The Dynamics and Distribution of some Plant Species on the Keen of Hamar, Shetland

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Abstract

Autecological and demographic studies on *Cerastium nigrescens* and *Arenaria norvegica* subsp. *norvegica* on the Keen of Hamar and Nikkavord, two ultramafic outcrops on Unst, are reported. The fluctuations in numbers of the two species on the Keen showed differences within the site but in general were related to low spring rainfall, and to number of day degrees above 5.6 °C.

Individuals of the two species were monitored on the Keen from June 1994 to November 1996. Plants of *Cerastium* showed Deevey type two curves and mature plants had a half life of 3.8 years. Most of the seeds germinated from July to November. Plants of *Arenaria* showed a Deevey type one curve with high mortality after flowering in the second year. Many *Arenaria* seedlings were recorded throughout the spring, summer and autumn. Seed bank measurements ranged from 12 - 13 m^{-2} for *Cerastium* and from 24 - 43 m^{-2} for *Arenaria.*

On Nikkavord, *Cerastium* plants occurred on wetter areas than the Keen plants but showed similar population dynamics to them. *Arenaria* plants sampled on Nikkavord showed bigger fluctuations in numbers and flowering frequencies than Keen plants.

Cerastium seeds were sown on Sobul, an ultramafic outcrop, about 6 km SW of the Keen, where the species did not occur naturally. There was germination and establishment after two years. Pilot studies on the Keen revealed the importance of soil surface microtopography for the establishment of *Cerastium* and *Arenaria.*

Keen and Nikkavord *Cerastium* leaves were more densely glandular pubescent than leaves of Faroese *Cerastium arcticum.* The glands produced fats, pectins and other polysaccharides and may be part of an adaptation to drought.

A nickel-rich fully vegetated area on the northern slopes of the Keen suggested that the lower nickel concentrations in the barest soils are not important in retarding successional processes.

Acknowledgements

I thank my supervisor Professor John Proctor for his patient support throughout the Ph.D and Dr. David Slingsby for his interest and enthusiasm. Dr. Roy Sexton interested me in the *Cerastium* hairs and gave me much help together with Linton Brown and Nicola Gray. I thank Dr. Tim Benton for the statistical advice, Dr. Stephen Carter for advice on soils and Alan Duncan for laboratory assistance.

I am grateful for financial support from NERC and from Scottish Natural Heritage (SNH), and to SNH staff for help, particularly Dr. Andrew Dowse and Paul Harvey. Donald Kennedy from the Scottish Wildlife Trust showed me the Beinn Iadain *Arenaria* site and Trondur Leivsson kindly collected *Cerastium* seeds from Streymoy. The Muckle Flugga Shore Station folk were friendly and welcoming, and I am grateful to Laurence Johnson for many lifts and to Wendy Dickson for photographs and seeds.

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CONTENTS

Chapter 1. Introduction

Ultramafic rocks are igneous or metamorphic rocks which are rich in ferromagnesian minerals. Iron and magnesium are always relatively high and silicon relatively low, but other than that they vary in their chemical and mineralogical composition (Proctor & Woodell 1975). In the past, biologists have often used the term 'serpentine' to describe ultramafic rocks, even though the rocks did not contain minerals of the serpentine group. The term ultramafic is used in this thesis.

Many ultramafic rocks have undergone a process of hydrothermal alteration (serpentinisation). The textural changes associated with serpentinisation result in different physical weathering of ultramafic rocks, which may also have an important affect on the soils (Proctor & Nagy 1992), although in temperate areas, at least, ultramafic soils generally reflect the chemical composition of the parent rock.

Ultramafic rocks generally have a vegetation which contrasts with that of the surrounding areas. Although, in Britain, the vegetation is not as distinctive as that reported for many other countries, several of the British sites have an open vegetation of low stature and are the habitat for rare taxa (Proctor 1992). Some sites have quite large areas of skeletal soils e.g. the Keen of Hamar, Shetland (the main study site in this thesis), Meikle Kilrannoch, Angus, and the Hallival/Askival area on the island of Rum. There have been several explanations for the low vegetation cover: low soil nutrient concentrations, high soil Mg/Ca quotients, high soil nickel concentrations, adverse physical factors, or a combination of two or more of these factors (Proctor 1992).

The Keen of Hamar is one of the more striking ultramafic sites in Britain (Proctor & Woodell 1975), having large expanses (about 22 ha) of poorly vegetated ochre-brown skeletal soils and these open soils are the habitat for many rare plants e.g. *Arabis petraea*, *Arenaria norvegica* subsp. *norvegica* and *Cerastium nigrescens,* and also unusual races (with no formal taxonomic status) of more common species e.g. *Rubus saxatilis*, *Plantago maritima* and *Rumex acetosa.*

Monitoring of some of the rare species from 1978-1993 (Slingsby *et al.* 1993) showed that there had been fluctuations in their numbers. The main purpose of this thesis was to investigate the population dynamics of two of the rare species, *Cerastium nigrescens* and *Arenaria norvegica* subsp. *norvegica* growing on the Keen and on the neighbouring Nikkavord ultramafic outcrop, which has much smaller areas of open soils. A second purpose of the thesis was to investigate some autecological aspects of *Cerastium nigrescens* in relation to its drought tolerance and the occurrence and possible function of its glandular hairs. Finally a subsidiary purpose was to shed further light on the role of nickel on the Keen in view of an earlier demonstration (Carter *et al.* 1987 a) of a very local, fully vegetated, nickel-rich area on its northern slopes.

The names of the vascular plants follow Stace (1991) and the bryophytes follow Watson (1981).

Site Descriptions

The Keen of Hamar

The Keen of Hamar, Unst, Shetland (National Grid reference HP 645098), is a hill of ultramafic rock rising to 89 m above sea level (Figs.1.1 and 1.2). It is made up of dunite with some pyroxenite on the eastern part of the site (Amin 1954).

The Keen comprises two parts, the Eastern Keen (a NNR of 30 ha) and the Western Keen (a SSSI of 11 ha) (Fig. 1.3) which are divided by a cattle corridor between areas of pasture. The Western Keen had been used for laying out winter feed for stock, prior to being fenced off in 1986, and now grazing is permitted at very low levels (0.4 sheep per ha), but this option is not currently taken up (Harvey 1997). The whole site had been grazed by farm animals in the past, but there has been no grazing on the Eastern Keen since the early 1970's (Harvey 1997). The Keen had been one of the major areas in the Britain for chromite mining in the nineteenth century (Rivington 1953), and the disused quarries are now full of water.

Fig. 1.1 The Keen of Hamar showing extensive areas of poorly vegetated soils.

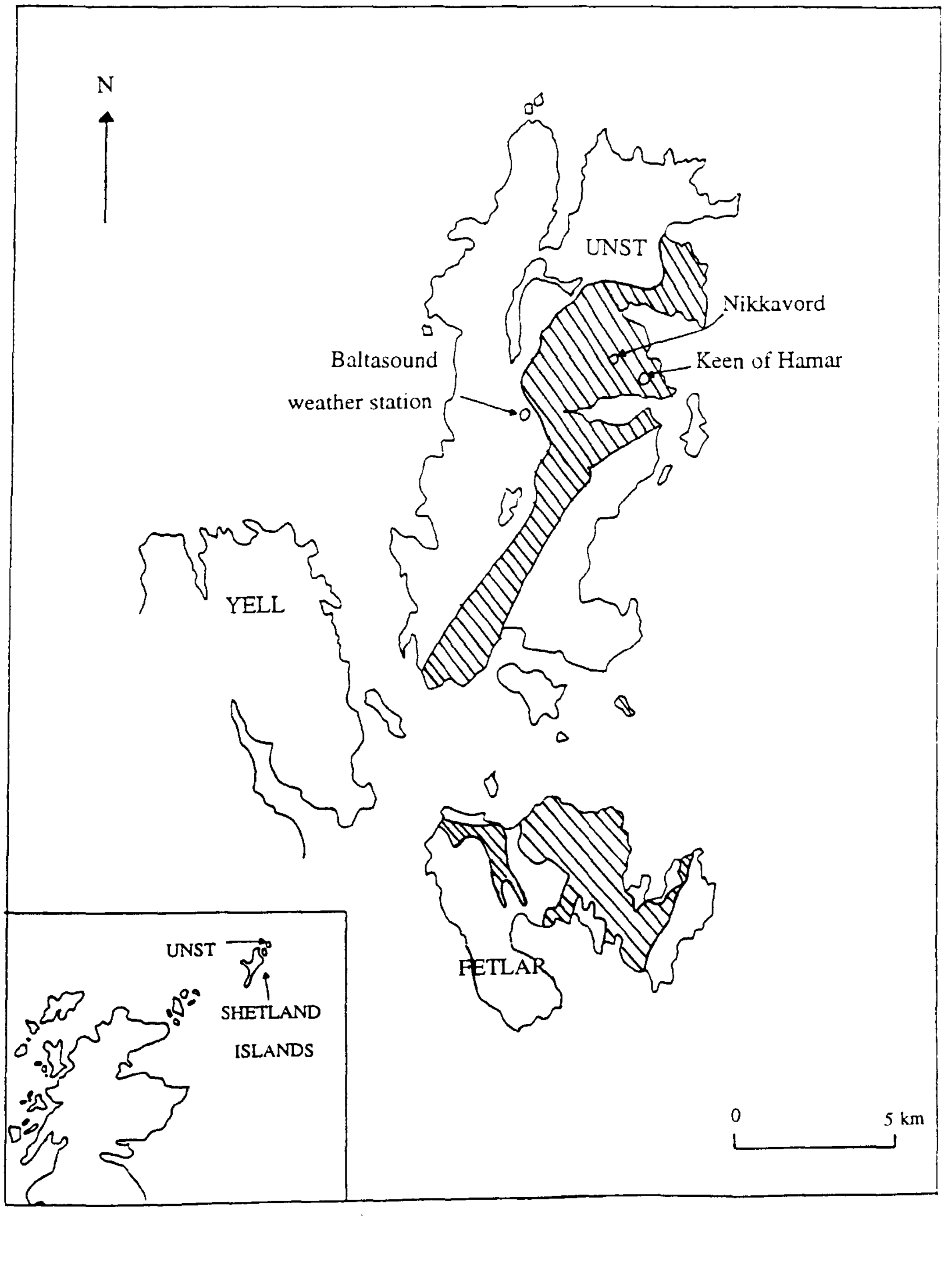


Fig. 1.2 The location of the Keen of Hamar, Nikkavord and the Baltasound weather station on Unst. ultramafic areas on Unst and Fetlar.

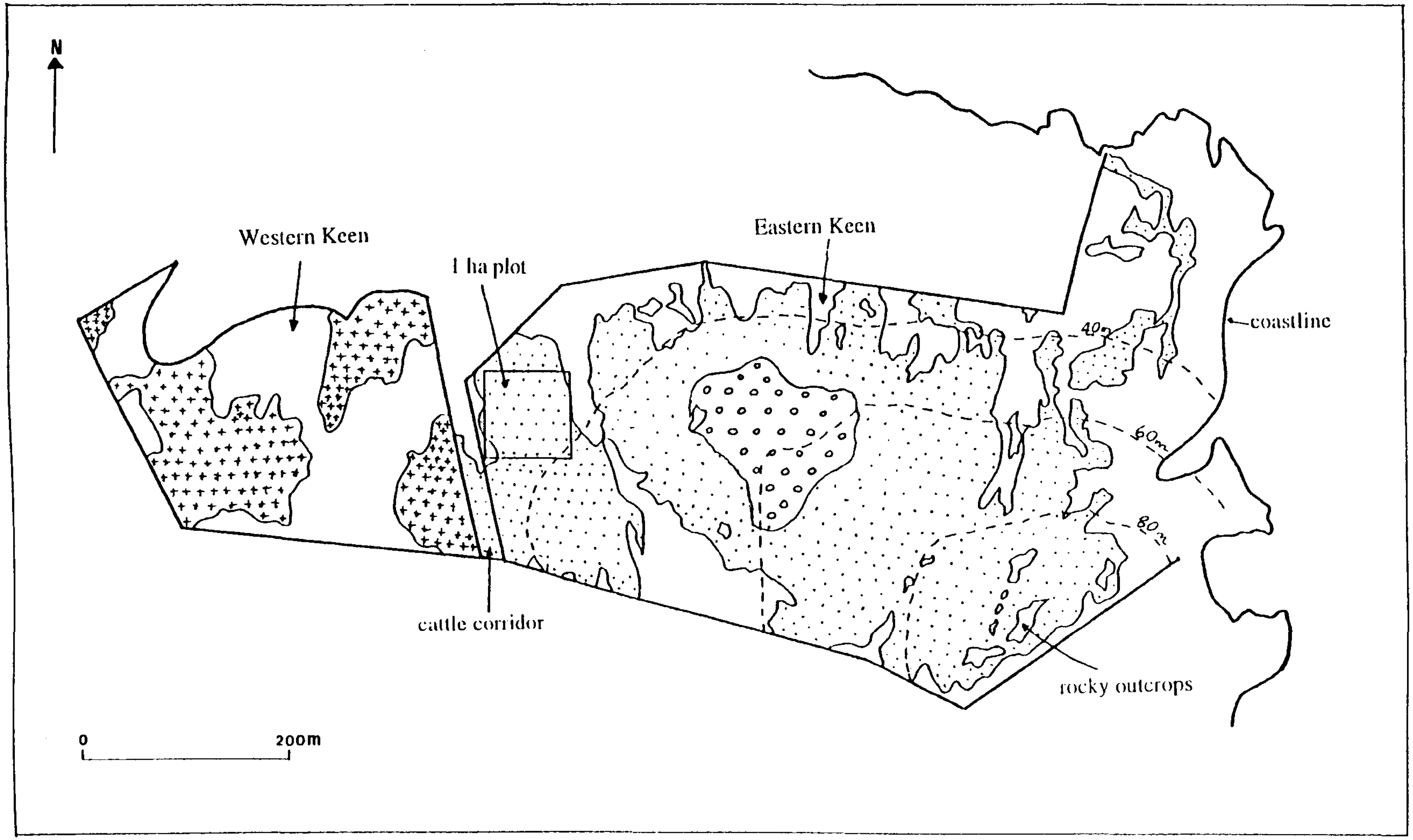


Fig. 1.3 Map of the Keen showing the location of skeletal soils. sparsely colonised soils, moderately colonised soils, well colonised soils.

Most of the neighbouring ultramafic outcrops on Unst support a sedge-grass heath which corresponds to the *Carex flacca-Carex pulicaris-Festuca* sociation of Spence (1970) and the *Antennaria dioica-Carex pulicaris* Association of Birse (1982). Much of the closed vegetation on unimproved parts of the Keen consists of this vegetation type, but the Keen is unique in having extensive open areas (about 22 ha according to Dore 1986) of poorly vegetated skeletal soils comprising a Species-poor debris in a mosaic with Species-rich debris (*sensu* Carter *et al.* 1987 a). The Species-rich group corresponds to the *Arenaria norvegica-Cardaminopsis petraea* sociation of Spence (1970) and the *Cerastium nigrescens-Armeria maritima* Association of Birse (1982). It has a distinct species composition with abundant *Armeria maritima, Plantago maritima,* and *Silene maritima* and includes the rarities *Cerastium nigrescens, Arenaria norvegica* subsp. *norvegica*, and *Arabis petraea.* The Species-poor group has lower numbers of the rarities and a higher abundance of *Anthyllis vulneraria.*

On the Western Keen there is Enriched debris (*sensu* Carter *et al.* 1987 a) which has many weedy species such as *Cerastium fontanum* subsp. *glabrescens*, *Sagina nodosa* and *Sagina procumbens* but there are also high numbers of the rarities including *Cerastium nigrescens* and *Arenaria norvegica* subsp. *norvegica* (Slingsby 1979).

In the past, many researchers had tried to explain why the skeletal soils had remained open, but several ecological factors, such as low major nutrient concentrations, metal toxicity and adverse climatic factors failed to account for the distinction from other ultramafic areas on Unst.

Carter *et al.* (1987 a) did extensive physical and chemical analyses on Keen soils. They confirmed that there were no observed toxic factors which might explain the retarded colonisation of the skeletal soils, but field descriptions of the soils and thin-section analyses revealed that the skeletal soils were derived from the underlying bedrock while soils supporting heathland were derived from ultramafic drift. The bedrock of the Keen has unusual weathering characteristics. In contrast to the surrounding ultramafic outcrops, where the bedrock forms rounded masses with few deep joints, the Keen is crossed by two sets of fractures breaking the rock into 1-5 cm fragments. The unusual weathering produces shallow, coarse-textured soils which have a low water-holding capacity and are prone to physical instability in the winter. Carter *et al.* (1987 a) suggested that moisture stress and soil instability were important factors in causing the retarded colonisation of skeletal soils.

There is one area on the north west slopes of the Eastern Keen where there is evidence of frost heaving in the form of stone stripes (parallel lines of alternating coarse and fine debris) (Fig. 1.4). These are known to be active, since they re-formed in a marked plot in the winter after the soil surface had been mixed (Carter *et al.* 1987 a). On these soils, the vegetation cover is very low (<5%). For the purposes of this study I have considered skeletal soils with three levels of plant cover: moderately colonised skeletal soils on the Eastern Keen (5-30% cover), sparsely colonised soils on the north west slope of the Eastern Keen (0-5% cover) and well colonised soils of the Western Keen (10-40% cover). Fig. 1.3 shows the distribution of these skeletal soils.

Nikkavord

Cerastium nigrescens and *Arenaria norvegica* subsp. *norvegica* are found on small areas of skeletal soils about two km W from the Keen (National Grid reference HP 628103) (Fig. 1.2). Nikkavord is strictly a low ultramafic hill with a summit of 133 m about 0.5 km NW of the skeletal soils, but the skeletal soils at the foot of the hill have usually been given the name of Nikkavord in the past and that name is retained here. Some of the skeletal soils are associated with fragmented bedrock ('associated debris' *sensu* Spence 1957) and the rest consist of 'unassociated debris' (*sensu* Spence 1957) which are small patches of a few m^2 in extent within the heathland (Slingsby 1982). As for the Keen the underlying bedrock is made up of dunite (Amin 1954). Nikkavord is part of the Crussafield/Heogs SSSI and there is pony grazing on the site.

Climate

The Keen has a submontane-oceanic climate. Table 1.1 shows the mean monthly rainfall and temperature records from a meteorological station (National Grid reference HP 607089) at 24 m at Baltasound, about 4 km W of the Keen, from 1959 to 1992 (Harvey 1997).

Fig. 1.4 Active stone stripes formed on the sparsely colonised slopes of the Eastern Keen

The mean annual rainfall was 1209 mm with May, June and July the driest months and, January, October, November and December, the wettest. The highest temperature recorded from 1959 to 1997 was 23.2 °C on 4 and 5 August 1982 and the lowest was -10.1 °C recorded on 27 December 1995. Shetland is often subject to low cloud and sea fog. It is also a windy place and there was an average of 46 days a year with gales from 1959 to 1992 (Harvey 1997). Carter *et al.* (1987 a) observed that rainless spells of seven consecutive days or longer occurred at least once in all but five years between 1959 and 1983 and that seven of the years had no rainfall for 10 consecutive days or longer. There was an extreme rainless spell in 1974, from 23 March to 7 May, a period of 46 days with 4.6 mm rain.

Table 1.1 Mean monthly rainfall (mm) and mean daily maximum and minimum temperatures (°C) for each month for the years 1959 to 1992 for a meteorological station at 24 m altitude at Baltasound, about 4 km W from the Keen (Harvey 1997).

	Jan	Feb	Mar	Apr	May	Jun
Rainfall	131	94	115	75	56	58
Maximum temperature	5.4	5.6	6.6	8.4	11.0	13.4
Minimum temperature	1.0	1.0	1.6	2.7	5.1	7.4

	Jul	Aug	Sep	Oct	Nov	Dec
Rainfall	65	76	116	132	147	144
Maximum temperature	14.7	14.9	12.7	10.4	7.4	6.2
Minimum temperature	9.0	9.2	7.7	5.8	2.8	1.6

Study Species

Cerastium nigrescens (H. Watson) Edmondston ex H. Watson

Cerastium nigrescens (Caryophyllaceae) (henceforth called *Cerastium*) is endemic to ultramafic soils on Unst, Shetland, where it was discovered in 1837 (Edmondston 1845). Its main station is on dry, open skeletal soils on the Keen of Hamar. Its only other extant locality is Nikkavord where it was refound in 1969 by L. Johnston (Scott & Palmer 1987) and where it grows very locally on associated debris, as for the Keen, and also on wetter gravelly flushes of unassociated debris (Slingsby 1982).

Cerastium is close to *Cerastium arcticum* Lange, a species of circumpolar distribution occurring in Scotland, Iceland, the Faroes, Fennoscandia, Greenland, Spitzbergen, Russia and arctic America, and is thought to be conspecific by some botanists (Brummit *et al.* 1987).

Cerastium is a dwarf perennial with more or less orbicular opposite fleshy leaves which are dark green tinged with purple. The flowers are large with five lanceolate scarious-margined sepals which are pubescent to glabrous. The corolla consists of five white clawed, bifid petals which enclose ten stamens and five fused styles. The petals are finely veined with green. In the glasshouse there was self fertilisation of isolated plants but individual flowers which were bagged with a fine synthetic fabric did not produce seeds. The flowers are scented and I observed many dipteran visitors to the flowers in the field. I collected some from 6-20 June 1995 which were identified by B. Laurence. Many of them are expected on flowers (B. Laurence pers. comm.) e.g. *Rhamphomyia morio* Zett. (Empididae), *Onesia agilis* Mg. (Calliphoridae) and *Helina communis* Des. (Muscidae) and may be pollinators.

The seeds are reddish brown and are covered in plates which form ridges on the seed coat. Soil movement and surface water flow are likely to be important for seed dispersal (see chapter 3). *Cerastium* was propagated from shoot cuttings without difficulty in the Stirling glasshouses in both John Innes Potting Compost (No. 2) and Keen soil. I also noticed that shoots from plants growing in Keen soil sometimes rooted back into the soil to form new shoots in the glasshouses, but I did not see this in the field.

Cerastium differs principally from *Cerastium arcticum* by its rounded succulent leaf form, purplish tinged leaves, dense glandular hairs and tight, tufted growth form. Lusby (1985) compared the morphology of *Cerastium arcticum* from five Scottish mainland populations with the Keen of Hamar taxon, using 29 morphological characters. He found that the Keen taxon had a shorter pedicel length than the mainland populations and sepals which were narrow at flowering yet very wide at the fruiting stage. The sepals were short in relation to the length of the petals and also the petals were wide in relation to their length. The Keen taxon also had generally shorter broader capsules. He found that there was some morphological variation between all the populations studied.

The *Cerastium* population growing on Nikkavord is the 'var. *acutifolium*' of Edmondston (1845). It differs in morphology from the Keen plants by having narrower less-fleshy leaves with a distinct tip and a more straggly growth form. Slingsby (1982) compared leaf shape and internode length of the two Unst populations of *Cerastium* in the field and found that they differed significantly in internode length and leaf shape. Indeed Slingsby & Carter (1986) from observing plants growing in their natural habitats considered var. *acutifolium* to resemble Faroese *Cerastium arcticum* in growth habit. Stuffins (1983) compared the morphology of the two *Cerastium* populations grown in a glasshouse and found in addition that var. *acutifolium* had smaller flowers, longer capsules and reduced pubescence compared with Keen plants. Figs. 1.5 a and b show the two Unst populations of *Cerastium* growing in the field.

***Arenaria norvegica* subsp. *norvegica* Gunnerus**

Arenaria norvegica subsp. *norvegica* (henceforth called *Arenaria*) within the aggregate *Arenaria ciliata* s.l. and family Caryophyllaceae has a disjunct distribution in Shetland, north-west Scotland, Iceland and Scandinavia. Within Britain it was first discovered in 1837 on Unst, Shetland (Edmondston 1845). On Unst it is most abundant on the ultramafic skeletal soils of the Keen of Hamar but is also found locally on small patches of similar skeletal soils at Nikkavord, Sobul and Clibberswick (Slingsby 1982). The continuing existence of these smaller populations was confirmed during my visit of 1995. *Arenaria* is sparsely distributed in western and northern Scotland, occurring on Rum and Eigg, and on a few mountains in Argyll, Inverness and Sutherland. There is a record from the Burren in Western Ireland, but despite many searches it has not be re-found (Webb & Scannell 1983). The species *Arenaria norvegica* is currently protected under Schedule 8 of the 1981 Wildlife and Countryside Act (Anon. 1981).

Arenaria is a plant of base-rich unstable open habitats and is found on screes, river shingle and rock ledges on soils derived from a variety of rock types. It is usually confined in its montane habitats to the sub-alpine and low alpine zones but can occur at or near to sea level throughout its distribution (Halliday 1960 a). It is found only on sites which are well drained (Halliday 1960 a, Coker 1969).

(a)

(b)

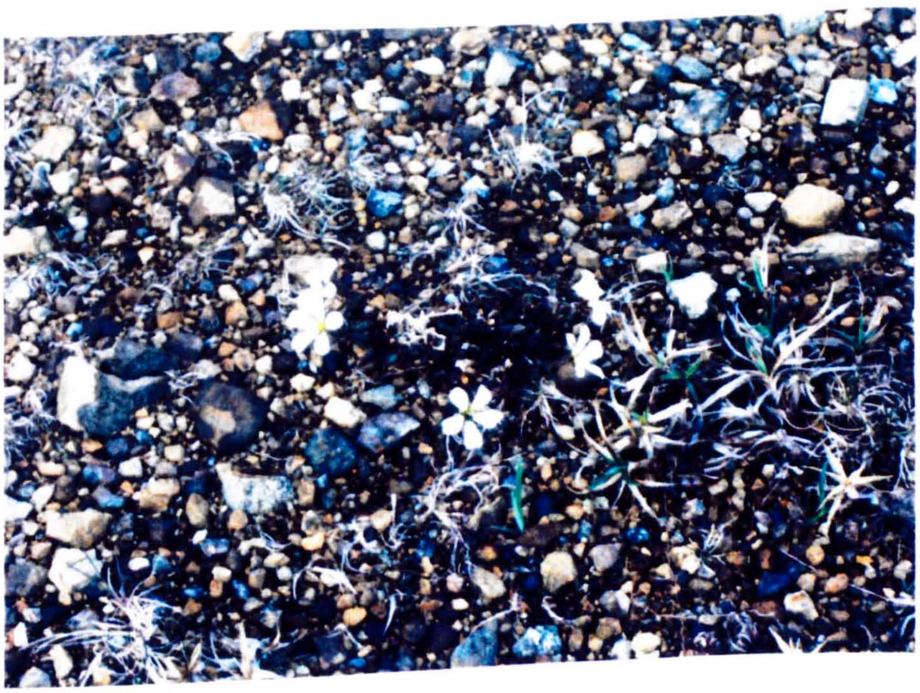


Fig. 1.5 Field populations of (a) Keen *Cerastium* showing a compact growth form and (b) Nikkavord *Cerastium* showing a straggly growth habit.

Arenaria is a perennial herbaceous chamaephyte with a low loose caespitose habit. Different populations of *Arenaria* show much uniformity in morphology (Halliday 1960a). Branching of the primary axis occurs early, and secondary and tertiary branching occurs freely, producing many non-flowering shoots. The leaves are dark green, opposite, obovate to spathulate, succulent and often glabrous. The roots are fine and wiry and are frequently exposed in the field (Fig. 1.6). D. Kennedy (pers. comm.) has recorded at least one instance of shoots from apparently dead *Arenaria* plants rooting themselves and producing new shoots at Beinn Iadain, Morvern, but I found no evidence of this on Unst. As for *Cerastium*, *Arenaria* was successfully propagated from shoot cuttings in the Stirling glasshouses.

The flower has two whorls of five stamens, the outer having swollen basal nectaries. The five (occasionally four) white petals slightly exceed the sepals which are almost always glabrous with a hyaline margin. The capsules dehisce by six teeth which are usually recurved. The black reniform seeds, which have many low, small tubercles, are dispersed chiefly by movement and detachment of the pedicels. On the unstable habitats on which *Arenaria* grows, soil movement is also likely to be important for dispersal and there are instances of dispersal of seeds by water (Halliday 1960 a).

Self fertilisation was efficient for bagged flowers in the Stirling glasshouses. The flowers are fragrant and the nectaries may also attract pollinators, but during this study and that of Halliday (1960 a) there were few observations of insect visitors in the field.

The subspecies *norvegica* interbreeds freely in cultivation with the annual and biennial subspecies *anglica* which grows on base-rich skeletal soils in Mid-west Yorkshire (Halliday 1960 b). The two taxa are given subspecific status on the grounds of geographical separation and morphological differences; the subspecies *norvegica* has a more compact habit, smaller flowers and broader less lanceolate leaves and less ciliation (especially at the base of the sepals) than subspecies *anglica* (Halliday 1960 b).

Fig. 1.6 One of the larger *Arenaria* individuals on the Keen showing an exposed root (r).

Non-ultramafic seed sources

I included a non-ultramafic population of *Cerastium arcticum* and *Arenaria* for comparative studies (Chapters 3 and 4). The *Cerastium arcticum* seeds were collected from a population growing on open, well-drained mineral soils overlying basalt bedrock from the margins of erosion scars on the north tip of Stremoy, the Faroes (62° 17'N, 7° 9'W) (Fig. 1.7). I chose Faroese *Cerastium arcticum* for comparison with Keen plants rather than the *Cerastium arcticum* plants from mainland Scotland, because the Faroese taxon is at no risk from any hybridisation with *Cerastium alpinum* (Hultén 1956) and also because of the interesting observations of Slingsby & Carter (1986) that the Faroese plant resembled the growth form of var. *acutifolium* from Nikkavord in its narrow pointed leaves and straggling growth form.

For *Arenaria*, seeds were collected from a non-ultramafic population from Beinn Iadain (571 m) in Morvern on the Scottish mainland (NGR NM693561), where *Arenaria* grows on the cliffs and screes on the north and south facing slopes (Fig. 1.7). Beinn Iadain is capped by 150 m of basalt, overlying successive layers of mudstone and greenstone over gneiss (Halliday 1960 a).

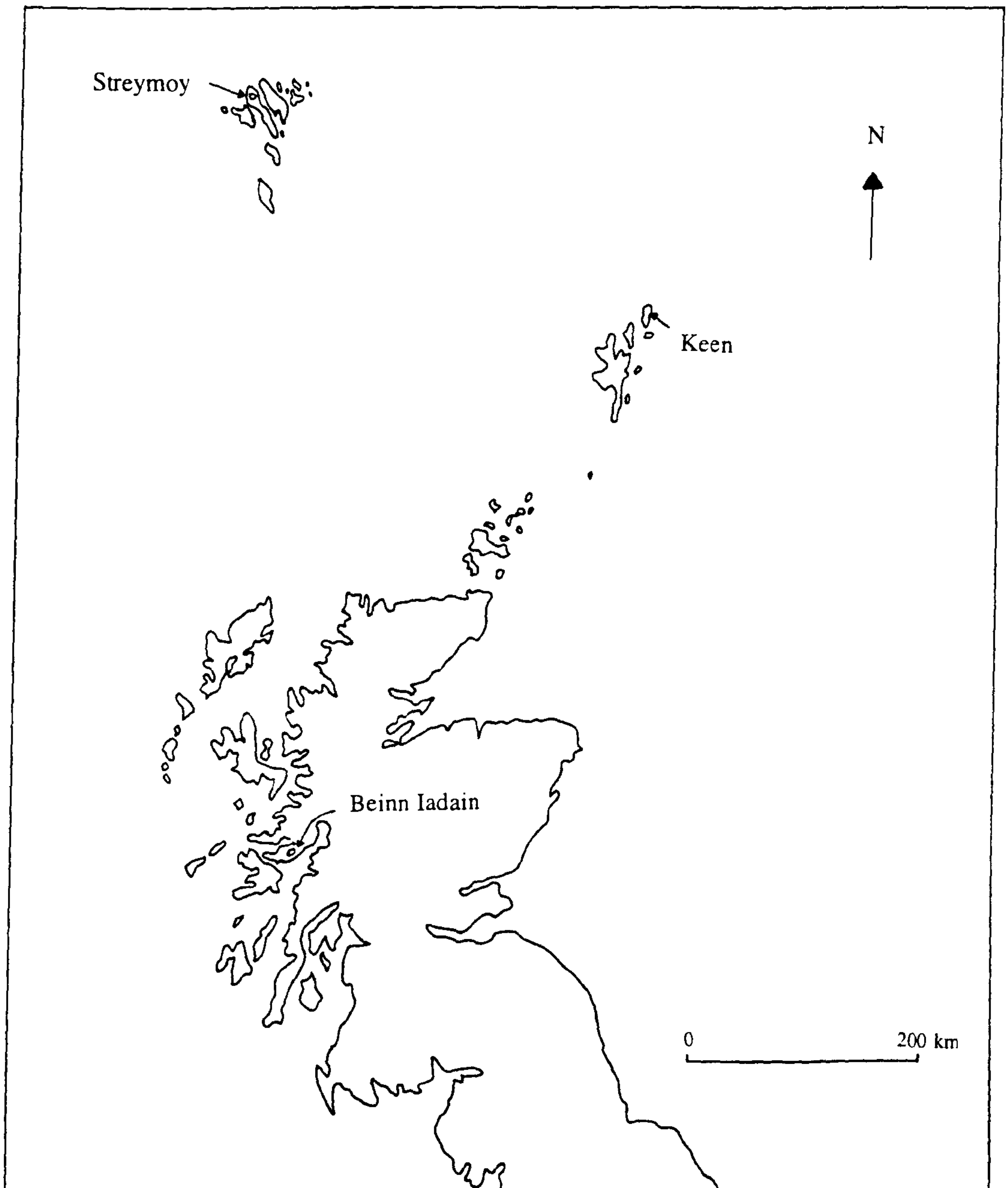


Fig. 1.7 The location of the Streymoy *Cerastium arcticum* population on the Faroe Islands and the Beinn Iadain *Arenaria* population in mainland Scotland.

Chapter 2. Population dynamics of *Cerastium* and *Arenaria* on the Keen and on Nikkavord.

Introduction

Slingsby *et al.* (in press) during 16 years of observations from 1978 to 1993 found that some of the arctic-alpine species of the Keen skeletal soils fluctuated greatly in numbers from year to year. He considered the four species, *Arabis petraea, Arenaria, Cerastium* and *Cochlearia officinalis*. The results were particularly striking for *Arenaria*: in 1991, 14 individuals were counted in a 1 ha permanent plot, while in 1987, 661 individuals were recorded in the same plot. It is not unusual for plant populations to exhibit large fluctuations in numbers (Menges 1986) and there are several examples of rare plants showing changes in population size from year to year e.g. in an eight-year study monitoring ten herbaceous perennials at Teesdale, NNR, (Bradshaw & Doody 1978), in 26 years of observations on *Lobelia urens* growing on two sites, one in Cornwall and one in Devon (Daniels *et al.* 1997), and in seven years of population counts of *Arenaria norvegica* subsp. *anglica* in Yorkshire (Walker 1995).

Detailed studies of the life history and population dynamics are important for the conservation of rare species (Schemske *et al.* 1994). The aim of this chapter was to describe and attempt to explain the changes in numbers of *Cerastium* and *Arenaria* plants by monitoring individuals from 1 June 1994 to 7 November 1996 and relating this to their autecology and climatic measurements. A further aim was to recommend a rapid monitoring method which could be used annually by SNH (Scottish Natural Heritage) staff.

Long term changes in plant numbers

D. R. Slingsby had monitored the composition of the plant community found on Keen skeletal soils with repeated recording of permanent plots. He counted total numbers of *Cerastium* and *Arenaria* plants in a 1 ha plot which he named the "rarity hectare," seven times from 1978 to 1993. There were also three

4 m x 4 m plots, his plots Q5 and Q6 set up in 1979 and Q43 set up in 1992, which were recorded as sixteen 1 m^2 sub-units. These plots will now be referred to as S5, S6 and S43 and are shown together with the 1 ha plot in Fig. 2.1. All the plots were positioned on the Eastern Keen. S6 and the 1 ha plot were on flat ground at the foot of the hill, S5 was on the north west slope of the hill and S43 was on the summit. Total numbers of *Arenaria* and *Cerastium* had been counted nine times in S5, eight times in S6 and twice in S43, to 1993. Seedlings were noted in S5, S6 and S43, but it is likely that very small seedlings were under-recorded. All recording was done in late July/early August (Slingsby *et al.* 1993). I continued counting numbers of the two species, not including small seedlings, in his plots in July 1994, 1995 and 1996.

D. R. Slingsby had also counted the total number of *Cerastium* and *Arenaria* plants on the whole site (41 ha) in 1978 and 1993, and in 1985 he counted plants on an area of 12 ha, which included all of the Western Keen and the 1 ha plot on the Eastern Keen (Fig. 2.1).

Cerastium

Fig. 2.2 a shows numbers of *Cerastium* plants recorded in S5, S6 and S43 from July 1979 to July 1996. S43 showed a small range from 20 plants in 1992 to 22 plants in 1995. S6 showed the largest range from eight plants in 1992 to 40 plants in 1995.

Fig. 2.2 b shows the numbers of plants counted in the 1 ha plot from 1978 to 1996. Total counts ranged from 55 in 1978 to 2226 in 1994. Total counts of *Cerastium* on the whole site (41 ha) in 1978 and 1993, and on the western part of the site (12 ha) in 1978, 1985 and 1993 are given in Table 2.1a.

Table 2.1 Total counts of (a) *Cerastium* and (b) *Arenaria* on the whole SSSI (41 ha) for 1978 and 1993 and on the western part of the site (12 ha) in 1978, 1985 and 1993. After Slingsby *et al.* (1993).

Year	**Total SSSI** (41 ha)	**Western part of the site** (12 ha)
(a) *Cerastium*		
1978	5857	4169
1985		7159
1993	6926	5027
(b) *Arenaria*		
1978	14453	9948
1985		9104
1993	4814	3051

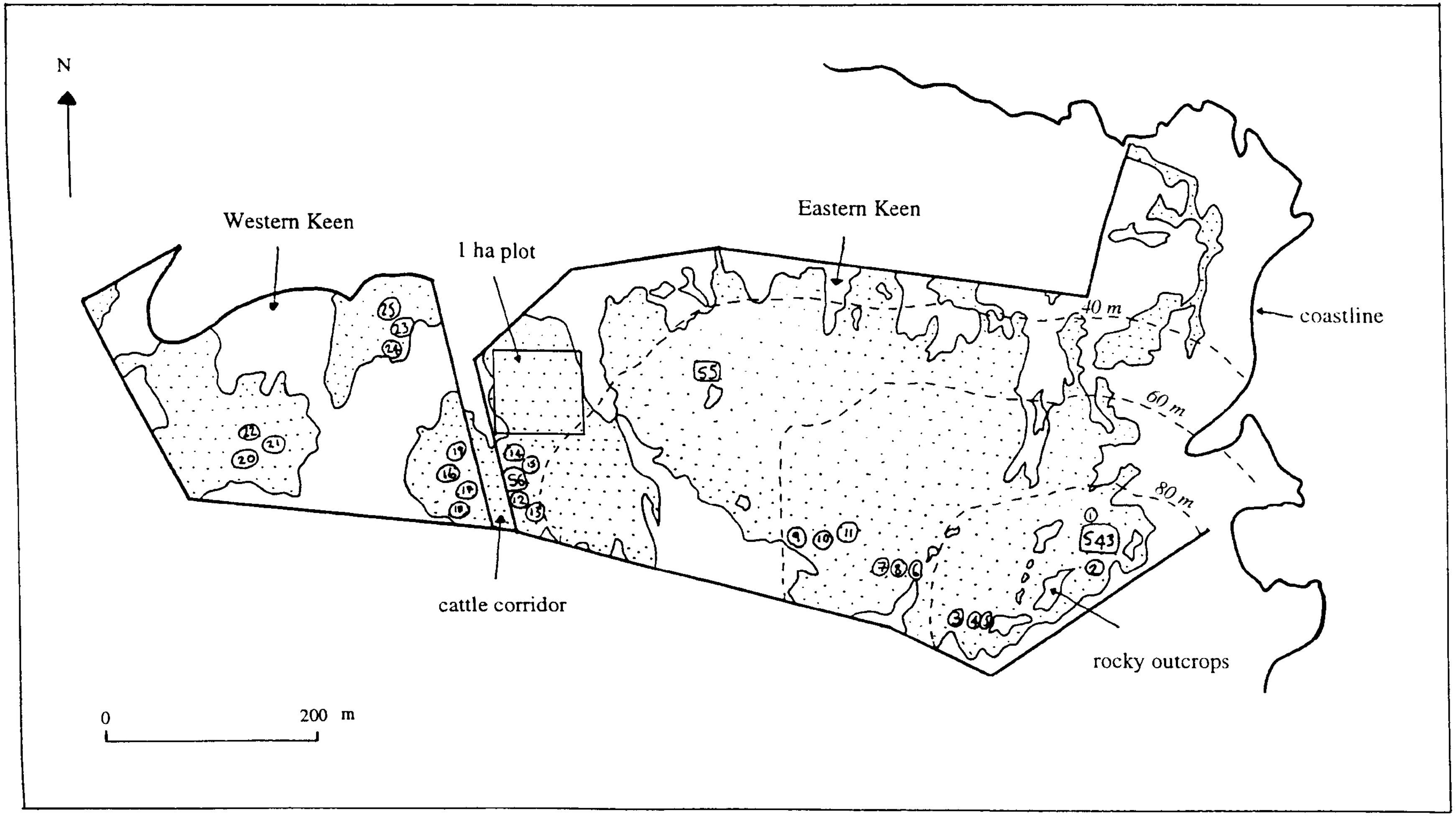


Fig. 2.1 Location of three 4m x 4m plots (S5, S6 and S43) and 25 1m x 1m quadrats (1-25) on the Keen in which *Cerastium* and *Arenaria* plants were recorded from 1 June 1994 to 7 November 1996. skeletal soils.

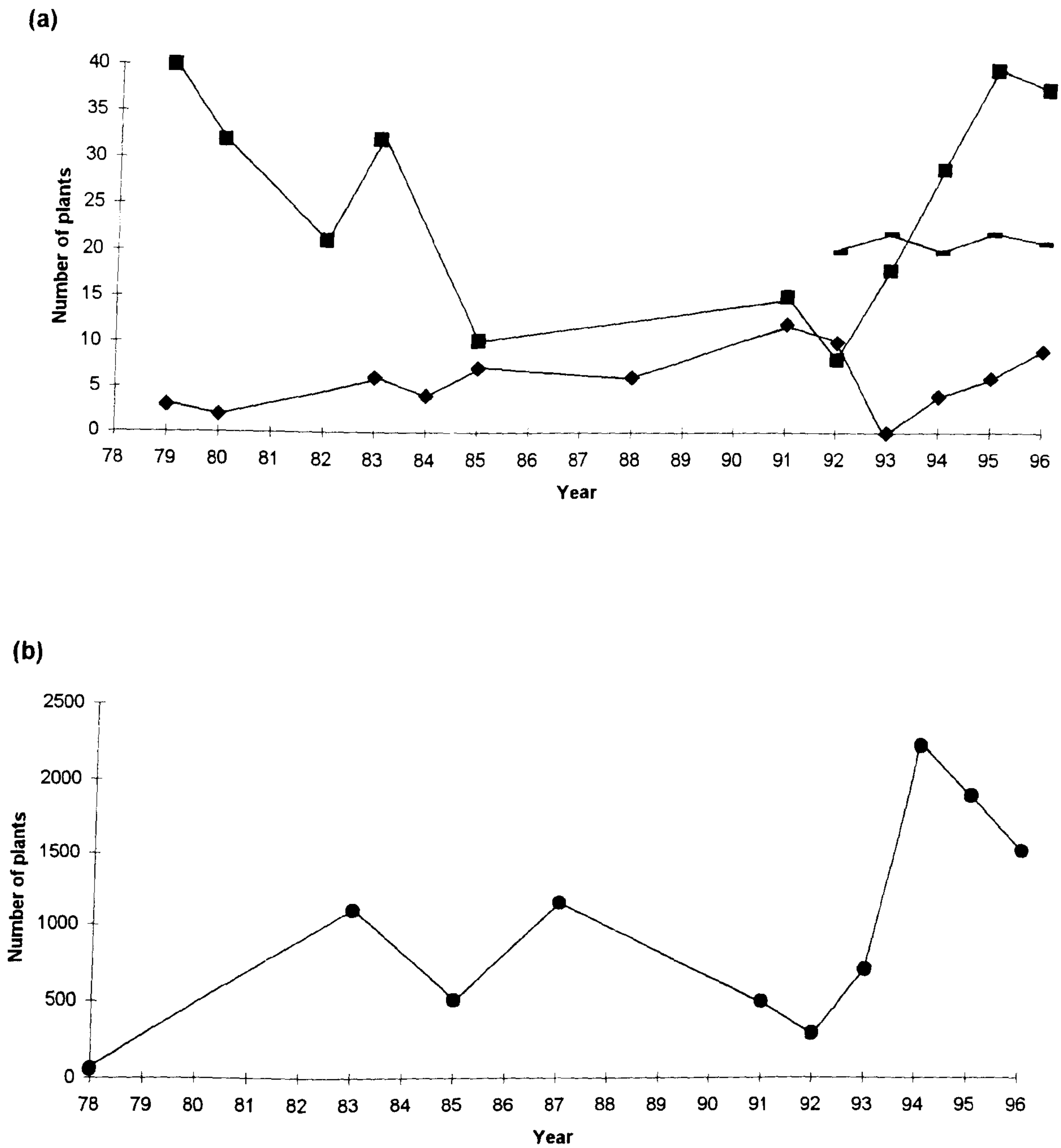


Fig. 2.2 Changes in numbers of *Cerastium* plants recorded on the Keen in (a) the three 4 m x 4 m plots S5 (♦), S6 (■) and S43 (–), and (b) the 1 ha plot from July 1978 to July 1996. Data were collected by D. R. Slingsby from 1978 to 1993 and by S. Kay from 1994 to 1996.

For the site as a whole, there was no clear pattern in changes in plant numbers. There was a very low number (55 plants) in the 1 ha plot in 1978, but numbers recorded over the whole site were 85% of those in 1993 (Table 2.1 a). In 1985, there were 521 plants recorded in the 1 ha plot and 10 in S6, but the 1985 count of the plants on the western part of the site showed higher numbers of plants recorded in 1985 than in 1978 and 1993 (Table 2.1 a). There were eight plants recorded in S6 and 293 plants in the 1 ha plot in 1992, but there were ten plants in S5. It appears that the patterns of change in the numbers of plants were localised.

Arenaria

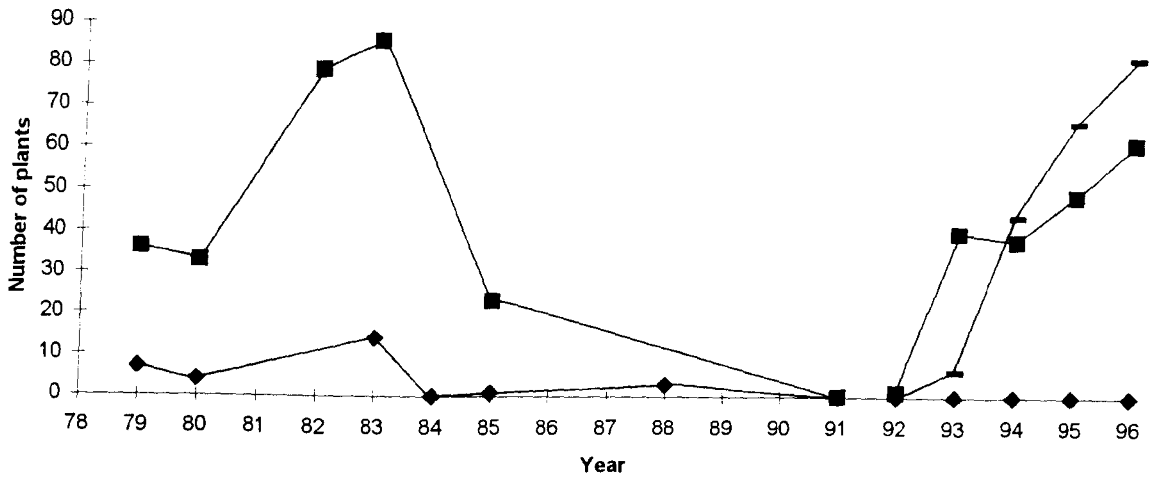
The numbers of *Arenaria* individuals counted from 1978 to 1996 in S5, S6, S43 and the 1 ha plot are shown in Fig. 2.3 a and b. There were higher numbers of plants in all the plots at the start of the period with a peak in 1983. The numbers of plants in all the plots were lower in 1985. There was a big fall in 1991 and 1992: in the 1 ha plot, from 661 plants in 1987 to 14 in 1991; in S6 from 23 plants in 1985 to none in 1991; in S5 no plants were recorded from 1991 to 1996. *Arenaria* made a rapid recovery, with numbers in the 1 ha plot increasing from 21 in 1992 to 468 in 1993, although plants counted over the whole site in 1993 were only a third of those in 1978 (Table 2.1 b).

Changes in plant numbers with climate

Daily rainfall and temperature data were obtained from Baltasound from July 1977 to September 1995, after which the voluntary data collector retired. Data from October 1995 to November 1996 were obtained from an automatic recorder at HP 625078 at 15 m about 4 km W from the Keen. Rainfall records for November 1995 and May 1996 and temperature data for April 1996 and May 1996 were not available owing to instrument faults.

In order to determine if yearly variation in numbers of *Arenaria* and *Cerastium* plants was correlated with the weather, the Spearmans's rank correlation coefficient was used to compare weather events which were thought to affect population numbers. These were: rainfall at the time of the most likely drought (monthly rainfall for April, May and June); rainfall at the time of the most likely flooding of

(a)



(b)

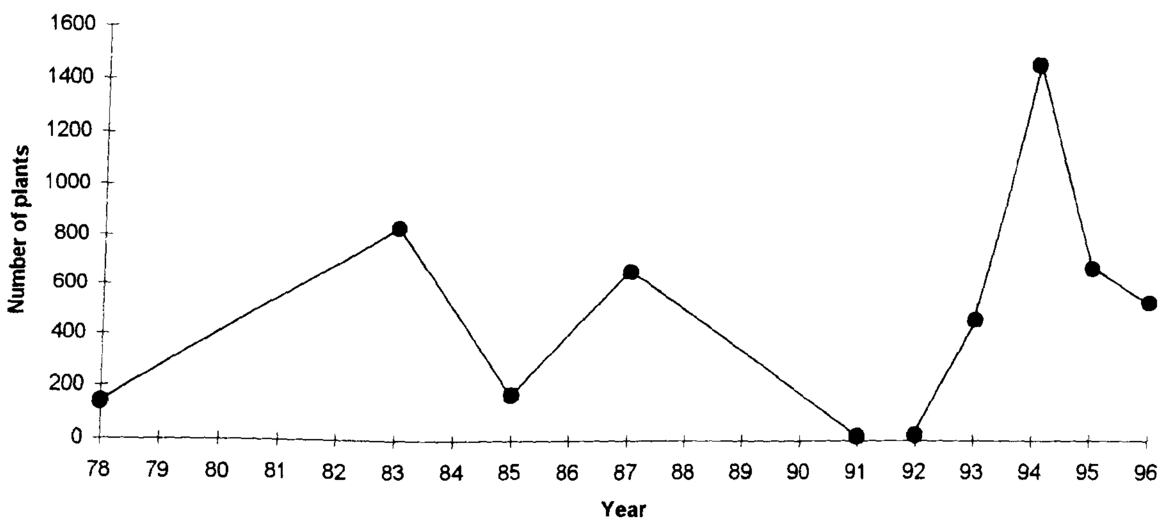


Fig. 2.3 Changes in numbers of *Arenaria* plants recorded on the Keen in (a) the three 4 m x 4 m plots S5 (◆), S6 (■) and S43 (—), and (b) the 1 ha plot from July 1978 to July 1996. Data were collected by D. R. Slingsby from 1978 to 1993 and by S. Kay from 1994 to 1996.

seedlings (monthly rainfall for August, September and October). Total annual rainfall was considered and also the annual frequency of number of days in the upper and lower quintiles of the rainfall data to find out if extremes of dryness or wetness had an effect on plant numbers.

Severe weather was calculated as the annual numbers of days with gales or with snow lying at 0900 GMT. An index of heat availability, the accumulated temperature was derived from day degrees above 5.6 °C, calculated using daily mean temperatures (Shellard 1959). An idea of winter and summer temperatures was estimated by the sum of daily degrees Celsius during the winter months (October to March) and the summer months (April to September).

The weather events were correlated with numbers of plants counted in S5, S6 and the 1 ha plot. The numbers of plants in S43 were not considered because there were only five years of data. Owing to the local extinction of *Arenaria* populations in S5 in 1991, data were only considered from 1979 to 1991. The weather was considered for the period July to July in the year previous to the plant count. There were missing weather records from 1995-96 and so the 1996 count was not included in the data set. There were also some missing severe weather records and daily rainfall and temperature values in 1995 and thus the 1995 count was not included when considering numbers of days in the upper or lower rainfall quintile and the temperature values. The numbers of plants in S5, S6 and the 1 ha plot and the climatic measurements are given in Appendix 1.

Table 2.2 and 2.3 shows the results of the Spearman's rank tests. Not all the weather events were independent causing a higher chance of Type 1 errors, therefore the results were only considered to be significant at a confidence level of $p<0.01$. No correlations were found between the number of plants and the total annual rainfall for either *Cerastium* of *Arenaria* but there were some positive correlations with spring monthly rainfall combinations. For *Cerastium* in the 1 ha plot and in S6 there was a trend towards higher numbers of plants with higher spring rainfall and there was a correlation between the numbers of individual plants and the (April+May+June) rainfall in S6 (Table 2.2:$r_{s10}=0.96$, $p<0.005$). For *Arenaria* there was a correlation between the (May+June) rainfall in the 1 ha plot (Table 2.3:$r_{s9}=0.85$, $p<0.01$).

Table 2.2 Spearman's rank correlations between numbers of *Cerastium* plants in S5, S6 and the 1 ha plot with daily and monthly weather events at a meteorological station at Baltasound, about 4 km W from the Keen from 1977 to 1995. (There were no severe weather records and daily rainfall and temperature values for 1995). The plant data were collected by D.R. Slingsby from 1978 to 1993 and by S. Kay in 1994 and 1995. * denotes significant correlations at $p<0.01$ and ** at $p<0.005$.

Weather event	**Correlation coefficient (r_s)** No. of plants in 1 ha plot n=9	**Correlation coefficient (r_s)** No. of plants in S6 n=10	**Correlation coefficient (r_s)** No. of plants in S5 n=11
Spring rainfall			
Apr	0.50	0.48	0.08
Apr + May	0.37	0.34	0.12
Apr + May + Jun	0.68	0.96 **	-0.02
May	0.18	-0.04	0.18
May + Jun	0.78	0.56	-0.34
Jun	0.35	0.39	-0.51
Autumn rainfall			
Aug	-0.15	0.11	0.15
Aug + Sep	-0.58	-0.20	0.23
Aug + Sep + Oct	-0.42	-0.23	0.16
Sep	-0.45	-0.24	0.01
Sep + Oct	-0.60	-0.33	0.08
Oct	-0.40	-0.53	0.43
Annual rainfall			
Total annual rainfall	0.17	0.29	-0.19
No. of days in the upper rainfall quintile	-0.42	-0.23	0.21
No. of days in the lower rainfall quintile	-0.52	-0.22	0.21
Severe weather			
No. of days with gales	0.12	-0.28	-0.15
No. of days with snow cover at 0900 GMT	0.31	0.49	-0.56
Temperature			
No. of day degrees above 5.6°C	-0.88 *	-0.66	0.57
Total degrees (°C) from October to March	-0.60	-0.64	0.70
Total degrees (°C) from April to September	-0.76	-0.61	0.09

Table 2.3 Spearman's rank correlations between numbers of *Arenaria* plants in S5, S6 and the 1 ha plot with daily and monthly weather events at a meteorological station at Baltasound, about 4 km W from the Keen from 1977 to 1995. (There were no severe weather and daily rainfall and temperatur values for 1995). The plant data were collected by D.R. Slingsby from 1978 to 1993 and by S. Kay 1994 and 1995. * denotes significant correlations at $p<0.01$ and ** at $p<0.005$

Weather event	Correlation coefficient (r_s) No. of plants in 1 ha plot n=9	Correlation coefficient (r_s) No. of plants in S6 n=10	Correlation coefficient (r_s) No. of plants in S5 n=7
Spring rainfall			
Apr	0.57	0.31	0.38
Apr + May	0.35	0.22	0.23
Apr + May + Jun	0.68	0.21	0.41
May	0.22	0.20	0.02
May + Jun	0.85 *	0.38	0.38
Jun	0.57	0.13	0.58
Autumn rainfall			
Aug	-0.07	0.07	0.47
Aug + Sep	-0.47	-0.35	0.36
Aug + Sep + Oct	-0.23	0.04	0.25
Sep	-0.34	-0.38	0.41
Sep + Oct	-0.52	-0.13	-0.13
Oct	-0.43	-0.33	-0.56
Annual rainfall			
Total annual rainfall	0.32	0.44	0.63
No. of days in the upper rainfall quintile	-0.14	0.01	0.34
No. of days in the lower rainfall quintile	-0.14	-0.20	-0.29
Severe weather			
No. of days with gales	0.19	0.23	-0.11
No. of days with snow cover at 0900 GMT	0.55	0.28	0.11
Temperature			
No. of day degrees above 5.6°C	-0.99 **	-0.73	-0.60
Total day degrees (°C) from October to March	-0.62	-0.40	-0.36
Total day degrees from April to September	-0.79	-0.15	-0.47

Both *Cerastium* and *Arenaria* showed significant negative correlations between the number of day degrees above 5.6 °C in the 1 ha plot (*Arenaria*: r_{s8}=-0.99, p<0.005; *Cerastium*: r_{s8}=-0.88, p=0.01), and there appeared to be a trend towards lower numbers of plants in milder winters and warmer summers. There were no significant correlations between the numbers of *Arenaria* plants in S5 and any of the weather events considered.

Methods

Recording of plants

D. R. Slingsby's three plots, S5, S6 and S43, included a range of densities of plants of *Cerastium* and *Arenaria* on the sparsely vegetated north western slopes (S5), moderately colonised skeletal soils on lower ground (S6), and moderately colonised skeletal soils on the summit of the hill (S43). All the plots were on the Eastern Keen. There were generally low numbers of plants in D. R. Slingsby's plots, with some 1 m x 1 m sub-units in each plot having no *Cerastium* or *Arenaria* plants.

In order to increase the sample size for each species, a further 25 1 m x 1 m quadrats were positioned on the skeletal soils of the Keen from 27 - 30 May 1994. Fifteen quadrats were positioned on the Eastern Keen; five on the summit of the hill (Q1-Q5), six on the western slopes (Q6-Q11), four on the lower ground (Q12-Q15). Ten quadrats were positioned on the Western Keen (Q16-25) (Fig. 2.1). The quadrats were placed in areas which were thought to be representative of the skeletal soil habitat and had individuals of either *Cerastium* or *Arenaria* within them. They were marked by coloured stones and located by compass bearings from the fixed point. From 1-7 June 1994, all individuals of the two species within the total of 73 1 m x 1 m quadrats were mapped using a 1m x 1m aluminium frame divided into 10 cm x 10 cm squares (Fig. 2.4).

Plants in all quadrats were re-recorded (including the mapping of recruits) on 13 occasions to 7 November 1996. They were recorded in July, September and November in 1994, 1995, 1996 and in May 1995 and 1996. There were two additional recordings in August 1994 and June 1995. All

Fig. 2.4 Aluminium frame (1 m x 1 m divided into 10 cm x 10 cm squares) used for mapping individual *Cerastium* and *Arenaria* plants in 73 permanent plots on the Keen and eight plots on Nikkavord.

recording was done in the first 15 days of the month with the exception of May 1995 and September 1996 when recording was in the last 15 days of the month (Table 2.4). This work was done within seven days. Any plants not relocated after two consecutive census periods were considered dead.

The quadrats were flooded from 2 - 5 November 1996 and it was difficult to relocate seedlings and record emergents. The study period was thus considered to start on 1 June 1994 and end on 30 September 1996. However plants recorded in June 1994 which were large and easy to relocate were recorded during the November 1996 census.

Table 2.4 Dates of repeated recording of individual plants of *Cerastium* and *Arenaria* in 73 1 m x 1 m quadrats on the Keen and in eight 1 m x 1 m quadrats on Nikkavord.

Year of recording	Dates of recording on the Keen	Dates of recording on Nikkavord
1994	1 - 7 June	8 June
	7 - 13 July	14 July
	8 - 14 August	15 August
	9 - 15 September	15 September
	3 - 7 November	8 November
1995	24 -31 May	25 May
	5 - 10 June	10 June
	5 - 10 July	11 July
	1 - 6 September	7 September
	8 - 12 November	12 November
1996	8 -13 May	14 May
	9 - 14 July	15 July
	25 - 30 September	30 September
	1 - 7 November	7 November

A further eight quadrats were set up on Nikkavord on 8 June 1994. Three were placed along the track running through the site (N4-N6), and five were placed in gravelly flushes (N1-N3, N7, N8) (Fig. 2.5). The dates of recording are shown in Table 2.4. Plants were mapped and re-recorded as for the Keen. Owing to the flooding of the quadrats in November 1994, September 1996 and November 1996, the data were considered to be unreliable for these three months and the Nikkavord recording was considered to end on the 15 July 1996.

Records were made of the following for each plant: dead material (on a subjective scale of 1-4), number of flowers, number of fertile fruits, and whether an individual was growing on a vegetated hummock

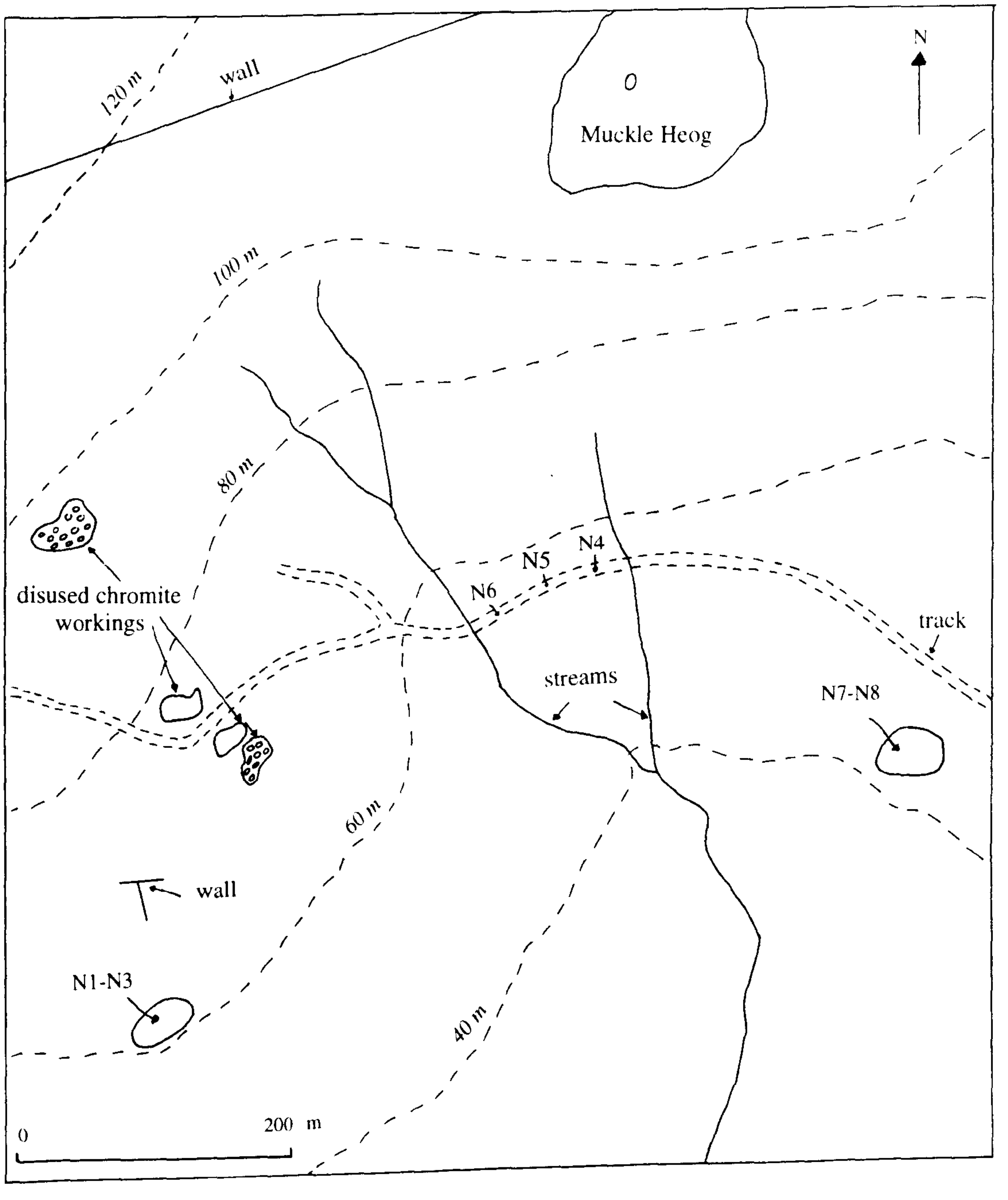


Fig. 2.5 Location of eight 1 m x 1 m quadrats (N1-N8) on Nikkavord in which *Cerastium* and *Arenaria* plants were recorded from 8 June 1994 to 15 July 1996.

i.e. growing on top of one of the cushion-forming species *Armeria maritima, Plantago maritima* or *Silene acaulis*. The size of *Cerastium* and *Arenaria* individuals was estimated by recording the number of shoots.

For both species, the number of seeds within one capsule was counted from each of 50 different plants along a transect across the Keen during 1995. Sometimes capsules looked ripe but contained only unripe seeds; in order to limit damage to the seeds, counting was done only in 1995 and the sample size was restricted to 50 capsules.

Seed banks

Soil samples of 10 cm x 5 cm and 5 cm depth were collected from the Keen from 7-8 June 1995 and 3-4 September 1995 to estimate the minimum (from the June samples) and maximum (from the September samples) seed bank. Samples were collected using stratified random sampling: 50 from the sparsely colonised skeletal soils of the Eastern Keen, 100 from the moderately colonised skeletal soils of the Eastern Keen and 50 from the well-colonised Western Keen. More samples were collected from moderately colonised soils because they covered a larger area.

The soils were spread out in trays to a depth of about 1 cm, in a heated glasshouse with PAR ranging from about 200 $\mu mol\ m^{-2}\ s^{-1}$ on a dull day to about 1400 $\mu mol\ m^{-2}\ s^{-1}$ on a bright day, and were watered with deionized water as necessary. Emergents were identified each week from 16 September 1995 to 16 April 1996. Chancellor (1966) and Muller (1978) were used to aid identification. Unidentifiable seedlings were transplanted to pots and grown where necessary until flowering.

The samples collected in September were placed in a cold room (4 °C) from 22 December 1995 to 5 January 1996 and put back in the glasshouses. On 6 January 1996 all the seed bank soil samples were turned over with a fork.

Data analysis

Depletion curves and survivorship curves were compared using the log-rank Peto and Peto test (Pyke & Thompson, 1986). This analysis is a non-parametric test resembling a chi-squared test which can be used to compare two or more cohorts of plants. Comparisons were between cohorts within the same year and cohorts in different years. The expected mortality was estimated in each cohort from the proportion of plants in each cohort at the start of each time interval.

Results

Population flux and density

During the study there were four dry spells of at least 19 days with less than 6 mm rain:

(a) 1 July to 20 July 1994, 20 days with 5.7 mm rain

(b) 9 June to 28 June 1995, 20 days with 5.0 mm rain

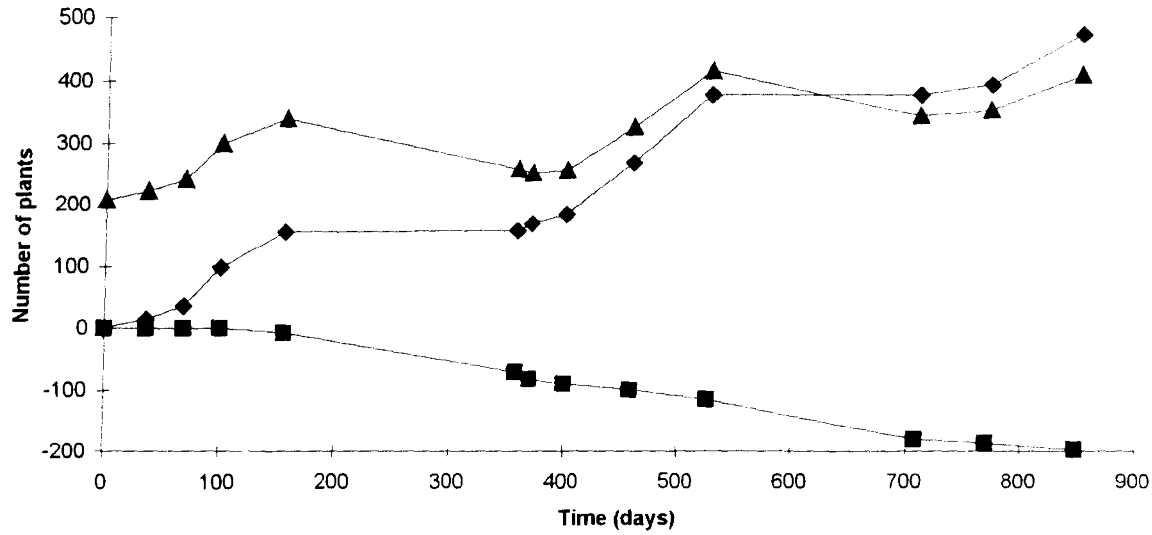
(c) 24 July to 11 August 1995, 19 days with 1.1 mm rain

(d) 2 September to 24 September 1996, 23 days with 5.2 mm rain

Cerastium

A total of 484 *Cerastium* seedlings were recorded in quadrats on the Keen during the study. There were 156 seedlings recorded from 7 June to 7 November 1994 and 225 seedlings recorded from 31 May to 12 November 1995. Most germination occurred during the summer and autumn after plants had set seed e.g. in 1995, 87% of seedlings germinated from 10 July to 12 November (Fig. 2.6 a). During the study there were 198 deaths. The highest mortality was during the winter. From July 1994 to July 1995, 63% of deaths were between November and May. Similarly, from July 1995 to July 1996, 64% of deaths were between November and May. On Nikkavord 43 seedling recruits were recorded in the quadrats. As for the Keen, most seeds germinated during the late summer and autumn (Fig. 2.6 b).

(a)



(b)

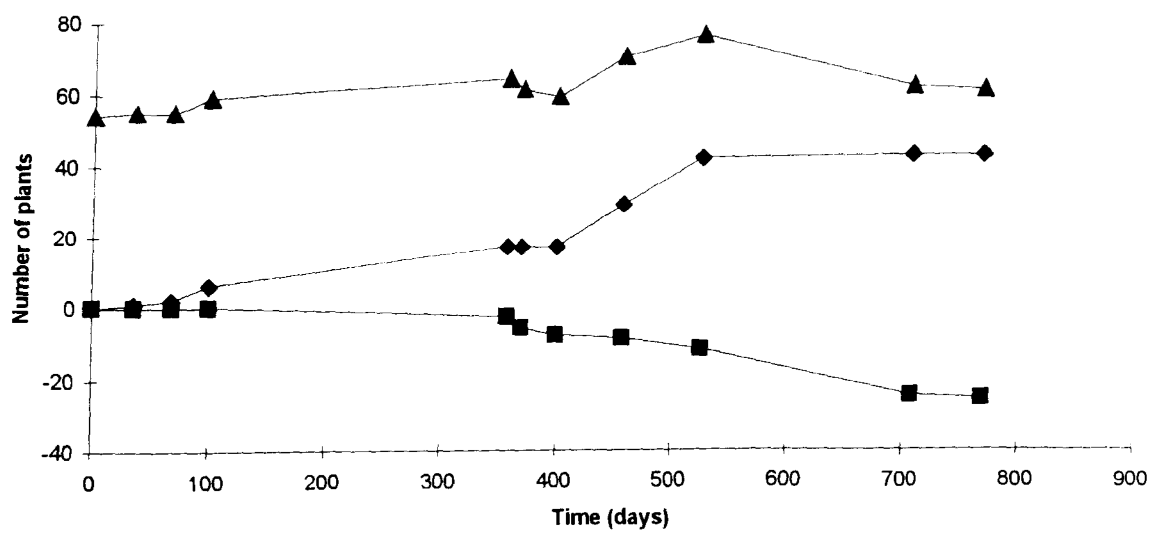


Fig. 2.6 Changes in numbers of *Cerastium* plants from 1 June 1994 to 30 September 1996 in 73 1 m^2 quadrats on the Keen (a), and from 8 June 1994 to 15 July 1996 (there were missing data for November 1994) in eight 1 m^2 quadrats on Nikkavord (b). (◆), cumulative gains; (■), cumulative losses; (▲), net population size.

Overall there did not appear to be an increased mortality of *Cerastium* during any of the dry spells on the Keen or on Nikkavord (Figs. 2.6 a and b).

On the Keen the highest density of plants was 47 per m^2 as recorded in Q24 on the Western Keen on 1 November 1996. On Nikkavord the highest density was 27 per m^2 as recorded in N3 on 12 November 1995. More than half of the quadrats on the sparsely colonised north west slopes of the Eastern Keen contained no *Cerastium*.

Throughout the study, 6-11% of *Cerastium* plants on the Keen were growing on vegetated hummocks. At any census time, more than 75% of the plants had over 25% (estimated subjectively) of their above-ground material comprised of dead stems and leaves still attached to the plant. There was a higher percentage of dead material during the winter.

Arenaria

During the study, 1352 *Arenaria* seedlings were recorded in the quadrats on the Keen. There were similar numbers of seedlings recorded in 1994 (462 seedlings from 7 June to 7 November) and 1995 (513 seedlings recorded from 31 May to 12 November). Germination occurred throughout the spring, summer and autumn of each year (Fig. 2.7 a). As for *Cerastium*, mortality was higher during the winter months. From July 1994 to July 1995, 68% of deaths were between November and May, and from July 1995 to July 1996, 74% of deaths were between November and May. On Nikkavord there were 578 seedling recruits recorded during the study. Ninety one percent of these were in three quadrats along the track running through the site (Fig. 2.5). As for the Keen, seeds germinated throughout the year, but there was a big flush of seedlings recorded from 8 November 1994 to 10 June 1995, 46% of the seedlings recorded in the quadrats throughout the study. Mortality was lower during the winter period than on the Keen. Forty percent of the deaths from July 1994 to July 1995 and 41% from July 1995 to July 1996 occurred between November and May.

Mortality of *Arenaria* was low during each of the dry spells on the Keen and on Nikkavord except on the Keen during the September 1996 dry spell (23 days with 5.2 mm rain), when there were 132 deaths

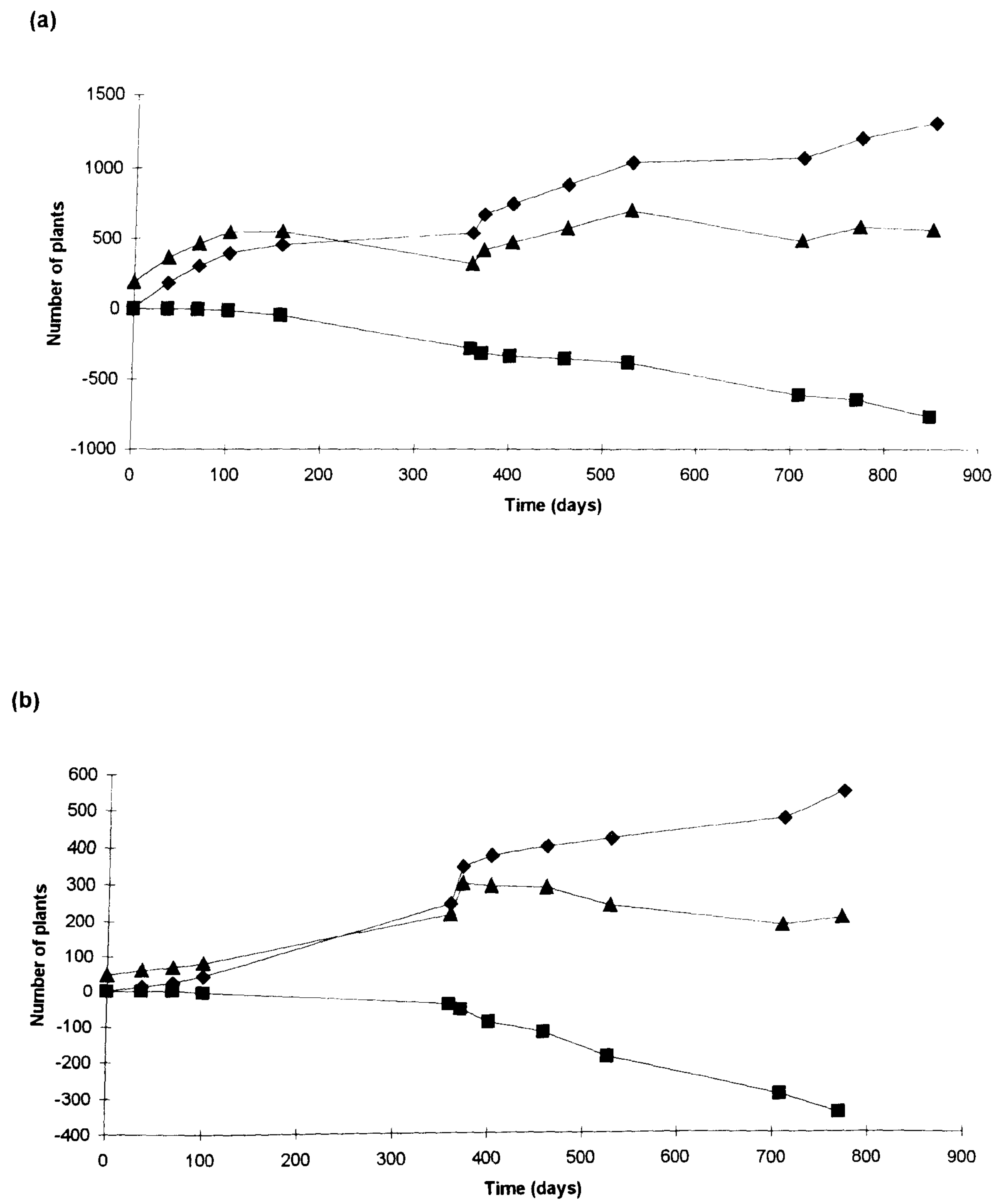


Fig. 2.7 Changes in numbers of *Arenaria* plants from 1 June to 30 September 1996 in 73 1 m^2 quadrats on the Keen (a) and from 8 June 1994 to 15 July 1996 (there were missing data for November 1994) in eight 1 m^2 quadrats on Nikkavord (b). (◆) cumulative gains; (■), cumulative losses; (▲), net population size.

recorded from 14 July to 30 September, 22% of the total number of deaths recorded in the quadrats during the study.

The highest density on the Keen was 41 plants per m^2 recorded in Q18 on the Western Keen on 12 November 1995. I recorded no *Arenaria* plants in S43 although I observed occasional plants in the sparsely colonised soils of this part of the Keen outside S43. On Nikkavord the density of plants in quadrats along the track was on two occasions greater than 100 plants per m^2: 110 plants were recorded in N6 on 12 November 1995 and 100 in N6 on 15 July 1996.

There were low numbers of *Arenaria* plants growing on vegetated hummocks (2-6% of the total plants). I did not observe an accumulation of dead material on *Arenaria* plants.

Cohort survivorship

Cerastium

On the Keen, plants of unknown age recorded from 1 - 7 June 1994 showed a constant mortality to November 1996 (Fig. 2.8 a). Table 2.5 a shows a life table describing survival and mortality of these plants. Out of 211 plants first recorded, 61% were still alive in November 1996. Assuming that the depletion curve remains constant, the half-life can be calculated using the formula for the half-life of a radioactive isotope where: half-life $\tau = \log_e 2/\lambda$ and $\lambda = 1/t \log_e(N_o/N_t)$. From July 1994 to July 1996, the half life of *Cerastium* plants of unknown age was 3.8 years.

In 1994 there were four cohorts recorded from 7 July to 7 November. Owing to low numbers of recruits in July and August 1994, these two cohorts were summed and renamed the Summer cohort. The survivorship curves for Summer, September and November cohorts are shown in Fig. 2.8 b. The log rank Peto and Peto test showed no significant differences between survivorship of the 1994 cohorts (χ^2_2= 0.17, p>0.05), and thus a summary cohort life table was calculated to September 1996 from the mean survivorship of these three cohorts (Table 2.5 b).

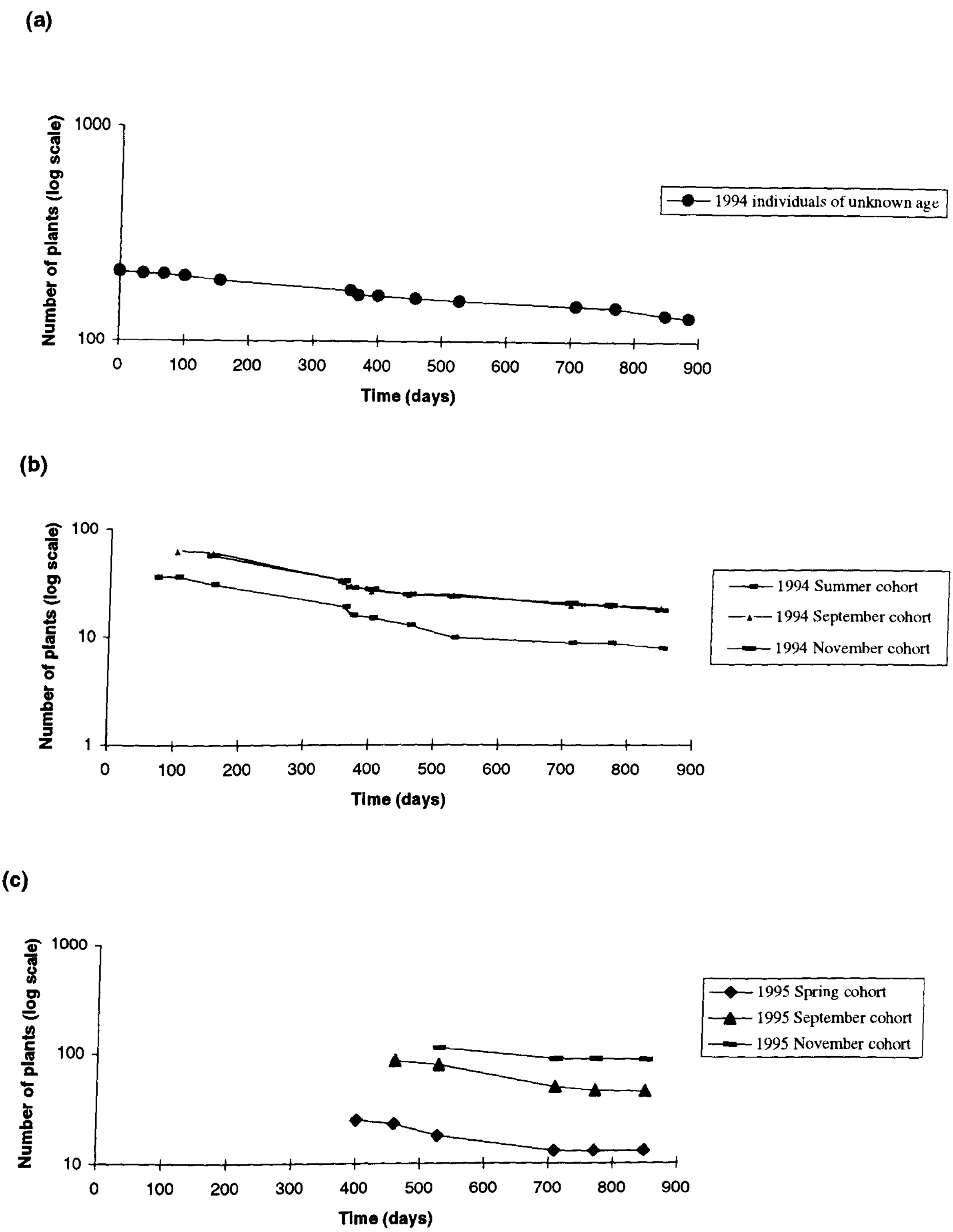


Fig. 2.8 Depletion curve for *Cerastium* individuals of unknown age recorded on the Keen from 1-7 June 1994 to 7 November 1996 (a) and survivorship curves for 1994 cohorts (b) and 1995 cohorts (c) to 30 September 1996.

Table 2.5 a Life table and fecundity schedule for Keen *Cerastium* plants of unknown age recorded from 1 - 7 June 1994. The last recording was on 7 November 1996. The number of seeds per plant in each year was calculated using the 1995 mean value of 20.4 seeds per capsule. The reproductive value was calculated according to the formula: $V_x = m_x + \sum_{i=1,\infty} (l_{x+i}/l_x)m_{x+i}$.

Census month	Number of plants	No. of days between census periods	Survival	Mortality	Mortality rate per month	Survival rate per month	Seeds per plant	Reproductive value
	N_x	x	l_x	d_x	$q_x = (30.5/x)(d_x/l_x)$	$p_x=1-q_x$	m_x	V_x
Jun 94	211	36	1.000	0.019	0.016	0.984		
Jul 94	207	32	0.981	0.009	0.009	0.991	26.2	67.9
Aug 94	205	32	0.972	0.019	0.019	0.981		
Sep 94	201	55	0.953	0.043	0.025	0.975		
Nov 94	192	203	0.910	0.095	0.016	0.984		
May 95	172	12	0.815	0.038	0.118	0.882		
Jun 95	164	30	0.777	0.005	0.006	0.994		
Jul 95	163	58	0.773	0.024	0.016	0.984	30.7	52.9
Sep 95	158	68	0.749	0.019	0.011	0.989		
Nov 95	154	182	0.730	0.038	0.009	0.991		
May 96	146	62	0.692	0.009	0.007	0.993		
Jul 96	144	78	0.682	0.057	0.033	0.967	25.2	25.2
Sep 96	132	37	0.626	0.014	0.019	0.981		
Nov 96	129		0.611					

Table 2.5 b Summary life table and fecundity schedule for *Cerastium* cohorts germinated from 7 June 1994 to 7 November 1994. Lx, dx, qx and px are given as mean values of the three (Summer, September and November) 1994 cohorts. Recording began on 7 July 1994 and the last recording was on 30 September 1996. The number of seeds per plant in each year was calculated using the 1995 mean value of 20.4 seeds per capsule. The reproductive value was calculated according to the formula:
$V_x = m_x + \sum_{i=1,\infty} (l_{x+i}/l_x)m_{x+i}$.

Census month	Total number of plants	No. of days between census periods	Survival	Mortality	Mortality rate per month	Survival rate per month	Seeds per plant	Reproductive value
	N_x	x	l_x	d_x	$q_x = (30.5/x)(d_x/l_x)$	$p_x=1-q_x$	m_x	V_x
Aug 94	36	32	1.000	0.000	0.000	1.000		
Sep 94	99	55	1.000	0.085	0.047	0.953		
Nov 94	149	203	0.943	0.400	0.063	0.937		
May 95	85	12	0.544	0.067	0.313	0.687		
Jun 95	75	30	0.476	0.031	0.067	0.933		
Jul 95	70	58	0.445	0.047	0.055	0.945	-	-
Sep 95	63	68	0.399	0.034	0.040	0.960		
Nov 95	59	182	0.365	0.053	0.024	0.976		
May 96	50	62	0.312	0.006	0.008	0.992		
Jul 96	49	78	0.306	0.026	0.034	0.966	4.1	4.1
Sep 96	45		0.280					

Plants of unknown age recorded in June 1994 showed a significantly higher survival than the summed 1994 cohorts when compared using the log rank test (Table 2.6: $x^2_1 = 50.98$, $p<0.005$). Percentage mortality of the summed 1994 cohorts was higher than it was for plants recorded in June 1994 between all census periods except for July to September 1996 when the mortality was similar (Table 2.6).

In 1995, there were five cohorts recorded from 24 May to 12 November. Owing to low numbers of recruits recorded in May, June and July, these three cohorts were summed and renamed the Spring cohort. Figure 2.8 c shows survivorship curves for the Spring, September and November 1995 cohorts. The log rank test showed significant differences between survival of the 1995 cohorts (Table 2.7:x^2_2 = 7.13, $p<0.05$). The cohorts recorded in September showed a higher mortality than the Spring and November cohorts. The September and November cohorts were summed to make Autumn cohorts. There was no significant difference between survival of the Spring and Autumn cohorts ($x^2_1 = 0.06$, $p>0.05$).

For comparison of survival of the 1994 and 1995 cohorts, numbers of emergents were considered over a roughly similar time interval. The 1994 cohort represented seeds germinated from 7 June to 7 November 1994 and the 1995 cohort represented seeds germinated from 31 May to 12 November 1995. Comparison of survival of the 1994 cohorts to September 1995 with that of the 1995 cohorts to September 1996 showed that the 1994 cohorts had a significantly higher mortality than the 1995 cohorts (Table 2.8:$x^2_1 = 18.87$, $p<0.005$). The mortality of the 1994 cohorts from May to July 1995 which included the June 1995 dry spell (20 days with 5 mm rain) was seven times higher than the mortality of the 1995 cohorts during the same months in 1996, although the numbers of deaths were low in both cases (Table 2.8). There were no dry spells from May to July in 1996, although the rainfall in May, June and July was below average.

Arenaria

On the Keen, no plants recorded from 1-7 June 1994 survived to November 1996 (Fig. 2.9 a, Table 2.9 a). The log rank test showed no significant differences between survivorship of the four cohorts

Table 2.6 Comparison of survival of *Cerastium* plants of unknown age recorded from 1 -7 June 1994 and 1994 cohorts (seeds germinated from 7 June to 7 November 1994) to 30 September 1996. * denotes significant differences between the June 1994 cohort and 1994 cohorts using the log rank x^2 test at p<0.05 and ** at p<0.005.

Time period of survival	Number of seedlings at start of time interval		Number of deaths		Percentage mortality		Log rank x^2
	June 94 cohort	1994 cohorts	June 94 cohort	1994 cohorts	June 94 cohort	1994 cohorts	
Nov 94-May 95	192	149	20	64	10.4	43.0	36.05**
May-Jul 95	172	85	9	15	5.2	17.6	9.38**
July-Sep 95	163	70	5	7	3.1	10.0	2.09
Sep-Nov 95	158	63	4	4	2.5	6.3	2.22
Nov 95-May 96	154	59	8	9	5.2	15.3	5.40*
May-Jul 96	146	50	2	1	1.4	2.0	0.10
Jul-Sep 96	144	49	12	4	8.3	8.2	0.00
TOTAL (Nov 94-Sep 96)	192	149	60	104	31.3	69.8	50.98**

Table 2.7 Comparison of survival of *Cerastium* 1995 Spring, September and November cohorts from 12 November 1995 to 30 September 1996. * denotes significant differences between Spring, September and November cohorts using the log rank x^2 test at p<0.05.

Time period of survival	Number of seedlings at start of time interval			Number of deaths			Percentage mortality			Log rank x^2
	Spr	Sep	Nov	Spr	Sep	Nov	Spr	Sep	Nov	
Nov 95- May 96	18	79	112	5	29	23	27.8	36.7	20.5	4.64
May-Jul 96	13	50	89	0	4	0	0	8.0	0	8.16*
Jul-Sep 96	13	46	89	0	1	2	0	2.2	2.2	0.029
TOTAL (Nov 95-Sep 96)	18	79	112	5	34	25	27.8	43.0	22.3	7.13*

Table 2.8. Comparison of survival of *Cerastium* 1994 cohorts (seeds germinated from 7 June to 7 November) to 6 September 1995 and 1995 cohorts (seeds germinated from 31 May to 12 November 1995) to 30 September 1996. * denotes significant differences between 1994 and 1995 cohorts using the log rank x^2 test at p<0.05 and ** at p<0.005.

Time period of survival	Number of seedlings at start of time interval		Number of deaths		Percentage mortality		Log rank x^2
	1994 cohorts	1995 cohorts	1994 cohorts	1995 cohorts	1994 cohorts	1995 cohorts	
Nov-May	149	203	64	54	43.0	26.6	6.85*
May-Jul	85	149	15	4	17.6	2.7	14.92**
July-Sep	70	145	7	3	10.0	2.1	6.38*
TOTAL (Nov-Sep)	149	203	86	61	57.7	30.0	18.87**

recorded in 1994 (x^2_3 = 2.2, p>0.05), and a summary cohort life table was drawn up as for *Cerastium* (Table 2.9 b). There was no significant difference between the survival of the plants recorded in June 1994 and the summed 1994 cohorts (x^2_1= 1.26, p>0.05). As for the plants recorded in June 1994, the 1994 cohorts showed higher mortality during the winter of 1995 and 1996 and also from July to September 1996 (Figs. 2.9 a and 2.9 b).

Figure 2.9 c shows survivorship curves for the 1995 cohorts. The log rank test showed no significant differences between the survival of the five cohorts recorded in 1995 (x^2_4 = 7.11, p>0.05). A summary life table was prepared for the 1995 June, July, September and November cohorts as for 1994 (Table 2.9 c).

For comparison of survival of the 1994 and 1995 cohorts, numbers of emergents were considered over a similar time period as for *Cerastium*. The log rank x^2 test indicated higher mortality of 1994 cohorts to September 1995, than 1995 cohorts to September 1996 (Table 2.10: x^2_1 = 35.65, p<0.005). Mortality of the 1994 cohorts during June and July 1995 which included the June 1995 dry spell (20 days with 5.0 mm rain), was four times higher than the mortality of the 1995 cohorts in the equivalent period in 1996 (Table 2.10). However mortality of the 1995 cohorts during August and September 1996 was four times higher than the mortality of the 1994 cohorts in the same months in 1995 (Table 2.10). There was a dry spell during both of these periods, in August 1995 (19 days with 1.1 mm rain) and in September 1996 (23 days with 5.2 mm rain).

Size of plants

Cerastium

Figure 2.10 a shows the size distribution of *Cerastium* plants on the Keen for each census month and Figure 2.10 b on Nikkavord. There is a trend towards increased numbers of plants in the smallest size category (mostly seedlings) on the Keen throughout the study period, and a decrease in the individuals

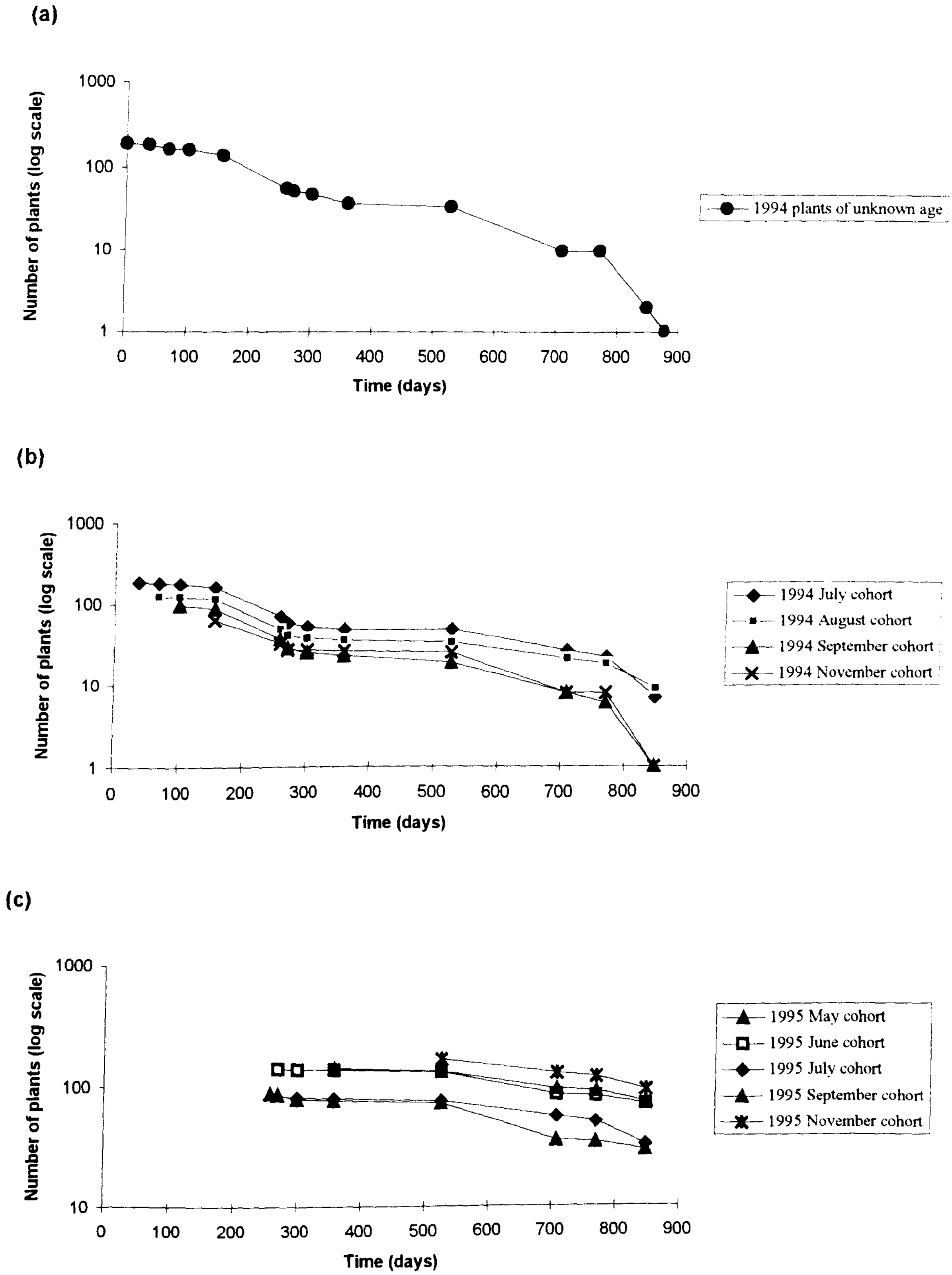


Fig. 2.9 Depletion curve for *Arenaria* individuals of unknown age recorded on the Keen from 1-7 June 1994 to 7 November 1996 (a) and survivorship curves for 1994 cohorts (b) and 1995 cohorts (c) to 30 September 1996.

Table 2.9 a Life table and fecundity schedule for *Arenaria* plants of unknown age recorded from 1 - 7 June 1994. The last recording was on 7 November 1996. The number of seeds per plant in each year was calculated using the 1995 mean value of 18.0 seeds per capsule. The reproductive value was calculated according to the formula: $V_x = m_x + \sum_{i=1,\infty} (l_{x+i}/l_x)m_{x+i}$.

Census month	Number of plants	No. of days between census periods	Survival	Mortality	Mortality rate per month	Survival rate per month	Seeds per plant	Reproductive value
	N_x	x	l_x	d_x	$q_x = (30.5/x)(d_x/l_x)$	$p_x=1-q_x$	m_x	V_x
Jun 94	188	36	1.000	0.027	0.023	0.977		
Jul 94	183	32	0.973	0.101	0.099	0.901	32.6	45.1
Aug 94	164	32	0.872	0.016	0.017	0.983		
Sep 94	161	55	0.856	0.117	0.076	0.924		
Nov 94	139	203	0.739	0.436	0.089	0.911		
May 95	57	12	0.303	0.021	0.178	0.822		
Jun 95	53	30	0.282	0.021	0.077	0.923		
Jul 95	49	58	0.261	0.059	0.118	0.882	39.7	46.6
Sep 95	38	68	0.202	0.016	0.035	0.965		
Nov 95	35	182	0.186	0.133	0.120	0.880		
May 96	10	62	0.053	0.000	0.000	1.000		
Jul 96	10	78	0.053	0.043	0.313	0.687	34.2	34.2
Sep 96	2	37	0.011	0.011	0.824	0.176		
Nov 96	0		0.000					

Table 2.9 b Summary life table and fecundity schedule for *Arenaria* cohorts germinated from 7 June 1994 to 7 November 1994. Lx, dx, qx and px are given as mean values of the four 1994 cohorts. Recording began on 7 July 1994 and the last recording was on 30 September 1996. The number of seeds per plant in each year was calculated using the 1995 mean value of 18.0 seeds per capsule. The reproductive value was calculated according to the formula: $V_x = m_x + \sum_{i=1,\infty} (l_{x+i}/l_x)m_{x+i}$.

Census month	Total number of plants	No. of days between census periods	Survival	Mortality	Mortality rate per month	Survival rate per month	Seeds per plant	Reproductive value
	N_x	x	l_x	d_x	$q_x = (30.5/x)(d_x/l_x)$	$p_x=1-q_x$	m_x	V_x
Jul 94	184	32	1.000	0.022	0.021	0.979	-	-
Aug 94	302	32	0.989	0.020	0.020	0.980		
Sep 94	389	55	0.979	0.077	0.044	0.956		
Nov 94	420	203	0.926	0.509	0.083	0.917		
May 95	185	12	0.417	0.074	0.457	0.543		
Jun 95	152	30	0.343	0.022	0.073	0.927		
Jul 95	140	58	0.320	0.018	0.030	0.970	10.2	26.0
Sep 95	132	68	0.303	0.019	0.030	0.970		
Nov 95	125	182	0.284	0.152	0.087	0.913		
May 96	63	62	0.132	0.017	0.067	0.933		
Jul 96	54	78	0.115	0.080	0.283	0.717	44.0	44.0
Sep 96	11		0.035					

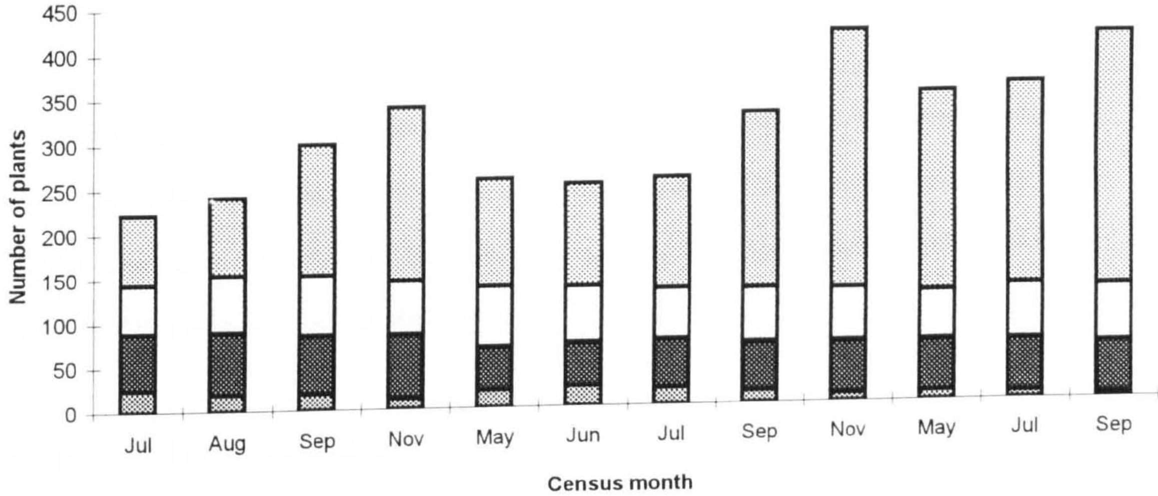
Table 2.9 c Summary life table and fecundity schedule for five cohorts germinated from 7 November 1994 to 12 November 1995. Lx, dx, qx and px are given as mean values of the five 1994 cohorts. Recording began on 24 May 1995 and the last recording was on 30 September 1996. The number of seeds per plant in each year was calculated using the 1995 mean value of 18.0 seeds per capsule. The reproductive value was calculated according to the formula: $V_x = m_x + \sum_{i=1,\infty} (l_{x+i}/l_x)m_{x+i}$.

Census month	Total number of plants	No. of days between census periods	Survival	Mortality	Mortality rate per month	Survival rate per month	Seeds per plant	Reproductive value
	N_x	x	l_x	d_x	$q_x = (30.5/x)(d_x/l_x)$	$p_x=1-q_x$	m_x	V_x
May 95	87	12	1.000	0.034	0.086	0.914		
Jun 95	220	30	0.983	0.048	0.050	0.950		
Jul 95	290	58	0.957	0.017	0.009	0.991	-	-
Sep 95	421	68	0.955	0.048	0.022	0.978		
Nov 95	562	182	0.926	0.293	0.054	0.946		
May 96	430	62	0.633	0.041	0.029	0.971		
Jul 96	370	78	0.650	0.140	0.079	0.921	11.1	11.1
Sep 96	293		0.546					

Table 2.10 Comparison of survival of *Arenaria* 1994 cohorts (seeds germinated from 7 June to 7 November 1994) to 6 September 1995, and 1995 cohorts (seeds germinated from 31 May to 12 November 1995) to 30 September 1996. ** denotes significant differences between 1994 and 1995 cohorts using the log rank χ^2 test at $p < 0.005$.

Time period of survival	Number of seedlings at start of time interval		Number of deaths		Percentage mortality		Log rank χ^2
	1994 cohorts	1995 cohorts	1994 cohorts	1995 cohorts	1994 cohorts	1995 cohorts	
Nov-May	420	364	235	91	56.0	25.0	44.93**
May-Jul	185	273	45	18	24.3	6.6	25.20**
July-Sep	140	255	8	60	5.7	23.5	66.66**
TOTAL (Nov-Sep)	420	364	288	169	68.6	46.4	35.65**

(a)



(b)

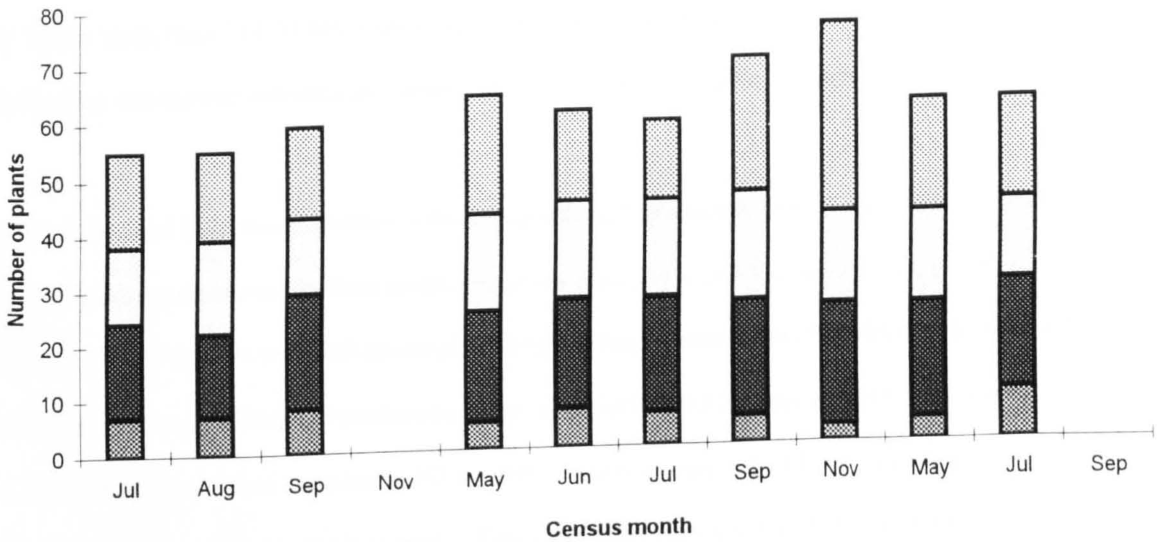


Fig. 2.10 Size distribution of *Cerastium* plants of unknown age recorded from 7 July 1994 to 30 September 1996 on the Keen (a) and from 14 July 1994 to 15 July 1996 on Nikkvord (there were missing data for November 1994) (b). , 1 shoot (includes seedlings); , 2-3 shoots; , 4- 10 shoots; , >10 shoots.

in the largest size category. On Nikkavord, plants appeared to maintain a more constant size distribution throughout the study period.

Arenaria

The size distribution of *Arenaria* plants on the Keen and on Nikkavord during each census month is shown in Fig. 2.11 a and b. On both sites there were higher numbers of plants in the smallest size category. There were generally higher numbers of plants in the larger size categories on Nikkavord than on the Keen especially in 1995 and 1996.

Flowering and seed production

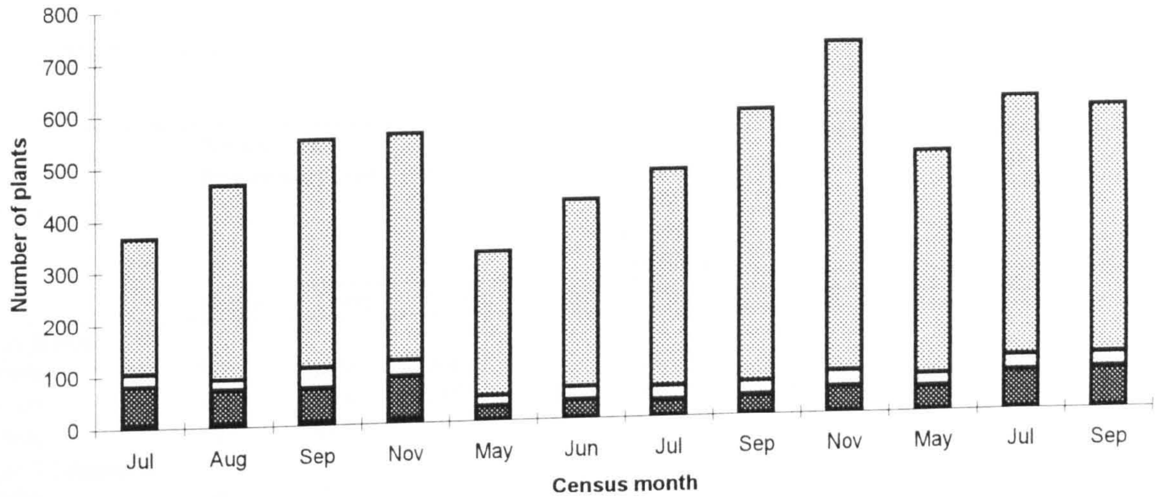
Cerastium

In 1995 a mean (±s.e.) of 20.4±0.9 seeds was recorded from capsules from Keen *Cerastium* plants. This value was used to calculate the number of seeds per plant in Table 2.5 a and b and Table 2.11.

Table 2.11 a and b shows a summary of flowering and seed production of *Cerastium*. Throughout the study, flowering plants on the Keen produced a mean (±s.e.) of 3.1±0.3 flowers per plant with a maximum of 65 flowers recorded on one plant in Q7 midway up the slope of the Eastern Keen in 1994. Flowering plants on Nikkavord produced a mean (±s.e.) of 2.2±0.2 flowers per plant with a maximum of 11 flowers recorded on one plant in N3 in 1995. Twenty six percent of Keen flowers and 29% of Nikkavord flowers failed to produce seeds. Keen plants produced a higher number of fertile flowers per plant than Nikkavord plants in each year and for both sites the number of fertile flowers per plant was lower in 1996 (Table 2.11).

The reproductive value of Keen *Cerastium* plants of unknown age recorded from 1-7 June 1994 is given in Table 2.5 a. This was calculated as the sum of the average number of offspring in the current year plus the sum of the average number produced in later years allowing for the probability of survival of existing plants (Silvertown & Lovett Doust 1993). The number of seeds per plant did not alter very

(a)



(b)

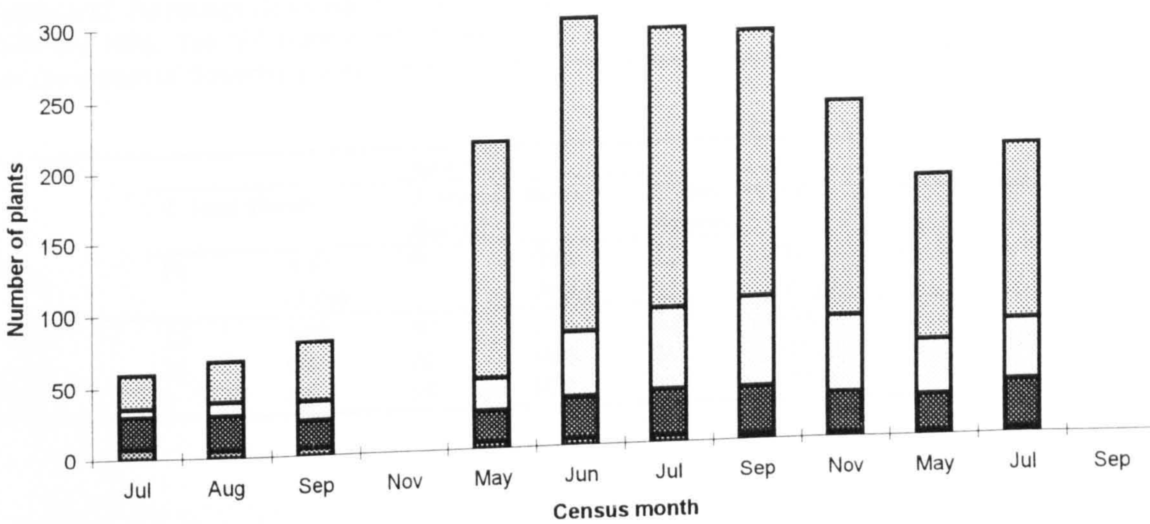


Fig. 2.11 Size distribution of *Arenaria* plants of unknown age recorded from 7 July 1994 to 30 September 1996 on the Keen (a) and from 14 July 1994 to 14 July 1996 on Nikkavord (there were missing data for November 1994) (b). , 1 shoot (includes seedlings); , 2-3 shoots; , 4-10 shoots; , > 10 shoots.

Table 2.11 Flowering and seed production of populations of *Cerastium* on (a) Keen and (b) Nikkavord in 1994, 1995 and 1996. The "total" columns refer to all plants and flowers including those which do not produce seeds. The "fertile" columns refer only to plants and flowers which produce seeds.

Year	Number of flowering plants		Number of flowers		Number of plants (July) (includes seedlings)	Flowers per plant		Seeds per plant
	Fertile	Total	Fertile	Total	Total	Fertile	Total	Total
(a) Keen								
1994	90	109	266	342	222	1.20	1.54	24.5
1995	90	105	245	351	258	0.95	1.36	19.4
1996	77	87	187	252	360	0.52	0.70	10.6
(b) Nikkavord								
1994	14	18	23	36	55	0.42	0.65	8.6
1995	24	27	46	65	59	0.78	1.10	15.9
1996	13	14	22	28	62	0.35	0.45	7.1

Table 2.12 Percentage flowering of *Cerastium* plants of different size classes on the Keen in 1994, 1995 and 1996. The "Fl" columns refer to the number of flowering plants. The "%Fl" columns refer to the percentage of flowering plants from the numbers in each size category recorded in July.

	Size class							
	1 (one shoot)		2 (two to three shoots)		3 (four to ten shoots)		4 (> ten shoots)	
Year	Fl	%Fl (July)	Fl	%Fl (July)	Fl	%Fl (July)	Fl	%Fl (July)
1994	15	19%	30	53%	22	35%	23	92%
1995	11	9%	29	49%	34	62%	16	84%
1996	9	4%	25	40%	37	62%	6	75%

much between years. Fifty three percent of Keen plants flowered for at least two years and 23% of plants flowered for three years. No seedlings recorded in 1994 produced seeds in 1995 (Table 2.5 b) and from the ten flowers recorded in 1996, there were nine capsules. All flowering plants from seeds which germinated in 1994 were recorded on the Western Keen. Only one seedling recorded in 1994 on Nikkavord flowered in 1996, but it failed to produce any seeds.

In the study quadrats, *Cerastium* flowers were observed from June to July in each year. Occasional flowering plants were observed elsewhere on the Keen during May and August. Plants growing on hummocks produced a total of 48 fruits from 1994 to 1996, 7% of the total fruits produced. Larger plants produced more flowers; from 1994 to 1996, 9% of the plants in the smallest size category flowered and 87% of the plants in the highest size category flowered (Table 2.12).

Arenaria

There was a mean (±s.e.) of 18.0±0.5 seeds per capsule from Keen *Arenaria* plants recorded in 1995. This value was used to calculate the number of seeds per plant in Table 2.9 a, b and c and Table 2.13.

A summary of flowering and seed production is given in Table 2.13. Throughout the study period, flowering plants on the Keen produced a mean (±s.e.) of 2.0±0.1 flowers per plant with a maximum of 34 flowers recorded in S6 on the lower parts of the Eastern Keen in 1996. Flowering plants on Nikkavord produced a mean (±s.e.) of 4.6±0.4 flowers per plant with a maximum of 54 flowers on one plant recorded in N6, along the track in 1994. Less than 10% of flowers on both the Keen and Nikkavord failed to produce any seeds. In contrast to *Cerastium*, Keen plants produced a lower number of fertile flowers per plant in each year than Nikkavord plants (Table 2.13). Nikkavord plants ranged almost ten-fold in the number of fertile flowers produced per plant in different years. Plants from both sites produced a lower number of flowers per plant in 1995 (Table 2.13).

As for *Cerastium*, the number of seeds produced from Keen *Arenaria* plants of unknown age recorded from 1-7 June 1994 did not vary much between years (Table 2.9 a). Eighteen percent flowered for at least two years and one percent flowered for three consecutive years.

Table 2.13 Flowering and seed production of populations of *Arenaria* on (a) Keen and (b) Nikkavord in 1994, 1995 and 1996. The "total" columns refer to all plants and flowers including those which do not produce seeds. The "fertile" columns refer only to plants and flowers which produce seeds.

Year	Number of flowering plants		Number of flowers		Number of plants (July) (includes seedlings)	Flowers per plant		Seeds per plant
	Fertile	Total	Fertile	Total	Total	Fertile	Total	Total
(a) Keen								
1994	130	134	331	383	367	0.90	1.04	16.1
1995	106	111	187	208	479	0.39	0.43	7.0
1996	226	229	358	380	609	0.59	0.62	10.6
(b) Nikkavord								
1994	38	40	324	346	59	5.49	5.86	98.8
1995	50	51	162	178	291	0.56	0.62	10.0
1996	100	102	352	369	203	1.73	1.82	31.1

Table 2.14 Percentage flowering of *Arenaria* plants of different size classes on the Keen in 1994, 1995 and 1996. The "Fl" columns refer to the number of flowering plants. The "%Fl" columns refer to the percentage of flowering plants from the numbers in each size category recorded in July.

	Size class							
	1 (one shoot)		2 (two to three shoots)		3 (four to ten shoots)		4 (> ten shoots)	
Year	Fl	%Fl (July)	Fl	%Fl (July)	Fl	%Fl (July)	Fl	%Fl (July)
1994	37	14%	15	63%	71	96%	7	100%
1995	60	14%	19	73%	24	80%	3	100%
1996	149	29%	17	59%	58	81%	2	100%

Arenaria individuals flowered and set seed within one year of germination; 16% of seedlings recorded in 1994 flowered and produced seed in 1995. The number of seeds per plant was low during the first flowering season e.g. for the 1994 cohorts the number of seeds per plant in 1995 was 10.2 (Table 2.9 b); for the 1995 cohorts the number of seeds per plant in 1996 was 11.1 (Table 2.9 c). For the 1994 cohorts, the number of seeds produced increased to 44.0 seeds per plant in 1996 a four-fold increase over the seeds produced in 1995 (Table 2.9 b). The number of flowers produced in 1996 which had germinated in the Spring and Autumn of 1995, were similar: there were 80 flowers produced from the Spring cohorts and 93 from the Autumn cohorts.

Arenaria plants had a long flowering season with flowers observed from May to November in study quadrats. The earliest flowering plant was seen on the site on 13 May 1994 and the latest on 12 November 1995. The proportion of fruits produced on hummocks from 1994 to 1996 ranged from 0.6 to 1.4% of the total numbers of fruits recorded. All the plants in the largest size category flowered and over 20% of the plants in the smallest size category flowered (Table 2.14). Some of the flowering plants were very small (less than two cm in length).

Seed bank

A total of 152 seedlings germinated from the June samples and 204 seedlings from the September samples (Table 2.15 a, b and c). The highest number of seedlings were recorded from the Western Keen samples (248 per m^2 for the June samples; 412 per m^2 for the September samples) and there were many seedlings of the ruderal *Cerastium fontanum* subsp. *glabrescens* recorded from this area.

A total of 12 *Cerastium* seedlings per m^2 were recorded from the June samples and 13 seedlings per m^2 from the September samples (Table 2.15 a, b and c). There was a maximum of 28 seedlings per m^2 recorded from the June samples on the Western Keen (Table 2.15 a). No *Cerastium* seedlings were recorded after the chilling treatment (Table 2.15 c).

As for *Cerastium*, seedlings of *Arenaria* were recorded from soils from all areas of the Keen including sparsely colonised soils which had few individuals (Table 2.15 a, b and c). The highest numbers of

Table 2.15 a Total number of emergents with mean (± s.e.) from bulked soil samples (three samples of 10 cm x 5 cm and 5 cm depth per tray) collected from the Keen from 7-8 June 1995. Seedlings were identified as they germinated from seed trays in glasshouses from 16 September 1995 to 16 April 1996. *Two plants of *Arabis petraea* grew from vegetative fragments.

Species	Sparsely -covered skeletal soil		Moderately -covered skeletal soils		Western Keen	
	Total (0.25 m^2)	Mean (± s.e.) n=17	Total (0.5 m^2)	Mean (± s.e.) n=34	Total (0.25 m^2)	Mean (± s.e.) n=17
Agrostis spp.	3	0.18 ± 0.12	2	0.06 ± 0.04	2	0.12 ± 0.08
Arabis petraea	6*	0.35 ± 0.14	5	0.15 ± 0.07	3	0.18 ± 0.09
Arenaria norvegica	1	0.06 ± 0.06	18	0.53 ± 0.15	5	0.29 ± 0.14
Armeria maritima	-	-	2	0.06 ± 0.04	-	-
Cerastium fontanum	2	0.12 ± 0.08	32	0.94 ± 0.25	27	1.59 ± 0.58
Cerastium nigrescens	1	0.06 ± 0.06	4	0.12 ± 0.06	7	0.41 ± 0.12
Cochlearia officinalis	-	-	4	0.12 ± 0.06	4	0.24 ± 0.13
Poa pratensis	-	-	1	0.03 ± 0.03	3	0.18 ± 0.09
Sagina procumbens	-	-	1	0.03 ± 0.03	3	0.18 ± 0.09
Silene uniflora	1	0.06 ± 0.06	2	0.06 ± 0.04	-	-
Thymus polytrichus	-	-	1	0.03 ± 0.03	6	0.35 ± 0.17
Unidentified herbs	2	0.12 ± 0.08	2	0.06 ± 0.04	2	0.12 ± 0.08
TOTAL	16		74		62	

Table 2.15 b Total number of emergents with mean (± s.e.) from bulked soil samples (three samples of 10 cm x 5 cm and 5 cm depth per tray) collected from the Keen from 3-4 September 1995. Seedlings were identified as they germinated from seed trays in glasshouses from 16 September to 22 December 1995. *Three *Arabis petraea* plants grew from vegetative fragments.

Species	Sparsely-covered skeletal soils		Moderately-covered skeletal soils		Western Keen	
	Total (0.25 m^2)	Mean (± s.e.) n=17	Total (0.5 m^2)	Mean (± s.e.) n=34	Total (0.25 m^2)	Mean (± s.e.) n=17
Agrostis spp.	1	0.06 ± 0.06	5	0.15 ± 0.06	17	1.0 ± 0.62
Arabis petraea	4	0.24 ± 0.10	8*	0.24 ± 0.11	3	0.18 ± 0.09
Arenaria norvegica	5	0.29 ± 0.14	11	0.32 ± 0.12	2	0.12 ± 0.08
Cerastium fontanum	1	0.06 ± 0.06	-	-	52	3.06 ± 1.24
Cerastium nigrescens	5	0.29 ± 0.14	7	0.21 ± 0.07	1	0.06 ± 0.06
Cochlearia officinalis	1	0.06 ± 0.06	3	0.09 ± 0.05	-	-
Sagina procumbens	-	-	7	0.21 ± 0.18	5	0.29 ± 0.14
Silene acaulis	-	-	2	0.06 ± 0.04	-	-
Silene uniflora	1	0.06 ± 0.06	-	-	-	-
Unidentified herbs	2	0.12 ± 0.08	4	0.12 ± 0.06	3	0.18 ± 0.09
TOTAL	20		47		83	

Table 2.15 c Total number of emergents with mean (± s.e.) from bulked soil samples (three samples of 10 cm x 5 cm and 5 cm depth per tray) collected from the Keen from 3-4 September 1995 after chilling treatment. Seedlings were identified as they germinated from seed trays in glasshouses from 5 January to 16 April 1996.

Species	Sparsely-covered skeletal soils		Moderately-covered skeletal soils		Western Keen	
	Total (0.25 m^2)	Mean (± s.e.) n=17	Total (0.5 m^2)	Mean (± s.e.) n=34	Total (0.25 m^2)	Mean (± s.e.) n=17
Agrostis spp.	1	0.06 ± 0.06	-	-	6	0.35 ± 0.34
Arabis petraea	1	0.06 ± 0.06	-	-	-	-
Arenaria norvegica	2	0.12 ± 0.08	19	0.56 ± 0.16	4	0.24 ± 0.10
Armeria maritima	-	-	-	-	1	0.06 ± 0.06
Cerastium fontanum	-	-	-	-	4	0.24 ± 0.16
Cochlearia officinalis	-	-	1	0.03 ± 0.03	1	0.06 ± 0.06
Hypericum pulcrum	-	-	1	0.03 ± 0.03	-	-
Plantago maritima	-	-	1	0.03 ± 0.03	-	-
Sagina procumbens	-	-	3	0.09 ± 0.09	2	0.12 ± 0.11
Scilla verna	-	-	4	0.12 ± 0.07	-	-
Thymus polytrichus	-	-	1	0.03 ± 0.03	-	-
Unidentified herbs	-	-	-	-	2	0.12 ± 0.08
TOTAL	4		30		20	

seedlings were recorded from moderately colonised soils: 36 seedlings per m^2 from the June samples; 60 seedlings per m^2 from the September samples. There was a flush of *Arenaria* seedlings in the September soil samples recorded after the chilling treatment (Table 2.15 c). The seedbank was higher in all areas in September than in June. A total of 24 seedlings per m^2 was recorded from the June samples and 43 seedlings per m^2 from the September samples.

Another rarity, *Arabis petraea,* both germinated from seed and grew from vegetative fragments. The highest numbers were recorded from sparsely covered skeletal soils: 24 seedlings per m^2 from the June samples; 20 seedlings per m^2 from the September samples. Low numbers of seedlings were recorded for *Armeria maritima, Plantago maritima* and *Silene uniflora* which are all well represented on the skeletal soils.

Discussion

There have been large fluctuations in numbers of *Cerastium* and *Arenaria* plants on the Keen over the past 18 years and correlations with the meteorological data show that numbers of both of these species on the lower ground on the Eastern Keen were lowest after a dry spring. The Baltasound weather station recorded an average of 296 rain-days (i.e. days with ≥ 0.2 mm rainfall) per year over a ten year period (Stirling 1982) and it may seem unlikely that drought is such an important factor in determining the population size. However, ultramafic soils often have a low water holding capacity and dry out rapidly after rainfall events. Gulmon *et al.* (1983) found that the soil water content in ultramafic Californian annual grassland closely reflected precipitation events to 0.45 m depth. Carter *et al.* (1987 a) estimated that summer droughts of seven consecutive days or longer on the Keen may exhaust the water reserves in the shallowest soils.

Many of the adaptations of plants widespread on shallow, rocky ultramafic soils are also an adaptation to drought (Walker 1954). Slingsby (1981) wrote an article on the Keen with the title: "Britain's most northerly desert" and it is true that many of the distinctive plants on the Keen skeletal soils do appear to show xeromorphic adaptations such as succulence, pubescence and extensive root systems (Proctor & Woodell 1971).

A spring drought may cause the death of plants directly through lack of water. On metalliferous soils, there may also be a concentration of metals by upward water movement and evaporation of surface layers. Antonovics (1972) observed a drop in population numbers of *Anthoxanthum odoratum* on a zinc mine in Wales after a dry summer and suggested that higher zinc levels may be the cause of the deaths. However the evidence suggests that nickel is more toxic in wet soils (Mitchell 1964, Robertson 1992) and it is unlikely that the toxic effects of nickel are the cause of a reduction in *Cerastium* and *Arenaria* numbers during a dry spring. The role of nickel on the Keen is discussed further in chapter 5.

A more likely possibility is that the interaction of drought and mineral nutrient shortage may be the cause of plant mortality. When little water is available, all ions become less mobile in the soil because air spaces replace water in the pores between soil particles, resulting in an indirect pathway from the soil to the root surface (Nye & Tinker 1977). Water stress therefore reduces the rate at which nutrients become available in soils and when little water is available, the indirect effects on plant nutrition may be as important as the direct effects of water stress (Chapin 1991).

Carter *et al.* (1987 b) found that the grass cover of skeletal soils increased greatly after phosphorus addition (originated in 1981), although it was not until 1985 that there was an accelerated increase in cover on the sparsely colonised skeletal soils. Data from 1988 onwards showed that the increase in grass cover had stopped and in some cases fallen back on the moderately colonised skeletal soils but the increased cover on the sparsely colonised soils was still evident in 1993 (Slingsby *et al.* in press). Clearly the low concentration of available phosphorus is an important factor in restricting the vegetation cover on the skeletal soils of the Keen.

Grime & Curtis (1976) observed that *Festuca ovina* was abundant on many abandoned pastures on areas of shallow soils in the limestone dales of Derbyshire but that *Arrhenatherum elatius* appeared to be unable to invade despite its close proximity. The results of field experiments suggested that *Arrhenatherum elatius* was vulnerable to desiccation under conditions in which root penetration was limited by nutrients, while *Festuca ovina* was able to tolerate moisture stress under conditions of nutrient stress. The species which have adapted themselves to growing on the Keen such as *Cerastium* and *Arenaria*, may have limited root growth due to phosphorus limitation and this may explain the reduction in numbers during a dry spring. I observed that the spring is the time of the fastest growth for both *Cerastium* and *Arenaria*, and it is likely that these species are more susceptible to nutrient deficiencies when they are actively metabolising.

There were negative correlations between the numbers of *Cerastium* and *Arenaria* plants in the 1 ha plot and the number of day degrees above 5.6 °C. The temperature of 5.6 °C is generally considered to be the critical temperature above which plant growth starts and is maintained in a European climate (Shellard 1959). Arctic plants have the ability to increase metabolic rates at low temperatures but at higher temperatures they cannot always sustain the higher metabolic rates (Crawford 1989) and on the Keen, it is possible that in years with a greater number of days with temperatures above 5.6 °C, *Cerastium* and *Arenaria* are not able to sustain the higher metabolic rates.

Interestingly, there were no correlations between any of the weather measurements and the number of *Cerastium* or *Arenaria* plants in S5. It is possible that correlations were not picked up because of the low number of plants and because only six years of data were available for *Arenaria.* Another explanation is that there may be other more important factors which are influencing the plant numbers on this part of the site. S5 is on the very sparsely colonised soils of the north western slopes, an area where there are active stone stripes. The instability of the soils caused by solifluction processes may be the cause not only of the low number of plants but also their fluctuations in numbers.

Slingsby *et al.* (in press) compared the distribution of *Cerastium* and *Arenaria* plants on the Keen in 1978 and in 1993 and found that there was a consistent area of population decrease on the north west summit and an associated increase on the lower parts of the Keen. From 1992 to 1996, the numbers of *Cerastium* plants in S43, which is on the north west summit, were remarkably constant compared with the numbers of plants in other plots during this time, and the pattern of fluctuations of *Arenaria* plants in this plot also appeared to be different from the plots on the lower areas. It seems likely that although the site area is only 41 ha it offers a varied environment for plants and the effects of climate and other factors such as cryoturbation, stone sorting and microtopography may vary greatly in different parts of the site. The sampling of plants in D. R. Slingsby's plots from 1978 to 1995 was within a limited area, and there are no estimates of precision and so it is difficult to draw conclusions about the whole site.

It is true that there are several sources of error for the data, and the relationships between numbers of *Cerastium* and *Arenaria* plants and weather events should be treated cautiously. There were different recorders each year and it is likely that there was a range in the ability of the recorders to identify seedlings. It is also possible that the correlations identified were Type 1 errors. The confidence level was reduced to $p<0.01$ in order to reduce the probability of erroneously finding significant results, but plant numbers from different years are not independent and this was not taken into account.

Nevertheless, there were very big fluctuations in numbers of *Cerastium* and *Arenaria* plants recorded in D. R. Slingsby's plots, and it seems likely that, at least on the lower parts of the site where there was a larger sample size, the numbers of plants recorded did reflect real changes in the population size. In general, the significant positive correlations between spring rainfall and numbers of *Cerastium* and *Arenaria* plants in the 1 ha plot and S6 were backed up by a trend towards positive correlations with other spring rainfall combinations. Similarly, there was a significant negative correlation between the number of both *Cerastium* and *Arenaria* plants in the 1 ha plot and the number of day degrees over 5.6 °C, and there was also a trend towards a negative correlation between the number of *Cerastium* and *Arenaria* plants and accumulated winter and summer temperatures in both the 1 ha plot and S6.

Clearly a dry spring and mild temperatures were factors which reduced the numbers of both *Cerastium* and *Arenaria* plants on the lower part of the Keen. The lower parts of the site are the main station for both species and it is possible that they may be susceptible to global warming. On a global scale spatially averaged temperatures have increased by as much as 0.4 °C, but it is difficult to interpret the evidence for long-term climate change and separate any trends from natural fluctuations in time and spatial variability (Houghton *et al.* 1990). Harrison (1997) considered monthly weather records from eight Scottish meteorological stations from the period 1964 to 1993 in order to try and identify any recent trends in climate. He found, among other things, that there were slight increases in maximum winter temperatures particularly in northern Scotland and that minimum temperatures were also higher during the winter away from the north-west coast. However he emphasised that these trends were mainly driven by the high temperatures of the last decade and may be short term effects.

From June 1994 to November 1996, populations of mature plants of *Cerastium* on the Keen showed a Deevey type two mortality with the number of plants decreasing exponentially with time (Deevey 1947). This conclusion is in line with many other population studies of long lived perennials e.g. Antonovics (1972), Harper (1967), Sarukhán & Harper (1973). Despite seasonal and annual fluctuations in climate, the risk of death to these plants remained constant with time. The seedlings which were recorded in 1994 and 1995 showed Deevey type two curves as for mature plants, although they had different decay rates, with the 1994 cohorts showing higher mortality than the 1995 cohorts, indicating that the chance of survival varied depending on the year in which the cohort was formed. Mature *Arenaria* plants and 1994 cohorts showed a Deevey type one curve with high mortality after flowering in the second year. Many annual and biennial plants have a Deevey type one curve e.g. *Cerastium atrovirens* (Mack 1976) and *Vulpia fasciculata* (Watkinson & Harper 1978). Like *Cerastium,* the 1994 *Arenaria* cohorts showed a higher mortality than the 1995 cohorts.

The period immediately following emergence is generally the most vulnerable stage in the plant's life (Fenner 1987). It is likely that during the present study, the seedling mortality was under-estimated because there were one to two months between census periods during the summer and there was a six month break in the winter. Any seedlings which germinated and died during these times would have been missed.

There were four dry spells from 1994 to 1996, and these did not have much of an overall affect on the numbers of *Cerastium* plants. There was a higher than expected mortality of the younger plants during the June 1995 dry spell but this was still relatively low (<20%). It seems likely that *Cerastium* can survive rainless periods even during the spring, a necessary attribute for its long-term persistence on the Keen. It shows xeromorphic adaptations with a compact growth form, and glandular, hairy, rounded leaves. The dead material attached to plants may reduce wind convection and evapotranspiration, protecting the plant from summer drought. The accumulation of insulating layers of dead leaves and fruiting stems is common in tundra herbs and helps to protect the growing parts from wind and abrasion (Fitter & Hay 1987).

There was a high mortality of established *Arenaria* adults during the September 1996 dry spell, but the younger plants showed a low mortality. It appears that the reasons for the high mortality during this dry spell were related to individuals coming to the end of their natural life rather than the climate. Overall, from 1994 to 1996, although there was an increased mortality of younger plants during some dry spells, it was never greater than 25% of the total plants. It appears that, like *Cerastium, Arenaria* has adapted to survive dry periods on the Keen and plants will suffer only when conditions are extreme. Halliday (1960 a) observed that *Arenaria norvegica* had more succulent leaves than other species in the *Arenaria ciliata* L complex and this may be an adaptation to drought.

From 1994 to 1996, there was higher mortality of both *Cerastium* and *Arenaria* during the winter. Most of the plants which were considered to be "dead" had disappeared altogether and therefore it was impossible to know the cause. Shallow ultramafic soils are susceptible to frost heaving (Rune 1953) and it is likely that this activity, together with general instability of soils and flooding may have been the main causes of death. I saw no evidence of herbivory, although there was one incidence of four *Cerastium* plants and three *Arenaria* plants being buried from soil from a rabbit scraping.

I recorded nearly three times as many *Arenaria* seedlings as *Cerastium* seedlings throughout the study and they germinated throughout the spring, summer and autumn of each year. There was no difference between the mortality of spring germinated or autumn germinated cohorts. It appears that *Arenaria* seeds germinate throughout the year; there will be a relatively high mortality of seedlings, but without unduly severe conditions, enough plants should survive in favourable microsites. Recording plants at only one time of the year does not take into account the seasonal differences in germination and thus the very large annual fluctuations recorded by Slingsby *et al.* (1993) may partly reflect short term changes in population numbers between different months.

Established *Cerastium* plants had a lower mortality than seedlings. This is in contrast to *Arenaria* for which there was no difference between mortality of mature plants or 1994 cohorts, implying that older plants were just as vulnerable as younger ones. All the mature *Arenaria* plants and most of the 1994 seedlings completed their life-cycle during the study period. However established *Cerastium* plants had a longer life than the period of study with a half life of 3.8 years.

It is not possible to ascertain whether the depletion and survival curves of mature plants and seedlings of *Cerastium* will remain constant in the future or whether severe weather conditions will cause an increase in mortality causing altered depletion and survival curves. In the latter case, the depletion and survival curves of *Cerastium* when observed throughout their whole life may alter their shape as stage follows stage (Begon *et al.* 1996). In the former case, changes in numbers of plants on the Keen may be related to poor germination success and seedling survival in years with unsuitable weather conditions. Recruitment tends to be the most sensitive part of the plant life cycle (Silvertown & Lovett Doust 1993). Bullard *et al.* (1987) showed that weather conditions were better correlated with recruitment than with mortality in *Primula scotica* which is endemic to the north coast of Scotland and Orkney.

Similar numbers of *Cerastium* seeds germinated in 1994 and 1995. Only long-term monitoring of the individual plants of *Cerastium* will be able to identify whether populations are regulated by germination success or whether there is higher mortality during stressful periods resulting in depletion and survivorship curves which alter with time. Recommendations for the long-term monitoring of *Cerastium* and *Arenaria* on the Keen are given in Chapter 6.

The open soils are the main habitat for *Cerastium* and *Arenaria* plants. However, I recorded 6-11% of the total numbers of *Cerastium* plants growing on vegetated hummocks. Plants on hummocks may benefit from the moderated temperature conditions. Hulm (1983) using a multichannel automated recorder between 29 July and 6 August 1982, found that there was a much greater diurnal temperature range on the open skeletal soils of the Keen than on heathland and also that maximum temperatures within a specimen of *Armeria maritima* were lower than those at the surface of the skeletal soils. The scale of the temperature recorder read from 0-25 °C on the Keen and on three days the maximum temperature was off the scale. On Nikkavord, the temperature recorder read from 0-50 °C and there was a maximum temperature of 31 °C recorded on the open soils on 31 July 1982 when the screen temperatures read 19 °C.

The pattern of flowering was different for *Cerastium* and *Arenaria.* The factors which control flowering in herbaceous perennials are highly complex and little understood (Harper 1977) and it is not uncommon for flowering to vary between years and between species on the same site. The flowering frequencies were more varied for *Arenaria.* Although it is impossible with data for two and a half years only, to know the cause of this variation, it can be speculated that the lower numbers of *Arenaria* plants flowering in 1995 were related to the drier spring. Several other studies have found a relationship between flowering frequency and the amount of rain in spring e.g. there was a positive correlation between early season precipitation and flowering frequencies in *Pinguicula vulgaris* on unstable calcareous soils in the Swedish subarctic (68°21'N, 18°49'E) (Svensson *et al.* 1993); there was a significant relationship between the total rainfall from 1 April to 3 June and the percentage of *Spiranthes spiralis* plants flowering in English chalk grassland (Wells 1981); low temperatures and drought in early summer delayed the onset of flowering and caused a decrease in seed set for *Fumana procumbens* (Dunal) Grenier et Godr. on Oland (Bengtsson 1993).

Most (92 %) of Keen and Nikkavord *Arenaria* flowers produced seeds. The 18 seeds per capsule recorded on the Keen was similar to that of 21 *Arenaria* seeds per capsule recorded by Halliday from Rum (Halliday 1960). There were only four seeds per capsule recorded by Walker (1995) for *Arenaria norvegica* subsp. *anglica* in Yorkshire. Over 25% of Keen and Nikkavord *Cerastium* flowers failed to produce seeds. This may be the result of failed pollinator visits; self fertilisation was not always effective in glasshouse grown plants in Stirling. Another possibility is that the seeds were aborted owing to resource limitations. Many plants control the number of seeds produced independently of pollination (Silvertown & Lovett Doust 1993).

Both *Cerastium* and *Arenaria* are polycarpic, although they show different strategies. *Cerastium* plants appear to have a relatively long reproductive life. No seedlings recorded in 1994 flowered in 1995 and the ones that flowered in 1996 were all found on the Western Keen where there are higher nutrients. *Arenaria* seedlings flowered within one year, although they produced a higher number of fruits in the second year, after which most of them died. Flowering *Arenaria* plants often had only a few remaining living leaves particularly in the second year, and by the time the fruits were produced, the plants looked dead. This behaviour is in common with annuals growing on nutrient deficient habitats which shows retranslocation of nutrients from the leaves to the seeds (Harper 1977).

Cerastium has a shorter flowering period, with nearly all of the plants flowering in June and July. The longer flowering period of *Arenaria* is characteristic of many species of disturbed habitats and will extend the period when the seeds are ripened and released (Harper 1977). Walker (in press) observed a similar prolonged flowering period for *Arenaria norvegica* subsp. *anglica* in Yorkshire, with plants flowering from May through to September and there were occasional records of plants flowering as late as December. For both *Cerastium* and *Arenaria*, as might be expected, there was a higher proportion of larger plants flowering, although some flowering plants of *Arenaria* were very small. When the above-ground parts of the plant are small, there may be extensive root systems below the ground as has been shown by Spence (1974).

Cerastium plants on Nikkavord showed similar population dynamics to those on the Keen. The main difference was that there were lower numbers of seedlings. In each year, Nikkavord plants produced lower numbers of flowers and hence less seeds. It is possible that the numbers of seedlings were limited by the number of seeds, but there might also have been a lower number of microsites available for germination. Miller (1994) found that seedling numbers of *Gentiana nivalis* were correlated with the amount of bare soil exposed in the autumn of the previous year rather than with seed production. Nikkavord *Arenaria* plants showed a rather different life cycle to those on the Keen. There were bigger fluctuations in numbers of plants and flowering frequencies. After a high flowering in 1994, there was a massive recruitment of seedlings during the winter of 1994/1995 resulting in very high numbers of seedlings during 1995 and a correspondingly lower flowering frequency. The winter mortality was lower than the Keen, with higher deaths during the growing season.

It should be emphasised that the sample size on Nikkavord was low. *Cerastium* plants were only considered on the wetter debris areas and the *Arenaria* plants sampled were mostly on the track passing through the site. Further sampling would have to be done in order to make conclusions about the site as a whole. Nevertheless, it has been demonstrated that *Cerastium* plants growing on a less well drained substrate on Nikkavord do show a similar behaviour to Keen plants. In contrast, *Arenaria* plants on the Nikkavord track have different population dynamics to those on the open soils skeletal soils of the Keen. It is not uncommon for plants to show demographic variation on different sites; Fowler & Antonovics (1981) found this to be so for *Plantago lanceolata* and *Salvia lyrata* (L) on plots which were only a few metres apart.

Gross (1990) when comparing different methods of estimating seed numbers in the soil, found that the highest species diversity was found with the germination method which I used. In this study it is likely that most of the species which have a seedbank were recorded, but that the abundance of seeds was underestimated. Germination conditions may not have been appropriate for all seeds, and the experiment was only for six months. Also the soil sample size was limited to one hundred for conservation reasons. Sparse species require a very large number of samples for precision (Thompson *et al.* 1997).

Nevertheless it has been established that both *Cerastium* and *Arenaria* have a seed bank which may have an important role in carrying the population across unfavourable periods. The quick recovery of *Arenaria* after two years of very low numbers in 1991 and 1992 is probably the result of seeds germinated from the seed-bank. Keen *Arenaria* seeds were still viable after two years of dry storage (chapter 3) but Halliday (1960 a) found a reduced germination of 25-50 % of *Arenaria* seeds after two years and after three years there was only a 5 % germination. It is not clear how Halliday's *Arenaria* seeds were stored. Keen *Cerastium* seeds were viable after two years of dry storage (chapter 3). A further implication of seedbanks is that they may be able to carry genotypes across several generations thus buffering the influence of contemporary selection and of genetic drift (Silvertown 1988).

Having identified seedlings of *Arabis petraea* from the seedbank studies, I was able to identify seedlings in the field; on the Keen, this species evidently reproduces by seedlings as well as vegetatively.

The long-term fluctuations of *Cerastium* and *Arenaria* populations from 1978 to 1995 have been related to extreme rainfall events, particularly low rainfall during the spring and to low temperatures. However, from June 1994 to November 1996, plant populations of *Cerastium* and *Arenaria* showed a remarkably constant death rate, with different causes of deaths throughout the year. Plants were hardly affected by the four dry spells throughout the study. It is possible that density stress continued to kill a more-or-less constant proportion of individuals with time. I noticed that seedlings which germinated in clumps had a high mortality. There were never more than 11 flowering *Cerastium* plants per m^2 and 20 flowering *Arenaria* plants per m^2 on the Keen despite higher densities. Nagy (1994) found that the flowering plants of some species growing on open ultramafic soils on Meikle Kilranoch were also widely spaced with 15 -20 per m^2 for *Cochlearia pyrenaica* subsp. *alpina* and 15 - 30 per m^2 for *Lychnis alpina*.

There certainly appeared to be density stress of *Arenaria* plants on the track on Nikkavord. There was a large recruitment of seedlings during the winter of 1994/1995 which was followed by a high mortality of seedlings during the growing season and a 10 times reduction in flowering frequency and seed production in 1995 compared to the previous year.

Competition may be important for vegetation dynamics in low productivity habitats (Taylor *et al.* 1990). Spence (1957) observed on the Keen, that although the total cover of a certain area was only about 1.5%, two plants which were well separated above ground were occupying the same horizontal and vertical planes below the ground, and he concluded that space-competition might exist when there is very low above-ground cover. Keen skeletal soils have a high stone content and are shallow (Carter 1982). McConnaughay & Bazzaz (1992) investigated the effect of fragmentation of physical space on plant growth, by using artificial root systems in their pot trials. They suggested that soils with a high stone content may reduce the efficiency of the root's ability to obtain nutrients. Klinkhamer & Dejong (1989), by modelling density regulations in sparse populations, concluded that even low levels of density dependence can be important in determining the number of plants in sparse populations.

Fowler (1988) emphasised that there is a very high degree of environmental variation, both spatial and temporal, confronted by plants of a single population. There can be misleading conclusions from descriptive studies. In the absence of density manipulations it is difficult to come to any conclusions regarding density dependence. Nevertheless it appears that there are density dependent and density independent factors operating on the Keen and on Nikkavord and their relative importance will vary in different areas and different years.

Cerastium and *Arenaria* show different life strategies to cope with the inhospitable Keen environment. *Cerastium* plants appear to have a long reproductive life and produce long-lived seeds. Seedling establishment is low, but survival of seedlings is relatively high. *Arenaria* plants, on the other hand, have a short life which is offset by copious seed production, long-lived seeds and frequent establishment.

Chapter 3. Seed germination and dispersal of *Arenaria* and *Cerastium*.

Introduction

For the conservation of a rare species, it is important to know the viability of the collected seeds and also how to germinate them. I considered Keen and Nikkavord *Cerastium* and *Arenaria* seeds and for the latter species also seeds from the non-ultramafic Beinn Iadain, and seeds from Keen plants which had been cultivated in John Innes Compost (No. 2) in Stirling.

The Royal Botanical Gardens of Kew (J. Terry pers. comm.) recommended agar as a germinating substrate (10 g of agar in 1 l water). Gibberellins are able to break dormancy in some seeds (Mayer & Poljakoff-Mayber 1989) and so agar was used with and without gibberellic acid (250 mg l^{-1}). I also used acid washed sand which has no added nutrients and John Innes Compost (No.1) (traditionally recommended by gardeners). Tests were done on chilled and unchilled seeds. The seed germination tests revealed that there were clear differences between the Keen, Nikkavord and Beinn Iadain *Arenaria* populations. I therefore investigated the seed germination on soils from the three sites.

Halliday (1960 a) observed that the Scottish mainland *Arenaria* populations appeared to have occupied most of the suitable habitats nearby. On Unst, *Arenaria* individuals are found on most of the well-drained, open, skeletal, base-rich soils from the hill of Clibberswick (about 3 km N of the Keen) to Sobul (about 6 km SW of the Keen) (Fig. 3.1).

However, *Cerastium* is restricted to the Keen and Nikkavord. Two old references quoted in Scott & Palmer (1987) possibly refer to *Cerastium* populations on Sobul, that of Hanbury (1885) "on the east side of the road between Baltasound and Uyeasound" and that of Druce (1922) "above the Loch of Watlee." However, despite several searches (e.g. Slingsby 1982), *Cerastium* has not been found and if it did occur on Sobul it is now extinct. Sobul has quite extensive areas of skeletal soils and bedrock

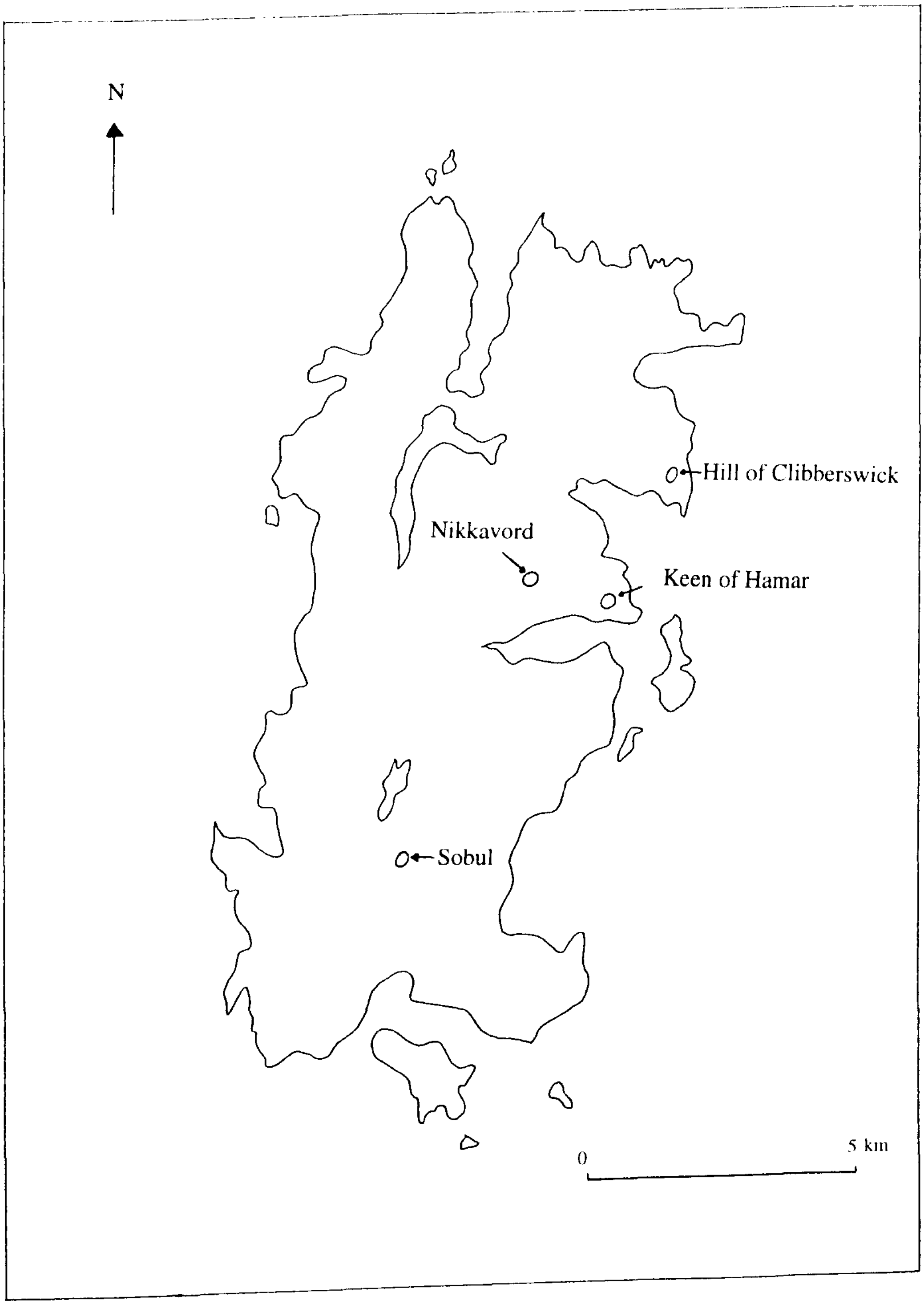


Fig. 3.1 The location of known *Arenaria* sites on Unst.

with deeply jointed fissures resembling those of the Keen and would appear to provide a suitable habitat (Slingsby 1982).

I planted *Cerastium* seeds on Sobul, to ascertain whether conditions on Sobul were unsuitable for germination or establishment or both, or whether *Cerastium* was absent from Sobul because of poor dispersal. The seeds were initially sown onto soils which had been cleared of surface stones (larger than about 5 mm in diameter) in order to provide a greater surface area of soil available for seed germination. Four months after sowing the seeds, I noticed that the soil within the plots had become compacted (probably by raindrops) and that the germination was low. I therefore set up a pilot study to investigate the role of soil surface microtopography on establishment and survival of both *Cerastium* and *Arenaria* on the Keen.

Methods

Source of seeds for investigations under controlled conditions

Table 3.1 shows the dates of collection of seeds from the two *Cerastium* seed sources and four *Arenaria* seed sources. The seeds were collected from ten plants selected at random from each population. All the seeds were stored in paper bags in the dark at room temperature after collection.

Table 3.1 Dates of collection of *Cerastium* and *Arenaria* seeds for seed viability and seed germination investigations. Keen (glasshouse) (a) refers to the collection date of seeds from the field and (b) the collection date of seeds from glasshouse grown plants

Seed source	Seed viability	Seed germination on acid-washed sand, JI compost, agar and field soils
Cerastium		
Keen	18 July 95	21 July 96
Nikkavord	18 July 95	21 July 96
Arenaria		
Keen(field)	18 July 95	22 July 96
Keen (glasshouse) (a)	-	18 July 95
Keen (glasshouse) (b)	-	27 July 96
Nikkavord	18 July 95	22 July 96
Beinn Iadain	-	22 August 96

Seed viability

The viability of Keen and Nikkavord *Cerastium* and *Arenaria* seeds was tested using the tetrazolium method (Freeland 1976) on 18 September 1995, 15 September 1996 and 12 September 1997. There were ten seeds from each population.

Seed germination under controlled conditions

Most of the collected seeds from each seed source (50 - 150 seeds from each population) were left to dry in paper bags at room temperature and refrigerated at about 5 °C from 14 October to 25 November 1996. The rest were stored in paper bags at room temperature in the dark. Twenty chilled and twenty unchilled seeds from each population (there were only ten Nikkavord *Cerastium* seeds) were tested for percentage germination on acid-washed sand on filter paper within Petri dishes, and on John Innes Compost (No. 1). The seeds from all treatments were kept in the Stirling growth rooms under a photoperiod of 16 h light and 8 h dark with a PAR of 200 μmol m^{-2} s^{1} from 6 January to 3 March 1997 and were watered daily with deionized water. The temperature was 20°C during the day and 15 °C during the night. All the seedlings were counted as they germinated. A further twenty chilled and unchilled Keen *Cerastium* and Keen and Nikkavord *Arenaria* seeds were put on Petri dishes containing 10 g l^{-1} agar with and without gibberellic acid (250 mg l^{-1}) and kept in the growth rooms from 4 August to 29 September 1997. (Insufficient Nikkavord *Cerastium* and Beinn Iadain *Arenaria* seeds were left for the germination on agar and this treatment was omitted).

Eight soil samples were collected randomly from moderately colonised skeletal soils of the Eastern Keen and from moderately colonised skeletal soils on Nikkavord on 18 July 1996. Another eight soil samples were collected randomly from the open areas on which *Arenaria* grew on Beinn Iadain on 22 August 1996. The soils were spread out in trays at room temperature. The soil samples from each site were then mixed and passed through an 8 mm sieve. The soils from each site were put into 12 trays (14 cm x 11 cm) to a depth of about 3 cm, and the total of 36 trays were placed in the growth rooms from 2

September to 20 December 1996 and watered as necessary with deionized water in order to remove any *Arenaria* seeds which germinated from the seed bank.

On 6 January 1997, three replicates of twenty chilled *Arenaria* seeds from each of the four provenances were scattered onto the Keen, Nikkavord and Beinn Iadain soils, so there were a total of 60 seeds from each population on each soil. The trays were placed in the growth rooms in a randomised block design and watered with deionized water as necessary to 17 February. Every two days, the germinated *Arenaria* seedlings were counted and removed.

The watering was stopped from 17 February to 17 March. The reason for the four week break was that an earlier trial of the germination of Keen *Arenaria* seeds on Keen soils had indicated a low germination during six weeks. The earlier experiment was considered to have finished and the trays were stacked on a shelf in the growth rooms. *Cerastium* seeds were sown onto the same trays of Keen soils about four weeks later and a few days after watering the soils, many *Arenaria* seeds germinated. It appeared that the break from watering had stimulated *Arenaria* germination. Therefore in the 1997 experiment involving seeds and soils from the three provenances, there were two four-week breaks from watering. The second break from watering was from 14 April to 12 May and the experiment was ended on 9 June.

Seed germination in the field

Table 3.2 shows the dates of collection of Keen *Cerastium* seeds and Keen (field) and (glasshouse) *Arenaria* seeds used in the field germination experiments. The seeds were collected from about 30 plants selected randomly from each population. The seeds were either sown after collection, or were stored in paper bags at room temperature.

Table 3.2 Dates of collection of *Cerastium* and *Arenaria* seeds for the field germination experiments. Keen (glasshouse) (a) refers to the collection date of seeds from the field and (b) the collection date from seeds of glasshouse grown plants. * refers to the sowing date.

Seed source	**Sobul and Keen cleared plots (31 March 95)***	**Sobul and Keen undisturbed plots (17 July 95)***	**Keen cleared and undisturbed plots (17 July 95)***	**Keen (field) and Keen (glasshouse) *Arenaria* seeds (30 August 95)***
Cerastium				
Keen	12 August 94	16 July 95	17 July 95	-
Arenaria				
Keen (field)	-	-	2 August 95	2 August 95
Keen (glasshouse)(a)	-	-	-	12 August 94
Keen (glasshouse)(b)	-	-	-	22 July 95

On 31 March 1995, 100 *Cerastium* seeds were sown on Sobul onto each of three replicate plots which had been cleared of stones larger than about 5 mm diameter. The plots were positioned in typical areas of Sobul skeletal soils and a location map of the plots is given in Appendix 2. In each plot the seeds were sown directly onto the ground surface about 1 cm apart within a 10 cm x10 cm square. A further three plots of 100 seeds were sown onto the Keen; one plot on the sparsely colonised skeletal soils of the north-west slope, one on the moderately colonised skeletal soils on the lower areas of the Eastern Keen, and one on the well colonised Western Keen. The surface stones were cleared as for the Sobul plots. On 17 July 1995 a further three replicate plots of 100 *Cerastium* seeds were sown onto undisturbed plots on Sobul with undisturbed plots on the Keen positioned in similar areas to the disturbed plots.

In order to investigate the effect of removing the surface stones on the germination success and survival of *Cerastium* and *Arenaria,* a further three replicate plots of 100 seeds of each species were sown onto cleared and undisturbed plots on the Western Keen (Fig. 3.2). The *Cerastium* seeds were sown on 17 July 1995 and the *Arenaria* seeds were sown on 30 August 1995. The plots were chosen to typify the stone surface layer and vegetation of the skeletal soils on the Western Keen and each cleared and undisturbed plot were positioned in pairs. The Western Keen was chosen for sowing because it afforded the least disturbance from visitors. A further three replicate plots of 100 *Arenaria* seeds which had been cultivated in the Stirling glasshouses were sown onto undisturbed plots on the Western Keen on 30 August 1995. *Arenaria* seeds collected from the field were used as a control and the seeds from the glasshouse and the seeds from the field were sown onto paired plots.

Fig. 3.2 Cleared and undisturbed 10 cm x 10 cm plots on which *Cerastium* seeds and *Arenaria* seeds were sown on the Western Keen.

Numbers of *Cerastium* and *Arenaria* seedlings were counted in all the plots on 13 November 1995, 13 May 1996, 18 July 1996, 29 September 1996, 5 November 1996 and 20 July 1997.

Data analysis

The total number of *Arenaria* seeds from each provenance which germinated from 6 January to 9 June 1997 on the Keen, Nikkavord and Beinn Iadain soils were compared using a two-way ANOVA test, with the two factors being the populations and the soils.

For the field sowing experiments, a two-way ANOVA test was used to compare the seedling germination on Sobul plots with the Keen plots sown on 31 March and on 17 July 1995. I considered the numbers of seedlings on the plots on two occasions, firstly on the 18 July 1996 (one year after sowing) and secondly on 20 July 1997 (two years after sowing). The data were transformed using the equation $\sqrt{(X + 0.5)}$, in order to homogenise the variance. A one-way ANOVA with the same transformation was used to find out if there were differences between the number of *Cerastium* or *Arenaria* plants on the cleared and undisturbed plots on the Western Keen on 18 July 1996 and 20 July 1997. Finally, the number of *Arenaria plants* recorded from plots with seeds from cultivated or field origin were compared using a one-way ANOVA test on 18 July 1996 and 20 July 1997 and there was homogeneity of variance so the data were not transformed.

Results

Seed viability

All the *Cerastium* and *Arenaria* seeds showed red-pink staining of the active mitochondria with tetrazolium salts, on 18 September 1995 and 15 September 1996 and 12 September 1997 indicating 100% viability.

Seed germination under controlled conditions

Cerastium

Table 3.3 shows the percentage germination of the Keen and Nikkavord chilled and unchilled *Cerastium* seeds on filter paper, John Innes compost (No.1) and agar. The two populations showed a similar germination under the treatments (although the sample size was low for Nikkavord seeds and there was no agar treatment). There was a high germination of both chilled and unchilled seeds on John Innes Compost (No.1), but there was no germination of unchilled seeds on filter paper. The seeds germinated within four weeks on John Innes compost (No. 1), but on filter paper they took up to eight weeks to germinate. There was some germination of Unst seeds on agar with a maximum of 70% germination of chilled Keen seeds on agar with gibberellic acid but there were fungal infections on the agar and this may have prevented some seeds from germinating.

Arenaria

On the filter paper there was no germination of Keen and Nikkavord *Arenaria* seeds but in contrast 90% of the Beinn Iadain seeds germinated within two weeks (Table 3.4). As for *Cerastium*, there was a high germination of both chilled and unchilled seeds on John Innes Compost (No.1). The agar with gibberellic acid also stimulated germination of Keen and Nikkavord seeds but this was sometimes low (e.g. 10% for unchilled Keen (field) and 15% for unchilled Keen (glasshouse) seeds). As for *Cerastium* the fungal infections on the agar may have prevented some seeds from germinating.

Germination of Keen (field) and Nikkavord seeds on soils from the Keen, Nikkavord and Beinn Iadain was poor during the first six weeks from 6 January to 17 February 1997 with a maximum of 25% germination of Keen seeds and 48% germination of Nikkavord seeds on Beinn Iadain soils (Fig. 3.3). Over 84% of the Beinn Iadain seeds and over 71% of the Keen (glasshouse) seeds germinated on all soil types during this time.

Table 3.3 Percentage germination of Keen and Nikkavord *Cerastium* seeds on filter paper, and John Innes Compost (No.1) in the Stirling growth rooms from 6 January to 3 March 1997 and of Keen *Cerastium* seeds on agar (10 g l^{-1}), with or without gibberellic acid (250 mg l^{-1}) from 4 August to 29 September 1997.

Provenance	**Filter paper**		**agar**		**agar with gibberellic acid**		**John Innes Compost No. 1**	
	Chilled	Unchd.	Chilled	Unchd.	Chilled	Unchd.	Chilled	Unchd.
Keen (n=20)	65%	0%	0%	0%	70%	40%	85%	75%
Nikkavord (n=10)	50%	0%	-	-	-	-	70%	60%

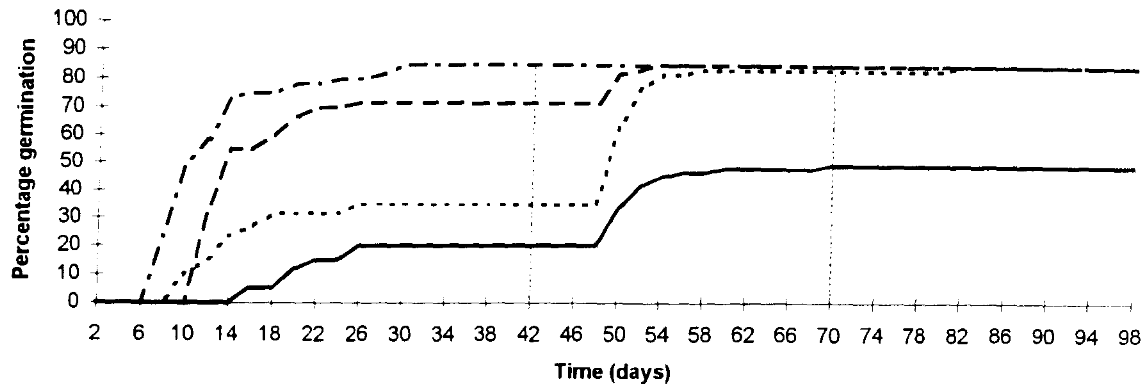
Table 3.4 Percentage germination of Keen (field), Keen (glasshouse), Nikkavord and Beinn Iadain *Arenaria* seeds on filter paper, and John Innes Compost (No.1) in the Stirling growth rooms from 6 January to 3 March 1997 and of Keen (field), Keen (glasshouse) and Nikkavord seeds on a agar (10 g l^{-1}) with or without gibberellic acid (250 mg l^{-1}) from 4 August to 29 September 1997.

Provenance	**Filter paper**		**agar**		**agar with gibberellic acid**		**John Innes Compost No. 1**	
	Chilled	Unchd.	Chilled	Unchd.	Chilled	Unchd.	Chilled	Unchd.
Keen (field) (n=20)	0%	0%	0%	0%	60%	10%	75%	60%
Keen (glasshouse) (n=20)	0%	0%	0%	0%	50%	55%	70%	80%
Nikkavord (n=20)	0%	0%	0%	10%	35%	15%	75%	70%
Beinn Iadain (n=20)	90%	-	-	-	-	-	100%	100%

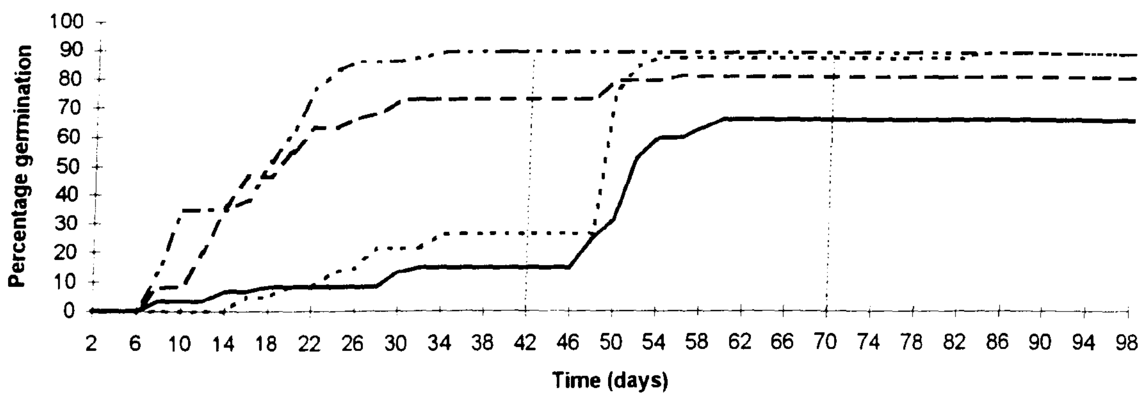
Table 3.5 Mean numbers (±s.e) of *Arenaria* seedlings recorded from Keen (field), Keen (glasshouse), Nikkavord and Beinn Iadain seeds on Keen, Nikkavord and Beinn Iadain soils in trays in the Stirling growth rooms from 6 January to 9 June 1997. There were three replicates of 20 seeds for each treatment.

Provenance / **Soil type**	**Keen (field)**	**Keen (glasshouse)**	**Nikkavord**	**Beinn Iadain**	**Total**
Keen	13.0 ± 1.0	16.7 ± 1.5	19.3 ± 0.7	20.0 ± 0	17.3 ± 0.9
Nikkavord	10.0 ± 2.0	17.0 ± 1.2	17.0 ± 2.1	17.0 ± 1.5	15.2 ± 1.2
Beinn Iadain	13.3 ± 1.2	16.3 ± 2.0	18.0 ± 1.2	18.0 ± 1.0	16.4 ± 0.8
Total	12.1 ± 0.9	16.7 ± 0.8	18.1 ± 0.8	18.3 ± 0.7	

(a)



(b)



(c)

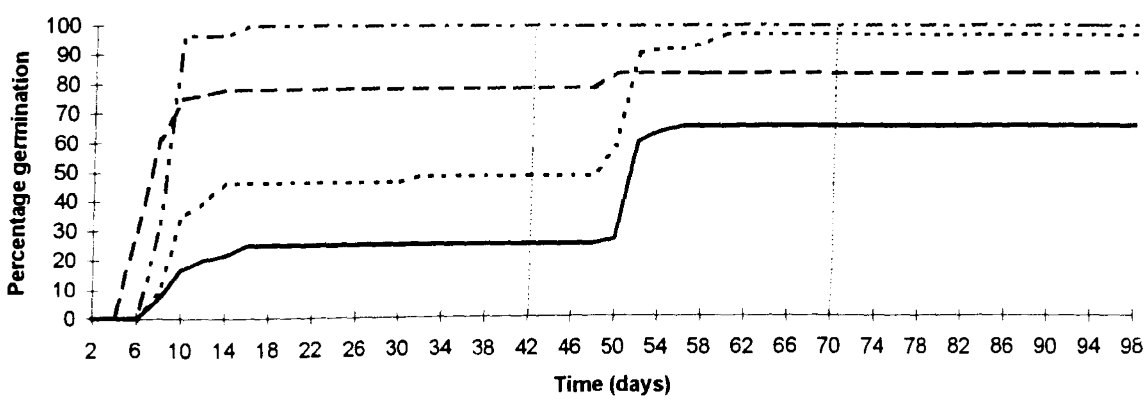


Fig. 3.3 Percentage germination of Keen (field) (——), Keen (glasshouse) (- - -), Nikkavord (-----) and Beinn Iadain (-·-·-) *Arenaria* seeds on trays containing (a) Keen soils, (b) Nikkavord soils and (c) Beinn Iadain soils from 6 January to 9 June 1997 in the Stirling growth rooms. After 42 days ( ) and after 70 days ( ) the trays were taken out of the growth rooms and not watered for four weeks and then were put back into the growth rooms and watered as before (the graph does not include the droughting time on the x axis.) There were three replicates of 20 seeds for each treatment.

After the four week drying period, from 17 February to 17 March there was a 100% increase in numbers of Keen (field) and Nikkavord seedlings recorded on all the soils (Fig. 3.3). There were low numbers of Keen (glasshouse) seedlings recorded, and no Beinn Iadain seedlings recorded during this time. After the second drying period, from 14 April to 12 May, two Nikkavord seeds germinated but no seedlings were recorded from the other populations.

Table 3.5 shows the mean numbers of seedlings from the four populations in each soil recorded from 6 January to 9 June 1997. There were no significant differences among the numbers of seedlings recorded on the different soils ($F_{2,30}=2.28$, $p=0.12$). However, there were differences between the numbers of seedlings recorded from the four provenances ($F_{3,30}=14.16$, $p<0.005$). The Tukey test showed that the Keen (field) seeds had a significantly lower germination than the Nikkavord seeds, Keen (glasshouse) seeds and Beinn Iadain seeds.

Seed germination in the field

Cerastium

The number of plants recorded in the three cleared plots (on which seeds had been sown on 31 March 1995) and the three undisturbed plots (on which seeds had been sown on 17 July 1995) on Sobul on six occasions from 13 November 1995 to 20 July 1997 are shown in Fig. 3.4 a and c. There was much variation among the number of plants recorded in each plot: e.g. from two to 20 plants in the cleared plots, and seven to 18 plants in the undisturbed plots, on 20 July 1997. There were new seedlings recorded at each census time but some of the recorded plants were larger and may have survived throughout the two years of recording. There were some plants outside the plots, up to a distance of 1 m from them. It is likely that some of the seeds sown were blown out of the plots, or flushed out by heavy rains. Twenty-four *Cerastium* plants were recorded outside the plots on 20 July 1997, giving a total of 92 plants on Sobul, roughly 15% of the number of seeds which were planted. On 20 July 1997 I observed that two of the plants had flowered, producing four fruits which contained seeds.

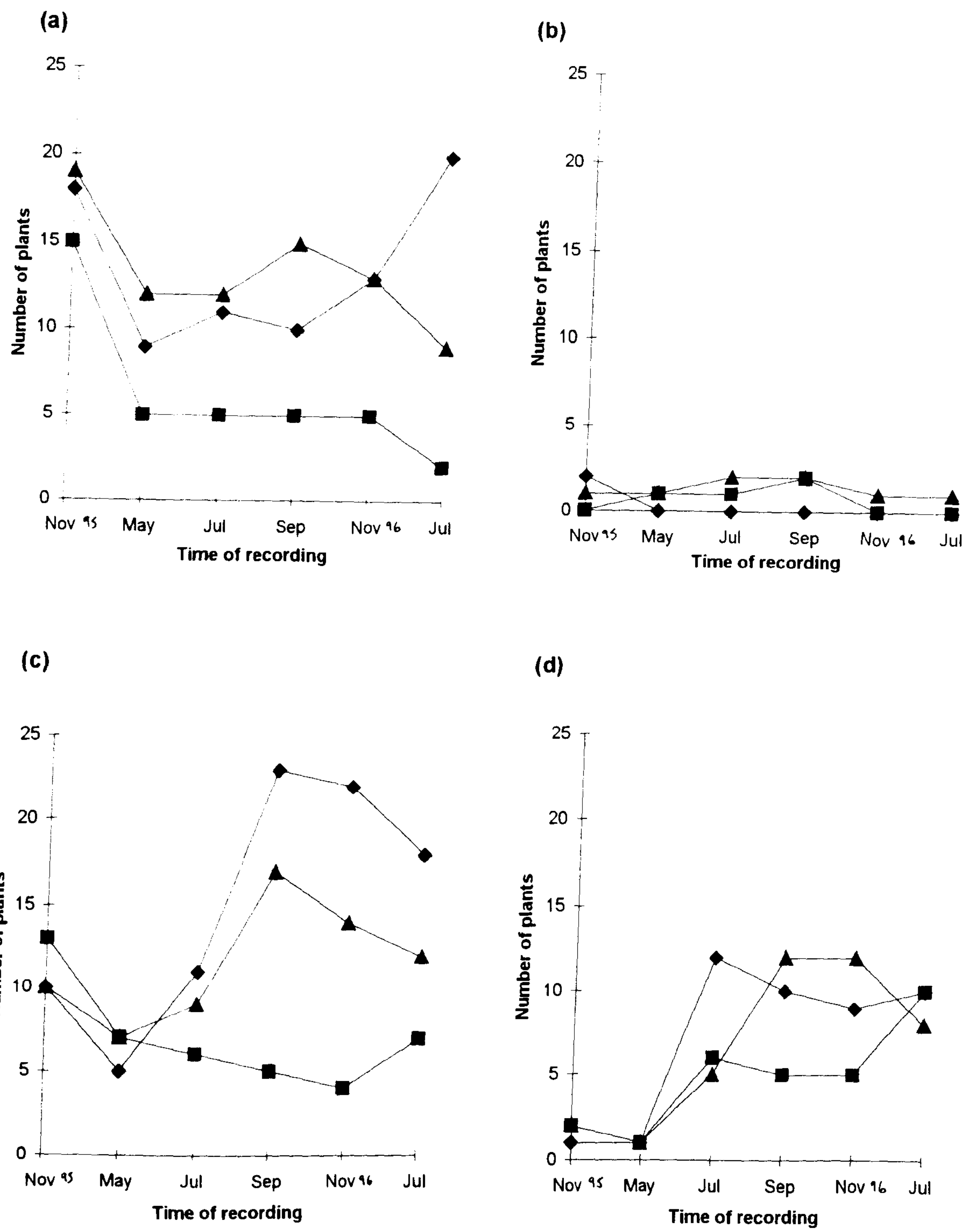


Fig. 3.4 Total numbers of *Cerastium* plants recorded from three replicate plots of 100 seeds sown onto (a) cleared plots on Sobul, (b) cleared plots on the Keen on 31 March 1995, (c) undisturbed plots on Sobul and (d) undisturbed plots on the Keen on 17 July 1995. Plants were recorded on 13 November 1995, 13 May 1996, 18 July 1996, 29 September 1996, 5 November 1996 and 20 July 1997.

Germination was poor in the cleared Keen plots (on which seeds had been sown on 31 March 1995) with only one plant recorded on 20 July 1997 (Fig. 3.4 b) but was higher in the undisturbed plots (on which seeds had been sown on 17 July 1995) with a total of 28 plants recorded on 20 July 1997 (Fig. 3.4 d). There were no significant differences between the number of plants in cleared and undisturbed plots recorded on 18 July 1996 ($F_{1,9}$=3.53, p=0.09), but on 20 July 1997, the undisturbed plots had slightly significantly higher numbers of plants than the cleared ones ($F_{1,9}$=5.61, p=0.04). There were slightly significantly higher numbers of plants on Sobul than on the Keen recorded on 18 July 1996 ($F_{1,9}$=6.54, p=0.03), and on 20 July 1997 ($F_{1,9}$=6.19, p=0.04).

There was a lot of variation in the numbers of *Cerastium* plants recorded in cleared and undisturbed plots on the Western Keen (on which seeds had been sown on 17 July 1995) (Fig. 3.5 a, b). There were no significant differences between the numbers of plants in the cleared plots or in undisturbed plots on 18 July 1996 ($F_{1,4}$=5.75, p=0.08), but there were significantly higher numbers in the undisturbed plots on 20 July 1997 ($F_{1,4}$=10.27, p=0.03) (Table 3.6). The plants which were recorded in the cleared plots were restricted to the edges of the plot near to stones. There were no flowering *Cerastium* plants in any of the Keen plots.

Arenaria

There were significantly higher numbers of *Arenaria* plants in the undisturbed plots than in the cleared plots on the Western Keen on 18 July 1996 ($F_{1,4}$=50.53, p=0.002) (Table 3.6). As for *Cerastium*, in the cleared plots the *Arenaria* seedlings were recorded around the edges. There was one flowering plant in one of the undisturbed plots which gave five flowers. There were also significantly higher numbers of plants in plots with the *Arenaria* (glasshouse) seeds than those with the *Arenaria* (field) seeds on 18 July 1996 ($F_{1,4}$=60.46, p=0.001) (Table 3.6). However, there were lower numbers of *Arenaria* plants in all the plots on 20 July 1997 (Figs. 3.5 c, d, e and f) and on this date there were no significant differences between the treatments (Table 3.6).

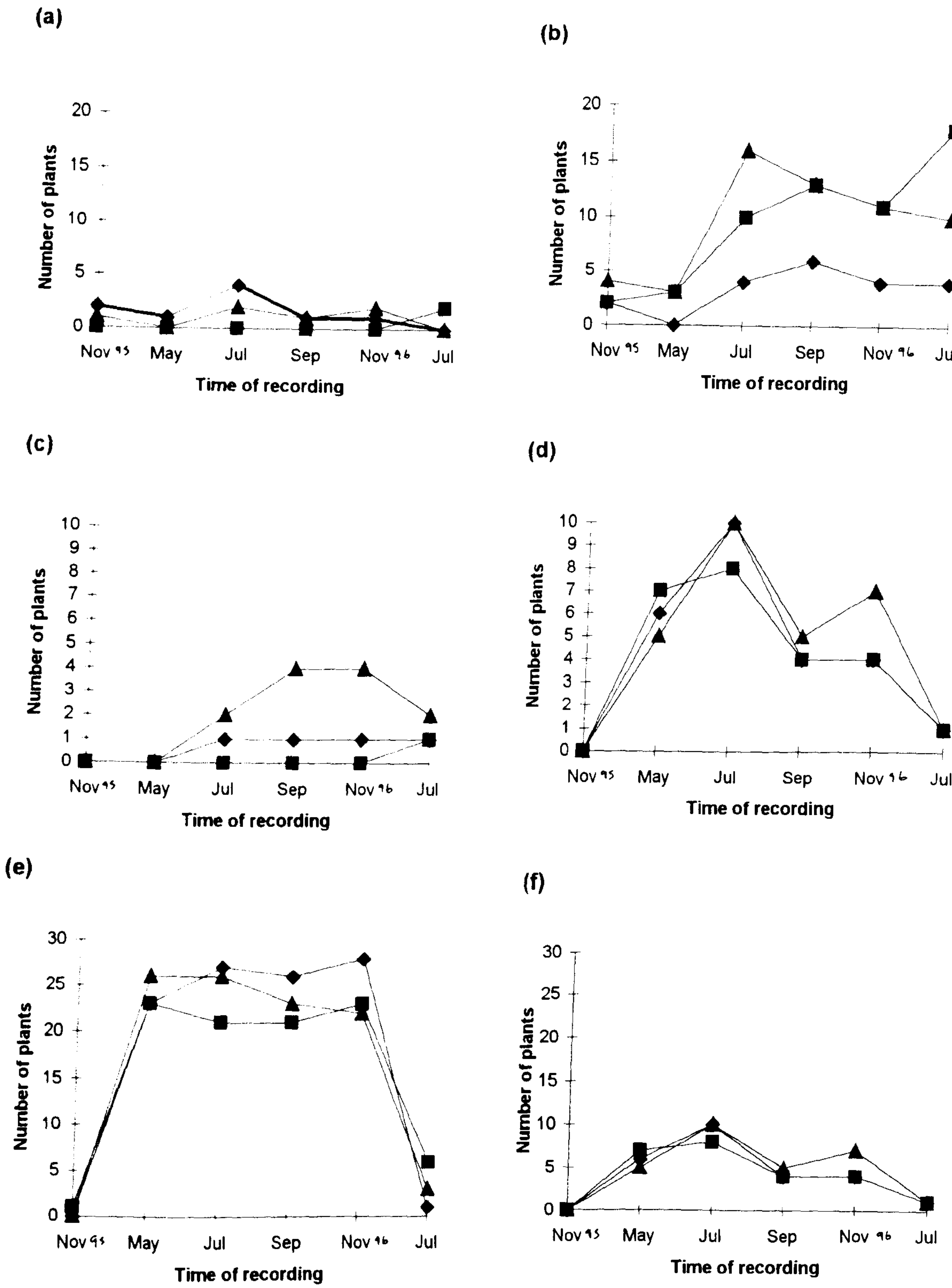


Fig. 3.5 Total numbers of plants recorded from three replicate plots of 100 seeds sown onto the Western Keen on (a) cleared plots and (b) undisturbed plots for *Cerastium* (c) cleared plots and (d) undisturbed plots for *Arenaria* and (e) *Arenaria* (glasshouse) seeds and (f) *Arenaria* (field) seeds sown onto undisturbed plots. Plants were recorded on 13 November 1995, 13 May 1996, 18 July 1996, 29 September 1996, 5 November 1996 and 20 July 1997.

Table 3.6 Results of one-way ANOVA tests comparing the numbers of plants germinated from 100 seeds sown onto three pairs of cleared and uncleared plots for *Cerastium* (a), and *Arenaria* (b) and for Keen (field) *Arenaria* seeds compared to glasshouse ones both sown onto undisturbed plots (c). The number of plants in each plot were considered on 18 July 1996 and 20 July 1997. The data for cleared and undisturbed plots for *Cerastium* and *Arenaria* were transformed using the equation $\sqrt{(x+0.5)}$ before analysis.

Treatment	F value (d.f. 1,4)	P value
(a) Cleared and undisturbed *Cerastium* plots		
Recorded on:		
18 July 1996	5.75	0.08
20 July 1997	10.27	0.03
(b) Cleared and undisturbed *Arenaria* plots		
Recorded on:		
18 July 1996	50.53	0.002
20 July 1997	1.00	0.37
(c) Keen (field) and Keen (glasshouse) *Arenaria* plots		
Recorded on:		
18 July 1996	60.46	0.001
20 July 1997	2.58	0.18

Discussion

Keen, Nikkavord and Beinn Iadain *Arenaria* seeds showed germination differences. None of the seeds from the Keen and Nikkavord populations germinated on filter paper and they germinated over a long period on Keen, Nikkavord and Beinn Iadain soils in the Stirling growth rooms. This implies that only a small proportion of the seeds from the Keen or Nikkavord populations entering the soil will germinate immediately. This "germination heteromorphism" will be a selective advantage for unpredictable sites on which the conditions for successful seedling establishment vary from year to year throughout the seasons (Silvertown & Lovett Doust 1993). This is in line with the population dynamics studies (chapter 2) in which *Arenaria* seedlings were recorded in permanent plots throughout the different seasons of 1994, 1995 and 1996.

Most of the Beinn Iadain seeds germinated within two weeks on filter paper and three weeks on the three soils, and a similar rapid germination has been found for *Arenaria* seeds in glasshouses from other Scottish mainland populations (Halliday 1960 a). However there are no field data on the germination of any Scottish mainland *Arenaria* populations and so it is not possible to know if the rapid germination is paralleled in the field.

The faster and higher overall germination of Keen (glasshouse) *Arenaria* seeds compared with Keen (field) seeds may have been a result of the higher nutrients in the potting compost used to grow the glasshouse seeds. The lower total germination of Keen (field) seeds compared with Nikkavord and Beinn Iadain ones, may be due to a lower germination of Keen seeds compared with the other populations. However, Keen seeds are 100% viable for at least two years and it is possible that the rest of the Keen seeds would germinate at some later date.

It is clear that Unst *Arenaria* seeds did not require a chilling treatment for germination, for there was >50% germination of both chilled and unchilled seeds on potting compost. There were no unchilled Beinn Iadain seeds in the investigations, but Halliday (1960 a) observed that the germination of Scottish mainland *Arenaria* seeds was high if the seeds were sown immediately (80-90% after three weeks). There was some germination of the Unst seeds on agar with gibberellic acid, and it is possible that fungi in the Petri dishes prevented more seeds from germinating.

The chilled *Cerastium* seeds germinated on acid-washed sand, but the unchilled ones did not. Most of the *Cerastium* seeds which were sown on the Keen and on Sobul on 17 July 1995 and had been collected from capsules on the same day, did not germinate until the following summer. This implies that the winter conditions stimulated germination. However, as for *Arenaria*, there was greater than 50% germination of unchilled seeds as well as chilled ones on potting compost.

The germination success and survival of *Cerastium* seeds on Sobul was as good as, if not better than on the Keen, with two flowering plants producing seeds. The Sobul population has established itself and is spreading. This implies that *Cerastium* plants had not been present on Sobul because the seeds were unable to disperse there from the Keen, and if there had been *Cerastium* populations on Sobul in the past, which became extinct, the population on this site was unable to re-establish.

There are several other examples demonstrating that dispersal can limit the distribution of a species even on a local scale: Primack & Miao (1992) found that four annual species growing in a woodland in Massachusetts, USA were apparently unable to reach in 20 years suitable sites less than 100 m away from large natural populations; Scherff *et al.* (1994) concluded that limited seed dispersal confined *Ranunculus adoneus* A. Grey to locations within alpine snowbeds in Pennsylvania, USA.

It is too early to say if the population will persist. There have been fluctuations of numbers of *Cerastium* plants on the Keen in the last 16 years which have been related to the climate (chapter 2). From 1995 to 1997 there were high numbers of *Cerastium* plants recorded on the Keen, and *Cerastium* seedlings on Sobul appeared to have established, but it is impossible to say if, in the event of unfavourable weather conditions, the smaller Sobul population will survive. *Cerastium* seeds were sown onto Sobul once before by L. Johnston (J. Proctor pers. comm.) and they apparently have not survived, although there are no details about the date of sowing, number of seeds sown, or the precise location. Nevertheless, the continual recruitment of young *Cerastium* seedlings throughout the two years of observations shows that this species had formed a seedbank on Sobul and this may enable the population to survive unfavourable periods.

There have been successful colonisations on other ultramafic sites, from species of both ultramafic and non-ultramafic origins. Kruckeberg (1986) reported the successful colonisation and spread of a population of *Silene paradoxa* L. onto an ultramafic site in western Washington. There were 27 transplants of *S. paradoxa* taken from three populations, from an ultramafic locality in Yugoslavia and two unknown sources, planted onto the site in 1963. In 1983, there were over 1000 plants.

An important question is why *Arenaria* has apparently dispersed more successfully on Unst than *Cerastium*. Neither species has specialised dispersal mechanisms but *Arenaria* seeds are smaller. The mean weight (± s.e.) of 100 *Arenaria* seeds collected from the Keen on 18 July 1995 was 0.260±0.004 mg and that of 100 *Cerastium* seeds collected from the Keen on 17 July 1996 was 0.364±0.007 mg. *Arenaria* seeds are smoother and may pass over rough surfaces more easily or be carried by the wind. Halliday (1960 a) observed that whole capsules of *Arenaria* were broken off in the wind; the capsule has a tight fit around the seeds, unlike the *Cerastium* capsule which holds the seeds loosely. If a *Cerastium* capsule was blown off, the seeds would probably fall out before the capsule had reached a new site.

There were low numbers of *Cerastium* and *Arenaria* plants recorded in all the sowing plots on the Keen and on Sobul, compared with the number of seeds first planted. There were some *Cerastium* plants on Sobul outside the plots but the total number of plants on Sobul recorded on 20 July 1997 was still only 15% of the number of seeds first planted. A few other seeds may be stored in the seedbank, but this number is likely to be low after two years. It appears that there are low numbers of "safe sites" (in the sense of Harper 1977) for the germination and establishment of *Cerastium* and *Arenaria* plants.

There was a big range in the numbers of plants recorded in all the sowing plots for *Cerastium* and *Arenaria* which demonstrates that both the Keen and Sobul are spatially heterogeneous. There are many reasons for this. Concentration of nutrients in the soil are patchy in space and time (Tilman 1982, Rorison 1987). Nagy (1994) found that there were large differences in the soil chemical factors at the microscale on the Scottish Meikle Kilrannoch ultramafic outcrop. Plants growing on the Keen are phosphorus limited (Spence & Millar 1963, Carter *et al.* 1987 b). A local nutrient input from animals and the process of cryoturbation may cause a patchy nutrient supply on a small scale and may influence seedling establishment.

The Keen has a range of slope, aspect, and soil depth (Carter 1982), and these will all affect the water relations of plants. Soil depth is likely to be particularly important. On ultramafic sites, studies have shown that soil depth has an important role both for plant communities e.g. a Californian ultramafic grassland (McCarten 1992), and for individual species e.g. *Lychnis alpina* on Meikle Kilrannoch, a Scottish ultramafic outcrop (Nagy & Proctor 1997).

Finally, heterogeneity of the of the soil-surface micro-environment will affect seed germination. Harper *et al.* (1965) demonstrated this in an experiment which involved sowing seeds of *Plantago lanceolata*, *P. media* and *P. major* onto an artificial seed bed, with seven different treatments including small alterations to the soil surface such as holes and compactions and a control. The seedlings were mapped as they germinated. There was a very fine scale of discrimination for differences in the soil-surface micro-environment for all the species, and there were also differences among the species.

Surface stones on the Keen will restrict the amount of space on which the seeds have direct contact with the soil, but the absence of stones causes a reduction in the numbers of both *Cerastium* and *Arenaria* plants compared to control plots in experiments carried out on the Western Keen. It is likely that the stones protect the seeds from exposure to high winds and also reduce evapotranspiration. Halliday (1960 a) noted that the protection afforded by variations in microtopography was important for *Arenaria* germination and survival throughout its range. I observed that the soil surface of the cleared plots had become compacted, probably by raindrops which can hit the ground forcefully when it is windy. Compacted soils may act as a physical impediment to seed germination and may also impede the gas flow to seedlings (Harper 1977).

The cleared and undisturbed experimental plots were within a relatively small area on the Western Keen, so it is perhaps unwise to draw conclusions about the rest of the site. There may be large variations in germination ability among seedlings from different parts of the Keen. However, *Cerastium* germination was poor on the cleared plots on other parts of the Keen (which were sown onto the site on 31 March 1995) and it seems likely that the effects of the stones would be just as important on the slopes and the summit of the hill on the Eastern Keen. Interestingly there were roughly the same number of *Cerastium* plants on cleared plots on Sobul as on undisturbed ones. This is because the stones had been displaced, probably by sheep, and after two and a half years, the stone surface layer of the cleared plots was similar to the undisturbed plots.

There was variation in the numbers of seedlings in the plots throughout time as well as space. For *Cerastium*, the differences in the numbers of plants in the cleared and undisturbed plots were only significantly different in 1997, which implies that the soil-surface microenvironment had more of an effect on survival of individuals than on initial establishment. For *Arenaria* there were higher numbers of seedlings in the undisturbed plots in 1996, but there were low numbers of plants in all the plots recorded on 20 July 1997 implying that some other factor was more important. Similarly, although the *Arenaria* (glasshouse) seeds showed a higher germination than the *Arenaria* (field) seeds during 1996, there were low numbers of all the seeds recorded in the plots on 20 July 1997. It seems likely that some climatic factor was the cause of the reduced *Arenaria* numbers recorded in July 1997.

Chapter 4. Leaf trichomes, glandular secretory material and drought tolerance of *Cerastium nigrescens* and *Cerastium arcticum*

Introduction

One of the most striking features of Keen *Cerastium* plants, is the dense glandular leaf trichomes which secrete a transparent and slightly sticky fluid. These trichomes are retained after three years in cultivation (Proctor & Woodell 1971). Lusby (1985) found that leaves from Keen *Cerastium* plants had more glandular trichomes than leaves from five Scottish mainland populations of *Cerastium arcticum*, although there were glandular and non-glandular trichomes recorded on leaves from all the populations. He did not consider the Nikkavord var. *acutifolium* in his study. There have been suggestions that the Keen leaves are more densely hairy than the Nikkavord ones (Stuffins 1983), but there are no data to support this.

Hairy plants tend to be found in dry habitats (Johnson 1975). Ehleringer *et al.* (1981) considered species of the genus *Encelia* in the coastal region of the north and south of the Western United States. In the wetter regions, they had glabrous leaves, and in the drier regions the species had more pubescent leaves. Smith & Nobel (1977) found that in the two Californian desert shrubs *Encelia farinosa* Grey and *Hyptis emoryi* Torr., the leaves were more hairy during the drier seasons of summer and autumn.

The presence of leaf trichomes is thought by many to be an adaptation to dry conditions (Fahn & Cutler 1992). Trichomes may reduce the transpiration rate by increasing the thickness of the boundary layer. However, studies have suggested that the effect on transpiration is not very great (Johnson 1975). Leaf trichomes may also affect the water economy of plants indirectly by reflecting solar radiation and causing a reduction of the heat load of the leaves; lowering the leaf temperature causes a reduction in transpiration. Leaf pubescence does increase leaf reflectance e.g. the leaf hairs of *Encelia farinosa* Grey reduced the absorbance of photosynthetically active radiation by as much as 56% compared with the non-pubescent *Encelia californica* Nutt. (Ehleringer *et al.* 1976).

Carter *et al.* (1987 a) estimated that summer droughts of seven consecutive days or longer on the Keen may exhaust the water reserves in the shallowest soils and they found that such rainless spells occurred at least once in all but five years between 1959 and 1983. It has been suggested that the hairy *Cerastium* leaves are a xeromorphic adaptation (Slingsby 1981, Lusby 1985). It was the aim of this chapter to quantify the density of leaf trichomes and the proportion of glandular trichomes on Keen and Nikkavord *Cerastium* and Streymoy *Cerastium arcticum*, to try and identify the substance secreted by the glandular trichomes, and to compare the drought tolerance of the *Cerastium* races.

Methods

Trichome Investigations

Source of glasshouse plant material

Cerastium seeds were collected from capsules of ten plants growing on the Keen and from ten plants from Nikkavord on 18 July 1995. *Cerastium arcticum* seeds were collected from Streymoy by T. Leivsson during August 1995. The seeds were refrigerated at 5 °C from 12 September to 26 October 1995 and then stored in paper bags in the dark. On 28 March 1996 about 50 seeds from the Keen, Nikkavord and Streymoy populations were germinated on acid washed sand in growth rooms at Stirling. Twelve seedlings from each population were transplanted into Keen soil in pots (11 cm in diameter) from 11 April to 26 April 1996 and also pots of John Innes Compost (No. 2) on 20 May 1996. All the plants were positioned in a randomised block design in unheated glasshouses in which the irradiance ranged from about 25 µmol m^{-2} s^{-1} on a dull day to 100 µmol m^{-2} s^{-1} on a bright day, and watered as necessary with deionized water. For all the trichome investigations the leaf samples were taken from the same position on each plant, three to four pairs of leaves away from the tip of the shoots.

Trichome density and form

In order to quantify the density of the trichomes and the proportion of glandular trichomes on each leaf, I counted, using a binocular microscope, the glandular and non-glandular trichomes on three leaves from each of six plants from each of the three populations growing on the two soils. The leaf trichomes were counted during December 1996. After counting, the leaves were placed on graph paper and their areas were determined.

A further ten leaves were collected from each of ten *Cerastium* plants on the Keen and ten *Cerastium* plants on Nikkavord on 20 July 1997. The leaves were placed on graph paper and the areas determined after collection, and then each leaf was put into a vial containing FAA (13 ml formaldehyde, 5 ml glacial acetic acid, 200 ml 50% ethanol). The trichomes were counted in Stirling using a binocular microscope on 28 July as for the previous ones.

On several occasions during December 1996 a whole leaf was carefully removed from three *Cerastium* plants of the three populations growing on the two soils and frozen in liquid nitrogen. The leaves were then observed under a 60A International Scanning Instruments scanning electron microscope (SEM) in order to see the distribution of the trichomes and to find out if there were pores at the tips of the glandular trichomes. On 29 February 1997 a small section of about 1-2 mm wide and 4-5 mm in length was cut from the leaf edges of plants from each provenance. Each section was then mounted in distilled water and observed using an optical Zeiss light microscope in order to compare the cells of the glandular and non-glandular trichomes.

Cell ultrastructure

On 12 December 1996, several small leaf sections about 1-2 mm wide and 1-2 mm in length were cut from Keen plants growing on John Innes Compost (No. 2) and on Keen soil, fixed in 2% glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.2) and kept at room temperature for 2 h. They were then refrigerated for 48 h. The leaf segments were vacuum infiltrated to enable the samples to sink and were kept for a further 12 h at room temperature. They were then dehydrated with graded ethanol, postfixed in 1% osmium tetroxide and embedded in London White Resin. Glandular trichomes were cut longitudinally using an ultramicrotome, placed under grids and stained with uranyl acetate and lead citrate. They were observed under a 275 Corinth transmission electron microscope (TEM).

Analysis of the glandular trichome secretory material

Specimens of fresh and embedded leaves were used for the histochemical tests. Sections of about 1-2 mm wide and 4-5 mm in length cut from the tip of each leaf were used for the fresh sections. The embedded material was prepared in the following way: small sections of about 1-2 mm wide and 4-5 mm in length were cut from the edge of the leaf and fixed in 2% glutaraldehyde in 0.1M sodium cacodylate buffer (pH 7.2), and kept at room temperature for two h. They were vacuum infiltrated and placed in a fridge overnight. The leaf segments were then dehydrated with graded ethanol and embedded in JB4 resin. The glandular trichomes were cut longitudinally using an ultramicrotome before staining.

All the staining methods used are described in Jensen (1962) except for the dimethylglyoxime method for nickel which is described in Pearse (1972). Fresh sections were required for the following tests: polysaccharides other than cellulose (Ruthenium red method), lipids (Nile blue procedure and Sudan Black method). Embedded sections were used to detect insoluble polysaccharides (Periodic Acid-Schiff's (PAS) reagent) and magnesium (titan yellow method). The dimethylglyoxime method for nickel was tested on both fresh and fixed sections. After staining, the fresh sections were mounted in glycerine jelly (70% gelatin in water containing 2% glycerine). All the sections were observed under an optical Zeiss light microscope. The staining work was done during March 1997.

Drought experiment

Source of seeds and soils

Cerastium seeds were collected from ten plants from the Keen on 20 July 1996. Unfortunately, there were insufficient field-collected Nikkavord or Streymoy seeds, so seeds from these two populations were collected from plants which had been cultivated in John Innes Compost (No.2) in the Stirling glasshouses. The seeds were harvested from ten Streymoy plants and seven Nikkavord plants from 18 June to 6 July 1996. The Nikkavord plants originated from seeds which had been collected from the Keen on 18 July 1995 and the Streymoy plants from seeds which had been collected by T. Leivsson during August 1995. The seeds from the three provenances were refrigerated from 14 October to 25 November 1996.

The Keen soils had been collected from moderately colonised soils on the Eastern Keen from 7-8 June 1995 and were spread out in trays in the Stirling glasshouses and watered regularly with deionized water from 16 September 1995 to 16 April 1996 for the seedbank investigations (Chapter 2). For the purpose of this experiment, the samples were dried from 16 - 30 April 1996 and then stored in bags in the dark. The soil was mixed and passed through an 8 mm sieve prior to use.

Droughting of plants

On 22 May 1997, about 50 seeds from each of the three provenances were germinated on John Innes Compost (No. 1). Although it is better to germinate plants on a substrate which has no added nutrients (e.g. acid-washed sand), compost was used because the seeds germinated over a shorter time period (Chapter 3), and it was possible to transplant 20 seedlings of roughly the same size from each population into Keen soil on 19 June 1997. Before transplanting, the seedlings were washed carefully in deionized water, and the length of the root and the shoot were recorded. Each seedling was planted into a 9 cm diameter pot which had been filled with 300 g of Keen soil and 100 g of deionized water which saturated the soil but did not flood it. The total of 60 pots were weighed (weight$_s$) and positioned in a randomised block design in the Stirling glasshouses. The plants were watered with deionized water regularly for six weeks.

On 30 July 1997, each pot was weighed and deionized water added to give weight$_s$. Water was withheld from ten individuals from each population (drought treatment) and the rest of the plants were watered daily to weight$_s$ (control). When 50% of the droughted plants were wilting (13 August), the droughted pots were weighed and then all the pots were rewatered daily to weight$_s$.

On 20 August there was a second drought treatment using the same plants and methods as for the first. This time the drought treatment was continued until all of the droughted plants had wilted and some showed signs of severe wilting with shrivelled, curled leaves. The droughted plants were rewatered on 9 September, after 20 days without water. The plants were then all watered regularly for four weeks. On 7 October 1997 the following were recorded: number of dead plants; number of plants with new growth at the nodes; number of plants with recovered leaves; number of recovered leaves; ratio of number of leaves on droughted plants compared with control plants.

Data analysis

A two-way ANOVA was used to compare the density of trichomes and the proportion of glandular trichomes on each leaf. For glasshouse-grown plants, three leaves had been sampled from each plant, and the average count was used in the statistical analysis. For the trichome density counts, the data were transformed using the equation $\log(x+1)$ and for the glandular hairs proportions, the data were transformed using the arcsin transformation in order to reduce the heterogeneity of the variance and give a normal distribution.

For the drought experiment, a one-way ANOVA was used to find out if there were differences in root or shoot length between the Keen, Nikkavord and Streymoy *Cerastium* seedlings (before they were transplanted into Keen soil). The water content of the soil was recorded as a percentage of the water which had first been added (100 g). A one-way ANOVA was also used to check that there were no differences between the % water contents of soils (recorded at the end of the two drought treatments) on which plants from each of the three populations had been grown.

Results

Trichome form and distribution

SEM photographs of Keen, Nikkavord and Streymoy leaves are shown in Figs. 4.1-4.3. The plants had been growing on John Innes Compost and the distribution of the leaf trichomes of plants growing on Keen soil was the same. Keen and Nikkavord leaves had many trichomes and these were distributed on all parts of the leaf (Figs. 4.1 and 4.2). Most of the trichomes were glandular, but there were some non-glandular ones which were more abundant on the leaf edges (Fig. 4.1). There were non-glandular trichomes on both leaf surfaces, and on the abaxial surface they were distributed near to the central vein. The trichomes of Streymoy leaves were almost entirely restricted to the leaf edges (Fig. 4.3) and most of them were non-glandular.

Sections from the edges of leaves from Keen, Nikkavord and Streymoy populations are shown in Fig. 4.4 a-d. The cells of both glandular and non-glandular trichomes were uniseriate and chloroplasts could be seen clearly in all the cells. The glandular trichomes had six to eight cells, and the non-glandular ones three to five. There appeared to be a greater number of shorter glandular trichomes on Nikkavord plants (Figs. 4.2 and 4.4 b) than on the Keen ones (Figs. 4.1 and 4.4 a), but there were no observed differences between the number of cells in the shorter or longer trichomes. There were four to six non-glandular trichomes at the base of Streymoy and Keen leaves (Fig. 4.4 d) and these were about three times as long as the other non-glandular trichomes, but there were none on Nikkavord leaves.

Trichome counts

There were significant differences between the density of trichomes on leaves of the three populations growing on John Innes Compost (No. 2) and on Keen soil ($F_{2,32}$=237.28, p<0.001). The Streymoy leaves had a lower mean density than the Keen ones and the Nikkavord ones (Fig. 4.5 a and b; table 4.1). When considering the field-grown plants as well as the glasshouse-grown ones, the Keen leaves had a significantly higher density of trichomes than those from Nikkavord ($F_{1,40}$=8.85, p=0.005).

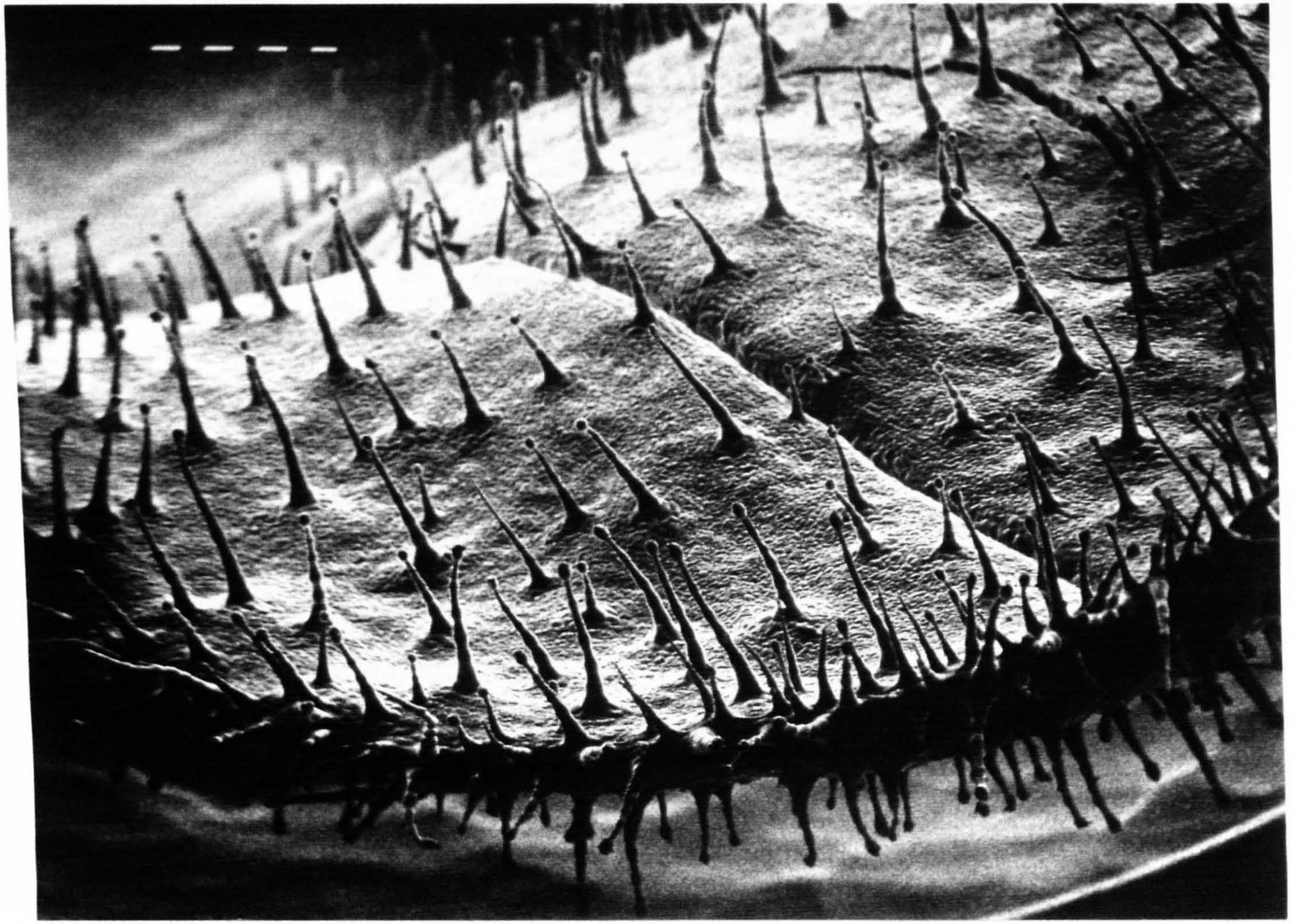


Fig. 4.1 SEM photograph (x26) of a Keen *Cerastium* leaf showing many trichomes on both leaf surfaces. The non-glandular trichomes are mostly on the edges of the leaf.

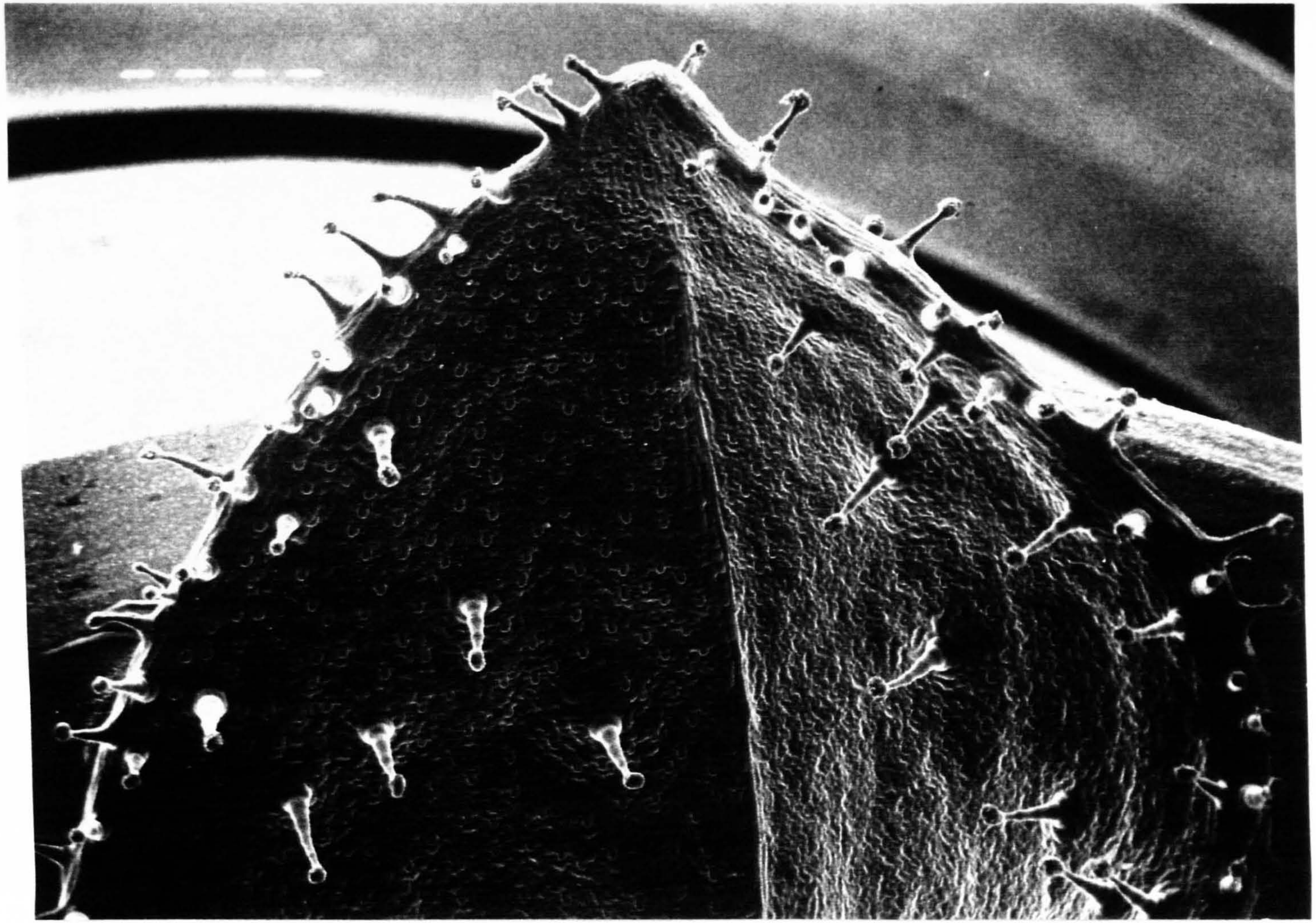


Fig. 4.2 SEM photograph (x25) of a Nikkavord *Cerastium* leaf showing glandular trichomes which are more abundant on the leaf edges

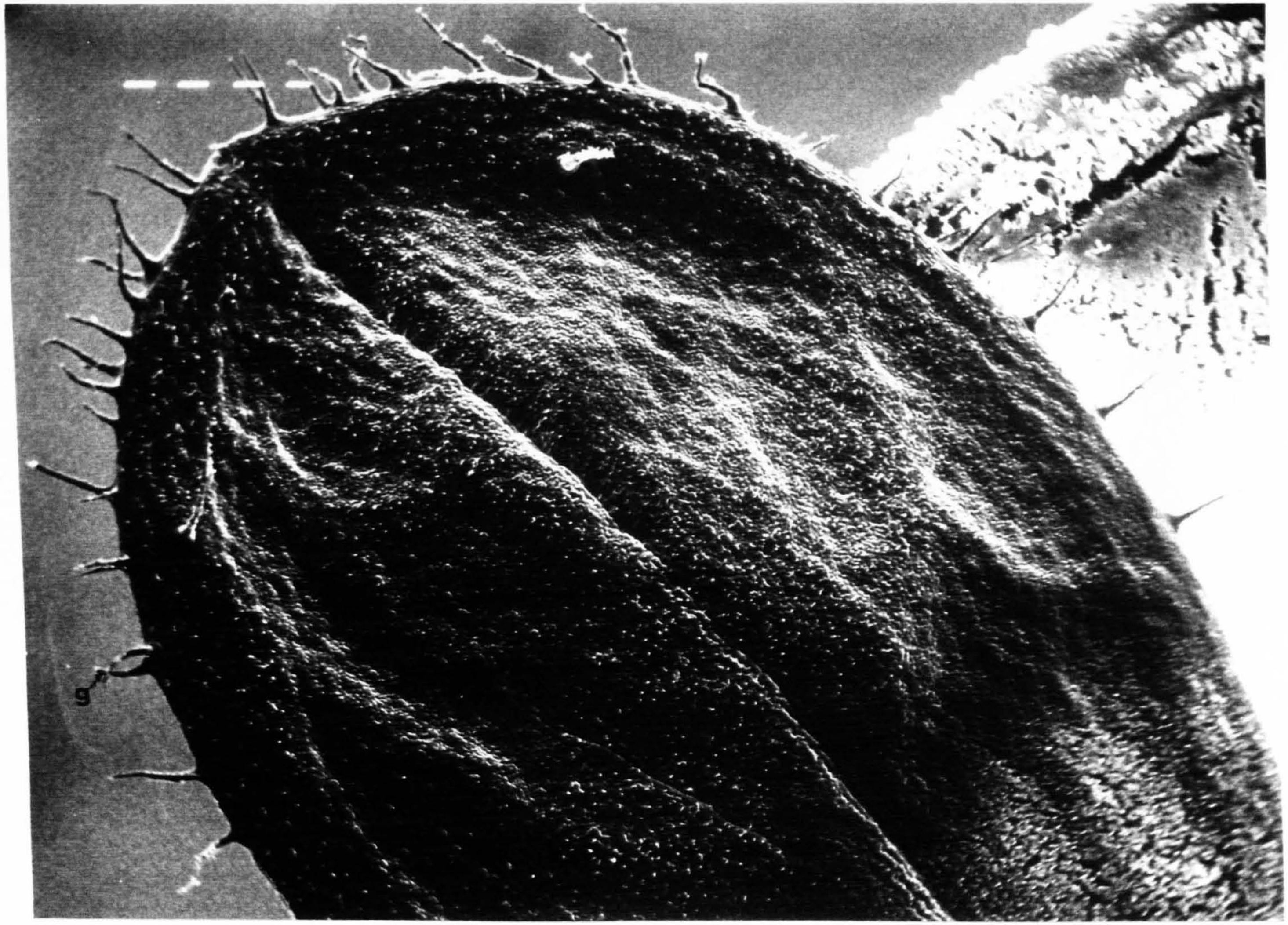


Fig. 4.3 SEM photograph (x25) of a Streymoy *Cerastium* leaf showing mainly non-glandular trichomes which are almost entirely restricted to the edges of the leaf. (There is one glandular trichome shown as g).

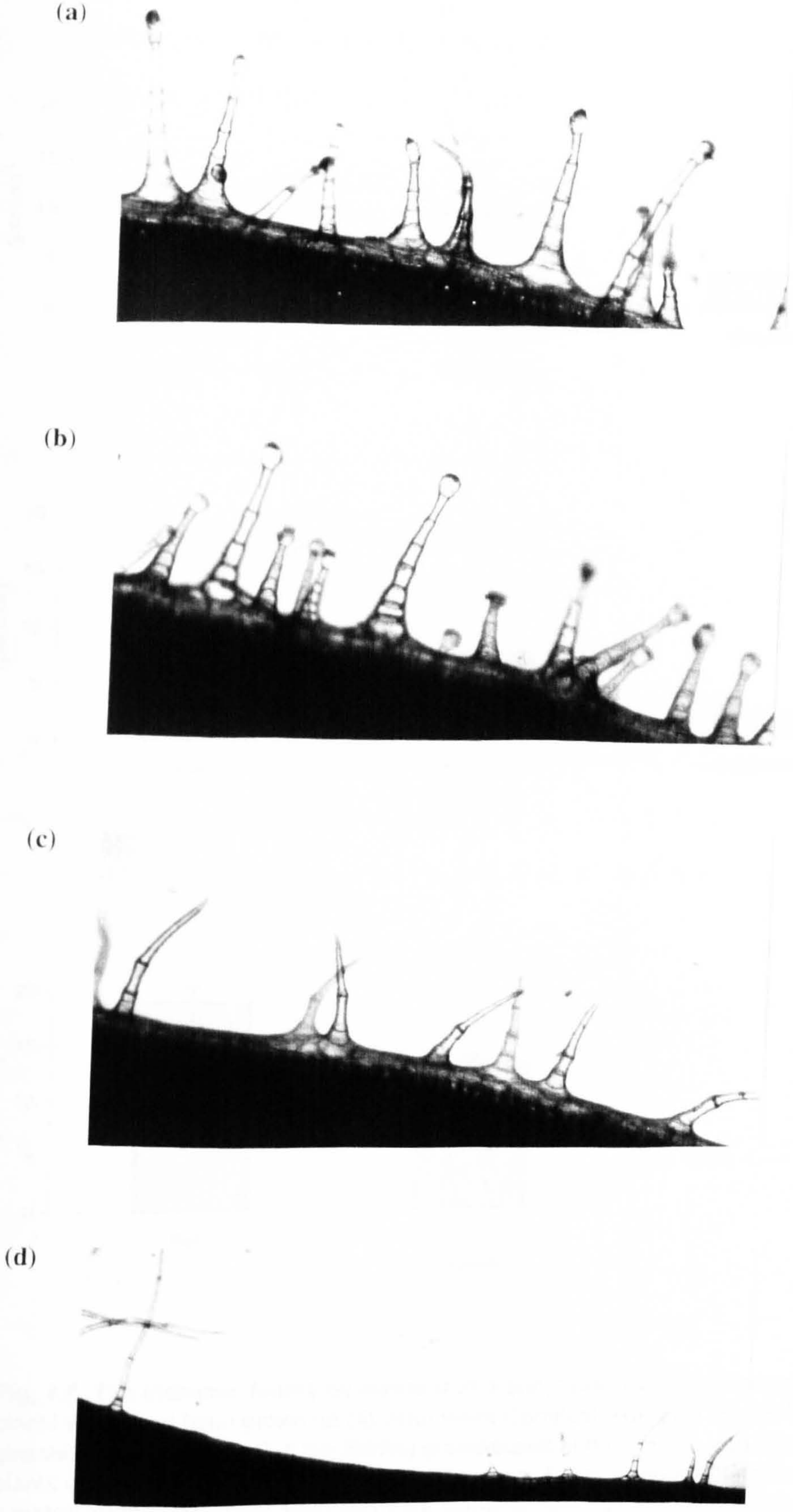


Fig. 4.4 Light micrographs of sections of leaf edges from (a) Keen (x20) (b) Nikkavord (x20) (c) Streymoy (x20) and (d) Streymoy (x10) *Cerastium* plants.

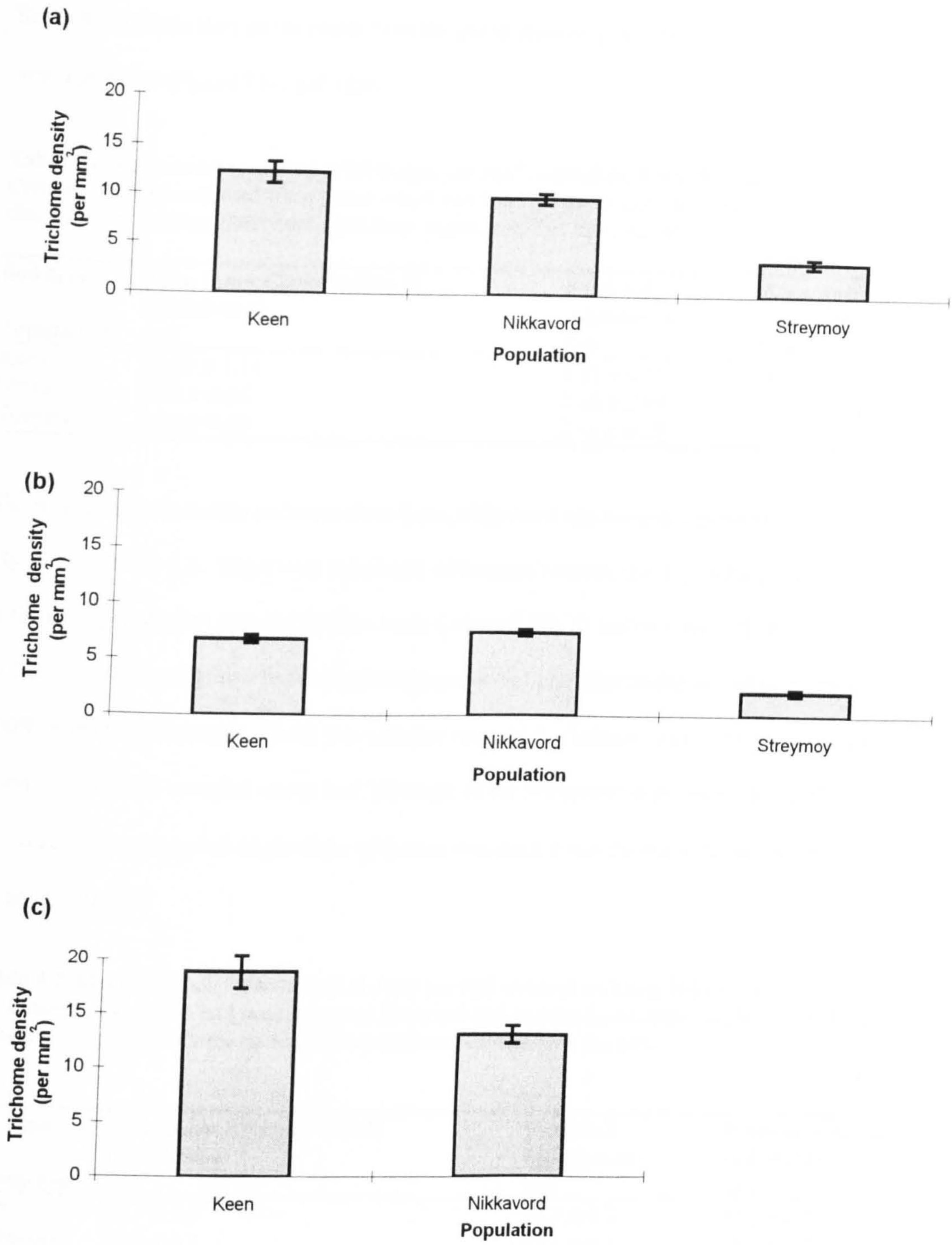


Fig. 4.5 The trichome density on leaves from Keen, Nikkavord and Streymoy plants which had been grown on (a) John Innes Compost (No. 2) in the Stirling glasshouses (b) Keen soil in the Stirling glasshouses and (c) Keen and Nikkavord plants collected from the field. The trichomes from the glasshouse plants were counted during December 1996 and from plants growing on the field during July 1997. The error bars represent the standard error of the mean.

However there was a big range in densities of leaf trichomes with a higher density of trichomes on the Keen (field) plants than on the plants from the glasshouses (Fig. 4.5; table 4.1) and these differences were significant ($F_{2,40}$=43.64, p<0.001).

Table 4.1 Mean number (± s.e.) of trichomes per mm² counted on Keen, Nikkavord and Streymoy *Cerastium* leaves collected from plants which had been grown in Keen soil and in John Innes compost (No. 2) in the Stirling glasshouses and from plants collected from the field.

Soil type Population	John Innes Compost (No.2) (glasshouse) n=6	Keen soil (glasshouse) n=6	Keen and Nikkavord soil (field) n=10
Keen	12.28 ± 1.11	6.81 ± 0.36	18.89 ± 1.54
Nikkavord	9.82 ± 0.54	7.46 ± 0.30	13.13 ± 0.82
Streymoy	3.54 ± 0.48	2.15 ± 0.28	-

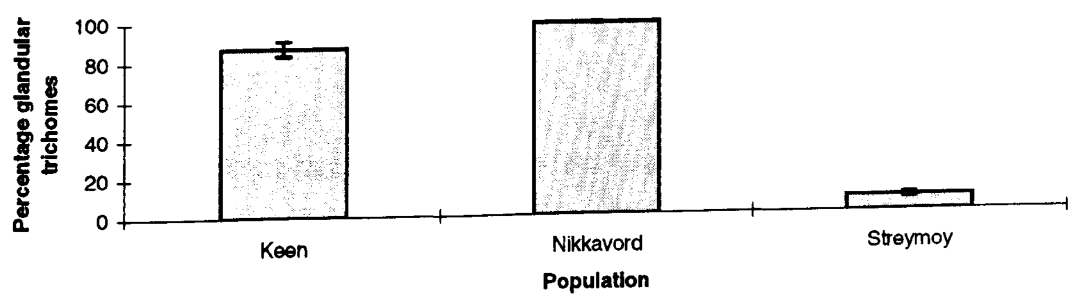
The % glandular trichomes on leaves from Keen, Nikkavord and Streymoy populations are shown in Fig. 4.6 and Table 4.2. There were significant differences between the % glandular trichomes on leaves of the three populations growing on John Innes Compost (No. 2) and on Keen soil ($F_{2,32}$=374.5, p<0.001). Nikkavord leaves had the highest proportion of glandular trichomes, which ranged from 97-100% of the total trichomes. There was a greater range of % glandular trichomes on Keen leaves, with a minimum of 65% recorded on one leaf, although, as for Nikkavord, some leaves had 100% glandular trichomes. The proportion of glandular trichomes was much lower for leaves from Streymoy with a range from 0-20%.

Table 4.2 Mean % (± s.e.) glandular trichomes per leaf counted on Keen, Nikkavord and Streymoy *Cerastium* plants which had been grown in Keen soil and in John Innes compost (No. 2) in the Stirling glasshouses and which were collected from plants collected from the field.

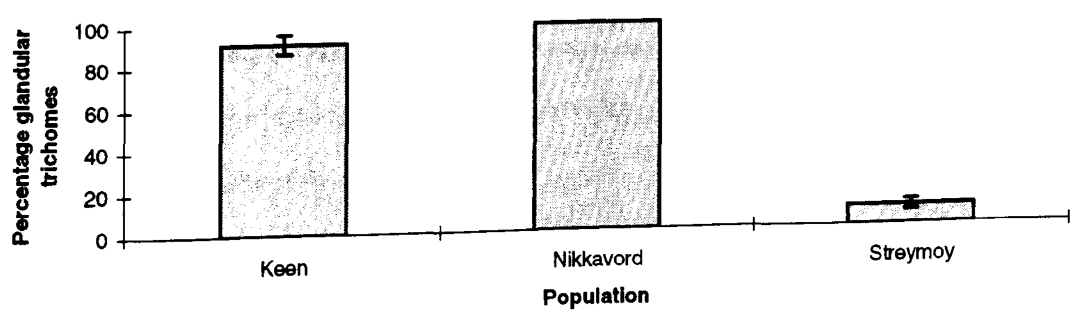
Soil type Population	John Innes Compost (No.2) (glasshouse) n=6	Keen soil (glasshouse) n=6	Keen and Nikkavord soil (field) n=10
Keen	86.7 ± 3.7	91.3 ± 4.7	95.3 ±1.0
Nikkavord	98.3 ± 0.2	99.4 ± 0.1	98.3 ± 0.3
Streymoy	7.5 ± 1.3	9.0 ± 2.6	

When considering the leaf counts on plants growing in the field as well as those grown in the glasshouses, a similar trend was observed; Nikkavord plants had a significantly higher % glandular trichomes than those from the Keen ($F_{1,40}$=21.8, p<0.001). There were no significant differences between the %glandular trichomes on leaves of Keen, Nikkavord or Streymoy plants which had been grown on Keen soil or on John Innes compost (No. 2) ($F_{2,32}$=2.45, p=0.13) or between the % glandular

(a)



(b)



(c)

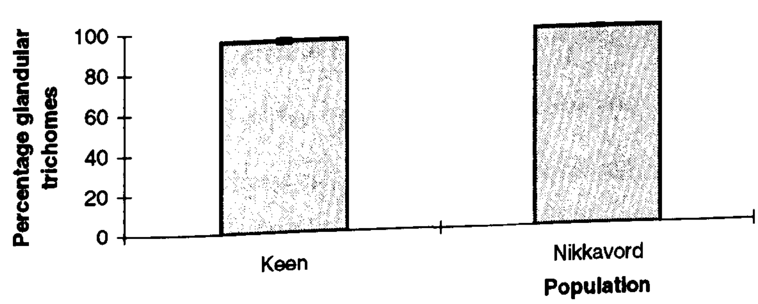


Fig. 4.6 Percentage glandular trichomes on leaves from Keen, Nikkavord and Streymoy plants which had been grown on (a) John Innes Compost (No. 2) in the Stirling glasshouses (b) Keen soil in the Stirling glasshouses and (c) Keen and Nikkavord plants collected from the field. The trichomes from the glasshouse plants were counted during December 1996 and from the plants growing in the field during July 1997. The error bars represent the standard error of the mean.

trichomes on leaves of Keen and Nikkavord plants from field or glasshouse-grown plants ($F_{2,40}$=2.49, p=0.10).

Cell ultrastructure

Figure 4.7 shows a sketch of a longitudinal section of a glandular trichome from a Keen *Cerastium* leaf with TEM photographs. The sketch was drawn in order to give an image of a complete trichome and to show the position of the photographs. The sketch shows some of the cell material in the head cell but in the neck cells, only the nuclei and chloroplasts were drawn in. In the leaf cells at the base of the trichome, there were many chloroplasts although only one of these was illustrated (Fig. 4.7 f). The photographs were taken from leaf trichomes of individuals which had been grown on Keen soil, but the structure of the trichomes was the same for plants which had been grown on John Innes Compost (No.2). The sections confirmed the light microscope observations, that each glandular trichome consisted of a longitudinal file of six to eight cells.

The nucleus in each of the trichome cells was large (Fig. 4.7 a). The cell walls were thickened and surrounded by a cuticle which detached from the cell wall in the head cell. The secretory substance appeared to accumulate in the space formed between the cuticle and the cell wall (Fig. 4.7 b). There was some granular material near to the tip of the head cell, in which lipid droplets, vesicles and mitochondria could be seen (Figs. 4.7 b and d). Some of the material between the cuticle and the cell wall of the head cell stained darkly, but it was not clear from these observations what it was. There were many plasmodesmata in the cell walls between adjacent cells (Fig. 4.7 c) and on this photograph, Golgi bodies can be seen, positioned near to the cell wall. There were occasional chloroplasts in all the neck cells of the trichome (Figs. 4.7 e). There was plenty of granular material near to the cell walls (Figs. 4.7 a, c and e), although it was not clear exactly what this was. There were also cell-wall incrustations (ingrowths of the cell wall towards the cell interior) (Fig. 4.8 e). The basal cell of the trichome had thickened cell walls. Moving into the leaf, the cells had thinner cell walls and many chloroplasts (Fig. 4.8 f).

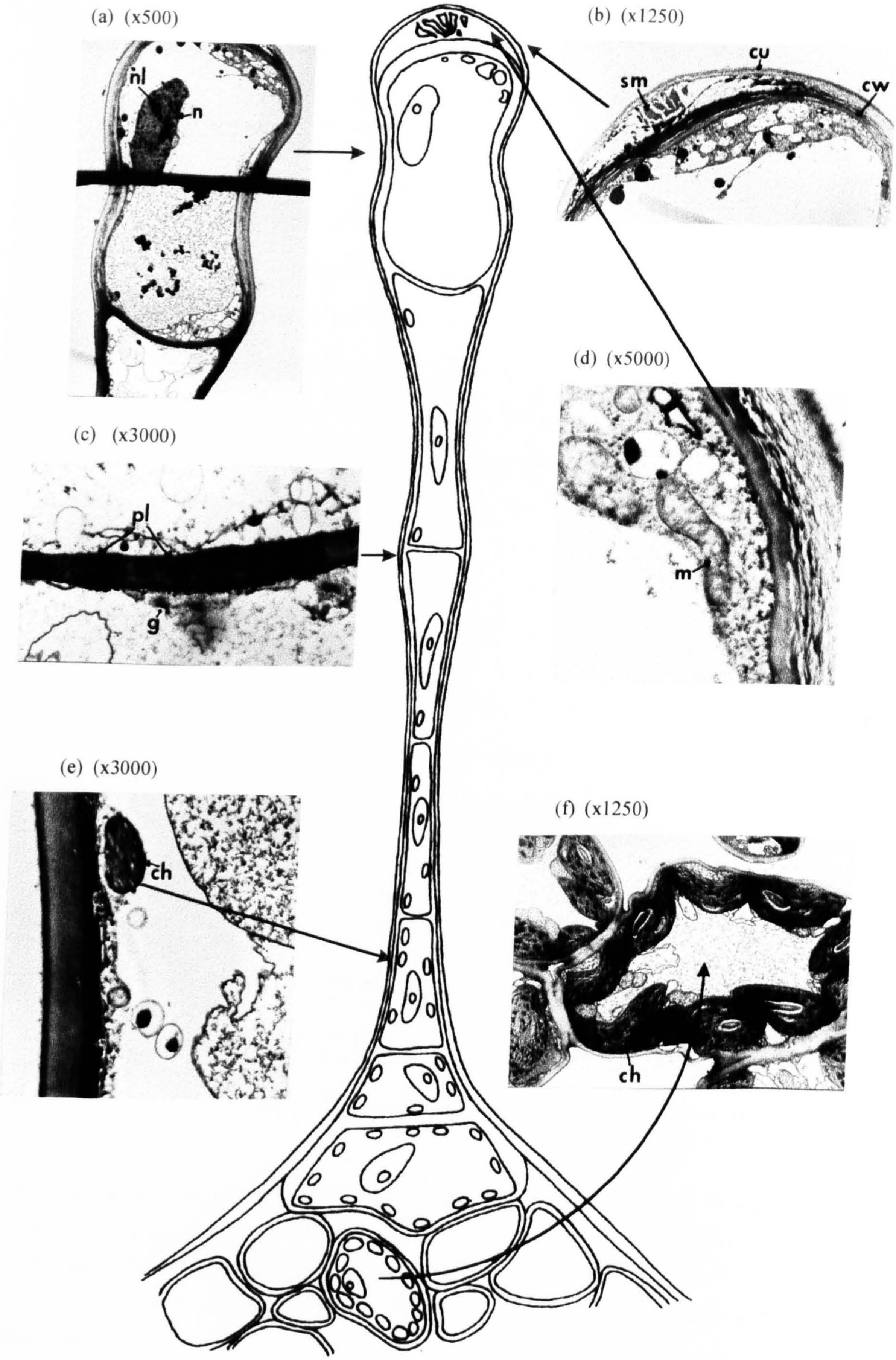


Fig. 4.7 Sketch of a longitudinal section of a glandular trichome (x500) from a Keen *Cerastium* leaf with TEM photographs to show the detail. n = nucleus, nl = nucleolus, sm = secretory material, cu = cuticle, cw = cell wall, g = Golgi bodies, pl = plasmodesmata, m = mitochondrion, ch = chloroplas

Analysis of glandular trichome secretory material

Figures 4.8 a-f show the results of the histological tests for the glandular trichomes. The staining was the same for Keen, Nikkavord and Streymoy leaf trichomes on the two different soil treatments. Fig. 4.8 a shows positive staining for lipids of glandular trichomes on a Keen leaf (Sudan black) and Fig. 4.8 b shows a Streymoy leaf with no staining of the non-glandular trichomes. There was also staining of lipids in the head cells of the glandular trichomes using the Nile blue method (Fig. 4.8 c) and staining of pectins using the Ruthenium red method (Fig. 4.8 d). There appeared to be positive staining of carbohydrates in the head cell of glandular trichomes using the PAS method (Fig. 4.8 e), although the staining was mostly for the cell wall (Figs. 4.8 e and f). There was no positive staining for nickel or magnesium for any of the trichomes.

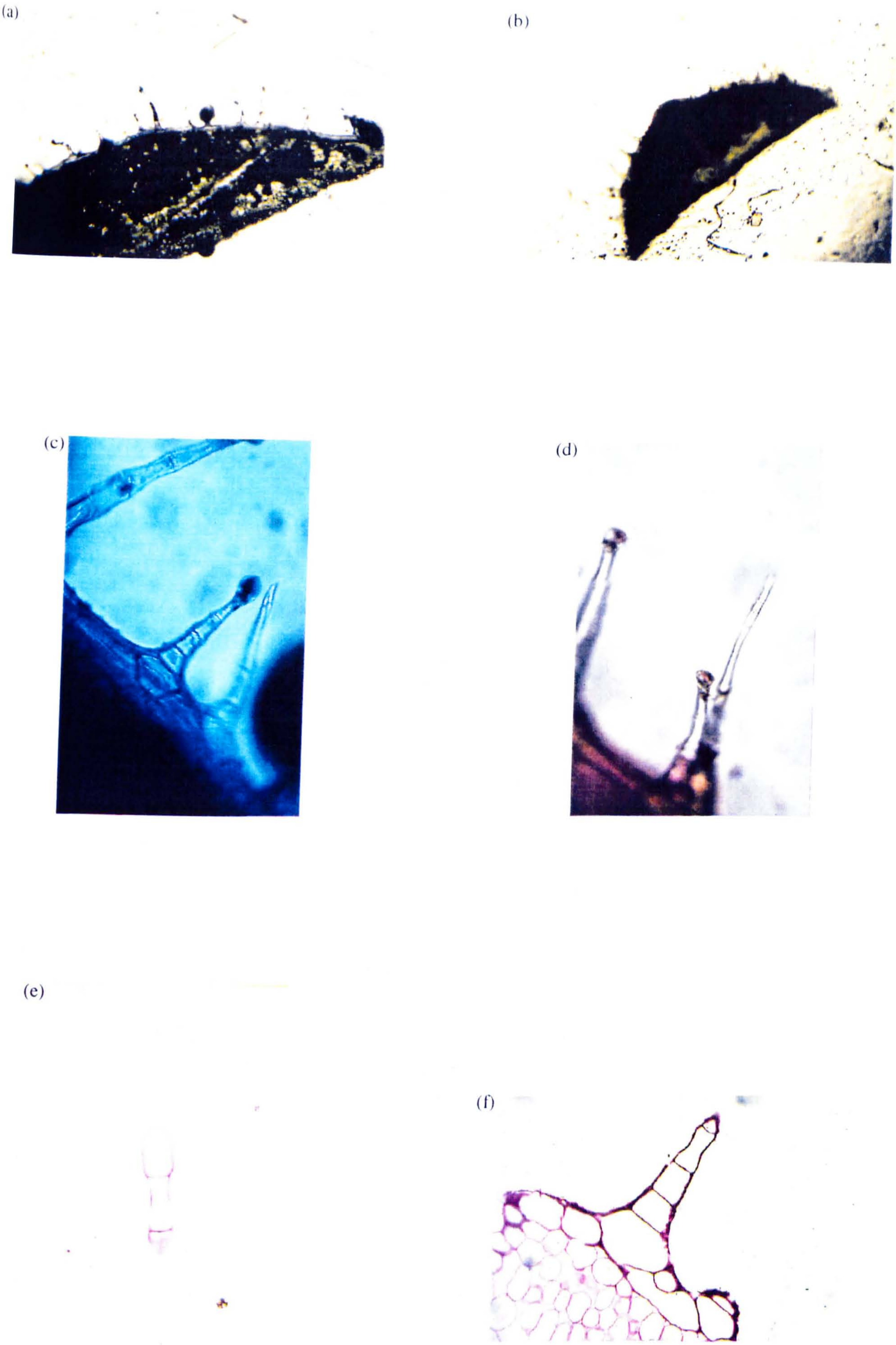
Drought experiment

Table 4.3 shows the mean (±s.e.) root and shoot lengths of the Keen, Nikkavord and Streymoy seedlings measured before the drought treatment. There were no differences between the root lengths of the seedlings ($F_{2,57}$=1.04, p=0.36), or the shoot lengths of seedlings from each provenance ($F_{2,57}$=0.96, p=0.40).

Table 4.3 Mean (±s.e.) root and shoot length (cm) of Keen, Nikkavord and Streymoy *Cerastium* seedlings measured before the drought treatment on 19 June 1997.

Population	Mean root length (±s.e). n=20	Mean shoot length (±s.e.) n=20
Keen	4.02 ± 0.26	2.64 ± 0.12
Nikkavord	3.42 ± 0.29	2.83 ± 0.14
Streymoy	3.83 ± 0.35	3.06 ± 0.17

There were no significant differences between the % water content of the Keen soils on which the Keen, Nikkavord and Streymoy individuals had been grown, after the first drought treatment ($F_{2,57}$=0.15, p=0.86) or the second ($F_{2,57}$=0.40, p=0.67) indicating that the plants from each population were exposed to the same amount of water stress. The mean (±s.e.) % water content of the soils after the first drought treatment was 24.96 ± 0.87 of the initial value and after the second was 14.62 ± 0.57.



ig 4.8 Results of histological tests on Keen (a,c,d,e,f) and Streymoy (b) glandular and non-glandular *Cerastium* trichomes. a) Sudan black (x8); (b) Sudan black (x8); (c) Nile blue (x25); (d) Ruthenium red (x25); (e) PAS (x63); (f) PAS (x63).

All the plants recovered within two days of the first droughting treatment. After the second drought, 90% of the plants survived (Table 4.4). Ten individuals (33%) regained turgor in the leaves, while the other plants survived by producing new leaves at the nodes (Figs. 4.9 a and b). There were no significant differences in the numbers of recovered leaves among the three populations ($F_{2,27}$=0.83, p=0.45) and the proportion of recovered leaves on droughted plants compared with the control ones for each population was similar (Table 4.4).

Table 4.4 A summary of observations on Keen, Nikkavord and Streymoy droughted and control *Cerastium* plants after the second drought. The observations were made on 6 October, four weeks after the end of the droughting treatment. Drt. refers to the drought treatment and Cont. the control.

Observation	**Keen**		**Nikkavord**		**Streymoy**	
	Drt. n=10	Cont. n=10	Drt. n=10	Cont. n=10	Drt. n=10	Cont. n=10
No. of dead plants	0	0	2	0	1	0
No. of plants with new growth at the nodes	9	-	7	-	9	-
No. of plants with recovered older leaves	4	-	4	-	2	-
No. of older leaves	28	108	20	78	11	65
Proportion of recovered leaves (from control)	26%	-	26%	-	17%	-

Discussion

Keen and Nikkavord plants had a much higher proportion and number of glandular trichomes on the leaves than Streymoy plants. This is in line with Lusby's (1985) observations of a higher proportion of glandular trichomes on leaves of Keen plants than on leaves of Scottish mainland populations of *Cerastium arcticum*. There were only two types of trichomes observed on any of the plants in this study, the glandular trichomes and the non-glandular ones. Lusby (1985) observed that *Cerastium arcticum* recorded from Ben Avon had three to four celled, very short, thick trichomes which were different from the trichomes of the other Scottish *Cerastium arcticum* populations.

The histochemical tests showed that the secreted substance included lipophilic material, pectins and other polysaccharides. There was no positive staining for nickel and this is perhaps not surprising given that nickel is not thought to be a major influence on the open soils of the Keen (Carter *et al.* 1987 a); non-tolerant species grown in Keen soils, or in water culture media simulating soil solutions analysed for the skeletal soils of the Keen, have shown no symptoms of nickel toxicity (Spence &

(a)

(b)

Fig. 4.9. Photographs of (a) Keen and (b) Faroese (Streymoy) *Cerastium* plants, four weeks after a 20 day drought treatment. The plants have recovered by producing new growth at the nodes.

Millar 1963, Proctor 1971a, Bowen 1983, Wilson 1981). It is however possible that the dimethylglyoxime method did not stain very low concentrations of nickel. It is not clear what the detection limits were for this mineral. There was also no staining for magnesium. The Mg/Ca quotient is moderately high in Keen soils, but is less than sites which are known to be toxic to plants (Carter *et al.* 1987 a). However, as for nickel, it is possible that low concentrations of magnesium were not stained; the titan yellow method will only give red staining if the concentration of magnesium is high (Jensen 1962) (although there are no detection limits given).

The head cells of the glandular trichomes had a large nucleus and this is characteristic of secretory cells (Lüttge 1971). Another important property of gland cells is the large numbers of mitochondria (Lüttge 1971, Fahn 1988). There were some mictochondria observed in the head cells but not many, and it is possible that some of them deteriorated during maturation of the head cell as has been suggested for trichomes of *Sorghum halepense* (L.) by McWhorter *et al.* (1995).

The plasmodesmata connecting the cells of the trichome showed a probable route for the transfer of secretory materials from the basal cell to the head cell. The cell wall protuberances may also play a role in transport processes (Lüttge 1971). The side walls of the basal cells were cutinized and thickened, a characteristic feature of secretory trichomes which prevents the secretory material from flowing back into the plant through the apoplast (Fahn 1988). It appeared that the secretory material accumulated in the space between the cell wall and the cuticle in the head cell but it was not clear how the secretory material was released. The secretory material may either have been released by rupture of the cuticular sheath (e.g. Antunes & Sevinate Pinto 1991) or by pores in the cuticle (e.g. Bruni *et al.* 1987). There were no pores observed under the SEM but pores can be very small and it is possible that they were missed. Many of the head cells observed under the TEM had collapsed but it was not clear whether the cells had collapsed during the preparation of the sections or whether the cuticles were ruptured during secretion.

An important question is why Keen and Nikkavord *Cerastium* leaves had large numbers of trichomes secreting lipophilic material, pectins and other polysaccharides. Fahn & Shimony (1996) found that the glandular trichomes of the desert shrubs, *Fagonia glutinosa* Del. and *F. arabica* L. growing in the southern Arava valley in Israel secreted polysaccharides and lipophilic compounds as for *Cerastium*. They observed that sand and other soil granules stuck to the surface of the trichomes. It was suggested that the trichomes, together with the epicuticular wax and the soil particles increased the thickness of the diffusion boundary layer and also had a role in insulation and increased light reflectance and that these were an adaptation to survival in the hot desert conditions. There were no soil particles stuck to the surface of Keen trichomes, but it is possible that the sticky secretion may have increased reflection which in turn would reduce temperature and water loss.

Keen and Nikkavord plants not only had a greater proportion of glandular trichomes, but also had a higher density of trichomes than the Streymoy plants. If the dense glandular trichomes were an adaptation to dry conditions it would be expected that the Unst plants would be more drought tolerant than the Streymoy plants. However under the conditions of the experiment there was no evidence that Unst plants were more drought tolerant than Streymoy ones.

At the end of the second drought of 20 days without water, the % soil water content had fallen to 14% and yet 90% of the droughted plants recovered by producing new growth at the nodes. The Streymoy plants appeared to be as well adapted to drought as the Keen and Nikkavord ones. The climate of Torshavn on Streymoy (about 30 km S of the *Cerastium arcticum* site) is similar to that of Baltasound (Berry & Johnson 1980), but *Cerastium arcticum* grows at a higher altitude on Streymoy (450 m) than on Unst (0-80 m). Cold winter temperatures and frozen soils can reduce water uptake and cause water stress in the winter (Billings 1974, Oberbauer & Billings 1981).

The drought experiment showed that the *Cerastium* populations were all able to recover after a dry spell even after most of the leaves had died, but there were no differences found between the populations. However, the experiment considered only the mortality of plants and the number of leaves produced. There were no measurements made of the plant water status or other plant responses such as stomatal conductance and photosynthetic rate. More detailed investigations would be needed to confirm that the glandular hairy Keen and Nikkavord populations were no more drought resistant than the Streymoy ones.

The many glandular trichomes on Keen and Nikkavord *Cerastium* leaves may have a role in plant defence against herbivores. I did not see many likely grazers e.g. gastropods on the dry open soils of the Keen but the possibility cannot be ruled out. There is also a possibility that the secreted polysaccharide material acted as an attractant and was a decoy to non-pollinating insects (normally, decoys are for ants, but I did not see any ants on the Keen). I observed many flies on flowering *Cerastium* plants and collected some from 6-20 June 1995 which were identified by B. Laurence. Most of the flies are expected on flowers and are probably pollinators (B. Laurence pers. comm.).

Both Keen and Nikkavord leaves were densely glandular hairy but the Keen leaves had a significantly higher density of trichomes than the Nikkavord ones (confirming the observations of Stuffins 1983) and also a significantly lower proportion of glandular trichomes. However, both the density of trichomes and the % glandular trichomes on Nikkavord leaves were within the range of the density and % glandular trichomes recorded on Keen leaves.

Interestingly, there were big differences in the leaf trichome density on plants from the different soil treatments. Leaves from the field-collected Keen and Nikkavord plants had a much higher density of trichomes than leaves from the glasshouse plants, and plants grown in John Innes Compost (No. 2) had a higher density of leaf trichomes than those grown in Keen soils when grown in the glasshouses. The reasons for this are unclear. It is possible that some site factors may have caused the increased pubescence observed in the field. Another possibility is that the *Cerastium* leaves alter in leaf hairiness at different times of the year; the glasshouse leaf trichomes were counted in December and the field-collected leaf trichomes were counted in July. A final suggestion is that the leaves were of different ages. It is known that Keen plants growing in John Innes Compost (No. 2) grow more quickly than they do in Keen soils (Proctor 1971 b). There are several examples showing that the density of trichomes on leaves alters with plant age (e.g. Maffei *et al.* 1989, Werker *et al.* 1993).

Chapter 5. Soil and plant analyses

Introduction

One of the features of ultramafic soils is that there are high concentrations of nickel (normally 500-10000 mg g^{-1} total nickel compared to 5-500 mg g^{-1} in non-ultramafic soils) (Proctor & Baker 1994). Although nickel is generally thought to be an important factor in causing the unusual features of ultramafic vegetation (Brooks 1987), its role is usually uncertain, since its potential toxicity can be modified by many factors (Proctor & Baker 1994).

Spence (1957) found high concentrations of nickel in the open skeletal soils of the Keen (220 µg g^{-1} acetic acid extractable) and also in *Agrostis stolonifera* plants growing on the open soils (118 µg g^{-1} dry matter). However, there was no evidence of nickel toxicity to oats or other non-tolerant species grown on the open Keen soils (Spence & Millar 1963, Proctor 1971a, Slingsby & Brown 1977, Proctor & Cottam 1982). During systematic soil sampling of the whole Keen, including closed vegetation as well as open, an area rich in nickel was found (119 µg g^{-1} exchangeable; 601 µg g^{-1} acetic acid extractable, 2.4 mg l^{-1}), (Carter *et al.* 1987 a). This area (referred to as the nickel-rich area) was not on the extensive barren areas of the site, but under relatively acid and organic soils which were well vegetated.

Bowen (1983) did more detailed sampling of soils from the nickel rich area (20 samples taken at 10 m intervals along a NS, EW transect). The concentrations of nickel were not as high as had been previously reported but there were two samples which had high nickel concentrations (31 µg g^{-1} and 37 µg g^{-1}) (exchangeable) and these were both higher than the concentrations recorded for the skeletal soils (a maximum of 26 µg g^{-1} as recorded by Carter *et al.* 1987 a). She found soils from the nickel-rich area produced nickel toxicity symptoms in oats in the Stirling glasshouses. Bowen (1983) also sampled plant leaves from the nickel rich area as well as from other parts of the Keen. The levels of nickel in all the plant samples were surprisingly low (maximum of 29 µg g^{-1} for *Calluna vulgaris* from the open soils).

I did further sampling of soils and plants from the nickel rich area at a finer scale that that of Bowen (1983). I included Keen open areas and a non-ultramafic site nearby at Burrafirth (NGR HP 614 149), about 8 km NW of the Keen, for comparison. In this chapter I have also reported the results of soil analyses from the other study sites considered in this thesis (Nikkavord and Beinn Iadain). Unfortunately there were no soil analyses from the Streymoy *Cerastium* site.

Methods

Vegetation description

The vegetation was sampled within a 10 m x 10 m plot in the nickel-rich area (Fig. 5.1). The plot was positioned in the centre of Bowen's (1983) transect (the two ends of the plot corresponded with her sample numbers six and 16, which were the samples which had higher soil nickel concentrations; Bowen 1983). Within each of eight 1 m x 1 m quadrats (positioned randomly in the plot) all the species were recorded and their abundance estimated following the DOMIN scale.

Soil chemical properties and particle size

Eight soil samples (to a depth of about 10 cm) were collected randomly from three 10 m x 10 m plots from different parts of the Keen: moderately colonised skeletal soils, sparsely colonised skeletal soils, and the nickel-rich area. Fig. 5.1 shows the location of the sampling areas. Eight samples were also collected randomly from Nikkavord (on areas of dry skeletal soils) and from Beinn Iadain (from areas of open soils associated with *Arenaria*). The Keen and Nikkavord samples were collected on 18 July 1996 and the Beinn Iadian ones on the 18 August 1996. Prior to analyses, the samples were air-dried, ground using a pestle and mortar, and sieved through a 2 mm mesh.

Soil pH was measured using a Corning-Eel Model 7 pH meter in both a 1: 2.5 soil : deionised water, and a 1: 2.5 soil : 0.01 M $CaCl_2$ solution. Loss-on-ignition (LOI) was determined in a muffle furnace at

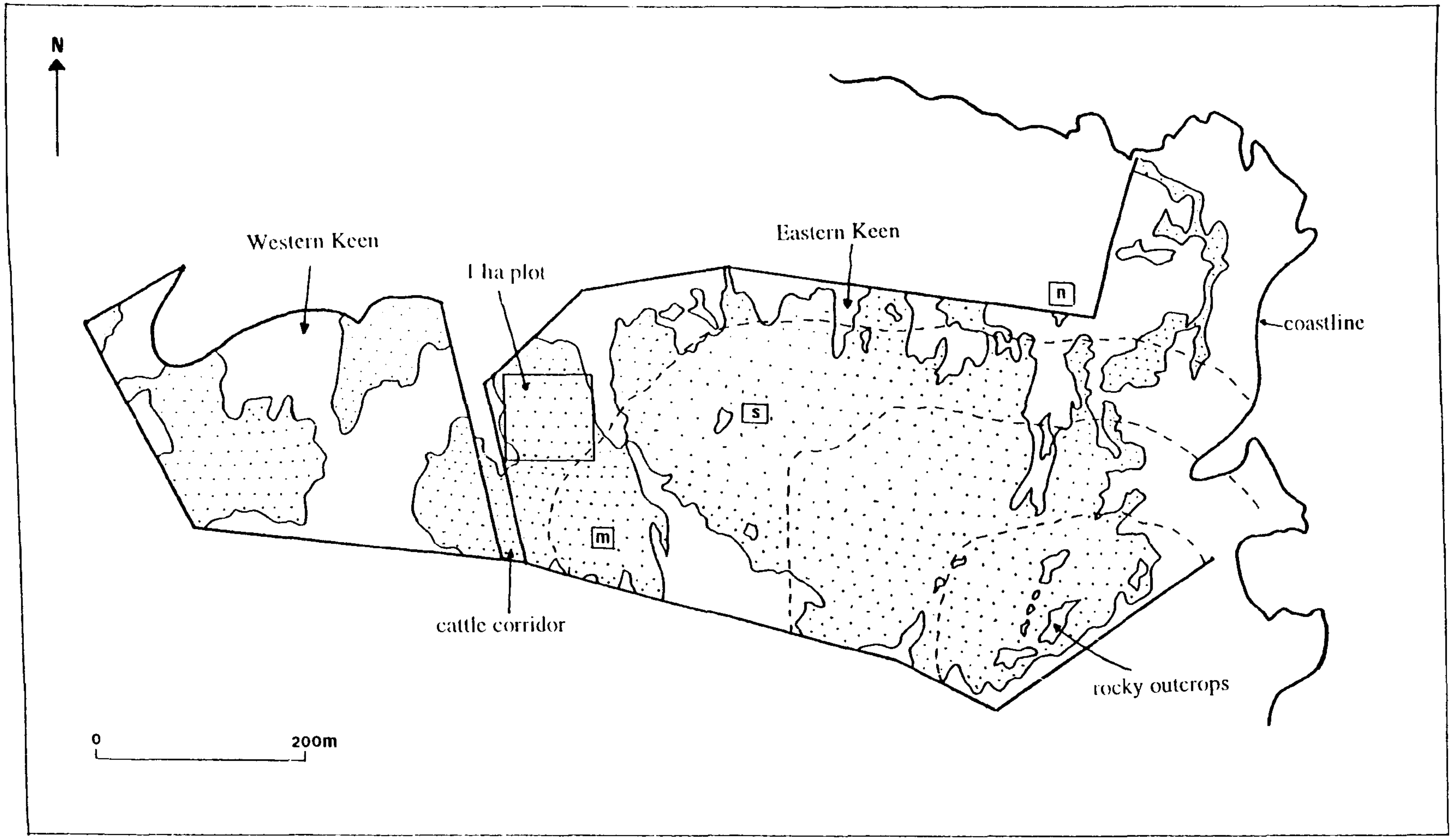


Fig. 5.1 Location of three 10 m x 10 m soil sample plots on the Keen. s sparsely colonised soils, m moderately colonised soils, n nickel rich area.

425 °C for 12 hours. Organic matter content of the skeletal Keen soils was analysed chemically by wet oxidation with excess potassium dichromate.

Soil exchangeable cations and nickel were extracted by leaching 5-g subsamples of soil with five successive additions of 20 ml of 1M ammonium acetate solution adjusted to pH 7. Leachates were then analysed by a Varian AA-575 S atomic absorption spectrophotometer with a nitrous oxide - acetylene flame for calcium and magnesium, and an air-acetylene flame for sodium, potassium and nickel. Total acidity and exchangeable aluminium were determined in 5 g subsamples of soil leached with five successive additions of 20 ml 1M potassium chloride solution. From each extract 10 ml were titrated with 2.5 mM sodium hydroxide solution using the indicator phenolphthalein. This titration corresponded to total acidity. After adding 10 ml of 1M potassium fluoride to the titrated solution, a subsequent titration with 5 mM hydrochloric acid determined the exchangeable aluminium. The difference between the two was equal to exchangeable hydrogen. Cation exchange capacity (CEC) was calculated from the sum of the total exchangeable cations plus total acidity. Percentage base saturation was calculated as the proportion of exchangeable cations (excluding aluminium and hydrogen) to CEC.

Available phosphorus in the soils was measured by extracting the soils using Olsen's reagent (0.5 M sodium bicarbonate buffered at pH 8.5). Phosphorus concentrations in the extracted solutions were determined colorimetrically using the ammonium molybdate-potassium stannous tartarate method. Particle size distribution of the soil samples was determined using the pipette method.

Plant nickel concentrations

For plant analyses, species were chosen which not only grew on the nickel-rich area, but also grew on either the skeletal soils of the Keen or on the open cliffs of Burrafirth. *Agrostis stolonifera, Armeria maritima* and *Plantago maritima* were common to all three habitats. The other three species, *Calluna vulgaris, Potentilla erecta* and *Succisa pratensis* were only found on two of the sites. On 22 July 1996, leaf samples (all above ground material for *Calluna vulgaris*) were collected from at least 30 plants of each species from each of the different areas, and sealed in a plastic bag. The samples were taken to Stirling within 48 hours, and washed carefully with deionized water. They were then air dried, ground, and stored at room temperature. For each sample, 1 g of oven dried (105 °C) plant material was digested in concentrated nitric acid (Allen 1989) using a block digester at 130 °C. The digests were then filtered (Whatman No. 540) and made up to 50 ml. Nickel concentrations were determined as above using a Varian AA-575 atomic absorption spectrophotometer.

Results

Vegetation description

Table 5.1 shows the estimated plant cover of the species sampled from the nickel-rich area. The vegetation had nearly full plant cover (Fig. 5.2). The area was damp but there was no standing water at the time of recording. Some of the species recorded are characteristic of wetter places e.g. *Schoenus nigricans* and *Pinguicula vulgaris.*

The most abundant species in the vegetation were *Molinia caerulea, Carex panicea* and *Schoenus nigricans,* although *Schoenus nigricans* was patchy. There were plenty of herbs present which are also found on the drier sedge-grass heath on other parts of the Keen e.g. *Linum catharticum, Thymus polytrichus, Euphrasia* sp. and *Thalictrum alpinum.* There were only two bryophytes recorded, and both of these had a low cover. The vegetation seemed to fit into the *Schoenus nigricans-Molinia caerulea* soligenous mire of Spence (1970), but there were also similarities with the *Carex panicea-Campylium stellatum* mire sociations described by McVean & Ratcliffe (1962). The community also fitted reasonably well into the *Schoenus nigricans* variant of the *Carex demissa- Juncus bulbosus/kochii* sub-community of the National Vegetation Classification, M10 *Carex dioica-Pinguicula vulgaris* mire (Rodwell 1991).

Soil chemical properties and particle size

Table 5.2 shows the results of the soil analyses. The influence of the parent material is clear, with the ultramafic sites having high nickel concentrations and high magnesium /calcium quotients compared

Fig. 5.2 The nickel-rich area showing a closed vegetation.

Table 5.1 Frequency of plant species (DOMIN scale) sampled in eight 1 m x 1m quadrats on the nickel-rich area of the Keen.

Species	**Quadrat number**							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Vascular plants								
Agrostis stolonifera		1	2	3	3	4	2	3
Antennaria dioica	2	1	2	3	2	1	2	
Armeria maritima		1				1		1
Calluna vulgaris	3		1	3			2	1
Carex flacca	3	3	4	3	2	5	4	3
Carex panicea	5	5	6	6	5	5	6	5
Carex pulicaris	3	3	4	3	3	2	2	2
Carex viridula subsp. *oedocarpa*	2	4	4		2		4	
Dactylorhiza purpurella	2		1	1				
Euphrasia sp.	2		1	1			1	
Festuca rubra	3	4	3	3	3	2	2	2
Leontodon autumnalis	1	1	1		2	1		
Linum catharticum	3	2	3	3	2	2	1	1
Molinia caerulea	5	6	5	5	5	6	6	6
Pinguicula vulgaris		1		1		1		1
Plantago maritima	4	3	4	3	3	3	3	3
Polygala vulgaris						1		
Potentilla erecta	2	2	3	3	3	3	4	3
Prunella vulgaris		2	1	1				
Rhinanthus minor			2	2		1	1	
Schoenus nigricans	6	5	3	7	4	2		5
Selaginella selaginoides	3	3	4	3	2	2	3	3
Succisa pratensis	3	3	3	4	3	3	4	4
Thalictrum alpinum	2	2	2	2	2	3	3	2
Thymus polytrichus	2		3	4		2	1	
Viola sp.			1			1		1
Bryophytes								
Campylium stellatum		1				2		1
Drepanocladus revolvens		1	1		1		2	1
Present outside quadrats								
Juncus articulatus								
Scilla verna								
Herb cover	9	8	8	9	9	8	9	9
Bryophytes	0	1	1	0	1	2	2	2
Bare ground	3	5	4	3	3	5	4	4
Dead material	5	6	6	5	5	5	5	4
Species number	19	21	24	21	17	22	19	19

Table 5.2 The mean values (with ranges in parenthesis) of soil chemical properties and particle size composition from soil samples (0-10 cm depth) taken from three locations on the Keen, from Nikkavord and from Beinn Iadain.

	Keen (Mod. colonised skeletal soils) n=8	Keen (Sp. colonised skeletal soils) n=8	Keen (Nickel-rich area) n=8	Nikkavord n=8	Beinn n
pH (H_2O)	**6.9**	**6.8**	**6.3**	**6.8**	**6**
	(6.8-7.0)	(6.7-6.8)	(6.1-6.4)	(6.6-6.9)	(6.0
pH ($CaCl_2$)	**6.5**	**6.5**	**6.0**	**6.4**	**5**
	(6.4-6.5)	(6.4-6.5)	(5.8-6.3)	(6.4-6.5)	(5.0
Loss on ignition (%)	**3.7**	**3.9**	**23.1**	**6.2**	**6**
	(3.2-4.3)	(3.2-5.2)	(16.1-31.2)	(5.2-7.3)	(4.4
Organic matter (%)	**1.3**	**2.4**	**n.d.**	**n.d.**	**n.**
	(1.0-1.7)	(1.9-2.9)			
Available P ($\mu g\ g^{-1}$)	**0.93**	**1.86**	**8.99**	**7.52**	**8.**
	(0-0.93)	(0-2.42)	(8.02-11.0)	(6.90-8.01)	(7.64
Exchangeable cations	**(meq kg^{-1})**				
K^+	**0.64**	**0.84**	**3.12**	**1.00**	**2.**
	(0.48-0.76)	(0.64-1.20)	(2.32-4.35)	(0.85-1.10)	(1.83-
Na^+	**2.87**	**2.73**	**14.80**	**4.25**	**2.**
	(1.22-3.65)	(2.09-3.05)	(9.92-17.49)	(3.74-5.31)	(1.17-
Ca^{2+}	**5.51**	**7.80**	**30.32**	**7.97**	**51**
	(3.49-9.38)	(6.39-11.18)	(22.26-38.62)	(6.69-10.53)	(41.92-
Mg^{2+}	**19.18**	**24.49**	**102.11**	**49.77**	**44**
	(16.54-21.48)	(21.81-27.98)	(79.20-134.54)	(43.69-61.80)	(33.41-
Mg/Ca quotient	**3.76**	**3.19**	**3.41**	**6.28**	**0.**
	(2.24-4.92)	(2.50-3.41)	(2.75-4.05)	(5.82-6.90)	(0.70-
H^+	**0.73**	**0.77**	**1.08**	**0.85**	**4.**
	(0.67-1.00)	(0.67-0.83)	(1.00-1.17)	(0.67-1.00)	(1.13-
Al^{3+}	**0**	**0**	**0**	**0**	**0.**
					(0.03-
Ni ($\mu g\ g^{-1}$)	**3.85**	**6.10**	**20.28**	**5.40**	**0.**
	(2.60-5.20)	(4.20-7.00)	(13.20-32.20)	(4.80-6.20)	(0.20-
CEC	**28.93**	**36.62**	**151.43**	**63.84**	**105**
	(23.06-34.23)	(32.08-43.63)	(117.95-195.82)	(59.51-79.50)	(88.19-
Base saturation (%)	**97.44**	**97.88**	**99.27**	**98.65**	**95**
	(96.48-98.29)	(97.40-98.35)	(99.01-99.49)	(98.39-98.95)	(89.42-
Particle fraction (%)					
clay	**14.5**	**13.4**	**19.4**	**10.3**	**8.**
	(13.4-15.8)	(11.8-15.0)	(17.0-21.0)	(7.8-15.0)	(7.8-
fine silt	**8.8**	**7.9**	**1.8**	**1.2**	**2.**
	(6.4-13.6)	(7.2-11.2)	(0-4.0)	(0-2.4)	(1.6-
medium sand	**14.2**	**14.5**	**5.8**	**6.7**	**5.**
	(10.4-17.6)	(12.0-16.8)	(5.3-6.7)	(5.6-8.0)	(2.4-
sand >63 μM	**16.7**	**19.4**	**7.5**	**15.2**	**11**
	(14.4-17.6)	(17.4-24.0)	(2.6-11.4)	(12.4-18.7)	(5.7-
sand >212 μM	**42.5**	**37.5**	**67.0**	**65.6**	**64**
	(28.6-52.1)	(32.6-42.9)	(59.5-75.4)	(64.2-69.3)	53.4-

with the non-ultramafic Beinn Iadian site. The high concentrations of sodium reflect the nearness of the sites to the sea. Soils from the nickel-rich area had higher nickel concentrations than from the skeletal soils. The nickel-rich area also stands out in having a higher loss-on-ignition than the other soils. When soils have a very low organic matter, the wet oxidation method is thought to be more accurate than the LOI method (e.g. Carter 1982). The wet oxidation method gave very low values of organic matter for Keen soils (<2.5%). The Keen soils also had lower concentrations of available phosphorus than the other soils, although the phosphorus concentrations of all the soils were low.

All the sites had a high proportion of sand (>70% of the particle size fraction). The nickel-rich area had a higher proportion of clay than the other sites, and the skeletal soils from the Keen, a higher proportion of silt.

Plant nickel concentrations

Table 5.3 shows the nickel concentrations of plants collected from the three sites. All the Burrafirth plant samples had very low concentrations of nickel which would be expected on soils which have low concentrations of nickel (0.2-0.6 $\mu g\ g^{-1}$ exchangeable). *Agrostis stolonifera* from the nickel-rich area had the highest concentrations of nickel in the shoots (103 $\mu g\ g^{-1}$) and this was five times as high as the nickel concentrations of *Agrostis stolonifera* recorded from plants collected from the moderately colonised skeletal soils (20.3 $\mu g\ g^{-1}$). There were no other clear interspecific or intraspecific differences between the nickel concentrations in the shoots of other plant species collected from Keen. (Table 5.3).

Table 5.3 Nickel concentrations in the shoots of some plant species ($\mu g\ g^{-1}$) collected from Keen moderately colonised skeletal soils, Keen nickel-rich soils and from Burrafirth. The value represents a bulked sample of at least 30 plants from each area.

Collection site / **Species**	**Keen** (Mod. colonised skeletal soils)	**Keen** (Nickel-rich area)	**Burrafirth**
Agrostis stolonifera	20.3	103	-
Armeria maritima	24.0	37.8	0.0
Calluna vulgaris	-	20.7	0.0
Plantago maritima	26.0	31.0	1.1
Potentilla erecta	-	27.0	2.2
Succisa pratensis	-	19.6	0.7

Discussion

The nickel concentrations from the soils of the nickel-rich area (13.2-32.2 $\mu g\ g^{-1}$) were within the range of values reported by Bowen (1983) (4.7- 37.0 $\mu g\ g^{-1}$). They were, however, lower than the concentration of 119 $\mu g\ g^{-1}$ of nickel recorded from one sample from this area in 1979 (Carter *et al.* 1987 a). It appears that the soils with very high nickel concentrations are localised; there may even be further areas with high soil nickel levels on the Keen which had been missed during previous sampling. This supports the view that the levels of nickel may vary over relatively short distances, even on the microscale (Proctor & Baker 1994).

The soil nickel concentrations were clearly higher in the nickel-rich area than in the skeletal soils. However, the vegetation showed no unusual features; there were many species growing in the nickel-rich soils (up to 24 species per m^2), and there was a closed vegetation cover. The nickel concentrations in the plant shoots from the nickel-rich area (19.6-103 $\mu g\ g^{-1}$) were higher than those recorded by Bowen (1983) (17.0-27.0 $\mu g\ g^{-1}$), but not as high as the nickel concentrations on Keen plants reported by Shewry & Peterson (1976) (e.g. 240 $\mu g\ g^{-1}$ for *Silene acaulis*) or for some other British ultramafic sites (e.g. the nickel concentration in one sample of *Plantago maritima* from ultramafic soils on Rum was 480 $\mu g\ g^{-1}$) (Looney & Proctor 1990).

There were higher nickel concentrations in *Agrostis stolonifera* leaves from the nickel-rich area (103 $\mu g\ g^{-1}$) than from the skeletal soils (20.3 $\mu g\ g^{-1}$), but Spence (1957) had reported nickel concentrations of 118 $\mu g\ g^{-1}$ in *Agrostis stolonifera* shoots from the open soils of the Keen. *Armeria maritima* and *Plantago maritima* are the two other species which were common to both the nickel-rich area and the skeletal soils. There was not a very big range in the nickel concentrations of the leaves for either species (24.0 $\mu g\ g^{-1}$-37.8 $\mu g\ g^{-1}$).

Slingsby & Brown (1977) did soil chemical analyses from several British ultramafic sites, and concluded that the soils analyses reflected pedological differences which were likely to have limited biological significance. It certainly seemed that the differences in the concentrations of nickel between the nickel-rich soils and the skeletal soils of the Keen were not reflected in the amounts taken up by the species sampled. It has been suggested that nickel availability can be reduced by chelation with soil organic matter (e.g. Halstead *et al.* 1969) and it is possible that the higher organic matter in the soils of the nickel-rich area reduced its availability to plants. It is worth bearing in mind, however, that Bowen (1983) found nickel toxicity symptoms in oats grown in soils from the nickel-rich area.

Shewry & Peterson (1976) did detailed plant analyses for several separate plants of a range of species growing on different parts of the Keen. They found large differences in the concentrations of shoot elements (including nickel) between individuals of the same species and marked differences between species in the mean concentrations of the elements. My results showed that *Agrostis stolonifera* shoots from the nickel-rich area had higher nickel concentrations than shoots of the other species, but on the Keen skeletal soils, there were similar nickel concentrations in the three plant species sampled. It is true that the plant samples which I collected were bulked, and so there was no estimate of the variation of nickel concentrations of plants within the nickel rich area.

It is worth pointing out that there were no root analyses and species may retain nickel in their root systems. Menezes de Sequeira & Pinto Silva (1992) found several examples of native species on Portuguese ultramafic soils keeping most of the nickel in the roots. Shewry & Peterson (1976) found higher concentrations of nickel in *Agrostis stolonifera* roots than in the shoots.

The results from the soil analyses from the areas associated with *Arenaria* on Beinn Iadain are in line with other studies (e.g. Halliday 1960 a, Coker 1969) reflecting soils with high calcium, low organic matter, and high sand content. The Nikkavord skeletal soils had similar chemical and physical properties to the Keen skeletal soils, although they appeared to have higher % organic matter and higher available phosphorus than the Keen soils. Certainly one of the important features of the skeletal soils of the Keen is the very low levels of nutrients.

Chapter 6. General Discussion

Summary of findings

The results from field monitoring of *Cerastium* and *Arenaria* individuals from June 1994 to November 1996, together with seed germination experiments in the field and under controlled conditions, have shown that *Cerastium* and *Arenaria* from the Keen show different strategies for surviving on the site.

On the Keen, established *Cerastium* plants appeared to be long-lived; 61% of plants which were recorded in June 1994 were still alive in November 1996. *Arenaria* plants, on the other hand, had a shorter life; no plants recorded in June 1994 survived to November 1996.

There was a high survival of both established plants and seedlings of *Cerastium* recorded on the Keen throughout the study period. There was a high survival of *Arenaria* plants for the first year, but there was a higher mortality of established plants and 1994 cohorts after flowering in the second year. It should be borne in mind that there were only four or five population censuses in each year and that an unknown number of seeds which germinated and died between censuses would not have been included in the data, and therefore it is likely that the mortality of seedlings of both *Cerastium* and *Arenaria* would have been underestimated.

On the Keen, most *Cerastium* seedlings were recorded during the summer and autumn. It is not clear whether the seeds originated from plants which had flowered and set seed in the same year, or whether the seeds had been in the seedbank. Most *Cerastium* plants flowered in June and July and seeds were ripe in July and August. An important question is whether newly shed *Cerastium* seeds require a chilling treatment for germination. The results from the germination experiments in the Stirling growth rooms using chilled and unchilled seeds were puzzling; chilled *Cerastium* seeds germinated on acid-washed sand and unchilled ones did not, but there was >50% germination of both chilled and unchilled seeds on potting compost. It is true that the conditions in the controlled environment of the Stirling growth rooms are different from those in the field, and it would be expected that seeds on Keen soil in the field would show different germination from seeds on acid-washed sand or potting compost in the Stirling growth rooms. Nevertheless, the successful germination of unchilled seeds on John Innes compost showed that a chilling treatment is not strictly necessary for germination.

The number of individuals recorded at various times of the year from November 1995 to July 1997 from seeds sown on the Keen and on Sobul in July 1995 gave an indication of the timing of germination of seeds in the field. Most of the *Cerastium* seeds which were sown on the Keen and on Sobul on 17 July 1995, and which had been collected from capsules on the same day, did not germinate until the following summer. This implies that most of the *Cerastium* seedlings recorded in the summer and autumn of each year originated from seeds in the seedbank and not from seeds shed in the same year.

For *Arenaria* there was seed germination on the Keen throughout the spring, summer and autumn. There was also a long flowering period, from May to November, giving a longer time during which seeds are ripened and released. As for *Cerastium*, the results of germination experiments in the Stirling growth rooms were not clear-cut but there was very low germination of fresh *Arenaria* seeds which had been sown on Sobul and on the Keen on 17 July 1995, as recorded on 13 November 1995, compared with the number of seedlings recorded in 1996 and 1997. Keen and Nikkavord *Arenaria* seeds germinated over a long period on Keen soil in the Stirling growth rooms compared with Beinn Iadain *Arenaria* seeds which mostly germinated within two weeks. It seems that only a small proportion of seeds from the Keen or Nikkavord populations entering the soil will germinate immediately and that many of the *Arenaria* seedlings recorded each year on the Keen originated from the seed bank.

On the Keen, both *Cerastium* and *Arenaria* were polymorphic, although *Cerastium* plants had a longer reproductive life than *Arenaria*; 23% of the *Cerastium* plants recorded in June 1994 flowered for three years, compared with only 1% of *Arenaria* plants. This is largely the result of *Arenaria* plants having a shorter life than *Cerastium*. *Arenaria* plants matured quickly with individuals setting seed the year following germination. In contrast, no *Cerastium* seedlings recorded in 1994 flowered in 1995 and only 6% flowered and set seed after two years.

Over 90% of Keen *Arenaria* flowers recorded from 1994 to 1996 produced seeds. The flowers appear to have no specialised pollination mechanisms and I did not observe insect visitors to the flowers in the field. It seems likely that the flowers were self pollinated. Certainly, self-fertilisation was efficient for bagged flowers in the Stirling glasshouses. There were many dipteran visitors observed on Keen *Cerastium* flowers and it is likely that some of these were pollinators. Self fertilisation was not always effective in the Stirling glasshouses and the 26% of Keen flowers which failed to produce seeds may be the result of failed pollinator visits.

On Nikkavord, *Cerastium* plants showed similar population dynamics to those on the Keen. *Arenaria* plants on Nikkavord showed bigger fluctuations in numbers and flowering frequencies than Keen plants. It should be emphasised, however, that the sample size on Nikkavord was low. *Cerastium* plants were only considered on the wetter debris areas and *Arenaria* plants were mostly on the track passing through the site. Further sampling would have to be done in order to make conclusions about the site as a whole.

There was successful germination and establishment of *Cerastium* seeds planted on Sobul, an ultramafic outcrop about 6 km SW of the Keen, where the species did not occur naturally. After two years, there were two flowering plants producing seeds. It would appear that *Cerastium* plants had not been present on Sobul because the seeds were unable to disperse there from the Keen. *Arenaria* is found on most of the well-drained, open, skeletal ultramafic soils on Unst, and has apparently dispersed and survived more successfully than *Cerastium*. Keen *Arenaria* seeds were found to be smaller, smoother and lighter than *Cerastium* ones and it is suggested that wind dispersal of *Arenaria* seeds was more effective. Of course, after two years only, it is impossible to know whether the Sobul *Cerastium* population will persist.

Cerastium and *Arenaria* both had seed banks on the Keen and undoubtedly this has an important role in carrying the population across unfavourable periods and may also reduce genetic drift by carrying genotypes across several generations. Seeds of the two species collected from the Keen were viable after two years in dry storage. There were young *Cerastium* seedlings recorded from plots on Sobul two years after Keen seeds had been sown onto the plots, indicating that seeds were viable in the soil for at least two years. The same appeared to be true for *Arenaria* seeds sown on the Keen, although there were very low numbers of both young seedlings and older plants recorded after two years and the possibility cannot be ruled out that younger seeds may have been blown onto the plots from surrounding flowering *Arenaria* plants. There was, however, a rapid recovery of *Arenaria* numbers recorded in D. R. Slingsby's plots on the Keen in 1993, after the very low numbers in the same plots in 1991 and 1992 and it seems likely that this was the result of germination from the seedbank.

Legg *et al.* (1997) emphasised the importance for the conservation management of rare Scottish plants of establishing one or two key factors which play a major role in limiting population size and stability. Once these have been identified, conservation management can be targeted accordingly. An important question is whether the number of *Cerastium* and *Arenaria* plants recorded were limited by the number of seeds or by some other factor such as the number of available microsites, competition with mature plants of the same or of another species, or seed and seedling predators. Field experiments showed that the surface layer of stones on the Keen was important for seed germination and establishment of *Cerastium* and *Arenaria*, but there were no experiments in which seeds were sown at different densities and so it is not possible to know to what extent the numbers of plants were limited by available microsites.

Cerastium leaves from the two Unst populations were found to be much more glandular hairy than leaves from a Streymoy *Cerastium arcticum* population. Keen and Nikkavord leaves were both densely glandular hairy but Keen leaves had a significantly higher density of trichomes than Nikkavord ones and also a significantly lower proportion of glandular trichomes. Histochemical tests revealed that the glandular trichomes secreted lipids, pectins and other polysaccharides. It is suggested that the densely glandular hairy Keen and Nikkavord leaves may be part of an adaptation to drought, although it is also possible that they may have a role in plant defence against herbivores or may act as a decoy for non-pollinating insects. The secretory material did not stain for nickel or magnesium (although it is true that there were no detection limits for either of the tests) and this in line with the suggestions that toxic concentrations of nickel or magnesium are not important for limiting plant growth on the skeletal soils of the Keen (Carter *et al.* 1987 a). The presence of a nickel-rich fully vegetated area on the northern slopes of the Keen with higher concentrations than the barest soils gives further evidence for the suggestion that nickel is not important in retarding successional processes.

There seems to be no very big danger for populations of *Cerastium* and *Arenaria* at present. My observations from monitoring the two species from 1994 to 1996 showed that there was a high survival of both species and they both have a seed bank which will enable them to recover from low numbers. Nevertheless, there had been fluctuations in numbers of the two species from 1978 to 1996 and the fluctuations showed differences within the site, but at least on the lower parts of the site, were related to low spring rainfall and to number of day degrees above 5.6 °C. It is not clear if seed banks of *Cerastium* and *Arenaria* plants last longer than two years, and a series of warm winters and dry springs may cause *Cerastium* and *Arenaria* populations on Unst to be threatened. Another rare plant, *Minuartia rubella*, which grew 'very sparingly on the serpentine hills near Baltasound' (Saxby 1903) has not been seen since 1953 (although there are some unconfirmed records of the plant being seen in the 1960s) and is now presumed to be extinct (Scott & Palmer 1987).

Monitoring recommendations

Monitoring of individuals of *Cerastium* and *Arenaria* in the field from June 1994 to November 1996 has given much information about the life cycles of the two species, which enables recommendations to be given for the long term monitoring of the two species.

Sixty-one percent of *Cerastium* individuals recorded in June 1994 were still alive in November 1996 and it would be interesting to find out the longevity of this species by continuing mapping of individuals in as many of the 73 1 m x 1 m permanent quadrats as possible, taking care to keep the same sample proportions of quadrats in the different debris areas (chapter 2). The maps and precise locations of the quadrats are in the Lerwick SNH office. It is thought that annual monitoring would be sufficient; from June 1994 to November 1996 there was a slow turnover of the Keen *Cerastium* population. It is recommended that monitoring is done in July, although if time permits, a re-survey in September would be able to confirm records (it is quite easy to miss seedlings and sometimes individuals appear to be dead but are alive). Such monitoring will give an idea of the age distribution of the population. There should also be records of the size of the plants (the number of shoots), and the number of flowers and fruits on flowering individuals, since these are important indicators of the condition of the population.

Arenaria is harder to monitor than *Cerastium*. There is high seed germination throughout the year. The fast turnover of the species results in difficulties in relocating individuals unless they are monitored frequently (a minimum of four times a year: May, July September and November). The study period was long enough to establish the longevity of this species. I therefore recommend a count of adults and seedlings in the quadrats. It should be emphasised that from June 1994 to November 1996, most of the population was made up of seedlings and small plants (chapter 2; fig. 2.11), and that it is necessary to have an indication of the size distribution of the population. It may be easier to simplify the four size categories which I used from June 1994 to November 1996, to seedlings and adults. As for *Cerastium*, the numbers of flowers and fruits produced should be recorded. There is a longer flowering season for *Arenaria* than *Cerastium* and therefore, ideally, plants should be monitored in July and in September. As for *Cerastium, Arenaria* plants should be recorded in as many of the 73 1 m x 1 m permanent quadrats as possible, taking care to keep the same sample proportions of quadrats in the different debris areas.

For the monitoring of rare plant populations, sampling should ideally be randomised within each recognisable stratum in the habitat (Palmer 1987). For this study, the samples were stratified so that there were quadrats on the different debris types throughout the site, although there was less sampling on the very open soils to the north of the site. It is true that quadrats were not placed randomly and therefore there are no confidence limits for the data, and it is impossible to know whether the individuals sampled were a representative sample of the population. In general there was bias towards sampling quadrats which already had either or both of the study species within them. Nevertheless, at the start of the study, 25% of the quadrats had no *Cerastium* plants and 33% had no *Arenaria* plants. Throughout the study, seedlings of either species were recorded in quadrats where they did not occur at the start, and plants of both species became extinct from some of the quadrats, but the proportion of quadrats with no plants remained roughly the same for both *Cerastium* and *Arenaria*. All in all, it is thought that monitoring of *Cerastium* and *Arenaria* plants in as many of the 73 1 m x 1 m permanent quadrats as possible, taking care to keep the same sample proportions of quadrats in the different debris areas, will at the very least be able to give an indication of any population changes on the whole site.

Unfortunately, since the voluntary data collector retired in September 1995, the weather records from the Baltasound weather station have been obtained from an automatic recorder and are rather unreliable. It may be worthwhile for SNH to try to find a replacement data collector or set up their own weather station. It has been found that the fluctuations in numbers of *Cerastium* and *Arenaria* on the Keen from 1978 to 1995 were related to spring rainfall and number of day degrees above 5.6 ^{O}C, but the data were collected from a restricted area and it would be worthwhile to confirm the trends.

Any monitoring work for *Cerastium* and *Arenaria* on Nikkavord should include sampling plots from the associated debris areas in the centre of the site, but it should be emphasised that monitoring on the Keen is the priority. However, it is well worthwhile monitoring the newly established *Cerastium* population on Sobul by counting the number of plants and recording the number of flowers and fruits on flowering plants. As for the monitoring of *Cerastium* on the Keen, this should be done annually in July.

There was no monitoring of the habitat quality on the Keen during the PhD, but this should be an important part of the monitoring program. Historical and photographic evidence suggests that the large expanses of open skeletal soils have not changed for the last few decades and it is likely that at least some of the debris habitat may have been in existence by the end of the late glacial period about 10,000 years ago (Carter *et al.* 1987 a). Nevertheless, there has been no grazing on the Keen since the early 1970's and it is possible that this may have a long term effect on the habitat quality.

Monitoring a species requires a lot of time and effort since at any time it is important to have an indication of the condition of the population, as well as an idea about the numbers of plants. It is also important to monitor a representative sample of the population and ideally there should be random samples. It is better to prioritise sites and species and set up a thorough monitoring plan than to monitor a wider range of sites and species in less detail, with the possibility of erroneous results.

Further research

The monitoring of individuals of Keen *Cerastium* and *Arenaria* populations from June 1994 to November 1996 gave much important biological information about the life cycles of the two species. However, it was not established whether or not recruitment of the two populations was seed limited. Simple experiments of sowing extra seeds and recording the number of recruits are able to answer this question (Crawley 1990). It is important when working with rare species not to waste seeds but certainly for *Arenaria* it is easy to produce many seeds from plants cultivated in glasshouses.

It was found that self pollination of *Arenaria* was efficient in glasshouse-grown plants, and most of the flowers produced seeds, therefore it seems unlikely that this species was pollinator limited. However, self pollination of *Cerastium* was not always effective in the Stirling glasshouses and there were dipteran visitors observed on flowers in the field which were probably pollinators. Over 25% of the flowers in the field failed to produce seeds, and it is possible that *Cerastium* is pollinator limited. It would be worthwhile to find out whether this was the case.

It was established that both *Cerastium* and *Arenaria* had a seed bank but it was not established how long seeds last in the soil. One way to answer this question would be to put freshly collected seeds of the two species into containers filled with Keen soil and dig them into the soil. It is easy to dig up the containers at various intervals e.g. annually, and test the seeds for viability and percentage germination.

There are many unusual forms of species growing on the Keen. I confirmed some of the morphological differences between Keen and Nikkavord *Cerastium*. To what extent this morphological variation is genetically or environmentally based is still unclear. Further research is required for *Cerastium* and also for other species which show morphological differences. Some of the unusual Keen forms show variation within the site. On the Keen, individuals of the distinctive form of *Plantago maritima* with the tight growth form and short pointed hairy leaves are found only metres away from plants which are much less hairy and have long thin leaves. It would be worthwhile to quantify the morphological variation of this species on the Keen and find out if there are any correlations with physical or chemical site factors. There would also be scope for reciprocal transplanting experiments both within the Keen and between other local sites.

There were clearly germination differences between Keen and Beinn Iadain *Arenaria* seeds and it would be interesting to follow this up and to consider ecological and physiological adaptations to the harsh Keen environment for other species.

There have been suggestions that drought may be an important factor which prevents natural successional processes on the Keen (e.g. Carter *et al.* 1987 a). It has been established in this thesis that there were lower numbers of *Cerastium* and *Arenaria* plants after a dry spring, but from June 1994 to November 1996, there was a high survival of both species during four dry spells. Keen *Cerastium* is glandular hairy and the fats secreted may have a role in increasing reflectance and reducing water loss, but this has not been tested. Experiments showed that Unst *Cerastium* and Faroese *Cerastium arcticum* leaves died back after a drought, but were able to recover by new growth at the nodes.

The actual role of drought, however is still unknown. It should be borne in mind that although there are quite long spells without rain, there are many fogs on the Keen and fogs can make a very significant contribution to rainfall. Similarly, dew in sandy soils near to the sea can provide an input of water to the vegetation (Crawford 1989). A field experiment involving manipulations of water and nutrients along the lines of Grime & Curtis (1976) might be able to elucidate the role of water and nutrients as limiting factors, but it should be pointed out that there would be several practical difficulties. The dry spells on Unst are unpredictable and there may be no results for several years. Also it would be important to use deionised water in such an experiment in order to prevent any unwanted nutrient inputs, and transportation of water to the Keen is not easy. An alternative approach is to consider if Keen populations of plants are more drought tolerant than populations of the same species growing elsewhere. This has been found to be the case for some species e.g. Lefèbvre & Simon (1979) found that *Armeria maritima* from a zinc-lead mine waste was more drought tolerant than *Armeria maritima* from seaside cliffs.

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Appendix 1

Table 1. Numbers of *Cerastium* and *Arenaria* plants in 1 ha plot with daily and monthly weather events at a meteorological station at Baltasound, about 4 km W from the Keen from 1978 to 1995. Plant data were collected by D.R. Slingsby from 1978 to 1993 and by S. Kay in 1994 and 1995. n.d; no data.

	1978	**1983**	**1985**	**1987**	**1991**	**1992**	**1993**	**1994**
***Cerastium* numbers**	55	1122	521	1176	505	293	719	2226
***Arenaria* numbers**	140	833	176	661	14	21	468	1463
Spring rainfall								
Apr	33	107	102	32	51	92	58	103
Apr + May	72	145	160	85	94	138	107	134
Apr + May + Jun	129	219	169	150	131	177	155	227
May	39	38	58	53	25	43	46	49
May + Jun	96	112	67	118	80	85	97	124
Jun	57	74	9	65	37	39	48	93
Autumn rainfall								
Aug	94	127	53	83	114	78	82	68
Aug + Sep	209	275	226	205	229	234	219	97
Aug + Sep + Oct	357	386	369	374	350	379	287	214
Sep	115	148	173	122	115	156	137	29
Sep + Oct	263	259	316	291	236	301	205	146
Oct	148	111	143	169	121	145	68	117
Annual rainfall								
Total annual rainfall	1180	1455	1054	1414	1081	1358	1292	1114
No. of days in the upper rainfall quintile	68	82	61	76	71	85	79	61
No. of days in the lower rainfall quintile	87	64	87	60	75	72	59	73
Severe weather								
No. of days with gales	41	60	48	59	35	56	61	19
No. of days with snow cover at 0900 GMT	24	12	23	18	4	9	15	27
Temperature								
No. of day degrees above 5.6 °C	229	221	225	223	257	257	223	208
Total degrees (°C) from October to March	838	859	824	746	977	1020	854	762
Total degrees (°C) from April to September	1740	1727	1729	1680	1789	1968	1795	1673

Appendix 1

Table 2. Numbers of *Cerastium* and *Arenaria* plants in S6 with daily and monthly weather events at a meteorological station at Baltasound, about 4 km W from the Keen from 1978 to 1995. Plant data were collected by D.R. Slingsby from 1978 to 1993 and by S. Kay in 1994 and 1995. n.d; no data.

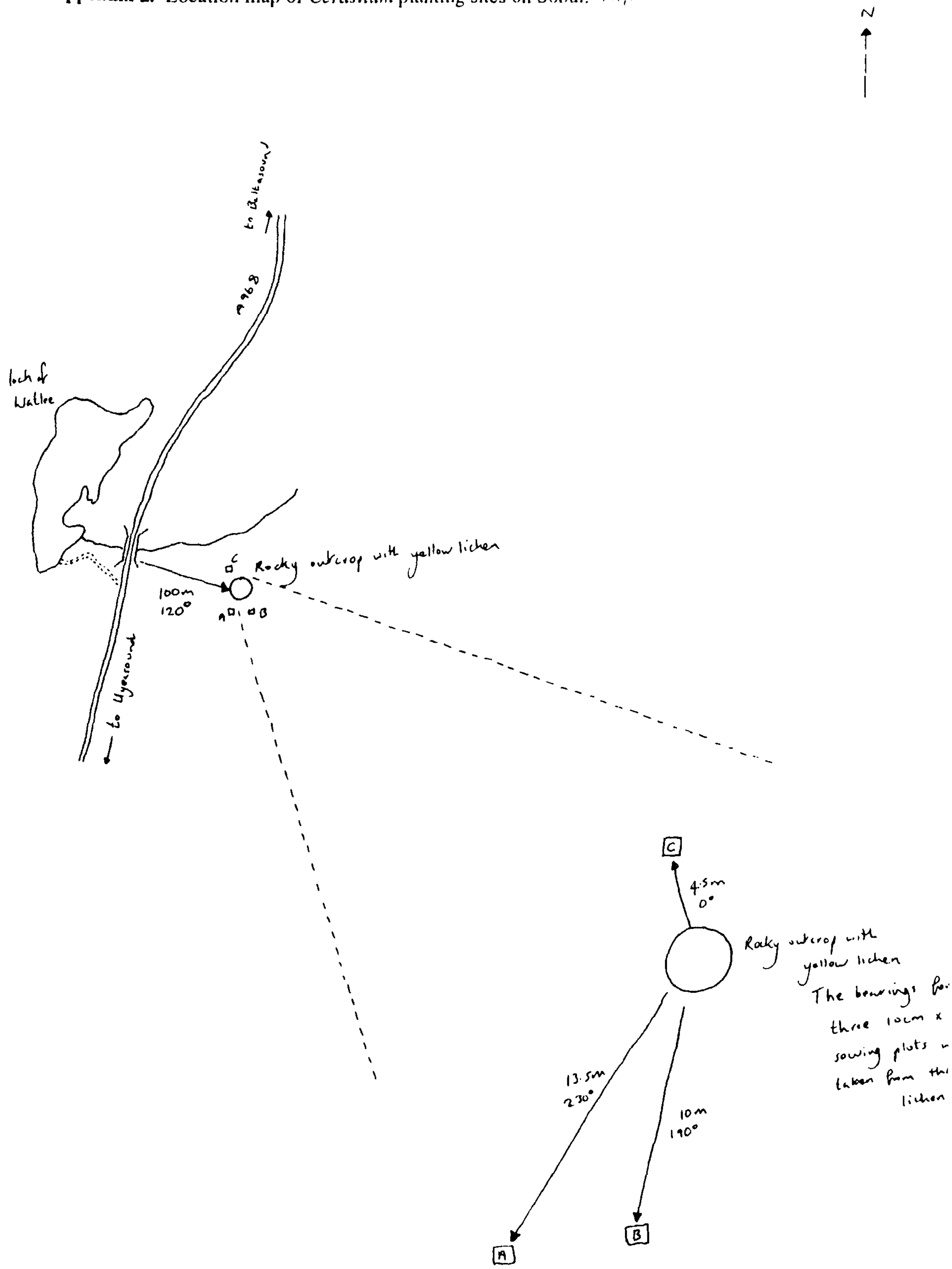
	1979	**1980**	**1982**	**1983**	**1985**	**1991**	**1992**	**1993**	**1994**	**1!**
***Cerastium* numbers**	40	32	21	32	10	15	8	18	29	4(
***Arenaria* numbers**	36	33	79	86	23	0	1	40	38	4!
Spring rainfall										
Apr	113	44	50	107	102	51	92	58	103	1!
Apr + May	225	58	121	145	160	94	138	107	134	2:
Apr + May + Jun	296	113	127	219	169	131	177	155	227	2!
May	112	14	71	38	58	25	43	46	49	31
May + Jun	183	69	77	112	67	80	85	97	124	98
Jun	71	55	6	74	9	37	39	48	93	3(
Autumn rainfall										
Aug	49	117	51	127	53	114	78	82	68	9(
Aug + Sep	192	340	148	275	226	229	234	219	97	17
Aug + Sep + Oct	284	468	423	386	369	350	379	287	214	28
Sep	143	223	97	148	173	115	156	137	29	80
Sep + Oct	235	351	372	259	316	236	301	205	146	19
Oct	92	128	275	111	143	121	145	68	117	11
Annual rainfall										
Total annual rainfall	1308	1180	1182	1455	1054	1081	1358	1292	1114	12
No. of days in the upper rainfall quintile	75	54	59	82	61	71	85	79	61	n.(
No. of days in the lower rainfall quintile	46	88	88	64	87	75	72	59	73	n.(
Severe weather										
No. of days with gales	34	48	38	60	48	35	56	61	19	n.d
No. of days with snow cover at 0900 GMT	53	17	22	12	23	4	9	15	27	n.d
Temperature										
No. of day degrees above 5.6 °C	201	230	207	221	225	257	257	223	208	n.d
Total degrees (°C) from October to March	664	800	677	859	824	977	1020	854	762	n.d
Total degrees (°C) from April to September	1648	1794	1821	1727	1729	1789	1968	1795	1673	n.d

Appendix 1

Table 3. Numbers of *Cerastium* and *Arenaria* plants in S5 with daily and monthly weather events at a meteorological station at Baltasound, about 4 km W from the Keen from 1978 to 1995. Plant data were collected by D.R. Slingsby from 1978 to 1993 and by S. Kay in 1994 and 1995. n.d; no data.

	1979	1980	1983	1984	1985	1988	1991	1992	1993	1994
***Cerastium* numbers**	3	2	6	4	7	6	12	10	0	4
***Arenaria* numbers**	7	4	14	0	1	3	0	0	0	0
Spring rainfall										
Apr	113	44	107	78	102	50	51	92	58	103
Apr + May	225	58	145	104	160	90	94	138	107	134
Apr + May + Jun	296	113	219	163	169	107	131	177	155	227
May	112	14	38	26	58	40	43	46	49	31
May + Jun	183	69	112	85	67	57	80	85	97	124
Jun	71	55	74	59	9	17	37	39	48	93
Autumn rainfall										
Aug	49	117	127	39	53	106	114	78	82	68
Aug + Sep	192	340	275	150	226	213	229	234	219	97
Aug + Sep + Oct	284	468	386	369	369	437	350	379	287	214
Sep	143	223	148	111	173	107	115	156	137	29
Sep + Oct	235	351	259	330	316	331	236	301	205	146
Oct	92	128	111	219	143	224	121	145	68	117
Annual rainfall										
Total annual rainfall	1308	1180	1455	1209	1054	1191	1081	1358	1292	1114
No. of days in the upper quintile	75	54	82	68	61	67	71	85	79	61
No. of days in the lower quintile	46	88	64	81	87	88	75	72	59	73
Severe weather										
No. of days with gales	34	48	60	68	48	33	35	56	61	19
No. of days with snow cover at 0900 GMT	53	17	12	20	23	14	4	9	15	27
Temperature										
No. of day degrees above 5.6 °C	201	230	221	225	225	230	257	257	223	208
Total degrees (°C) from October to March	664	800	859	801	824	924	977	1020	834	762
Total degrees (°C) from April to September	1648	1794	1727	1756	1729	1777	1789	1968	1795	1673

Appendix 2. Location map of *Cerastium* planting sites on Sobul. (A, B and C)



Appendix 3. Morphological races on the Keen.

Several of the species which occur on ultramafic rocks within Britain are morphologically distinct (Proctor & Woodell 1971). The Keen is no exception and has many species which look different to the more usual forms of the species growing elsewhere. Two of the more distinctive ones are *Rubus saxatilis* and *Plantago maritima*.

Rubus saxatilis (henceforth called *Rubus*) has no stolons and occurs on the Keen as emergent shoots (Fig. 1 a). It is the var. *borealis* of West (1912) who described it as 'a distinct reddish brown to nigrescent dwarf variety with rugose leaves, usually two fully grown with a smaller third one, with under surfaces pressed to the ground.' I saw occasional flowering plants on the Keen but no fruits. Slingsby (1979) reported possible references to *Rubus* fruits in the past (Slingsby 1979).

Plantago maritima (henceforth called *Plantago*) has hairy, short, succulent, pointed leaves and a dense growth form. Druce (1922) described the more hairy plants with broader shorter leaves growing on the ultramafic outcrops of Unst as a new species, *Plantago edmondstonii*. However there is a lot of variability in leaf shape and hairiness of plants on the Keen and on the other ultramafic sites on Unst. Fig. 2 a shows an example of one of the more extreme Keen forms.

I compared the growth of Keen forms of *Rubus* and *Plantago* in John Innes Compost (No. 2) in Stirling with more usual races of the same species growing elsewhere. The comparison also included Keen and Nikkavord *Cerastium nigrescens* and Streymoy *Cerastium arcticum*.

Rubus

Four *Rubus* cuttings were collected from each of three Shetland sites: the Keen (NGR HP 645098), Catfirth (NGR HU 437 538) and Stackaberg, Fetlar (NGR HU 613 928). Catfirth is a small limestone ravine and Stackaberg an ultramafic rocky hill which does not show many ultramafic characteristics because the summit is largely composed of metagabbro and phyllites (Slingsby *et al.* 1983). Keen and

(a)

(b)

Fig.1 (a) Keen *Rubus* in the field (b) Keen, Fetlar and Catfirth *Rubus* after two years in cultivation in a Bridge of Allan garden.

(a)

(b)

Fig. 2 (a) Keen *Plantago* in the field (b) Keen and Burrafirth *Plantago* after six months in cultivation in the Stirling growth rooms.

Stackaberg cuttings were collected on 6 July 1995 and Catfirth ones on 8 July 1996. They were transplanted into large pots of John Innes Compost (No. 2) after collection and grown in a Bridge of Allan garden (NGR NS 787 974). Observations were made during two years. As for the plants on the Keen, *Rubus* leaves died back during the winter. Stolons were produced on all the races during the summer months (Fig. 1 b) and the plants flowered but there were no fruits. Keen and Fetlar plants retained their purple coloration in cultivation which is in contrast to the observations of Scott & Palmer (1987) who found that the dark colour of Keen *Rubus* was lost in cultivation.

Plantago

Plantago seeds were collected from the Keen and from Burrafirth, a non-ultramafic site (NGR HP 614 149) on 24 September 1996. They were germinated on acid washed sand and five seedlings were transplanted into pots of John Innes Compost (No. 2) on 12 April 1997 and grown in the Stirling growth rooms. After six months in cultivation (6 October 1997), the Keen individuals had lost much of their distinctiveness. They maintained the tight growth form, but the leaves were longer, thinner and less hairy (Fig. 2.b).

Cerastium

Keen and Nikkavord seeds were collected from the Keen on 22 July 1996. Streymoy seeds were collected from plants which were cultivated in Stirling glasshouses and had been collected from Streymoy during August 1995. They were germinated on acid washed sand and twelve seedlings from each population were transplanted into pots of John Innes Compost (No. 2) on 26 April 1997. Ten plants from each population were grown in the Stirling glasshouses and the rest were grown in a Bridge of Allan garden. After six months there appeared to be much plasticity in growth form. In the glasshouses, Keen plants were less tufted with trailing shoots (Fig. 3 a), but out of doors, they maintained the tight growth form in the field compared with the spreading Streymoy plants (unfortunately the garden Nikkavord plants died).

(a)

(b)

Fig. 3 (a) Keen *Cerastium* after six month's growth in the Stirling glasshouses (b) Keen and Faroese (Streymoy) *Cerastium* after six month's growth in a Bridge of Allan garden.

Clearly the growth form of Keen *Cerastium* plants is plastic. However, other features of *Cerastium* are maintained in cultivation. Proctor & Woodell (1971) found that after three years in cultivation Keen *Cerastium* leaves were still round and glandular hairy. Stuffins (1983) found that var. *acutifolium* maintained narrower leaves after growing individuals for 14 weeks in potting compost in glasshouses.