weak green light in a darkroom.

3. Experiment B. Growth cabinet experiment to investigate the effects of burial under different depths of J.I. Compost, on seed germination and seedling emergence

For each species, the design was 6 treatments x different number of replicates x 45 seeds (arranged in 3 separate groups of 15). 45 seeds were placed on a sheet of Whatman's no.3 filter paper in each of 24 9 cm petri-dishes. Eight of these dishes were untreated, so that the seeds in them were exposed to light. Four dishes were each surrounded by a double layer of aluminium foil. In four dishes the seeds were covered to a depth of 2 mm

¹ The size of the experiment was limited by the number of large Tilia leaves I could find.

with dry, sterilized, unsieved J.I. Compost. Another group of four dishes had their seeds buried to 5 mm, and the final group of four dishes had seeds buried to 10 mm. In the sixth treatment one 9 cm petri-dish was filled to a depth of 5 mm with dry sterilized J.I. Compost which had been sieved through a 2 mm sieve, and 45 seeds were placed on the soil. All the petri-dishes had lids but were not sealed.¹

4 g of distilled water was added to all the dishes which did not contain soil, and the final weight of each dish was noted so that the correct weight of water could subsequently be replaced. In the treatments involving burial, 4 g of distilled water was added to the filter paper and seeds, the soil was placed over them, water equivalent to 35% of the weight of the soil was added, and the final weight of each dish was recorded. In the sixth treatment, water equivalent to 35% of the weight of the dry soil was added to the dish. I found that the dishes needed 'topping up' with water every 4-5 days. The four dishes in the 'dark treatment' were only examined and watered under weak green light in a darkroom.

All the dishes were randomised in a growth cabinet maintained at 20°C² with a 16-hour day. The cabinet had 'natural fluorescent' tubes providing an illumination of about 2150 lx at petri-dish level (with gauze). The experiment began on 8 September 1970.

¹ Seeds were not placed near the edges of the filter papers; gaseous diffusion (e.g. of CO₂ and O₂) might be greater down the sides of a dish than through soil.

² The experiment was performed under 'constant' conditions so that comparative experiments could be done later under similar conditions.

4. Measurement of mean inflorescence heights. It was not worthwhile to number the inflorescences of a species and select a random sample. A stick was thrown several times in the sampled area, and I measured the heights from the ground of the centres of the 10 or 20 inflorescences which were nearest the tip of the stick each time.

5. Collection of plants for the determination of mean seed production

Mean seed production in Arenaria serpyllifolia and Veronica arvensis was determined by collecting all the plants of a species on the same ant-hill. The ant-hills themselves were not selected by a random procedure; they were merely mounds with high densities of the species. Inflorescences of Carex flacca, Poterium sanguisorba, Plantago lanceolata and Leontodon hispidus were collected from my plot by selecting the nearest inflorescences to a stick thrown about in the sampled area.

6. Experiment C. The sowing of seeds on ant-hills and in the sward in my Beacon Hill plot in 1969

For each species, the design was 5 blocks x 2 treatments x 3 sowing densities. The perspex template (Fig. 42) was placed over 33 large mounds in the control plot in turn, and its corners were marked with wooden pegs. The ant-hills which received the seeds of a particular species were chosen arbitrarily. At sowing¹ the template was placed in position on the ant-hill and 25, 0, and 100 seeds respectively were sown into

¹Seeds falling naturally onto the ant-hill surface in early summer might be buried by soil heaped up by the ants. Burial might impose seed dormancy. In my experiment, seed sowing occurred in late summer and early autumn, so that a lower proportion of seeds than usual might have been buried at germination time.

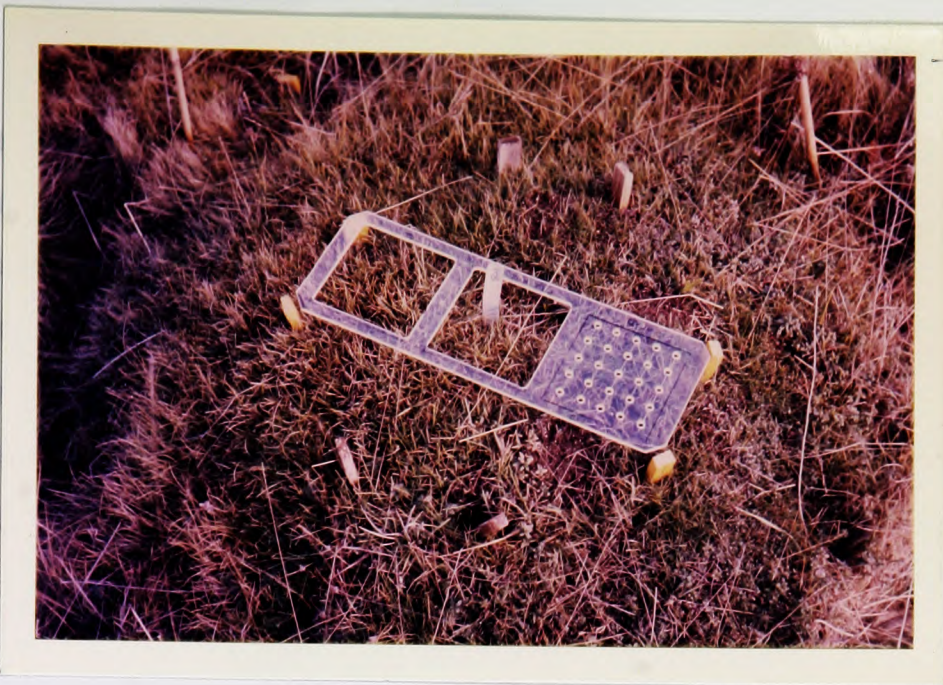


Fig. 42. Experiments C & D. The use of a perspex template and wooden pegs in marking out 100 cm² seed-sowing plots on ant-hills.

three 100 cm² quadrats.

A 'surrounding vegetation area' 30 cm from each mound in a random direction was selected and the vegetation cut to 7.5 cm. This area was cut from time to time with shears to maintain the vegetation at 7.5 cm. The corners of the template were again marked with wooden pegs and seeds of the same species were sown into the sward at the same three densities as for the mound.

Unfortunately many seeds sown in September 1969 did not germinate because there was a complete drought from 21 September to 1 November.¹ The total number of seedlings present in each quadrat was recorded at intervals.

7. Experiment D. The sowing of seeds on ant-hills in my Beacon Hill plot in 1970

The design was 5 sowing densities x 5 replicates. 24 large mounds, some inside the control area and others on the north-

¹Wheat drilled in the field next to my plot on 25 September did not germinate for 5 weeks.

eastern side of it, were prepared by marking the corners of the perspex template with wooden pegs. 5 replicates of each of the seed densities 0, 3, 10, 30 and 100 seeds/100 cm² quadrat were sown for each species, but the different seed densities of a species were not necessarily sown onto the same mounds. The total number of seedlings present in each quadrat was recorded at intervals. Seedlings of particular species were mapped, and in Poterium sanguisorba the number of leaflets per leaf of each surviving seedling was recorded.

5.3. RESULTS

5.3.1. Arenaria serpyllifolia¹

A. serpyllifolia is a winter annual which is frequently confined to ant-hills in calcareous grasslands (sections 3.3. & 3.4). What factors affect the sizes of Arenaria populations on the mounds, and why are they restricted to ant-hills?

At Beacon Hill, flowering plants occur from mid-May to October, but the flowering peak is from mid-May to late June. These flowering plants produce, on average, about 104 seeds per year.² This estimate is based on two independent determinations,

¹ Many of the Arenaria individuals on Beacon Hill cannot be dogmatically assigned to either A. serpyllifolia or A. leptoclados. Thus my 'A. serpyllifolia' may include some A. leptoclados individuals. Clapham (1969) notes that intermediates occur in Derbyshire and Clapham et al. (1968) make A. leptoclados a subspecies of A. serpyllifolia.

² Salisbury (1942, p.131) found that 31 plants produced 20841.6 capsules/plant, giving a mean seed output of 3583, over thirty times my estimates. On 21 August 1971 I collected 7 'interesting' Arenaria plants from an ant-hill; these were not a representative sample of the plants there. The plants had a mean of 195 capsules, similar to Salisbury's estimate. One plant had 702 capsules, another 431 and another 193. I feel that Salisbury (1942) probably over-estimated the normal seed production of many species.

assuming that each capsule contains 16.75 seeds¹ (mean of 40 capsules taken from Aston Rowant on 7 August 1970). All 48 plants on an ant-hill at site C on Beacon Hill (see map, Appendix 29) had a mean of 5.98 capsules per plant (100.15 seeds per plant) on 7 August 1970. All 63 plants on another mound at the same site had a mean of 6.44 capsules per plant (108) seeds per plant) on 21 August 1971.

The black, papillose seeds, weighing about 66 μ g (two independent estimates each on 1000 seeds, gave means of 60.9 and 70.3 μ g),² have an after-ripening period, which Ratcliffe (1961) found to last 6 weeks in the Peak District. They are dispersed from the flask-shaped capsules when the wind rocks the plant, by rain-wash (Ridley, 1930), by herbivores, or when the dead plant keels over in late summer. The after-ripening period may be primarily an adaptation to 'avoid' germination during the driest and hottest months of the year (e.g. Ratcliffe 1961). It may also prevent the premature germination, in the upright capsules, of those ripe Arenaria seeds which are not dispersed immediately. Because of the after-ripening period, A. serpyllifolia survives the period of intense soil-heaping by ants and rabbits in June, July and August as a seed.

Nevertheless, burial of seeds during this period might reduce the proportion which germinate or the degree of seedling emergence. In Experiment B, burial of Arenaria seeds under 5 mm or 10 mm of unsieved J.I. Compost greatly reduced the proportion which produced emergent seedlings (Fig. 43). Perhaps

¹ Salisbury (1942) found 17.2 ± 0.3 seeds per capsule in eighty A. serpyllifolia capsules.

² Seeds of this and other species were stored in envelopes in the laboratory until needed.

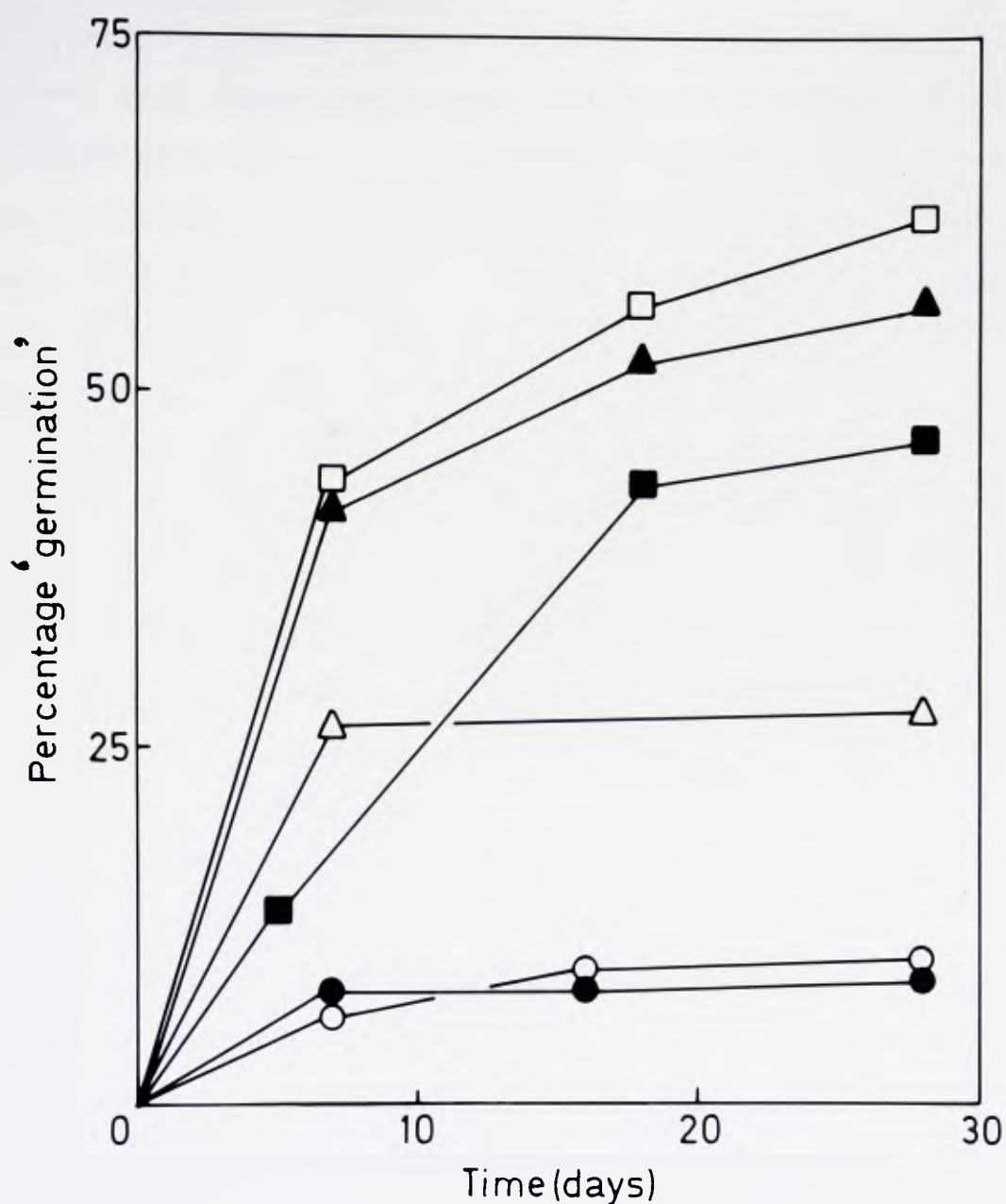


Fig. 43. Effect of burial on the germination of *Arenaria serpyllifolia* seeds (collected 15 July 1970) in Experiment B (8 September 1970).

- On 5mm of sieved J.I. compost.
- On filter paper, in the light.
- ▲ On filter paper, under 2mm of J.I. compost.
- △ On filter paper, in the dark.
- On filter paper, under 5mm of J.I. compost.
- On filter paper, under 10mm of J.I. compost

the seeds germinated at depth, but the seedlings died before they reached the soil surface. Alternatively, seed dormancy might have been imposed (e.g. by high CO_2 concentrations in the soil atmosphere, Harper 1957) or induced (e.g. by producing a light-requirement for germination in the seed, Wenson & Wareing 1967) by burial. Whatever the cause, it seems possible that deeply-buried A. serpyllifolia seeds on ant-hills might not produce healthy seedlings. After all, the seed reserves are minute. Since most dense A. serpyllifolia populations occur on bare soil on active ant-hills, up to 20% of the seeds reaching the ant-hill surface in a year might be buried to >1 cm depth (subjective estimate, based on my experience).

Since flowering-time is staggered, germination-time is also staggered; germination occurs during ^{the} first rainy weather after after-ripening is complete. Peak germination on Beacon Hill is usually in August, but sometimes in early September if August is dry. I have only one reliable estimate of the proportion of seeds reaching the ant-hill surface which germinates in a year. On 3 October 1969, 625 A. serpyllifolia seeds, with 99.0% viability under 'standard germination conditions' were sown onto mounds in my control plot in Experiment C. Most of the germination occurred during a week of warm wet weather before 19 November 1969, by which time 255 seedlings had emerged. Assuming no seedling mortality, 41% of the seeds produced seedlings.

I investigated the extent and causes of seedling mortality in Arenaria seedlings in great detail in 1971, because by that time several pieces of evidence suggested that seedling mortality

was considerable. For instance:

(i) 715 seeds (collected in August 1968 and with 98.7% viability under 'standard conditions') were sown on mounds in my plot on 22 August 1970 in Experiment D. By 31 May 1971, eleven plants had fruited, producing 33 capsules (553 seeds at 16.75/capsule) between them. Thus only one out of every 64 viable surface-sown seeds produced a fruiting plant in the next year,¹ and since 300 seedlings had been seen in the previous year, many seedling deaths must have occurred.

(ii) On 25 August 1970, I noticed over 200 A. serpyllifolia seedlings on an ant-hill in my plot, and over 100 on another. As a result of rabbit scratching, which had buried many of the plants, only 20 seedlings remained on each mound on 2 September 1970.

(iii) I mapped all 405 seedlings present on two mounds in my plot on 20 September 1970. Only 150 remained by 10 October. I attributed 125 of the 255 deaths to rabbit scratching and the consequent burial, 113 to desiccation of seedlings on the south sides of the mounds in a long spell of hot dry weather, 2 to shading by Fagus leaves, which produced etiolation and death, and one to grazing (by molluscs?).

(iv) On 13 August 1971 one of these ant-hills already had over a hundred seedlings in the cotyledon stage. Over fifty of them had been washed away by heavy rain by the end of the day.

¹ In comparing this result with that of the later experiment (Tables 20 & 21, Fig. 43) one must bear in mind that rabbits did not have access to this experiment, whereas rabbit scratching was the major cause of seedling mortality in the later experiment.

Thus on 18 August 1971 I marked out 20 16 cm² quadrats, each containing an accessible group of A. serpyllifolia seedlings, on seven different mounds. The total number of seedlings in each quadrat at the start of the observations ranged from 380 to 13. I examined the quadrats at intervals from 8 September 1971 to 27 July 1972, and recorded the total numbers of seedlings with 0, 2, 4, 6 etc. true leaves, the number of 'newly-germinated' seedlings (which were left in situ), and any causes of seedling mortality. This procedure enabled me to separate 'newly germinated' seedlings from my original 'cohort' to some extent. I undoubtedly made errors in counting dense seedling populations, but the results (Table 20, combined and plotted in Fig. 44), are substantially correct.

Table 20. *Arenaria serpyllifolia*. Decline in numbers with time in a cohort of seedlings followed in twenty* 16 cm² quadrats on ant-hills at Aston Rowant N.N.R. in 1971/2

No.	1971			<u>Recording date</u>			1972	
	18 Aug.	8 Sept.	30 Sept.	1 Nov.	7 Jan.	15 Apr.	1 Jun.	27 July
1	225	205	82	73	34	14	5	3
2	151	126	85	78	66	8	1	1
3	380	309	243	52	12	10	1	
4	102	79	66	40	19	5	2	1
5	80	64	32	8	4	3	2	1
6	87	4	2					
7	93	26						
8	30	1						
9	48	45	28	23	19	3		
10	318	259	227	132	80	55	11	
11	101	40	29	21	18	7	7	5
12	14	4	3	1	1	1	1	1
13	15	5						
14	99	37						
15	93	60						
16	55	53	40	8				
17	32	11	5	5				
18	95	11	10	10				
19	31	17	2	1				
20	29	11	4					
	2078	1367	858	452	253	106	30	12

* quadrats 1-12 were at site C, and quadrats 13-20 at site H, on the map of Aston Rowant N.N.R. in Appendix 29.

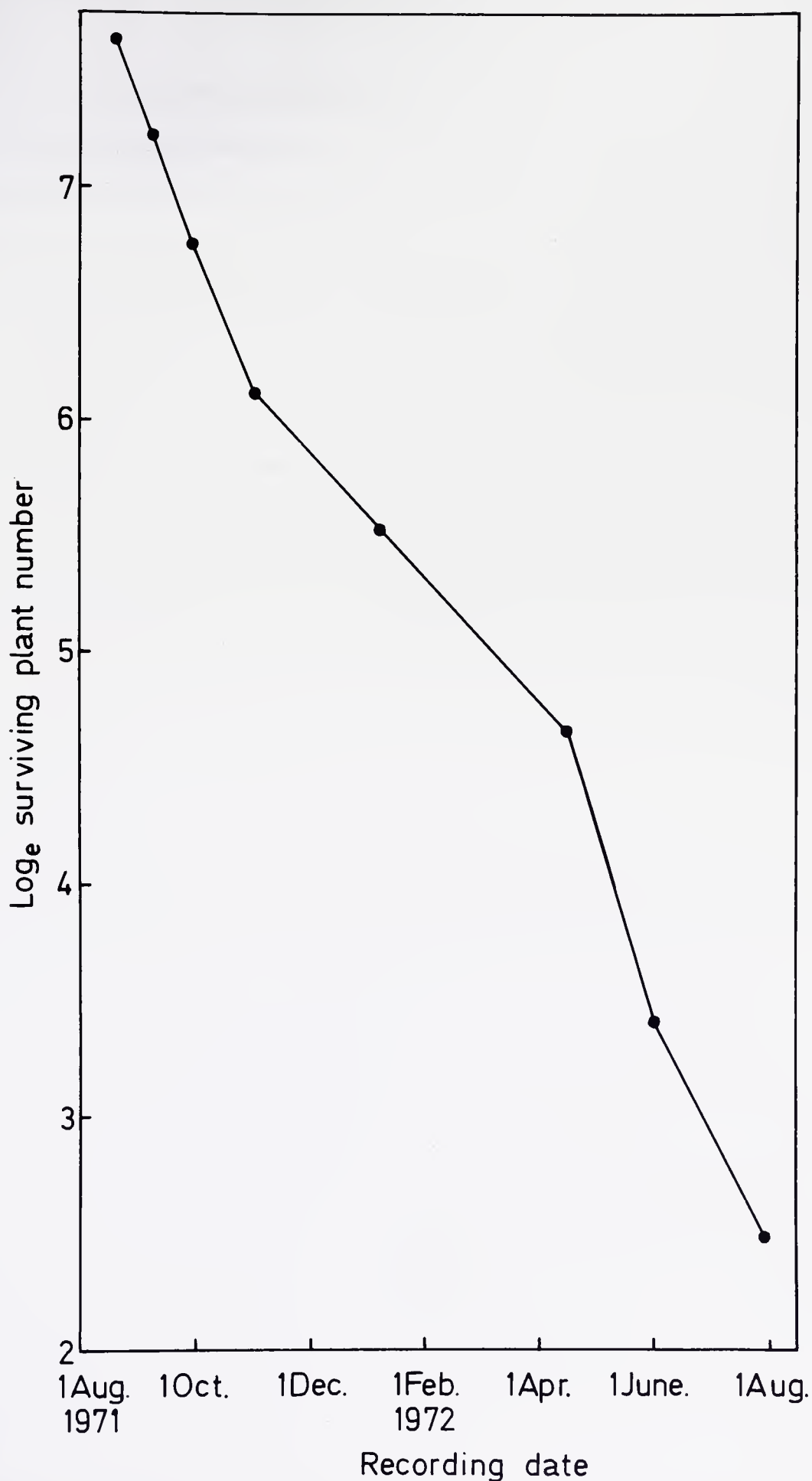


Fig.44. Decline in number of a 'cohort' of 2078 seedlings of *Arenaria serpyllifolia* on mounds on Beacon Hill. The line $\log_e y = 7.72 - 5.035t$, where y is the surviving number of plants and t is the time in years, accounted for a significant ($P < 0.001$) proportion of the total variation in plant number, giving a half-life of 0.14 years.

The 'cohort' originally consisted of 2078 seedlings.

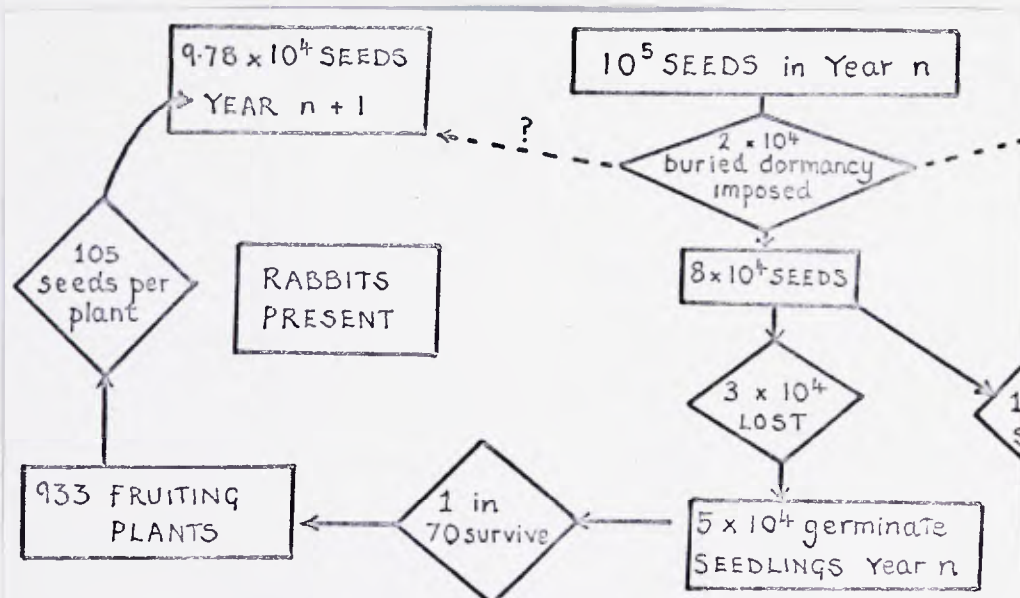
There was a rapid decline in seedling numbers, the main cause of mortality (Table 21) being rabbit scraping, and the resulting

Table 21. Factors which caused seedling mortality in the 'cohort' of seedlings of *A. serpyllifolia* which was followed from 18 August 1971 to 27 July 1972

- (i) Rabbit scraping and the associated heaping of soil over seedlings by rabbits was the main cause of seedling mortality. They obliterated the seedlings in 9/20 quadrats. In others, it killed the smaller seedlings but 'selected out' the larger ones.
- (ii) Heaping-up of soil over plants by ants (Q1, 2, 3, 5). This killed seedlings in late summer and autumn and eliminated old, poorly-developed seedlings (2-6 true leaves), which over-wintered, in spring.
- (iii) Smothering of seedlings by rabbit droppings (Q1, 2, 4, 5), *Fagus sylvatica* leaves (Q1, 16) or *Sorbus aria* leaves (Q3, 10) caused seedling etiolation and death.
- (iv) Digging by the green woodpecker (*Picus viridis*), Q13.
- (v) Grazing by snails and slugs (Q1, 2, 5, 9, 11, 12). This, like burial, seemed to stimulate branching.
- (vi) Fungal infections (Q2, 3). Quadrat 3 had 380 seedlings on 18 August and 300 were still present on 30 September. But on 1 November, only 60 remained. A dense network of fungal hyphae connected those plants still standing. Most seedlings had yellowed leaves, and their hypocotyls were shrivelled at soil level.
- (vii) Competition with other species, e.g. *Acrocladium cuspidatum* (Q4), *Bryum caespiticium* (Q3, 4, 10) and *Helianthemum chamaecistus* (Q4). Shading caused etiolation and death. Seedlings with their roots in *B. caespiticium* clumps were often still at the 2-6 leaf stage in April 1972.
- (viii) Self-thinning (Q3). A dense seedling carpet, with up to three layers of cotyledons, produced etiolated seedlings which remained in the cotyledon and 2-leaved stages for much longer than elsewhere; this probably made the seedlings susceptible to other hazards, like fungal infection.
- (ix) Desiccation during hot weather in early September 1971 (Q15, 20). In quadrats on the south sides of ant-hills the seedlings appeared scorched and shrivelled up. The root system of small *Arenaria* seedlings is rarely more than 2 cm deep, and soil temperatures on the south sides of ant-hills can exceed 40°C at this time of year.

heaping of soil over the plants. Seedlings which developed most rapidly in summer and autumn were those most likely to fruit and produce abundant capsules in 1972.¹ Most seedlings have only 2-4 true leaves at the beginning of winter and die without setting seed, but those seedlings most likely to fruit overwinter with 16-20 more leaves. A negative exponential regression of seedling numbers on time explained a highly significant ($P < 0.001$) proportion of the total variation in seedling number, and gave a seedling 'half-life' of 0.14 years. 30 plants fruited in 1972, and since the 12 plants remaining on 27 July had produced 56 capsules between them, the 30 fruiting plants had probably produced about 140 capsules, or about 2345 seeds (at 17.75 per capsule). Only one in 69 of the seedlings present on 18 August had produced a fruiting plant.

Fig. 45. A crude quantification of Arenaria serpyllifolia's life cycle.



¹ Seedlings produced from seeds which germinated in autumn seemed much more susceptible to environmental hazards. For instance, of 255 newly-germinated *Arenaria* seedlings present on 5 mounds in my plot on 19 November 1969, 87 (mostly still in the 2- or 4-leaved stage) remained in April 1970, and none fruited. Newman (1963) noticed the same phenomenon in *Aira praecox*.

Fig. 45 shows a rudimentary quantification of Arenaria's life-cycle, using many of the measurements which I have made. Much of the absolute and most of the relative mortality in the life-cycle occurs at the seedling stage. The tiny seeds produce small seedlings highly susceptible to environmental hazards.

Why are fruiting Arenaria plants strikingly absent from the vegetation surrounding ant-hills? In Experiment C, 625 seeds, with 99% germination under 'standard conditions', were sown into swards on 3 October 1969. Only 8 seedlings were seen and all died rapidly. Since I was not certain how many seeds had germinated, I sowed ten groups of 20 seeds each into short (1-2 cm) open turf on my plot on 4 September 1971, and examined the sites every 2-3 days. Although the germination of the sample under 'standard laboratory conditions' was 67.5%, only two seedlings appeared in the field, one on 28 September and the other on 25 October. Abundant Arenaria germination occurred on mounds nearby during this time. If the seeds had germinated in the swards, I would have seen the cotyledons. Either the seeds had been destroyed by predation or parasitism, or they had not germinated.

The possibility that dormancy of Arenaria seeds might be imposed under a sward by the increase in the proportion of far-red to red light (Pigott 1967, Taylorson & Borthwick 1968) was investigated in Experiment A. The results in Table 22 show that dormancy was imposed on Arenaria seeds under a leaf canopy in experimental conditions.¹ Since A. serpyllifolia seedlings

¹ The experiment needs to be repeated and followed up by using filters. Does the response of Arenaria seeds to the quality of light change with the age of the seed? How are seedlings affected under swards by the 'quality' of light?

Table 22. Experiment A, October/November 1969. Germination response of *Arenaria serpyllifolia* seeds (collected 26 August 1968) when surrounded by two layers of *Tilia* leaves

Design: 4 treatments x 2 'dishes' x 50 seeds.

Final number of germinated seeds per 'dish
(after 27 days)

<u>Laboratory</u> <u>Light</u>	<u>Light</u>	<u>Laboratory roof</u> <u>Dark</u>	<u>2 layers</u> <u><i>Tilia</i> leaves</u>
50	47	30	0
50	48	35	1

Analysis of variance on untransformed data

<u>Source</u>	<u>d.f.</u>	<u>M.S.</u>	<u>F₀</u>
Among treatments	3	1036.8	307.2***
Within treatments	4	3.4	
	7		

The following differences between treatments are significant (P 0.05) by Gabriel's (1964) sum of squares simultaneous test procedure:

<u><i>Tilia</i> leaves / Lab. light.***</u>	<u>Dark / Lab. light.**</u>
<u><i>Tilia</i> leaves / Roof light.***</u>	<u>Dark / Roof light.**</u>
<u><i>Tilia</i> leaves / Dark.**</u>	

(**, 0.01 > P > 0.001; ***, P < 0.001).

have little chance of survival in a sward,¹ it might be a selective advantage to the species if the seeds could remain dormant until conditions changed. However, the importance of this process under field conditions is questionable since many seeds must become buried.

¹Grime & Jeffrey (1965) showed that although *Arenaria* grows rapidly in full daylight it has poor shade survival; 'small seeds are liabilities in shaded environments'.

5.3.2. Veronica arvensis and other winter annuals

Veronica arvensis is confined to ant-hills at several sites (Table 13), but on Beacon Hill it occurs mainly on ant-hills on the northern slopes. It resembles Arenaria serpyllifolia in its biology and life-cycle, but I have not studied it in such great detail.

V. arvensis has a flowering peak in early May. The seeds, which weigh $146 \mu\text{g}^1$ (mean of 497 seeds collected from Beacon Hill) are rapidly dispersed from the ripe capsules, but they have an after-ripening period, which Ratcliffe (1961) found to last for 12 weeks in the Peak District. Thus germination occurs in rainy periods from the beginning of August onwards.

Those seeds which have been buried by heaped soil in the intervening months may not germinate. In Experiment B, germination was inhibited under 5 mm or 10 mm of unsieved J.I. compost (Fig. 46).² Moreover, some collections of V. arvensis seeds contain a high proportion of seeds with a light requirement for germination. For instance, when seeds collected from Beacon Hill on 26 June 1968 were germinated in groups of 50 under 'standard conditions' (19 January 1969), 287/297 (96.3%) germinated in the light in 17 days but only 74/200 (37%) germinated when the petri-dishes were surrounded by two layers of aluminium foil. M.J.D. Percival (1969, pers. comm.) found that germination of V. arvensis seed collected from Breckland was inhibited by darkness, burial, and CO_2 concentrations of 2-4% in air. The responses of the seeds of winter annuals to burial, and the importance of burial in their life-cycles on ant-hills, merit further investigation.

¹Salisbury (1942) gives $122 \mu\text{g}$.

²Seedling emergence was lower; but when the soil was excavated, no evidence of germination followed by seedling death was seen.

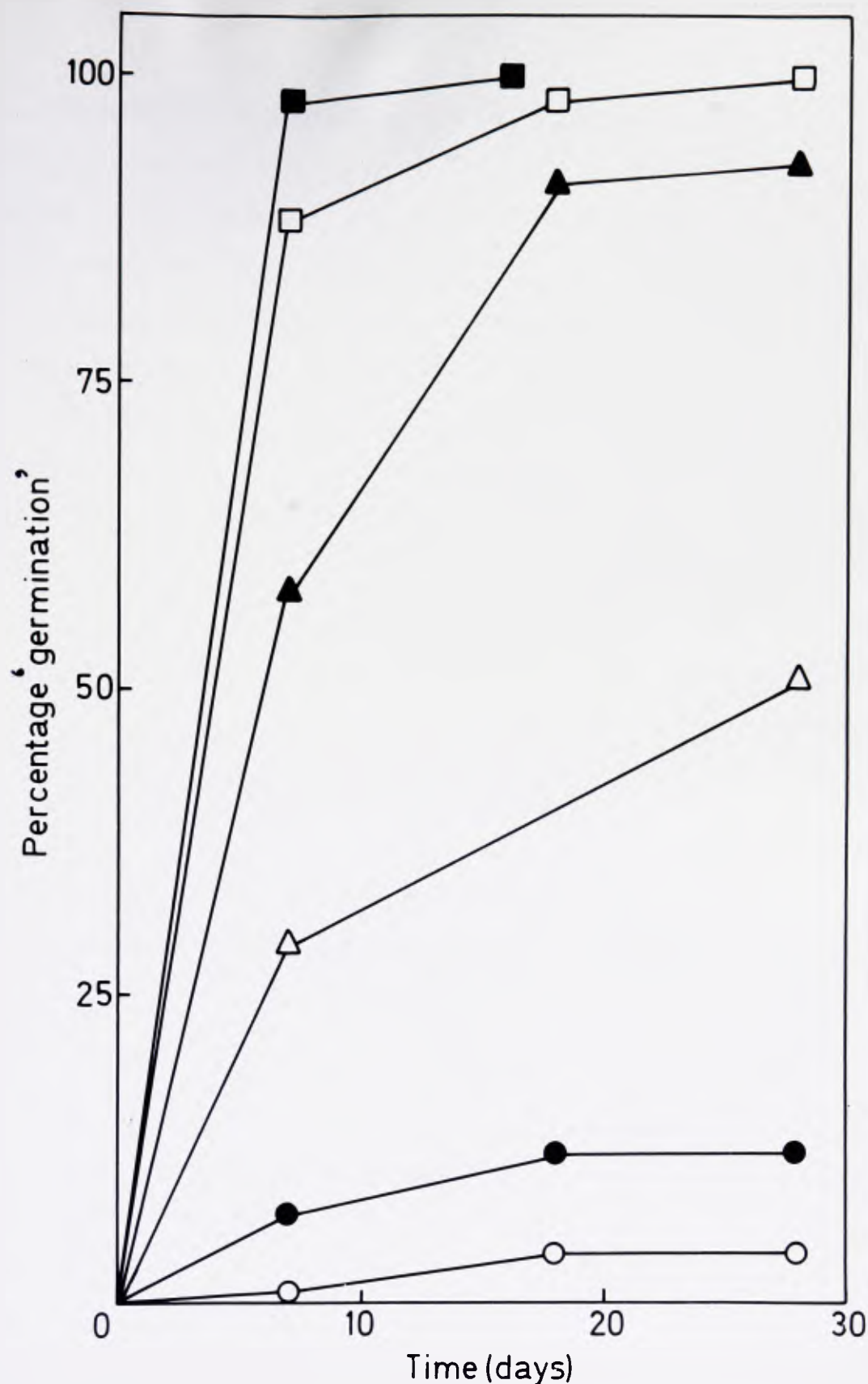


Fig.46. Effect of burial on the 'germination' of *Veronica arvensis* seeds (collected 10 July 1969) in Experiment B (8 September 1970).

- On 5mm of sieved J.I. compost.
- On filter paper, in the light.
- ▲ On filter paper, under 2mm of J.I. compost.
- △ On filter paper, in the dark.
- On filter paper, under 5mm of J.I. compost.
- On filter paper, under 10mm of J.I. compost.

None of the V. arvensis seeds sown in Experiments C & D ultimately produced a mature plant and so I cannot quantify Veronica's life cycle on the mounds. Some seedlings died through self-thinning, some through mollusc grazing, and many newly-germinated seedlings were smothered by soil heaped up by the ants in August and September.

500 seeds were sown into swards in my plot on 12 September 1969 in Experiment C. Eleven seedlings were seen, which all became tall and etiolated. Two persisted until the following April. Germination of V. arvensis seeds, like those of Arenaria serpyllifolia, was inhibited in Experiment A when the petri-dishes were covered with two layers of Tilia leaves (Table 23).

Table 23. Experiment A, October/November 1969. Germination response of Veronica arvensis seeds (collected 10 July 1969) when surrounded by two layers of Tilia leaves

Design: 4 treatments x 2 'dishes' x 50 seeds.

Final number of germinated seeds per 'dish' (after 27 days)

<u>Laboratory</u> <u>Light</u>	<u>Light</u>	<u>Laboratory roof</u> <u>Dark</u>	<u>2 layers</u> <u><u>Tilia</u> leaves</u>
48	46	40	0
50	48	49	1

Analysis of variance on untransformed data

<u>Source</u>	<u>d.f.</u>	<u>M.S.</u>	<u>F₀</u>
Among treatments	3	1080.2	96.01***
Within treatments	4	11.25	
	7		

The following differences between treatments are significant ($P < 0.05$) by Gabriel's (1964) sum of squares simultaneous test procedure:

Tilia leaves / Dark***

Tilia leaves / Lab. light***

Tilia leaves / Roof light***

(***, $P < 0.001$).

Myosotis ramosissima is very similar to Arenaria serpyllifolia and Veronica arvensis in its biology¹ and its response to ant-hills. Other members of this 'natural' group of winter annuals are Cardamine hirsuta, Catapodium rigidum, Cerastium semidecandrum, Erophila verna, Myosotis discolor, Saxifraga tridactylites and some others mentioned by Ratcliffe (1961).

5.3.3. Cerastium holosteoides

The perennial herbaceous chamaephyte C. holosteoides was very frequently confined to ant-hills at the sites which I studied (Table 13). C. holosteoides is a wide-ranging species, with $2n = 136-152$, and may, like Erophila verna, consist of large numbers of 'pure lines'. Some of these races might be annual (Hutchinson 1955, Clapham et al. 1962), and in its biology and response to ant-hills, C. holosteoides greatly resembles the winter annuals; but when four plants from Beacon Hill were grown up in a cold frame at the laboratory, and five plants on ant-hills on the north side of Beacon Hill were examined at intervals, all lived for over two years. The prostrate creeping rootstock produces several flowering and non-flowering shoots, some of which remain green all winter.

Reproduction of C. holosteoides on ant-hills is almost entirely by seed. It flowers from May to September on the mounds at Beacon Hill, producing perhaps 38.3 ± 3.3 seeds² per capsule

¹ M. ramosissima resembles V. arvensis and A. serpyllifolia in the causes of its seedling mortality, its poor germination and seedling survival in swards, and the imposition of dormancy in its seeds by two layers of Filix leaves. Its seeds have a mean weight of 278 μ g (sample of 36). The hooked bristles on the fruiting calyces may aid dispersal by animals and birds.

² The flowers of C. holosteoides, like those of the other winter annuals which I have mentioned, are predominantly self-pollinated (Clapham et al. 1962).

(Salisbury 1942).¹ The red-brown tubercled seeds (weighing 177 μ g, Salisbury 1942) are released from the wide-open capsules, usually held at an angle of less than 45° to the horizontal, when the plant is jolted by wind or animals. Fruiting heads are often bitten off by rabbits, e.g. on 18 August 1971, 8 plants on an ant-hill on the north side of Beacon Hill had 23 inflorescences, 9 of which had been removed.

Observations on the germination of seed sown on mounds in my plot at various times of year, on seedlings in the field and on germination under fruiting plants at the laboratory all indicate that most C. holosteoides seeds germinate in autumn (especially September)² and some germinate in spring.³ On 22 August 1970 I sowed 715 seeds (collected in September 1968 and with 94% germination in 'standard laboratory conditions') on ant-hills in my plot in Experiment D. 209 seedlings were seen, but they rapidly disappeared. Mortality was mainly due to the heaping of soil over the seedlings by ants, and partly due to shading and etiolation by dense Helianthemum, but rabbits and sheep did not affect seedling deaths because the seeds had been sown on mounds in my control plot. The seedlings gave rise to 4 fruiting plants of Cerastium in 1971, bearing at least 10 capsules between them, a total seed production of 383 if Salisbury's estimate is applied. Thus the rate of seedling mortality of C. holosteoides on ant-hills seems to be of the

¹ Salisbury (1942) found a mean of 168.1 ± 24 capsules per plant per year on plants growing in short, semi-open herbage, giving a mean seed output of 6463 ± 1009 . This is probably an order of magnitude higher than the seed production of C. holosteoides on Beacon Hill ant-hills.

² I have not investigated the possibility that seeds of Cerastium from Beacon Hill ant-hills might have an after-ripening requirement.

³ Wareing (1966) gives C. holosteoides as an example of a species with seeds which have no marked germination periodicity in the laboratory.

same order of magnitude as that of the winter annuals. Its ability to set abundant fruit in the summer after germination contributes to its survival on ant-hills. It can also grow up through heaped soil by the elongation of its rootstock and the production of new rosettes at the tip; chamaephytes seem to have an advantage over hemicryptophytes on ant-hills in this respect. Thymus drucei, Helianthemum chamaecistus, Veronica officinalis and V. chamaedrys can also continually put their buds above the surface of soil heaped over them.

In Experiment C, C. holosteoides had a higher germination rate and longer seedling survival under swards than the winter annuals. Of 650 seeds sown in swards on 20 September 1970, 50

Table 24. Experiment A, October/November 1969. Germination response of Cerastium holosteoides seeds (collected 4 September 1968) when surrounded by two layers of Tilia leaves

Design: 4 treatments x 2 'dishes' x 50 seeds

Final number of germinated seeds per dish (after 27 days)

<u>Laboratory</u> <u>Light</u>	<u>Light</u>	<u>Laboratory roof</u> <u>Dark</u>	<u>2 layers</u> <u><u>Tilia</u> leaves</u>
44	47	46	3
46	47	47	24†

† The leaf cover on this 'dish' was accidentally broken. The seedlings inside were ± horizontal, leaning towards the gap.

Analysis of variance on untransformed data

<u>Source</u>	<u>d.f.</u>	<u>M.S.</u>	<u>F₉</u>
Among treatments	3	535.0	9.6*
Within treatments	<u>4</u>	55.75	
	7		

The following difference between treatments is significant ($P < 0.05$) by Gabriel's (1964) sum of squares simultaneous test procedure:

Tilia leaves / Roof light* (*, $P < 0.05$).

were seen to have germinated, and 6 of the 36 which had appeared in autumn 1970 survived until at least 19 May 1971. All these surviving seedlings had 2-4 leaves and were etiolated, and two of them had developed purple colourations on the leaves, so that their long-term survival in swards was improbable. In Experiment A, Cerastium seeds did not have a light requirement for germination, but their germination was inhibited under two layers of Tilia leaves (Table 24). This mechanism might impose some dormancy under dense swards, where in any case the seedlings are unlikely to survive for long, but the absence of C. holosteoides from short open turf on Beacon Hill is a mystery (see section 3.4 for a possible explanation).

5.3.4. Thymus drucei¹

T. drucei is consistently much more abundant on ant-hills than on the sward (Chapter 3). Its initial invasion of ant-hills, and its vigour there, depend on its rapid vegetative spread, and its ability to grow up through heaped soil. Other factors which might favour its growth on mounds are (i) its resistance to rabbit grazing (Tansley & Adamson 1925); grazed Thymus stems were never seen, (ii) its xeromorphic character, and (iii) the low densities of the shoots and roots of other species on ant-hills.

Thymus shoots colonise young mounds when existing plants are covered by heaped soil as the mounds expand. Further soil heaping would cause repeated branching, allowing Thymus to make up an increasing proportion of the total percentage cover on ant-hills with increasing volume (Chapter 4), and producing a

¹The biology of Thymus drucei is summarised by Pigott (1955).

complex 'root' system ramifying within the mound.¹ Established T. drucei plants on ant-hills often have woody, much-branched 'root' systems penetrating the underlying chalk, which may be 40-60 cm below the top of the mounds. On two out of 3 ant-hills excavated, most of the shoots on the surface came from a single rootstock, even when Thymus had 60% cover on a large mound Thymus shoots form dense prostrate cushions on parts of mounds or mounds where severe soil heaping is absent, with adventitious roots every 6-12 cm, and pairs of axillary branches growing from each node. When buried, both axillary and apical shoots grow vertically through heaped soil. In experimental burials of Thymus shoots on ant-hills on my plot in August 1971 Thymus grew up through 3 cm, but not 6 cm, of suddenly heaped soil.² However, I noted several times during the surveys described in Chapters 3 & 4 that Thymus had grown up through 2-6 cm of soil heaped up previously that summer.³

Thymus flowers profusely and sets abundant seed on ant-hills, although in 1971 no seeds were produced by the 5-10% of inflorescences in my plot which were infected by the acarine gall-mite Eriophyes thomasi. The nutlets weigh 145 µg (mean of 9 seeds) and are dispersed by a flicking mechanism. Most seedlings appear in August-October, but they are subject to such high mortality that I have only noted establishments of Thymus from seed on a mound in two cases. For example, on 25 October 1971 I marked a population of 58 Thymus seedlings, 53 of which had

¹ This hypothesis could be tested by examining the variation in the number of annual growth rings in Thymus with depth.

² Under natural conditions, heaping of soil by ants would be more gradual.

³ Pigott (1955) noted that Thymus drucei could withstand 5 cm of burial in a year.

just germinated and were on the cotyledon stage. None remained on 31 October. On 26 September 1971 I marked 15 seedlings, with 4-10 true leaves, on two ant-hills. They had all disappeared four days later. Thus establishment of Thymus from seed on active ant-hills is much less important than the vigorous growth of its shoots in producing the dominance of Thymus on the mounds.

5.3.5. Helianthemum chamaecistus¹

Helianthemum, like Thymus drucei, is frequently much more abundant on ant-hills than in the surrounding vegetation (Chapter 3). Like Thymus, it is a xeromorphic woody perennial chamaephyte which often has a much-branched woody stem system ramifying through the mounds and a root system reaching the underlying chalk. It probably invades ant-hills vegetatively, on the three mounds dominated by Helianthemum which I have excavated, all the shoots came from the same plant, and so none of the abundantly-produced seeds had produced an established individual.

Unlike Thymus drucei, which invades bare soil by prostrate branches which run across the surface, Helianthemum invades beneath the surface, its horizontal stems throwing up vertical leafy shoots when covered with bare soil. Any one of these shoots could itself subsequently become a horizontal stem with axillary branches. In autumn, new axillary shoots begin to develop below the soil surface on parts of existing shoots. If the apex dies in winter, growth of the axillary shoots continues in spring.

Several estimates indicate that H. chamaecistus shoots can also grow up through 3-4 cm of suddenly-heaped soil. When a

¹The biology of H. chamaecistus is summarised by Proctor (1956).

bucketful of sterile J.I. compost was dumped in my plot in 1970, a Helianthemum shoot grew up through 6-7 cm of soil. On an excavated ant-hill in my plot (10 October 1971) one axillary shoot started from 7.6 cm below the surface. Helianthemum shoots grew up through 6 cm of soil deposited on two ant-hills in my plot in August 1971, but the shoots were already 1.5-2.5 cm above the surface of the mound and heavy rain reduced the depth of the smothering soil. On the other hand, H. chamaecistus shoots in a mound excavated on 17 August 1970 were covered by 4-5 cm of heaped soil and were losing their chlorotic leaves.

The effects of the burial of Helianthemum shoots on their subsequent growth were examined in a greenhouse experiment described in Table 25. In the control shoots, growth was apical

Table 25. The effects of burial on the growth of the shoots of a Helianthemum chamaecistus plant in the greenhouse

Method. A single plant was taken from Beacon Hill in December 1969 and grown up in a heated greenhouse. By October 1970, shoots ran in all directions from the central stock, overhanging the sides of the pot. On 31 October 15 numbered jewellers' tags were tied onto the longest shoots and detailed notes were made on the morphology of each shoot. The ends of 5 randomly-selected shoots were buried to 5 cm in individual 5 cm pots, 5 were buried to 2 cm and the remainder were left unburied as controls. On 3 January 1971 detailed notes and measurements were made again.

Mean increases in shoot length

<u>Controls</u>	<u>Under 2 cm soil</u>	<u>Under 5 cm soil</u>
3.7 cm	2.24 cm	-2.0 cm.

except when the apex of the main shoot was damaged, when it became axillary. Under 2 cm of J.I. compost, three of the five shoots grew apically to produce stems with their leaves projecting above the surface. The apex of the fourth shoot died but an axillary branch grew rapidly and emerged from the heaped soil.

The apex of the fifth shoot also died but branches appeared and grew at the node immediately above the soil surface. All the shoots buried 5 cm deep also responded in this way.

Seed dispersal is inefficient and establishment from seed is sporadic. The seeds, which weigh 1177 μg (mean of 200 seeds collected 11 September 1968) are often released only when the pedicel breaks and the fruiting capsule falls onto the soil surface and disintegrates. 300 Helianthemum seeds sown in Experiment C onto ant-hills in my control plot on 2 September 1969 only gave rise to 3 seedlings altogether before 10 September 1971. The seeds require scarification before germination, under 'standard conditions', probably because of an impermeable testa or cuticle, but then exhibit 100% germination, often extruding mucilage. In the field the scarification requirement may be slowly satisfied by microbial action or the movement of mineral soil particles during freezing and thawing. Although its seedlings appear robust, most Helianthemum shoots on an ant-hill come from plants which have grown up with the mound.

5.3.6. Cirsium acaule¹

C. acaule is a perennial mesophytic rosette hemicryptophyte with a horizontal, branched, sympodial rhizome which allows it to produce large clones vegetatively in short chalk grassland swards. Nevertheless, it is strikingly absent from ant-hills (Chapter 3). In the survey of my plot described in Chapter 4, C. acaule occurred in 90 of the 103 surrounding vegetation quadrats, often with a cover of 5-10%, but I saw only 46 rosettes on 206 mounds.

¹The biology of Cirsium acaule is summarised by Pigott (1968).

All the rosettes on ant-hills which were not on the absolute margin were completely isolated and must have come from fruit dispersal and germination. Vegetative reproduction in Cirsium acaule is much too slow to be important in ant-hill invasion. Thus the factors most likely to influence the population size of Cirsium on the mounds are the density of viable achenes produced in the sward,¹ the efficiency with which they are dispersed, the germination rate of the fruits which reach the tops of ant-hills and the rate of decline in numbers of the seedlings.

I investigated Cirsium's viable fruit production and dispersal in Beacon Hill in 1971. I estimated the production of viable fruits in two Cirsium populations at 139.6 and 205.5 viable achenes/m² respectively (Table 26). On Beacon Hill Cirsium acaule begins to flower in late July and most of the viable fruits are released from the beginning of September onwards. Pigott (1968, 1970) showed that the number of viable fruits set by C. acaule inflorescences is influenced by the weather from the time when the first flowers open to the time when the last fruits are dispersed. This is because the availability of pollinators and the weather determine the proportion of florets pollinated, and the percentage of fertilized ovules which produce fully-grown embryos increases with temperature. August 1971 was warmer than average and 14.85 and 11.9 viable achenes were produced per capitulum.²

¹I have never seen Cirsium flowering on an ant-hill.

²From Pigott's (1970, p.37) map of the mean numbers of viable achenes produced per capitulum at 13 sites in September 1963 one might expect 8-10 viable fruits per capitulum at Aston Rowant.

Table 26. Data from two populations of *Cirsium acaule* at Aston Rowant N.N.R. (1971)

POPULATION	1	2
Letter on map of reserve (Appendix 29)	P	M
Date sampled	31 August 1971	
Sampled area (m)	150 x 25	30 x 25
Random 0.25 m ² quadrats sampled	20	15
Mean number of <i>Cirsium</i> rosettes/m ²	31.2	25.3
% of rosettes producing inflorescences	28.2	66.3
Mean number of inflorescences/rosette	1.07	1.03
Mean number of inflorescences/m ²	9.4	17.3
Number of inflorescences ¹ examined	20	20
Mean number of florets/inflorescence	71	75.4
Total number of fruits recovered/infl.	57.75	68.9
Mean number viable ² fruits recovered/infl.	14.85	11.9
Mean number underdeveloped ³ fruits/infl.	9.3	14.3
Mean number empty ⁴ fruits/infl.	29.7	25.6
Mean number deformed ⁵ achenes/infl.	3.9	17.2
Mean number viable achenes produced/m ²	139.6	205.5
Mean number seedlings/m ²	0.6	1.08
Number ant-hills examined	15	15
Mean number <i>Cirsium</i> rosettes seen/mound	0	0.4

¹ Only ripe fruiting heads, about to release their fruits, were examined.

² 'Viable' fruits weigh over 3 mg and are full and three-cornered.

³ Underdeveloped fruits have incomplete embryo development; they appear turgid, but can be broken with difficulty when prodded with a needle.

⁴ Empty fruits have developed to full size but have not been fertilised; they are empty when prodded with a needle and usually weigh about 1 mg.

⁵ Deformed fruits include cylindrical, brown, fungus-infected fruits and small flat empty ones. They weigh < 0.6 mg.

However, many apparently 'viable' fruits are not released from the inflorescences. For instance, fungal infection (especially by Botrytis cinerea Fr) increases in frequency from the end of August onwards, and is not only an important cause of achene inviability, but sometimes destroys viable seeds or binds them to the receptacle so that they cannot be dispersed. On 3 September 1971 36 (84%) out of 43 random fruiting inflorescences of C. acaule from site M bore signs of fungal attack. The inflorescences act as cups which catch rain and dew, and the receptacles are infected first. Infection spreads to the fruits and the peduncle, and the peduncles frequently disintegrate, leaving the capitula (which may still contain 'viable' fruits) to decay in the sward. Further viable achenes are killed by the orange larvae of Dasyneura spp. (Diptera, Cecidomyiidae), which were found in several fruiting capitula in 1969 and in 8 out of 14 collected from site M (population 2) in September 1971. In one head, they were present in fruits of viable weight. A high proportion of the viable achenes which have not been infected by Botrytis or invaded by Dasyneura larvae is not dispersed because the pappi readily break off, leaving their viable fruits behind in the receptacle. This was noted frequently on Beacon Hill in 1969-71.

The achenes, which weigh $4190 \mu\text{g}^1$ (mean of 40 'viable' fruits), are released from the capitula (2-5 cm above the soil surface) on warm days when their hygroscopic pappi expand and the achenes are drawn out of the inflorescences. On still days, the achenes and their pappi remain clumped around the capitula, and if early September is wet, no dispersal may occur at all.

¹Pigott (1968) found $4490 \mu\text{g}$.

On windy days, however, the viable fruits may be blown further. On 1 September 1971, a warm dry day with a high wind, large numbers of Cirsium pappi were released from population 2 (site N), and I examined all 400 pappi which, over 124 minutes, became caught in a 6.6 length of wire netting 8 m upslope and upwind from the nearest C. acaule plants. 16 of them had viable achenes attached. However, I have only seen two viable Cirsium acaule fruits which have reached the tops of mounds naturally.

'Viable' C. acaule achenes can germinate and produce seedlings on ant-hills. 80 fruits of viable weight were sown in two petri-dishes under 'standard germination conditions' on 13 September 1971. 34 germinated, but many seedlings became infected by fungi immediately on emergence of the radicle,¹ and only 21 remained by 13 October. On 16 September 1971 20 C. acaule achenes from the same collection were sown into each of three 100 cm² quadrats on the tops of ant-hills in my plot. No germination occurred until the spring of 1972, when 13 fruits (22%) germinated. However, there was considerable soil-heaping by the ants in these quadrats, and by 27 July 1972, only two seedlings remained, one of which had its leaves half buried. When the heaped soil was excavated, four dead Cirsium seedlings were found underneath.

C. acaule does not normally flower until at least a year old (Pigott 1968) but the small, stunted plants found on ant-hills would probably not produce viable fruits until they were much older, and then probably not at a rate to maintain Cirsium on the mound.

¹Pigott (1970) notes that Cirsium seedlings often die through 'damping off'.

Thus there are several reasons for the striking absence of Cirsium acaule from ant-hills. The number of viable fruits produced is lowered by the weather, predation and parasitism. Their dispersal is hindered by the low level of the capitula, the high frequency of pappi lost before dispersal, the weather and the heavy achenes. The production of vigorous seedlings on the mounds may be affected by fungal parasitism, and their survival is probably poor because they are susceptible to burial. Seedling development is slow on ant-hills and no flowering plants were seen there.

5.3.7. Poterium sanguisorba

Poterium sanguisorba is a perennial mesophytic rosette hemicryptophyte with a deep woody root system and a vertical rootstock bearing one or more rosettes of pinnate leaves. Although it is a frequent colonist of bare soil (Ridley 1930), mole-hills (Appendix 2), erosion terraces, and soil bared in fence-laying or track making, P. sanguisorba is usually very uncommon on ant-hills (Chapter 3 & Table 27) considering the high density of its rosettes in 'typical' calcareous grassland swards. Since new rosettes are only produced slowly from existing rootstocks, at a distance of less than 2 cm, the invasion of L. flavus mounds by Poterium probably depends entirely on establishment from 'seed'. Thus I shall discuss factors like the density of viable fruits produced in the sward, their dispersal and germination, the survival rate of Poterium seedlings on ant-hills and the ability of Poterium on the mounds to set viable fruit.

Table 27. Data from three populations of *Poterium sanguisorba* at Aston Rowant N.N.R. (1971)

POPULATION	1	2	3
Letter on map of reserve (Appendix 29)	G	B	M
Sampled area (m ²)	210	500	400
Vegetation height (cm)	15-20	10-12	4-10
Grazing	± None	Rabbits	Sheep
Other notes	Brachypodium-rich. <i>Poterium</i> plants very large and old.	Dense, mossy turf.	More open. Mainly <i>Poterium/Cirsium</i> rosettes.
Date sampled	27 Aug.	27 Aug.	1(&3) Sept.
Random 0.25 m ² quadrats sampled	10	10	7 (+ 10)
Ant-hills sampled	10	12	9
Mean number <i>Poterium</i> rosettes/m ²	63.2	110.4	414.3
Percentage of rosettes flowering	28.5	13.4	8.0
Mean number flowering rosettes/m ²	18	14.8	28.6(22)
Mean number seedlings*/m ²	0	6.4	97.1
Mean number seedlings*/ant-hill	0.1	0.4	3.2

* A 'seedling' was a plant with cotyledons and/or at least one trifoliate leaf.

Each *P. sanguisorba* 'inflorescence' bears 1-10 globose 'flower heads', each of which has several male, female and hermaphrodite flowers. Pollen transfer is mainly by wind. I made 10 collections of 20 intact fruiting heads on 4 July 1970 at sites J, K, L & M on Beacon Hill (see map, Appendix 29), and estimated that on average 3.37 fertile fruits were produced per 'flower head'.¹ Assuming that the mean number of 'fruiting heads'

¹ Several fruiting heads sometimes came from the same inflorescence. 1715 fruits were collected, i.e. 8.575 per fruiting head. 733 (42.7%) of these were large enough to contain viable embryos, i.e., 3.665 per fruiting head. 87.7-96.5% of these 'viable' fruits germinated under 'standard conditions' in a month. These 'standard conditions' included five 16-hour nights in a dark refrigerator at 2-5°C, since alternating temperatures enhanced germination. Assuming that 92% of the fruits which had appeared 'viable' were viable, a mean 3.37 fertile fruits per fruiting head were produced on sites J, K, L & M in 1970 if my sample was representative.

per inflorescence is 1.5, and applying my 1970 estimate of viable fruit production to three dense populations of Poterium surveyed in 1971 (Table 27), the mean viable fruit productions in populations 1, 2 & 3 in 1971 were 91, 74.8 and 127.9 viable fruits/m² respectively. I saw little sign of any predation or parasitism which might reduce the number of viable fruits released.¹

The fruits are dispersed in July when the 'fruiting heads' disintegrate. Each consists of an ellipsoid or quadrangular coarsely reticulate persistent calyx tube enclosing 1 or 2 achenes, and weighs 3.37 µg (mean of 400 fruits).^{2,3,4} Inefficient dispersal⁵ of these heavy fruits onto the mounds may contribute to the relative absence of Poterium from ant-hills. Although the fruits are released from mean 'fruiting head' heights of 21-27.4 cm,⁶ most of them probably fall almost vertically. When viable fruits have been sown onto ant-hill soil in August or September (1969-71) they rapidly disappear; many are buried, either by ant activity or rain beating the soil, long before they germinate. The effect of burial under ant-hill soil on seedling emergence was investigated in the laboratory experiment described in table 28. Slight burial enhanced

¹On 8 July 1971, 18 rabbit droppings, examined from ant-hills within population 2 (Table 27), contained 10 Poterium 'fruit cases', 6 of which contained apparently viable achenes.

²This estimate includes fruits containing both one and two viable achenes.

³Salisbury (1942) gives 9000 µg.

⁴Most 'fruits' weigh <1000 µg and are inviable.

⁵Ridley (1930) notes dispersal by Linnets.

⁶27.4±0.62 cm (124 'heads', control on my plot, 15 August 1969).
25.17 cm (82 'heads', population 2, 4 September 1971).
20.98 cm (70 'heads', population 3, 1 September 1971).

Table 28. Emergence of *Poterium sanguisorba* seedlings from fruits buried at different depths in ant-hill soil

Methods: I added 1-2 cm peat to the base of 16 15 cm diameter plastic pots, and filled them with J.I. compost to within 6 cm from the top. After watering, I sprinkled about 1 cm of unsieved ant-hill soil, which had been sterilised at 105°C for 48 hours, onto the surface. I placed 15 large *Poterium* fruits (collected 26 August 1971), which had 92.5% viability in standard germination tests run concurrently, in each pot. I broadcasted sterilized ant-hill soil onto the surface to give the required depths of 0, 0.2, 0.5 and 1 cm. Each treatment was applied to 4 pots; the experiment was laid out in four randomised blocks in a cold frame on 12 September 1971 and read finally on 26 October 1971.

Design: 4 treatments x 4 pots x 15 fruits.

Results: Number of fruits which had produced emergent seedlings after 45 days. Total number of seedlings given in parentheses

Burial depth (cm)	0	0.2	0.5	1.0
	3(4)	9(9)	8(9)	4(5)
	6(6)	3(3)	7(8)	1(1)
	2(3)	5(5)	9(12)	3(4)
	7(8)	8(8)	8(8)	3(4)
Totals	18(21)	25(25)	32(37)	11(14)

Analysis of variance on untransformed data

Source	d.f.	M.S.	F _s
Among groups	3	20.4	5.27*
Within groups	12	3.88	

The following difference is significant ($P < 0.05$) by Gabriel's (1964) sum of squares simultaneous test procedure:

1 cm burial/0.5 cm burial* ($*, P < 0.05$).
 > 0.01

germination; although the results were not statistically significant, they may be biologically important. As a fruit becomes embedded more and more in the soil, the proportion of its surface area from which water is likely to evaporate decreases, and the proportion in contact with the water-supplying substrate increases, so that there will be more chance of the critical water levels for germination being reached in a fruit if it is buried (hypothesis of Harper & Benton, 1966). However, seedling emergence was reduced when Poterium fruits were buried under 1 cm of ant-hill soil.

In the burial experiment, 86 out of 240 fruits sown (36.8%) produced emergent seedlings, although 11 of these (13%) each gave rise to two seedlings. When 'viable' fruits from the same collection (August 1970) were sown onto ant-hills in my plot in groups of 25 on 28 September 1971, 12 out of 300 (40.3%) had produced seedlings by 27 July 1972. Only 14% (100 out of 715) of fruits (from the same collection) sown onto mounds in my plot on 8 September 1970, in Experiment D, had given rise to seedlings by May 1971. Thus viable Poterium fruits can germinate successfully on ant-hills, but only 14-40% of those sown (92% germination under 'standard conditions') produce emergent seedlings.¹

The decline in number of the 100 Poterium plants resulting from Experiment D was followed in detail in 1970-72 and is illustrated in Fig. 47. 70 seedlings appeared in autumn 1970,²

¹ Fungal infection might cause some death of viable fruits in the field, since in the laboratory (25 October 1970) I noted that 'of the 100 or so petri-dishes on my bench which contain seeds or fruits...only those which contain Poterium sanguisorba fruits have a high incidence of algal and fungal infection'.

² Both Anderson (1927) and Salisbury (1952) mention that P. sanguisorba fruits germinate mainly in September.

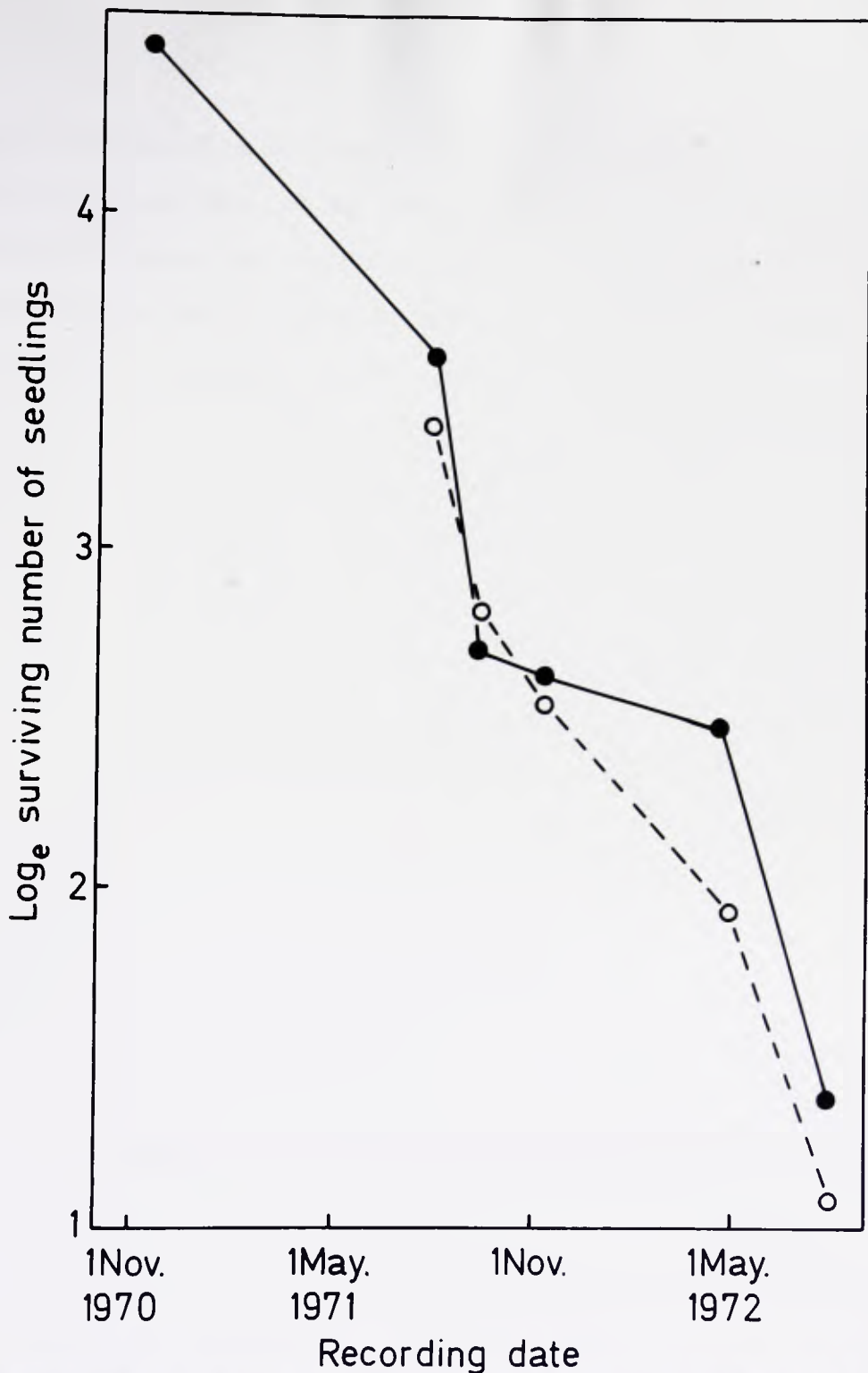


Fig.47. Decline in numbers in 2 cohorts of *Poterium sanguisorba* 'seedlings' on ant-hills in my Beacon Hill plot (Experiment D).

Cohort 1 (●). A negative exponential regression with $b = -1.558$ (where the time was in years) accounted for a significant ($P < 0.01$) proportion of the total variation in seedling number, giving a half-life of 0.439 years.

Cohort 2 (○). A negative exponential regression with $b = -2.048$ (where the time was in years) accounted for a significant ($P < 0.01$) proportion of the variation in seedling number, giving a half-life of 0.338 years.

4 of which remained on 27 July 1972. Another 30 seedlings came up in spring 1971, 3 of which survived ^(August 1972). The main cause of mortality, where the cause could be assigned, was burial of the seedlings by soil heaped by the ants, which was responsible for 30 deaths. Poterium seedlings are well adapted to withstand light burial, because leaves which die are replaced by larger ones, and petiole etiolation can keep the terminal leaflets above the soil surface; for instance, one tiny seedling excavated had leaf petioles 1-2 cm long beneath soil level. However, most of the seedlings I followed were very small and stunted for their age, those a year old being still in the 3- or 5-leaflet-per-leaf stage (which is reached after 25 days by Poterium plants on J.I. compost in a cold frame) with leaves only 1-3 cm long. When this size, they can be killed by only 1 cm of soil heaping. Fig. 47 shows that seedling mortality may be relatively greater from May to September than in the ~~rest~~ ^{rest} of the year, and I attribute this mainly to the catastrophic effects of burial in spring and summer. Burial particularly affects the smaller, more stunted seedlings, leaving the most vigorous plants in the 'cohort' to become established. Burial might also increase the chance of 'fungal infection', which caused 11 deaths in seedlings unaffected by burial. Necrotic spots first appeared on the upper surfaces of the leaflets, which later turned grey-green. A bright purple colouration occurred beneath the leaflets, and sometimes flecked patterns and half-leaflet infections were seen on the upper surfaces. The leaves gradually died, sometimes having purple blotches or red, globular, fungal fruiting bodies.¹ The third obvious cause of seedling

¹ Seedlings dying naturally from burial had brick-red and bright yellow patches on their leaves.

mortality, which killed 4 seedlings, was competition with dense Helianthemum chamaecistus. I deduced that this was occurring when seedlings which were very shaded developed slowly in comparison with unshaded seedlings nearby, and ultimately died. The remaining deaths were from obscure or uncertain causes.

If Poterium rosettes could flower on ant-hills and set viable fruit there, the species would be more likely to survive on the mounds, despite its meagre output of five fruits per inflorescence. I have only seen one P. sanguisorba rosette flowering on an active ant-hill, and then its peduncle was only 5 cm high. Poterium plants growing on bare chalk (e.g. at site A in the map in Appendix 29) usually also produce short peduncles bearing only a single 'flower head'. When I provided some of these plants with a nutrient-rich substrate free of moisture stress by growing them on J.I. compost in an unheated frame, they grew luxuriantly and produced tall inflorescences with numerous 'flower heads'. Thus water or nutrient stress might limit the flowering on ant-hills of P. sanguisorba rosettes which have reached the required age or developmental stage to flower. Rosettes established on the mounds are usually far smaller than those in the surrounding pasture with the same number of leaves and the same number of leaflets per leaf. Many of them must reach the required age to flower; Anderson (1927) stated that young Poterium plants do not flower in the first summer, but of the 100 seedlings which appeared in Experiment D, 19 survived until their second summer. However, I doubt if many P. sanguisorba plants on ant-hills reach the required physiological state (e.g. enough assimilate accumulated)

to flower before they die. An estimate of the developmental stage reached by a Poterium rosette is the mean or the maximum number of leaflets per leaf, since Poterium first produces four trifoliate leaves, then two or four 5-foliate leaves, and then pairs of 7-, 9-, 11- ... foliate leaves in strict progression. Table 29 shows that the rate of development of P. sanguisorba rosettes on ant-hills in the field was much slower than under conditions of ample water and nutrient supply in an

Table 29. Relative rates of development of Poterium seedlings on ant-hills at Aston Rowant N.N.H. and in an unheated frame on the laboratory roof

Ant-hills. Fruits sown 22 September 1970 on my Beacon Hill plot.

Laboratory roof. Fruits sown 13 September 1971 in J.I. compost in 15 cm plastic pots.

Number of seedlings of a given size from the same cohort' remaining on the sampling date

Maximum No. of leaflets per leaf	<u>Ant-hills</u> Days from sowing						<u>Laboratory Roof</u> Days from sowing		
	54	321	350	415	578	677	12	38	193
cots.	50								
3	20	33	7	3			16		
5		14	8	7	6				
7		14		4	3			12	
9			1		3	2			
11									
13						1			
15									2
17									6

unheated frame at the laboratory. Table 30 shows that the average 'developmental age' of Poterium rosettes is much lower on ant-hills than in the surrounding vegetation. This difference probably results in a much smaller proportion of flowering rosettes on the mounds than off them.

Table 30. Mean numbers of leaflets per leaf on *Poterium* plants on ant-hills and in the surrounding vegetation

Method. On 1 October 1971 I determined the mean number of leaflets per leaf on all 41 *Poterium* plants found on eight random ant-hills at site H (see map of Aston Rowant N.N.R., Appendix 29). Similar counts were made on 41 'random' *Poterium* rosettes in the nearby sward.

Frequency distribution of numbers of *Poterium* plants with various mean numbers of leaflets per leaf

Mean number of leaflets per leaf	Ant-hills	Surrounding vegetation
3	1	
3-4.9	9	3
5-6.9	11	5
7-8.9	11	2
9-10.9	4	4
11-12.9	3	7
13-14.9	2	8
15-16.9		2
17-18.9		5
19-20.9		3
21		2

A significant ($P < 0.01$) proportion of the total variance in plant number in Fig. 47 was explained by a negative exponential regression of plant number on time (in both cases), giving seedling half-lives of 0.44 and 0.34 years respectively, as compared with 0.14 years in *Arenaria serpyllifolia*. The mortality rate is lower in *Poterium* than *Arenaria* for several reasons. *P. sanguisorba* seedlings with their second true leaf appearing usually have radicles 4-5 cm deep, and they are much less susceptible to death by rain-wash or desiccation than *Arenaria* seedlings. *Poterium* leaves and leaflets are bitten off by molluscs without destroying the plant, but *Arenaria* seedlings are easily killed by snail or slug grazing. Shading often kills *Arenaria* plants, but *Poterium* seedlings start life

with 40 times more photosynthetic capital and their leaves can grow upwards fast and overtop the Thymus and Helianthemum with which they are growing. A normal P. sanguisorba seedling with one true leaf has a hypocotyl of 2 mm and a leaf petiole 8-10 mm long, but when shaded the hypocotyl may reach 15 mm and the leaf petiole 18 mm. Thus Poterium, unlike Arenaria, can often establish itself in swards from 'seed'. In Experiment C equal numbers of Poterium fruits were sown onto ant-hills and into the sward on 21 October 1969. 14 seedlings appeared on the mounds and 17 in the swards, and on 2 September 1970 five rosettes remained on the ant-hills and four had established themselves in the surrounding vegetation, one having reached the 7-leaflet per leaf stage. Yet despite their robustness, Poterium sanguisorba seedlings develop slowly on the mounds and are susceptible to burial by ant-heaped soil. The other main factor which accounts for their relative absence from ant-hills is the poor 'dispersability' of the fruits.

5.3.8. Leontodon hispidus

L. hispidus is a perennial rosette hemicryptophyte, with a perennating rootstock, which is often far more abundant in the surrounding vegetation than on the ant-hills nearby (Chapter 3). Nevertheless, in dense populations it produces many more viable fruits per unit area than Poterium sanguisorba or Cirsium acaule, and fruit dispersal is far more efficient than in those species, so that seedlings are frequent on the mounds in autumn and mature Leontodon plants are more frequent than those of Poterium and Cirsium on mounds of all sizes and activities. Once established on ant-hills, Leontodon rosettes may spread

vegetatively, but since rosettes joined to the same rootstock have a mean distance apart of 0.98 cm (13 observations), vegetative reproduction is unlikely to be important in the initial invasion of mounds. I excavated all the rosettes on an ant-hill where Leontodon seemed to be invading the top (Fig. 48) and found that although numerous separate groups of rosettes occurred (Table 31), invasion had been due to fruit dispersal.

Table 31. Leontodon hispidus. Frequencies of groups of 1, 2, 3 ... rosettes on a mound on my Beacon Hill plot

No. of rosettes/group	1	2	3	4	5	6	7
No. of groups found	32	15	5	7	0	0	6

Fig.48. 2 September 1970.

Ant-hill in my plot with
Leontodon hispidus
'invading' the side and
some rosettes flowering.



I estimated the viable fruit production in a dense population of Leontodon hispidus rosettes in my control plot in both 1969 and 1970. On 10 August 1970 there were 170.8 L. hispidus rosettes per square metre there (mean of 13 random 0.25 m² quadrats). 3.2% of these were flowering (5.54/m²), and since ten complete fruiting heads had produced a mean of 72.4 'viable' fruits per inflorescence,¹ the mean viable achene production was 399.9/m². On 14 August 1969 31.6 inflorescences/m² occurred in the same population (mean of 70 0.25 m² quadrats), giving a mean viable fruit output of about 2288/m², if the 1970 estimate of 72.4 viable achenes per head is used. Abundant fertile fruit is set by Leontodon in the sward in most years. Nevertheless, its output of viable achenes, and hence the rate at which it can invade ant-hills, may be severely reduced by grazing in spring and summer. For instance, in 1969 Leontodon set much more viable fruit inside the control plot, which had been fenced against rabbits and sheep a year before, than outside (Fig. 49). Within 15 m of the control plot, 1.62 inflorescences/m² appeared (mean of 80 random 0.25 m² quadrats) by 12 September 1969, much later than the 31.6 inflorescences/m² which were found inside the control. Mean peduncle height was 12.4±0.84 cm (40 samples) outside the control but 29.7±0.57 cm (124 samples) inside it.²

¹ A mean 86.3 fruits per inflorescence were produced. 13.9 per head were sterile, recognised initially by their white colour, flattened appearance and flexibility, and later by their inability to germinate. The remaining 72.4 achenes per head had over 98% germination in 39 days under 'standard conditions'.

² The effects of grazing are confounded with possible pre-existing differences in the density or vigour of Leontodon rosettes. L. hispidus rosettes appeared just as dense outside the control as inside it; the data for surrounding vegetation quadrats 71-96 in Appendix 28 show that Leontodon had a high percentage cover outside the control on the NE side.



Fig. 49. 5 July 1969. Leontodon inflorescences produced much more abundantly inside than outside my control plot in the year after it had been fenced. 10 sheep had grazed the vegetation outside the plot from 18 April to 19 May, and 8 sheep from 19 May-10 June.

The viable fruits weigh 1050 μg (mean of 100 samples) with a pappus of 370 μg ^{included} and are dispersed by wind from a mean height of 12-30 cm. Dispersal is much more efficient in Leontodon hispidus than in Cirsium acaule because the lighter fruits are released from a greater height, and the pappus is rigid, not hygroscopic. High densities of Leontodon fruits are often found on the mounds in autumn; for instance, on 25 September 1970 I mapped all the L. hispidus achenes on four randomly-selected ant-hills in my control plot and found 456 fruits/ m^2 of ant-hill surface. The data in Table 32 show that the fruits frequently reached the summits of the mounds.

Once the achenes of L. hispidus have fallen onto ant-hill soil they may be buried by soil heaped up by the ants, although there may be less than three weeks between peak fruit dispersal

Table 32. Distribution of *Leontodon hispidus* fruits, within 5 concentric rings, on maps of 3 random ant-hills

Method. Each map was a perpendicular projection of the ant-hill surface onto a plane piece of paper, with the positions of *Leontodon* fruits marked in. 5 concentric approximate circles, centred on the summit, were drawn, with radii 0.2, 0.4, 0.6, 0.8 and 1.0 times the radius of the mound. The numbers of *Leontodon* fruits within each annulus were summed over the 3 mounds.

Results. Column 3 gives the area of each annulus as a proportion of the total ant-hill area, if the ant-hill is regarded as a plane circle. Column 4 gives the number of fruits expected in each annulus on this basis, if the distribution of fruits were independent of position.

Annulus	Total no. of fruits found /annulus	Area of annulus as proportion of total area	†Expected no. of fruits on this basis
Centre-0.2r	40	0.04	14.8
0.2-0.4r	67	0.12	44.4
0.4-0.6r	84	0.20	74.0
0.6-0.8r	91	0.28	103.6
0.8-1.0r	88	0.36	133.2

† $\chi^2_{[4]} = 72.63^{***}$ Thus the summits of these ant-hills apparently received significantly more fruits than expected if fruits were randomly-distributed, and the bases less. However, on a hemispherical three-dimensional ant-hill, each successive annulus, from the summit to the base, is likely to present a smaller proportion of its total area to a vertically falling fruit.

time and peak germination time. Those fruits which fall into cracks in the soil, being kept upright by their pappi, germinated more frequently than those just lying on the surface. Yet deeper burial might impose dormancy; in Experiment B *Leontodon* fruits had dormancy imposed by burial under 5 or 10 mm of J.I. compost in growth cabinets, just like the seeds of *Arenaria serpyllifolia* and *Veronica arvensis*. When 600 de-papused *L. hispidus* achenes (1969) were sown 3.5 cm deep in ant-hill soil, pasture soil and sterilized sand treatments, 50 to a pot,

in January 1970, only one of the 600 possible seedlings emerged in spring (0.2%) and another ten plants came up in autumn (1.7%).

Leontodon achenes germinate on the mounds mainly in autumn. On 25 September 1970 37 'seedlings' (in the cotyledon to 3-leaf stage)/m² were recorded on the four random mounds surveyed. This tallies with an estimate of 46.5/m² obtained on 15 November 1970 when seedlings were counted in 80 100 cm² quadrats on 20 random ant-hills. Three independent crude estimates suggested that 5-9% of achenes landing on the mounds produced seedlings in 1970. Firstly, of 625 fruits sown onto the mounds in Experiment C on 23 January 1970, 30 (4.8%) germinated. Secondly, 37-46.5 seedlings/m² were found on ant-hills in my plot in 1970 (see above) but I estimated that 456 fruits/m² had fallen there. Thus about 9% of achenes had given rise to seedlings in autumn 1970.¹ Thirdly, when the same 4 mounds mapped on 25 September 1970 were surveyed again on 14-16 September 1971, 9 of the 374 Leontodon fruits mapped in 1970 produced surviving seedlings. Since 13 (41.9%) of the 31 seedlings present in 1970 still remained in 1971, an estimated $9 \times \frac{31}{13}$ (21.5) of the achenes present on the mounds in 1970 actually germinated, i.e. 5.6%.

The rates of decline in seedling numbers found in two experiments on ant-hills are summarised in Fig. 50. For instance, of 32 seedlings marked in 1970, only 3 remained in November 1971. Six of the 29 seedling deaths occurred through

¹In view of the slow rate of development of small Leontodon plants on ant-hills, mentioned later, some of these plants might have come from achenes which germinated in 1969; but 1970 seedlings were usually quite distinct.

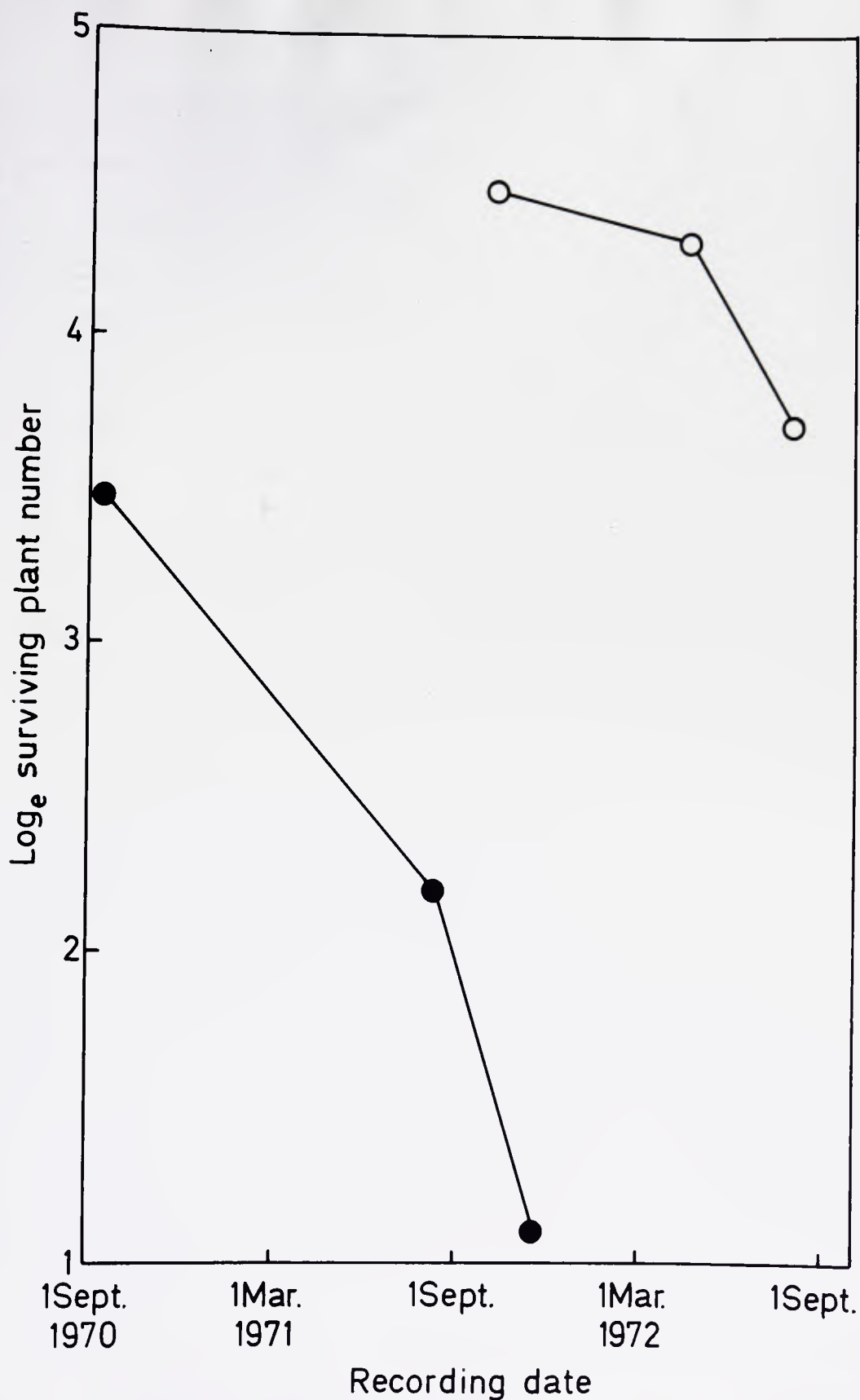


Fig.50. Decline in number in 2 'cohorts' of Leontodon hispidus seedlings on ant-hills in my Beacon Hill plot. Negative exponential regressions on time did not account for a significant (5% level) proportion of the total variation in seedling number in either case (and yielded 'half-lives' of 0.38 years (●) and 0.83 years (○))

burial. Of 75 seedlings mapped on mounds in my control plot on 2-4 October 1971, ten later died of burial in the summer of 1972. Even large Leontodon rosettes were found dying under heaped soil when active mounds were dissected. In August 1971 I covered 5 L. hispidus 'seedlings' (in the two-leaf stage) with 1 cm of ant-hill soil, which buried at least half their leaf area. On 4 October the plants were still in the same state, except that the leaves of 3 of them were reddening. All had disappeared by 11 January 1972. On 4 October I excavated numerous slightly-buried L. hispidus seedlings; Leontodon leaves respond to burial by etiolation (some plants had petioles 2 cm long) and I gained the impression that burial had probably stunted their rate of development.

Yet Leontodon seedlings growing on bare ant-hill soil develop slowly anyway, and remain small; this may increase the probability that they might be killed by burial. In the survey of 4 mounds in my control plot on 25 September 1970 and 14-16 September 1971 I recorded the size of all the 'seedlings'. In 1971 none of the 13 seedlings surviving from 1970 had a leaf more than 2.5 cm long, and three of those with two true leaves in 1970 had only two true leaves a year later (Table 33). None

Table 33. Rates of development of surviving Leontodon seedlings from September 1971-72

<u>1970</u>	<u>1971</u>
cotyledons	4 true leaves
1 true leaf	2, 4 or 6 true leaves
2 true leaves	2, 3 or 4 true leaves
3 true leaves	3 or 5 true leaves.

of the rosettes approached 'flowering size' in 1971, and the slow rate of development of even the surviving seedlings makes it

likely that many will fall prey to environmental hazards before they can flower. Their susceptibility to burial may be one of the factors causing the concentration of Leontodon rosettes near the margins of the mounds (section 4.3). Nevertheless, some large Leontodon plants flower vigorously on the tops of ant-hills, and rosettes inside the perimeter of active ant-hills often flower profusely and reproduce vegetatively. The relationship between the distance of achenes from the summit and the proportion which germinate, the rate of development of the seedlings and the rate at which they die would be worth further investigation. Leontodon hispidus maintains larger populations on ant-hills than Poterium sanguisorba and Cirsium acaule mainly because its fruit dispersal is much more efficient, and partly because its rosettes frequently flower on the mounds.

5.3.9. Plantago lanceolata¹

P. lanceolata is a perennial rosette hemicryptophyte which often has a lower cover on ant-hills than in the surrounding vegetation (Chapter 3). It resembles Leontodon hispidus in its biology and its reaction to the mounds, but I have not studied it in such great detail. The density of Plantago rosettes on ant-hills remains the same with increasing ant-hill volume, and this is partly due to vegetative reproduction; groups of rosettes joined to a common rootstock are frequent on the mounds. However, the centre of each rosette in a group is usually within 2 cm of its neighbour, and since P. lanceolata cannot spread far or fast vegetatively, most dispersal onto mounds and effective reproduction there is probably by seed.

¹ The biology of Plantago lanceolata is described by Sagar & Harper (1964).

5 complete P. lanceolata inflorescences collected from my control plot on 20 January 1970 had a viable seed production of 49.1 per inflorescence.¹ Vigorous rosettes often produce several inflorescences. Under ungrazed conditions, the seed output of Plantago can be considerable; in the first year after fencing my control (1969), 31.17 inflorescences/m² (mean of 20 random 0.25 m² quadrats) were produced in the 40 m² area of the control plot which had the densest population of P. lanceolata rosettes. This is equivalent to a viable nutlet production of 1306/m². However, under grazed conditions the density of inflorescences, the height of the peduncles² and the number of viable seeds produced per spike can be drastically reduced. Plantago is very palatable to sheep and decreases under heavy grazing (Sagar & Harper 1964), and seedlings appear in cattle faeces (Ridley 1930). Thus the grazing intensity in the sward may indirectly affect the population sizes of P. lanceolata on ant-hills by reducing its seed production in the surrounding vegetation.

The nutlets weigh 1550 µg (Salisbury 1942) and are dispersed mainly by wind³ from an inflorescence height which often exceeds 15 cm in the sward. Dispersal seems more efficient than in Poterium sanguisorba but less efficient than in

¹ There were 58.4 nutlets per spike. Most of them were immediately placed under 'standard germination conditions' and after 363 days, 239 (84.15%) of the 284 seeds sown had germinated, giving a viable seed production equivalent to 49.1 per inflorescence.

² In 1969 the vegetation outside my control plot was grazed by sheep from 18 April to 10 June. Plantago lanceolata flowered a month later outside than inside the control plot and whilst its mean inflorescence height was 28.9 ± 0.65 cm inside the control (125 samples), it was 9.5 ± 0.30 cm (120 samples) outside it.

³ The adhesiveness of the mucilaginous seed coat may aid dispersal by animals (Sagar & Harper 1964).

Leontodon hispidus. The seeds reaching the mounds from the surrounding vegetation are augmented by those produced by rosettes which have flowered on the ant-hills. Plantago frequently flowers on the mounds, although the peduncles are usually less than 10 cm tall and the number of flowers per inflorescence is usually lower than in the sward. When I took 4 tiny P. lanceolata rosettes, each with one short peduncle bearing a small inflorescence, from ant-hills in my plot in 1969 and grew them up on J.I. compost in individual pots in an unheated frame at the laboratory, they all grew large, and had produced 7, 12, 15 and 23 inflorescences respectively by 3 August 1970. The low vigour of flowering of Plantago rosettes on mounds is thus probably due to some feature(s) of the ant-hill micro-environment (e.g. micro-climate, water or nutrient stress, grazing or competition); but its ability to flower on ant-hills probably allows it to maintain higher population sizes there than otherwise.

Plantago seeds reaching the ant-hill surface may be buried, but the nutlets can produce seedlings after germinating 3.5 cm down. In January 1970 I buried Plantago seeds in an experiment on an unheated roof. The design was 3 treatments (ant-hill soil, pasture soil and sterilised sand) x 4 pots x 50 nutlets (1969) buried at 3.5 cm depth. In spring 1970 538 (89.7%) of the seeds germinated and the majority put cotyledons above the surface. This behaviour differed greatly from that of Leontodon fruits in the same experiment (section 5.3.8).

The ability of Plantago nutlets to germinate from depth

might be one reason¹ why a greater proportion of its seeds germinate on ant-hills than the fruits of Leontodon. On 21 October 1969 I sowed 615 P. lanceolata nutlets, with 74% viability in 27 days under 'standard conditions', onto mounds in my plot in Experiment C. Some germination occurred in each autumn and spring² from autumn 1969 to autumn 1971, when the experiment was discontinued, and by that time 150 seeds (33% of those viable) had germinated at least. Several nutlets produced red radicles, with no root hairs, which did not penetrate the soil. Burial caused deaths of 27 seedlings. Naturally-sown Plantago seedlings which were buried and dying were often seen. I did not study the decline in number of Plantago lanceolata seedlings in detail, but the data I have are summarised in Fig. 51. Four independent estimates, each based on two or three points, show almost identical death rates for P. lanceolata seedlings on ant-hills. For example, 65 Plantago seedlings occurred on four mounds in my plot in September 1970, but only 15 (20%) of these remained a year later. Those in the cotyledon stage in 1970 had 3 true leaves a year later, those with one leaf in 1970 had 2-4 leaves in 1971 and those with 2 true leaves in 1970 had 3-5 by 1971. All the surviving plants remained small; thus P. lanceolata seedlings might be susceptible to burial on the mounds partly because of their slow rate of development, like those of Poterium sanguisorba.

¹ Germinating P. lanceolata nutlets secrete a sticky mucilage; Harper & Benton (1966) suggested that the mucilage imbibes water and spreads around the seed, greatly extending the pathways for water flow.

² Spring-germinating seedlings were recorded in field notes about 5 times more frequently than autumn-germinating seedlings.

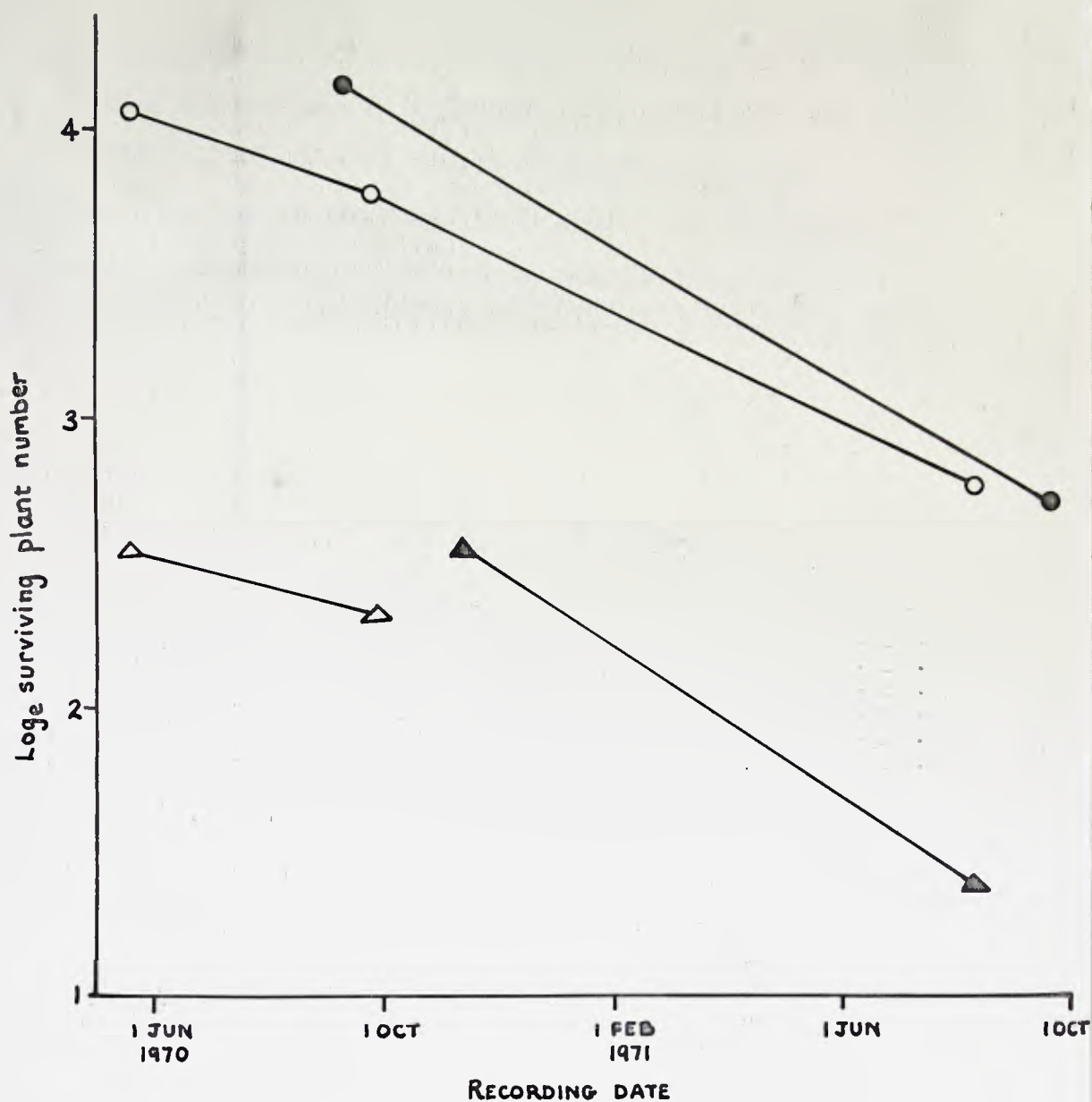


Fig. 51. Decline in numbers in four 'cohorts' of *Plantago lanceolata* seedlings on ant-hills in my Beacon Hill plot.

and Leontodon hispidus.¹

Thus although Plantago lanceolata reproduces vegetatively on ant-hills and frequently flowers there, its rosettes may have a lower density on ant-hills than in the surrounding vegetation partly because of the dispersal barrier and partly because of the interaction between the stunted growth of its seedlings and their susceptibility to burial.

5.3.10. Carex flacca²

C. flacca is a perennial semi-rosette hemicryptophyte which has a much greater cover around large ant-hills than on them (Chapter 3). The patterns of its rosettes on mounds of various sizes and activity are described in section 4.3.

Carex flacca is a frequent member of closed chalk grassland swards, but has vigorous far-creeping rhizomes by which it invades bared soil on the chalk, mole-hills, ant-hills, and erosion hollows on steep slopes. It differs from the other species which are less abundant on ant-hills than in the sward in having vigorous vegetative dispersal and negligible reproduction by fruit.³

¹ Yet the seedlings of all three of these species can become established in swards. Some data for Loterium are given in section 5.3.7; see also Grime (1963). Of 500 fruits of L. hispidus sown in short swards in Experiment C on 20 January 1970, 42 germinated, and nine months later 11 seedlings in the 2-leaf stage were still present. In Experiment C, 615 Plantago seeds were sown into swards on 21 October 1969 and 33 seedlings were found; ten of these reached the 2-leaf stage and one or two probably became established. Sagar (1960) found that considerable recruitment from seed occurred in a Plantago lanceolata population in a cattle-grazed meadow near Oxford.

² The biology of Carex flacca is described by Taylor (1956).

³ Fragaria vesca is similar; see Chapter 3 and Fenn (1948).

C. flacca can produce considerable densities of viable fruit in some years. On 19 August 1970 there were 72.6 Carex rosettes/m² in my control plot (mean in 13 0.25 m² quadrats). 8.31/m² (11.4%) were flowering,¹ equivalent to 16.6 female spikes/m². Applying my 1969 estimates of 36.9 viable nutlets per female spike² to this figure, C. flacca produced about 513 viable fruits/m² in my plot in 1970. Each fruit contains a maximum of one nutlet. Inflorescence production can be severely depressed by grazing (field notes) but I have no quantitative evidence.

However, dispersal onto the mounds seems very inefficient. The mean height of fruiting female spikes of Carex was estimated at 21.7±0.48 cm (123 samples, 15 August 1969) in my control plot and 15.35±1.0 (20 samples, 12 September 1969) outside it. Yet many fruits are not released for some time and the peduncles and stem become more and more arched with age, bringing the nutlets nearer the ground. The viable fruits have a mean weight of 705 µg (100 nutlets) and drop vertically into the sward.³

Moreover, once viable fruits reach the ant-hill surface they rarely germinate and produce established seedlings. When nutlets collected in September 1969 were sown under 'standard

¹ Taylor (1956) states that although shoots may live for several years they flower only in the first.

² 18 female spikes collected from my plot in 1969 had a mean 77.7 nutlets per spike. On 18 January 1970 the nutlets from each spike were placed in separate petri-dishes and kept under 'standard conditions' for a year. A mean of 36.9 fruits per spike germinated. Taylor (1956) found 95% of empty nutlets in some populations.

³ I have never seen a Carex flacca rosette flowering on an active ant-hill.

conditions' in the laboratory on 18 January 1970 the proportion of fruits which germinated rose to a peak between 18 May and 18 June 1970, and then declined. Taylor (1956) also mentioned that C. flacca nutlets have an after-ripening period and show a clear germination peak in the laboratory about nine months after ripening. Thus most germination in the field may well occur in the spring after the fruits have been produced. When nutlets collected on 3 September 1969 (with 47.6% viability under 'standard conditions') were sown on 23 January 1970 in Experiment C, none (out of 615 sown) had germinated on the mounds by 2 September 1970 and only 3 (out of 615) had germinated in the swards by that date. Only 4 C. flacca seedlings were seen on ant-hills during the whole study. As Taylor (1956) states, 'seedlings are of very rare occurrence under natural conditions'.

Most effective reproduction in Carex flacca is by rapid rhizomatous spread. For example, when I dumped a bucketful of sterile J.I. compost onto the sward just outside my control plot, it was rapidly invaded by C. flacca. A year later, in September 1971, a Carex rhizome 23 cm long was present, with two side-shoots, 5 and 6 cm long respectively, all 3-5 cm below the soil surface. 11 rosettes occurred, i.e. about 3 cm apart. C. flacca rhizomes which are invading ant-hills or mole-hills often produce rosettes 5-7 cm apart.

Burial seemed to be the main cause of mortality in Carex flacca¹ (see also sections 4.3. & 4.4). For instance, on

¹ Since I have not yet investigated the population biology of C. flacca rosettes on ant-hills I do not know what the average life-span of a C. flacca rosette might be. Burial might merely hasten the end of an already short existence.

17 August 1970 I found over 20 Carex rosettes which were buried, chlorotic and dying beneath 4-5 cm of newly-heaped soil on the same mound. When I sprinkled 2 cm of soil over the centres of 5 Carex rosettes on ant-hills in my plot in August 1971, three died by 3 October but the other two remained healthy. Nevertheless, numerous field observations suggest that burial might be an important factor influencing the population sizes and the patterns of Carex rosettes on active mounds. Competition in the dense vegetation just inside the periphery of the mound might also be important in regulating the rate of reproduction of Carex rosettes.

5.3.11. Pseudoscleropodium purum

P. purum is a perennial pleurocarpous moss with a weft growth form and a capacity for indefinite growth. Like Pleurozium schreberi at the north end of Rhossili Down (section 2.3.3), Pseudoscleropodium purum on Beacon Hill is often much more frequent on north-facing than south-facing aspects of ant-hills (section 3.3). The greater abundance of pleurocarpous mosses like Pseudoscleropodium and Pleurozium on northerly than southerly slopes has been noted before (e.g. Watson 1960, Suominen 1969 and references therein) but has never been satisfactorily explained.¹

¹ The hypothesis that P. purum may occur on north-facing aspects more frequently than on south-facing aspects because soil-heaping by the ants and Pseudoscleropodium burial is concentrated on the south sides falls down because burial is only concentrated on the southern sides of mounds at one or two sites, buried Pseudoscleropodium is hardly ever found on the south sides of ant-hills, P. purum is often concentrated on the northern sides of abandoned mounds, and it can grow up through a little heaped soil anyway.

Magdefrau (1935) showed (see results in Table 34) that most water conduction in P. purum is external, i.e. the moss is 'ectohydric'.¹ Water uptake from the ground or the air occurs via capillary spaces which lie between the overlapping leaves, or between these and the stem. Conduction is so inefficient that it will only prevent desiccation at high relative humidities. At low relative humidities water is rapidly lost from P. purum (Irmscher 1912); since water can be absorbed through the leaf surfaces, a continuous cuticle is probably absent and water is easily lost from the leaves. The P. purum stems often seem desiccated for long periods in summer, even on the northerly sides of ant-hills.²

Table 34. Water conduction in Pseudoscleropodium purum kept for 24 hours at 70% relative humidity (Magdefrau 1935)

	<u>External</u>	<u>Internal</u>	<u>Central strand</u>	<u>Rhizoids</u>
Water conducted (g/0.2g dry weight)	3.62	0.13	(+)	(+)

A slight reduction in the water content of pleurocarpous mosses below 100% saturation often causes a drastic lessening of the photosynthetic rate (e.g. Hikosawa et al. 1964). In winter, photosynthesis in P. purum is probably limited mainly by low temperatures. Longton & Greene (1969) showed that Pleurozium schreberi grew mostly from April to November, in an environment

¹ Zachari (1956) showed that water conduction through the central strand of Pleurozium schreberi was negligible.

² Desiccation of P. purum on the south side of ant-hills might result in high enough leaf temperatures to kill the plant, because the loss of heat from a leaf due to the latent heat of evaporation of water would not occur once the moss was desiccated. However, the apical cell is well protected by a group of leaves and its death through high temperatures seems unlikely.

which was not water-stressed to the same extent as ant-hills in grassland. In summer, Pseudoscleropodium's water content is probably the main factor limiting its photosynthetic rate. Most of its growth on the mounds may occur in spring and autumn. Since P. purum would be fully hydrated for much longer periods in spring and summer on north-facing than south-facing slopes, its total net assimilation rate might well be considerably higher on northern than southern aspects. In fact, it might be unable to exceed compensation point over the whole year on south-facing slopes.¹

An alternative hypothesis is that a certain degree of desiccation exceeding a critical period could itself cause death, if the cells plasmolysed and broke down. This would be more likely to occur in moss reaching the south side, than in P. purum growing on northerly aspects; in fact, the present pattern might be the result of a particularly dry year 5 or 10 years ago. However, during droughts P. purum may be rehydrated by dew at night.

I first tried to test three hypotheses: (i) that the percentage water saturation of P. purum was the same on north- and south-facing aspects of ant-hills, (ii) that the increase in dry weight per unit time was the same on both aspects, and (iii) that the growth increments were the same on northern and southern slopes. All these experiments failed because my techniques involved the transplantation of moss clumps, which rapidly died, even when their bases had been firmly buried in ant-hill soil. Since I had to leave P. purum in situ for

¹ Pseudoscleropodium purum has a higher frequency on NW than NE slopes of ant-hills on Beacon Hill (Fig. 16). It might be hydrated for longer periods on NW than NE slopes, because P. purum moistened at night would lose its water by evaporation more quickly on the E than the W slopes.

adequate experimentation, I set up the experiment described in Table 44.

Unfortunately many of the tagged shoots either broke off or were interfered with by grazing animals, so that I did not determine the increments in Pseudoscleropodium growth over a long period. However, the collection of shoot tips provided some results (Table 35). On 6 September 1971 all the P. purum shoots were moist, swollen and bright yellow-green, and over 93% of the basal leaf cells were living in both treatments. Several days followed on which the air temperature exceeded 20°C. On 11 September 1971 the terminal 2 cm of the shoots on the north sides of the mounds were light yellow-green but the rest of the moss remained a brilliant bright yellow-green colour. On the south-facing sides, however, P. purum was bone dry and most of the moss had become light grey-green. Over 50% of the shoots had turned white at the tips up to 1 cm (often to 2 cm) from the apex. When I again sampled the shoots, and counted the proportion of the basal cells in the leaf which re-plasmolysed, the analysis of variance (Table 35) confirmed that the percentage of dead cells in the leaves of Pseudoscleropodium was significantly ($P < 0.001$) greater in the moss growing on the south sides than in that on the north. Although this did not prove that the apical cell was likely to die, the rapid reaction of Pseudoscleropodium to southern aspects suggested that desiccation (or high leaf temperatures) might be the ultimate cause of death.¹ However, the experiment has been examined six times since then, and the majority of P. purum

¹ This might merely have been the reaction of P. purum acclimatized to growing on northerly aspects to its sudden transfer to the south sides.

Table 35. Percentage dead¹ cells in *P. purum* leaves collected from 5 mounds on which the moss faced north (N.1-5) and five ant-hills on which it faced south (S.1-5).

Method On 5 September 1971 ten mounds small enough to dig underneath, and with *P. purum* on their north sides, were selected on the south side of my plot. I dug underneath each and then turned 5 of the ant-hills, selected at random, through 360°, and the other 5 through 180°, leaving the moss facing south.

The design was 2 treatments x 5 replicates x 3 shoot tips x 100+ cells examined in each. On two occasions (5 & 11 September 1971), 3 shoot tips, each about 1cm long, were collected from the *P. purum* on each of the ten ant-hills. I selected shoot tips which were representative of the moss on that particular mound. The shoots were placed in water for an hour, and the terminal 2mm of each was transferred to a separate slide. The leaves were dissected from each shoot tip and mounted in a drop of water.

The microscope was racked across the basal 5 or 6 rows of cells of the first leaf found, and the numbers of 'plasmolysed' cells and examined cells were recorded. When the first leaf was small or damaged a second and occasionally a third had to be looked at until at least a hundred cells had been surveyed.

<u>5 September 1971</u>				<u>11 September 1971</u>		
N1	0	0	0	4	16	23
N2	0	3	1	7	24	11
N3	9	0	8	0	8	10
N4	1.5	0	1	12	6	3
N5	48	21	7	3	5	14
S1	12	7	1	93	14	5
S2	2	0	17	25	8	26
S3	8	4	9	36	0	26
S4	9	0	2	45	46	55
S5	2	1	4	0	98	32

Analyses of variance (after angular transformation)

<u>Source</u>	<u>df.</u>	<u>M.S.</u>	<u>F_s</u>	<u>df.</u>	<u>M.S.</u>	<u>F_s ...</u>
Treatments	1	9.6	0.05 N.S.	1	2305.9	7.92
Ant-hills within treatments	8	205.6	3.2 *	8	177.7	0.52 N.S
Error	20	64.6		20	366.4	
	29			29		

(N.S., $P > 0.05$; *, $0.05 > P > 0.01$; ..., $P < 0.001$)

1. 'Living' cells (i) Cell contents bright green, chloroplasts large, spherical.
(ii) Chloroplasts confined to half the cell.
(iii) Colourless chloroplasts distributed throughout the cell volume.
- 'Dead' cells (i) Plasmolysed, with colourless chloroplasts.
(ii) Highly refractive, bubbly cytoplasm in centre of cell volume, chloroplasts absent.
(iii) Cells empty.
2. Plastic number-tags on nylon thread were tied onto 5 shoots of *P. purum* on each mound, 1cm from the tip.

shoots have survived on southern aspects of the mounds. For instance, on both 22 April and 27 July 1972, Pseudoscleropodium seemed just as healthy on southerly aspects as in the controls. On two of the mounds, moss which had been present at the base of the south side (transferred to the north side when the ant-hills were rotated) was growing particularly well at the bottom of the north. It would be worth repeating the experiment in which the increments in P. purum growth on northerly and southerly aspects are compared, on mounds in an ungrazed area.

5.4. DISCUSSION

The factors which affect the population sizes of the first ten species discussed in this chapter are summarized in Fig. 52. Survival of species on the mounds is especially influenced by the 'dispersability' of their fruits and seeds, the resistance to burial of their seedlings and mature plants, and their ability to flower precociously on ant-hills. Although the work described in this chapter provides a basis for further investigation of the reactions of these species to the mounds, several important problems need to be solved before their life-histories can be quantified in detail. For example:

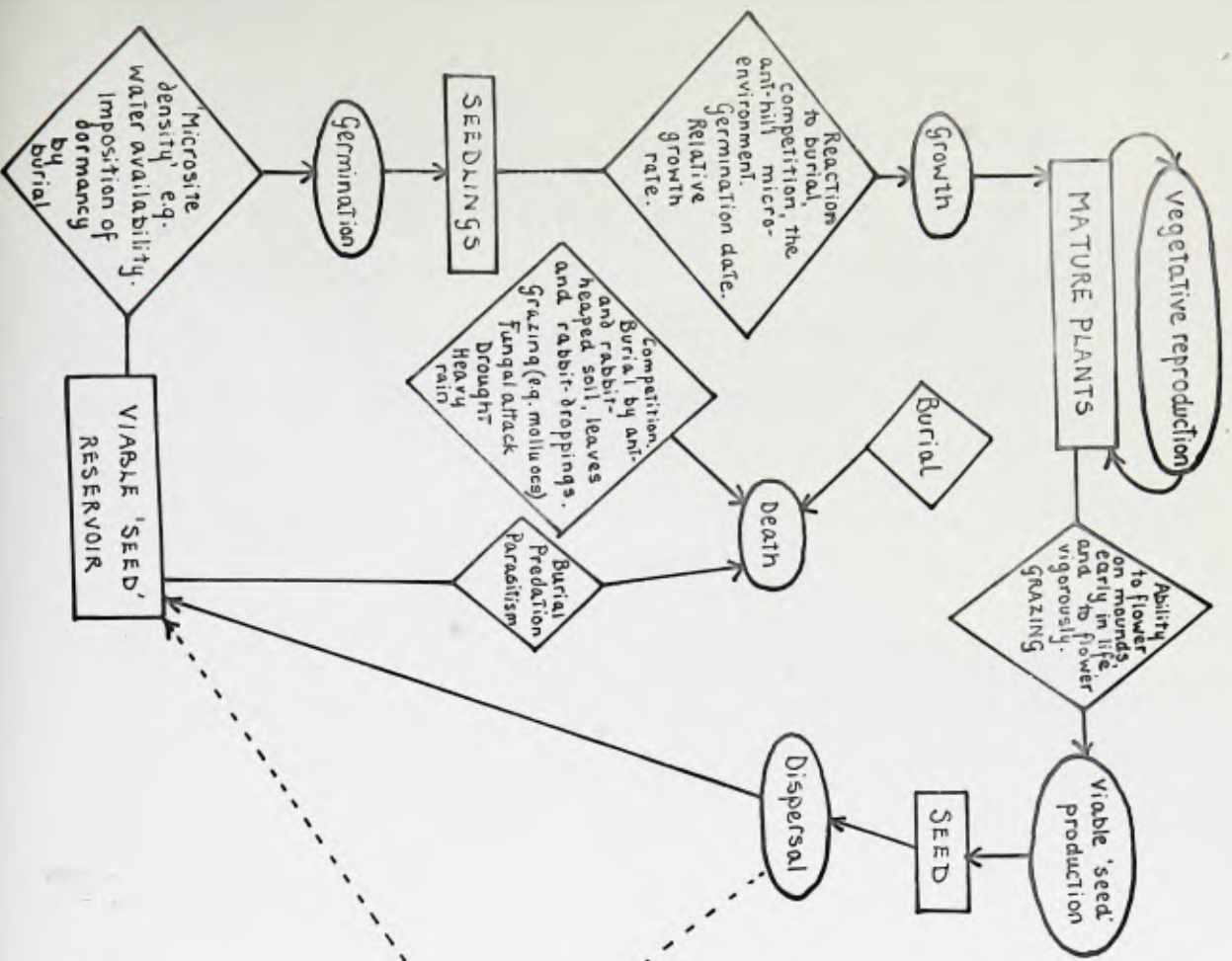
(i) Fluctuations in viable fruit production with time.

The viable fruit production of many species is greatly affected by climate differences between years and the intensity of grazing, so that measurements must be made over several years to be reliable.

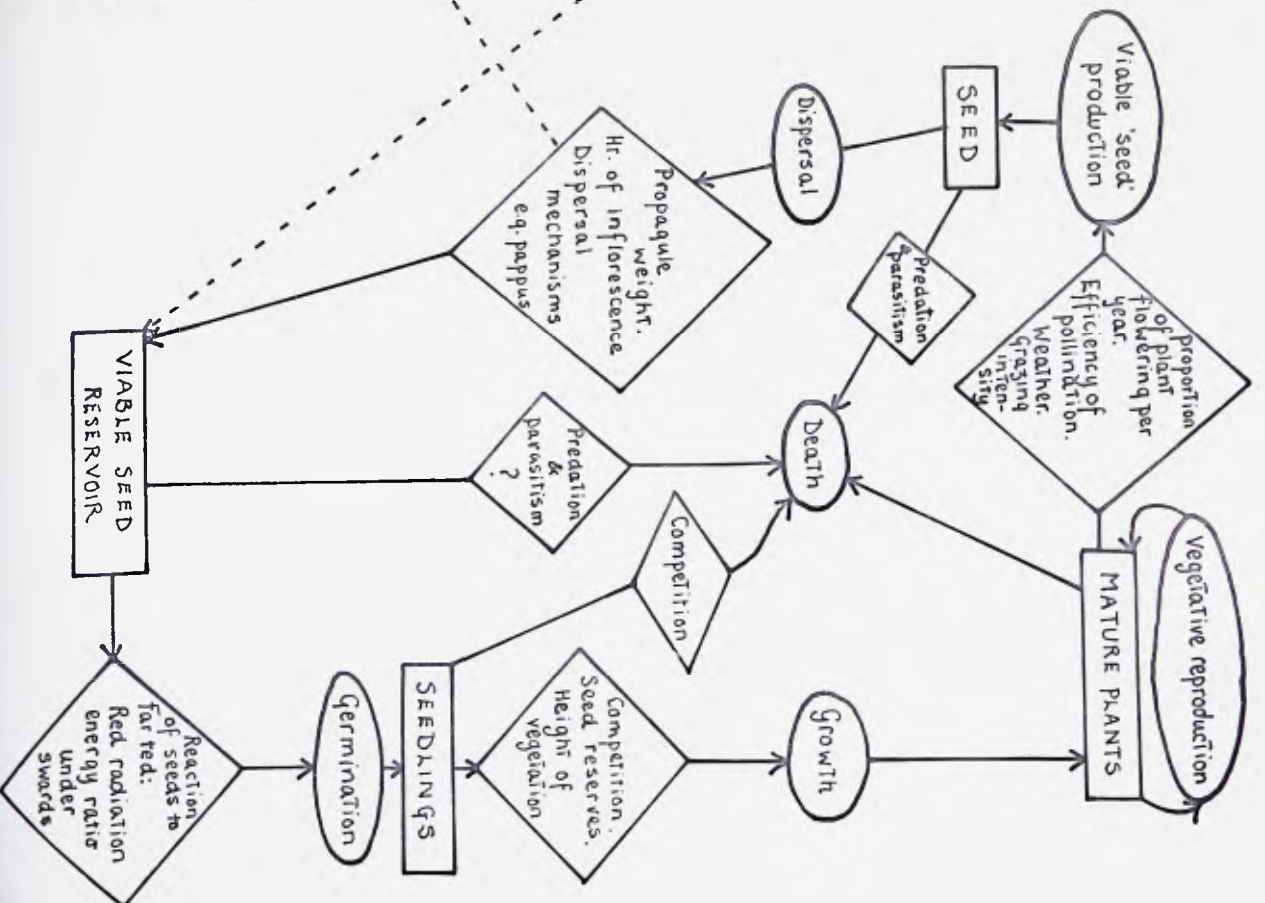
(ii) Dispersal. I could not quantify the life-cycles of Cirsium acaule, Poterium sanguisorba, Leontodon hispidus, Plantago lanceolata, and Carex flacca without knowing the density

FIG. 52.

ANT-HILLS



SURROUNDING VEGETATION



of their fruits reaching the mounds. The proportion of viable fruit which falls onto ant-hills can be estimated by collecting soil from the mounds and the surrounding pasture just after dispersal, keeping the samples moist and counting the seedlings which emerge. For instance, 70 Carex flacca seedlings emerged from 25 pasture samples but none came up in equal weights of ant-hill soil (Table 15).¹ A large sample size would be needed to obtain reliable estimates.

Alternatively, seeds reaching the ant-hill or surrounding soil could be caught in trays of sterile soil, or on vaselined slides. When I placed vaselined slides on mounds in my control plot they were rapidly disturbed or removed by deer or birds.

By estimating the probability that the fruits of a species will fall a given distance away from the parent plant, basing the model on empirical evidence,² one could predict the proportion of fruits reaching the mounds. Fruits marked before dispersal could be collected in and recovered from soil samples or trays of sterile soil placed at various distances from the inflorescence.

¹ One is assuming that the germination rates of fruits reaching both types of soil surface before the samples were taken were identical, and that over the years the fruits have declined in numbers at the same rate in both soils.

² The data of Hesselmann (1934, 1938) on pine, Kohlermann (1950) on ash, and Poole & Cairns (1948) on Senecio jacobaea all suggest a negative exponential model for the distribution of fruits with distance from the parent plant. However Salisbury's (1942) experimental results on the dispersal of seeds of Papaver argemone, P. dubium and P. hybridum yielded truncated normal distributions, as did my data for the distribution of the male flowers from the trunk in Prunus monspessulanum in the Oxford Botanic Garden (1 May 1972). Emerging seedlings of Verbascum thapsus followed a leptokurtic normal distribution with distance from the parent (Salisbury 1961).



Fig. 53. As a mound increases in size, seeds dispersed onto it are less likely to reach the summit.

- (iii) Changes in the incoming seed densities, and the proportion of the surface area covered by heaped soil, with increasing ant-hill size.

As a mound increases in height and basal area, the proportion of fruits produced in the sward which reach the summit probably declines (Fig. 53). The greater density of fruits arriving at the bases than the tops of large mounds may contribute to the greater concentration of rosettes there. Thus not only might the density of fruits in soil samples decline from the margin towards the centre, but the rate of decline may increase with the size of the ant-hill.

The volume of soil heaped onto a mound by the ants may fluctuate considerably from year to year (Table 2) but it rarely exceeds 1600 cm^3 (Appendix 25) and it rarely increases with mound size. Imagine randomly-distributed seedlings occurring at the same density over the surfaces of a small and a large ant-hill. A greater proportion of seedlings might be buried in a year on the small mound than the large one.

- (iv) Significance of burial in imposing dormancy in the field.

To assess the rôle of burial in imposing dormancy on the seeds

of a species, one needs to know the mean frequency distribution (over the whole ant-hill surface) of the seeds with depth at the time of germination. This could be found by collecting soils from successively deeper levels of the mound and determining the number of seeds in each sample; alternatively, by recording soil levels, one could find the frequency distribution of the height of soil heaped onto the ant-hill surface since the seeds landed there. By comparing the frequency distribution of seeds with depth with the results of experiments in which seeds had been sown onto mounds, covered with various depths of ant-hill soil, and emergent seedlings counted, one could estimate the proportion of seeds landing on ant-hills which had dormancy imposed on them by burial.

(v) The rate of seed decay in soil. The rates at which viable seeds decline in number in ant-hill soils could be investigated by sowing marked seeds and recovering them at intervals.¹ This technique could be used over periods of years if the marker remained detectable. The rate at which predation, parasitism and loss of viability deplete the numbers of viable seeds in soil² could also be estimated by burying known numbers of seeds in wide-mesh bags, recovering them at intervals, and assessing the numbers of viable seeds remaining.³

¹ In July 1970 I marked 500 seeds each of Arenaria serpyllifolia and Cerastium holosteoides with fluorescent paint (Naylor 1972) and sowed them in groups of 100 on ant-hills in my control plot, covering each group with 2 cm of soil. No seedlings appeared before mid-September, when I recovered the soils, but I only found 2 seeds of Arenaria and 4 of Cerastium when the soils were examined under an ultra-violet lamp.

² Roberts (1970) estimated that 22% of viable weed seeds in vegetable crops were lost each year.

³ Several replicates of each of a wide range of densities would have to be placed underground. This is because density-dependent effects might occur; for instance, a higher proportion of seeds might be attacked by fungi at high densities than at low densities.

(vi) The cause of seedling mortality. Seedlings often disappear for no apparent reason, but the proportion of deaths to which causes can be assigned probably increases with the frequency with which seedlings are examined. Thus time-lapse photography might be worth while, especially on ant-hills, where dense seedling populations often occur on bare soil. Yet seedlings not dying from one cause may die from another. For instance, if some groups of Arenaria serpyllifolia seedlings had not been killed by rabbit-scraping (section 5.3.1) they might have been eaten, self-thinned, or buried.

(vii) The 'stunted' growth of some seedlings on ant-hills. The 'long-lived non-flowering habit apparently induced in many of the herbs on ant-hills' (Grubb 1967, pers. comm.) is still a mystery. The rate of development (and decline in number) of seedlings of a species needs to be compared in the sward and on the mounds. The factors limiting the growth of the seedlings of perennials on ant-hills might be studied in water or nutrient addition experiments.

(viii) The decline in numbers of mature plants. The turn-over in numbers of mature plants must be investigated as well as the decline in seedling numbers, if the life-cycles of species on ant-hills are quantified more fully. I have concentrated on seedlings because the scanty data available (Tamm 1956) indicate that mortality is relatively greater in the seedling stage than in established plants, at least in grassland perennials.

5.5. SUMMARY

I describe some of the factors influencing the patterns of eleven species in relation to ant-hills at Beacon Hill,

Aston Rowant N.N.R., Oxon. in 1969-72. The species which are less abundant on ant-hills than in the surrounding vegetation flower infrequently on the mounds and tend to have heavy, inefficiently-dispersed fruits and seedlings which develop slowly and are susceptible to burial. I consider some of the problems in quantifying the life-cycles of these species on ant-hills.

CHAPTER 6

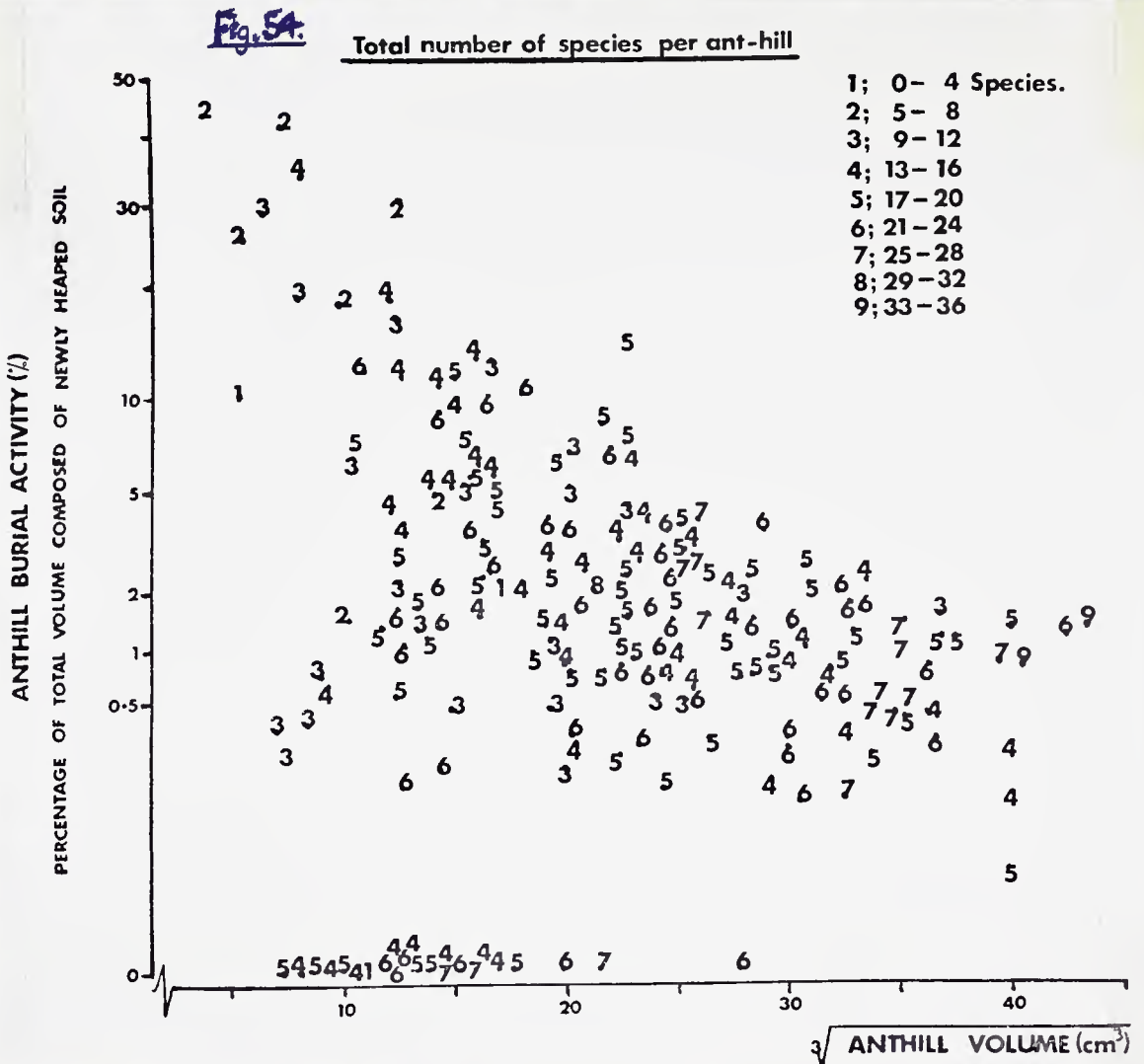
SPECULATIONS

In this chapter I discuss some general features of ant-hill ecology and relate them to 'ecological theory'.

The vegetation in two habitats which have wind-blown sand deposited on the surface greatly resembles that of ant-hills. Farrow (1925) described heavily rabbit-grazed Festuca ovina-Agrostis tenuis grassland at Cavenham Heath in Breckland. His species list includes Aira praecox, Arenaria serpyllifolia, Erophila verna, Filago minima, Myosotis arvensis, M. discolor, M. ramosissima, Ornithopus perpusillus, Sagina procumbens, Thymus drucei, Trifolium dubium, Veronica arvensis, V. serpyllifolia, Polytrichum piliferum and Dicranum scoparium, all species confined to ant-hills in certain areas. Salisbury (1952) lists the characteristic species of late yellow dunes and includes Aira praecox, Erophila verna, Filago minima, Myosotis ramosissima and Trifolium dubium. Not only does the species composition of fixed calcareous dunes resemble that of chalk grassland around ant-hills, but the soil changes which occur with dune succession are the same as those which occur on ant-hills when soil-heaping ceases (section 4.4): decreased mobility, increased organic matter (and water-retaining capacity), and the leaching out of bases from the surface. The addition of sand or soil to the surface of grasslands, dunes, or ant-hills provides an element of 'environmental unpredictability' which prevents the formation of a closed vegetation cover (with its associated soil changes), affects the species composition and

continually maintains the area at a 'lower stage of succession'.

Succession, at least in animal communities, is frequently accompanied by an increase in 'species diversity' (Margalef 1968, Odum 1969). Species diversity has two components, 'species-richness' and 'equitability'.¹ Since ant-hills begin as heaps of bare soil, they are 'new' environments, and one might expect that their 'species-richness' might increase with increasing size (age?) and decreasing activity. This was the case for the mounds on the north-east side of my Beacon Hill plot (Fig. 54). I compared the 'equitability' or evenness of



¹ I have not discussed species diversity in terms of any of the indices available (e.g. Pielou 1969) because these confound species-richness and equitability, and have no obvious biological meaning.

species abundances on large ant-hills with that of the surrounding vegetation by constructing dominance-diversity curves (Whittaker 1965, 1970) for eight sites selected at random from the seventeen surveyed in less detail (Chapters 2 & 3). For two of these areas the dominance-diversity curves were similar for ant-hills and the sward.¹ The curves for the mounds were more concave than those for the grassland at three sites, but for the remaining three places, including West Hill (Fig. 55), the ant-hill curves were much more concave. These data indicate that there tend to be fewer species of intermediate abundance and many more rare species on large ant-hills than in the surrounding vegetation.² This confirms my impression that the plant community on ant-hills is made up of a 'fortuitous juxtaposition' of species which can arrive there and withstand the environmental conditions ('Gleasonian', e.g. Gleason 1939), whilst in the surrounding sward the balance of species is more the result of the selection of species in relation to one another for competitive efficiency ('Clementsian', e.g. Clements (1928); see also Goodall 1966).

Species selected for high competitive efficiency may devote a low proportion of their net assimilation to reproduction and a high proportion to perennation, vigorous root growth and leaves which overtop those of neighbours (Harper 1967). This has become known as K-selection (MacArthur & Wilson 1967), and it is tempting to speculate that the species which are most

¹ These two sites were Harding's Down and the south end of Rhossili Down. Both had very few species.

² My comparisons are valid because the total number of species was similar in ant-hill and pasture curves and the species composition of both curves in a set was almost identical. Comparisons between the curves for communities with different species complements mean little, (e.g. Lloyd et al. 1971).

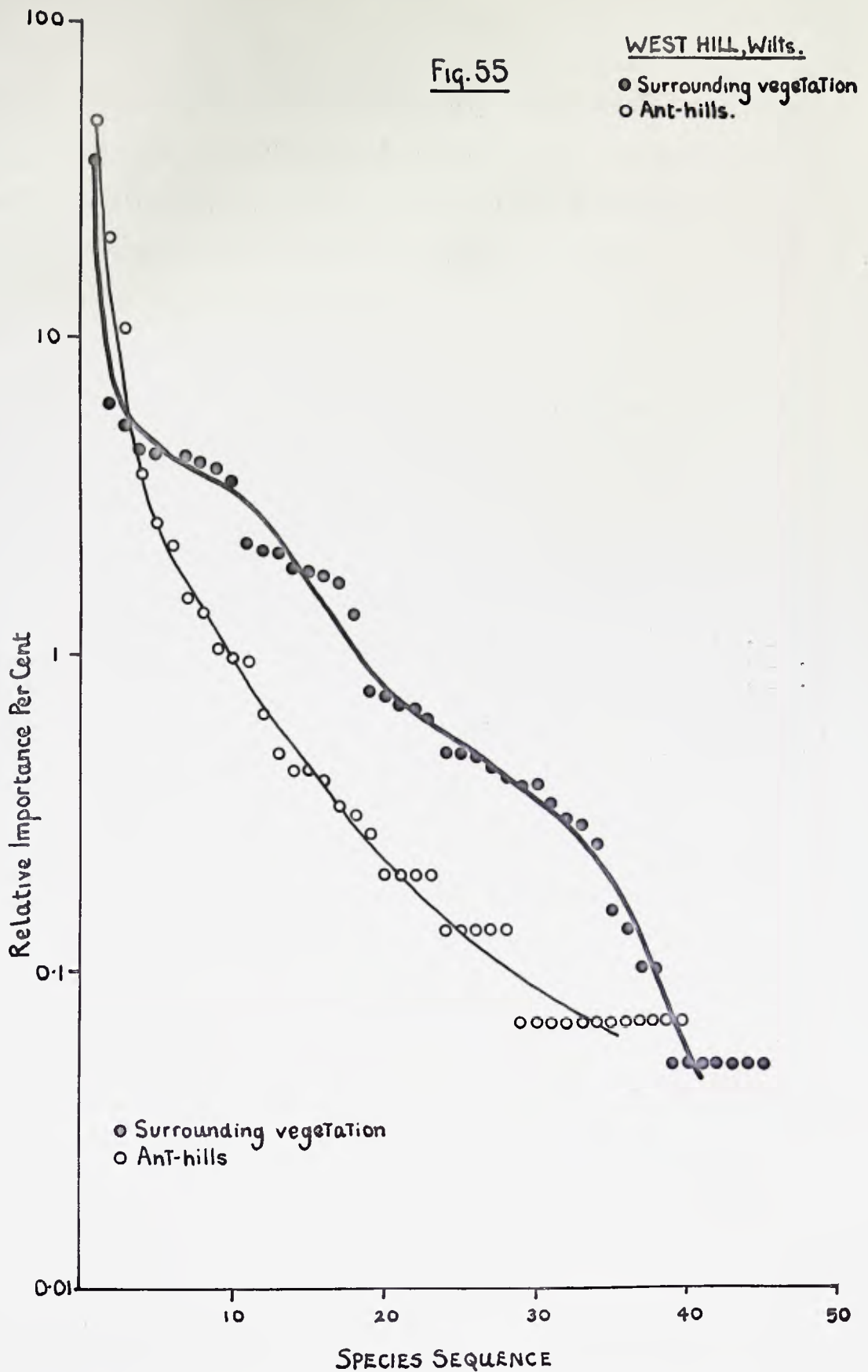


Fig. 55. West Hill, Wilts. Dominance-diversity curves for ant-hills and surrounding vegetation quadrats. The 'relative importance' of a species is its total percentage cover in the eight samples (ant-hill or pasture) expressed as a percentage of the total cover of all species in the eight samples. The species are ranked in order of decreasing 'relative importance'.

strikingly absent from ant-hills are those which are most K-selected.¹ If natural selection were mainly directed towards maintaining a species in its existing environment, long-range propagule dispersal would be unimportant compared with the ability of the species to establish itself in a closed sward from seed. Cirsium acaule, Poterium sanguisorba, Leontodon hispidus and Plantago lanceolata can all become established from seed in chalk grassland swards (Chapter 5), and are among the calcareous grassland species with the heaviest fruits. In establishment, much of the seeds' energy and the initial net assimilation of the seedling must go into vigorous root and shoot growth; consequently, the seedlings of K-selected species may not reproduce early in life. Cirsium acaule, Poterium sanguisorba, Leontodon hispidus and Plantago lanceolata seedlings on ant-hills did not flower in their first and second summers. Thus the inability of these species to become abundant on ant-hills seems partly the result of their selection to occupy closed communities. Their heavy fruits and inability to flower early prevent them from maintaining themselves at a high density in a community of an earlier successional stage. It is interesting that Poterium sanguisorba, Leontodon hispidus and Cirsium acaule (see also Pigott 1968) are among the species which are frequent in calcareous grasslands but uncommon on calcareous 'fixed dunes' (Hope-Simpson 1955).

Of the species which 'prefer' ant-hills, the winter annuals (like Arenaria serpyllifolia) cannot become established

¹ This cannot be entirely true, because under favourable conditions Carex flacca must put a considerable proportion of its total net assimilation into vegetative reproduction.

in short swards (Chapter 5), and Helianthemum chamaecistus and Thymus drucei occur in short calcareous grassland but are rapidly eliminated when it is fenced against grazing animals. Winter annuals occur in temporarily open habitats; there, selection probably favours the production of large numbers¹ of seeds light enough² to reach new patches of bared soil, the investment of a high proportion of the total net assimilation in reproduction, and a short life cycle. MacArthur & Wilson (1967) showed mathematically that the probability of 'quick success' for a propagule colonising an island³ is maximised when r/λ is large, where r is the 'intrinsic rate of natural increase' of the species and λ is the birth rate of the plants in the population. r/λ becomes larger as a life-cycle shortens. Helianthemum and Thymus are abundant on the mounds because of their vigorous growth through heaped soil. Cerastium holosteoides combines the ability to withstand burial, the capacity to flower on ant-hills in its first year and the production of numerous light seeds.

The species with roughly equal abundances on and off ant-hills are frequently stoloniferous and able to grow up through heaped soil to some extent (e.g. Agrostis stolonifera, Campanula rotundifolia, Festuca rubra, Galium verum, (Lotus corniculatus)) or short-lived (e.g. Euphrasia officinalis agg., Gentianella amarella, Linum catharticum, Medicago lupulina, Senecio jacobaea).

¹ In winter annuals every surviving plant flowers, and since the flowers are usually self-pollinated (Clapham et al. 1962) the proportion of ovules ultimately fertilised and released as viable seeds may be high. In the rosette species uncommon on ant-hills only some rosettes flower each year, and seed set depends on cross-pollination.

² Small seeds are liabilities in swards. As Salisbury (1942) states, 'the larger the supply of food material provided by the parent plant in the seed ... the more advanced the phase of succession that the species can normally occupy.'

³ Ant-hills can be thought of as islands in a sea of potentially-colonising species.

The ant-hill environment acts as a sieve, letting through short-lived species and those which can grow up through heaped soil, and excluding those with poor fruit dispersal, seedlings susceptible to burial, and an inability to flower on the mounds. If a time-lapse film could be taken of a chalk grassland sward, and speeded up, the species most likely to colonise ant-hills might be those jumping around like jumping-jacks, and the species least likely to invade might be the most statuesque.

Ant-hills thus reveal that the species in the surrounding vegetation are distinct 'characters'. The term 'niche' has often been used to express the fact that species in the same community differ in certain ways. It was first defined by Grinnell (1917) to mean the place where a species lived, and then by Elton (1927) to represent the rôle of a species in a community, 'its profession, not its address'. Different species could occupy the same niche in different communities. Hutchinson (1957) visualised the niche of a species as a hyper-volume in a multidimensional space of which the co-ordinates were various attributes of the species or the environment.^{1,2}

The niche concept has mainly developed in animal ecology. The niches of plant species growing in the same habitat are not so easily separated, because almost all higher plants occupy the same 'trophic level', their food intake cannot be defined precisely, they are static, so that behavioural patterns cannot be investigated, and they grow closely intermixed under constant competitive pressure. Nevertheless, it should be possible to

¹ Harper (1968) mentions that the seedlings and adult plants of the same species might occupy different 'niches'.

² In view of the four different definitions of 'niche' which I have mentioned, the definition should always be stated when the term is used.

define the 'niche' of a plant species on a large scale by its place in a multidimensional hypervolume in which the axes are features of the macro-environment. Then, on a smaller scale, species commonly growing together could be separated by quantitative features of their 'population biology', like their mean turnover times, the proportion of their net assimilation entering reproduction and so on. A detailed quantitative comparison of the life cycles of species on and off ant-hills would be a logical follow-up to my work, and would allow the 'niches'¹ of grassland species to be defined.

¹By 'niches' I mean plant niches as I have re-defined the term in the previous two sentences.

REFERENCES

Appendix references are listed separately (after Appendix 29).

- Aitcheson, P.A., Smart, D.A. & Greig, J. (1967). Observations on ant-hills at Rhossili Down, Oxford University Botany School field course project report, unpublished.
- Anderson, V.L. (1927). Studies of the vegetation of the English chalk. V. The water economy of the chalk flora. *J. Ecol.* 15, 72-129.
- Bailey, N.T.J. (1959). Statistical Methods in Biology. English Universities Press. London.
- Baxter, F.P. & Hole, F.D. (1967). Ant (*Formica cinerea*) Pedoturbation in a Prairie soil. *Proc. Soil. Sci. Soc. Am.* 31, 425-28.
- Black, M. (1969). Light-controlled germination of seeds. *Symp. Soc. exp. Biol.* 23, 193-217.
- Beckett, P.H.T. (1960). Aston Rowant Soils II. Unpublished report in Hemsley & Woodman (1960).
- Boorman, L.A. & Woodell, S.R.J. (1966). The topograph, an instrument for measuring microtopography. *Ecology*, 47, 869-70.
- Clapham, A.R. (1969) (Ed.). Flora of Derbyshire. Derby Museum & Art Gallery.
- Clapham, A.R., Tutin, T.G. & Warburg, E.F. (1962). Flora of the British Isles. 2nd. Edn. Cambridge University Press.
- Clapham, A.R., Tutin, T.G. & Warburg, E.F. (1968). Excursion Flora of the British Isles. 2nd. Edn. Cambridge University Press.
- Clements, F.E. (1928). Plant succession and indicators. Hafner (reprinted 1963), New York.
- Collingwood, C.A. (1957). The species of ants of the genus *Lasius* in Britain. *J. Soc. Br. Ent.* 5, 204-14.
- Czerwinski, Z., Jakubczyk, H. & Petal, J. (1971). Influence of Ant hills on the Meadow Soils. *Pedobiologia* 11, 277-85.
- Dandy, J.E. (1969). Nomenclatural changes in the 'List of British Vascular Plants'. *Watsonia*, 7, 153-78.
- Davies, J. (1966). Molehills and pasture reversion. *J. Br. Grassld. Soc.* 21, 148-49.

- Dixon, H.N. (1924). The student's handbook of British mosses. 3rd. Edn. Sumfield & Day, Eastbourne.
- Elton, C.S. (1927). Animal Ecology. Sidgwick & Jackson, London.
- Elton, C.S. (1959). Note in Wytham Woods Ecological survey, 24 July 1959 (C.E. 13 p.57) unpublished.
- Elton, C.S. (1966). The Pattern of Animal Communities. Methuen, London.
- Farrow, H.P. (1925). Plant life on East Anglian heaths, being observational and experimental studies of the vegetation of Breckland. Cambridge University Press.
- Gabriel, K.R. (1964). A procedure for testing the homogeneity of all sets of means in analysis of variance. *Biometrics*, 20, 459-77.
- George, T.W. (1940). The structure of Gower. *Q. Jl. geol. Soc. Lond.* 96, 131-98.
- Gleason, H.A. (1939). The individualistic concept of the plant association. *Am. Midl. Nat.* 21, 92-110.
- Goodall, D.W. (1952). See p.139.
- Goodall, D.W. (1966). The nature of the mixed community. *Proc. ecol. Soc. Aust.* 1, 84-96.
- Goodland, R.J.A. (1965). On termitaria in a savanna ecosystem. *Can. J. Zool.* 43, 641-50.
- Gould, W. (1747). An account of British ants. Cited in Donisthorpe, H. St.J.K. (1927). British Ants Their Life History and Classification. London.
- Govier, R.N., Nelson, M.D. & Pate, J.S. (1967). Hemiparasitic nutrition in Angiosperms. I. The transfer of organic compounds from host to Odontites verna (Bell.) Dum. (Scrophulariaceae). *New Phytol.* 66, 285-97.
- Govier, R.N., Brown, J.G.S. & Pate, J.S. (1968). Hemiparasitic nutrition in Angiosperms. II. Root haustoria and leaf glands of Odontites verna (Bell.) Dum. and their relevance to the abstraction of solutes from the host. *New Phytol.* 67, 963-72.
- Green, F.H.W. (1959). Note on water balance added to Hemsley & Woodman (1960).
- Greig-Smith, P. (1964). Quantitative Plant Ecology. 2nd. Edn. Butterworths, London.

- Griffiths, J.W. (1968). Studies in chalkland ecology with special reference to the flora of ant-hills. M.I. Biol. thesis, Institute of Biology, London.
- Grime, J.P. (1963). An ecological investigation at a junction between two plant communities in Coombedale on the Derbyshire limestone. *J. Ecol.* 51, 391-402.
- Grime, J.P. & Jeffrey, D.W. (1965). Seedling establishment in vertical gradients of sunlight. *J. Ecol.* 53, 621-642.
- Grinnell, J. (1917). The niche relationships of the California thrasher. *Auk*, 34, 427-33.
- Grose, D. (1957). The Flora of Wiltshire. Wiltshire Archaeological and Natural History Society, Devizes.
- Grubb, P.J., Green, H.E. & Merrifield, R.C.J. (1969). The ecology of chalk heath: its relevance to the calcicole-calcifuge and soil acidification problems. *J. Ecol.* 57, 175-212.
- Haarlov, W. (1960). Microarthropods from Danish soils. *Oikos* Suppl. 2, 1-176.
- Harper, J.L. (1957). The ecological significance of dormancy and its importance in weed control. *Proc. 4th int. Congr. Pl. Prot.* pp.415-20.
- Harper, J.L. (1967). A Darwinian approach to plant ecology. *J. Ecol.* 55, 247-70.
- Harper, J.L. (1968). The regulation of numbers and mass in plant populations. Population Biology and Evolution (Ed. by H.C. Lewontin), pp.139-58. Syracuse University Press.
- Harper, J.L. (1969). The role of predation in vegetational diversity. *Diversity and Stability in Ecological Systems* (Ed. by G.W. Woodwell & H.H. Smith), *Brookhaven Symp. Biol.* 22, 48-61.
- Harper, J.L. & Benton, R.A. (1966). The behaviour of seeds in soil. II. The germination of seeds on the surface of a water supplying substrate. *J. Ecol.* 54, 151-166.
- Hemsley, J.H. & Woodman, M.J. (1960). Management plan for Aston Rowant N.N.R., Oxfordshire. Nature Conservancy, South Region.

- Hesselsmann, H. (1934 & 1938). Reference 660 cited in Geiger, R. (1965). The climate near the ground. Harvard University Press, Cambridge, Massachusetts.
- Hokosawa, T., Odani, N. & Tagawa, H. (1964). Causality of the distribution of corticolous species in forests with special reference to the physico-ecological approach. *Bryologist*, 67, 396-411.
- Hope-Simpson, J.F. (1955). Book review of 'Downs and Dunes: their Plant Life and its Environment' (Salisbury, E.J.). *J. Ecol.* 43, 311-5.
- Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harb. Symp. quant. Biol.* 22, 419-27.
- Hutchinson, J. (1955). British Wild Flowers. Vol.1, Penguin, Harmondsworth.
- Imscher, E. (1912). Über die Resistenz der Laubmoose gegen Austrocknung und Kälte, *Jb. wiss. Bot.* 50, 387-449.
- James, P.W. (1965). A new check-list of British lichens. *Lichenologist*, 3, 95-153.
- Jennings, R. (1965). The Vegetation of Ant-hills on Chalk Grassland. Nature Conservancy, unpublished.
- Kershaw, E.A. (1964). Quantitative and Dynamic Ecology. Arnold, London.
- Kohlermann, L. (1950). Reference 72 cited in Geiger, R. (1965). The Climate near the ground. Harvard University Press, Cambridge, Massachusetts.
- Lambley, P.W. (1967). Special Investigation into Ant-hills. B.Sc. Honours thesis, University of Leicester Botany Department.
- Leach, W. (1931). The importance of some mosses as pioneers on unstable soils. *J. Ecol.* 19, 98-102.
- Lee, K.E. & Wood, T.G. (1971). Termites and Soils. Academic Press, London.
- Lloyd, P.S., Grime, J.P. & Horison, I.E. (1971). The grassland vegetation of the Sheffield region. 1. General features. *J. Ecol.* 59, 863-86.
- Longton, R.E. & Greene, S.W. (1969). The Growth and Reproductive Cycle of Pleurozium schreberi (Brid.) Mitt. *Ann. Bot.* 33, 82-105.

- MacArthur, R.H. & Wilson, E.O. (1967). The Theory of Island Biogeography. Princeton University Press.
- Mägdefrau, K. (1935). Untersuchungen über die Wasserversorgung des Gametophyten und Sporophyten der Laubmoose. Z. Bot. 29, 337-75.
- Margalef, R. (1968). Perspectives in Ecological Theory. University of Chicago Press.
- Mellanby, K. (1971). The Mole. Collins, London.
- Messenger, G. (1971). Flora of Rutland. Leicester Museums, Leicester.
- Naylor, R.E.L. (1972). Aspects of the population dynamics of the weed Alopecurus myosuroides Huds. in winter cereal crops. J. appl. Ecol. 9, 127-39.
- Newman, E.I. (1963). Factors controlling the germination date of winter annuals. J. Ecol. 51, 625-38.
- Nixon, G.B.J. (1951). The association of ants with aphids and coccids. Commonwealth Institute of Entomology, London.
- Odum, E.F. & Pontin, A.J. (1961). Population density of the underground ant, Lasius flavus, as determined by tagging with P32. Ecology, 42, 186-8.
- Odum, E.F. (1969). The strategy of ecosystem development. Science, N.Y. 164, 262-70.
- Paton, J.A. (1965). Census Catalogue of British Hepatics. British Bryological Society, Truro.
- Perring, F.H. (1959). Topographical gradients of Chalk Grassland. J. Ecol. 47, 447-81.
- Pfeiffer, H. (1933). Von sukzessionsauslosender Tätigkeit mancher Rasenameisen. Beih. Repert. Spec. nov. Regni veg. (Feddes rep. Beihefte) 71, 224-31.
- Pickles, W. (1936). Populations and territories of the ants Formica fusca, Acanthomyops flavus and Myrmica ruginodis at Thornhill (Yorks.). J. Anim. Ecol. 5, 262-70.
- Pickles, W. (1940a). The effects of ants on the acidity of soils. Ent. Mon. Mag. 76, 49-52.
- Pickles, W. (1940b). Fluctuations in the populations, weights and biomasses of ants at Thornhill, Yorkshire from 1935-9. Trans. R. ent. Soc. Lond. 90, 467-85.

- Pielou, E.C. (1969). An Introduction to Mathematical Ecology. Wiley, New York.
- Pigott, C.D. (1955). Biological Flora of the British Isles: Thymus L. J. Ecol. 43, 365-87.
- Pigott, C.D. (1967). Ecological effects of red/far red light. Research Talk, Botany School, Oxford, 2 February.
- Pigott, C.D. (1968). Biological Flora of the British Isles: Cirsium acaulon (L.) Scop. J. Ecol. 56, 597-612.
- Pigott, C.D. (1970). The response of plants to climate and climatic change. The Flora of a Changing Britain (Ed. by F. Ferring), pp.32-44. Classey, Hampton, Middlesex.
- Pigott, C.D. & Taylor, K. (1964). The distribution of some woodland herbs in relation to the supply of nitrogen and phosphorus in the soil. J. Ecol. 52 (Suppl.), 175-85.
- Pontin, A.J. (1955). Colony foundation and competition between ants. D.Phil. thesis, University of Oxford.
- Pontin, A.J. (1957). An investigation of the interaction between Lasius flavus (F.) and L. niger (L.). Proc. R. Ent. Soc. Lond. (C), 22, 49
- Pontin, A.J. (1958). A preliminary note on the rearing of aphids by ants of the genus Lasius (Hym., Formicidae). Ent. Mon. Mag. 24, 9-11.
- Pontin, A.J. (1959). Some records of predators and parasites adapted to attack aphids attended by ants. Ent. Mon. Mag. 25, 154-5.
- Pontin, A.J. (1960a). Observations on the keeping of aphid eggs by ants of the genus Lasius (Hym., Formicidae). Ent. Mon. Mag. 26, 198-9.
- Pontin, A.J. (1960b). Field experiments on colony foundation by Lasius niger (L.) and L. flavus (F.) (Hym., Formicidae). Insectes sociaux, 7, 227-30.
- Pontin, A.J. (1961a). The prey of Lasius niger (L.) and L. flavus (F.) (Hym., Formicidae). Ent. Mon. Mag. 27, 135-7.
- Pontin, A.J. (1961b). Population stabilization and competition between the ants Lasius flavus (F.) and L. niger (L.). J. Anim. Ecol. 30, 47-54.

- Pontin, A.J. (1963). Further considerations of competition and the ecology of the ants Lasius flavus (F.) and L. niger (L.). J. Anim. Ecol. 32, 565-74.
- Pontin, A.J. (1968). Personal communication. 7 July 1968.
- Poole, A.L. & Cairns, D. (1940). Ref. 167 cited in Salisbury, E.J. (1961). Weeds & Aliens. Collins, London.
- Potts, G.R. (1970). Recent Changes in the Farmland Fauna with Special Reference to the Decline of the Grey Partridge. Bird Study, 17, 145-66.
- Proctor, M.C.F. (1956). Biological Flora of the British Isles: Helianthemum Mill. J. Ecol. 44, 675-92.
- Ratcliffe, D. (1961). Adaptation to Habitat in a Group of Annual Plants. J. Ecol. 49, 187-203.
- Ridley, H.W. (1930). The Dispersal of Plants throughout the World. Reeve, Ashford.
- Roberts, H.A. (1970). Viable weed seeds in cultivated soils. Rep. natn. Veg. Res. Stn. for 1969. 25-38.
- Ross, B.A., Tester, J.R. & Breckenridge, W.J. (1968). Ecology of mima-type mounds in northwestern Minnesota. Ecology 49, 172-77.
- Sagar, G.R. (1960). The biology of some sympatric species of grassland. D.Phil. thesis, University of Oxford.
- Sagar, G.R. & Harper, J.L. (1964). Biological Flora of the British Isles: Plantago lanceolata L. J. Ecol. 52, 211-21.
- Salisbury, E.J. (1942). The Reproductive Capacity of Plants. Bell, London.
- Salisbury, E.J. (1952). Downs and Dunes. Their Plant Life and its Environment. Bell, London.
- Salisbury, E.J. (1961). Weeds and Aliens. Collins, London.
- Salt, G., Hollick, F.S.J., Raw, F. & Brian, M.V. (1948). The arthropod population of pasture soil. J. Anim. Ecol. 17, 139-50.
- Smith, A.J.R. (1964). A Bryophyte Flora of Glamorgan. Trans. Br. bryol. Soc. 4, 539-96.
- Sokal, R.R. & Rohlf, F.J. (1969). Biometry. Freeman, San Francisco.

- Stevenson, F.J. (1964). Organic acids in Soil. Soil Biochemistry (Ed. by D.A. McLaren, G.H. Peterson), pp.119-146. Dekker, New York.
- Suominen, J. (1969). The plant cover of Finnish railway embankments and the ecology of their species. Ann. Bot. Fenn. 6, 183-235.
- Tamm, C.O. (1948). Observations on reproduction and survival of some perennial herbs. Bot. Notiser, 3, 305-21.
- Tamm, C.O. (1956). Further observations on the survival and flowering of some perennial herbs. Oikos, 7, 273-92.
- Tansley, A.G. (1939). The British Isles and their Vegetation. Cambridge University Press.
- Tansley, A.G. & Adamson, R.S. (1925). Studies of the Vegetation of the English Chalk. III. The Chalk Grasslands of the Hampshire-Sussex Border. J. Ecol. 13, 177-223.
- Taylor, F.J. (1956). Biological Flora of the British Isles: Carex flacca Schreb. J. Ecol. 44, 281-90.
- Taylorson, R.B. & Northwick, H.A. (1968). Light filtration by foliar canopies: significance for light-controlled weed seed germination. Weed Sci. 17, 48-51.
- Thomas, A.S. (1962). Ant-hills and termite mounds in pastures. J. Br. Grassld. Soc. 17, 103-08.
- Urbain, A.-J. & Marty, P. (1920). Influence du travail souterrain des taupes sur la flore des pâturages du Cantal. C.r.hebd. Séanc. Acad. Sci., Paris, 171, 581-3.
- Veronov, B.P. (1968). Über die Wühltätigkeit des Maulwurfes (Talpa europaea L.). Pedobiologia, 8, 97-122.
- Walloff, N. & Blackith, R.E. (1962). The growth and distribution of the mounds of Lasius flavus (Fabricus) (Hym: Formicidae) in Silwood Park, Berkshire. J. Anim. Ecol. 31, 421-37.
- Warburg, E.F. (1963). Census Catalogue of British Mosses. British Bryological Society, Ipswich.
- Wareing, P.F. (1966). Ecological aspects of seed dormancy and germination. Reproductive Biology and Taxonomy of Vascular Plants (Ed. by J.G. Hawkes), pp.103-121. Pergamon, Oxford.

- Watson, B.V. (1960). A Quantitative Study of the Bryophytes of Chalk Grassland. *J. Ecol.* 48, 397-414.
- Watt, A.S. (1971). Factors controlling the floristic composition of some plant communities in Breckland. The Scientific Management of Animal and Plant Communities for Conservation (Ed. by R. Duffey & A.S. Watt), pp.137-152. Blackwell Scientific Publications, Oxford.
- Wesson, G. & Wareing, P.F. (1967). Light requirements of buried seeds. *Nature*, Lond. 213, 600-1.
- Whittaker, R.H. (1965). Dominance and diversity in land plant communities. *Science*, N.Y. 147, 250-60.
- Whittaker, R.H. (1967). Gradient analysis of vegetation. *Biol. Rev.* 42, 207-64.
- Whittaker, R.H. (1970). Communities and Ecosystems. Macmillan, London.
- Williams, C.B. (1964). Patterns in the Balance of Nature. Academic Press, London.
- [Williams, C.B. (1970). Population dynamics of two perennial grasses in Australian semi-arid grassland. *J. Ecol.* 58, 869-875.]
- Zacherl, H. (1956). Physiologische und ökologische Untersuchungen über die innere Wasserleitung bei Laubmoosen. *Z. Bot.* 44, 409-36.
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- Goodall, D.W. (1952). Some considerations in the use of point quadrats for the analysis of vegetation. *Aust. J. sci. Res. Ser. B.* 5, 1-41.

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1. Sample Collection & Treatment.

N end of Rhossili Down On 18 May 1968 one bulked soil sample was collected from each of the twenty ant-hills and sixteen surrounding vegetation quadrats whose vegetation had earlier been sampled in detail (see Ch. 2 & Appendices 8 & 9). Four separate cylinders of soil were taken from the top 5cm of mineral soil in each sampled area, and bulked. In the laboratory, I removed vegetation (including roots) and litter. The samples were air-dried for ten days. The fraction of each sample which passed through a standard 2mm sieve was placed in a sealed polythene container at laboratory temperature (15-25°C) until analysis.

Aston Rowant. On 21st August 1969 twenty-five ant-hills on my Beacon Hill plot were selected for sampling. The first 19 were chosen at random after all the mounds on the plot had been numbered. The final six were chosen because they had been abandoned by L. flavus colonies, and unoccupied mounds had not been represented in the original sample. Bulked samples were collected from the top 5cm of mineral soil of each ant-hill, and from 0.25m² quadrat placed 30cm away from each mound in a random direction. They were air-dried for 14 days but otherwise treated like the Rhossili Down samples; analyses were performed on the fraction which passed through a standard 2mm sieve.

2. Methods of AnalysisA. pH

Rhossili Down (N end) pH was measured with a Pye glass electrode bench pH meter, on duplicate samples of a 1:2.5 ratio by weight of dry soil to distilled water. The electrode was placed at the liquid/soil junction, as suggested by Peech (1965).

Aston Rowant. pH was measured in exactly the same way, but on a 1:2.5 ratio by weight of dry soil to 0.01 M CaCl₂.

B. Exchangeable H⁺ (m.eq./100g).

Rhossili Down (N end), Brown's (1943) crude method was used. 2.5g of soil was placed in 25 cm³ of 1N Ammonium acetate (adjusted to pH 7). The suspension was shaken intermittently for one hour, its pH was read with a Pye glass electrode bench pH meter and the concentration of exchangeable Hydrogen ions was obtained from the curve in Jackson (1958), p. 76.

C. CaCO₃ (%)

Aston Rowant 50ml Erlenmeyer flasks, each containing about 10cm³ of 3N Hydrochloric acid, were weighed and sealed. Known weights (about 3g) of soil were added carefully. The flasks were gently agitated every half hour, until two hours after the soil had been put in, when the flasks & contents were reweighed. The loss of weight of the flask was assumed to be due to loss of CO₂ from CaCO₃.

D. Total exchangeable bases (m.eq./100g)

Rhossili Down. Brown's (1943) method was used. 2.5g of soil was placed in 25cm³ of 1N Acetic acid and the suspension was shaken intermittently for an hour. The pH values were read on a Pye glass electrode bench pH meter and the concentration of total exchangeable metallic cations was obtained from the curve in Jackson (1958) p. 69.

E. Organic matter (%)

Aston Rowant. The Walkley-Black method (Jackson 1958) was used on 0.5g soil samples which had passed a 0.2mm sieve. After adding the concentrated H₂SO₄, the solutions were heated to 200°C to produce more complete oxidation, and a conversion factor of 1.12, not 1.34, was used.

F. Extractable phosphorus (pp.m)

Aston Rowant. 5g of soil was extracted with 100cm³ of 0.5M NaHCO₃ adjusted to pH 8.5 (Jackson 1958), and the extracted phosphorus was determined colorimetrically, using a molybdate method.

G. Total Nitrogen(%)

Aston Rowant A finely-ground soil sample was passed through a 0. sieve and subjected to a micro-Kjeldahl digestion. The ammonia was determined by the Conway method.

H. %Stones The weight of the original sample retained by the 2mm sieve was expressed as a percentage of the total air-dry weight of the sample before sieving.

APPENDIX 2. Vegetation of mole-hills in chalk grasslands.

In these notes f = regenerated from root fragments, v = invaded vegetatively and s = seedlings seen on molehills (MH).

- (i) Beacon Hill, Aston Rowant N.N.R.. Molehills formed March 1970 at N. (see map, Appendix 29).
2nd May 1970. MHs projected above surrounding soil. Total plant cover below 4% on every MH. All species present on 15 MH recorded. Those with highest frequencies were: Poterium sanguisorba (fs, 15), Festuca rubra (11), Carex flacca (v, 10), Helictotrichon pratense (8), Plantago lanceolata (fs, 7), Leontodon hispidus (s, 6), Campanula rotundifolia (v, 6). Nine seedlings occurred altogether.
7th August 1970. Total plant cover below 25% on every MH; some rosettes had expanded.
28th September 1971. MH soil at level of surrounding soil. Total plant cover below 70% on every MH. Same MHs difficult to find. Most frequent species Poterium, Festuca, Carex, Leontodon, Sedum acre, Linum catharticum, Raphrasia spp and Arenaria serpyllifolia occasionally present.
- (ii) Beacon Hill, Aston Rowant N.N.R.. North side at D (see map, Appendix 29).
18th August 1971. MHs projected above surrounding soil. All species present on 10 MH recorded. Those with highest frequencies were Galium verum (f, 10), Plantago (f, 9), Carex (f, v, 8), Lotus corniculatus (v, 8), Veronica chamaedrys (v, 7), Festuca (5). Most plants had invaded vegetatively. Very few seedlings seen.
- (iii) Stockton Down, Wilts (see Appendix 13). 25th August 1969. "MHs colonised by species absent from ant-hills, e.g. Carex flacca, Poterium sanguisorba, Cirsium acaule."
- (iv) Camp Down, Wilts (see Appendix 13). 14th July 1969. "Molehills abundant. Colonised mainly by Cirsium acaule, Poterium sanguisorba, Plantago lanceolata, and P. media."
- The same group of species invades other bare patches, e.g. chalk rubble and erosion hollows, e.g.:
- (v) Beacon Hill, Aston Rowant N.N.R.. North side at A (see map, Appendix 29).
15th August 1971. Topsoil had been excavated for track 3 years previously, leaving compacted chalk rubble. About 15% plant cover, including Poterium sanguisorba (f), Cirsium acaule, Plantago lanceolata (f), Carex flacca, Leontodon, Arenaria, Theris arvensis.
- (vi) Beacon Hill, Aston Rowant N.N.R. at P (see map, Appendix 29).
1st March 1968. Erosion terraces formed (sheep walking?) on steep slope. Fresh soil in hollows colonised by Poterium sanguisorba, Carex flacca, Plantago lanceolata.

SYMBOLS USED IN APPENDICES 4-7 and 10-22.

A = animal

B = bird

C = cattle(cows,bullocks & horses)

G = grazed

GG = very heavily grazed

H = horse

I = irregular

M = mole-hill.

M.R. = not recorded

P = pecks

S = sheep

SV = surrounding vegetation

T = trampling

species recorded, although often not rooted in the sample area.

Significance Tests

NS., $P > 0.05$

. , $0.05 > P > 0.01$

.. , $P < 0.01$

B = exact Binomial test.

NT = not tested

T = t-test for paired comparisons

W = Wilcoxon signed - ranks test

for matched pairs (two-tailed).

APPENDIX 3. Explanation of the symbols in, and some of the methods used in collecting the data for Appendices 4-7&10-22 in which 17 sites and the vegetation on and off their ant-hills are described.

The key to the symbols is glued to the facing page, and when folded upwards it can be consulted whilst appendices are read.

In this Appendix I give the evidence that L. flavus mounds are regularly-distributed (Section 1), mention how environmental features of ant-hills were estimated (Section 2), list identification difficulties (Section 3) and describe how significance tests were performed (Section 4). The same method was used to sample the vegetation on and off the mounds at the Gower sites (Chapter 2, Appendices 4 - 7), the calcareous grassland sites (Chapter 3, Appendices 10-22), and on my Beacon Hill plot (Chapter 4, Appendix 28). The technique is described in section 2.2.1, p.24 of the text.

1. Evidence that L. flavus mounds are regularly-distributed.

<u>Source</u>	<u>Site</u>	<u>Method</u>	<u>Result (sample size in brackets)</u>
Aitcheson et al (1967)	Rhossili Down, Gower, Glam.	Hopkins (1954)	A = 0.504** (50)
Calculation on map of Pontin (1963)	Bowling Alley, Wytham Woods, Berks	Hopkins (1954)	A = 0.45** (25)
Waloff & Blackith (1962)	Ascot, Berks	Clark & Evans (1964)	P < 0.0001 (60)
Blackith et al (1963)	Chagford, Devon,	Clark & Evans (1964)	P < 0.01 (25)
			P < 0.01 (10)

(**P < 0.01)

2. Recording of site details and ant-hill characteristics. Details of parent material and drift were obtained from the latest editions of the O.S. Geological Survey 1/65000 drift maps, sheets 246, 254, 281, 297, 298 and 519.

The height of each mound was estimated by placing a measuring tape beside the ant-hill, perpendicular to the slope of the pasture, on the north, south, east and west sides in turn, and gauging the height of the summit. The four estimates were averaged.

The diameter of the base of the mound was measured by holding the tape parallel to the slope of the pasture, above the ant-hill, and reading off the distance between the apparent intercepts of the ant-hill margin on the tape. Two estimates were made, one north to south, the other east to west, and were averaged.

A mound's height and diameter were used to calculate its surface area and volume. Few ant-hills were hemispherical; most had the shape of segments cut off a sphere. Thus for mounds whose height (h) ≤ radius (r) the following formulae, derived from Green (1966), p.184-9 were used to estimate surface area and volume:

$$S.A. = \pi(r^2 + h^2)$$

$$V = \frac{\pi h(3r^2 + h^2)}{6}$$

When the height exceeded the radius, I calculated the surface area and volume of the mound as those of a hemisphere atop a cylinder.

I estimated vegetation height by measuring the distance of my hand from the ant-hill surface, when I held it parallel to the surface so that it was pricked by several leaves.

% Bare soil was the percentage cover of soil which was not obscured by the perpendicular projection onto it of the aerial parts of plants.

Soil heaped up by the ants in the year of sampling could be distinguished from the rest of the ant-hill by its dry, crumbly, porous structure; it also covered the stem and leaf bases of plants growing on the mound. Its volume was estimated, using the depth of plant burial and a vision of a 100 cm³ beaker as my guide. The estimates were corrected to "measured volumes" by the regression equations $\hat{M} = 11.42 + 1.57 \hat{E}$ (for 1969 and 1970) and $\hat{M} = 16.12 + 0.98 \hat{E}$ (for 1971) derived in Appendix 25, to give the "volumes of newly-heaped soil" in the appendices. The accuracy of these assessments of soil volume is also discussed in Appendix 25.

A comparative index of the extent of soil heaping on different mounds (% ant-hill activity) was calculated by expressing the corrected "volume of newly heaped soil" on each mound as a percentage of the total mound volume.

5. Identification difficulties.

(i) Festuca ovina and F. rubra were separable but the extra information gained by determining them and their percentage covers was not worth the extra time needed to sample each quadrat. These species were often lumped, but Festuca spp. in the tables does not necessarily mean that both species were present in my samples. For example, F. rubra only was seen at several chalk grassland sites.

(ii) I cannot distinguish Leontodon hispidus and L. taraxacoides vegetatively. Flowering L. hispidus was much commoner at the sampled sites than flowering L. taraxacoides, and I have recorded all Leontodon rosettes whose leaves have forked hairs as L. hispidus in the tables.

(iii) Arenaria serpyllifolia and A. lentocladus have been "lumped" under A. serpyllifolia for the same reason.

(iv) I sometimes found difficulty in separating, in the vegetative state, Cynosurus cristatus from small Lolium perenne, Helictotrichon pratense from Poa pratensis, and Agrostis tenuis from A. stolonifera.

(v) Young plants of (a) Holcus lanatus, Arrhenatherum and Trisetum,

(b) Scabiosa columbaria and Leucanthemum vulgare, (c) Viola hirta and V. riviniana, (d) Galium mollugo and G. verum often caused trouble.

Unknown bryophytes were collected and determined microscopically. Many identifications were checked by A. R. Perry and I compared others with a reference collection of species named by him. The bryophytes collected were often scrappy and never fruiting, so that it was often difficult to identify e.g. Barbula and Bryum spp. In the tables I have enclosed percentage cover estimates, or the names of genera or species, in parentheses whenever I am at all uncertain about the identification.

4. Significance tests.

The results of tests of significance of the null hypothesis, that the true percentage cover of each species on and off the mounds was the same, are given in the final columns of each table. The symbols are explained in the key. At each site, I considered only those species which had four or more occurrences in either or both of the ant-hill and surrounding vegetation samples. Firstly, when the percentage cover values for a species, on and off the mounds, were extremely different or extremely similar, I noted either that there was a highly significant difference in its abundance on and off the mounds, or that the difference was not significant, as the case may be. Secondly, attention was confined to samples in which the species had one or more cover value of 4% or more, and at least six occurrences in either or both the ant-hill or surrounding vegetation samples. Two-tailed Wilcoxon signed-ranks tests for matched pairs were applied to these data. This quickly applied, non-parametric test is more conservative than a t-test or its equivalent analysis of variance, and so I noted the cases in which the difference in abundance of a species on and off the mounds was almost significant at the 5% level by Wilcoxon's test. Then t-tests for paired comparisons were applied both to these cases, and to the remaining samples in which a species had one or more cover estimate of at least 4%. For all samples to which t-tests were applied, the difference in percentage cover between ant-hills and surrounding vegetation quadrats were normally distributed about a zero mean, although the distribution was highly leptokurtic. Thus the data were not transformed before t-tests were carried out; when the percentage cover values were all small the assumptions underlying the t-test were usually satisfied and the test was sensitive, but when some of the cover values were large, the tests were conservative.

There remained those cases in which the cover of the species did not exceed 3% on any ant-hill or in any quadrat. Here I applied an exact test for frequency data based on the Binomial distribution. I calculated the exact probability of obtaining the observed ratio of occurrences of the species on and off the ant-hills if $p = q = 0.5$.

In all the significance tests described above, the blocks from which a species was absent were ignored.

APPENDIX 4. Llanmadoc Down, Gower, Glamorgan

Comparison of ant-hill (AH) and surrounding vegetation (SV)

O.S. GRID REFERENCE SS 438926

SITE VISITED IN June 1970

SITE POSITION From the B4271 between Llangennith and Burry Green a road runs northwards to Llanmadoc via the side of Llanmadoc Down. From the house nearest Llanmadoc on this road I took a path up the Down which led over ancient earthworks arranged in concentric circles. The site was on the other side of the earthworks overlooking a farmhouse.

Site was at 170 m. sloping 10° to the south.

Extremely exposed to winds and rain. Within 2.5 km. of sea. Mean total annual rainfall = 1105 mm.

Common Land.

AREA SAMPLED 15 x 15 m. containing an estimated 100 mounds, i.e. a density of 444/ha.

VEGETATION HISTORY Neolithic earthworks present. Site probably grazed by commoners' sheep and cattle for more than 400 years.

SOIL DETAILS Parent material is Old Red Sandstone (Devonian) - red marls?. Drainage good. An A₀ horizon (matted humus) 2.0 cm. thick covered a grey-brown loam. Parent material was reached at 20-25 cm.

PRESENT VEGETATION *Pteridium* covers most of the Down, except on and near the circular ridges and hollows of the earthworks; in the pioneer stage, it was invading the site. *Potentilla erecta* and *Linula campestris* are abundant in the SV.

AHs all "mature"; most dominated by *Festuca rubra* and *Polytrichum juniperinum*

Site grazed by rabbits, sheep and horses.

RESULTS are overleaf. The methods and symbols used are described in Appendix 3. The numbers in the table are subjectively-estimated percentage covers of all species in 8 blocks, each consisting of a randomly-selected AH and a 0.25m^2 quadrat placed 0.5 m. away from it, in a random direction, in the SV.

	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	SIG
Mean All Ht. (cm)	16	18	21	17	15	23	25	29									
Mean All Diam. (cm)	78	58	71	51	48	70	74	77									
All Volume (10 ³ cm ³)	40	27	45	21	15	51	61	81									
Volume N.H.S. (corr.) (10 cm ³)	3	4	8	18	4	5	14	4									
Activity (%)	+	•2	•2	•9	•2	•1	•2	+									
Animal Activity	RDC SDG	RSC		RSC		RSC			RDC SDG	RSC SD	G		G	RSC RD	RSC SD		
Vegetation Ht. (cm)	1	2	3	4	2	3	2	3	4	2	3	5	7	3	4	N.R.	
% cover Bare Soil	1	2	1	6	2	1	1	1									
Agrostis tenuis	40	9	3	2	8	6	6	3	30	50	3	35	25	15	25	15	*T
Aira praecox	1	1	1	1		1		1									*B
Anthoxanthum odoratum	3		4	1	3	4	1	2	8	7	5	15	12	10	5	10	**W
Carex pilulifera											1	2		1	1		NSB
Festuca ovina	70	55	35	30	50	60	55	30	60	70	40	65	65	80	80	75	*W
Galium saxatile	5	2	12	1	25	25	12	7	9	1	3	1	3	3	3	7	NST
Lusula campestris	1				1	1		1	9	6			22	5	6	12	*W
Potentilla erecta	2				2			1	4	3	35	5	2	2	7	10	*W
Rumex acetosella	1	1	10	3	1	2	1		1		1	3	2				NST
Pteridium aquilinum									8	1	6	1	6				*T
Dicranum scoparium	4	4	1		8	6	8	35	1	1	13			2	9	1	NST
Hypnum cupressiforme	12				3						12	4			6	5	NST
Pleurozium schreberi	4				1				1	1	14	1			2	5	NST
Polytrichum juniperinum	4	40	55	70	17	22	50	30			8	5					**W
Rhytidiadelphus squarrosus					1				1	1	10	4	1	7	7	12	**W

HERA species

Ceratodon purpureus AH1(1%), AH6(3%).
Cladonia rangiferina AH1(1%)
Erica cinerea AH5 (1%), 7(6%).
Fissidens taxifolius AH6 (2%)
Polytrichum piliferum AH8 (3%)
Pohlia nutans AH1 (6%), 6(1%)

Cerastium holosteoides SV7(1%)
Hieracium stricta SV3(7%)
Pseudoscleropodium purum SV1(1%), 6(1%),
 7(1%).
Deschampsia flexuosa AH1(1%), SV1(1%),
 3(3%)

APPENDIX 5 Harding's Down, Gower, Glamorgan.

Comparison of ant-hill (AH) and surrounding vegetation (SV)

O.S. GRID REFERENCE SS454907

SITE VISITED IN June 1970

SITE POSITION From the track which skirts the northerly edge of the Down, I climbed the path up the most westerly earthwork. At the top, across a ditch, the site was about 75 m. down the hill on the SW side.

Site was at 137 m., sloping 5° to the SW.

Fairly exposed to winds and rain. Within 5 km. of sea.

Mean total annual rainfall = 1105 mm.

Common Land.

AREA SAMPLED 30 x 20 m. containing an estimated 200 mounds, i.e. a density of 3333/ha.

VEGETATION HISTORY Neolithic earthworks present nearby. Site probably grazed by commoners' sheep and cattle for more than 400 years.

SOIL DETAILS Parent material is Upper Old Red Sandstone (Devonian); Quartz and red conglomerate. Site well-drained, with a flush, dominated by Juncus effusus, leaving the lower side. Soil a grey-brown loam, very similar to Llanadoc Down (App.4.)

PRESENT VEGETATION Most of the Down was covered by Pteridium, under which AHs were absent. Closely-grazed patches of grassland, with AHs, occurred along paths, in and around earthworks, and at the sampled site. This site was surrounded by Pteridium with some closely-grazed Ulex (gallii?) bushes up to 2m.

AHs all "mature", with little soil-heaping; Polytrichum juniperinum was abundant on the tops.

Site very closely grazed, especially by sheep and horses. Droppings of sheep, rabbits, and birds present; peck-marks occurred in the sides of the mounds.

RESULTS are overleaf. The methods and symbols used are described in Appendix 3. The numbers in the table are subjectively-estimated percentage covers of all species in 8 blocks, each consisting of a randomly-selected AH and a 0.25 m² quadrat placed 0.5m. away from it, in a random direction, in the SV.

	AH								SV								SIG
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Mean AH Ht. (cm)	16	24	21	24	17	56	30	24									
Mean AH Diam. (cm)	57	91	64	92	48	79	44	69									
AH Volume (10 ³ cm ³)	25	87	57	88	18	115	19	55									
Volume N.H.S. (corr.) (10 cm ³)	6	11	20	2	17	6		5									
Activity (%)	.5	.1	.5	+ 1.0		+		.1									
Animal Activity	CG	CGP	CG	CG		CG	DC	DC	CGD	CG	CG	CG	CG	CG	CG	G	
						ED			SR	RD	RD	RD	D				
Vegetation Ht. (cm)	2	3	1	2	1	2	2	2	1	1	1	2	2	1	4	3	
% Cover Bare Soil	1	1	10	2	22	1		1									
<i>Agrostis tenuis</i>	3	4	8	15	10	8	6	3	6	15	50	45	40	50	13	30	**W
<i>Aira praecox</i>	2	4	1	2	2	3			2	3	1	4	1	8			NSNT
<i>Anthoxanthum odoratum</i>				3	6	1		1		4	4	1	12	4		1	NST
<i>Carex pilulifera</i>		1					1								6	3	
<i>Festuca ovina</i>	50	70	30	70	60	60	25	68	80	80	70	60	80	70	55	80	*W
<i>Galium saxatile</i>	5	5	8	10	25	6	8	10	9	2	9	1	2		4	9	NST
<i>Luzula campestris</i>	1	2	4	5	2	1	1	2	17	6	10	8	6	4		4	*W
<i>Rumex acetosella</i>		2	1	12	2	1	1	10			2	20		3		1	NST
<i>Dicranum scoparium</i>	50	15	18	20	1	25		2	1	2	1	1	2	1	3	1	*T
<i>Hypnum cupressiforme</i>	8	15	2						25	5	5	1	6	1	7	3	NST
<i>Pleurozium schreberi</i>							1			2	1				3		
<i>Polytrichum juniperinum</i>	15	7	30	4	7	10	70	10							2	1	**W
<i>Rhytidiadelphus squarrosus</i>	1	1			1	1			12	20	15	1	25	3	9		*W

Recorded for AH 1, 3, 6 that Luzula occurred in a ring around the edge and Polytrichum juniperinum and Dicranum dominated the bare soil on the tops of the mounds.

EXTRA species

Gladonia rangiformis AH1 (1%)

Pohlia nutans AH2 (1%)

Polytrichum piliferum AH6 (10%)

Juncus effusus AH7 (1%)

Potentilla erecta AH7 (1%), SV7 (4%), 8(3%)

Ptilidium ciliare AH1 (1%), SV7(1%), 8(1%)

Sieversia decumbens AH8(1%), SV7(2%), 8(1%)

Carex sp. SV8(1%)

Euthyrium proclonum SV6(1%)

Hypochaeris radicata SV6(1%)

Urtica (longirostris) SV4(1%), 6(1%)

Nardus stricta SV1 (5%), 7(10%), 8(2%)

Rhytidiadelphus triquetrus SV8 (6%)

Sagina procumbens SV6(1%)

APPENDIX 6 Cefn Bryn, Gower, Glamorgan.

Comparison of ant-hill (AH) and surrounding vegetation (SV)

O.S. GRID REFERENCE SS488902

SITE VISITED 21st June 1970.

SITE POSITION Cefn Bryn is the largest O.R.S. hill in Gower. Site near the car park at the highest point of the Reynoldston-Cillibion road, about 100 m from road, 100 m. NW of car park, alongside the path to Frog Moor.

Site is at 150 m., level. Extremely exposed to sea gales.

Mean total annual rainfall = 1105 mm.

Common Land.

AREA SAMPLED 75 x 40 m. containing an estimated 400 mounds, i.e. a density of 1555/ha.

VEGETATION HISTORY Arthur's Stone, nearby, is a Neolithic burial tomb. Site probably grazed for centuries by commoners' sheep and horses.

SOIL DETAILS Parent material is Upper Old Red Sandstone (Devonian) - quartz and red conglomerate. Drainage good; lower down the hill a bog with Erica tetralix Molinia, Eriophorum etc. exists. Several auger borings showed that an A₀ horizon 2-5 cm. deep (matted plant remains) was underlain by a red-brown sandy soil, varying in depth from 15-90+ cm., which was podsolised in places.

PRESENT VEGETATION SV tall, tussocky, with many inflorescences remaining ungrazed; the high proportion of Nardus, Sieglingia and Ulex possibly reduced the grazing intensity. The site had probably been burnt in Spring 1969 or Spring 1970, since many dead, recently-burnt Ulex stems were present, regenerating from the base.

Most AHs "mature", but two small active mounds and two "incipient" mounds seen. The large mounds often had angular shapes, with vertical sides and flat tops, instead of the usual rounded contours. Holes and scrapes on the summits were possibly due to grazing animals. The tops and south sides of the AHs often bore parched, dead vegetation; there had been no rain in the area for five weeks.

Site grazed lightly by sheep and ponies. Several unidentified bird droppings found on mounds.

RESULTS are overleaf. The methods and symbols used are described in Appendix 3. The numbers in the table are subjectively-estimated percentage covers of all species in 10 blocks, each consisting of a randomly-selected AH and a 0.25m² quadrat placed 0.5m. away from it, in a random direction, in the SV.

AH

SV

	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	SIG	
Mean AH Ht. (cm)	29	28	19	22	27	21	31	30	22	17												
Mean AH Diam. (cm)	93	124	62	98	80	39	96	121	46	64												
AH Volume (10 ³ cm ³)	114	132	53	87	79	17	130	133	24	50												
Volume N.H.S (corr.) (cm ³)	90	90			294		27	43														
Activity (%)	+	+			+		+	+														
Animal	CHS	CHS			RD		GD	ST		STD	SG	SCT		G		CT	CT		CT	CT		
Activity	TSHD	TSHD																				
Vegetation Ht. (cm)	7	8	10	8	6	5	4	6	1	4	6	2	19	4	10	8	10	11	5	7		
% cover																						
Bare Soil	40	15	1	10	7	6	2	15	50	20												
Agrostis tenuis	2	2	25	10	1	2	8	2	20	4	15	50	20	27	6	15	6	2	17	17	NST	
Aira praecox	2	1		1	1			1	1	1											*W	
Anthoxanthum odoratum	1	3	1	2	1	2	4	2		1	6	15	3	2	3	6	5	3	4	3	*W	
Carex pilulifera	1	1	2		2	1	1	1	1	1			1	1	3			1	2		NSB	
Erica cinerea		1			6			1	3	1											NST	
Festuca ovina	55	78	90	70	70	90	75	80	36	70	75	50	85	80	90	85	80	92	85	75	NSW	
Galium saxatile	2	4	3	5	3	2	3	1	3	1	4	2	3	5	5	4	10	4	2	2	NST	
Luzula campestris		1		1		1	1				7	1		1	3	2	2		7		NST	
Nardus stricta							2				2	5				8	7		6	4	*W	
Polygala (serpyllifolia)				1				1		1				1	1		1		1	1	NSB	
Potentilla erecta				1		1	1	1		1		1	1		2		1	1	1	1	NSB	
Rumex acetosella agg.		1	1										1	1								
Sieglingia decumbens					5	2	5	1	2		2	4	2	6	6	8	8	17	14	2	25	*W
Ulex galii			5	3	1	1		1		6				2	2	1			4		10	NSNT
Polytrichum juniperinum	4	4		4	18		7	2	1												*W	
Pseudoscleropodium purum											4			1	1	1	8	6	5	1	*W	
Rhytidiadelphus squarrosus											2	1	1			25	8		4	1	*W	

Parched, brown, dying vegetation was noted on AH1, 2, 5 and 9.

EXTRA species

Agrostis stolonifera AH6(1%)
Campylodon pyriformis AH3(2%), 10(1%)
Ceratodon purpureus AH10(3%)
Dicranum sponarium AH4(10%), 7(18%), 8(1%)
Polytrichum piliferum AH4(1%), 8(1%)

Erica tetralix SV10(4%)
Hynum compressiforme SV4(1%)
Rumex acetosa SV3(1%)
Molinia caerulea AH1(1%), SV1(10%), 3(1%)

APPENDIX 7. Southern end of Rhossili Down, Gower, Glamorgan.

Comparisons of ant-hill (AH) and surrounding vegetation (SV)

O.S. GRID REFERENCE SS416884

SITE VISITED 24th June 1970

SITE POSITION The site was the first large patch of grassland on the seaward side of the path leading up Rhossili Down from Rhossili to "the Beacon". Its centre was about 70 m. from the path.

Site is at 150 m., sloping 4° to the WSW.

Extremely exposed to south-westerly winds and rain. Annual rainfall 1105 mm. Receives some sea spray and much sea mist; within 1 km. of sea. One of the windiest places in southern Britain.

Common Land. Administered by National Trust.

AREA SAMPLED 60 x 20 m, containing an estimated 450 mounds, i.e. a density of 3750/ha.

VEGETATION HISTORY

Neolithic monuments occur on Rhossili Down. Site probably grazed by commoners' sheep and cattle for more than 400 years.

SOIL DETAILS

Parent material is Upper Old Red Sandstone (Devonian) - quartz and red conglomerate. Two trowel profiles were dug. An Ao (matted plant remains) horizon 0.5-2 cm. thick overlaid a red-brown sandy loam, with quartz pebbles increasing in frequency with depth. Parent material was encountered 20-24 cm. down. Mean pH of two samples taken from top 5 cm. of mineral soil was 4.5 (measured on 1:25 ratio of air-dried soil to distilled water by weight).

PRESENT VEGETATION

The presence of *Koeleria*, *Poa pratensis*, *Achillea millefolium* and *Hieracium pilosella* suggests that the soil might be more neutral than at the other Gower sites I sampled.

Mounds all large; flowering *Thymus drucei* occurred there.

Grazed mainly by sheep; numerous sheep droppings found. Probably also grazed by horses, rabbits and hares.

RESULTS are overleaf. The methods and symbols used are described in Appendix 3. The numbers in the table are subjectively estimated percentage covers of all species in 8 blocks, each consisting of a randomly-selected AH and a 0.25m^2 quadrat placed 0.5m away from it, in a random direction, in the SV.

	AH								SV								SIG
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Mean AH Ht. (cm)	17	24	24	15	19	20	20	20									
Mean AH Diam. (cm)	62	77	73	37	59	48	51	54									
AH Volume (10 ³ cm ³)	29	61	58	10	29	22	24	28									
Volume N.H.S. (corr.) (cm ³)	0	0	0	19	19	0	59	27									
Activity (°)				.2	+		.2	.1									
Animal Activity	OG	D			RD	G	G	G	OG	GR	G	G	G	G	G	G	
					G					SD	SD			SD	SD	RD	
Vegetation Ht. (cm)	5	3	4	2	3	3	2	3	3	5	4	4	5	3	5	4	
% cover Bare Soil			1		1		2	2									
<i>Agrostis tenuis</i>	16	20	22	15	10	15	15	15	30	30	55	45	50	50	35	20	**W
<i>Aira praecox</i>	1	2	1	1		1	1	2	1	1	1				1		NSB
<i>Anthoxanthum odoratum</i>	1		1	1					1		1		2				
<i>Carex (caryo- phyllaea)</i>	1	1	1			1	1	1	2	1			1	1	2	1	NSB
<i>Festuca ovina</i>	80	60	70	80	80	70	70	60	70	60	80	80	60	70	85	80	NSI
<i>Galium saxatile</i>	10	10	5	20	8	18	7	5	9	2	5	4	13		9	10	NSI
<i>Hieracium pilosella</i>							2				3	2			3	2	*T
<i>Hypochoeris radicata</i>									4		3	1	1			2	**T
<i>Luzula campestris</i>	1		1		1	1			3		8	2	3	4	1	3	*W
<i>Poa pratensis</i>	2							1	6	3				2			
<i>Rumex acetosa</i>	1	3	1	1							1	1	1				NSNT
<i>Veronica officinalis</i>	1				1		7		1		1		1	1	1		NSNT
<i>Dicranum scoparium</i>	6	5	2	6		3		8			1						*W
<i>Hypnum cupressiforme</i>	2	1	1			1		1	2		4			1	2	1	NSNT
<i>Pleurozium schreberi</i>	4								2		4					6	
<i>Polytrichum juniperinum</i>	3	10	1	5	17	3	2	35									**TT
<i>Polytrichum piliferum</i>	10	25	20			10	7	3									**TT

EXTRA species

Gladonia imoxa AH2(2), 6(1).
Gladonia pyxidata AH2(3), 6(1), 8(1).
Gladonia rangiformis AH3(1).
Dicranum bonjeanii AH1(1).
Brillania tovarisci AH6(2).
Lonicoclea bidentata AH1 (1), 3(2).
Thymus drucei AH3 (1).

Achillea millefolium SV1(1), 4(1), 6(1).
Koeleria cristata SV1 (1), 3(1), 6(4).
Erius Gongirostema SV1 (1).
Poa annua SV2(5).
Pseudoclerodendron purum SV1 (1).
Rhytidadelphus squarrosus SV3 (1), 4(1).
Siecklingia decumbens AH6(2), SV6(2).
Ptilidium ciliare AH1 (1), 6(1), SV8(1).

APPENDIX 8. Site Details for Northern end of Rhossili Down (Text, Section 2.3.

O.S. GRID REFERENCE SS 418904

SITE VISITED ON numerous occasions

SITE POSITION Along path from Hillend to the Beacon, a concave, grassy area just below dense Pteridium and Calluna. Site is at 140 m. sloping 7° to the north. Photograph in Fig. 7, p. 26.

Extremely exposed to south-westerly winds and rain, although somewhat sheltered by the rocky crests on either side. Annual rainfall 1105 mm. (Oxford Atlas). Receives some sea-spray and much sea mist. Golding & Stodhart (1952) estimated long-term annual average wind speed at 10.7 m/sec.

Common land, administered by National Trust.

AREA SAMPLED 40 x 25 m, containing 497 mounds, i.e. a density of 4970/ha.

VEGETATION HISTORY Neolithic monuments occur on Rhossili Down. Site probably grazed by commoners' sheep and cattle for more than 400 years. Pteridium has spread on the Down in the last 50 years (anecdotal evidence).

SOIL DETAILS Parent material is Upper Old Red Sandstone (Devonian) - quartz and red conglomerates. Site drainage good; in wet weather water runs away in a flush at the base of the site. Detailed descriptions of one ant-hill and one soil profile made 24th June 1970. The soil under the sward was 15-20 cm. deep, highly podsolised, with an A₀ horizon of 4 cm. of mor humus, a mean pH of 4.4, no earthworms, quartz stones which increased in size and density down the profile, and MnO₂ granules in the B₂ horizon.

The ant-hill soil showed secondary podsolization; i.e. curved eluvial and illuvial horizons were developing in the mound. That leaching of bases from the surface was occurring was confirmed by pH measurements of successive horizons: A₁ 4.425, A₂ 4.6, A₃ 4.9 B₁ (at level of A₀ in surrounding soil).

5.1 (All pH measurements made in duplicate on a 1:2.5 ratio by weight of dry soil to distilled water using a Pye bench glass electrode pH meter). A₀ horizon absent. Stoneless. Ratio of space to solid reached 10-20%, because of ant chambers and channels, which were present even in the B₂ horizon.

PRESENT VEGETATION Described in text, section 2.3. Inflorescences of Anthoxanthum and Luzula frequent in sward. Nardus stricta and Sieglingia decumbens probably under-recorded.

Ant-hills all "mature"; no "incipient" mounds were found. Aira praecox frequent, Thymus drucei and Sedum anglicum locally frequent, on mounds. Tops of ant-hills dominated by Polytrichum juniperinum and P. piliferum.

Site appeared over-grazed in winter, but in summer, grazing did not keep pace with vegetative growth. Grazed mainly by sheep (droppings abundant), partly by cows, horses, rabbits and hares.

APPENDIX 9.

North side of Rhossili Down, March-April 1968. Percentage covers of all species recorded on 20 random ant-hills and 16 random in² surrounding vegetation quadrats, using 120 point quadrats per sample.

	ANT-HILLS																				SURROUNDING VEGETATION QUADRATS																χ^2 (1)	† SIG
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16		
<i>Agrostis tenuis</i>	29	60	79	78	33	45	25	72	39	77	28	33	52	55	42	61	38	45	42	74	67	68	85	92	79	62	78	83	68	61	68	57	68	81	61	42	167.0	**
<i>Anthoxanthum odoratum</i>	2	15	1	7			1	7		2			2	2	2	2	2		2		2	19	5	5	6	2	29	3	28	31	24	11	12	8	18	14	209.6	**
<i>Festuca ovina</i>	44	45	22	37	46	19	65	26	50	18	27	30	26	39	27	52	77	54	31	30	77	24	22	27	27	38	19	23	17	37	40	42	52	47	38	61	0.35	NS
<i>Galium saxatile</i>	5		8	10	2	12	1	7	7	9	9	27	8	9	29	17	13	17	21	6	5	18	7	7	6	12	7	4	2	17	5	26	16	7	1	22	1.17	NS
<i>Juncus</i>																																						
<i>campestris</i>				2		1							1	1								6	3	10	7	7	4	5	9	7		27	6	2	21	161.0	**	
<i>Potentilla erecta</i>																											2			2	1	6	2		6	27.6	**	
<i>Rumex acetosella</i>			8	14		4		7		7					1	1	7				1					1	5	1	1	3		2	2	2	3	1	6.5	*
<i>Veronica officinalis</i>				7			1						8		1															1	1		2					
<i>Dicranum scoparium</i>	1		2			27				1			2	6	12					32	3				4									2	53.4	**		
<i>Hypnum cupressiforme</i>	3						2	2			4		1	5		2	2	2	1	4	2					1	2		1	1				1	9.1	**		
<i>Pleurozium schreberi</i>	10		19	4		17	7	5	2	3	11	54	29	39	13	14	22	3	6		7	8	6	7	7	57	1	7	4	20	6	14	5	1	4	11	7.4	**
<i>Pohlia nutans</i>		1		2			2								2	1																					6.4	*
<i>Polytrichum juniperinum</i>	25	5	22		62	16	15	1	22	17	72	14	19	15	8	23	22	2	32	19							5			2							418.6	**
<i>P. piliferum</i>	5	17	2			11	31	21	32		3	29	32	13	22	15	6	20	26	12							2										306.4	**
<i>Pseudoscleropodium purum</i>																5					1							5	2	1								
<i>Ptilidium ciliare</i>									1																								1					
<i>Rhytidiadelphus squarrosus</i>		10	7				2	2	10	38		1	14	2	2	3			7		7	4	2		3	4	2	3	3	3	2	2	1	4		3	11.0	**
<i>Lichen (Peltigera sp.)</i>	2					1	2										2																					

EXTRA species

Carex pilulifera AH4(6%), AH11(1%)

Erica cinerea AH1(51%), AH17(1%)

Polytrichum formosum AH5(1%), AH13(2%)

Serratodon maritimus AH5(1%), AH7(4%), AH8(7%)

Gladonia sp. AH15(2%), AH18(2%)

Sedum anglicum AH20(1%)

Linum affine AH9(2%)

Oxalis acetosella SV11(1%), Unknown moss SV12 (1%)

Plantago lanceolata SV5(1%), SV11(1%)

Pteridium aquilinum SV5(1%)

Saxifraga decumbens SV3(2%), SV11(1%)

Vaccinium myrtillus SV16(3%)

† For each species the point-quadrat data were pooled for (a) ant-hill samples (b) point-quadrat samples. Using these data, the independence of the area sampled and species frequency was tested in a 2 x 2 contingency table. Significance tests were two-tailed. *0.05 > P > 0.01, **P < 0.01.

APPENDIX 10. Scratchbury and Cotley Hills, Wiltshire.

Comparison of ant-hill (AH) and surrounding vegetation (SV)

O.S. GRID REFERENCE ST 915437

SITE VISITED ON 12th July and 23rd August 1969

SITE POSITION I climbed the bridleway beginning at ST 917430; just past the second tumulus along the path (ST 916436) I turned left and descended the hill. The site was half-way down the slope to the railway line.

Site is at 145 m., sloping 15° to the south-west. Exposed.

Owned by Ministry of Defence, and leased to tenant at South Farm, Norton Bavant. S.S.S.I.

AREA SAMPLED 20 x 40 m., containing an estimated 150 mounds, i.e. a density of 1875/ha.

VEGETATION HISTORY O.S. 1/2500 edition (surveyed 1886) shows site as grassland. Probably too steep to have been ploughed.

SOIL DETAILS Parent material Middle Chalk (Cretaceous). Junction with Upper Chalk is upslope, nearby. Soil was a dark brown earth with very occasional chalk fragments and no A₀ horizon. Chalk rubble was encountered at 17 cm. depth.

PRESSENT VEGETATION.

Only "mature" AH present. Thymus (mainly on south-facing sides) and Lotus were abundant on the mounds, Arenaria and Cerastium were frequent.

Grazed by mature cows. But grazing pressure slight, and droppings scarce. No signs of rabbits.

RESULTS are overleaf, continued below. The methods and symbols used are described in Appendix 3. The numbers in the table are subjectively-estimated percentage covers of all species in 8 randomised blocks, each consisting of a randomly-selected AH and a 0.25 m² quadrat placed 0.3 m away from it, in a random direction, in the SV.

ADDITIONAL SPECIES

Arenaria serpyllifolia AH6(1%), 7(1%)
Cerastium holosteoides AH5 (2%), 7(1%), 8(1%)
Gentianella amarella AH1(1%), 2(2%), 4(1%)
Viola hirta AH6(1%)

Asperula cynanchica AH6(1%), 7(1%). SV1(1%)
Campanula clonata AH5(6%). SV2(2%), 5(2%)
Holcus lanatus AH1(1%). SV3(1%)
Scabiosa columbaria AH2(1%). SV1(1%), 2(1%)

Camptothecium lutescens SV7(1%)
Carlina vulgaris SV2(2%)
Gynadenia conopsea SV1(2%), 2(2%), 5(1%)
Leontodon autumnalis SV8(1%)
Medicago lupulina SV3(4%), 8(1%)
Picris hieracioides SV6(4%)
Roa trivialis SV4(1%)
Primula veris SV3(4%), 6(4%)
Ranunculus acris SV4(1%)
Succisa pratensis SV2(1%), 6(3%), 7(1%)

	AH								SV								SIG	
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8		
Mean AH Ht. (cm)	25	27	24	30	28	38	38	23										
Mean AH Diam. (cm)	49	42	69	65	44	57	70	46										
AH Volume (10 ³ cm ³)	31	28	55	65	31	73	101	26										
Volume N.H.S. (corr.) (cm ³)	16	6	5	20		7	30	5										
Activity (%)	.1	+	+	+	0	+	+	+										
Animal Activity			CT												CT			
Vegetation Ht. (cm.)	2	3	4	2	2	3	2	1	5	9	8	6	6	5	7	4		
% cover Bare Soil	15	10	15	30	4	4	10	10			5			4				
<i>Agrostis stolonifera</i>	2			1	1	1						1	2			1	NSB	
<i>Eriosa media</i>		3		1														
<i>Campanula rotundifolia</i>		1	2	1		2	1	1	1			1		2		1	NSB	
<i>Carex caryophyllacea</i>	4	3	1		2	2		1	2	2						3	NSW	
<i>Carex flacca</i>	1	5			5				25	13	27	20	15	20	25	23	**W	
<i>Centaurea nigra</i>	2								8	5	10	7	4		5	5	*W	
<i>Cirsium acaule</i>									25	30	12	7	20	10	4	12	**NT	
<i>Cynosurus cristatus</i>	4			4				1						4		3		
<i>Dactylis glomerata</i>	3		2					1	4	5	5	4	3	4	3	4	**W	
<i>Daucus carota</i>		2			1	1							1		1	1		
<i>Euphrasia officinalis</i>																		
agg.	1	1	1			1	1	1		1		1		1		1	NSB	
<i>Festuca</i> spp.	60	65	75	55	60	75	65	75	70	70	65	70	55	65	60	70	NST	
<i>Galium verum</i>			2		10		1	1			1		5				NST	
<i>Helianthemum chamaecistus</i>	2	7	6	13	1	7	23	8	2	2	2	1	5		1	2	*WT	
<i>Heliotrichon pratense</i>	2	2	1	4		1		1	4	12	8	4	2	5	6	4	*W	
<i>Heliotrichon pubescens</i>	2								1	3						1		
<i>Hiera cium pilosella</i>				5			1	1			4	9	4	4	4	2	*W	
<i>Hippocrepis comosa</i>	4				10	1			9	2	6	2			2	5	NST	
<i>Hypochoeris radicata</i>	2				2			2			4	2	4	4	2	2	*W	
<i>Koeleria cristata</i>	2	1	1		2	2	1	2	2	3	2		2	4	2	3	*T	
<i>Leontodon (hispida)</i>	2		2		2	1			9	8	2	4	10	13	9	9	*W	
<i>Leucanthemum vulgare</i>	2	2	2			1						1			3	1	NSB	
<i>Linum catharticum</i>	1		1	1					1	1	1	1	1	1		1	NSB	
<i>Lolium perenne</i>		1							2	3	1							
<i>Lotus corniculatus</i>	60	25	17	2	12	25			12	12		8	4	4	4	9	NST	
<i>Pastinaca sativa</i>		1							1	1	1	1					NSB	
<i>Pimpinella saxifraga</i>	1		2			2		1							1	1	1	NSB
<i>Plantago lanceolata</i>	1	3	1	3	3	1		1	10	7	6	7	15	30	13	10	**W	
<i>Plantago media</i>	4	9	4	2	3	2	1		12	9	9	7	6	7	16	11	*W	
<i>Poterium sanguisorba</i>									4	5	5	12	6	14	4	5	**NT	
<i>Prunella vulgaris</i>		3		7					2				3	1	1		NSW	
<i>Senecio jacobaea</i>	2	1	2						2			5			2	1	NSW	
<i>Thymus drucei</i>		25	13	23	2	16	25	20	2	3	3	2			3	1	*W	
<i>Trifolium pratense</i>									1	4	1			5	4	3	*W	
<i>Trifolium repens</i>		2									3			3		2		
<i>Zerna erecta</i>						2	8		4				10		1			
<i>Pseudoscleropodium purum</i>								8				2	1		6			

NSB species are on previous page.

APPENDIX 11. West Hill, Wiltshire.

Comparison of ant-hill and surrounding vegetation.

O.S. GRID REFERENCE SU014357

SITE VISITED ON 15th July and 25th August 1969.

SITE POSITION I left the road from Wylve to Dinton at SU007351 and moved eastwards along the track beside Grovely Wood. At about SU014350 I turned north and walked down the valley, along a field margin, towards "Church end Ring". I reached a scrubby field with a fence across its southern edge. The site was about 150 m. north of this fence, in the narrowest part of the field, above the footpath.

Site was at 157 m., sloping 20° to 20° north of east. Sheltered to the north and south by tall bushes of Viburnum and Crataegus, with Lonicera.

AREA SAMPLED 25 x 20 m., containing about 60 mounds, i.e. a density of about 1200/ha.

VEGETATION HISTORY O.S. 1/2500 edition (surveyed 1886) shows site as grassland. Probably never ploughed.

SOIL DETAILS Parent material is Upper Chalk (soft, with flints) (Cretaceous). No A₀ horizon. Rich brown earth to 17 cm., when chalk rubble encountered.

PRESENT VEGETATION.

Typical chalk grassland sward; Cirsium acaule, Carex flacca, Plantago media abundant, and inflorescences of Plantago lanceolata, Euphrasia, Scabiosa and Succisa prominent.

Most AH large, several massive. Several incipient mounds seen in shorter vegetation. All flora dominated by closely-grazed Festuca sp. with much Thymus and Helianthemum. Many mounds on or near the site covered with dead and decaying Festuca.

Fairly heavily grazed by bullocks. 6 rabbits were seen and rabbit droppings, burrows and scrapes were frequent on the mounds.

RESULTS are overleaf, continued below. The methods and symbols used are described in Appendix 3. The numbers in the table are subjectively-estimated percentage covers of all species in 8 randomised blocks, each consisting of a randomly-selected AH and a 0.25 m² quadrat placed 0.5m. away from it, in a random direction, in the SV.

EXTRA species (continued)

Plantago major AH1(2%)

Veronica arvensis AH7(1%)

Heissia crispa AH1(1%)

Agrostis stolonifera AH6(1%). SV7(1%)

Dactylis glomerata AH5(1%). SV7(5%)

Gentianella amarella AH1(1%). SV1(1%), 3(1%)

Scabiosa columbaria AH1(2%). SV1(1%), 8(1%)

Fissidens adiantoides AH1(1%). SV7(1%)

Lolium perenne SV1(1%)

Quercus robur SV2(1%)

Pastinaca sativa SV1(1%), 5(1%), 8(1%)

Ranunculus acris SV3(2%)

Rhytidadelphus squarrosus SV3(3%)
8(1%)

Veronica chamaedrys SV3(1%)

	AH								SV								SIG
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Mean AH Ht. (cm)	30	27	33	37	25	37	32	32									
Mean AH Diam. (cm)	57	44	64	103	62	87	68	43									
AH Volume (10 ³ cm ³)	53	31	71	177	47	133	75	36									
Volume N.H.S. (corr.) (cm ³)	30	19	27	59	51	27	55	19									
Activity (%)	+	+	+	+	.1	+	+	+									
Animal Activity																	
Vegetation Ht. (cm)	1	1	2	1	2	1	1	1	5	6	4	7	4	7	3	8	
% cover Bare Soil	8	4	15	15	12	10	15	7				3					
Asperula cynanchica	2	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	NSNT
Briza media			1			1		1			3	4	6	5	5	8	*W
Campanula rotundifolia	1	1	1	2	2	2	4	3	1	1	1	2	1	1	1	1	NST
Carex caryophylla	2		1		1			2	5	2	3	2	2	6	2	5	**W
Carex flacca								12	12	9	16	5	17	6	13	**W	
Cirsium acaule								25	10	3	5	8	6	10	11	**W	
Daucus carota											1	2	1			1	NSB
Euphrasia nemorosa	1		1	1	1	1		2	1	3				1	2	1	NSB
Festuca spp.	60	75	65	70	65	75	65	65	80	75	70	65	70	55	60	60	NST
Galium mollugo	7		4			4	10	4	3	2	2			2	2		NST
Helianthemum chamaecistus	25	13	17	20	19	5	15	5	4	4	4	5	3	5	5	1	*W
Helictotrichon pratense	3		1	1	2	1	1	5	3	5	4	3	4	4	1	1	NST
Hieracium pilosella	1			1				2	1					3	1		NSB
Hippocrepis comosa					1			10	9	10	4	10	2	10	7	**W	
Koeleria cristata	2		2	3	14	1	1	2	3	4	4	4	3	3	2	4	NST
Leontodon hispidus	2		2	2	2	1		3	3	6	6	6	10	8	7	6	**W
Leucanthemum vulgare	1					1	1	1	1	1	2	1		3	1	2	NSB
Linum catharticum	1	1		1	1	1		1	1	1	1	1	1			1	NSNT
Lotus corniculatus		12						15	5		4	2	4	2	4		NST
Pimpinella saxifraga	1		1					1	1	1	1	1	1	1	1	1	NSB
Plantago lanceolata	2	3		1	2		1	2	7	10	11	12	6	4	4	9	**W
Plantago media	1	1						4	10	10	10	3	17	8	4	**W	
Polygala vulgaris								2		1	1	2		1	1	*B	
Poterium sanguisorba								6	9	4	11	12	12	3	5	**NT	
Prunella vulgaris			1	1		1		3	2	1	2	1		1	2	*T	
Senecio jacobaea	2					1		2				1	3	2			
Serratula tinctoria								2	4	2	8	4	3	3	8	**W	
Succisa pratensis			1					10	4		2	11	16	12	4	*W	
Thymus drucei	40	28	14	55	38	20	22	32	5	3	3	3	2	5	2	3	**W
Pseudoscleropodium purum	5	5	15	2			15	4	15	10	5	20	7				NSNT

ADDITIONAL species (continued on previous page)

<u>Arenaria serpyllifolia</u> AH4(1%), 8(1%)	<u>Acrocladium cuspidatum</u> SV2(1%)
<u>Campothecium lutescens</u> AH6(1%), 8(4%)	<u>Amblystegium serpens</u> SV1 (1%)
<u>Cerastium holostaeoides</u> AH4(1%)	<u>Brachythecium rutabulum</u> SV8(1%)
<u>Fissidens taxifolius</u> AH8(1%)	<u>Bryum capillare</u> SV1(1%)
<u>Fragaria vesca</u> AH8(1%)	<u>Carlina vulgaris</u> SV1(2%), 2(1%), 7(3%)
<u>Holcus lanatus</u> AH4(1%), 6(1%), 7(2%)	<u>Cynosurus cristatus</u> SV2(1%)
<u>Picris hieracioides</u> AH1 (2%)	<u>Helictotrichon rubescens</u> SV2(7%), 4(1%), 6(2%)
<u>Pottia lanceolata</u> AH1(1%)	<u>Hymenochaeria radicata</u> SV2(1%)

APPENDIX 12. Camp Down, Wiltshire.

Comparison of ant-hill (AH) and surrounding vegetation (SV)

O.S. GRID REFERENCE SU 118558

SITE VISITED ON 14th July, and 25th August, 1969

SITE POSITION I left the road which descends Camp Down half-way between the bends at SU 116359 and SU 118559, and climbed the north-facing slope of the Down. The site was about 50 m. above the road.

Site is at 92 m, sloping 20-25° towards 10° west of north. Exposed, but with some scattered bushes of Juniperus, Crataegus and Rosa up to 3m.

Owned by Earl of Chichester, S.S.S.I.

AREA SAMPLED 25 x 25 m., containing about 80 mounds, i.e. a density of 1280/ha

VEGETATION HISTORY O.S. 1/2500 edition (1877-9) shows site as arable land.

SOIL DETAILS Parent material is Upper chalk (soft, with flints) (Cretaceous). No A₀ horizon. Rich brown earth to 17 cm, when chalk rubble encountered.

PRESENT VEGETATION

Galium verum very abundant both on the AHs and in the SV. Grazed by cattle, mainly in winter, for several years. Rabbit droppings abundant on mounds. Mole-hills present.

RESULTS are overleaf, continued below. The methods and symbols used are described in Appendix 3. The numbers in the table are subjectively-estimated percentage covers of all species in 8 randomised blocks, each consisting of a randomly-selected AH and a 0.25 m² quadrat placed 0.3 m. away from it, in a random direction, in the SV.

ADDITIONAL species

Phleum bertolonii AH4(1%)
Scabiosa columbaria AH5(3%)
Achillea millefolium AH2(2%), SV3(5%), SV7(2%)
Crenis capillaris AH2(1%), SV2(4%), 4(1%).
Hippocrepis comosa AH5(45%), SV7(15%)
Trisetum flavescens AH2(5%), 4(5%), SV2(2%)
Poa pratensis SV1(1%)
Polygala vulgaris SV7(1%)
Pseudoscleropodium purum SV7(2%), 8(4%)
Rosa sp. SV5(1%)

Acrocladium cuspidatum SV7(15%), 8(1%)
Alopecurus pratensis SV5(2%)
Anthyllis vulneraria SV5(2%), 4(4%)
Brachythecium rutabulum SV8(1%)
Centaurea scabiosa SV6(4%)
Cirsium arvense SV2(13%)
Fissidens adianthoides SV7(1%), 8(4%)
Fissidens taxifolius SV6(1%)
Filipendula vulgaris SV1(2%), 2(1%),
3(2%)
Gentianella amarella SV7(1%)
Geranium molle SV1(1%), 2(1%)
Lolium perenne SV1(1%)
Plantago major SV6(1%)

	AH								SV								SIG
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Mean AH Ht. (cm)	32	52	35	25	17	19	52	19									
Mean AH Diam. (cm)	74	71	78	62	32	35	65	36									
AH Volume (10 ³ cm ³)	85	81	105	46	9	15	69	15									
Volume N.H.S. (corr.) (cm ³)	27	51	51	19	19	51	43	74									
Activity (%)	+	.1	+	+	.2	.4	+	.6									
Animal Activity							RD										
Vegetation Ht. (cm)	5	5	4	5	3	3	4	5	4	7	6	6	4	12	7	8	
% cover Bare Soil	10	15	15	17	5	20	10	25	5		5		7	5			
<i>Agrostis stolonifera</i>	1	1		2		1		1	4	2	3		4	1			NST
<i>Arrhenatherum elatius</i>		5								4	2		5				
<i>Briza media</i>							1			1	1	1	2	1		1	NSB
<i>Campanula rotundifolia</i>		1	1				1		1			1	1		1	1	NSB
<i>Carex caryophylla</i>						1	1				2			1	2	1	NSB
<i>Carex flacca</i>					1	2	1	2	15	5	8	8	10	7	10	9	**W
<i>Cirsium acaule</i>								2			5	2	15	5	16	50	*W
<i>Cynosurus cristatus</i>								2	2	2	2	5	7	6	4	3	**W
<i>Dactylis glomerata</i>		2	1	1				5	9	4	4					5	**T
<i>Daucus carota</i>						1		1	4	5	5	2	11	3	5	5	**W
<i>Euphrasia nemorosa</i>			1			1	1	1			1	10	2	1	1	2	NST
<i>Festuca ovina</i> & <i>F. rubra</i>	85	70	75	85	75	70	75	50	70	65	75	50	50	60	65	60	NST
<i>Galium mollugo</i>		2				1				1				2	1		
<i>Galium verum</i>		55	15	5	10	7	10	4		15	4	6		15	8		NST
<i>Helianthemum chamaecistus</i>					5			27					2			1	
<i>Helictotrichon pratense</i>						5	1	4	1	1	4	5	8	4	9	14	**W
<i>Helictotrichon pubescens</i>							1		1		1			5			
<i>Hieracium pilosella</i>					2								5	2	4	3	*T
<i>Holcus lanatus</i>	1		4	6		1				2		1		2		1	NSNT
<i>Koeleria cristata</i>		5	1		2	5	4	5	4	2	5	6	2	4	4	1	NST
<i>Leontodon hispidus</i>	1	1	2		5	1	2	5	12	10	8	22	2	14	5	5	*W
<i>Leucanthemum vulgare</i>								1	2					2	1		
<i>Linum catharticum</i>	1		1	1		2	1	1	2	1	1	1	1	1	1	2	NSB
<i>Ltus corniculatus</i>					2	1	10	2	1		4	4		10	5	6	NSW
<i>Medicago lupulina</i>	1	1	4			5	5	5	2	8	1	1		3		2	NSW
<i>Pastinaca sativa</i>		2						2	1	1	1				1		NSB
<i>Pimpinella saxifraga</i>						1		4			1				2	2	NST
<i>Plantago lanceolata</i>	1	2	2	1	5	9	1	2	6	8	8	7	5	19	10	11	**W
<i>Plantago media</i>	1	2	1	2	7		2	2	10	8	11		5	16	4	9	*W
<i>Poterium sanguisorba</i>								5	9	8	4	12	13	14	8		**NT
<i>Prunella vulgaris</i>	1	5	2	2		1	5	1	7	8	5	2	2				NSW
<i>Ranunculus acris</i>										1	2	1	1		1	1	*B
<i>Senecio jacobaea</i>		4	4		4		2		2	2	7	6	2			5	NSW
<i>Succisa pratensis</i>									9	6	4	6	8	7	8	7	**NT
<i>Thymus drucei</i>	50				5		12	2									NST
<i>Trifolium pratense</i>					1	2				1	2	2	2	8	2	5	**W
<i>Trifolium repens</i>				5					6	5	5	6	6				*T
<i>Veronica arvensis</i>	1	2	1	1													NSB
<i>Zerna erecta</i>									4	2	2	2	9		2	16	*W

EXTRA species are on previous page.

APPENDIX 13. Stockton Down, Wiltshire.

Comparison of ant-hill (AH) and surrounding vegetation (SV)

O.S. GRID REFERENCE ST 960370

SITE VISITED ON 12th July and 25rd August 1969

SITE POSITION I took the metalled road from Park Bottom to Stockton Earthworks, leaving it, to the right, where the 500 ft. contour crosses it on the map. I crossed tall vegetation (abundant Cirsium arvense) for about 40 m, and found ant-hills on a ncient earthworks amongst Juniperus scrub.

Site is at 152 m., sloping 2° to the north-east. Sheltered by Juniperus scrub to one side, and a hill to the south west.

Owned by M. Stratton, Codford St. Mary, Wilts. S.S.S.I.

AREA SAMPLED 75 x 25 m., containing about 250 mounds, i.e. a density of 1533/ha.

VEGETATION HISTORY O.S. 1/2500 edition (surveyed 1886) shows site as grassland. Some of the scrub probably grew up after myxomatosis decimated the rabbit population in 1954.

SOIL DETAILS

Parent material is Upper Chalk (soft, with flints) (Cretaceous). Rich brown earth about 18 cm. deep.

PRESENT VEGETATION

SV 12-18 cm. high, with inflorescences of Poterium Scabiosa, Pimpinella and Gymnadenia common, and tufts of Carex humilis prominent. Near Juniperus bushes the vegetation was less species-rich, dominated by Xerna, Helictotrichon pratense, Carex flacca and Poterium, with some Brachypodium sylvaticum.

Some mounds were exceptionally large; rare incipient AHs occurred in the shorter vegetation.

Normally ungrazed, except by rabbits, whose recent dunging patches occurred on some mounds. However, in spring 1969 the site was grazed by cattle and sheep. Four times as many orchids had appeared as usual (local farmland, pers. com.). Molehills present.

RESULTS are overleaf, continued below. The methods and symbols used are described in Appendix 3. The numbers in the table are subjectively-estimated percentage covers of all species in 8 randomized blocks, each consisting of an AH (the nearest to a random point) and a 0.25 m² quadrat placed 0.5 m. away from it, in a random direction, in the SV.

EXTRA species (continued)

Euphrasia nemorosa AH6(1%). SV4(2%), 6(1%).

Senecio jacobaea AH5(1%). SV8(3%)

Gymnadenia conopsea SV4(1%), 6(1%)

Primula veris SV5(5%), 8(9%)

Succisa pratensis SV8(7%)

Viola hirta SV6(3%)

	AH								SV								SIG
Mean AH Ht. (cm)	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Mean AH Diam. (cm)	32	16	27	35	28	17	28	28									
AH Volume	67	38	74	67	72	55	57	60									
(10 ³ cm ³)																	
Volume N.H.S.	74	11	70	85	67	21	48	50									
(corr.) (cm ³)	74	106	0	16	16	22	16	16									
Activity (%)	.1	1	0	+	+	.1	+	+									
Vegetation Ht. (cm)	3	3	4	2	6	1	5	7	12	18	14	13	20	15	12	20	
% cover Bare Soil	10	70	14	6	4	10	3	3									
<i>Achillea</i>																	
<i>millefolium</i>											3	1	8	1			NST
<i>Brisa media</i>		2						1			1		2				
<i>Campanula</i>																	
<i>rotundifolia</i>	1	2	1	2	1	1		1	1	1	1	1	1		1		NSB
<i>Carex caryophylla</i>		2						4			3		3				
<i>Carex flacca</i>	1	2			2			10	9	10	9	15	20	12	7		**W
<i>Carex humilis</i>	3	3		4		6	3	3	24	40	20	12	40	55			*W
<i>Cirsium acaule</i>									21	10	4	42	4	26	3	2	**W
<i>Dactylis glomerata</i>					4			2			1			2		3	
<i>Daucus carota</i>	1							1	1		1			1			
<i>Festuca sp.</i>	60	17	70	70	85	50	95	80	40	75	90	80	70	30	70	50	NST
<i>Filipendula</i>																	
<i>vulgaris</i>								1	2		2	3	5	1	3	1	*W
<i>Galium verum</i>	1		2	1	2			1			2						NSB
<i>Helictotrichon</i>																	
<i>pratense</i>	4	1	1	2	1		2	6	9	7	7	8	4	7	14	70	**W
<i>Helictotrichon</i>																	
<i>pubescens</i>	1		1		1			1	2			3	5	1		5	NST
<i>Hieracium pilosella</i>	1					1					3	3		3			
<i>Hippocrepis comosa</i>		1		1						2	2	4		7	2		*T
<i>Koeleria cristata</i>	10	9	7	17	6	7	4		5								**W
<i>Leontodon (hispidus)</i>	3				2				5	16	11	12	2	12	10	3	*W
<i>Leucanthemum</i>																	
<i>vulgare</i>			3	2	2	2		4		16	3			3	3	1	NST
<i>Idem catharticum</i>	1	1	1	1	1	1		1		1	1			1		1	NSB
<i>Lotus corniculatus</i>	10	2	3		2	1		1	3	3	16	6	3	3	11	2	NST
<i>Pastinaca sativa</i>	1		1					1			1	1					
<i>Pimpinella</i>																	
<i>saxifraga</i>	2			1				2	2		1	2		3	1	2	NST
<i>Plantago</i>																	
<i>lanceolata</i>	4			1	3	2	1	6	19	10	3	8		8	3	3	NST
<i>Plantago media</i>	2								8		7	9		10	6		*T
<i>Polygala vulgaris</i>								2	1	1	1			1			NSB
<i>Poterium</i>																	
<i>sanguisorba</i>								1	15		8	8	25	3	25	20	*W
<i>Prunella vulgaris</i>			1								1				1		
<i>Scabiosa</i>																	
<i>columbaria</i>	2							1	4		5	2					
<i>Thymus drucei</i>	1	2	2	35	6	50		20	1	1	1	1		3			*W
<i>Zerna erecta</i>									3					2	2	7	*T
<i>Pseudoscleropodium</i>																	
<i>purum</i>						14				5	15	20	5	2			NST

Additional species (continued on previous page)

Agrostis stolonifera AH5(5%), 5(2%)
Asperula cynanchica AH2(1%), 4(1%)
Centaurium erythraea AH4(1%)
Holcus lanatus AH5(14%)
Lolium perenne AH2(1%)
Veronica arvensis AH8(1%)

Acrocladium cuspidatum SV2(1%), 5(1%)
Brachypodium sylvaticum SV4(1%)
Campythecium lutescens SV2(1%), 5(7%)
Carlina vulgaris SV7(1%)
Coeloclossum viride SV2(1%), 4(1%), 6(1%)
Fissidens adiantoides SV4(1%)
Galium mollugo SV3(2%)

APPENDIX 14. White Sheet Downs, Wiltshire.

Comparison of ant-hill (AH) and surrounding vegetation (SV)

O.S. GRID REFERENCE ST 805555

SITE VISITED ON 11th July 1969

SITE POSITION Approached along unmetalled road from ST 825544; I walked off the road to the right at ST 805551, and found the site on the western side of a valley, 150 m. from the road.

Site is at 198 m, slopes 10-15° to 30° south of east.

AREA SAMPLED 40 x 25 m., containing about 200 AHs, i.e. a density of 2000/ha.

VEGETATION HISTORY O.S. 1/2500 edition (surveyed 1885-6) shows site as grassland.

SOIL DETAILS

Parent material is Middle Chalk (Cretaceous). Soil 25 cm. deep; 15 cm. of Brown Earth, with few chalk fragments, was underlain by 8 cm. of chalk rubble.

PRESENT VEGETATION.

AHs in this valley only seen on slopes facing SE-NE. No "incipient" mound seen. AHs had low soil heaping activity, but frequently dominated by *Thymus drucei*.

Site grazed by young bullocks; bare patches, due to their trampling, frequent in sward. One hare seen.

RESULTS are overleaf, continued below. The methods and symbols used are described in Appendix 3. The figures in the table are subjectively estimated percentage covers of all species in eight randomised blocks, each consisting of one AH (the nearest to a random point) and a 0.25² quadrat placed 0.5 m. away from it, in a random direction, in the SV.

EXTRA species (continued)

Polygonum bertolonii AH6(2%), 8(4%)

Trifolium dubium AH1(3%), 7(2%)

Veronica arvensis AH1(1%)

Festuca pratensis AH4(6%), SV4(5%)

Leucanthemum vulgare AH5(1%), SV2(2%)

Lasula caespiticia AH2(3%), SV1(3%), 8(1%)

Polygala vulgaris AH6(1%), SV7(2%)

Pseudoscleronodum purum AH5(7%), 6(2%), SV6(2%)

Scabiosa columbaria AH7(4%), SV4(4%), 5(4%)

Euphrasia nemorosa SV5(1%)

Hyssopus cuneusiformis SV5(1%)

Lonchoclea bidentata SV3(1%)

Polygonum pratense SV8(2%)

Plantago major SV2(7%), 8(2%)

Ranunculus bulbosus SV7(2%)

	AH								SV								SI
Mean AH Ht. (cm)	22	19	57	55	25	50	26	58									
Mean AH Diam. (cm)	65	54	75	62	74	72	75	75									
AH Volume (10 ³ cm ³)	45	25	105	68	57	74	67	115									
Volume N.H.S. (corr.) (cm ³)	51		15														
Activity (%)	+		+														
Animal Activity									TB						CT	CT	
Vegetation Ht. (cm)	4	3	4	4	5	5	5	5	5	5	4	5	5	2	5	2	
% cover Bare Soil	10		2	2		2	5	2							15	5	
<i>Agrostis stolonifera</i>	4			2	1	1			5							2	NST
<i>Asperula cynanchica</i>		1	2			15		5			5						NST
<i>Brisa media</i>		2		1	5					2	4		1			6	NST
<i>Campanula rotundifolia</i>		2	1			1	2										NST
<i>Carex caryophylla</i>	1					1	2		5	2	2	2		1	1		NST
<i>Carex flacca</i>				4					28	5	6	20	8	8	7		*W
<i>Cerastium holos- teoides</i>	4	4				1	2	1									*T
<i>Cynosurus cristatus</i>	5		6		9	4	5	5	5	5	5	7	10	5	8	20	*W
<i>Dactylis glomerata</i>	2		1	5	2		2		5	4	4	2	5	6			NST
<i>Festuca sp.</i>	80	80	80	80	85	70	50	70	60	20	60	70	45	55	50	75	*W
<i>Galium mollugo</i>			2	2	2				2		2						*W
<i>Galium verum</i>			5	6	6	5	8	7					5				*W
<i>Helianthemum chamaecistus</i>			10	6				2			2						
<i>Helictotrichon pratense</i>											5	5		5	2		*T
<i>Helictotrichon pubescens</i>		1			2			1				5	1	1			
<i>Hieracium pilosella</i>			4	5			1	2		7	5	2			4		NST
<i>Holcus lanatus</i>	5				4	5		5						5	1	10	NST
<i>Koeleria cristata</i>		2	2	4	4		2	2	2		5	5	2	5	5	2	NST
<i>Leontodon hispidus</i>			1			5			2	1			1	5			NST
<i>Linum catharticum</i>	2	4	1	1	1	1			2		1	1	1	1	1		NST
<i>Lotus corniculatus</i>	20	15	2	2	5	1		20	5	1	5			8	1		NST
<i>Medicago lupulina</i>	7	5			4	5		3		2							NST
<i>Plantago lanceolata</i>	6	10	1		4	4	5	2	25	12	4	7	20	7	12	2	*W
<i>Plantago media</i>		2		5	1				4	20		2	5			2	NST
<i>Poterium sanguisorba</i>				2	5		1	13	7	15	10	7	20	8			*W
<i>Prunella vulgaris</i>	5					2		8	4			2	4	5	5		*W
<i>Ranunculus acris</i>		2				1	1	1	6	1	2	2	1	2	1	1	NST
<i>Senecio jacobaea</i>	4		1	5		2		2	5		5	4	5	4	6		NST
<i>Succisa pratensis</i>		4			2			7	55						2		NST
<i>Thymus drucei</i>		15	30	35		30	75	40			15	5			1		*W
<i>Trifolium pratense</i>	2	4	2		4				7	5		7		5	5		NST
<i>Trifolium repens</i>	5	15			4				5	2	5		4	5		5	NST
<i>Trisetum flavescens</i>	2	2			2		2	1									NST
<i>Zerna erecta</i>	5	5			1				2								NST

Additional species (continued on previous page)

Arenaria serpyllifolia AH1 (15)

Crataegus monogyna AH5 (15)

Crenis capillaris AH2 (10)

Oenlis repens AH5 (10)

Callis perennis SV6 (15), 7 (2)

Camptothecium lutescens SV1 (7), 2 (2), 3 (2)

Cirsium acaule SV6 (12)

Daucus carota SV5 (15)

APPENDIX 15. Site near Brixton Deverill, Wiltshire.

Comparison of ant-hill (AH) and surrounding vegetation (SV)

O.S. GRID REFERENCE ST 857391

SITE VISITED ON 11th July and 22nd August 1969

SITE POSITION I took the track leading from Brixton Deverill (ST 865389) to Woodcombe Farm (ST 846392). The site was below the track, on the left, just past the first gate (at ST 858392).

Site is at 152 m., sloping 10-15° to the south.

AREA SAMPLED 55 x 40 m., containing about 300 mounds, i.e. a density of 2143/ha.

VEGETATION HISTORY O.S. 1/2500 edition (surveyed 1886) shows site as grassland.

SOIL DETAILS

Parent material is Middle Chalk (Cretaceous). Soil is a Brown Earth, 20 cm. deep, containing few chalk or flint fragments.

PRESENT VEGETATION

Some incipient AHs found. Cerastium, Euphrasia, Medicago, Thymus and Asterula seemed frequent on mature mounds.

Grazed by cows. Some AHs had been destroyed, probably by cattle lying.

RESULTS are overleaf, continued below. The methods and symbols used are described in Appendix 3. The figures in the table are subjectively estimated percentage covers of all species in eight randomised blocks, each consisting of one ant-hill (the nearest to a random point) and a 0.25 m² quadrat placed 0.5 m. away from it, in a random direction, in the surrounding vegetation.

EXTRA species (continued)

<u>Plantago major</u> AH7(8%), 8(5%), SV6(10%)	<u>Phleum pratense</u> SV6(1%)
<u>(Saxifraga granulata)</u> AH8(1%), SV7 (1%)	<u>Ranunculus bulbosus</u> SV3(1%)
<u>Helianthemum chamaecistus</u> AH8(15%), SV8(1%)	<u>Rhytidadelphus squarrosus</u> SV4(7%)
<u>Gemmaula rotundifolia</u> AH2(4%), 6(1%), 7(2%)	<u>Taraxacum officinale</u> agg. SV7(2%)
<u>Cerastium holosteoides</u> AH5(2%), 6(3%), 7(1%)	<u>Viola hirta</u> SV5(2%)
<u>Eca biosa columbaria</u> AH3(5%), 7(6%)	
<u>Trifolium dubium</u> AH2(2%), 5(2%)	
<u>Trisetum flavescens</u> AH5(4%), 6(3%), 8(2%)	
<u>Odontites verna</u> AH6(1%)	

	AH								SV								SIG
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Mean AH Ht. (cm)	22	21	16	17	24	33	29	27									
Mean AH Diam. (cm)	32	53	51	28	62	49	48	52									
AH Volume (10 ³ cm ³)	15	28	8	7	43	47	58	58									
Volume N.H.S. (corr.) (cm ³)	0	27	19	27	15	59	19	19									
Activity (%)	0	•1	•2	•4	+	1.1	+	+									
Animal Activity																	
Vegetation Ht. (cm)	4	2	3	3	2	3	3	2	4	5	6	6	5	15	7	8	
% cover Bare Soil	0	15	7	20	10	8	2	2			7	5	7	2	4	5	
<i>Agrostis stolonifera</i>	3					1	1	1	2	3						2	NSWT
<i>Asperula cynanchica</i>		5		27		4	5		2	1			3	1			NST
<i>Briza media</i>				4	3				3	1	2	2	2		1	1	NST
<i>Carex caryophylla</i>				5	2		2	2	2					5		1	NST
<i>Carex flacca</i>	2	1			5		2		18	17	17	15	7	6	22	12	**W
<i>Cirsium acaule</i>									5	8	8	13	6	20	2	10	**W
<i>Cynosurus cristatus</i>	3	4	1	2	5				3	8	8	5	6			2	NST
<i>Dactylis glomerata</i>			2		3	1	1	3	8	8	10	5	12	10	10	6	**W
<i>Daucus carota</i>		2	3					1	1								NSB
<i>Euphrasia</i> sp.	5	1	4	1	2	2	2	5	1	1		2	2		2	1	NST
<i>Festuca</i> sp.	70	70	30	20	60	70	60	50	50	30	20	40	30	40	40	35	*W
<i>Galium verum</i>					10	4	5	4		6			4	12	3		NSWT
<i>Helictotrichon</i> pratense			10	10			2	1	3				2		2		NST
<i>Holcus lanatus</i>	5		7		2	3			2	6						2	NST
<i>Hypochoeris radicata</i>									2	2	2		2				NSB
<i>Koeleria cristata</i>						1	1	2		2						2	
<i>Leontodon (hispidus)</i>	2				9		3	3	8	12	8	13	10	3	5	14	**W
<i>Leucanthemum vulgare</i>						3	7	3							4	3	
<i>Linum catharticum</i>	1	1	1	1	1	1	1	1		1	1	2	2	1	1	2	NSB
<i>Lolium perenne</i>	3	1	7	7	7	1	1	6	5	5	7	12	15	30	20	20	*W
<i>Lotus corniculatus</i>	60			12	5		25	1	7	4	7	10	5	10	9	2	NST
<i>Medicago lupulina</i>	2	1	7		6	1	2		3	2	3		4		3	1	NST
<i>Pastinaca sativa</i>			2	1	2		1										NSB
<i>Plantago lanceolata</i>	3	6	2	16	7	4		2	13	8	10	12	4	15	11	5	NST
<i>Plantago media</i>	5		8	2	5				5		6	6	4		8	5	NST
<i>Poterium sanguisorba</i>	1						1		15	15	10	4	10	15	14	15	**W
<i>Primella vulgaris</i>	10	2	32		5	1	5	4	4	5	7	5	4		4	3	NST
<i>Ranunculus acris</i>							1		2	3	5	2		3	1		*T
<i>Senecio jacobaea</i>		5			3				5	4	2	6	5				NST
<i>Succisa pratensis</i>	2						2		9	10	15	12	10	15	20	15	**W
<i>Thymus drucei</i>	10	6		6	8	50	13	65									**W
<i>Trifolium pratense</i>				2	4	4	3		3	2	8	3	9	6	10	4	**W
<i>Trifolium repens</i>					2				4	2	5	8	4				*T

Additional species (continued on previous page)

<i>Centaurea nigra</i> AH7(2%), SV7(3%), 8(6%)	<i>Campanula glomerata</i> SV7(5%), 8(2%)
<i>Galium mollugo</i> AH5(2%), SV8(1%)	<i>Oxypis capillaris</i> SV2(2%), 4(2%)
<i>Gentianella anarella</i> AH7(2%), SV7(2%), 8(3%)	<i>Primula veris</i> SV1(4%), 2(5%), 6(5%)
<i>Phleum bertolonii</i> AH1(5%), SV2(2%), 5(4%)	<i>Acrocladium cuspidatum</i> SV8 (1%)
<i>Pimpinella saxifraga</i> AH7(2%), 8(5%), SV3(2%)	<i>Luzula campestris</i> SV2(1%)

I visited Lullington Heath N.N.R. (O.S. Grid Reference TQ 544017) and Fore Down nearby in October 1971 to examine the ant-hills investigated by Grubb et al (1969) (abbreviated as GGM). The vegetation zones, and the sites which I sampled, are shown on the map below. Data from these three sites are given in Appendices 17, 18, and 19. Here I discuss some of GGM's methods, data, and conclusions, especially their section "plant life of the ant-hills" (GGM p. 200-4).

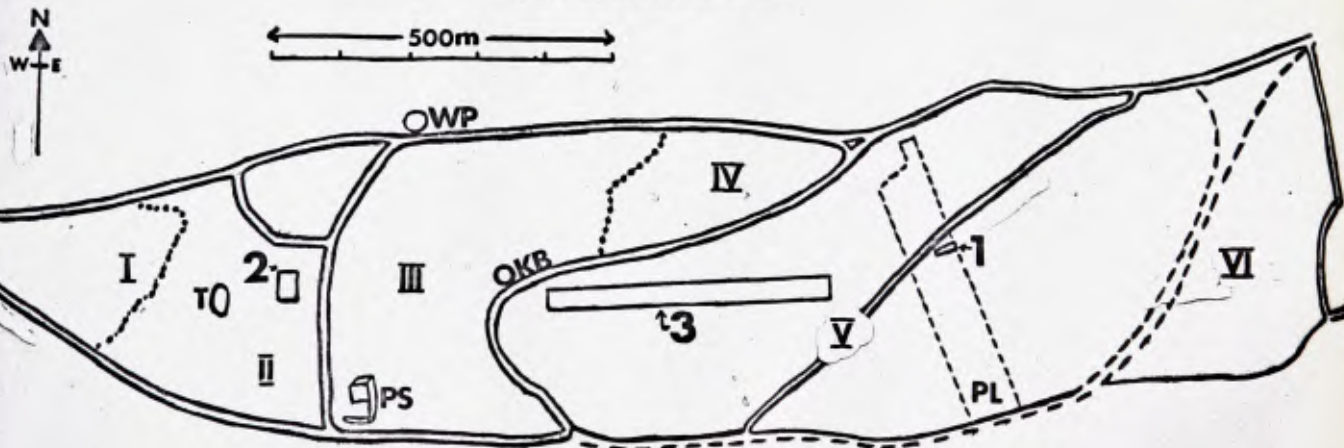
(i) GGM do not explain how their sampling units, the "tops of ant-hills", were delimited. GGM Table 7, p.201 shows that they found 9 species in Zone II on 8 active ant-hills (I found 20 species there on 7 active mounds), and in Zone V they found 16 species on 10 active mounds (I found 29 species on 8 occupied mounds at SITE 5). The discrepancy between their data and mine, may partly be due to GGM's smaller sampling area. For instance, Achillea, Filipendula and Poterium occur mainly on the sides of the mounds; I recorded them, but GGM did not.

(ii) GGM state (p.202) that Thymus spp and Asperula cynanchica characterise active ant-hills in Zones V and VI but do not understand their rarity on mounds in Zone II. However, one must distinguish (a) areas, near bomb-sites and furrows in Zones II, V and VI (e.g. SITE 1, SITE 5 Quadrats 6-8 in the following appendices) where Thymus is abundant both on the ant-hills and in the short turf nearby, from (b) tall chalk heath in Zones II and V, where Thymus is uncommon both on ant-hills and in the sward (see SITE 2 data, and SITE 3, quadrat 1-5). In this area, Thymus was probably common on and off the mounds before myxomatosis struck the rabbit population in 1954. Why does Festuca rubra dominate the mounds there now?

Festuca grows much less vigorously on shallower than deeper soils (e.g. on the bomb sites and soils of intermediate depth nearby). This may be because of its sensitivity to drought. Its poor growth enables a diverse vegetation to exist over shallow soils (see Appendices 17 and 19). Mounds there must be constantly invaded by Thymus from the sward. On the deeper, moister, loessic soils, however, a luxuriant growth of Festuca may have been possible after myxomatosis to form "tall chalk heath". This probably ameliorated the microclimate on the ant-hills, and allowed Festuca there to grow tall, ousting Thymus. Thymus would not be available in tall chalk heath to reinvade mounds or to colonise new ones.

GGM (p.202) also seem puzzled that Hieracium pilosella, Plantago lanceolata, Medicago lupulina and Euphrasia nemorosa are commoner on active mounds in "secondary grassland" (bomb hollows etc) than in tall chalk heath. These species are abundant in bomb hollows. Yet once Hieracium, Plantago and Medicago had been shaded out by

LULLINGTON HEATH



NUMBERS SHOW POSITIONS OF SAMPLED ANT-HILL SITES.

ROMAN NUMERALS SHOW ZONES OF GRUBB et al (1969)

OKB=OLD KILN BOTTOM

T=TUMULUS

PL=AREA PLOUGHED 1953

WP=POND

PS=PUMPING STATION

tall Feather in "chalk heath", and killed by soil-heaping on active mounds there, the constant invasion of propagules required to maintain their numbers on the mounds would no longer occur.

(141) GCM state (p.202) that ant-hills of the "secondary grassland" (Zone VI and bomb sites) tend to be smaller than those in tall "chalk heath" in Zones II and V, and mention that mounds on shallower soil may be slower-growing. This may be so; but the hills in the "secondary grassland" all have a recent origin, since Zone VI was ploughed up to 1919 and the bomb-hollows in Zones II, V and VI were formed in the Second World War.

APPENDIX 17.

Islington Heath, Sussex. Site 1

Comparison of ant-hill (AH) and surrounding vegetation (SV)

O.S. GRID REFERENCE TQ 546017

SITE VISITED ON 21st to 23rd October 1971

SITE POSITION See map in Appendix 16. Half-way along ride from TQ548018 to TQ 544014, on south side. Furrowed area of tall chalk heath, notched into Ulex scrub, which surrounds it on three sides.

Site is at 154 m. and $\pm$ level.

Owned by Eastbourne Water Board, let to Forestry Commission, sublet to Nature Conservancy.

AREA SAMPLED 35 x 10 m., placed across ridges and furrows at right angles, containing about 120 AHs, i.e. a density of 3429/ha.

VEGETATION HISTORY

The site was uncultivated in 1785, 1845 and 1878 (maps) and was probably chalk heath closely grazed by rabbits and sheep. It was ploughed by the Forestry Commission in 1955 but trees were never put in. Furrows up to 0.5 m. wide run between "ridges" about 1m. wide. Rabbit grazing present, but negligible.

SOIL DETAILS

Parent material is Upper Chalk (Upper Cretaceous). Perrin (1956) suggested that there had been considerable loess deposition in the area in the Pleistocene.

In the furrows a dark brown silty loam with peds <3 mm. overlies chalk rubble, which becomes very dense at 5-7 cm. depth but occurs to 15-17 cm. Flints are frequent on the surface, and chalk stones up to 3 cm. long are distributed throughout the profile. An Ao horizon is absent.

On the ridges a structureless clay loam 15-16 cm. deep overlies impenetrable chalk rubble. Flints are almost absent from the surface, and very occasional stones, up to 2 cm. long, occur in the profile. A patchy Ao horizon up to 1.5 cm. (10 determinations) is present.

PRESENT VEGETATION

The furrows have a short (1-2 cm.) vegetation with depauperate Hieracium pillosella (about 70% cover), Festuca, Plantago, Poterium and Viola riviniana. Himantoglossis comosa, Thymus drucei, Medicago lupulina, Bellis, Anthyllis vulneraria, Carex flacca, Hymenocorys, Camptothecium lutescens, Fissidens tardifolius, Cladonia rangiferina, Bryum capillare, Weissia (controversa), Parhelia (convoluta), Euphrasia nemorosa, Linum catharticum, Cremis capillaris, and Arenaria serpyllifolia were also frequent there.

The ridge vegetation is dominated by tall (25-30 cm. high) Festuca rubra with abundant Poterium and Epilipendula. Occasional bushes of Ulex europaeus (0.6-0.9 m. high), Erica cinerea and Calluna occur there.

Mature AHs seemed even-aged. 5 "incipient" mounds were found at the base of tall vegetation on the ridges. All 42 "mature" mounds examined had >90% of their volume on the ridges. Linum catharticum, Arenaria serpyllifolia and Cerastium holosteoides were frequent on AHs and more or less confined to them.

Observations No signs of grazing were seen, but I saw some rabbit droppings on AHs and the ride nearby.

RESULTS are overleaf. Methods and symbols used are described in Appendix 3. Numbers in the table are subjectively-estimated percentage covers of all species in 8 blocks, each consisting of one random AH and a 0.25 m² quadrat placed 0.3 m. away from it, in a random direction, in the SV.

	AH								SV								SIG
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Mean AH Ht. (cm)	14	15	33	19	29	33	22	26									
Mean AH Diam. (cm)	67	45	65	57	83	57	77	50									
AH Volume (10 ³ cm ³)	27	14	73	28	92	59	58	34									
Volume N.H.S. (100 cm ³) (corr.)	11	0	8	4	7	3	6	1									
Activity (%)	4	0	1	1	7	5	1	3									
Animal activity	RD						RD	RD									
Vegetation Ht. (cm)	10	16	9	10	8	7	8	7									
Total No. seedlings	21		>36	5	8		4	1		3				1			
Depth to horizon (mm)		8							10	9	10	1	3		5	3	8
% cover Bare Soil	4	0	3	1	3	0	2	1									
<i>Achillea millefolium</i>				1	1	1	3	1		3	6	2	3	1	1	2	NST
<i>Agrostis stolonifera</i>	1				1						1					1	
<i>Agrostis tenuis</i>	1	1				3	2	1		1	5	2		1	2		NSW
<i>Anthoxanthum odoratum</i>	1	1	1	1	2	1	1	1	1	4	1	2	2	4	1	1	NST
<i>Arenaria serpyllifolia</i>	2		1	1	1		1	1									*B
<i>Arrhenatherum elatum</i>	1		1	1	1	1					1	1		2	4	2	NSW
<i>Carex caryophyllaea</i>	1											1		1	1	1	NSB
<i>Carex flacca</i>		3					1	1	2	4		1	1	2	2	1	*W
<i>Crepis capillaris</i>	1		1	1	1							1	1				NSB
<i>Filipendula vulgaris</i>		1			1		1	1	10	10	7	7	6	3	8	18	*W
<i>Festuca rubra</i>	80	95	75	85	85	60	70	55	97	90	90	92	90	90	95	85	*W
<i>Galium mollugo</i>	1		1	1	1	1		1					1				NSB
<i>Galium verum</i>	3	1	6	1	2	5	2	3	5		1		4	9			NST
<i>Helictotrichon pratense</i>	1	3		2		1	1		2	1		1	6		3	1	NST
<i>Hieracium pilosella</i>		1		3	2		1					5	2				NSNT
<i>Holcus lanatus</i>	1	2	1		1			1	1		2	1	1	1			NSB
<i>Koeleria cristata</i>	1	4	30	4	2	2	1	1	1	4	10	15	8	4	2	6	NST
<i>Lotus corniculatus</i>	1			1				1		1		1			1		
<i>Medicago lupulina</i>				1	1		1					1					
<i>Plantago lanceolata</i>	1	2		2	1		2	7	1		1	5	2			2	NST
<i>Poterium sanguisorba</i>					1		2		5	4		1	11	3	12	13	*W
<i>Prunella vulgaris</i>	1			1	1							1					
<i>Rumex acetosa</i>	1	1	1	1	1		1	1	1	1		1	1	1			NSB
<i>Thymus drucei</i>	4	3	3	12	13	43	35	10		1		2	1				*W
<i>Viola riviniana</i>	1	1					1	1	1	2	3				1		NSNT

EXTRA species (continued overleaf)

Asperula cynanchica AH1 (1%), 5(4%), 8(50%).
Eriza media AH5(1%), 7(2%), 8(1%)
Erva (erythrocarmum agg.) AH1(1%), 3(1%)
Cerastium holosteoides AH1(1%), 4(1%)
Daucus carota AH2(1%)
Leontodon hispidus AH8(1%)
Trisetum flavescens AH1 (1%), 2(1%)
Erica cinerea AH1(15%), 6(5%), SV6(6%)

Agrostis canina SV3 (6%)
Anthyllis vulneraria SV (1%)
Calluna vulgaris SV4 (2%)
Dactylis glomerata SV5(1%)
Dicranum scoparium SV4 (1%)
Euphrasia nemorosa SV4 (1%)
Luzula campestris SV6(2%)
Pimpinella saxifraga SV1 (1%)
Potentilla erecta SV2 (2%)

EXTRA species (continued)

Fragaria vesca AH5(1%), 5(1%), SV5(2%)

Poa pratensis AH2(1%), SV1(1%)

Sieclinia decumbens AH1(1%), SV2(1%), SV5(1%)

Veronica chamaedrys AH1(2%), SV1(2%)

Veronica officinalis AH5(1%), SV5(1%)

Zerna creata AH8(1%), SV8(2%)

Senecio jacobaea SV7(5%)

Viola hirta SV4(1%)

COMMENTS

(i) 4 seedlings were found in SV quadrats. 3 Rumex acetosa seedlings occurred in SV2 on an incipient AH. One unidentified seedling grew on a patch of bare soil in SV6. In contrast, over 75 seedlings, over 50 of which were Arenaria serpyllifolia, were present on the 8 AHS.

(ii) AH2 was the only mound which appeared abandoned, and the only one which had a measurable A₀ horizon.

APPENDIX 18.

Lullington Heath, Sussex, Site 2.

Comparison of ant-hill (AH) and surrounding vegetation (SV)

O.S. GRID REFERENCE TQ 553018

SITE VISITED ON: 21st to 23rd October 1971

SITE POSITION See map in Appendix 16. I walked due east from the tumulus at TQ 557018 and found the site two-thirds of the way towards the bridleway which runs from TQ 558015 to TQ 54009.

Site is at 125 m., sloping 3° to the E.
Owned by Eastbourne Water Board.

AREA SAMPLED 50 x 45 m., containing about 70 AH, i.e. a density of 519/ha.

VEGETATION HISTORY

Celtic field systems occurred across the site (aerial photographs). The area was uncultivated in 1878 (6" O.S. map), and both before and after this time it was probably covered with chalk heath and *Ulex*, maintained by sheep and rabbit grazing (Grubb et al 1969). After myxomatosis a tall, dense mat of *Festuca rubra* and large bushes of *Calluna*, *Erica*, *Ulex* and *Rubus* became established in the "chalk heath" at Lullington (Thomas 1960, 1963).

SOIL DETAILS

Parent material is Upper Chalk (Cretaceous). An A₀ horizon of irregular depth, reaching 2 cm. under dense *Festuca*, overlies a dark brown silty loam, with peds <5 mm. diameter. Occasional chalk stones <10 cm. long occur throughout the profile to 18 cm., where chalk stones and flints become dense. Perrin (1956) suggested that this soil type on the Lullington reserve arose through loess deposition on an erosion pavement of flints in periglacial times. The distribution of rubble through the upper soil profile may be due to Celtic cultivation.

Grubb et al (1969) p. 191, Table 3 found that the pH of the top 1 cm. of mineral soil in this area was in the range 5.0-5.9. The active AHs, however, had a pH in the range 6.0-7.9.

PRESENT VEGETATION

Prominent bushes of *Viburnum lantana* (2), *Ulex europaeus* (2), *Crataegus* (5) and *Calluna vulgaris* (20-30) stick out from a dense turf of *Festuca rubra* about 50 cm. high. *Erica cinerea* is present, and dense patches of *Rubus fruticosus* occur

Most AHs "mature", active, and partly hidden by *Festuca*.

Occasional signs of (rabbit) grazing were seen, and rabbit droppings occurred on about half of the mounds.

RESULTS are overleaf. Methods and symbols used are described in Appendix 3. Numbers in the table are subjectively-estimated percentage covers of all species in 8 blocks, each consisting of one random AH and a 0.25 m² quadrat placed 0.5m. away from it, in a random direction, in the SV.

	AH								SV								SIG
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Mean AH Ht. (cm)	26	31	15	21	25	27	22	28									
Mean AH Diam. (cm)	65	55	59	56	67	44	58	65									
AH Volume (10 ³ cm ³)	51	52	16	51	52	30	18	59									
Volume N.H.S. (corr, 100 cm ³)	9	27	6	20	16		35	5									
Activity (%)	2	5	4	6	5		19	9									
Animal activity	RDG				RD	G	RD	RD									
Vegetation Ht. (cm)	11	25	11	20	12	10	8	14	30	32	26	51	25	25	33	32	
Total no. seedlings	1	1	5	7	7				1		1						
Depth Ao horizon (mm)	5								61			22	8	121	20	10	
% cover Bare Soil	2	8	8	8	7		70	2	2								
<i>Achillea millefolium</i>				2		1		1	4			5	2				
<i>Agrostis stolonifera</i>	1	1					1	2		1		15	5			5	NST
<i>Agrostis tenuis</i>		1		2	5	8	4	2						10		2	NST
<i>Anthoxanthum odoratum</i>						1			1	1	1						
<i>Arrhenatherum elatius</i>		1	1			1		1		1					7		
<i>Filipendula vulgaris</i>						1		1	1	6	5	5	5	16	4	7	**W
<i>Festuca rubra</i>	95	90	95	90	92	95	30	100	95	99	95	80	85	85	90	95	NST
<i>Helictotrichon pratense</i>							1			1	1	2	1	1			NSB
<i>Holcus lanatus</i>	1	1	1		2			1	1		2	2	6	5	1	7	*T
<i>Koeleria cristata</i>	2	1	2	5	1	1		1	22	2	4	5	20	1	6	6	*W
<i>Poterium sanguisorba</i>									6	17	8	2	2		55	5	*W
† <i>Rubus fruticosus</i> agg				8	1			2			9	20	5			2	NST
<i>Rumex acetosa</i>	1		1	1							1	1	1	6	7	1	NST
<i>Thymus drucei</i>	1		1	2			1	7	1								NST

EXTRA species

Artemisia annua AH4(1%)
Fragaria vesca AH1 (1%)
Hypericum sp. AH2 (1%)
 † *Lathyrus pratensis* AH3(1%)
Myosotis sp. (seedlings) AH5(1%)
Solanum dulcamara AH2(1%)

Lonicera periclymenum AH2(5%), SV2(5%)
Viola riviniana AH5(1%), SV1(1%), 5(2%)

Carex flacca SV1 (1%), 2(1%)
Cirsium arvense SV5(3%)
Galium verum SV3(2%), 8(8%)
Leontodon hispidus SV3(12%)
Lotus corniculatus SV3(1%)
Plantago lanceolata SV5(1%)
Sonchus oleraceus SV2(1%)
Taraxacum officinale SV3(1%), 6(1%)

APPENDIX 19. Illington Heath, Sussex, Site 5

Comparison of ant-hill (AH) and surrounding vegetation (SV)

O.S. GRID REFERENCE TQ545016 - TQ541016

SITE VISITED ON 22nd-24th October 1971

SITE POSITION See map in Appendix 16. Site runs from the top to the bottom of the grassy spur situated about 20 m. above, and to the south of, the track which runs through "Old Kiln Bottom". It included areas 5, 4 and 8 sampled by Grubb et al (1969) p. 182-4.

Site is at 122 m. (Wend) - 81.5 m. (E end), sloping 5° to the NE.
Owned by Eastbourne Water Board.

AREA SAMPLED 400 x 30 m. (1.2 ha), containing an estimated 300 AH, i.e. a density of 250/ha.

VEGETATION HISTORY Similar to that of Site 2 (Appendix 18.), except that *Crataegus* is commoner at Site 5, and that less than 1% of the site area consists of areas hollowed out by mortar bombs in the Second World War.

SOIL DETAILS

Parent material is Upper Chalk (Cretaceous). Loess deposition occurred in periglacial times. In the upper (E) half of site, a dark brown stoneless silty loam 10-17 cm. deep covers a rubble of chalk and flints. The A₀ horizon is irregular but reaches 1.5 cm.

In the lower (W) half of the site, the undisturbed soils are usually stoneless, about 8 cm. deep, with no A₀ horizon, overlying chalk rubble. The bomb sites mainly occur here; their soils differ from those around in having flints on the surface and chalk lumps and flints up to 8 cm. long distributed throughout the shallow (3-8 cm. deep) profile.

Grubb et al (1969) p. 191 show (Table 3) that the pH of the top 1cm. of mineral soil under "chalk heath" vegetation in this area is 4.5-6.4. Active ant-hills, however, had a pH in the range 6.0-7.9. The soil in bomb hollows had a pH of 7.5-7.8.

PRESENT VEGETATION

Dense turf 15-30 cm. high, dominated by *Festuca rubra*, in which several large patches of *Ulex* (to 6 m. across, 2m. high) and many bushes of *Rubus* are prominent throughout the area. The upper 100 m. of the site had numerous large bushes of *Calluna* and *Crataegus* and 5 individuals of *Viburnum lantana*.

The bomb sites bear vegetation 1-2 cm. tall in which many species (e.g. *Poterium sanguisorba* with leaves 3-4 cm. long, *Festuca rubra*, *Leontodon hispidus* and *Plantago lanceolata*) are small and stunted. 7 bomb-sites were examined; typical species included *Hieracium pilosella*, *Lotus corniculatus*, *Thymus drucei*, *Dicranum scoparium*, *Anthyllis vulneraria*, *Medicago lupulina*, *Gladonia arbuscula*, *C. rangiformis*, *C. fimbriata*, *Elasidema taxifolius*, *Linum catharticum*, *Centaureia erythraea*, *Carlina vulgaris*, *Euphrasia nemorosa*, and *Gentianella amarella*. *Weissia (crissa)*, *Bryum capillare* and *Eucalypta stuebeliana* also occurred.

Most mounds "mature" and "active"; two "incipient" AH found. The AH were typically dominated by *Festuca rubra* except near bomb sites, where they often seemed smaller and to bear a more diverse flora.

Although the whole site was crossed 5 times, only two intensely-grazed mounds, but no rabbit droppings were seen; thus rabbit influence is almost absent.

RESULTS are overleaf. Methods and symbols used are described in Appendix 3. Numbers in the table are subjectively-estimated percentage covers of all species in 8 blocks, each consisting of one random AH and a 0.25 m² quadrat placed 0.5 m. away from it, in a random direction, in the SV.

	AH								SV								SIG
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Mean AH Ht. (cm)	23	18	17	15	20	24	22	50									
Mean AH Diam. (cm)	40	35	64	38	56	61	62	64									
AH Volume (10^3 cm^3)	19	12	29	10	30	42	39	62									
Volume N.H.S. (corr, 10^2 cm^3)	8	7	17	12	8	9	3	2									
Activity (%)	4	6	6	12	3	2	•7	•3									
Vegetation Ht. (cm)	15	9	6	20	10	11	8	6	25	25	25	27	28	23	17	15	
Total No. Seedlings			10	2	3			5									
Depth to horizon (mm)	0	0	0	0	0	0	0	0	61	31	2	15	15	0	21	0	
% cover Bare Soil	15	18	40	50	8	5	8	8	2		15				5		
<i>Achillea millefolium</i> 1			1			1	5		1		15			2		2	NSW
<i>Agrostis stolonifera</i>			1					1			1	1			2		
<i>Agrostis tenuis</i>			8						1	1	2	4					NSWT
<i>Arrhenatherum elatius</i> 1	1	1	1		1		2	1	3		1	3		2	2		NSB
<i>Briza media</i>	1	8	1									1					
<i>Carex flacca</i>	1	2			1	1			2	1		2	1	1	1	10	NST
<i>Filipendula vulgaris</i>								1	17			6	7	15	1	3	*F
<i>Festuca rubra</i>	85	80	50	50	90	70	60	50	90	85	40	95	90	85	90	70	NST
<i>Galium mollugo</i>			12	1		1	30	10									NST
<i>Galium verum</i>					1	8		2								1	
<i>Helictotrichon</i> <i>pratense</i>		1							2	5	1		5	1			*T
<i>Holcus lanatus</i>			3		1	1	1	1			2			8	4		NST
<i>Koeleria cristata</i>		3			1	1	2	9	5	2	1	5	5	6	3	1	NST
<i>Leontodon hispidus</i>					1		1	1		2			1			15	
<i>Plantago lanceolata</i>			1		1		1	1									NSB
<i>Poterium sanguisorba</i>	1					1		1	13	40	3	13	30	12	6	20	*F
<i>†Rubus fruticosus</i>				4	7		4			2	40	8			2		NST
<i>Rumex acetosa</i>			1					1			3				2		
<i>Thymus drucei</i>		2				35	10	30								3	NST

EXTRA species

Arenaria peruvillifolia AH3(1%), 6(1%), 7(1%).
Asperula cyna nobilis AH5(1%), 5(1%)
Centaurea nigra AH5(1%)
Cremis capillaris AH5(1%)
Fragaria vesca AH5(1%)
Helictotrichon pubescens AH1 (1%)
Medicago lupulina AH5(1%)
Prunella vulgaris AH7(1%)
Scabiosa columbaria AH3(1%)
Veronica officinalis AH7(1%)

Anthoxanthum odoratum AH1(1%), 6(1%), SV8(1%)
Dactylis glomerata AH5(2%), SV7(11%)
Knautia arvensis AH3(1%), SV8(1%)

Carex corymbulosa SV2(1%), 8(1%)
Crataegus monogyna SV7 (2%)
Eleusine (adianthoides) SV8(2%)
Hypericum pulchrum SV2(2%)
Idonotum vulgare SV2(3%)
Pimpinella saxifraga SV8(1%)
Polypodium vulgare SV8(1%)
Ranunculus bulbosus SV8(1%)
Succisa pratensis SV6(5%), 8(5%)
Viola hirta SV2(2%), 3(1%)
Zewa erecta SV3(1%)

Hieracium pilosella AH3(1%), SV8(2%)
Viola riviniana AH3(1%), SV5(1%)

Appendix 20. Aston Rowant N.N.R., site 1. Comparison of ant-hill and surrounding vegetation.

O.S. GRID REFERENCE SU 727974

SITE VISITED Many times; sampled 16th June 1970.

SITE POSITION Marked on map of Aston Rowant N.N.R. in Appendix 29. On the north-facing slope of Beacon Hill, to the west of the track which runs from my plot to the Icknield Way, a band of grassland extends round the hill, with Juniperus scrub above and below it. The site was 5 m. from the path, sloping about 8° to the north, at an altitude of 198m.

AREA SAMPLED 40 x 25m

VEGETATION HISTORY The site has probably never been ploughed; it was shown as grassland by Jefferys (1767), Davis (1797), and the 1/2500 O.S. map of Oxfordshire, sheet 47(8) (1881). The area had closely rabbit-nibbled turf in 1953 (reserve records).

SOIL DETAILS Parent material is Upper Chalk (Cretaceous), with no drift. There is an A₀ horizon 1-2 cm. deep. The mineral soil consists of a Brown Earth 12-15 cm. deep. Small chalk stones increase in size and frequency down the profile.

PRESENT VEGETATION Springy, rabbit-grazed turf rich in Festuca rubra, Thymus drucei and bryophytes. Several species frequent in heavily rabbit-grazed areas are present, e.g. Senecio jacobaea, Cirsium palustre, C. arvense, Rubus fruticosus, Bryonia dioica.

Most ant-hills mature and heavily grazed. Annuals e.g. Arenaria serpyllifolia, Veronica arvensis, are frequent on mounds.

RESULTS are overleaf; the methods and symbols used are described in Appendix 3. The figures in the table are subjectively-estimated percentage covers of all species in eight 'blocks', each consisting of a random ant-hill, and a 0.25m² quadrat placed 0.3m away from it, in a random direction, in the surrounding vegetation.

	AH								SV								SIG
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Mean AH Ht. (cm)	24	26	26	18	25	22	13	30									
Mean AH Diam (cm)	68	55	55	40	47	35	42	75									
AH Volume (10 ³ cm ³)	52	59	39	14	29	16	10	80									
Volume N.H.S. (10 cm ³)	11	5	15	3	4	8	11	17									
Activity (%)	.2	.1	.3	.2	.1	.3	.5	.2									
Animal Activity	RD	G	RGS	NG	RD	G	G	GG	G						G		
		RD	D	D		RD	RD	RD									
Mean Veg. Ht. (cm)	2	3	1	4	6	3	3	2	4	9	9	20	8	18	6	6	
% cover Bare Soil	3	1	8	1	2	3	9	4									
Campanula																	
rotundifolia	1	1	1		1	1	1	1	1	1	1		1	1	1	1	NSNT
Carex caryophylla		1	1		2	1	1				1		1	1			NSNT
Festuca spp.	80	85	80	90	80	80	75	75	70	80	90	75	65	95	70	65	NST
Fragaria vesca		1		1				1		16	1	4	1	2	1	9	*W
Galium mollugo	8							1	5						1	4	
Galium verum		6	1		5			1	1			1	2				NSNT
Helianthemum chamaecistus				5	10	1						2					
Koeleria cristata	2	6		4		6	1	1	2	6	4	4	4	5	1	1	NSNT
Prunella vulgaris			1		1		1			1			1		1	1	NSNT
Rumex acetosa			1				1			1	1			1	1		NSNT
Sedum acre	1		1				1	1									NSB
Senecio jacobaea	1			1			1		1						1	1	
Thymus drucei	6	6	25		5	6	13	25	30	20	6		9	3	22	40	NST
Veronica arvensis	1		1		1		2	1									NSB
Veronica chamaedrys	3	4	1	16	3	3	4	2	4	3	2	5	2	3	2	3	NST
Acrocladium																	
cuspidatum		1				2						3		1			
Dicranum scoparium	1						1	1	6	10	1		22	3	5	7	*W
Hylocomium splendens						6			10	14	30		17	6	17	5	*W
Pseudoscleropodium purum	3	5	4	5	7	8	1	1	2		1	5		4	2	20	NST
Rhytidiadelphus																	
squarrosus	7		2	25	5	8	3	1	5	3	1	6	3	4	4	1	NST

EXTRA species

Arenaria serpyllifolia AH2(1%), 3(1%), 7(1%)

Brachypodium sylvaticum AH2(1%), 5(1%).

Cerastium lutescens AH6(1%)

Cerastium semidecandrum AH1(1%)

Holcetostrichen pratense AH5(1%)

Linum undulatum AH7(1%)

Myosotis ramosissima AH1(1%), 7(1%), 8(1%)

Trisetum flavescens AH1 (2%), 2(1%)

Achillea millefolium AH5(1%), SV3(3%), 6(1%)

Agrostis stolonifera AH1(3%), 3(1%), SV2(8%)

Carex flacca AH5(1%), SV4(1%), 5(1%)

Cirsium acaule SV1(6%), 7(1%), 8(1%)

Cirsium arvense SV2(4%)

Cirsium palustre SV3(2%), 4(20%), 5(15%)

Crepis canicularis SV1(3%), 2(3%), 7(2%)

Knautia cuneosiformis SV1(4%)

Lotus corniculatus SV4(6%)

Potentilla reptans SV4(2%)

Sida sanguinea SV3(1%)

Rhytidiadelphus triquetrus SV3(1%), 7(1%)

Veronica officinalis SV8(14%)

Luula caespiticia AH1(1%), SV1(2%)

Hieracium pilosella AH3(1%), SV1(13%),
7(50%)

Appendix 21 , Aston Rowant N.N.R., Site 2. Comparison of ant-hill
and surrounding vegetation.

O.S. GRID REFERENCE SU 727971

SITES VISITED Many times; sampled 13 & 14 October 1971.

SITE POSITION. Marked on the map of Aston Rowant N.N.R. in Appendix 29 .
In my Beacon Hill plot, near the fence along the S.W. side.

Site is at 244 m altitude and slopes 3° to the SSW. Sheltered by a spinney on the southern margin, which has dense Fagus, Taxus, Crataegus, Rosa etc. up to 6-8 m tall.

AREA SAMPLED. 15 x 25 m, containing 70 mounds, i.e. a density of 1866/ha.

VEGETATION HISTORY Shown as grassland by Jefferys(1767) and Davis(1797), and then as open scrub on the 1/2500 O.S. map of Oxfordshire(1881).

However the area was almost certainly ploughed between 1880 and 1920 (local farmer, in reserve records). It was probably kept open by sheep and rabbits until 1954, when the whole area was free of scrub (Thomas(1960), Rawes, M. (pers. comm.)). No invading shrubs were present in 1959 (Myerscough and Harley(1959)), but now several Rosa plants and seedlings of Quercus, Crataegus and Betula occur.

SOIL DETAILS Parent material is Upper Chalk (Cretaceous); site is just free of drift. There is no A horizon; chalk rubble is encountered at 12cm under a Brown Earth. The pH of the top 5cm of the profile is 7.1-7.4 (3 determinations in 0.01M CaCl₂).

PRESENT VEGETATION The sward is about 10cm tall with Fragaria, Helianthemum Leontodon and the luxuriant growth of bryophytes prominent.

Most of the ant-hills are large and 'active'. A consistent pattern of species exists on the mounds; Helianthemum and Thymus occupy the tops and south sides, where most soil-heaping occurs, and Festuca spp. and mosses (Pseudoscleropodium purum, Rhytidiadelphus squarrosus & Maia spp.) dominate the northern sides. Establishment of Leontodon, Fragaria and Plantago is also concentrated on the north-facing slopes. Some of these patterns are illustrated in Fig.18. of the text.

A small rabbit colony exists in the area, and the site is grazed occasionally with a low density of sheep.

RESULTS are overleaf; the methods and symbols used are described in Appendix 3 . The figures in the table are subjectively-estimated percentage covers of all species in eight 'blocks', each consisting of a random ant-hill, and a 0.25m² quadrat placed 0.3m away from it, in a random direction, in the surrounding vegetation.

EXTRA species (continued).

Scabiosa columbaria AH7(1%).

Brachythecium velutinum AH4(2%). SV7(1%).

Briza media AH2(1%), 8(1%), SV2(4%).

Camptothecium lutescens AH3(2%). SV3(1%).

Dactylis glomerata AH6(1%). SV8(1%).

Rhodobryum roseum AH1(1%). SV1(1%).

Poterium sanguisorba SV6(1%), 8(10%)

Ranunculus bulbosus SV8(1%)

Senecio jacobaea SV2(1%), 3(1%)

Trifolium repens SV4(1%)

Viola hirta SV1(1%), 3(1%), 5(1%)

	AH								SV								SIG
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Mean AH Ht. (cm)	22	31	25	18	35	31	27	35									
Mean AH Diam. (cm)	72	74	129	50	104	71	65	96									
AH Volume (10 ³ cm ³)	49	84	170	20	171	76	52	148									
Volume H.H.S. (10 cm ³)	170	25	10	10	55	30	33	30									
Activity (%)	3	•3	•1	•6	•3	•4	•6	•2									
Animal Activity	RD	RD	RD	RD	RD	RD	RD	RD									
	G	GS		G	S	G		GS									
Mean Veg. Ht. (cm)	5	4	4	4	7	4	4	4	11	7	12	8	18	10	9	10	
Total No. seedlings			1		15		2	1		5		1					
% cover Bare Soil	25	7		4	14	1	1	8									
<i>Agrostis stolonifera</i>	1		1	1		1					1	1		1			NSNT
<i>Anthoxanthum odoratum</i>			1		1		1	1			1			1	2	2	NSNT
<i>Brachypodium sylvaticum</i>	1		1		4				1	1	5		35				NST
<i>Campanula rotundifolia</i>		1	1		1		2		1	1	1	6		1	1	1	NSW
<i>Carex flacca</i>	1						1		1	2	2	1	1	1	4		**T
<i>Crepis capillaris</i>		1	1		1		1			1	1		1	2			NSNT
<i>Festuca spp.</i>	20	20	18	40	50	20	35	40	75	50	40	65	40	65	50	50	**W
<i>Fragaria vesca</i>	1	3	3	3	5	1	1	2	9	14	8	1	7	5	1	4	NST
<i>Galium mollugo</i>					1	1			8	2							
<i>Galium verum</i>				2	1	2	1	1		4				2	1	2	NSW
<i>Helianthemum chamaecistus</i>	26	40	15	45	20	55	45	15	6	12	10	40	7	28	14	5	**W
<i>Heliotropium pratense</i>		1	1	1				1						4	1		
<i>H. pubescens</i>	1		1			1	1	1	2	1	1	1			2	2	NSB
<i>Hieracium pilosella</i>							1	1			3		1	4	1		NST
<i>Holcus lanatus</i>		1	2	2	1	1	2	1	1	2	2	4	1	2	2	5	**T
<i>Koeleria cristata</i>	1	1	1	2	2	1	1	1	6	2	1	2	2	5	10	19	NST
<i>Leontodon hispidus</i>	2	2	4	1	1	2	5	1	8	11	15	2	8	15	20	16	**W
<i>Linum catharticum</i>	1		1	1	1					1	1	1		1	1		NSNT
<i>Lotus corniculatus</i>			1	1		1		1	1	1	1	1	2	1	1	1	NEW
<i>Medicago lupulina</i>		1	5			1	5										NST
<i>Plantago lanceolata</i>		5	4		1	2				2	10		1	5	1	1	NST
<i>Poa pratensis</i>		1			1	1						3	25				
<i>Prunella vulgaris</i>			1	1	1	1	1			1	1	1		1			NSNT
<i>Thymus drucei</i>	18	20	35		30	18	4	40	2	2	2			1	1		*W
<i>Trisetum flavescens</i>		2	5	1	2	1		1			4				1		*T
<i>Veronica chamaedrys</i>	1	1	1	5	2			1		1	1	2	2			5	NSW
<i>Veronica officinalis</i>	1				1					2	1						
<i>Dicranum bonjeanii</i>		4	2		1		5		1		2	1		1	1		NSW
<i>Pseudoscleropodium purum</i>	7	7	1	5		20	5	15	5	10	5	1		5	1	5	NSW

EXTRA species (continued on previous page)

Bryum bicolor AH8(1%)
Bryum capillare AH5(1%)
Campylidium chrysophyllum AH5(1%)
Fissidens adiantoides AH7(1%), 8(1%)
Fissidens taxifolius AH5(1%)
Linum affine AH7(1%)
Linum (longirostrum) AH3(8%)

Cirsium acaule SV1(5%), 6(2%)
Cirsium arvense SV8(1%)
Fissidens cristatus SV1(1%)
Gentianella spurella SV3(1%)
Lathyrus pratensis SV1(1%), 8(1%)
Luzula campestris SV3(1%), 8(2%)
Potentilla erecta SV4(1%)
Potentilla reptans SV2(2%)

Comparison of ant-hill and surrounding vegetation

O.S. GRID REFERENCE SU 728967

SITE VISITED Many times; sampled on 30 & 31 October 1971

SITE POSITION. Marked on the map of Aston Rowant N.N.R. in Appendix 29. Site is in the coomb on the south side of Beacon Hill, in the grassland plot above the arable field, and encompasses most of the flatter ground in the base of the valley.

Site is at 183-198m altitude, sloping 8° towards the south-west.

Now obliterated by the M40 motorway.

AREA SAMPLED 130 x 110m, containing about 650 ant-hills, i.e. a density of 455/ha.

VEGETATION HISTORY Grassland covered the area in Jefferys(1767) and Davis(1797), but the site was shown as arable in the O.S. 1/2500 map of Oxfordshire, sheet 47(8)(1881). Probably ploughed until the 1920s, but since then has reverted to grassland.

SOIL DETAILS Parent material is Middle Chalk (Cretaceous).

Two profiles were dug. The depth of the A₁ horizon is given in the results overleaf. A structured dark red-brown loam occurred to 15-17cm, with minute chalk fragments appearing in the lower 3-4cm. Below this, 5cm of chalk rubble, with stones increasing in size downwards, covered chalk rock.

PRESENT VEGETATION Tall grassy patches were separated by a network of sheep tracks. In the northern half of the site the vegetation was more species-rich than on the southern half, where coarse grasses like Arrhenatherum, Dactylis, Helictotrichon spp. and Zerna erecta were more abundant.

The anthills were all 'mature'. Arenaria was frequent, and Cerastium holosteoides occasional, on ant-hills throughout the area. In the southern half of the plot, the mounds rarely bore Thymus and Medicago etc. Many of these mounds had been invaded by tall grasses, and an A₂ horizon was starting to form in the absence of recent soil heaping by the ants.

Sheep had grazed the site in winter and early spring. Mounds on the north side of the plot had closely-grazed vegetation and abundant rabbit droppings. Yet the density of sheep-tracks and the evidence of rabbit activity both decreased as I walked south.

RESULTS are overleaf; the methods and symbols used are described in Appendix 3 . The figures in the table are subjectively-estimated percentage covers of all species in eight 'blocks', each consisting of a random ant-hill, and a 0.25m² quadrat placed 0.3m away from it, in a random direction, in the surrounding vegetation.

EXTRA species(continued).

Sonchus sp. AH2(1%).

Trifolium pratense AH7(1%)

T.repens AH2(1%),6(12%),7(1%)

Achillea millefolium AH7(1%),
SV7(2%).

Barbula (convoluta) AH7(2%).SV7(1%).

Bryum (erythrocarpum agg.) AH4(1%),
7(1%).SV7(1%).

Cerastium holosteoides AH7(1%).
SV7(1%).

Luzula campestris SV1(1%)

Mnium (longirostrum) SV7(2%)

Phleum bertolonii SV6(1%)

Sieglingia decumbens SV8(1%)

Viola hirta SV7(1%)

V.riviniiana SV7(1%)

Filipendula vulgaris AH4(1%).SV4(1%).

Galium mollugo AH2(1%),7(1%).SV1(1%)

Potentilla reptans AH7(1%).SV2(1%),8(1%).

Senecio jacobaea AH2(2%).SV6(2%),8(1%)

	AH								SV								SIG
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Mean AH Ht. (cm)	17	16	23	27	15	16	27	16									
Mean AH Diam. (cm)	68	85	53	110	46	47	73	38									
AH Volume (10 ³ cm ³)	32	50	31	137	15	16	68	10									
Volume N.H.S. (10cm ³)	36		32		61	31		11									
Activity (%)	1		1		4	2		1									
Animal Activity	RD	RD	RD		RD	RD	RD	RD									
Depth A ₀ horizon (mm)	GS	G	G		G	G	EGS								T	T	
Mean Veg. Ht. (cm)	7	7	11	9I 20	6	5	2	9	71 20	3	8I 23	8I 17	12I 13	5I 10	3	15 6	
Total No. seedlings	>24	19	2	>15	7	1		5	2	6	1	3	17	3	22	2	
% cover Bare Soil	6	5	7	4	45	2	25	3									
<i>Agrostis stolonifera</i>	1	1	1	4						1							NOT
<i>Arenaria serpyllifolia</i>	1	1				1		1									NSB
<i>Arrhenatherum elatius</i>	1			20				1	1	1				1	1		NSNT
<i>Briza media</i>	1	1	1	1	1	1	2	4		2	2		1	2	6	4	NET
<i>Campanula</i> <i>rotundifolia</i>		2			10	1	2	6		1				1		1	NET
<i>Carex flacca</i>					1				1	3	1	1	3		2	2	*W
<i>Cirsium acaule</i>							3	1	2	11	3			5			
<i>Crepis capillaris</i>				1						1	1				3	1	
<i>Dactylis glomerata</i>		1	5	1	4	1	1		36	1	1	20	15	2	3	1	NSNT
<i>Daucus carota</i>		1		1					1			1		1			
<i>Festuca</i> spp.	60	70	60	65	25	50	75	45	55	55	55	45	65	60	65	65	NSW
<i>Galium verum</i>	1	1	3	2	1		1	2	1	1	1	1		1	1	1	NSB
<i>Helictotrichon</i> <i>pratense</i>	1	2	1	5	2	1	1	1	4	5	1	2	3	6	1	6	NET
<i>H. pubescens</i>		1	2	4	1	1		5	5	3	1	14	3	6	2	2	NST
<i>Hieracium pilosella</i>				1						2				1	1		
<i>Holcus lanatus</i>		1		2	1	1	1	2	1	1		1	1	4		6	NSNT
<i>Leontodon hispidus</i>	1	3	1	1	3	2	2	1	2	12	10	2	12	11	15		*W
<i>Linum catharticum</i>	1	1	1	1	1			1	1	1	1	1	1	1	1	1	NSB
<i>Lotus corniculatus</i>		1	1	1	4		1	2	3	2	1	1	2	2	1	2	NSNT
<i>Medicago lupulina</i>		1	12	1	2		2			1	2		4		6	1	NSNT
<i>Pimpinella saxifraga</i>	1			1				1	1			1		1	1	1	NSB
<i>Plantago lanceolata</i>			3			1			3	1	4	1		5	2		*W
<i>Poa pratensis</i>	1		2	1						1					2	2	
<i>Poterium sanguisorba</i>						1				1	2		3	5	1		*T
<i>Prunella vulgaris</i>			1							1	1		1		2	1	NSB
<i>Ranunculus repens</i>				1						1	4	1	1		1	1	NET
<i>Scabiosa columbaria</i>			1		3				3	3	2		1		5	1	NET
<i>Thymus drucei</i>	30	32	20			45	1	25		5	1			2	1	1	*T
<i>Trisetum flavescens</i>	3	2				1	1			1	1		1	1	1		NSNT
<i>Veronica chamaedrys</i>		1		1	2		1	8								1	NET
<i>Zerna erecta</i>			7	4				1	1		45	10	5		1	2	*W
<i>Acrocladium cuspidatum</i>								1		1			3	2	2	1	NSB
<i>Brachythecium</i> <i>velutinum</i>	1			1					2						1		
<i>Pseudoscleropodium</i> <i>purum</i>	4	1	6	1	25	2	7	10	3	9		6	2	6	1	20	NSW

EXTRA species (continued on previous page)

<i>Agrostis tenuis</i> AH2(1%)	<i>Anthoxanthum odoratum</i> SV2(1%), 7(5%)
<i>Barbula (cylindrica)</i> AH4(1%)	<i>Brachythecium rutabulum</i> SV8(1%)
<i>Bryum (caespitium)</i> AH4(1%), 7(4%), 8(2%)	<i>Carex caryophylla</i> SV2(1%)
	<i>Centaurea scabiosa</i> SV7(1%)
<i>B. capillare</i> AH1(2%)	<i>Fissidens adianthoides</i> SV2 (1%)
<i>Fissidens taxifolius</i> AH7(1%)	<i>Gentianella amarella</i> SV2(1%), 7(1%)
<i>Myosotis ramosissima</i> AH2(1%)	<i>Helianthemum chamaecistus</i> SV7(1%)
<i>Rubia peregrina</i> AH2(1%)	<i>Leucanthemum vulgare</i> SV6(6%)

APPENDIX 23. North side of Rhossili Down, Gower, Glamorgan.

Experiment to compare the viable seed "banks" in soil taken from the tops of ant-hills (AH) and from the pasture (SV)

SAMPLE COLLECTION

I selected 25 random ant-hills within the 40 x 25 m. area in which vegetation had been sampled. On 4th to 6th December 1968 I took 4 soil cores from the top half of each ant-hill, and four cores from a 0.25m² quadrat placed 0.5 m. away from each mound in a random direction. The cores were each 5 cm. deep and about 2.2 cm. in radius, and collected with a steel corer.

SAMPLE TREATMENT

I carefully removed vegetation and roots from the cores, but retained the Ao (litter) horizon because seeds might have been embedded in it. After air-drying the cores until 1st January 1969 to kill fauna and root fragments, I weighed them, large stones being removed where possible. The total weight of soil collected from each ant-hill was compared with the total weight of soil collected from its associated pasture quadrat. When one exceeded the other by more than 5%, soil was removed from the bases of the cores of the heavier sample until it was within 5% of the weight of the lighter sample of the pair. Then the cores in the same sample were broken up and mixed together. Samples were stored in polythene containers at laboratory temperature (15-25°C) until March 1st-3rd 1969.

EXPERIMENTAL METHOD

I transferred each sample to a plastic dish 15 cm. in diameter and 4.5 cm. high. I added oven-sterilised silver sand as needed to make the depth of "soil" in each dish up to 5 cm. The samples were watered with distilled water and placed in an unheated glass frame on the Botany School roof. The two samples in each pair were kept together, but pairs were randomised. I kept the soils moist with distilled water throughout the experiment, which ended on 25th October 1970. On 11 occasions, roughly at intervals of 1½ months in Summer (less frequently in Winter), I removed all the seedlings I could identify, and thoroughly churned up the soil in each pot. On occasions 2, 4, 6, 8 and 10 I re-randomised the blocks and watered the soils with nutrient solution (composition as Rorison 1967). Five dishes filled with J.I. compost were randomised amongst the blocks. Eight weed seedlings appeared in these dishes, and these species have been excluded from the results overleaf.

SOURCES OF ERROR

(i) Identification errors. Aira and Festuca might sometimes have been confused at first, but even by May 1969 Aira seedlings could easily be recognised by their tufted habit, flattened sheaths and large ligules.

(ii) No credence can be put on the absolute numbers of seedlings identified in this experiment. Viable seeds were probably lost, for instance, by:

- a) germination in moist samples brought to the lab, followed by death on air-drying;
- b) injury or disintegration, when I used a pestle or spatula to break up the air-dry soil cores;
- c) germinating under the crust which sometimes formed on the soil surface and being unable to penetrate it;
- d) germinating too deep to put cotyledons above ground;
- e) having just germinated, when the soil was churned up;
- f) decay;
- g) natural death or predation by animals. Although I sprayed the experiment with Malathion several times, centipedes, woodlice and even earthworms were found in the pots;
- h) having dormancy induced by the treatments I applied;
- i) being still present, viable but not germinated when the experiment ended.

However, since both samples of each pair were treated alike, the number of seeds which germinated in AH and SV samples can be used to estimate the true ratio of viable seeds in the two soil types, with two provisos;

(j) that dormancy had not been induced in some seeds of a species in either AH or SV soils by particular environmental conditions. Then a greater proportion of seeds taken from one soil type might show continuous induced dormancy than seeds of the same species taken from the other soil type;

(k) Because of their lack of crumb structure, AH soils crusted more easily and were more difficult to wet than soils taken from the SV. The ratio of seedlings appearing is only a good indication of the ratio of viable seeds present in the soils if the "microsite density" for germination of seeds of a particular species is the same in the pots containing both soil types.

RESULTS

SPECIES		1	2	3	4	5	6	7	8	9	10	11	12	14	15	16	17	18	19	20	21	22	23	24	25	TOTAL	SIG	
<i>Agrostis stolonifera</i>	AH				1						2				1						1					5	NS	
	SV		1	2						1	4													1		9		
<i>Agrostis tenuis</i>	AH	5	1	17		1	4		4	2	4	3	2	7	1	5	2	1	9	6						14	95	
	SV	16	20	7	15	3		5	52	79	25	3	1	18	13	10	1	10	35	13	8	24	34	12		7	515	**
<i>Aira praecox</i>	AH	20		1	37	2	48	29	7	54	4	35	61	6	3	11	24	22	32	1	87	37	49	12	7	613		
	SV		2	4	12	2	5		4	1			4	6	5	2		2	14		2	7	4	4	2	85	**	
<i>Anthoxanthum odoratum</i>	AH			2		2		1											1							6		
	SV		1		6	2	1		2	3	6			5	1	1		1	1		10	2	1	1		45	**	
<i>Festuca ovina</i>	AH		1		3			3	2		2			3				4	4	2			3	2		29		
	SV	5	13	8	2	3	3	8	5	3	22	3	10	7	7	10	3		20	4	1	2		7		176	**	
<i>Galium saxatile</i>	AH	20	5	3	2	3			6	1	6	1	1	3	1	22	2		2	34	4	1	18	2	7	145		
	SV	16	15	4		7		5	21	4	17	2	6	5	1	13	8	2	4	38	16	6	4	6		219	NS	
<i>Luizula campestris</i> s	AH																									0		
	SV	1	2																1					1		7	NS	
<i>Potentilla erecta</i> ta	AH					1													1			1	3			5		
	SV		5	5	4	1		4				1	21	1		1		1	2					1		48	*	
<i>Rumex acetosella</i>	AH		1			1				4	9	2	2		1		1	1				1				28		
	SV	1		1		1				185	5	3		10		11	3	13	3		4	1			5	244	NS	
<i>Sieglingia decumbens</i>	AH																									0		
	SV					1		1		10					1	1		2						1	1	18	*	
Unidentified	AH																1		2							5		
	SV	4		1					2								1					1		1	1	11		

†Two-tailed Wilcoxon signed-ranks tests for matched pairs were used.
N.S., $P > 0.05$; * $0.05 > P > 0.01$; ** $P < 0.01$.

Also appeared:

Calluna vulgaris s. SV25(1).
Carex pilulifera AH AH8(1), SV5(5), 16(3)
Dactylis glomerata SV15(1).
Holcus lanatus SV21(1)
Luizula campestris SV1(1), 2(2), 13(2),
 19(1), 24(1)
Hordeum stricta SV11(1)

Plantago lanceolata SV6(3), 9(1)
Plantago maritima AH(1), SV6(1), 12(1), 16(2), 19(1), 24(1)
Salix anglica AH19(1)
Veronica officinalis AH22(1), SV9(1), 12(1), 14(2).

APPENDIX 24. Beacon Hill plot. Experiment to compare the viable seed "banks" in soil taken from the tops of ant-hills (AH) and from the pasture (SV)

SAMPLE COLLECTION

I selected 25 random AH from the 1947 numbered mounds in my plot by using random number tables. Mounds with diameters <30 cm. were not sampled. On 22nd to 23rd April 1969 I took a turf 20 x 20 cm. and 5 cm. deep from the summit of each AH, and a similar turf from the SV, 0.5 m. away from each mound in a random direction.

SAMPLE TREATMENT

In the laboratory, I carefully removed vegetation and roots from the soils. The Ao (litter) horizon was retained (when present) since seeds might have been embedded in it. I air-dried the soils until 1st May 1969 and then weighed them, large stones being removed when possible. The total weight of soil collected from each AH was compared with the total weight of soil collected from its associated pasture quadrat. When one exceeded the other by more than 5%, soil was removed from the base of the heavier sample until it was within 5% of the weight of the lighter sample of the pair. Samples were broken up and stored in polythene containers at laboratory temperature (15-25°C) until March 1970.

EXPERIMENTAL METHOD

Samples 1, 2 and 3 were placed in turn on a 2 mm. sieve and washed with a strong jet of water. The seeds were caught on a 0.02 mm. sieve underneath, but the samples were reduced in volume because silt and clay particles were washed through both sieves. The remaining 22 samples were not treated in this way. Each sample (or parts of it) was placed in a plastic dish 15, 22.5 or 50 cm. in diameter, as needed to give a soil depth of 3 cm. Samples were put in an unheated glass frame on the Botany School roof. The two samples in each pair were kept together, but pairs were randomised. I kept the soils moist with tap water throughout the experiment, which ended on 3rd November 1971. On 14 occasions, roughly at intervals of one month in summer (less frequently in winter), I removed all the seedlings I could identify, and thoroughly churned up the soil in each pot. On occasions 2, 4, 6 etc. I re-randomised the blocks; ten dishes filled with J.I. compost were randomised amongst the blocks.

RESULTS

The results are given overleaf for all species except Festuca sp. and Agrostis stolonifera, three seedlings of which appeared in the control pots. The symbols beside the species names in the table below, represent the results of testing the null hypothesis that the true number of seedlings of a species identifiable from ant-hill and pasture samples was the same.

SOURCES OF ERROR

The sources of error listed at the end of Appendix 23 also apply to this experiment, except for "identification errors".

RESULTS (Further results overleaf)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	TOTAL	† SIG	
<i>Arenaria serpyllifolia</i>	AH	2		1										1	1		10	1			2	37	41	59	7	1		143	**W
	SV																									1	1	1	
<i>Carex flacca</i>	AH																											0	**W
	SV		1			5		4	15	2			2		13	1	11	4			11	1		2				70	
<i>Fragaria vesca</i>	AH	4	4	4	2				1		1		1																
	SV	41		1	17	7		2	51	1						5	1		2	1		2	1			1	1	28	NSW
																2			1			1				2	1	127	
<i>Helianthemum chamaecistus</i>	AH	5		1	2	4	1		6	6			5	5	1													38	NSW
	SV	49	2	5	11	1		21	20	7		6	1			2			1				1	2				125	
<i>Holcus lanatus</i>	AH	5	5	1					14																			26	**W
	SV	20	27	15	29	15		57	51	4					1		4											275	
															1		42								18				
<i>Leontodon hispidus</i>	AH										1																	2	*W
	SV	1		2	2											1	1			1						1		11	
<i>Linum catharticum</i>	AH	1			5						43			21		2						13		1				84	NS
	SV	0					11					11		9		2	5				2	3						52	
<i>Plantago lanceolata</i>	AH				1		1																					9	NS
	SV	2			1		6						1			5		2							2	1		14	
<i>Prunella vulgaris</i>	AH	2	2	1				3	2		10						1	2			1							24	NS
	SV	1			7		2	1	2		1	1	1		3	2	3		1	2	1	8				1	37		
<i>Thymus drucei</i>	AH				2			1	2	1	12	1	5				2	1										29	NSW
	SV				1										1	1		2	1	1		1					8		
<i>Veronica chamaedrys</i>	AH	11	70	67	2					2	1		15															177	NS
	SV	12	53	55	34	1		1	1	8						1	2	1			1	4						181	
<i>Viola hirta</i>	AH							1																				1	**W
	SV	3		5	6	4		53	10	4						2												92	
																										2			

† Two-tailed Wilcoxon signed-ranks tests for matched pairs were used.

... = $P > 0.05$; * = $0.05 > P \geq 0.01$; ** = $P < 0.01$.

Remaining seedlings from Aston Rowant soils

- Agrostis tenuis SV5(1)
Anthoxanthum odoratum SV5(3)
Aphanes arvensis AH3(1), SV21(1)
Arrhenatherum elatius SV4(1).
Asterula cymatophylla SV15(1)
Bellis perennis SV7(1)
Carex corymbifolia SV1(1), SV5(1)
Cerastium holosteoideum AH20(4), 21(1), SV21(1)
Chaenorchium minus AH2(2), 4(1), 13(1), 15(1), 19(1).
SV4(1), 15(1)
Cirsium acule SV5(1)
Cirsium arvense SV6(4)
Crenis capillaris AH12(2), 17(2), 18(1).
SV2(1), 3(7), 4(1), 12(1), 18(7), 23(1), 24(5)
Dactylis glomerata AH3(1)
Galium aparine AH25(1)
Galium mollugo SV1(1), 2(4)
Helictotrichon pratense SV2(1), 7(4), 15(4)
Koeleria cristata SV5(1)
Lotus corniculatus SV5(1), 15(2), 24(1), 17(1), 20(1)
Lucula campestris SV1(1), 2(1), 7(2)
Matricaria recutita SV15(1)
Medicago lupulina AH2(1), 4(2), 8(4), 17(1).
SV1(1), 6(1)
Myosotis ramosissima AH1(1), 3(1), 13(1).
SV2(2), 6(1)
Roa pratensis SV15(2)
Polycala serpyllifolia AH10(4)
Portentilla erecta SV5(1)
Poterium sanguisorba AH6(1).
SV4(3), 5(1), 13(1)
Ranunculus repens AH4(1), SV5(45), 16(1)
Rubus fruticosus AH2(1), 3(1), 8(2), 18(2).
SV1(4), 4(5), 6(1), 7(2), 8(1), 13(1), 15(1), 21(1)
Sambucus nigra AH1(1), 2(2), 3(1), 7(1).
SV1(1), 2(5), 3(2)
Senecio jacobaea SV4(1), 21(1)
Taraxacum officinale agr. SV5(1), 8(1)
Trifolium repens SV8(1)
Trisetum flavescens SV2(1), 7(1), 8(2), 16(1)
Urtica dioica SV4(1)
Veronica arvensis A1(1), A5(1)
Veronica officinalis AH1(1), 11(1), 12(1). SV3(1)
Viola riviniana AH21(1). SV7(1)

Unidentified: AH1(3), 12(3), 17(2), 18(1), 25(1).
SV1(4), 8(1), 15(1), 21(1)

APPENDIX 25 Relationships between (i) my estimates of the volume of newly-heaped soil and the actual volume heaped onto ant-hills; (ii) volume of soil heaped onto the same mound in two successive years.

On 17th August 1970 and 17th August 1971 I estimated the volume of soil newly-heaped onto the same 51 ant-hills on my Beacon Hill plot. On both occasions, the newly-heaped soil was collected from the same 20 of these mounds with a spoon. Soil from each ant-hill was poured into a measuring cylinder to assess its volume. The results are summarised in Fig 56, overleaf.

DISCUSSION

These data suggest that my estimates of heaped soil volume are reliable. Since I had underestimated heaped soil volume in 1970, I changed my concept of it, and in 1971 almost perfect estimates ($b = 0.98$) were obtained.

The significant ($P < 0.01$) correlation between soil heaping in 1970 and 1971 on the same mounds strengthens my belief that a single estimate of the volume of newly heaped soil may give a reliable indication of building activity on a mound over several years.

SOURCES OF ERROR

- (i) it was often difficult to collect soil from around the bases of plants;
- (ii) it was sometimes difficult to decide where new soil ended and old began;
- (iii) the regression lines would be inaccurate if the volume of soil in a measuring cylinder differed from its volume on the mound. Nevertheless, the correlation coefficient between measured and estimated volumes would remain high.

FIG. 56 (overleaf)

FIG 56 a (Top). Relationship between estimated and measured volumes of newly heaped soil in both 1970 and 1971. Bartlett's three-group method was used to calculate both regressions, since both estimated and measured soil volumes were random variables.

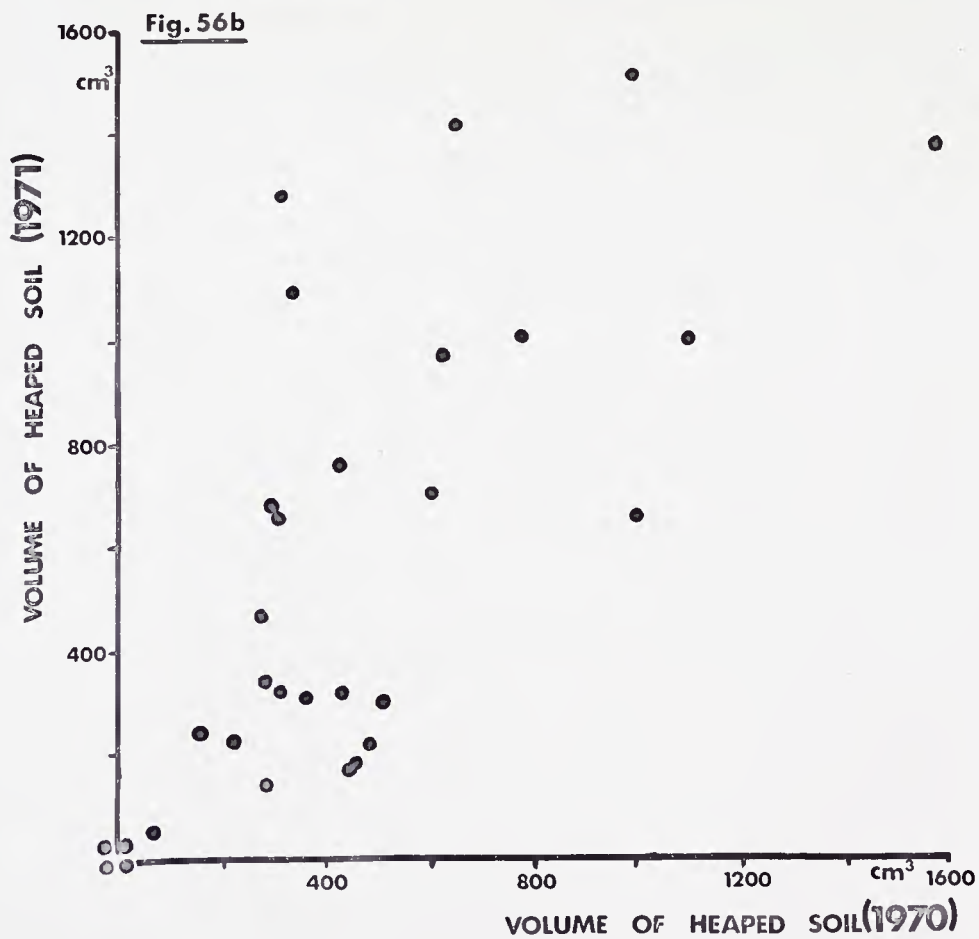
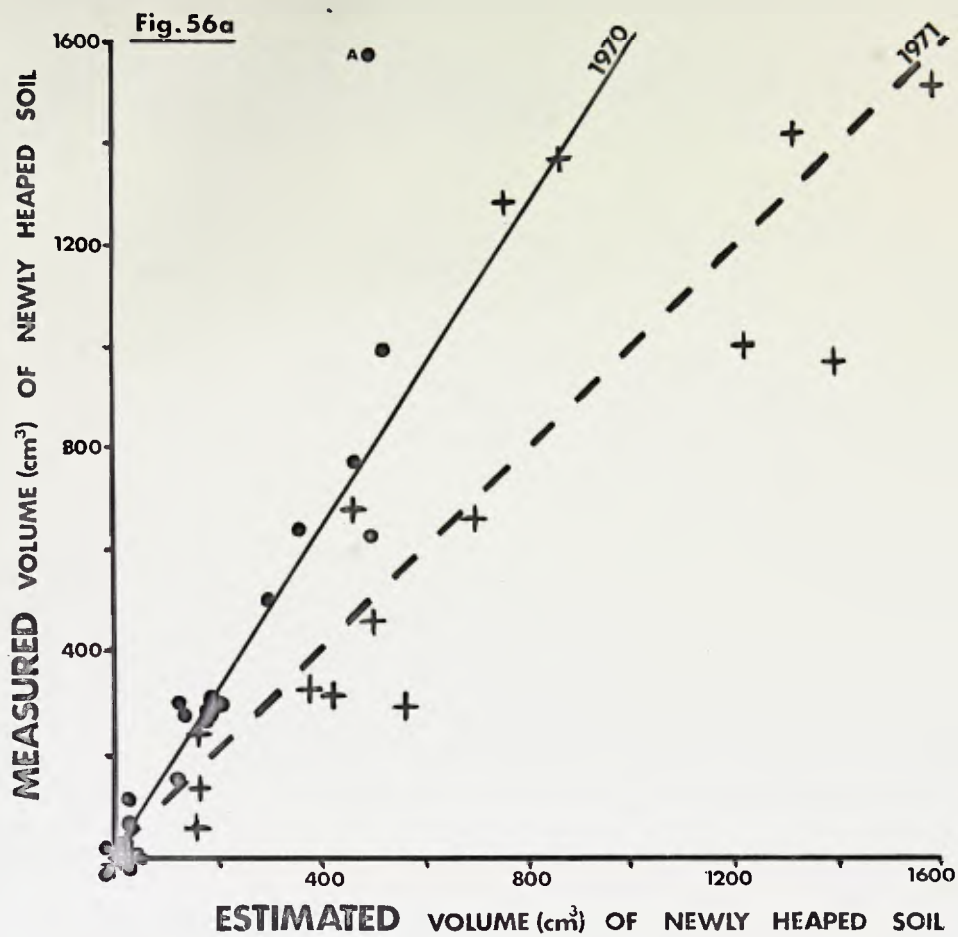
1970. Black dots, continuous line. The correlation coefficient between measured and estimated volumes was $r(16) = 0.90$ ($P \leq 0.01$ from $\rho = 0$)

The line represents the regression equation $\hat{M} = 11.42 + 1.57 \hat{E}$, where M = measured value; E = estimated value. Point A was not included in the regression calculations (suggestion of Dr. M. G. Bulmer); all the vegetation on this ant-hill was buried, so that I could not easily gauge the volume of heaped soil.

1971. Crosses, dashed line $r = 0.91$ ($P \leq 0.01$ from $\rho = 0$) Line represents the equation $\hat{M} = 16.12 + 0.98 \hat{E}$

FIG 56 b (Bottom). Volume of newly-heaped soil on the same 50 ant-hills in two successive years. $r(28) = 0.71$ ($P < 0.01$ from $\rho = 0$). For 19 mounds, volumes of collected soil measured in 1970 and 1971 are plotted. For 11 ant-hills, field estimates (E) made in both years were converted to M by using the appropriate regression equations.

The 3 correlation coefficients given above were recalculated, using a square root transformation of both variates. $r = 0.96$ ($P \leq 0.01$) in all three cases.



APPENDIX 26. Estimation of the precision of subjective sampling on a percentage scale

I sampled two 0.25 m² quadrats and an ant-hill, on my Beacon Hill plot, five times each between 28th September and 6th October 1971, to investigate the precision of my subjective estimates of percentage cover.

METHODS

I selected and marked three sampling points, representative of species-rich (Q1), less diverse (Q2) and ant-hill (AH) vegetation. Q1 bore short vegetation 2-4 cm. high but Q2 was covered with tussocky grasses to 12 cm. high.

I estimated the percentage covers of all species present in each area on an integer scale (1-100). Species with less than 1% cover were given +. I also noted Bare ground (%) and the time taken in sampling. Results are overleaf.

COMPARISON WITH EXPECTED PRECISION OF POINT QUADRAT RECORDING

I confined my attention to the 27 cases in which a species had a mean percentage cover exceeding 2% in a sampled area, and calculated the mean % covers and their 95% confidence limits. Then, for comparison, I obtained the expected 95% confidence limits of the means for 1000, 500, 348(Q1), 268(Q2), and 220(AH) randomly arranged point quadrats from the table of binomial confidence limits in Rohlf & Sokal (1969) (Table W, p. 203-14), using their formulae for interpolation. The table summarises the outcome:

Number of point quadrats recorded	Total sampling time (mins)	% of confidence limits at 100 points per hour.	% of confidence limits narrower for point quadrats than subjective estimation
1000	600		48%
500	500		30%
348 (Q1)	209	}	15%
268 (Q2)	161		
220 (AH)	152		

*Actual recording time for five subjective estimates.

This method, the best I could devise, only provides a very crude quantitative comparison, which must be interpreted cautiously. A mean 167 minutes of subjective estimation achieved about the same "precision" as expected in 600 minutes of point quadrat recording at 100 points per hour. This does not mean, say, that half an hour of subjective estimation would yield the same "precision" as two hours' point quadratting.

DISCUSSION

Yet these data, together with the considerable agreement between all five samplings of the same area, suggest that my estimates of percentage cover by eye were at least as precise per unit time, and probably more so, than point-quadrat recording would have been. Nevertheless, 100 points per hour is an optimistic (for me) rate of working; for example, it does not take into account the number of leaf-layers through which the pins must be followed, or the time taken to move and set up the topograph. Other factors which increase recording time or reduce the precision of point-quadrat recording are mentioned in Table 16, p 48.

I thus attach considerable credence to comparisons between my subjective estimates of percentage cover. Two sources of experimental error are worth mentioning, the first tending to increase precision and the second tending to reduce it. Firstly, I remembered the % cover of Thymus on the ant-hill when I sampled it for the second and third time. I sometimes recalled the positions of Ranunculus (Q1), Agrostis (Q2), and Carex flacca, Gladonia rangiformis (AH). Secondly, on 2nd October I realised that I had been slightly underestimating % cover and made a conscious shift in my estimates; the highest total covers in both

Q1 and Q2 were recorded on that day. Thus the results probably reflect as large a fluctuation in my concept of percentage cover as might occur unconsciously over a longer period.

OTHER SOURCES OF ERROR IN SUBJECTIVE RECORDING

(i) The largest estimation errors occur in the mosses Pseudoscleropodium (Q2) and Dicranum spp (Q2); thus the % covers of mosses given in this thesis should be interpreted cautiously (cf Watson 1960 p.399).

(ii) Only in one of the fifteen samples were all the species in the area recorded; in the first ant-hill sample, ten species were missed! Thus the number of species recorded in a sample only roughly indicates its species richness; many rare species are not found in a single recording.

<u>Quadrat</u>	Q1	Q2	Q3
Total number of species/quadrat	47	29	31
Mean no. of species recorded	39.2	27.6	23.8

(iii) 4th October was misty. Because mosses and lichens were much more prominent when hydrated than when dry, Bryum, Barbula, Cladonia - rangiformis (AH) and Camptothecium (Q1) were seen for the first time. Most sampling described in this thesis was done on dry days, and I probably missed many dehydrated bryophytes.

(iv) On 30th September, I was extremely tired. The lowest total numbers of species in both Q1 and AH were recorded on that day.

Results of repeated samplings of the same three areas on Mt. Beacon
Hill plot. Values are subjectively estimated percentage covers.

Date recorded (1971)	28	30	2	3	4	30	2	5	4	5	30	3	4	5	6
	9	9	10	10	10	9	10	10	10	10	9	10	10	10	10
Time taken (mins)	28	33	41	55	52	23	29	34	38	37	23	26	38	21	24
No. species recorded	40	36	37	41	42	29	27	27	28	27	21	25	26	23	24
Total plant cover (%)	104	102	124	116	112	147	163	156	141	145	101	89	86	87	89
Bare ground (%)	1	1	2	2	2						20	20	20	22	20
<i>Achillea millefolium</i>	1	1	2	2	1										
<i>Agrostis stolonifera</i>				1	+	+	+	+	+	+		+	+	+	+
<i>Asperula cynanchica</i>						5	4	3	2	3					
<i>Bellis perennis</i>	2	2	3	3	3						1	+	1	1	1
<i>Campanula rotundifolia</i>	+	+	1	1	+										
<i>Carex caryophylla</i>					+	1	1	1	1	+					
<i>Carex flacca</i>	3	3	3	3	4	2	2	2	2	2	+	+	+		+
<i>Carlina vulgaris</i>	1	1	2	1	1	2	2	2	2	2		+			
<i>Cirsium acaule</i>	7	8	9	7	8	3	3	3	3	2					
<i>Crepis capillaris</i>	+		1	1	+	1	1	1	1	1	1	1	1	+	1
<i>Dactylis glomerata</i>	1	+	+	+	+										
<i>Euphrasia nemorosa</i>	+				+						+		+		
<i>Festuca sp.</i>	30	35	40	35	35	70	60	70	70	72	45	38	35	40	40
<i>Fragaria vesca</i>	1	+	1	1	+	9	7	6	5	5	+	+	+	+	+
<i>Galium mollugo</i>											+	1	+		
<i>Galium verum</i>											1	+	+	+	+
<i>Gentianella amarella</i>	2	1	1	1	1	+	+	+	+	+	+	+	+	+	+
<i>Helianthemum chamaecistus</i>	8	5	7	6	7	7	7	5	5	6	10	10	15	9	11
<i>Heliototrichon pratense</i>	1					+	+				+	+	+	+	+
<i>H. pubescens</i>		1	1	1	1	+	1	1	+	+					
<i>Hieracium pilosella</i>	2	1	2	2	1	3	3	3	4	3		+	+	+	+
<i>Holcus lanatus</i>	+	+	+	+	+	1	+	+	+	+					
<i>Koeleria cristata</i>	3	2	2	2	2										
<i>Leontodon hispidus</i>	11	10	15	18	15	10	15	12	12	14	6	3	3	2	3
<i>Linum catharticum</i>	+	+	+	+	+	+	+	1	1	1	+	+	+	+	+
<i>Lotus corniculatus</i>	2	3	2	3	2	3	3	4	2	1	2	+	+	+	+
<i>Medicago lupulina</i>											7	7	5	6	5
<i>Plantago lanceolata</i>	12	12	16	12	14						2	2	2	1	1
<i>Poa pratensis</i>	1	+				+			+	+				+	+
<i>Polygalavulgaris</i>		+	+	+	+										
<i>Prunella vulgaris</i>	1	3	2	+	2	1	2	1	2	2	2	2	2	2	2
<i>Ranunculus bulbosus</i>	1	+	+	+	+										
<i>Senecio jacobaea</i>	1	1	1	1							1	+	+	+	+
<i>Taraxacum officinale</i>	1			+											
<i>Thymus drucei</i>	1	2	2	3	4	6	7	5	5	4	20	20	20	22	20
<i>Trisetum flavescens</i>	+	1	1	+	1	1	1	2	2	2		+		+	+
<i>Veronica chamaedrys</i>	+	1	+	1	+										
<i>Veronica officinalis</i>	+			+		1	1	1	+	+	+	1	+	+	+
<i>Viola hirta</i>	3	3	1	3	3	3	3	2	2	2		+			
<i>Barbula (convoluta)</i>													+		
<i>Brachythecium velutinum</i>	1	+	+	+	+										
<i>Bryum (erythrocarpum agg)</i>														+	+
<i>Camptothecium lutescens</i>					+										
<i>Campylium chrysophyllum</i>	2	1	2	1	1										
<i>Dicranum spp.</i>	1	1	3	1	1	8	25	25	14	14					
<i>Eurhynchium spp.</i>			+	1	+										
<i>Fissidens sp.</i>	+	+			+										
<i>Hypnum cupressiforme</i>	+	+	+	+	+										
<i>Lophocolea bidentata</i>	+	+	+	+	+										
<i>Mnium (punctatum)</i>	1	+	+	+	+										
<i>Neckera complanata</i>						+		+	+						

<i>Pseudoscleropodium purum</i>	+	1	1	1	+	2	10	5	2	4	1	+	+	1
<i>Rhodobryum rosetta</i>	1		+	+	+									
<i>Rhytidiadelphus squarrosus</i>						5	1	2	2	2				
<i>R. triquetrus</i>						1	3	+	+	1				

Cladonia rangiformis

C. arbuscula

+ + + + +

Present, but not recorded.

APPENDIX 28. Results of survey of 206 ant-hills (AH) and 105 surrounding vegetation (SV) quadrats on the north side of Mt Beacon Hill plot, August - October 1969

The site is described, methods used in collecting the data are explained, and the results are analysed in Chapter 4, p 44. This appendix lists the raw data.

Quadrat records for the most frequent species, and "environmental" data associated with each sample, are listed in the large table. G = signs of grazing, D = droppings (mainly rabbit), S = scratching, T = trampled (path). AHs are numbered 1-206 and SV quadrats 1-105. Each even-numbered AH is associated with a SV quadrat, i.e. AH2 and SV1 were sampled together, AH4=SV2, AH6=SV3 etc. Vegetation height can be worked out from Figs. 2 and 57; mound volume and surface area, and the number of species in a sample, can be calculated from data in the table; but the numbers of individuals of Leontodon, Carex flacca, Poterium Cirsium, Plantago lanceolata and Hieracium, and their burial, have been left out owing to lack of space.

Records of the less frequent species are given below:

LESS FREQUENT SPECIES IN SAMPLE

- Acinos arvensis AH190 (1%)
Agrimonia eupatoria SV9(4%)
Anthoxanthum odoratum SV55(4%), 58(1%), 59(1%), 74(1%), 100(1%), 101(1%), 103(1%).
 AH105(1%), 121(1%), 205(20%).
Artemisia axerollifolia AH5(1%), 15(1%), 51(1%), 51(1%), 71(1%).
Arrhenatherum elatius SV11(2%), 12(1%), 15(2%), 16(1%), 17(4%), 18(1%), 40(8%),
 42(12%), 43(1%), 95(1%).
 AH 57(1%), 80(3%), 81(3%), 86(1%), 206(1%).
Campanula glomerata AH 74(1%)
Carlina vulgaris SV4(1%), 24(1%), 51(2%), 69(1%), 72(1%), 75(1%), 79(2%), 80(1%),
 81(1%), 82(1%), 86(1%), 88(1%), 89(1%), 90(1%), 93(1%).
 AH129(1%), 138(1%), 139(1%), 142(1%), 144(1%), 150(1%), 168(1%),
 175(1%), 193(2%), 195(1%)
Catanodium rigidum AH202(1%)
Cerastium holosteoides AH9(1%), 10(1%), 22(1%), 54(1%), 55(1%), 62(2%), 65(1%),
 73(1%), 111(1%), 151(1%), 160(1%)
Cirsium arvense SV1(7%), 10(1%)
Cirsium palustre SV3(11%)
 AH45(6%)
Coeloglossum viride SV2(1%), 25(1%), 39(1%), 41(1%)
Crataegus monogyna SV5(1%), 28(1%), 40(2%), 42(1%)
Dactylis glomerata SV9(2%), 12(2%), 13(2%), 42(4%), 45(8%), 55(8%), 74(1%), 82(2%),
 84(3%), 85(3%), 86(3%), 87(5%), 88(1%).
 AH19(3%), 25(2%), 26(2%), 27(1%), 84(3%), 86(2%), 88(1%), 147(1%),
 168(1%), 169(1%), 172(3%), 173(4%), 181(1%).
Deschampsia caespitosa AH12(20%), 53(15%), 76(14%)
Erigeron acer SV94(1%),
 AH110(1%)
Filipendula vulgaris SV103(1%)
Himnocypris comosa SV13(1%)
Hypochoeris radicata SV34(3%), 37(1%), 52(2%), 55(1%), 57(2%), 62(2%), 65(2%),
 65(2%), 67(3%), 69(3%), 74(1%), 75(1%), 79(1%), 92(1%),
 95(3%), 96(1%), 99(2%), 103(1%).
 AH49(2%), 51(1%), 54(1%), 64(1%), 127(1%), 135(1%), 151(1%).
Luzula campestris SV82(1%), 103(1%).
 AH174(1%), 196(1%), 206(1%).
Myosotis ramosissima AH9(2%), 51(1%).
Pastinaca sativa SV69(1%).
 AH24(1%), 200(1%), 203(1%)
Pteris hieracioides SV17(1%), 92(2%).

Plantago media SV23(4%), 81(1%).
AH5(1%), 163(1%).

Rosa pratensis SV9(1%), 11(1%), 96(1%).
AH25(2%), 156(1%), 159(1%), 182(1%), 185(1%), 186(1%), 194(1%), 196(1%),
198(1%).

Polysiala vulgaris SV44(1%), 64(1%), 73(1%), 84(1%), 89(1%), 100(1%).
AH104(1%), 160(1%), 195(1%).

Potentilla erecta SV93(1%).

Potentilla reptans SV10(1%), 11(1%), 15(1%), 33(1%), 44(1%), 54(1%), 60(1%).
AH17(1%), 20(1%), 25(2%), 60(1%), 61(1%), 156(1%), 186(1%), 203(1%),
206(1%).

Poterium sanguisorba SV14(7%), 19(1%), 33(9%), 34(6%), 35(1%), 36(5%), 37(5%), 39(3%),
48(1%), 56(10%), 63(1%), 67(1%), 81(1%), 93(1%), 95(6%), 97(3%),
98(3%), 99(4%), 103(1%).
AH44(1%), 66(2%), 72(1%), 98(2%), 101(1%), 112(1%), 190(1%),
193(1%), 197(2%), 200(1%), 202(1%).

Ranunculus bulbosus SV14(1%), 20(2%), 30(2%), 51(1%), 52(1%), 34(1%), 55(1%),
47(1%), 51(1%), 55(1%), 59(1%), 69(1%), 87(1%), 91(1%),
92(1%), 97(1%), 102(1%).
AH26(1%), 102(1%), 110(1%), 185(1%), 191(1%), 196(1%), 197(1%).

Ranunculus repens SV21(2%), 24(2%), 52(1%), 50(1%), 50(1%), 53(2%), 56(1%).
AH16(1%), 83(1%).

Rhamnus catharticus AH132(1%).

Rosa sp. SV7(1%), 29(1%), 49(1%).
AH193(1%).

Rubus sp. SV15(6%).

Scabiosa columbaria SV45(1%), 44(1%), 86(2%).
AH26(1%), 201(1%).

Sida sanguinea SV5(1%), 52(1%).

Taraxacum officinale agg. SV2(1%), 43(2%).
AH42(1%), 49(1%), 50(1%), 69(1%), 76(1%), 144(1%), 147(1%),
158(1%), 182(1%), 193(1%).

Trifolium dubium AH1(1%), AH2(1%), 24(1%), 63(1%), 157(1%), 206(2%).

Trifolium pratense SV18(1%).

Veronica arvensis AH120(1%), 121(2%), 169(1%), 185(1%).

Viburnum lentum SV1(4%), 24(1%).

Zerna erecta SV44(1%), 50(4%).

Barbula cylindrica AH151(1%), 184(1%), 199(1%).

Brachythecium rutabulum SV67(1%), 93(1%), 99(1%).
AH81(1%), 94(10%), (158(1%)), 171(1%), 180(1%).

Brachythecium velutinum SV45(1%), 74(1%), (79(1%)), 84(1%), 85(1%), 88(1%), 96(1%),
102(1%).
AH49(1%), 76(1%), 140(1%), 145(1%), 150(1%), 152(1%),
153(1%), 169(1%), 171(1%), 172(1%), 173(1%), 176(1%),
(177(1%)), 180(1%), 184(1%).

Briza (bicolor) SV71(1%).
AH153(1%), 170(1%), 173(1%).

Briza caespiticia AH7(1%), 69(1%), 78(2%), 107(1%), 110(1%), 114(1%), 137(1%),
139(1%), 151(1%), 199(1%).

Briza capillare AH88(1%), 90(1%), 110(1%).

Briza (erythrocarpa) agg. AH20(1%), 57(1%), 61(6%), 65(1%), 85(1%), 144(1%), 148(1%),
151(1%), 160(1%), 166(1%), 180(1%), 182(1%), 184(1%),
194(1%).

Campylium chrysophyllum SV75(1%), 85(1%), 103(1%).
AH149(1%), 180(1%), 184(1%).

(Cistophyllum piliferum) AH156(1%), 161(1%), 180(1%).

Ctenidium molluscum SV16(1%), 25(1%), 35(4%), 41(2%), 64(3%), 68(1%).

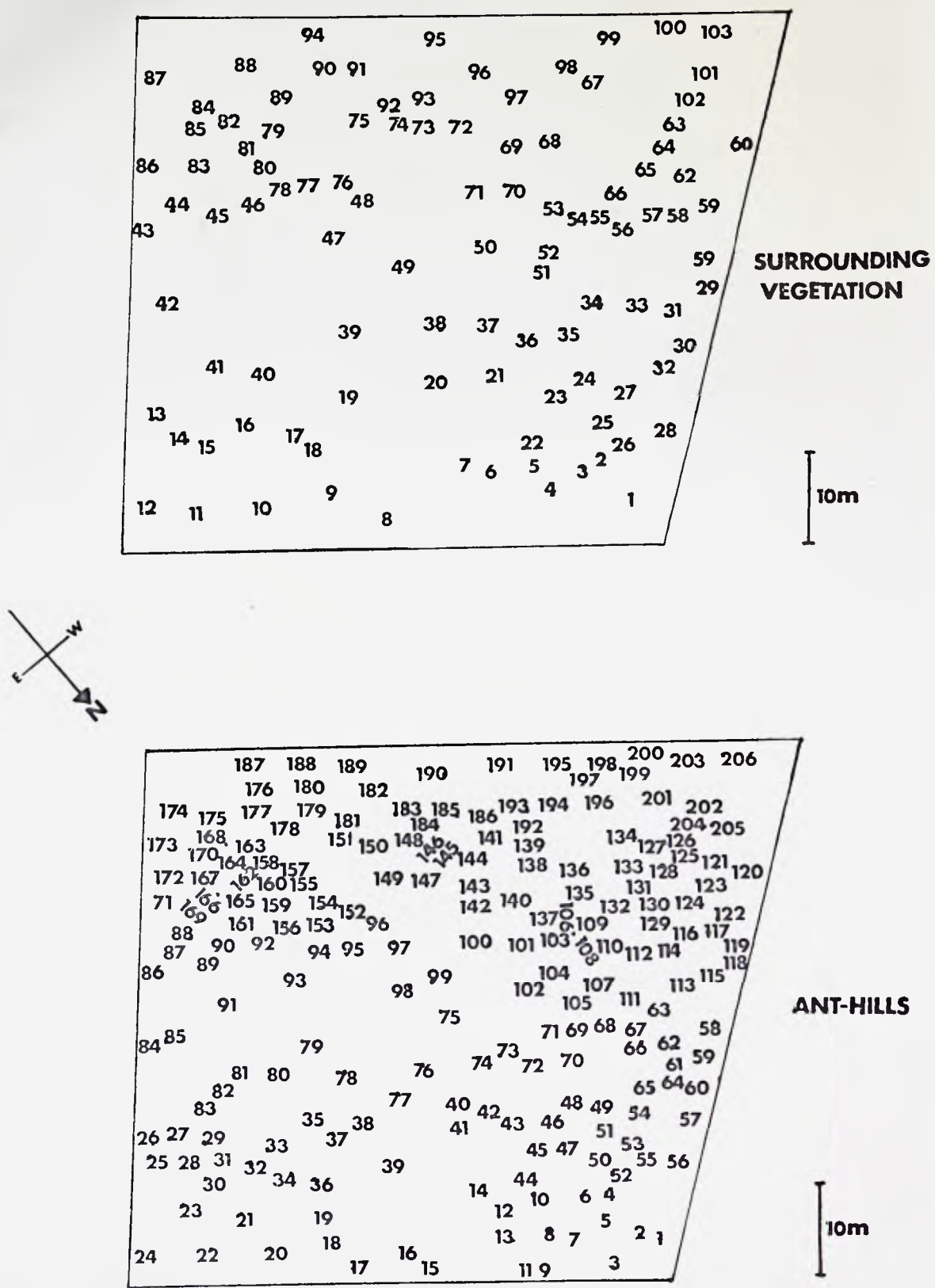
(Eurychium confertum) SV28(1%), 86(1%), 87(1%), 101(1%).
AH97(1%), 141(1%), 148(1%), 162(1%), 164(1%), 165(1%),
184(1%).

Eurychium proelungum SV75(1%), 79(1%), 89(1%), 102(1%).
AH56(1%), 105(1%), 183(2%).

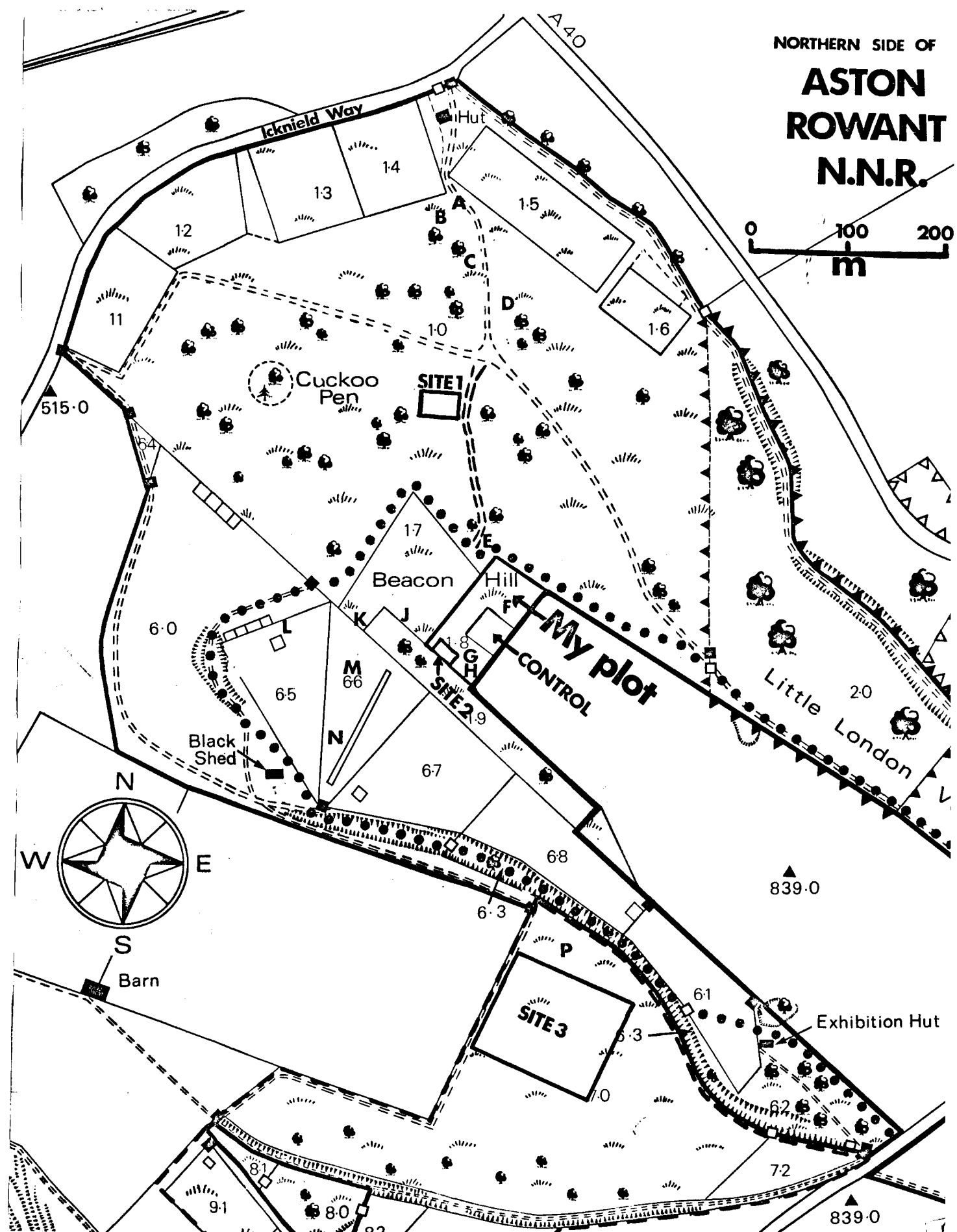
(Eurychium swartzii) SV29(1%).
AH65(1%).

- Rhynchium strictum* SV31(1%), 46(1%), 74(1%), 88(1%), 97(1%), 99(1%), 101(1%), 103(1%).
AH171(1%), 193(1%)
- Fissidens (adianthoides)* SV37(1%), 45(3%), 46(1%), 64(2%), 68(1%), 72(2%), 74(2%), 77(1%), 79(1%), 83(2%), 85(1%), 92(1%), 93(1%), 96(2%), 99(1%), 101(1%), 102(2%), 103(1%).
AH149(1%), 154(1%), 180(1%), 184(1%), 185(1%), 198(1%), 199(1%).
- Fissidens (cristatus)* SV57(3%), 63(2%), 66(3%), 67(2%), 69(2%), 71(4%), 75(2%), 81(1%), 82(1%), 84(3%), 86(2%), 94(1%), 95(1%), 98(1%).
AH69(1%), 87(1%), 105(1%), 106(1%), 113(2%), 128(1%), 131(1%), 133(1%), 134(1%), 136(1%), 142(1%), 145(1%), 146(1%), 149(1%), 150(1%), 153(1%), 155(3%), 156(1%), 157(2%), 160(1%), 164(1%), 165(1%), 179(1%).
- Fissidens (tardifolius)* SV35(1%), 41(1%), 46(1%), 70(1%), 71(1%), 75(1%), 77(2%), 81(1%), 89(2%), 96(1%), 97(1%).
AH74(1%), 139(1%), 144(1%), 148(1%), 151(1%), 173(1%), 176(1%), 177(1%), 178(1%), 184(1%), 193(1%), 199(1%).
- Frullania tamarisci* SV31(1%), 48(1%), 74(1%), 81(1%), 82(3%), 84(1%).
- Hylocomium splendens* SV19(1%), 22(1%), 23(1%), 52(3%), 83(1%).
AH21(1%)
- Hycomium compressiforme* SV57(2%), 45(1%), 64(4%), 65(1%), 67(6%), 74(1%), 77(3%), 78(1%), 81(1%), 82(1%), 94(1%), 95(1%), 98(1%), 99(1%), 100(1%), 101(1%).
AH127(3%), 128(1%), 132(1%), 199(1%).
- Lonchoclea bidentata* SV45(2%), 62(2%), 77(1%), 82(1%), 84(2%), 86(2%), 87(2%), 90(3%), 94(1%), 101(1%).
- Mnium (affine)* SV85(1%), 87(1%), 101(1%), 103(2%).
AH88(3%), 173(7%).
- Mnium punctatum* SV79(1%), 81(2%), 85(2%), 87(5%), 88(1%), 90(1%).
AH16(1%), 56(1%), 57(1%), 127(1%), 129(1%), 158(1%), 160(1%), 166(1%), 171(3%), 174(25%), 175(4%), 177(1%), 180(2%), 187(15%), 197(1%), 199(1%).
- Mnium undulatum* SV28(1%).
AH57(1%), 89(2%)
- Neckera complanata* SV35(3%), 63(1%), 64(2%), 67(1%), 70(1%), 71(1%), 72(1%), 74(2%), 75(1%), 77(1%), 81(1%), 83(1%), 91(1%), 96(1%), 97(1%), 101(1%).
AH134(1%), 184(1%)
- Porella platyphylla* SV41(2%), 86(1%).
AH69(1%)
- Cladonia rangiferina* SV48(1%), 63(1%), 67(1%), 70(1%), 75(1%), 79(1%), 81(3%), 82(1%), 84(1%), 88(1%), 89(1%), 92(1%).
AH127(1%), 162(1%), 177(1%).

Appendix 27 (Fig 57)
SAMPLED PATTERN AT N.E. END OF MY BEACON HILL PLOT



Appendix 29. Folding-out map of Aston Rowant N.I.R., showing sampled sites.



Appendix references

- Aitcheson, P.A., Smart, D.A. & Greig, J.(1967). Observations on ant-hills at Rhossili Down. Oxford University Botany School field course project report, unpublished.
- Blackith, R.E., Siddorn, J.W., Waloff, N. & Van Emden, H.F.(1963). Mound nests of the yellow ant, Lasius flavus L., on waterlogged pasture in Devonshire. Ent.Mon.Mag.99(4th series,24),48-49.
- Brown, I.C.(1943). A rapid method of determining exchangeable hydrogen and total exchangeable bases of soils. Soil Science 56, 383-7.
- Clark, P.J. & Evans F.C.(1954). Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology, 35, 445-53.
- Davis, R.(1797). A new map of the county of Oxford from an actual survey....London.
- Golding, E.W. & Stodhart, A.H.(1952). The selection and characteristics of wind-power sites. Electrical Research Association Report C/T 108, London.
- Grubb, P.J., Green, H.E. & Merrifield, R.C.J.(1969). The ecology of chalk heath: its relevance to the calcicole-calcifuge and soil acidification problems. J.Ecol.57, 175-212.
- Harley, R.M. & Myerscough P.J.(1959). Aston Rowant N.N.R.- Botanical Survey. Reserve management plan, Unpublished.
- Hopkins, B.(1954). A new method for determining the type of distribution of plant individuals. Ann.Bot., Lond., N.S. 18, 213-27.
- Jackson, M.L.(1958). Soil Chemical Analysis. Constable, London
- Jeffreys, T.(1767). The county of Oxford surveyed.... London.
- Pfeiffer, H.(1953). Von sukzessionsauslosender Tätigkeit mancher Rasenaneisen. Beih. Repert.Spec.nov.Regni. veg.71,224-31
- Peech, M.(1965). Hydrogen Ion Activity. Ch.60 in C.A. Black(Ed.) Methods of soil analysis, Part 2, pp. 914-26.
- Perrin, R.M.S.(1956). Nature of 'chalkheath' soils. Nature, Lond.178, 31-2.
- Pontin, A.J.(1963) Further considerations of competition and the ecology of the ants Lasius flavus(F) and L.niger(L.).J. Anim.Ecol 32, 563-74.
- Rohlf, F.J. & Sokal R.R.(1969). Statistical Tables. Freeman, San Francisco.
- Rorison, I.H.(1967). A seedling bioassay on some soils in the Sheffield area. J.Ecol. 55, 725-41.

Appendix references (continued)

- Thomas, A.S.(1960). Changes in Vegetation since the Advent of Myxomatosis. J.Ecol. 48, 287-306.
- Thomas, A.S.(1963). Further changes in vegetation since the advent of myxomatosis. J.Ecol. 51, 151-86.
- Waloff, N. & Blackith, R.E.(1962). The growth and distribution of the mounds of Lasius flavus(Fabricus)(Hym: Formicidae) in Silwood Park, Berkshire. J.Anim.Ecol.31, 421-37.
- Watson, E.V.(1960). A Quantitative Study of the Bryophytes of Chalk Grassland. J.Ecol. 48, 397-414.