The distribution of Acaena novae-zelandiae T. Kirk. (the Piri-Piri Burr) on lindisfarne national nature reserve

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The Distribution of *Acaena novae-zelandiae* T. Kirk. (the Piri-Piri Burr) on Lindisfarne National Nature Reserve

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SUMMARY

1) The aims of this study were to map the present distribution of *Acaena* on the Snook and Shiel of Lindisfarne and to relate that distribution with the major factors determining where *Acaena* grows. Past distribution was compared to investigate invasion dynamics and predict future spread.

2) Mapping was done by pacing out a grid of 25m × 25m and sampling, using a 1m × 1m quadrat, at each intersection on the grid. For each quadrat percentage cover of *Acaena*, *Ammophila* and bare ground were recorded as well as the presence of paths and warrens. Aspect was also recorded and a subjective record of habitat type was made.

3) The greatest abundances of *Acaena* were found on the Shiel and in patches around the edges of the Snook, this correlates with the presence of yellow dunes. The Shiel is the most probable site of introduction to the island so it is not surprising that *Acaena* is most abundant here.

4) Preferred habitat of *Acaena* is open, yellow , and to a certain extent fixed, dune habitat, with ten to 50 percent of *Ammophila* and one to 30 percent bare ground; no *Acaena* was found in the slacks. There is, however, no association with aspect, but *Acaena* is associated with paths.

5) This preference for open ground and low vegetation cover is probably due to an inability of seeds to establish in densely vegetated areas, and because *Acaena* is a poor competitor in the vegetative phase.

6) Rate of spread of *Acaena* appears to have been constant since its introduction. It has certainly not shown any signs of decreasing in the last 29 years, despite a decline in the number of colonisation events. This indicates that vegetative spread is more important than colonisation.

7) *Acaena* threatens the rare flora of Lindisfarne, but so far control is ineffective and there is little that can be done about the problem. *Acaena* is not, however, affecting the rare species in the slack (nor is it likely to in the future); the lower areas of the transitional stages are similarly uninvaded offering refuge to a number of orchid species.

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1. INTRODUCTION

There are 56,000 hectares of dune land in the UK (Doody 1985) and these include examples of all major dune types, but are typically undulating dune machair, dune heath, dune grassland and areas of blown sand deposited over other formations (such as shingle or cliffs). Sand dunes are found extensively around the British coastline, with the majority in the Western Islands, Orkney and east Scotland, Wales, northern and south-west England (Figure 1.1). Northumberland has a substantial amount of dune system, of which Lindisfarne is the largest site (and the only one protected for conservation).

Despite a seemingly harsh environment, large and old dune systems with well developed slacks and stable inland parts have a rich and diverse flora. For example, in 800 hectares of Braunton Burrows approximately one sixth of British vascular plants are represented. Salisbury (1952) notes that there are 400 species of vascular plant to be found in dune systems. This represents the number of truly native species and a more recent survey has found more than 900 species of vascular plants inhabiting dune systems (Ranwell 1972).

On the calcareous dunes at Lindisfarne (Holy Island) there are extensive slacks with an unusually diverse flora. These slacks are largely responsible for the area's inclusion in a National Nature Reserve (Garson 1985). Of particular interest are the large populations of orchids; *Dactylorhiza incarnata* (Early Marsh), *D. purpurella* (Northern Marsh), *D. fuchsii* (Common Spotted) and *Epipactis palustris* (Marsh Helleborine) all occur within the slacks. Other noteworthy species are *E. dunensis* (the Dune Helleborine), which occurs in only five localities in England (of which this is the only one on the east coast), and *Corallorhiza trifida* (the Coralroot Orchid). Also found at Lindisfarne is the rare Wintergreen species *Pyrola rotundifolia* (Round-leaved Wintergreen).

This biological richness of sand dune systems may be at least partially related to the wide range of habitat conditions and ecological niches present (Willis 1989). At Lindisfarne there are calcareous dunes and slacks, as well as gradations to a more acidic, *Agrostis stolonifera* (Creeping Bent) type of slack. The eastern end of Holy Island exhibits luxuriant dune meadows with a wide diversity of grass species and moss-rich communities are well developed on parts of the stable dunes (Ratcliffe 1977).

Sand dunes form where there is an adequate supply of material sized 0.2-2.0mm in diameter. The critical physical factor for dune formation is the presence of a

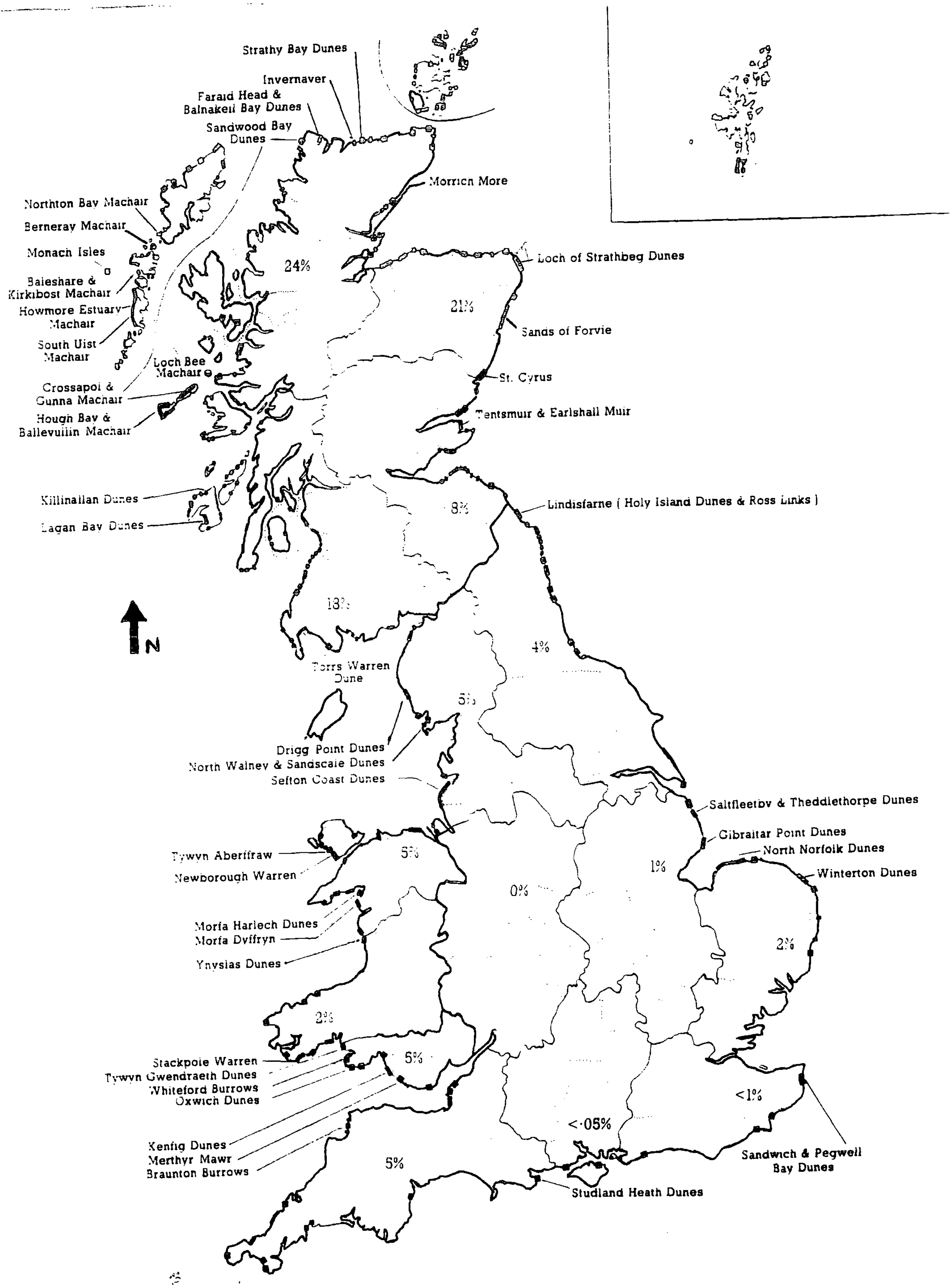

Figure 1.1 - Distribution of Nationally important sand dunes around the British coastline. The area of dunes in each NCC Region are given as a percentage of the total area of dunes in Great Britain (based on a map from Doody 1985).

large beach which is exposed for long enough at low to allow the coarse sandy sediments to dry and be carried inland by ~~of~~fshore winds (Doody 1991). The dunes at Lindisfarne, formed on a large sand flat which is exposed for long periods at low tide, have existed for more than 10,000 years. They are presumed to have accreted post-glacially. on/

The second phase in sand dune formation is the stabilisation of mobile sand by vegetation. Plant cover reduces the velocity of tidal water or the air stream, on higher dunes, and allows particles to sediment out. Vegetation also catches and holds particles that might otherwise drain away, thus increasing accretion. The root systems of these plants helps to bind the surface sediments and reduce its mobility (Barnes 1977). The growth and stability of a dune system depends largely on the existence of a barrier to reduce surface wind speed, increase accretion and reduce erosion. While static objects will perform this function they soon become buried in sand whereas plants do not, they grow with the dune.

In Britain the primary dune building species is *Ammophila arenaria* (Marram grass), although in the north *Elymus arenarius* (Lyme grass) is also important. The first colonists of embryo dunes and the drift line are species that can withstand occasional tidal inundation and high salinity conditions. *Ammophila arenaria* can not cope with high salinity and the initial colonist of dune systems is often *Agropyron pungens* (Sea Couch), which can withstand occasional tidal inundation and often establishes within reach of spring tides. ? A. farctus

These grasses share at least one characteristic; burial in sand stimulates them to further growth. A. farctus ? *A. pungens* and *E. arenarius* do not exhibit as rapid a rate of growth as that exhibited by *A. arenaria* though, and are limited to areas where sand deposition does not exceed 30cm per year. While these two species are the earliest colonist they are rapidly replaced by *A. arenaria*, which can grow at a rate of greater than 1m per year, and can therefore withstand accretion rates in excess of such a depth (Boorman 1977).

This pattern of replacement of species continues as the dunes get older; while *A. arenaria* remains dominant until the fixed dune stage there are a number of species that colonise the dune system and are subsequently replaced. Through this pattern of variation in space, sand dunes are seen to exhibit succession through time (summarised in Figure 1.2). The first stages of pioneer dune, colonised by *A.* farctus *pungens*, *E. arenarius* and then *A. arenaria,* are replaced by mobile, or yellow dunes. These possess a relatively large surface of bare sand and are still considerably mobile. The dominant vegetation is still *A. arenaria*, which forms tufts providing protection for other plants, although these must be able to withstand accretion of fresh sand. Following the early yellow dunes are more stable yellow dunes, here again *A. arenaria* is still dominant and the community is fairly open.

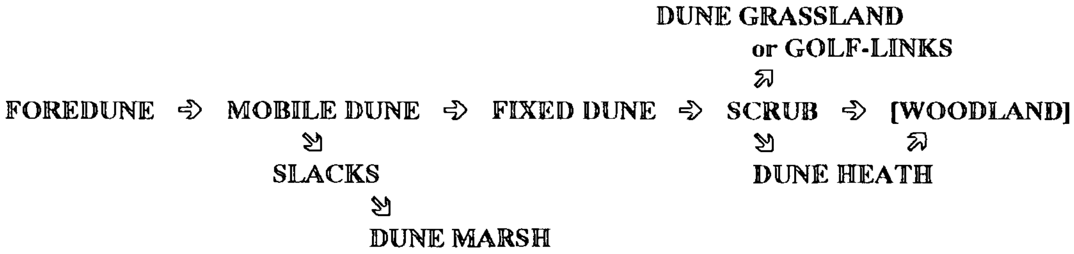

Figure 1.2 : Summary diagram of the possible successionary stages of a sand dune system.

The next successional stage is fixed, or grey, dune where *A. arenaria* is still present but is much less abundant and is no longer dominant. At this stage accretion, if it still occurs, is much reduced and mosses begin to play a considerable role in colonisation. There is a more or less continuous carpet of varied vegetation, but even here there are disturbed areas within the carpet that allow colonisation by short-lived annuals. There are often well developed slacks present at these stages, with a wide and varied flora. Dune slacks, especially the drier slacks, often become dominated by a short, scrubby growth form of *Salix repens* (Creeping Willow) and in well developed, old slacks this may begin to encroach on the side of the fixed dunes themselves. This *S. repens* dominant vegetation can be seen to a large extent in the fixed dune slacks of the Snook on Lindisfarne.

The ultimate vegetation that develops on a dune system can be of several types; from fixed dune, scrub can develop and in this habitat the major species can be variable. *Calluna* dominated scrub may develop into dune heath; alternatively scrub may consist of *Ligustrum vulgare* (Privet) and *Sambucus nigra* (Elder). If allowed to develop without the interference of man, woodland may form behind the scrub; on calcareous soils this consists of *Quercus* (Oak), and shrubs such as *Corylus avellana* (Hazel) and *Crataegus oxycantha* (Hawthorn). On more acidic sands pine woods are likely to establish. Another possibility is that scrub reverts to dune grassland.

monogyna

On Lindisfarne the earlier stages of dune formation are extensively covered with *A. arenaria*. There are also small communities of *E. arenarius* and *A. pungens* on areas of young dune fringing the island. The more stable dunes have reduced cover of *A. arenaria* and exhibit a greater diversity of flora. The slacks of this stable system are extremely diverse indeed, but dominated by *S. repens* in the drier areas. The dunes at Lindisfarne lack the characteristic climax communities of dune lands, such as scrub, heath and woodland, especially on the western section of the island. Here succession appears to be halted at the fixed dune stage, although dune grassland has developed in some areas; dune grassland is more common on the eastern part of the island. On the

Shiel at Lindisfarne succession has not progressed further than an advanced yellow dune stage.

As with all British habitats sand dunes are not a completely natural ecosystem (although it is one of the more natural ones in the British Isles) and ha~~s~~ been ve/ extensively utilised by man in the past for grazing of domestic stock and for rabbit warrens especially. This close association with man and the openness of parts of the habitats might suggest that it would be particularly vulnerable to invasion by alien plant species. Crawley (1987) lists a number of characteristics that increase the invasibility of a habitat:

a) low average levels of plant cover,
b) frequent periods of disturbance,
c) close proximity to man (or managed by man),
d) a large pool of potential invaders,
e) few generalist herbivores,
f) large area,

and, with the possible exception of large surface area, these would seem to apply to dune systems. In many parts of the dune system there is certainly a large degree of open community and sand dunes are naturally disturbed by the sea and winds. They have a long history of use by humans both agriculturally and recreationally and it might be imagined that the sea would provide a large number of potential invaders. Apart from domestic stock and rabbits there appear to be very few generalist herbivores. — invertebrates?

Invasive species have an important potential impact on the communities which they invade. Invasive plants often compete with natives, generally to the detriment of the indigenous species. The introduction of a single species can have huge effects on an ecosystem by disturbing the balance of species present. Animals species may then follow these plant invaders and cause further disruption (Elton 1958).

There are a large number of invaders in dune systems, of the 900 species noted by Ranwell (1972) more than half are thought to have been introduced by humans or birds. The majority of these invaders, however, are generally associated with forestry plantations established in the late stages of sand dune succession and in fact seaside communities are usually poor in aliens. This is probably because seaside plants are very wide spread for the simple reason that the sea is such a good disperser that it has already brought most potential colonists to suitable habitats (Crawley 1987). All communities are invasible to some extent, however, and one example of a sand dune invader is the plant species that was under investigation in this project.

Acaena novae-zelandiae (Piri-Piri Burr), previously thought to be *Acaena anserinifolia*, is an invader from the Antipodes. It has established itself on various sand dunes ecosystems around the coast of Britain (Figure 1.3). This coastal distribution

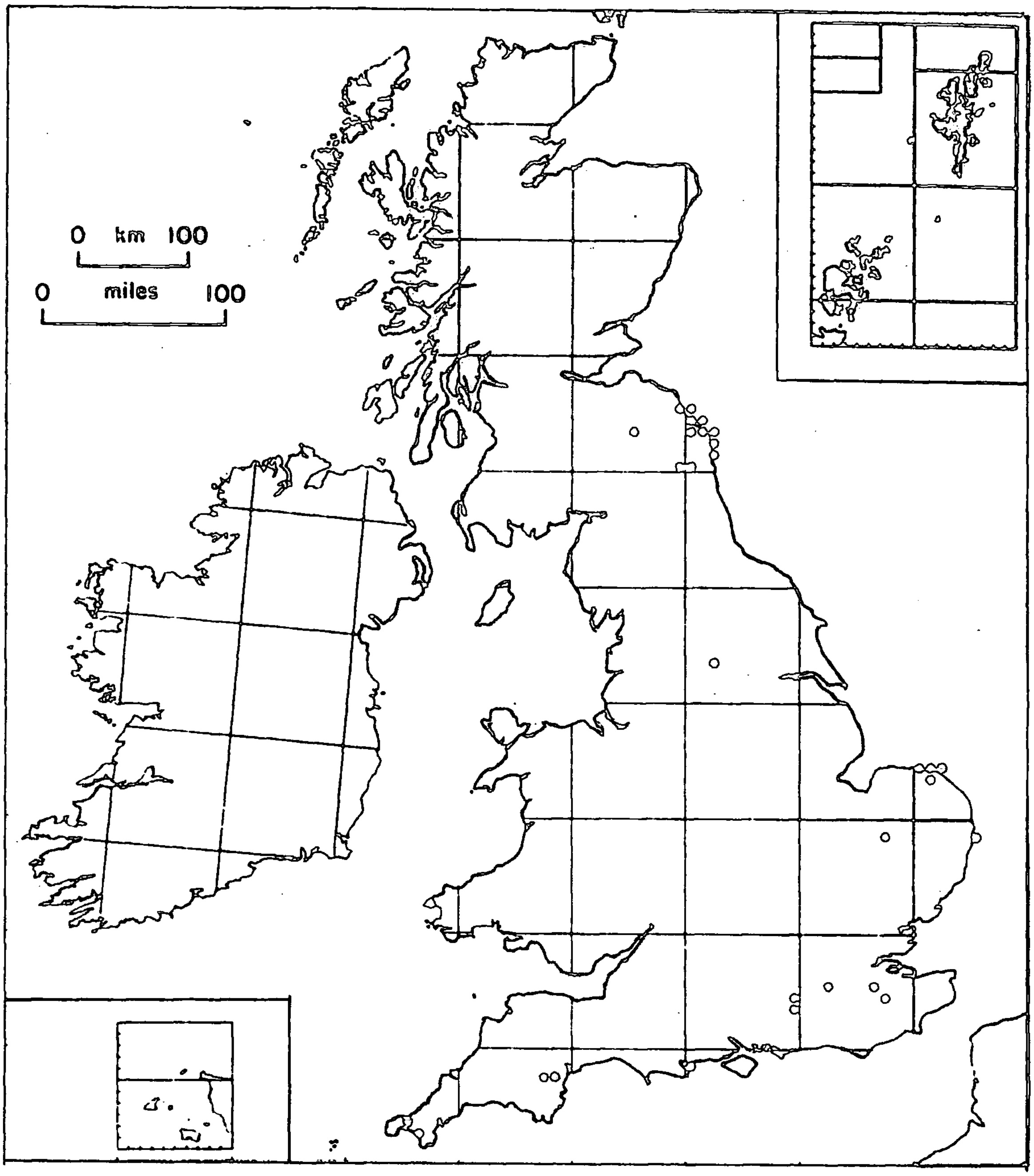

Figure 1.3 - Distribution of *Acaena novae-zelandiae* in the British Isles. Each dot represents at least one record in a 10km National Grid-square (from Glynn & Richards 1985).

possibly relates to frost sensitivity, although the species is also common on the chalk downs of the south, but it has not been recorded from the rest of Europe (Glynn & Richards 1985). The plant arrived in England from New Zealand or southern Australia, probably transported in wool fleeces or brought over by plant collectors as a garden ornamental; another possible method of introduction is in imported seed from New Zealand. *Acaena novae-zelandiae* seeds were found in samples of New Zealand's Chewing's Fescue sent to the Cambridge Testing Station (Lousley 1956). This plant is the subject of this study and will be referred to as *Acaena* throughout.

In New Zealand the plant is found in a wide range of habitats including stable dunes, cliffs, grassy slopes, open scrub and track-sides near the coast. It is not certain that the species has any native habitat in New Zealand, and the species is thought to be an invader here also; having originated and evolved in Australia (Glynn & Richards 1985). In both New Zealand and Australia it is considered a weed of pasture land. Despite being kept under relatively close control in this system, by grazing pressure from domestic stock and competition from other pasture species, the burrs cause problems by easily becoming embedded in the wool of sheep. Once caught in the wool the burrs are very difficult to remove and also stain the fleeces a reddish colour; both of these actions depreciate the value of the wool.

The first record of the species in Britain was in 1901 at a site on the edge of Haynor Down in Devon (Keble Martin & Fraser 1939). Today there are records from 29 ten kilometre grid squares in Britain (Figure 1.3). The populations are all relatively small with the exception of large populations at Kelling Heath in Norfolk and at Studland in Dorset, with the largest population at Lindisfarne in Northumberland.

The first record of *Acaena* in the Northumberland area was in 1911 of a firmly established colony on the banks of the Tweed below Leatherfoot, Roxburghshire (Fraser 1911). A population was first recorded at Lindisfarne in 1939. The plants growing in Tweedside, Yorkshire and Devon were probably introduced from the woollen mills, as were the populations in Bedfordshire, Worcestershire and Kent where wool shoddy was used as a manure (Lousley 1956).

A. novae-zelandiae is an attractive looking plant, with flowers crowded into globular heads about a centimetre across and exhibited on stiff upright stalks (up to 15cm). In May and June the heads are greyish-green, but they turn red as the spines develop fruit and then brown as these fruits ripen.

In Britain, unlike the situation in New Zealand and Australia the burr is not a pasture land weed, the possible threats it poses are not to agriculture but to out native wildlife. The burrs have been known the embed themselves in the plumage of young birds crippling them and leading to their death. The reason for this study, however, is due to the possible threat the burr poses to the rare and varied flora of the dune slacks on Lindisfarne National Nature Reserve by competing with these rare species. Several surveys of *Acaena* have been carried out on Lindisfarne in the past, including mapping its distribution (Hargreaves & Peach 1965, Dollman + Darlington 1965, and Culwick 1982).

The aims of this project were:

a) to map the current distribution of *Acaena* on the Snook and Shiel of Lindisfarne;

b) to relate the abundance of *Acaena* with habitat factors;

c) to compare the current distribution with previous records in order to assess the dynamics of the invasion of *Acaena* at this site;

d) to predict future patterns of spread and identify the habitats at risk form further invasion of the alien weed.

2. STUDY SITE

The area studied in this project covers approximately 107 hectares of the sand dune ecosystem on Holy Island (total area of the island is approximately 546 hectares) and is within the Lindisfarne National Nature Reserve in Northumberland. Lindisfarne lies between 1-2 km off the Northumberland coast, about 125 km north of Durham and is the chief dune system in Northumberland (Salisbury 1952). The island is approximately 2.5 km long from north to south and 1.5 km long from east to west with a long narrow peninsular of dunes stretching a further 2.5 km towards the mainland. It is on this peninsular of calcareous dunes that the study took place (Figure 2.1).

Holy Island gets its name from its long history as a religious settlement. The first habitation of Lindisfarne is thought to have occurred in 635, when Aidan arrived with a group of Irish monks (Graham 1992). Although there are records of human activity on the island dating back much further than this, as yet there is no evidence to suggest there was any settlement on the island prior to 635. Archaeological finds, of struck flint, in the claggy, sandy dune land of the island date back to 8,000 BC, the Mesolithic period (Magnusson 1985). The coastal profile of the Island at O.D. has not changed significantly for at least 500 years (Garson 1985), although today the island is accessible by a causeway from the Northumberland coast which is flooded for about five hours at high tide.

Sand dunes are unique in that they are one of only a few ecosystems in our present landscapes in which the full successional cycle through time is exhibited by changes in patterns through space. On the Snook area of Lindisfarne it is possible to see successional stages of sand dune vegetation from very young, mobile dunes, through large yellow dunes, to fixed, grey dunes and dune slack. The Shiel is a narrow neck of dunes that joins the Snook to the main mass of the Island. In this area dunes are primarily yellow dunes or young dune; there is not a complete successional gradation and the system has only reached the later yellow dune stage.

The dunes at Lindisfarne are up to 15m high on the Snook and on the Shiel some are greater than 20m. They are formed over boulder clay and limestone outcrops and are largely covered in *Ammophila arenaria* and so are relatively stable. The Snook's low-lying slacks remain moist in the driest summers and may be inundated with water for six months in a wet year.

While the yellow and, to some extent, the fixed dunes of Lindisfarne are relatively species poor the slacks, which cover much of the Snook, are unusually diverse. This dune system is also the site of the largest population of the invasive species under study in this project, *Acaena novae-zelandiae*.

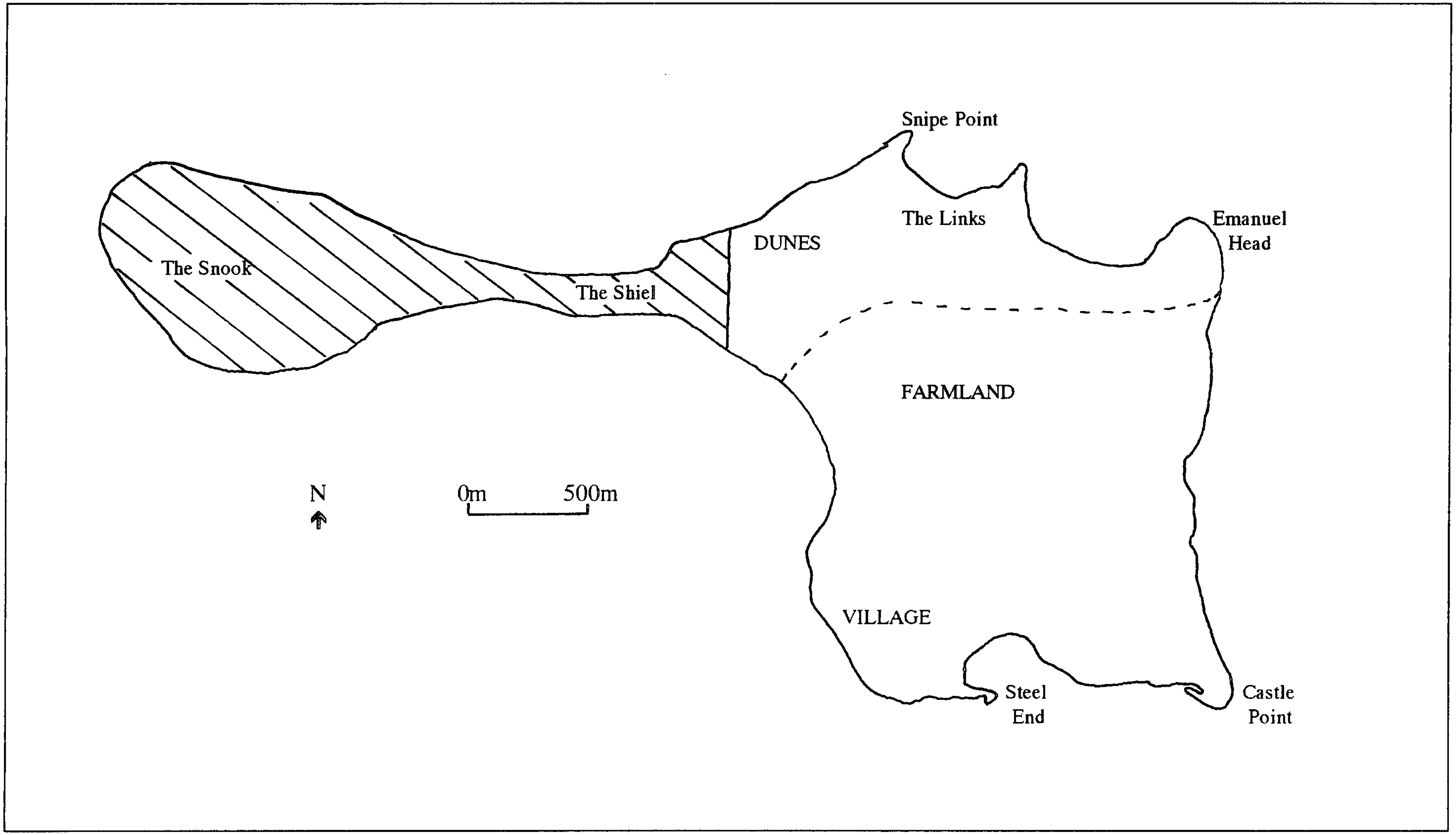

Figure 2.1 - Map of Lindisfarne (Holy Island), showing the extent of the study site (shaded).

3. METHODS

This study involved field work to map the distribution of *Acaena novae-zelandiae* on Lindisfarne as it is found at present and the collection of habitat variables that might affect *Acaena* distribution. Previous maps of *Acaena* distribution were examined to compare changes in distribution over time.

Field Data

The mapping of *Acaena* distribution in the field was carried out by first producing 25m x 25m a grid which was overlaid on an enlarged contour map of the Snook and Shiel of Holy Island, the study area. Fieldwork involved taking vegetation samples from 1m x 1m quadrats at each point on the grid. The correct course across and along the island was maintained by using a compass to keep on a direct bearing north to south and the west to east (or vice versa) respectively at each 25m interval. Each quadrat was numbered, and that number recorded on the grid. In this way, for each quadrat its position on the island could easily be determined and later plotted on a map. In total data for 1709 quadrats were collected.

At each quadrat point several variables were recorded; percentage cover of *Acaena*, *Ammophila arenaria* and bare ground within each 1m x 1m quadrat. Spatial distribution of *Acaena* was also recorded on a scale of 1-5, where:

1 = one small patch (not more than 5% of the quadrat),
2 = several small patches (each one not more than 5% of quadrat),
3 = one large clump (5-30% of the quadrat),
4 = several large clumps (each clump 5-30% of quadrat),
5 = large mat of continuous cover (greater than 30% of quadrat).

Some attempt was made to classify the dune type and habitat in which the quadrat occurred:

1 = young, mobile dune,
2 = young dune by causeway structure (southern edge of the island),
3 = yellow dune slope,
4 = yellow dune habitat on level ground (dune top or lower ground),
5 = fixed dune slope,
6 = fixed dune habitat on level ground,
7 = dune - slack transitional habitat,
8 = dry or grassy slacks,
9 = damp or wet slack.

For some of the statistical analysis habitat categories 3 and 4, 5 and 6, and 8 and 9 were amalgamated to produce a series of new habitat categories (1-6). The major species in each 1m x 1m quadrat were recorded as was aspect. Aspect was recorded in categories form zero to eight, where zero represents level ground (i.e. without aspect) and one to eight represent 45^{o} bearings around the compass starting at North.

Map Generated Data

This involved overlaying the 25m by 25m grid used in this survey on the maps produced by earlier surveys and at each grid point recording the presence or absence of *Acaena*. In this way corresponding points on each map could be achieved and equivalent maps showing presence or absence of *Acaena* in three different years (1965, 1978 and 1994) could be produced. As a result, data from these three years could be compared.

The 25m by 25m grid was also overlaid on the National Vegetation Classification map produced for Lindisfarne (Woolven & Radley 1988). By doing this a rough estimate of the NVC class/habitat type at each quadrat point could be obtained and recorded.

Map Production

Maps of the distribution and changes in distribution of *Acaena* were produced using three dimensional surface graphs in Microsoft Excel.

Statistical Analysis

Chi-squared tests and correlations were performed on the quadrat data to analyse the relationships between these habitat variables and to see whether any of them differed to a greater or lesser extent than expected. Principle Component Analysis was also performed on the variable data to attempt to identify the principle factors responsible for the distribution and abundance of *Acaena*. Multiple regression was carried out to produce a model predicting *Acaena* distribution at each site according to the attributes of that site with respect to the other variables.

4. RESULTS

4.1 Distribution of *Acaena*

A map of *Acaena* abundance (scaled into categories) showed a definite pattern to *Acaena* distribution (Figure 4.1). Very high densities of *Acaena* are found on the Shiel, with a more scattered distribution and generally lower abundance to be found on the Snook. When compared with a map of the topological features of the dunes at Lindisfarne (Figure 4.2) *Acaena* distribution shows greater abundances on areas of high dunes, especially those at the edges of the Snook and on the Shiel; these consist mainly of yellow dunes. Far less *Acaena* appears to be found in low-lying (slack) areas.

In order to compare the changes of distribution in the data obtained from 1965 to 1994 maps of simply presence or absence had to be produced since no detailed data were available with regards to absolute abundance. Presence/absence data were available from surveys carried out in 1965 (Hargreaves and Peach 1965), 1977 (Culwick 1982) and from this survey (1994); maps could therefore be produced for these three years (Figures 4.3, 4.4 and 4.5). The size of map produced in the 1965 survey meant that only 1324 quadrats were represented rather than the 1709 quadrats collected in 1994 and taken from Culwick's map of 1977; the 1965 map is smaller than those for 1977 and 1994. This series of maps show a clear pattern of overall increase in *Acaena* between 1965 and 1994.

While Figures 4.3, 4.4 and 4.5 show obvious overall increases in *Acaena* between 1965 and 1977, and 1977 and 1994, it is also possible to see that there are some areas of the study site in which *Acaena* appears to be decreasing between these years. To highlight areas change between 1965 and 1977, and then 1977 and 1994 separate maps were drawn to show the areas of increasing and decreasing *Acaena* between these years (Figure 4.6 and 4.7).

As expected both Figures 4.6 and 4.7 show a far greater area of increasing *Acaena* than decreasing. The maps also show a fairly random distribution throughout the study site of areas of both increasing and decreasing *Acaena*, with possibly a slight bias towards the Shiel and edges of the island in terms of increasing *Acaena*.

Tabulating the exact number of quadrats in which *Acaena* is increasing and decreasing allows a more quantitative assessment of the changes in *Acaena* distribution between 1965 and 1994 (Table 4.1). From Table 4.1 it is possible to see that, surprisingly, there is a greater increase in the total number of quadrats with *Acaena* in

4. RESULTS

4.1 Distribution of *Acaena*

A map of *Acaena* abundance (scaled into categories) showed a definite pattern to *Acaena* distribution (Figure 4.1). Very high densities of *Acaena* are found on the Shiel, with a more scattered distribution and generally lower abundance to be found on the Snook. When compared with a map of the topological features of the dunes at Lindisfarne (Figure 4.2) *Acaena* distribution shows greater abundances on areas of high dunes, especially those at the edges of the Snook and on the Shiel; these consist mainly of yellow dunes. Far less *Acaena* appears to be found in low-lying (slack) areas.

In order to compare the changes of distribution in the data obtained from 1965 to 1994 maps of simply presence or absence had to be produced since no detailed data were available with regards to absolute abundance. Presence/absence data were available from surveys carried out in 1965 (Hargreaves and Peach 1965), 1977 (Culwick 1982) and from this survey (1994); maps could therefore be produced for these three years (Figures 4.3, 4.4 and 4.5). The size of map produced in the 1965 survey meant that only 1324 quadrats were represented rather than the 1709 quadrats collected in 1994 and taken from Culwick's map of 1977; the 1965 map is smaller than those for 1977 and 1994. This series of maps show a clear pattern of overall increase in *Acaena* between 1965 and 1994.

While Figures 4.3, 4.4 and 4.5 show obvious overall increases in *Acaena* between 1965 and 1977, and 1977 and 1994, it is also possible to see that there are some areas of the study site in which *Acaena* appears to be decreasing between these years. To highlight areas change between 1965 and 1977, and then 1977 and 1994 separate maps were drawn to show the areas of increasing and decreasing *Acaena* between these years (Figure 4.6 and 4.7).

As expected both Figures 4.6 and 4.7 show a far greater area of increasing *Acaena* than decreasing. The maps also show a fairly random distribution throughout the study site of areas of both increasing and decreasing *Acaena*, with possibly a slight bias towards the Shiel and edges of the island in terms of increasing *Acaena*.

Tabulating the exact number of quadrats in which *Acaena* is increasing and decreasing allows a more quantitative assessment of the changes in *Acaena* distribution between 1965 and 1994 (Table 4.1). From Table 4.1 it is possible to see that, surprisingly, there is a greater increase in the total number of quadrats with *Acaena* in

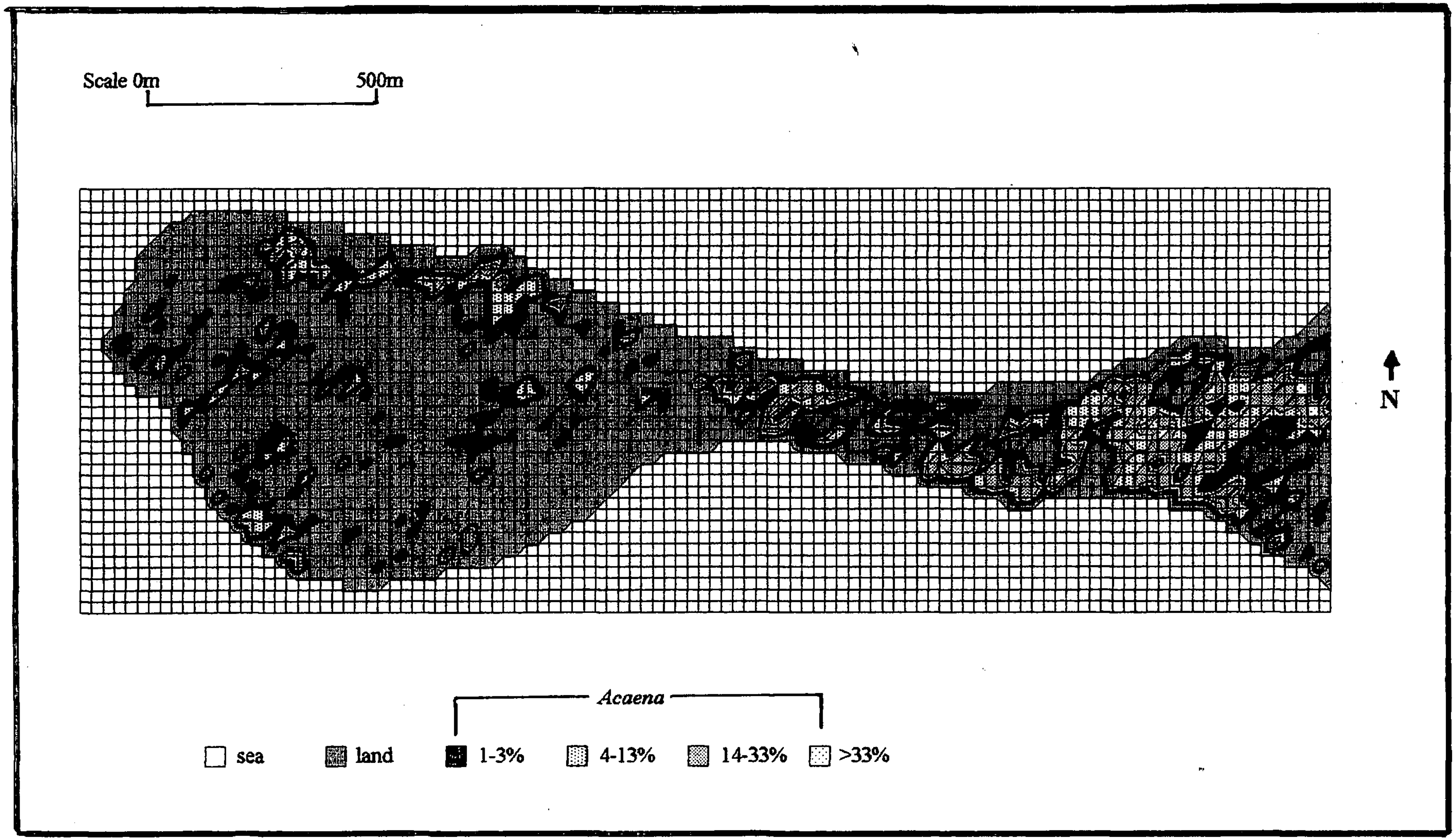

Figure 4.1 - Distribution of *Acaena* (in scaled categories) on the Snook and Shiel of Lindisfarne Island in 1994.

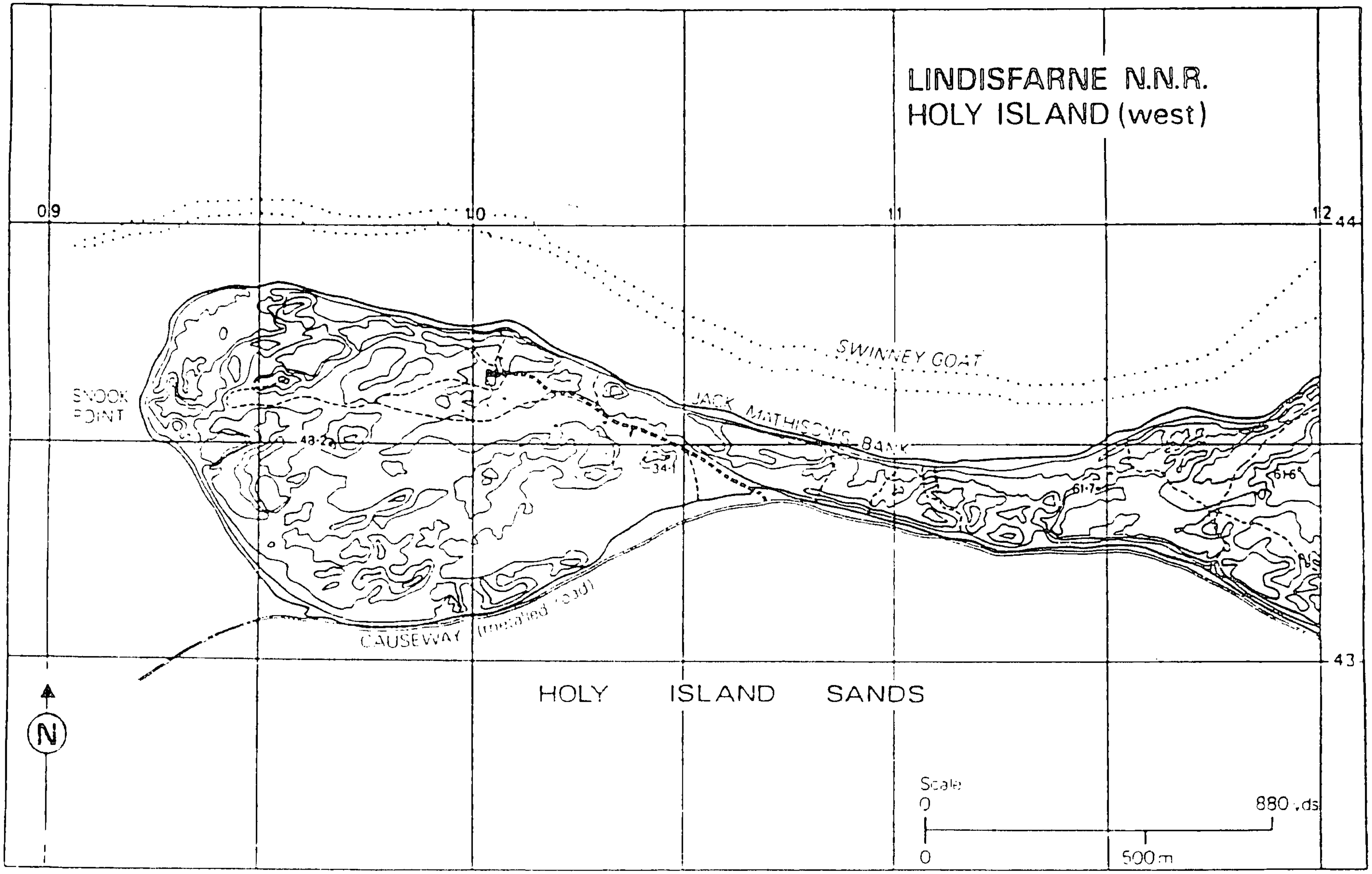

Figure 4.2 - Contour map of the Snook and Shiel of Lindisfarne Island.

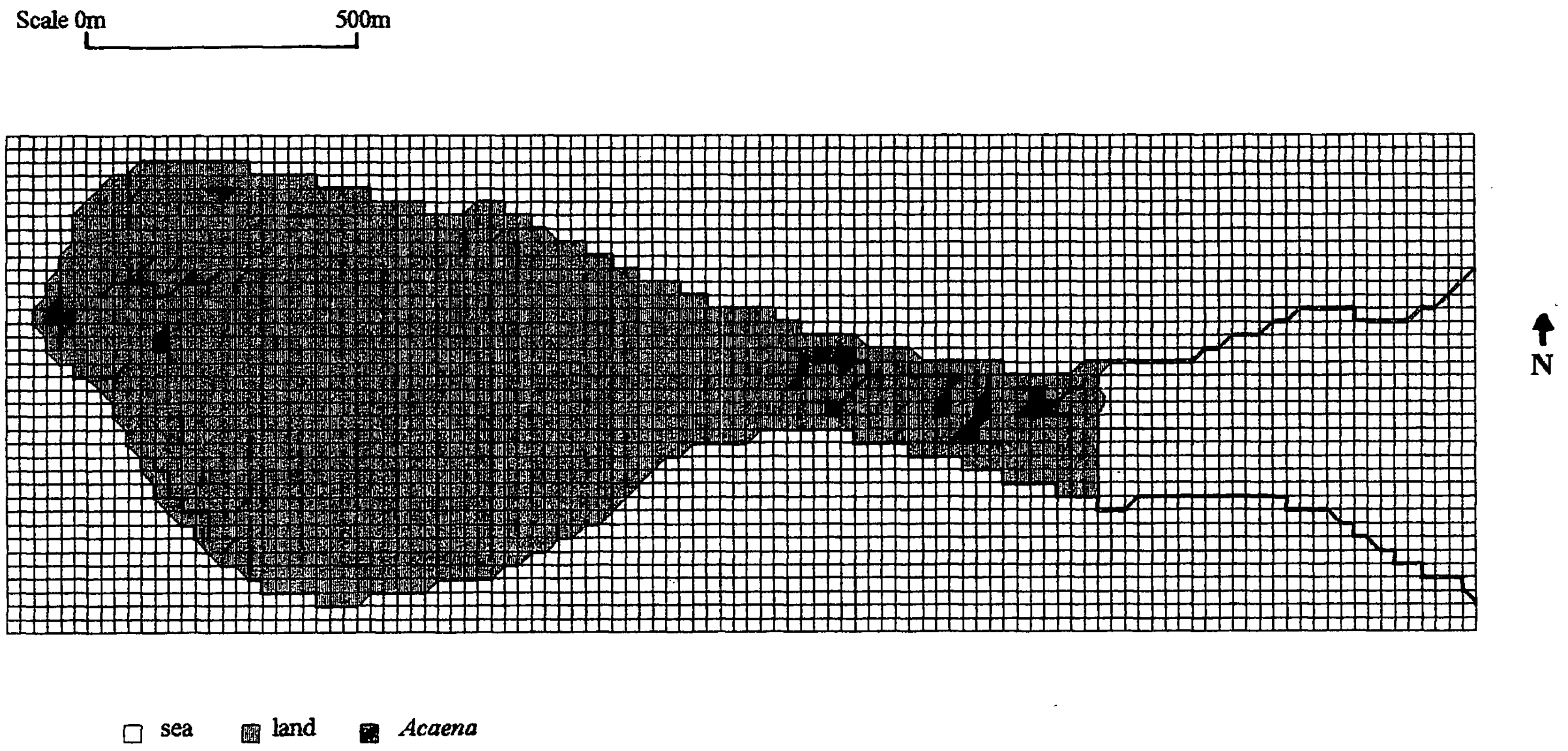

Figure 4.3 - Areas of *Acaena* presence on the Snook of Lindisfarne Island in 1965.

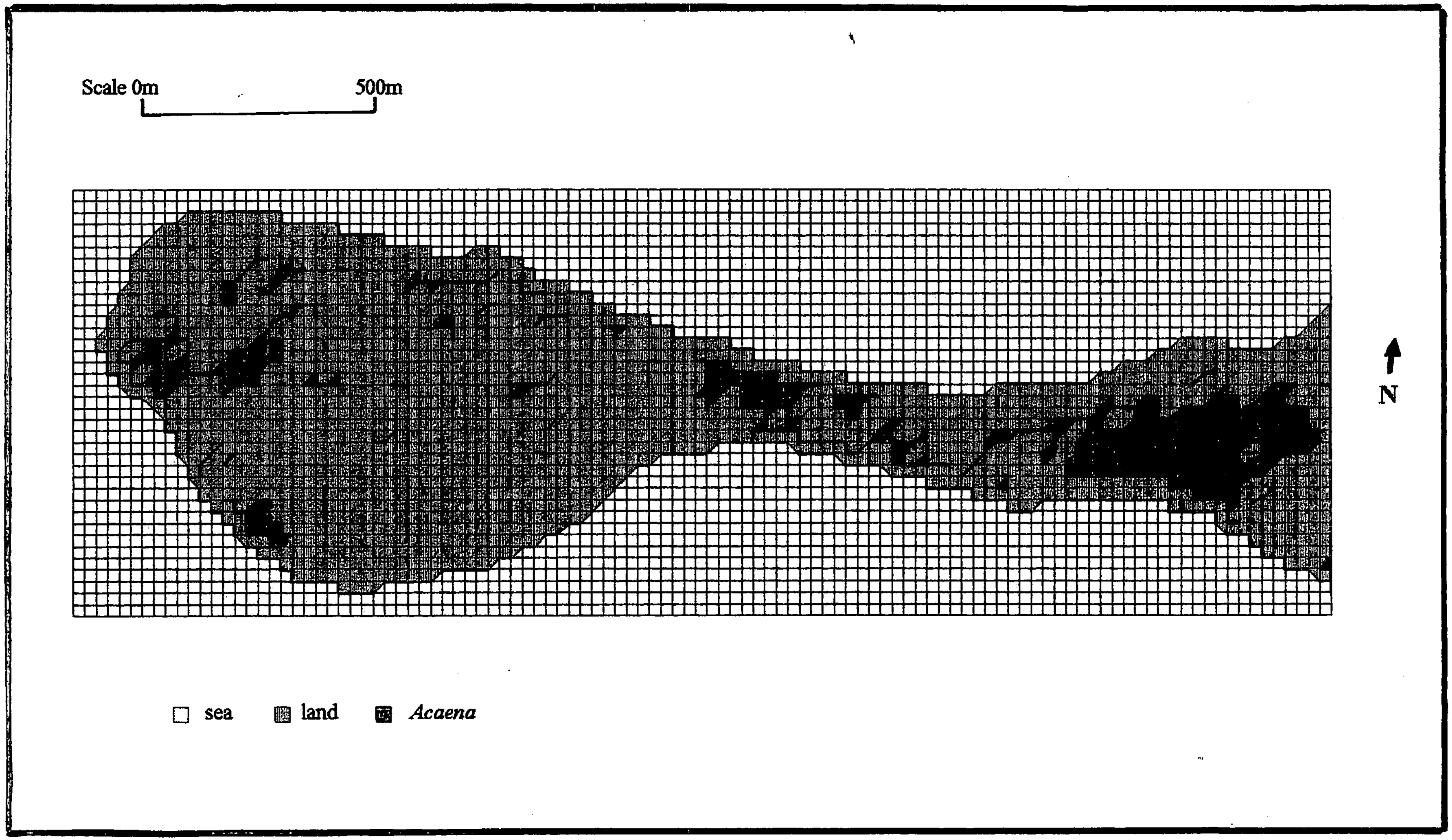

Figure 4.4 - Areas of *Acaena* presence on the Snook and Shiel of Lindisfarne Island in 1977.

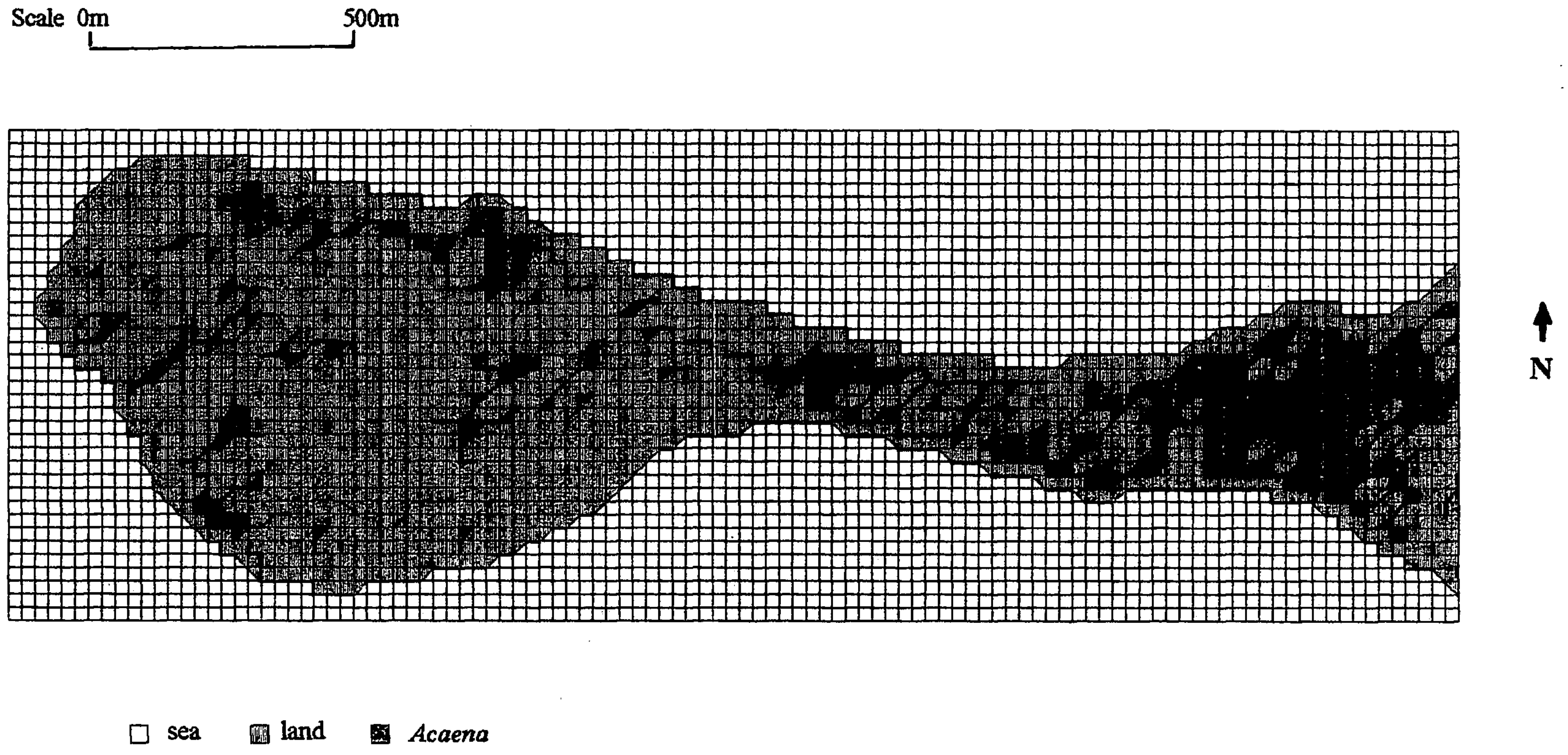

Figure 4.5 - **Areas of *Acaena* presence on the Snook and Shiel of Lindisfarne Island in 1994.**

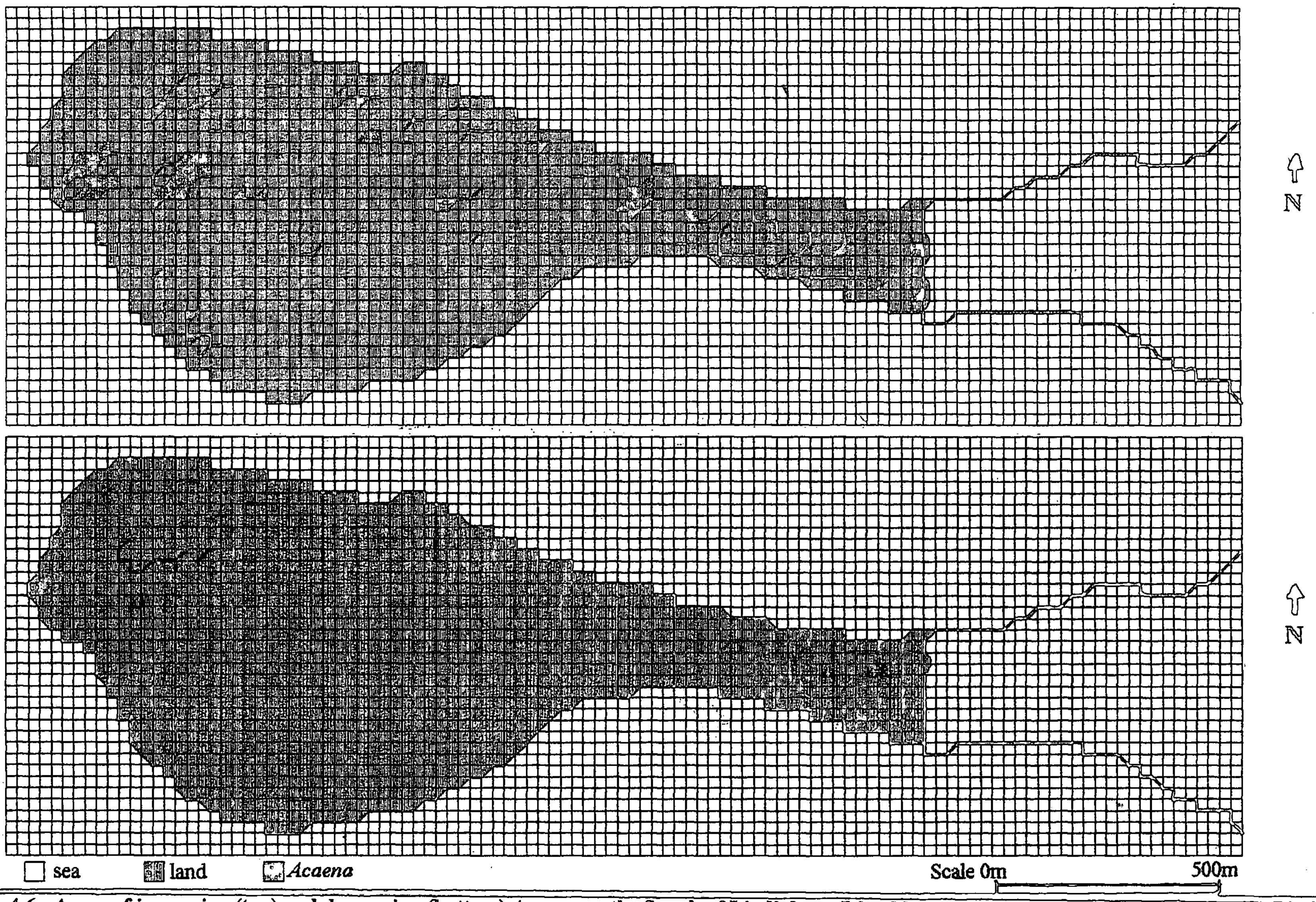

Figure 4.6 - Areas of increasing (top) and decreasing (bottom) *Acaena* on the Snook of Lindisfarne Island between 1965 and 1977.

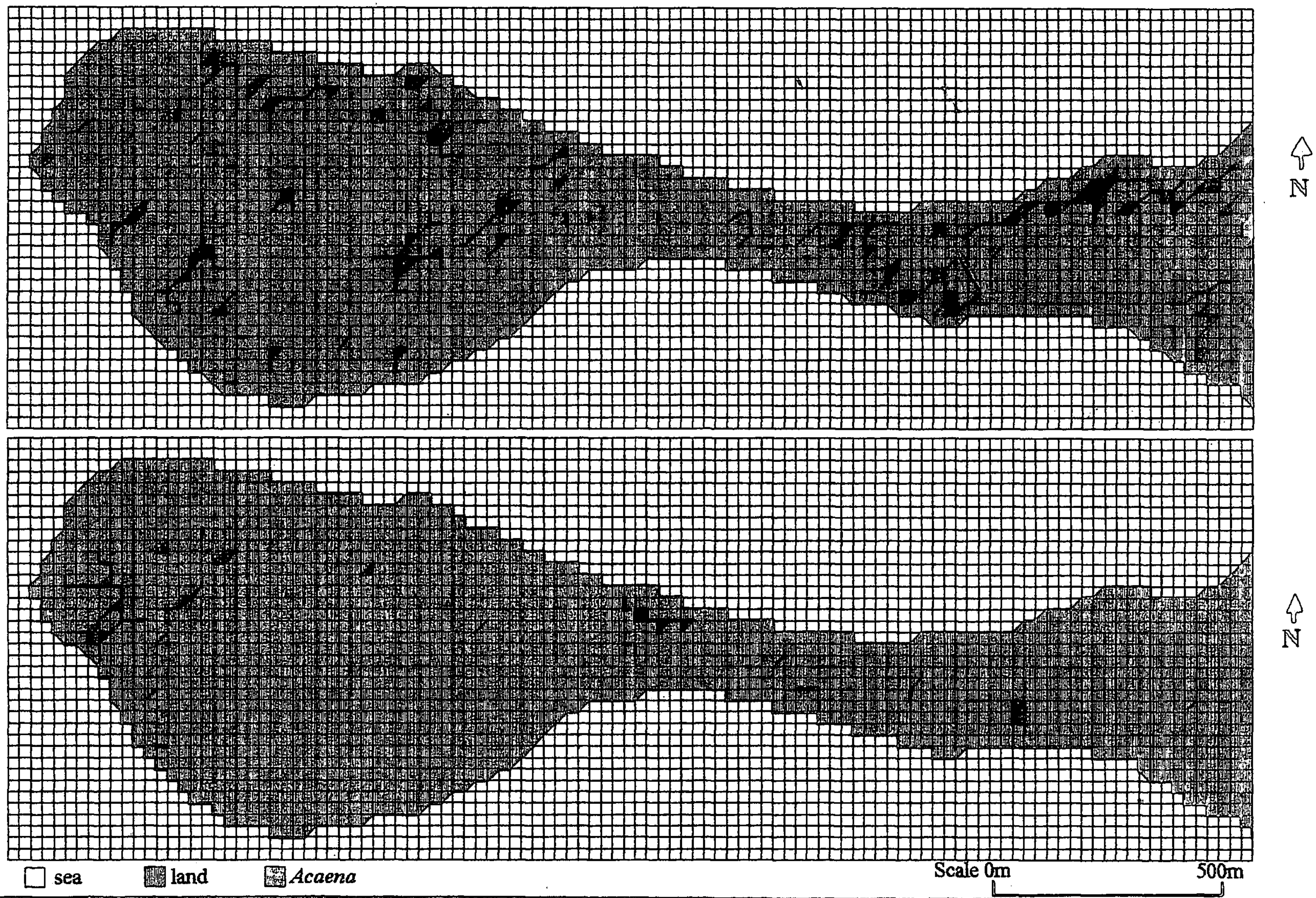

Figure 4.7 - Areas of increasing (top) and decreasing (bottom) *Acaena* on the Snook and Shiel of Lindisfarne Island between 1977 and 1994.

between 1977 and 1994 than between 1965 and 1977. The difference calculated per year, however, shows an increase of 10.1 quadrats per year between 1965 and 1977 compared with only 8.1 quadrats per year between 1977 and 1994.

Table 4.1 - Total number of quadrats in which *Acaena* increases, decreases or exhibits no change between 1965, 1977 and 1994. For quadrats exhibiting no change samples are split into those with and those without *Acaena* present.

	Number of quadrats				
Year	**No change (*Acaena*)**	**No change (no *Acaena*)**	**Increasing**	**Decreasing**	**Total increase**
1965-1977	74	915	228	107	121
1977-1994	173	756	266	129	137
1965-1994	86	790	353	95	258

4.2 Rate of Spread of *Acaena*

Once the maps of *Acaena* distribution, and of the changes in that distribution, had been produced analysis was carried out to relate the overall increases in *Acaena*, from 1965 to 1994, to rate of spread. For this analysis only data from 1324 quadrats were used rather than the total 1709 so that the 1965 data could be included in the analysis. To give a picture of the rate of spread of this invasive species the square roots of the areas occupied by *Acaena* in 1965, 1977 and 1994 were represented graphically (Figure 4.8)

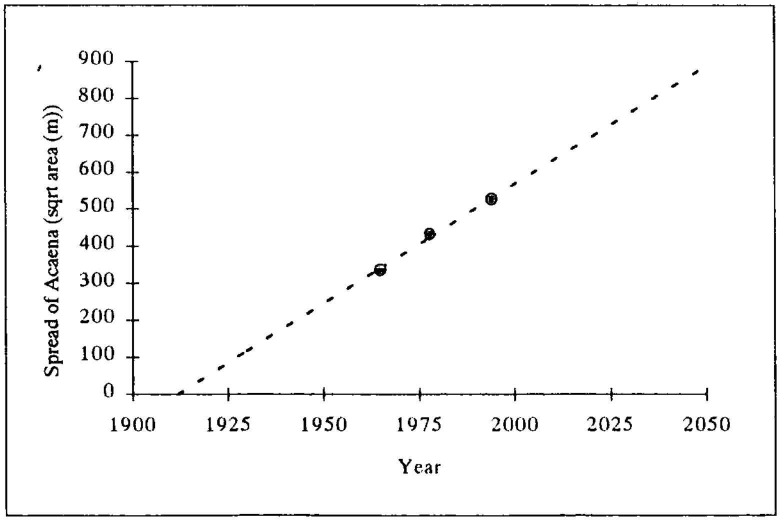

Figure 4.8 - The square root of the area occupied by *Acaena* in 1965, 1977 and 1994. A regression line has been fitted (this line takes them form $y = 6.43x - 12295.7$, for which $r^2 = 0.99$).

Although there are only three data points on the graph the regression line is a relatively good fit, as indicated by an r^2 value of 0.99. The goodness of fit of a straight line would indicate that rate of spread has been relatively constant between 1965 and 1994, with a rate of approximately 41.4m^2 per year. When the regression line is extrapolated out it is found to cross the x-axis at about the year 1912. If it is assumed that rate of spread has been constant since *Acaena* first invaded this values represents the probable time of the species introduction into the area.

The next step in the investigation into the invasion dynamics of *Acaena* was to attempt to record the number of new colonisation events in each of the three years that data were ~~was~~ available for. The aim of this exercise was to see whether the increases in range by *Acaena* were by vegetative growth in areas where *Acaena* was already present or by colonization of new areas by seed, or both. To do this isolated patches of *Acaena* were recorded; an isolated patch, or fo~~ci~~us, is defined as one or two adjacent quadrats with *Acaena* present completely surrounded by quadrats without any *Acaena*. In this way areas of *Acaena* that could only have established by colonization events from seed were defined. Number of foci was then plotted against time (Figure 4.9).

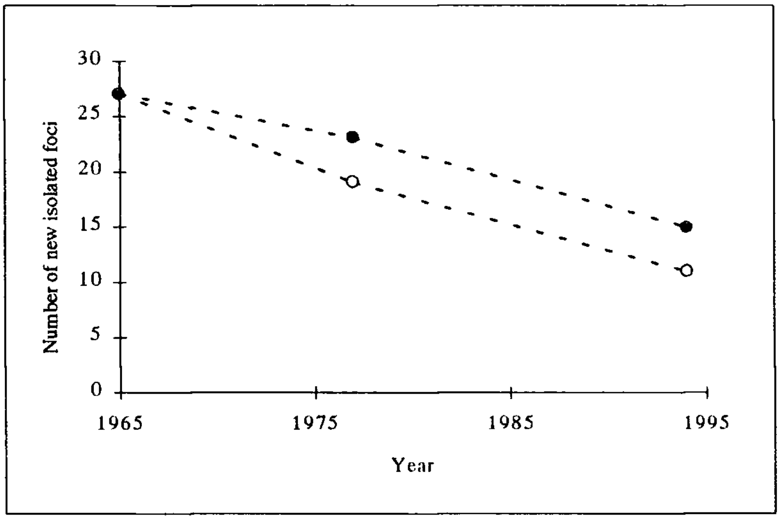

Figure 4.9 - The number of isolated foci recorded in 1965, 1977 and 1994. Closed circles represent the total number of foci recorded whilst open circles are foci recorded in areas where they were not present in any of the previous years.

Number of foci is steadily decreasing between 1965 and 1994; by 1994 the number has dropped to approximately half the level exhibited in 1965. Although *Acaena* is spreading to cover a greater area of Lindisfarne, the number of new colonisation events is actually falling. This suggests that *Acaena* is spreading more by vegetative expansion than through the distribution of seed.

4.3 National Vegetation Classification Data

Overlaying the 25m × 25m grid on a map of NVC habitat types produced information on the amount of the study site represented by each of the NVC categories (Woolven & Radley 1988) present in the study area (codes and habitat descriptions for NVC data are found in Appendix 1). This data is presented with the proportion of each NVC category on the study site that is covered by *Acaena* (Table 4.2). To show the trends in *Acaena* abundance in relation to successional stage a further histogram has been produced in which NVC classes are amalgamated into broader, successional categories (Figure 4.10).

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Table 4.2 - Number of quadrats represented by each NVC category present in the study site and the proportion of those quadrats that have *Acaena* present.

? number with Acaena

NVC Code	Habitat Description	No. of quadrats	% with *Acaena*
SD10d	Dune grassland, many bryophytes, few vascular sp.	426	260
SD10L	Dune grassland, lichen rich.	157	60
SD10	Dune grassland, undifferentiated.	138	26
SD16	*Potentilla - Carex* slack (calc. sand, acidic water).	133	7
SD6f	*Ammophila* dune (*Poa* understory).	111	62
SD9/10	Foredune - undifferentiated grassland transition.	106	53
DG	Undifferentiated dune grassland.	77	56
SD15d	*Salix - Holcus* slack (often dune-slack interface).	75	12
SD10/MG1.1	Tall, species poor dune grassland.	57	34
SD9	*Ammophila - Ononis* dune, undifferentiated.	55	21
SD8	*Leymus - Ammophila* dune, also present is Couch.	41	22
SM	Saltmarsh.	37	2
SD15	*Salix - Holcus* undiff. slack (low salinity, high Ca).	36	11
SD10/15	Transitory stage, dune to slack.	36	2
SD6a/b	*Ammophila* dune, high sand deposition.	33	5
T26	Sparsely vegetated, stabilized shingle.	27	24
SD6e	*Ammophila* dune (*Festuca* understory).	25	18
SM/SD15/16	Saltmarsh - slack transition communities.	24	1
T25	Narrow dune-saltmarsh transition.	20	7
T10	Tall-species poor grassland.	20	0
SD14(a)	*Ammophila - Phleum* dune.	17	9
T21	Saltmarsh - dune transition.	16	0
T7	Transitional vegetation (dune-slack).	14	6
SD5	*Elymus farctus* foredune	14	5
SD10/14	Dune grassland, *Ammophila - Phleum* transition.	11	3
T18	Sparsely vegetated, exposed shingle.	8	1
T23	Sparsely vegetated, eroding sand cliff.	7	4
SD7a	*Leymus arenarius* dune - open community.	6	5
T1	Sparsely vegetated, exposed shingle.	5	0
BS	Bare sand.	4	3
BSH	Bare shingle.	4	3
T34	Dune influence lacking, cliff exposure clay.	4	3
BG	Bare ground.	2	1
T8	Water filled slack.	2	0
T16	Pool with approx. 10cm water.	2	0
T4	Very wet slack.	1	0
T27	Fenced bare sand blowout.	1	0
T97	Wet area.	1	0

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The largest area covered by a single category on study site is the habitat type SD10d, which is a class of dune grassland rich in bryophytes and lichens, with few vascular plants. Also very common is SD10L, another type of dune grassland (with a lichen-rich sub-community) and SD10, also dune grassland. The relatively acidic slack habitat SD16 is the fourth commonest type.

Acaena is found in high proportions on sparsely vegetated ground and dune grassland types. Far less is found in slack communities, especially very wet slacks, and in saltmarsh areas. Very exposed habitats also appear to be low in *Acaena*. It is interesting to note that there are in fact very few NVC habitats that have no *Acaena* in at all.

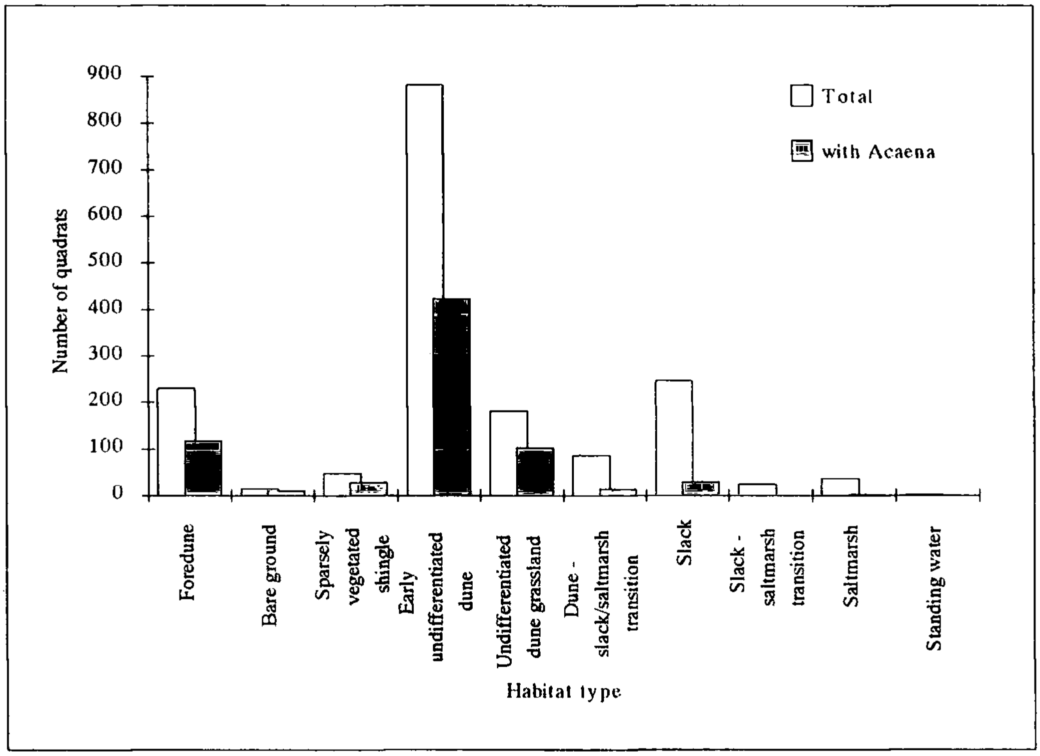

Figure 4.10 - Number of quadrats in the total sample represented by the successional stages defined from the NVC data and the number of quadrats in each of these stages in which *Acaena* is present.

combined ?

When the NVC habitats are split into broader successional categories the most common category is that of early undifferentiated dune; slacks, foredune and undifferentiated dune grassland are also quite common. *Acaena* is seen to be far more abundant in the earlier stages of the successionary cycle, than in the more stabilized habitats. The most densely covered habitats are bare ground, vegetated shingle and undifferentiated grassland. The lack of samples for these first two categories might lead to errors; it is likely that *Acaena* is most abundant on the undifferentiated dune.

Where *Acaena* was relatively abundant (present in greater than five quadrats), and known to be increasing within an NVC category, graphs were produced of the square root of the area covered by *Acaena* in each of the three years (Figure 4.11(a) to (l)). From these graphs information about the rate of spread in these NVC categories could be investigated.

It is possible to see from Figure 4.11 that in general *Acaena* is increasing in each of these habitat categories, but not with the same consistency as the overall increase in *Acaena*. Although this may be due to the much smaller numbers of samples involved. Most of the increase is to be seen in the dune grassland habitats as would be expected, but in some of these habitats the area of *Acaena* is beginning to level off and even appears to be dropping in some cases (SD9, SD9/10and SD10d).

More unexpected are the large increases in *Acaena* seen in Figure 4.11 (j) and (k). These are both slack categories (SD15 and SD15d) and here *Acaena* appears to be spreading rapidly. The third slack category (SD16) shows a relatively stable *Acaena* cover, as does the transitory stage between slack and dune (T7).

Table 4.3 shows the numbers of new foci recorded for these twelve NVC categories in the three different years that data ~~is~~ are available for. Despite a general increase in *Acaena* in the majority of these classes, the number of foci in virtually all cases decreases or remains approximately the same. Unfortunately a lack of samples in the data reduces the significance of any conclusions that might be drawn from such data.

Table 4.3 - Number of new foci found in the years 1965, 1977 and 1994 for twelve of the NVC categories represented on the study site.

Vegetation Type		**Year**	
	1965	**1977**	**1994**
SD6f	3	1	0
SD9	1	0	0
SD9/10	0	1	0
SD10	3	3	4
SD10d	5	3	4
SD10L	5	2	3
SD10/14	1	0	0
DG	3	0	0
T7	2	0	0
SD15	0	2	1
SD15d	0	1	0
SD16	4	1	0

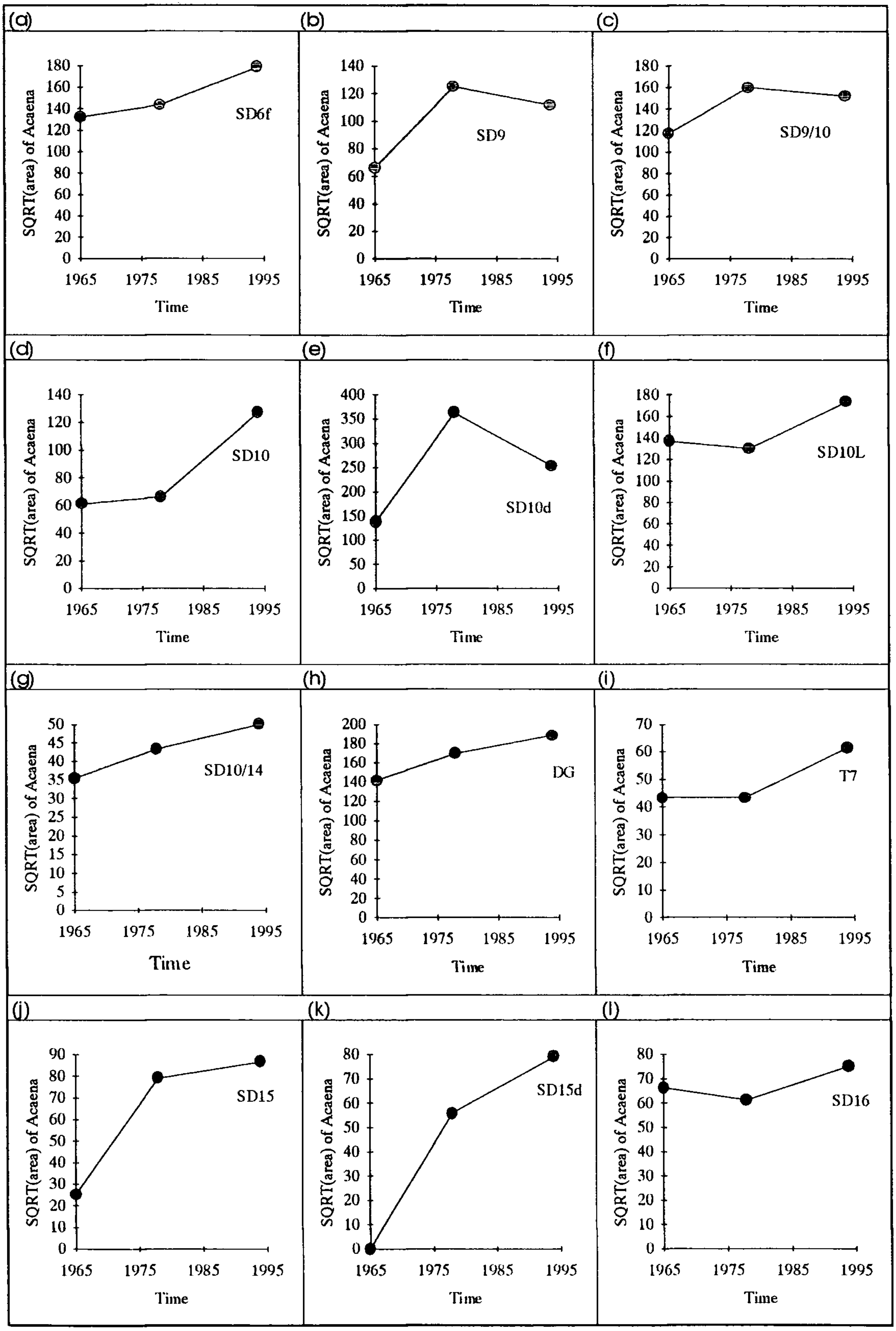

Figure 4.11 - The rate of increase in *Acaena* in different NVC categories (a) to (l), where rate of increase is measured as the change in the square root of the area occupied with time.

4.4 Habitat Variables

Correlations among the habitat variables recorded in the field were undertaken. A general correlation was performed on the entire data set, involving eight variables, using both raw and ranked data (Tables 4.4 & 4.5).

Table 4.4 - Correlation values for the unranked data from the eight variables collected in the field. The sample size is 1652 and any result >0.062 is significant at the 5% level, results of >0.081 are significant at the 1% level. Significant values are marked in bold.

	% *Acaena*	*Acaena* dist.	Habitat type	Aspect	War-ren	Path	%*Amm-ophila*	%Bare ground
% *Acaena*	1							
Acaena distribution	**0.834**	1						
Habitat type	**-0.221**	**-0.292**	1					
Aspect	**0.221**	**0.273**	**-0.270**	1				
Warren	-0.027	0.053	-0.040	**0.102**	1			
Path	**0.268**	**0.297**	**-0.179**	0.003	0.036	1		
% *Ammophila*	**0.092**	**0.182**	**-0.640**	**0.193**	**-0.150**	0.037	1	
Bare ground	-0.026	-0.033	**-0.360**	**0.086**	0.045	0.024	-0.029	1

Table 4.5 - Correlation values for the ranked data from the eight variables collected in the field. The sample size is 1652 and significant values are marked in bold.

	% *Acaena*	*Acaena* dist.	Habitat type	Aspect	War-ren	Path	%*Amm-ophila*	%Bare ground
% *Acaena*	1							
Acaena distribution	**0.929**	1						
Habitat type	**-0.261**	**-0.263**	1					
Aspect	**0.276**	**0.273**	**-0.283**	1				
Warren	0.033	**0.078**	0.045	**0.097**	1			
Path	**0.308**	**0.296**	**-0.168**	0.003	0.036	1		
% *Ammophila*	**0.251**	**0.270**	**-0.650**	**0.256**	**-0.113**	**0.069**	1	
% Bare ground	0.055	0.056	**-0.390**	**0.161**	**0.133**	0.060	**0.074**	1

Tables 4.4 and 4.5 show a large number of significant correlations between the eight recorded variables. *Acaena* shows relationships that are significant at the 1% level with five of the other seven variables. The only variables *Acaena* is not significantly correlated with are warren and bare ground. When both ranked and unranked data are used *Acaena* is seen to be negatively related to habitat type, indicating the *Acaena* is most abundant in the earlier successional stages and less abundant in the later stages.

Acaena and *Ammophila* are positively correlated, this relationship becomes more significant when ranked values are used. This might suggest that the variables are not linearly related. *Ammophila* is related to all the other variables which might suggest that the way in which *Ammophila* affects *Acaena* will be complex and itself affected by the relationship between *Ammophila* and the other variables.

There is a significant, positive correlation between *Acaena* and the presence of paths, which are negatively related to habitat type just as *Acaena* is. Aspect is also positively related to *Acaena*, as well as being positively correlated to *Ammophila* and negatively related to habitat in the same way as *Acaena* is.

Acaena distribution and percentage cover of *Acaena* are very highly correlated and distribution is correlated with the other variables in a very similar way to *Acaena* itself. When percentage cover of *Acaena* is plotted against mean distribution score (Figure 4.12) it is seen that as the percentage cover of *Acaena* within a quadrat increases so the distribution score of *Acaena* changes. At higher abundances larger clumps of *Acaena* exist and small patches become far less common. *Acaena* spreads in such a way that at higher abundances, rather than finding lots of small patches of *Acaena*, there are a few large patches; an increase in the size of the patches already present occurs, not a increase in the number of small patches. This suggests that *Acaena* is exhibiting clonal growth rather than dispersing to new areas and growing there.

This large number of significant correlations shows that it is likely that all these variables are important in explaining the distribution and abundance of *Acaena*. Although the way in which they do so is likely to be complex and with just the correlation values it is difficult to interpret these relationships correctly. It is, therefore, necessary to look at the relationships between the variables in more detail.

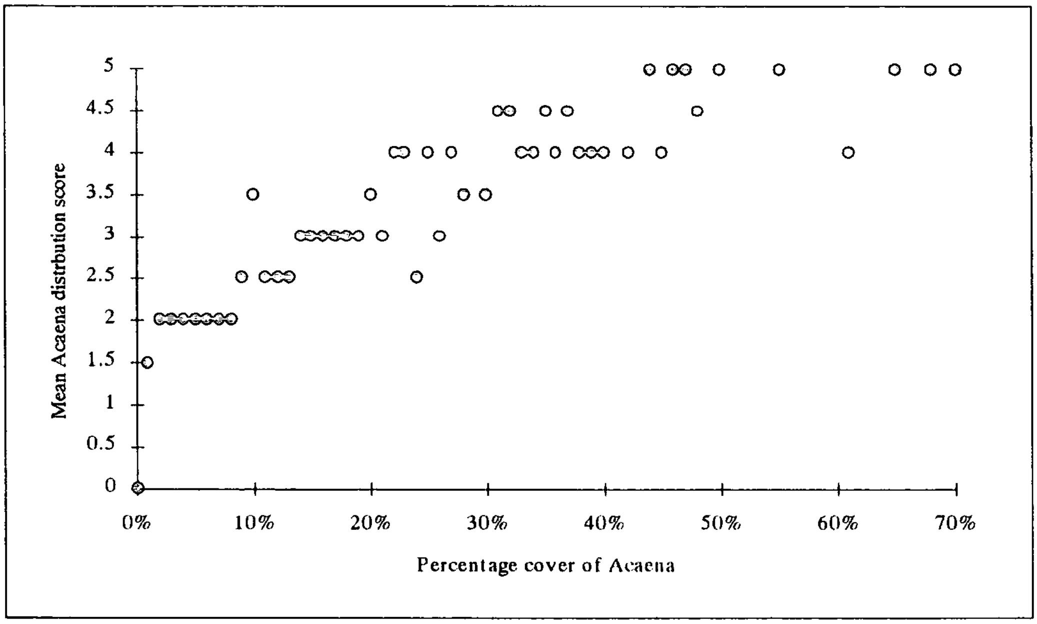

Figure 4.12 - The average distribution score is plotted for each percentage of *Acaena* recorded.

Habitat

Habitat shows significant correlations with the abundances of *Acaena, Ammophila* and bare ground. There is also a significant relationship with the presence of paths, although not with warrens. The percentage of quadrats occupied by each of these variables within each habitat type is shown in Figure 4.13. *Acaena* shows a decrease in presence in the slack habitat and to some extent the transitional stage, this drop in presence is also exhibited by the other four variables. Other than a reduction of presence at this late stage in the successional cycle there appear to be no similarities between the patterns of the four variables and *Acaena*, except between *Acaena* and path. The presence of paths and *Acaena* through out the successional cycle appear to mirror one another; both show reduced densities both in the slacks and young dune habitats, and peak in the yellow dune habitat.

When these relationships are investigated further using Chi-square tests it is possible to see that the observed presence of *Acaena* differs significantly from the expected in virtually all habitat types ($\chi^2_{(5)}$ = 509.47, significant at the 0.1% level; full Chi-square tables in Appendix 2). If a Chi-square analysis is also undertaken between path and habitat type the results are significant ($\chi^2_{(5)}$ = 175.26, which is significant at the 0.1% level) and the table of Chi-square values (Appendix 2) follows a very similar pattern to that of the analysis between *Acaena* and habitat. *Acaena* and path are both less common than expected in the young dunes, dune-slack transition and slack itself, with a greater presence than expected in the yellow and fixed dunes. Observed and expected values are approximately equal in the causeway dunes for both *Acaena* and path presence.

These similarities in distribution suggest that the way in which *Acaena* is distributed within habitats may be affected by the presence of paths or that the presence of *Acaena* near paths is an effect of habitat type. The relationships between habitat type and the other three variables do not show the same patterns as the relationship between *Acaena* and habitat, although each variable shows a significant difference between the observed and expected with regards to presence and absence (tables in Appendix 2), even warren. This suggests that the way in which *Ammophila*, bare ground and warren all interact with *Acaena* is not directly related to habitat. With the possible exception that where *Acaena* is absent these variables may also often be at reduced densities due to the fact that all four variables are at lower abundances in the slack habitat.

In order to get a clear picture of the changes in abundances of *Acaena*, *Ammophila* and bare ground over the successional cycle exhibited in the dunes a graph was produced to show mean percentage cover of each of these variables at each stage (Figure 4.14). For this graph the habitat category of causeway dune has been left out because it does not fit into the successional cycle; possibly because of effects exerted by the causeway structure itself.

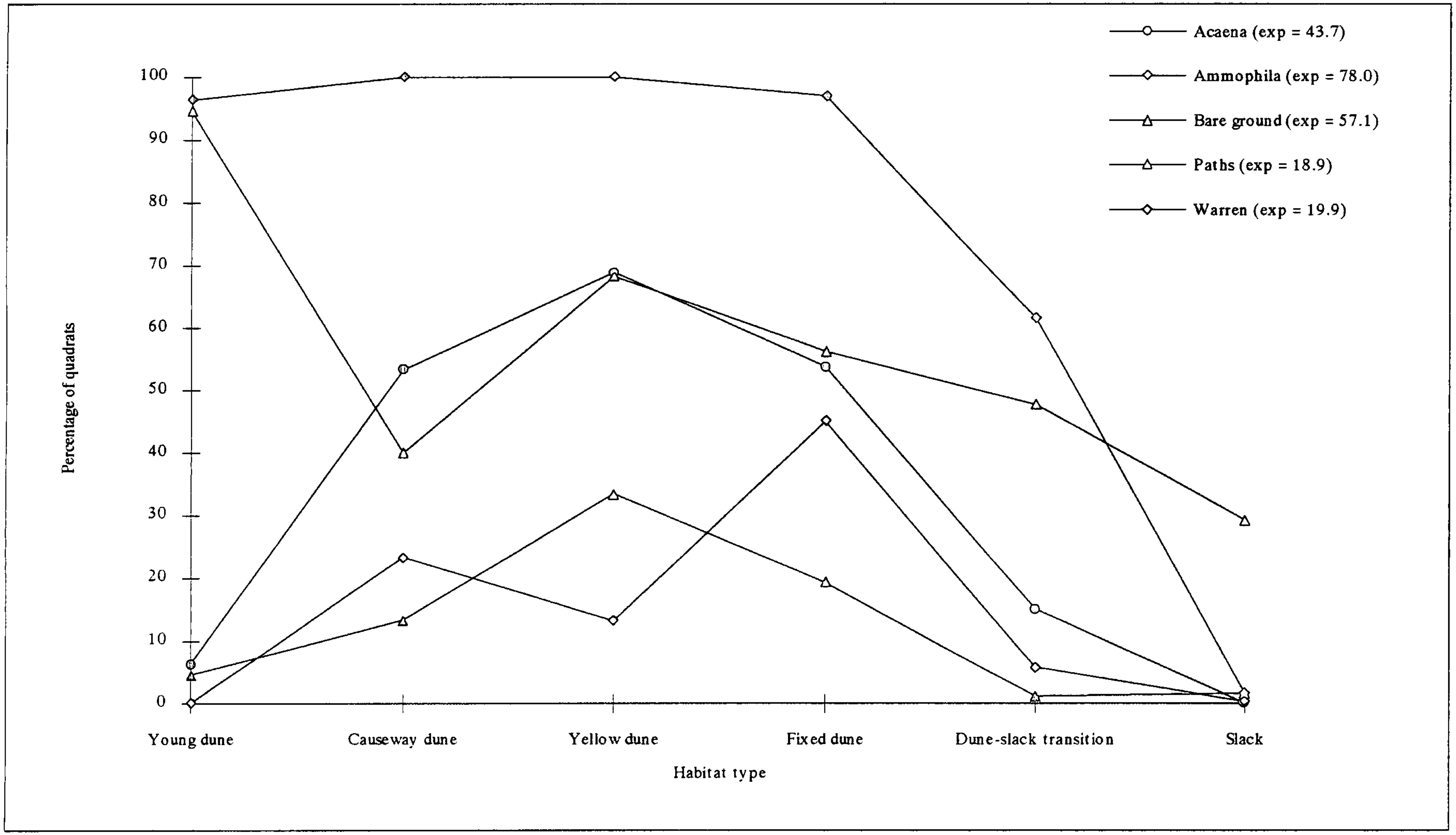

Figure 4.13 - Observed values of the percentage of quadrats with *Acaena*, *Ammophila*, bare ground, paths and warrens present are plotted for each habitat type. Percentage of quadrats expected (where expected values are the same in each habitat type) are recorded in the legend.

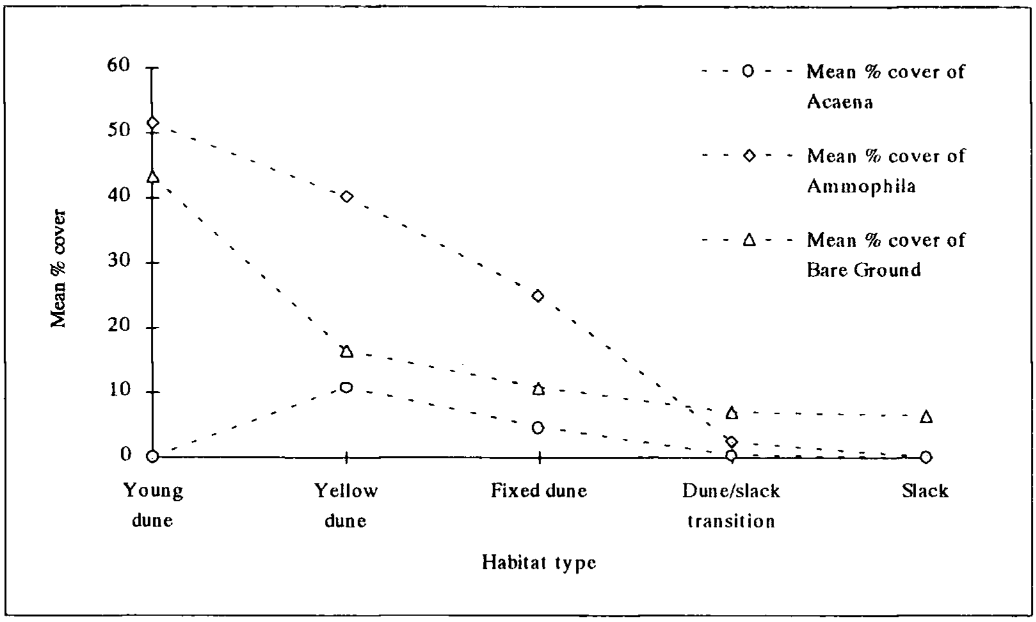

Figure 4.14 - Mean percentage cover of *Acaena*, *Ammophila* and bare ground are plotted against habitat category to show the changes in abundance of these variables, throughout the successional cycle, in relation to each other.

Absolute abundance of *Acaena* throughout the successional cycle shows a similar pattern to that exhibited by changes in presence and absence. Bare ground and *Ammophila* are both very abundant in the young, mobile dunes; *Ammophila* abundance then drops of at a relatively rapid, constant rate to very low abundances in the transitional habitat, and virtually nothing in the slacks. Density of bare ground drops sharply between the young dunes and yellow dunes and then steadily decreases along the successional gradient.

Aspect

The way in which Aspect was measured means that two variables are actually recorded. A measure of purely aspect is included, recorded in eight categories (north, north-east, north-west, south, south-east, south-west, east and west), and including a level category means that quadrats occurring on a slope can be distinguished from those on the level.

Acaena abundance and aspect (both true aspect and slope) are significantly positively correlated. Chi-square analysis of aspect with *Acaena* presence and absence shows that the observed values of *Acaena* differ significantly from the expected where $\chi^2_{(8)}$ = 155.98, significant at the 0.1% level (Chi-square tables in Appendix 2). When these results are examined in detail it is found that significantly less *Acaena* is present in the level aspect category than expected, while significantly more is found on south and west facing slopes.

There is also a significant correlation between habitat and aspect and it is possible that since habitat influences *Acaena* distribution, it may affect the relationship between *Acaena* and aspect or *Acaena* and slope. When a Chi-square analysis is done on the six habitat categories with five aspect categories, Level, North, South, East and West (where east is an amalgamation of east, northeast and southeast and west is an amalgamation of west, northwest and southwest), the overall Chi-square value is significant at the 0.1% level ($\chi^2_{(20)} = 676.03$). This means that the observed and expected values differ significantly.

The main contributor to this result is from the slacks, significantly more of the level aspect is slack than expected and significantly less of all the other aspect categories are slack. This shows a relationship between habitat with slope and level categories rather than aspect. The fact that much less *Acaena* is found in the level category reflects a relationship between slope and level rather than aspect *per se*. It is also possible that the fact that *Acaena* is not found in slacks is influencing the fact that is far less common than expected on the level. Indeed when the slack data is excluded and the analysis repeated on simply level or slope there is no significant difference.

When an analysis is performed on *Acaena* on purely aspect itself (i.e. excluding the aspect level category, and therefore the slack data also) the observed values are seen to differ significantly from expected ($\chi^2_{(7)} = 22.81$ which is significant at the 1% level; full Chi-square tables in Appendix 2). There is significantly more *Acaena* on the south and west slopes and less on the north slopes than expected.

Chi-square analysis was done on habitat and aspect *per se*, which involves excluding level aspect category (and therefore the slack data) so that habitat can be compared to aspect alone with out the result being disrupted by differences between slope and level ground. When these data are excluded observed and expected values still differ ($\chi^2_{(12)} = 108.33$ which is significant at the 0.1% level; for full tables see Appendix 2) and it is possible that this relationship could affect the differences seen between observed and expected values when aspect and *Acaena* are compared.

The main cause of difference between observed and expected is that more of the young dunes are found on north-facing slopes and less on the south-facing ones. The reverse appears to be true for causeway dunes, in general there are more than expected on the south facing slopes and less on north-facing slopes.

It is known that *Acaena* is more common on the causeway dunes than expected and less common on the young dunes at the northern edges of the island. It is also known that causeway dunes are more commonly south-facing than north-facing, while the young dunes are significantly more common on north-facing slopes and less common on south-facing ones than expected. In this way the abundance of *Acaena* in specific habitats could affect its relationship with aspect. To assess whether this was the case a Chi-square analysis was carried out on the two habitats in which *Acaena* was most abundant and which appeared to be least biased in terms of aspect; yellow and fixed dune. When this analysis was carried out there were no significant deviations of the observed values of *Acaena* presence and absence in true aspect categories from those expected.

The presence of paths, which showed a similar pattern to *Acaena* in its distribution throughout the different habitats, shows no significant deviation from the expected values in relation to either aspect or slope. This is surprising since *Acaena* shows a negative relationship to level ground because of slacks being level, while paths show no relationship with level ground even though they are significantly less abundant in slacks.

Ammophila arenaria

Ammophila is significantly, positively correlated with *Acaena*, in what is probably a non-linear fashion. When Chi-square analysis is carried out on these two variables, significantly less *Acaena* than expected is found where *Ammophila* is absent. Distribution of *Acaena* within scaled categories of *Ammophila* differs significantly from expected ($\chi^2_{(10)}$ = 406.79, significant at the 0.1% level). There is a humped relationship between *Ammophila* and *Acaena* abundance; a greater abundance of *Acaena* occurs at middling levels of *Ammophila* than expected and less at high and very low levels (Figure 4.15). This relationship remains even when the slack data is removed (Chi-square tables with and without slack data in Appendix 2).

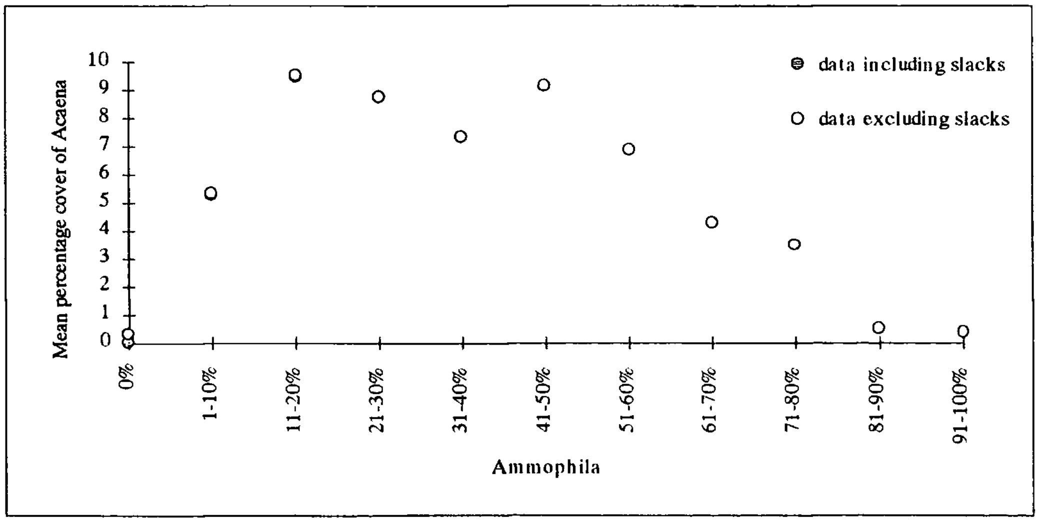

Figure 4.15 - Mean percentage cover of *Acaena* in each *Ammophila* abundance class for both slack included and excluded data.

Chi-square analysis show significantly more warrens and paths are present where there is also *Ammophila* present and less where it is absent that expected (Tables 4.6 and 4.7). These relationships are likely to arise because of the fact that all three variables are generally very common in the yellow and fixed dune habitats

Table 4.6 - Observed and expected values for path presence and absence in areas of *Ammophila* presence and absence. $\chi^2_{(1)} = 76.44$, significant at the 0.1% level.

Path	*Ammophila*		No *Ammophila*	
	obs	exp	obs	exp
present	308.00	248.35	15.00	74.65
absent	1006.00	1065.65	380.00	320.35
sum	1314.00	1314.00	395.00	395.00

Table 4.7 - Observed and expected values for warren presence and absence in areas of *Ammophila* presence and absence. $\chi^{(2)}_{(1)} = 115.66$, significant at the 0.1% level.

Warren	*Ammophila*		No *Ammophila*	
	obs	exp	obs	exp
present	326.00	252.19	2.00	75.81
absent	988.00	1061.81	393.00	319.19
sum	1314.00	1314.00	395.00	395.00

Further Chi-square analysis was done on the presence and absence of paths and warrens within scaled categories of *Ammophila* where it is present, (tables in Appendix 2). There are significant differences between observed and expected and these differences are represented graphically (Figure 4.16).

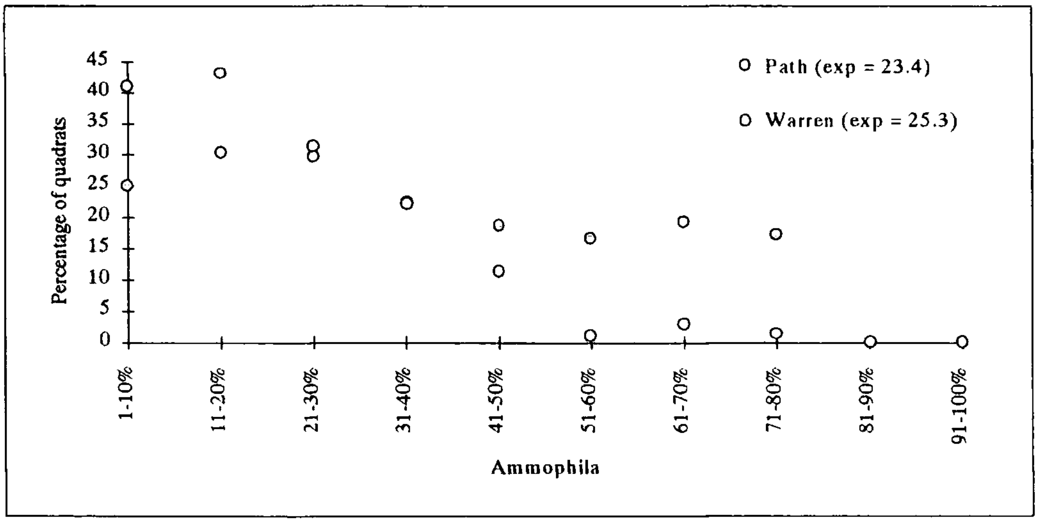

Figure 4.16 - The percentage of quadrats with paths and warrens in for observed values (% of quadrats expected in each habitat type are recorded in the legend) is plotted against *Ammophila* abundance. For paths $\chi^2_{(5)} = 30.03$, which is significant at the 0.1% level and for warrens $\chi^2_{(5)} = 176.02$, which is significant at the 0.1% level.

These patterns are very similar to that seen when percentage cover of *Acaena* is plotted for different *Ammophila* abundance classes. While both paths and warrens are more common than expected where *Ammophila* is abundant as *Acaena* is, they are significantly more common at reduced densities of *Ammophila* than at higher densities. This gives a humped relationship with both path and warren which is similar to the humped relationship seen between *Acaena* and *Ammophila*.

This suggests that the relationship between *Ammophila* and *Acaena* may be affected by the relationship between *Acaena* and paths, or warrens. Alternatively the presence of *Acaena* by warrens or paths may be the result of the relationship between *Acaena* and *Ammophila*.

Bare Ground

Acaena does not exhibit a significant relationship with the amount of bare ground present in the initial correlations performed on the data. When Chi-square analysis is carried out on the data, however, the observed and expected results differ significantly; $\chi^2_{(10)}$ = 145.39 which is significant at the 0.1% level (full tables in Appendix 2). There is significantly less *Acaena* present where there is no bare ground than is expected. In general though, where bare ground is present, *Acaena* is more common than expected at low densities and less common in areas with large amounts of bare ground.

If the slack data is excluded (see Appendix 2) there is no longer a significant difference between the observed and expected presence of *Acaena* where there is no bare ground. This suggests that *Acaena* is not commonly found in areas with no bare ground because these are often slack areas. The total Chi-square values for this analysis is still significant ($\chi^2_{(10)}$ = 71.1, significant at the 0.1% level) and shows that *Acaena* is more common than expected at low densities of bare ground and less common at higher densities. The way in which *Acaena* abundance is affected by density of bare ground is represented graphically (Figure 4.17).

When Chi-square analysis is done on bare ground with the presence of warrens and paths the observed results are seen to differ significantly from what is expected in a similar way to the results obtained when *Acaena* and bare ground are compared. There are significantly ($\chi^2_{(8)}$ = 74.74, significant at the 0.1% level; tables in Appendix 2) less warrens than expected in areas where there is no, or very little, bare ground; warrens are also lacking from areas where there is a high density of bare ground. More warrens than expected are found at middling to low densities, just as *Acaena* is.

Chi-square analysis of path with amount of bare ground also shows a humped pattern, resembling that displayed by the relationship between *Acaena* and bare ground. Less paths than expected are found at very low and very high densities of bare ground ($\chi^2_{(8)}$ = 30.02, significant at the 0.1% level; tables in Appendix 2).

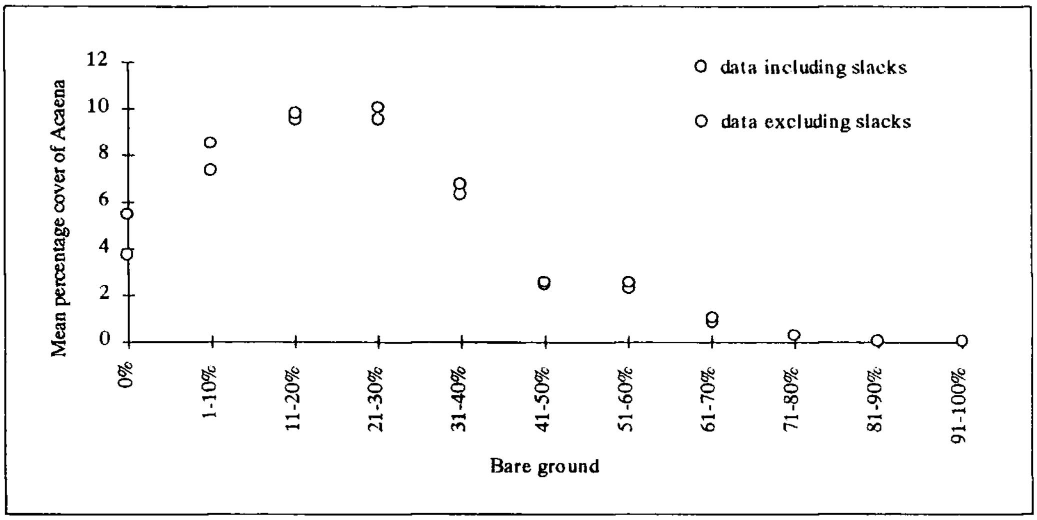

Figure 4.17 - Mean percentage cover of *Acaena* in each bare ground abundance class for both slack included and excluded data.

Paths and Warrens

Acaena is significantly correlated with the presence of paths; when a Chi-square analysis is done on this data far more paths than expected are found where *Acaena* is present. The fact that both *Acaena* and paths have a negative relationship with slacks may affect there relationship with each other. When the analysis is repeated, however, and the slack data excluded the same result is shown (Table 4.8). There is a true positive relationship between presence of *Acaena* and paths; *Acaena* is more commonly found where paths are present than where they are not.

Table 4.8 - Observed and expected values for *Acaena* presence and absence in areas with paths ($\chi^2_{(1)}$ = 165.74, significant at the 0.1% level) and without paths ($\chi^2_{(1)}$ = 86.34, significant at the 0.1% level).

	Slack data included				Slack data excluded			
Acaena	Paths		No Paths		Paths		No Paths	
	obs	exp	obs	exp	obs	exp	obs	exp
present	240.00	137.02	485.00	587.98	237.00	165.78	485.00	556.22
absent	83.00	185.98	901.00	798.02	70.00	141.22	545.00	473.78
sum	323.00	323.00	1386.00	1386.00	307.00	307.00	1030.00	1030.00

Chi-square analysis shows a significant difference between the observed and expected values when *Acaena* and warren presence are compared; there are more warrens where *Acaena* is present (Table 4.9). This again might be considered to be an effect of the relationship between *Acaena* and warrens with slack, and indeed when the analysis is repeated excluding slack samples there is no significant difference exhibited.

It is therefore likely that there is no true relationship between presence of *Acaena* and presence of warren.

Table 4.9 - Observed and expected values for *Acaena* presence and absence in areas with and without warrens ($\chi^2_{(1)}$ = 25.78, significant at the 0.1% level).

Acaena	Warrens		No Warrens	
	obs	exp	obs	exp
present	180.00	139.15	545.00	585.85
absent	148.00	188.85	836.00	795.15
sum	328.00	328.00	1381.00	1381.00

Multivariate Statistics

A multiple regression analysis was performed on the data using *Acaena* abundance as the dependant variable and *Ammophila* abundance, density of bare ground, warren and path presence and aspect as independent variables. The model produced was ineffective at explaining *Acaena* distribution and only included three of the variables. The fact that only a few variables were used and the large number of correlations between them indicates that the model was largely ineffective because the variables involved are all explaining the same variation. While these are likely to be important in explaining the distribution of *Acaena*, they are highly inter-related and not the only variables involved.

Principle Components Analysis was also performed on the data to attempt to show the major factors responsible for the variation in *Acaena* distribution. Again the variables used were *Ammophila* abundance, density of bare ground, path and warren presence and aspect; the variables were standardized and centred before the analysis was undertaken.

From this analysis two factors were extracted with Eigenvalues of greater than one. The percentage of variation that these explain, however, is not very good:

Factor 1	24.2%
Factor 2	23.1%.

The scree plot (Figure 4.18) shows that the percentage of variation explained does not fall off as sharply as it should after the second Factor. The Kaiser-Meyer-Olkin Measure of Sampling Adequacy is rather low (KMO = 0.435) suggesting that the data is not suitable for analysis in this way, even though the Bartlet Test of Sphericity is significant (Bartlet = 154.113, significant at the 0.01% level).

The Factors extracted (Table 4.10) are basically the same, with Factor one being a gradient of high *Ammophila* to low values of bare ground and reduced densities of warrens. Factor two represents a gradient from high densities of warrens to low abundances of *Ammophila*. When *Acaena* abundance is plotted against Factor one (Figure 4.19) it shows a humped relationship similar to those seen when *Acaena* is compared at different levels of *Ammophila* and bare ground.

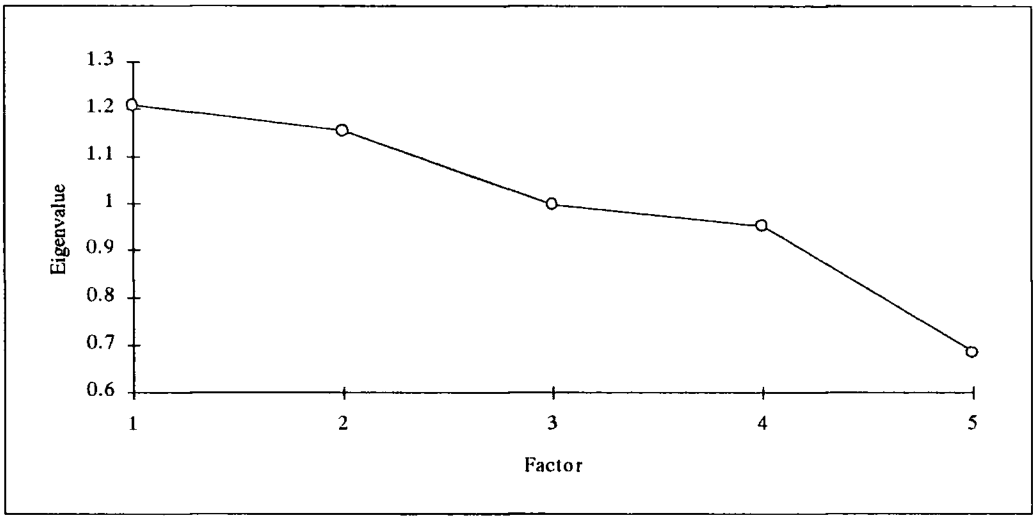

Figure 4.18 - Scree plot for PCA using *Ammophila* abundance, bare ground abundance, path and warren presence and aspect.

Table 4.10 - Factors extracted by PCA using *Ammophila* abundance, density of bare ground, presence of warrens and paths, and aspect.

Variable	Factor 1	Factor 2
Ammophila	0.7762	-0.3557
Aspect	0.7293	0.3797
Bare ground	0.1827	0.5187
Path	0.1467	0.1829
Warren	-0.1380	0.7733

ere

The data was also run through a DECORANA programme to see if Detrended Correspondence Analysis could explain the data better than PCA. The Eigenvalues were very low, however, and the results were not considered worth interpreting.

This lack of success in using multivariate techniques to interpret what are clearly important factors affecting *Acaena* distribution indicates that the way in which the variables are affecting the distribution is too complex and inter-related to be conducive to such analysis. Although these variables are important there are likely to be other variables involved and since these were not measured, and therefore not included in the analysis, PCA can not give a suitable solution.

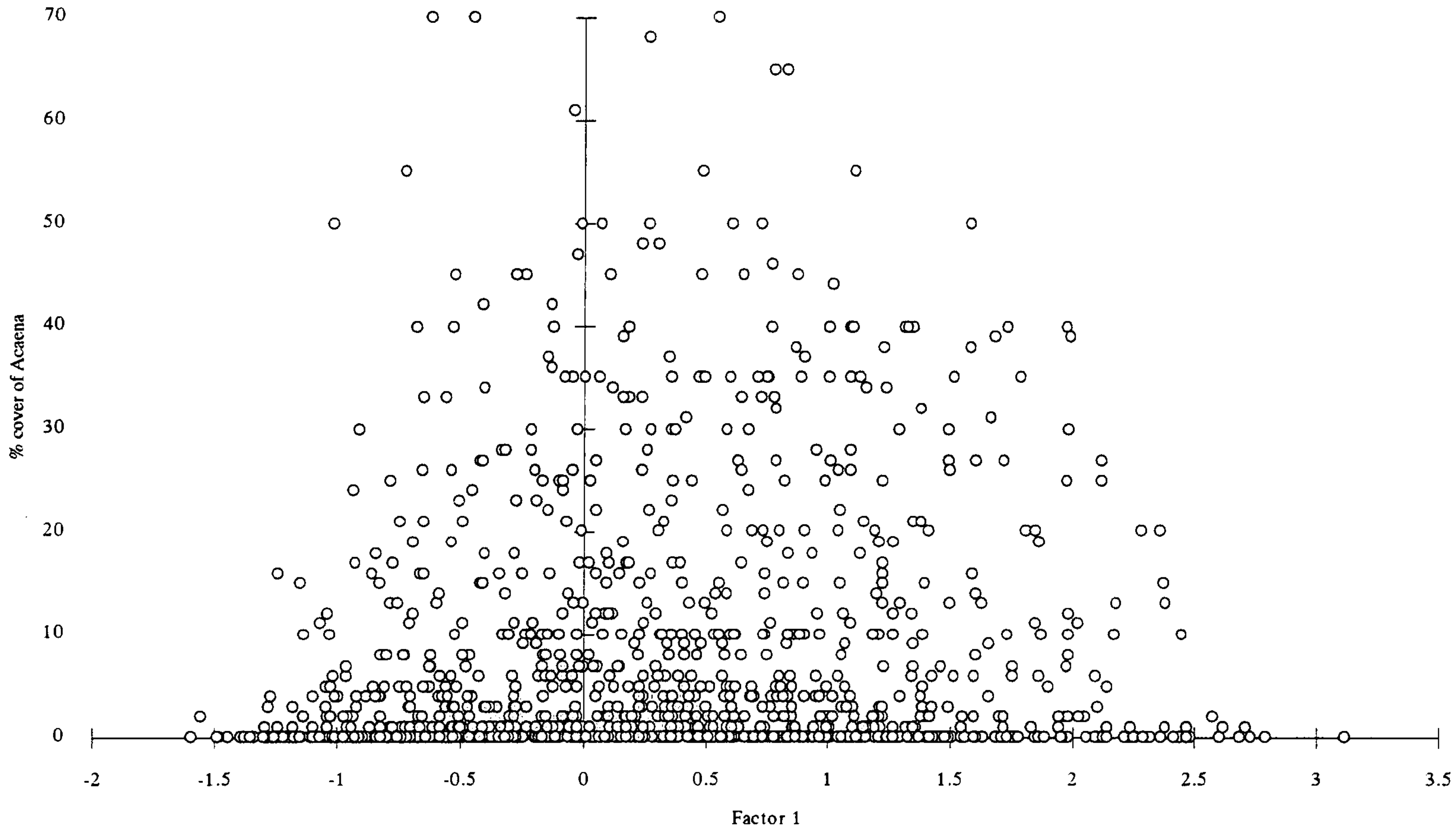

Figure 4.19 - Percentage cover of *Acaena* is plotted against Factor 1 from PCA analysis.

5. Discussion

This study aimed to map *Acaena* distribution on Lindisfarne and to find the major factors associated with this distribution. The fact that *Acaena* is an invasive alien makes close monitoring a necessity if the potential threat the species poses be to native British flora is to be assessed. ? Lindisfarne possesses a range of botanically important species, mainly orchids, that could be threatened by the spread of a species such as *Acaena*. Mapping an invading species distribution is important to identify whether or not it interacts spatially with this rare flora. Identification of preferred habitat means that the degree of interaction can be investigated.

Consideration of the past distribution of *Acaena* may provide a means of finding patterns of spread and investigating invasion dynamics of the species. Once this is known predicting future spread and ,therefore, future interaction of the alien with native plants becomes possible.

The results of mapping *Acaena* distribution on the Snook and Shiel of Lindisfarne show that a very large area of the study site is covered by this invasive species. Of the 1709 quadrats sampled *Acaena* was found to be present in 42%, suggesting that almost half the island has been invaded. Particularly high levels were found on the Shiel.

The site of the first introduction of *Acaena* is considered to be the Shiel (Culwick 1982), which might account for its abundance here. Two theories concerning the method of introduction, from seeds washed from woollen mills or from burrs attached to human visitors at the site, are conducive to the theory that the Shiel is the original site of introduction. Seeds washed down from the Tweed in flood water could quite conceivably wash up on the Shiel. This area is the main recreational site within the dunes and is therefore likely that any seeds brought in by human activity would arrive here first.

A third theory of how the species reached the island is as a garden escape; several *Acaena* species were recorded as being planted in the castle gardens as ornamentals. There is, however, no record of the invading species, *Acaena novae-zelandiae* being cultivated, and this is considered an unlikely method of introduction in this case.

From the Shiel *Acaena* has spread to the Snook where it is most common in patches around the edges of the island. If a contour map is compared with the map of distribution it can be seen that *Acaena* is more common in areas in which dunes have formed, typically the less stable, yellow dunes, rather than lacks or lows. Within the study site yellow dunes are found most commonly on the Shiel and around the edges of the Snook.

This association is clarified when *Acaena* presence is compared with habitat using a Chi-square analysis. *Acaena* is most abundant in yellow dune habitats, and is also relatively common on fixed dune and on the dunes formed near the causeway. It is significantly more common in these habitats than expected. *Acaena* is also seen to be significantly less common in dune slack, dune-slack transition and on very young, mobile dunes.

Culwick (1982) noted that the preferred habitat of *Acaena* was south-facing dune with moderate to low percentage cover of *Ammophila* and a high proportion of bare ground. This correlates with the observation that *Acaena* is most abundant on yellow dunes since these are often associated with moderate levels of *Ammophila* and a high degree of bare ground.

Analysis done in this project confirmed Culwick's statement that *Acaena* is found where *Ammophila* is moderately abundant. A humped relationship between *Acaena* and *Ammophila* is observed; while *Acaena* is significantly less abundant than expected at zero and very low levels of *Ammophila*, the invader is most abundant when *Ammophila* cover is between ten and fifty percent.

When the relationship between *Acaena* presence and bare ground is examined *Acaena*, while significantly more common than expected where there is bare ground, is found to be associated with relatively low levels of bare ground. *Acaena* is most common where there is between one and 30 percent bare ground; this result is contrary to Culwick's conclusion that *Acaena* is associated with high levels of bare ground.

These conclusions are validated by results from Principle Components Analysis. The primary factor drawn from PCA shows distribution along an axis from high *Ammophila* to high disturbance, in terms of warren, path and bare ground presence. When *Acaena* distribution along this axis is observed it exhibits a clearly humped relationship.

Ammophila and *Acaena* are both associated with the dunes and are rare in transitory habitats and slack. Dune habitats are often relatively open, and this type of habitat suits *Acaena* since it is not a good competitor in the vegetative phase (Glynn & Richards 1985). Seedlings are shaded out by tall vegetation and can not establish, although once established *Acaena* can tolerate partial shading. An intolerance of shading explains the fact that *Acaena* is most abundant in moderate rather than high levels of *Ammophila*.

Bare ground is necessary to provide areas where seed can penetrate and seedlings establish. Too much bare ground, however, might constitute too great a level of disturbance, open areas are affected by wind, and unvegetated sand is unstable.

These areas might be too disturbed for the seedlings to establish. The reason for a lack of *Acaena* on the young dunes is likely to be the presence of too much disturbance; the sand is unstable and continually shifting. Young dunes are also characterised by a high density of *Ammophila*; *Acaena* would encounter shading in this habitat.

The fact that *Acaena* requires open areas to colonise and does not compete well explains its absence in slacks and transitory habitats. Slack systems represent a completely different habitat to any of the dune types; they are characterised by an almost complete absence of *Ammophila* and very little bare ground. Water is readily available due to the close proximity to the water table and these habitats are generally more nutrient rich as minerals leached from the dunes collect in the slacks (Boorman 1977). The overall effect of this is that slacks present a far more hospitable environment, and consequently exhibit a far greater variety and abundance of vegetation than the neighbouring dune habitats.

The lack of bare ground means that *Acaena* is unable to penetrate by seed. The high percentage cover of vegetation, and in some cases the tall willow and grass cover, means that even if seedlings could establish *Acaena* would be out competed. *Acaena* has invaded the transitional habitat to some extent, possibly through vegetative expansion from neighbouring dune habitat, but it has not affected the slacks at all as yet.

Culwick's work also mentions a relationship between *Acaena* presence and aspect. Initially analysis in this study also showed that *Acaena* was more often associated with south- and west-facing slopes than expected and less associated with north-facing slopes; this is an artefact of habitat type. *Acaena* is more common on south facing slopes because it is more common than expected on causeway dunes which tend to be mainly south-facing. It is less common on northern slopes because of a lack of *Acaena* on young, mobile dunes of which the majority are north-facing. When these data are excluded there is no relationship with aspect.

Theoretically this relationship between aspect and young dunes or causeway dunes should not exist. Those dunes described as causeway dunes in this study should have the same habitat semblance as young dunes. They occupy the same position in the successionary stage of the dune system as the young dunes, and fringe the island in the same way. The only difference between them is that the young dunes are mainly north-facing while the causeway dunes are south-facing and are bordered by the causeway.

There are, however, large differences in the vegetation they display. The young dunes are very unstable with dense stands of *Ammophila* and in some cases E*lymus arenarius*, but very little other vegetation; *Acaena* is very rare in this habitat. The causeway dunes offer a more stable community, they have far more in common with the later stages of yellow dune formation than with young dunes. Broad-leaved species such as *Senecio* and *Taraxacum* are common, and *Acaena* is found at moderate levels not differing greatly from the expected.

These differences are unlikely to be caused by aspect alone, since there are no such differences exhibited between different aspects in the other habitat types. Although the majority of young dune habitat is north-facing and causeway dune south-facing there are some sites representing all aspects present in both, again indicating that aspect is an unlikely cause of the differences. It is quite possible, however, that the habitats differ because of the presence of the causeway structure itself.

The new causeway was opened in 1954 and under went construction in 1965 to extend it and raise it above the level of the sand (Weighman 1983). Previously the only a~~ss~~ccess to the island was the perilous journey across the inter-tidal sands themselves. The construction of a permanent structure fringing the southern boundary of the island has led to a reduction in the movement and deposition of sand along that edge and hence to a stabilisation of the habitats there. The differences artificially induced in this habitat type mean that it does not fit into the natural successional cycle and have apparently made it more susceptible to invasion by this alien species.

It is important to have established that there is in fact no relationship of *Acaena* with aspect. If *Acaena* had been more common on the south-facing slopes, then the northern slopes could have provided a refuge (from *Acaena*) for other species. This is not the case, however, and any conservation plans or *Acaena* controls implemented must not rely on north-facing refuges and should take account of the fact that no relationship is found.

The conclusion from this study is that the preferred habitat of *Acaena* is relatively open, yellow dune, with low to moderate abundance of *Ammophila* and a low density of bare ground; no *Acaena* was found in the slacks. Unlike Culwick's work no relationship was found with aspect.

Acaena is seen to be associated with the presence of both paths and warrens. Unlike the relationship between warrens and *Acaena*, which is an artefact of the relationship between both *Acaena* and warrens with slack, *Acaena* appears to be genuinely associated with paths. This association may arise because the dispersal of *Acaena* seeds relies on epizoochory (the plant possesses spiny burrs). Paths might represent the areas most commonly travelled by animals (in the form of humans and their pets, or rabbits) and so these are areas that *Acaena* will most commonly disperse to.

This manner of dispersal might led to the assumption that warrens would also be associated with *Acaena* if rabbits are a vehicle of dispersal. The lack of such an association does not show that rabbits do not carry the burrs but simply that rabbit travels are not confined to the areas around warrens. For example warrens are rarely found in the slack, since the burrows risk becoming inundated with water, but rabbits often feed in the slacks, which represent areas of readily available green vegetation, such as orchid shoots and willow buds. In fact rabbits are in fact probably responsible for much of the spread of *Acaena* across the island. Studies in Kent have seen that *Acaena* is spreading along the runways of the rabbits and it is likely that a similar situation has occurred here (Lousley 1956).

When path presence is compared with habitat type it shows a very similar pattern to that of *Acaena* with habitat. Paths and warrens both show similar patterns to *Acaena* when compared at different abundances of bare ground and *Ammophila*. This might suggest that *Acaena* is common in the middle stages of sand dune succession because it has more opportunity to establish here due to a greater frequency of dispersal to these areas.

Presence of paths, however, is not a completely literal representation of animal activity. Although there are a greater number of paths in the yellow and fixed dunes, this does not necessarily mean that these habitats are visited with greater frequency. It is quite possible that paths are less common in the slacks because they are flat and there is not the same need to stay on a well defined path as there is in the rougher terrain of the dunes. Well defined, permanent paths may be less common in the young dunes because the continually shifting sand covers them up.

In this way seeds are probably transported to all habitats with fairly similar frequencies. The conditions under which *Acaena* can grow are more important in determining its abundance in a particular area than the presence of paths. Another reason for an association between *Acaena* and the presence of paths is that paths represent good areas for *Acaena* to colonise and grow. Tall vegetation is trampled down so *Acaena* would not experience shading, and disturbance from human feet leads to patches of bare ground where *Acaena* seeds can establish. *Acaena* is often seen to from a dense mat of plant material across paths in the dunes. The conditions paths provide for *Acaena* to grow in might, at least partially, explain their association.

The National Vegetation Classification survey carried out in 1988 (Woolven & Radley) produced a map over which it is possible to lay the grid used to map *Acaena*. Habitats found commonly on Lindisfarne generally represent undifferentiated dune, and this can be clearly seen if the specific NVC types are amalgamated into broader successional habitats. Foredune, dune grassland and slack habitats are also relatively common.

The amount of *Acaena* found in these habitat types follows a similar pattern along the successionary stage as that exhibited when the habitat categories collected with the quadrat data are used. Moderate cover of *Acaena* in the younger dunes, higher cover in the later dune stages, very little in the transitional stages and less in the slacks and slack-like habitats. It is interesting to note, and worrying from a conservational point of view, that there are very few NVC habitats that are free of *Acaena*. This suggests that virtually all habitats are invasible to some extent.

The use of a grid system for mapping *Acaena* on the island allowed the comparison of *Acaena* distribution from different years in an analogous fashion. There will be some errors involved in overlaying the grid of quadrat points on these maps since there are some discrepancies between the maps as to the shape of the island. Taking into account the sensitivity of the grid used, however, (i.e. 25m by 25m) it is likely that such discrepancies are not of very great importance.

When comparing the distribution of *Acaena* in the three different years only a simple presence/absence score could be used. Previous methods of mapping involved walking over the island in a zigzag fashion so that the entire area of the island was seen from a maximum of 5m (Culwick 1982), or by walking around contours (Hargreaves & Peach 1965). It is much harder to assess the amount of ground covered by *Acaena* in a non-defined area than it is in a uniform, specified area such as a quadrat. Possibly, it is for this reason that previous work has used only single, or few, categories to record cover. By using a 1m x 1m quadrats in the systematic method employed by this survey, however, it was possible to record the actual percentage cover quickly and efficiently at each site. The few categories recorded in previous studies did not correspond to percentage cover so presence/absence had to be used when comparing distribution in different years.

A comparison of the maps shows an overall increase in *Acaena* between 1965 and 1994, there are, however, sites of both increase and decrease recorded. It is possible that the areas of decrease may represent errors in converting the older maps to the system used in this project. Alternatively these points may actually represent areas of *Acaena* decline. *Acaena* may have colonised these areas and then died out; during the seedling stage the species is very sensitive to frost and drought and plants are killed by water-logging (Culwick 1982).

To give a measure of the rate of spread of *Acaena*, square root of the area occupied was calculated. Other methods may be used to measure spread, such as radial increase and aerial circumference but square root of the area is generally considered the best (Hengeveld 1989). The simplest measure of range is radius but this incurs difficulties when species expand asymmetrically, and circumference is difficult to interpret as it is derived from surface area.

The size of a population is often proportional to its area and as it expands its area will relate to time in a simple way, thus using area is an appropriate method of measuring rate. It does, however, assume that the increase in rate is constant which does not always apply.

Increase in *Acaena* per year between 1965 and 1977 is greater than between 1977 and 1994, but the difference in increase is quite small. If a regression line is fitted the r^2 value is very high (0.99) indicating that increase is very nearly linear. The dynamics of an invading species characteristically show a sigmoidal shape; initially increase is very slow, then there is a very rapid rate of expansion with the species filling available habitat at a rapid rate. Exponential growth can not continue indefinitely and as the suitable habitat is filled, rate of spread decelerates and reaches a plateau.

Acaena does not appear to follow this characteristic pattern, there is no indication that the rate of spread is reaching a plateau and rate appears to be constant during the 29 year period between 1965 and 1994. If the regression line through rate of spread is extrapolated it passes through the x-axis at about the year 1912. This represents the approximate time of the first records of *Acaena* in the area, it is therefore realistic to assume that rate of spread has been relatively constant since its first introduction to the Northumberland area. *Acaena* has not shown the characteristically slow initial invasion response. It is possible that *Acaena* was present in a static population some time before the first records, but being a rather unusual and noticeable plant this is unlikely. The first record in England was only as early as the 1900's, so *Acaena* could not have been present much earlier than that time, if at all.

Acaena exhibits two methods of expansion, the first being long distance diffusion. The spiny burr heads of *Acaena* stick tenaciously to fur and clothing and can be carried for long distances. Plants also exhibit strong vegetative growth (Culwick 1982), a form of neighbourhood diffusion. These two processes combine to cause a process of expansion known as hierarchical diffusion (Hengeveld 1989). Long distance dispersal provides a number of sites from where the species can invade the neighbouring area.

The relative importance of these two methods of expansion was investigated. Despite an increase in overall cover of *Acaena* the number of new colonisation events has declined rapidly between 1965 and 1994, in fact the number has halved. This indicates that expansion is becoming mainly vegetative since *Acaena* is still increasing at the same rate but the rate of colonisation is declining. *Acaena* is no longer dispersing to new habitats as effectively but rather expanding to fill the habitats it is already present in.

A possible reason for this reduction in colonisation events is that there is a reduction in the number of sites suitable for germination. Seedlings require open areas to germinate since they may be shaded out in tall, denser vegetation (Glynn & Richards

1985). Culwick (1982) suggests that the principle factor affecting germination is the availability of water, *Acaena* is not well adapted to germinate in such a dry environment. In this way recruitment depends on the availability of 'safe sites' for germination and a reduction in colonisation may reflect a reduction in such sites. As *Acaena* spreads over the island suitable sites are occupied and less are available for colonisation.

If individual NVC habitats are examined, *Acaena* is seen to be increasing in a large number of these categories, even in some of the transitional and slack habitats. This increase, and indeed actual presence, of *Acaena* in the NVC slack categories is surprising when it is considered that this study found no *Acaena* in any of the 1m x 1m quadrats sampled in the slacks (as defined by this study).

These discrepancies may be due to errors incurred in overlaying the grid of quadrats on the NVC map. Alternatively they might be due to differences in classification of habitat type. In this study a simple categorisation of slack was made based on a subjective judgement. NVC categories represent communities defined from the list of species present and their abundance's (Malloch 1989). What might be considered slack, in the Woolven and Radley (1988) survey, with respect to the species composition might have been classified as transitional habitat for reasons of aspect or other attributes during this study.

As with the overall distribution of *Acaena*, despite an increase in presence, the number of colonisation events in approximately 75 percent of the NVC categories data was calculated for are decreasing. Interestingly, in some of the dune habitats the rate of spread appears to be levelling off, possible because all suitable space within that habitat has been filled.

A reduction in the number of colonisation events in these dune habitats may be responsible for the plateaux observed in several of the dune habitats, however it is more likely to be due to the filling of available space within these habitats. Overall, *Acaena* is still increasing even though colonisation is declining, indicating that vegetative expansion is becoming more important than seed dispersal. If this is the case there must be some other factor limiting *Acaena* growth within the habitats showing a levelling in *Acaena* presence since it has certainly not filled the total area of these habitats present on the island.

The obvious importance of vegetative growth as a means of expansion may give cause to question the presence, within this *Acaena* species, of such an effective long distance dispersal process. It is found, however, that the dispersal distances of *Acaena* seeds are in fact not that great. Culwick (1982) found that the majority of seeds actually fall within the boundary of the parental clone (average dispersal distance 26cm) and are not able to germinate due to parental suppression. There are a few seeds dispersed to distances exceeding 18m, but seeds tend to be dispersed as a single unit (due to aggregation into seed heads) and location is often dependent of the habits of the dispersing animal. For example large collections of seed are to be found around rabbit warrens, the rabbits often free themselves of the burrs before entering their burrows.

Further evidence of the importance of vegetative expansion comes from the relationship exhibited between *Acaena* abundance and distribution. The greater the percentage cover of *Acaena* within a quadrat the more clumped/aggregated the distribution becomes. This indicates that expansion is largely vegetative within a localised area. Seed dispersal, however, could also lead to clumping; seed heads (burrs) contain approximately 100 seeds and dispersal as a single unit would frequently result in localised aggregation (Culwick 1982).

The observation that *Acaena* does not appear to be slowing its spread is not good news for the future conservation of this important Reserve. *Acaena* is an alien species in Britain and therefore to be discouraged under most circumstances, but more specifically it represents a potential threat to the rare species growing within the dune flora of Lindisfarne.

The large mats of dead *Acaena* material allow very few species to grow beneath, except *Ammophila* which can penetrate the layer. The soil under these mats is loose and has a low organic content resulting in a species poor community. The presence of a greater botanical richness in areas not colonised by *Acaena* suggests that it is crowding out these additional species.

Various forms of control have been tried; several herbicides have been used in trial plots, including Roundup and SBK Brushwood killer. These trials have been largely unsuccessful, resulting in eradication of *Acaena* and also the majority of other species present (no information is available as to which species are the first to recolonise treated area) or in *Acaena* being largely unaffected by treatment. Use of SBK brushwood killer showed the structure of *Acaena* leaves renders it resistant, the small, shiny leaves shed the droplets of herbicide before they do any damage.

Mechanical removal has also been tried, but pulling up the plants by hand is exceeding ineffective. The man power that would be required to remove *Acaena* completely is immense and the disturbance to the dunes that occurs from uprooting the plants merely makes them a more suitable areas for *Acaena* seeds to establish.

The final method of control considered was that of biological control. Two organisms were suggested as control agents, a sawfly native to Chile that had been used as a control in New Zealand in the 1900,s and a Chrysomelid beetle (Hortica) which feeds on *Acaena* in South America. Support for the introduction of these alien species was not overwhelming, however, and the plans were shelved. Consequently no forms of control have been widely implemented on the island and *Acaena* has spread largely unchecked.

Virtually half the island has already been invaded to some extent, this distribution has, however, so far been associated with the yellow dunes in general. These dunes are naturally relatively open habitats and *Acaena* may not actually be affecting that great a range of species in these areas. *Acaena* may in fact be stabilising these areas at a greater rate than would normally occur. Whether *Acaena* then allows plants of a later colonary stage to establish, however, is debatable. There is some evidence that *Lotus corniculatus* is able to compete with *Acaena* in the later dune stages (Culwick 1982).

Acaena is relatively abundant in the causeway dunes, fixed dunes and yellow dunes, of which there are approximately 47, 46 and 31 percent of sites as yet totally uninvaded. In terms of habitat type alone these sites represent potentially invasible area and collectively compose approximately 26 percent of the study area. Some of these sites are probably uninvaded because they are unsuitable for reasons such as too much bare ground or too dense *Ammophila*. This observation is supported by evidence that *Acaena* abundance appears to levelling off in some of the dune habitats, and the fact that the number of new colonisation events is declining might be interpreted as positive news for the reduction of future spread. The fact that the overall rate of spread has appeared to have decreased very little in the past 17 years, however, would indicate that while some areas might be unsuitable there is still plenty of invasible habitat available and *Acaena* is quite capable of invading this vegetatively.

More positive observations are that the species is rare in transitional habitat and absent in the slacks. These are the sites inhabited by the most botanically important species, the orchids. It is likely, due the high proportion of vegetated ground in the transitional sites that *Acaena* has invaded these areas through vegetative expansion since conditions are not conducive to the establishment of seed. Vegetative spread is therefore also likely to be the method employed to invade the slack habitats which are likewise unfavourable to seed.

Acaena has failed to penetrate the slacks by this manner for greater than 17 years however. Culwick (1982) reports that *Acaena* is common on the small dunes within slacks in 1977, indicating that there has been plenty of opportunity to spread to the slacks vegetatively. This evidence, when considered in conjunction with the information that *Acaena* is unable to establish by seed, and is killed either in seedling form or as an adult plant by water-logging conditions, leads to the following conclusion. *Acaena* is unlikely to invade the slacks, and indeed the lower areas of the transitional habitats, in the future, either vegetatively or otherwise, due to their proximity to the winter water level.

If this conclusion is correct *Acaena* is unable to interfere with the slack dwelling orchids such as *Epipactis palustris* (the Marsh Helleborine) and *Corallorhiza trifida* (the Coralroot orchid). One of the most important species occurring in this site is *E. dunensis* (the Dune Helleborine), this orchid grows within the transitional habitat and may be affected by the invasion of *Acaena* to some extent. The lower areas of the transitional habitat (within the range of the winter water level) will, however, offer refuges within which this and other species growing in the dune - slack transition will be unaffected by *Acaena*.

In conclusion, it would be expected that future spread of *Acaena* on Lindisfarne is inevitable, at least within the dunes themselves. To gain a clearer picture of the rate of spread and the invasion dynamics of *Acaena* it would be useful to have more information on past distribution. More importantly, however, to observe how rate of spread is changing at present, further surveys are necessary sometime in the near future.

Although effective prediction of *Acaena* distribution was not possible with the variables collected in this survey, it is probable that if further variables were recorded, for example pH, organic content and water content, it would be possible to predict suitable (invasible) habitat and, therefore, the pattern of future spread of *Acaena*. It would have been favourable if such variables could have been collected during this study but unfortunately the time available was not sufficient and a longer study is required for such an in depth investigation.

Another area of work on this invasive species that would prove interesting would be studies investigating the species present in the same habitats as *Acaena*. Continuing research into the interactions and changes occurring between these species through time would give some idea as to the potential menace of *Acaena* to the native flora of this duneland system.

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Appendix 1

National Vegetation Classification nomenclature and descriptions of habitat types:

BG	Bare ground.
BS	Bare sand.
BSH	Bare shingle.
SD5	*Elymus farctus* foredune - can be species poor. Generally consists of strand-line species; although more mesotrophic species are found if the area sheltered. Usually found just above the high-tide level.
SD6a/b	*Ammophila arenaria* dune - *Ammophila* is dominant & often the only species present. Occurs in areas of high sand deposition.
SD6f	*Ammophila* dune (*Poa pratensis* understory) - displays a large range of 'weedy' herbs. Low, but still significant, sand deposition.
SD6e	*Ammophila* dune (*Festuca rubra* understory). Low, but still significant, deposition of sand.
SD7a	*Leymus arenarius* dune - a generally open community where *Leymus* is the main dune building grass (no *Ammophila* is present).
SD8	*Leymus arenarius, Ammophila arenaria* dune (couch grass is also present). These three grasses are abundant, also present are a range of strand-line species.
SD9	*Ammophila arenaria, Ononis repens* dune - undifferentiated *Ammophila* dune with a lot of *F. rubra* and *O. repens.* Relatively low sand deposition means the community is fairly open. *Acaena* is abundant in this habitat.
SD9/10	Transitory stage between SD9 & 10 - foredune to undifferentiated grassland.
SD10	*F. rubra, Galium verum* dune grassland (undifferentiated).
SD10d	*F. rubra, G. verum* dune grassland - with a large number of bryophytes and lichens, but with few vascular plants. Low calcium content.
SD10L	*F. rubra, G. verum* dune grassland - lichen-rich sub-community.
SD10/14	*F. rubra, G. verum* dune grassland / *Ammophila - Phleum arenarium* transition.
SD14(a)	*Ammophila - Phleum* dune - well drained dune, often with steep slopes; found in areas subject to drought.
DG	Undifferentiated dune grassland.
SD10/MG1.1	Tall, species poor dune grassland.
SD10/15	Transitory stage between SD10 & 15 - dune grassland to slack.
SD15	*Salix repens, Holcus lanatus* undifferentiated slack - with low salinity; calcium rich.
SD15d	*S. repens, H. lanatus* dune slack, *H. lanatus, F. rubra* sub-community - often the interface of dune & slack. Low salinity, high calcium content and generally drier.
SD16	*Potentilla anserina, Carex nigra* slack - less calcareous sand with incoming ground water more acidic.
SM/SD15 (or 16 or 10)	Salt marsh - slack transitional communities.
SM	Saltmarsh.
T1	Sparsely vegetated, exposed shingle - encrusting lichen common.
T4	Very wet slack, a lot of bare mud.
T7	Transitional vegetation - dry dune grassland with *S. repens* growing through.
T8	Water filled slack (*Ranunculus flammula*).
T10	Tall species-poor grassland.
T16	Pool with approximately 10cm of water.
T18	Sparsely vegetated, exposed shingle.
T21	Salt marsh / dune transition

T23	Sparsely vegetated, eroding sand cliff.
T25	Narrow dune / salt marsh transition.
T26	Sparsely vegetated, stabilized shingle.
T27	Fenced, bare sand blow-out.
T34	Dune influence lacking except for infrequent clumps of *Ammophila*. Cliff exposure clay with a layer of pebbles.
T97	Wet area.

Appendix 2

Chi-square tables

Chi-square analysis of habitat type with presence and absence of *Acaena*.

Observed	**Habitat Type**						
Acaena	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	7.00	16.00	402.00	284.00	13.00	0.00	722.00
absent	103.00	14.00	181.00	244.00	73.00	315.00	930.00
sum	110.00	30.00	583.00	528.00	86.00	315.00	1652.00
Expected							
Acaena	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	48.08	13.11	254.79	230.76	37.59	137.67	722.00
absent	61.92	16.89	328.21	297.24	48.41	177.33	930.00
sum	110.00	30.00	583.00	528.00	86.00	315.00	1652.00
Chi-sq							
Acaena	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	35.09	0.64	85.04	12.28	16.08	137.67	286.80
absent	27.25	0.49	66.02	9.54	12.49	106.88	222.67
sum	62.34	1.13	151.06	21.82	28.57	244.55	**509.47**

$\chi^2_{(5)}$ = 509.47, significant at the 0.1% level.

Chi-square analysis of habitat type with presence and absence of paths.

Observed	**Habitat Type**						
Path	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	5.00	4.00	195.00	102.00	1.00	5.00	312.00
absent	105.00	26.00	388.00	426.00	85.00	310.00	1340.00
sum	110.00	30.00	583.00	528.00	86.00	315.00	1652.00
Expected							
Path	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	20.77	5.67	110.11	99.72	16.24	59.49	312.00
absent	89.23	24.33	472.89	428.28	69.76	255.51	1340.00
sum	110.00	30.00	583.00	528.00	86.00	315.00	1652.00
Chi-sq							
Path	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	11.97	0.49	65.45	0.05	14.30	49.91	142.17
absent	2.79	0.11	15.24	0.01	3.32	11.62	33.09
sum	14.76	0.60	80.69	0.06	17.62	61.53	**175.26**

$\chi^2_{(5)}$ = 175.26, significant at the 0.1% level.

Chi-square analysis of habitat type with presence and absence of *Ammophila*

Observed	**Habitat Type**						
Ammophila	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	106.00	30.00	583.00	512.00	53.00	5.00	1289.00
absent	4.00	0.00	0.00	16.00	33.00	310.00	363.00
sum	110.00	30.00	583.00	528.00	86.00	315.00	1652.00
Expected							
Ammophila	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	85.83	23.41	454.90	411.98	67.10	245.78	1289.00
absent	24.17	6.59	128.10	116.02	18.90	69.22	363.00
sum	110.00	30.00	583.00	528.00	86.00	315.00	1652.00
Chi-sq							
Ammophila	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	4.74	1.86	36.08	24.28	2.96	235.89	305.81
absent	16.83	6.59	128.10	86.23	10.53	837.62	1085.90
sum	21.57	8.45	164.18	110.51	13.49	1073.51	**1391.71**

$\chi^2_{(5)}$ = 1397.71, significant at the 0.1% level.

Chi-square analysis of habitat type with presence and absence of bare ground.

Observed	**Habitat Type**						
Bare ground	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	104.00	12.00	398.00	297.00	41.00	92.00	944.00
absent	6.00	18.00	185.00	231.00	45.00	223.00	708.00
sum	110.00	30.00	583.00	528.00	86.00	315.00	1652.00
Expected							
Bare ground	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	62.86	17.15	333.14	301.71	49.14	180.00	944.00
absent	47.14	12.85	249.86	226.29	36.86	135.00	708.00
sum	110.00	30.00	583.00	528.00	86.00	315.00	1652.00
Chi-sq							
Bare ground	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	26.93	1.54	12.63	0.07	1.35	43.02	85.54
absent	35.91	2.06	16.83	0.10	1.80	57.36	114.06
sum	62.84	3.60	29.46	0.17	3.15	100.38	**199.60**

$\chi^2_{(5)}$ = 199.60, significant at the 0.1% level.

Chi-square analysis of habitat type with presence and absence of warrens.

Observed	**Habitat Type**						
Warren	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	0.00	7.00	77.00	238.00	5.00	1.00	328.00
absent	110.00	23.00	506.00	290.00	81.00	314.00	1324.00
sum	110.00	30.00	583.00	528.00	86.00	315.00	1652.00
Expected							
Warren	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	21.84	5.96	115.75	104.83	17.08	62.54	328.00
absent	88.16	24.04	467.25	423.17	68.92	252.46	1324.00
sum	110.00	30.00	583.00	528.00	86.00	315.00	1652.00
Chi-sq							
Warren	**Young dune**	**Causeway dune**	**Yellow dune**	**Fixed dune**	**Dune-slack transition**	**Slack**	**sum**
present	21.84	0.18	12.97	169.16	8.54	60.56	273.25
absent	5.41	0.05	3.21	41.91	2.12	15.00	67.70
sum	27.25	0.23	16.18	211.07	10.66	75.56	**340.95**

$\chi^2_{(5)}$ = 340.95, significant at the 0.1% level.

Chi-square analysis of aspect categories with presence and absence of *Acaena* (including the level aspect category).

Observed	**Aspect**									
Acaena	**Level**	**North**	**North-east**	**East**	**South-east**	**South**	**South-west**	**West**	**North-west**	**sum**
present	214.00	133.00	11.00	52.00	25.00	217.00	10.00	45.00	18.00	725.00
absent	567.00	163.00	13.00	39.00	15.00	146.00	8.00	20.00	13.00	984.00
sum	781.00	296.00	24.00	91.00	40.00	363.00	18.00	65.00	31.00	1709.00
Expected										
Acaena	**Level**	**North**	**North-east**	**East**	**South-east**	**South**	**South-west**	**West**	**North-west**	**sum**
present	331.32	125.57	10.18	38.60	16.97	153.99	7.64	27.58	13.15	725.00
absent	449.68	170.43	13.82	52.40	23.03	209.01	10.36	37.42	17.85	984.00
sum	781.00	296.00	24.00	91.00	40.00	363.00	18.00	65.00	31.00	1709.00
Chi-sq										
Acaena	**Level**	**North**	**North-east**	**East**	**South-east**	**South**	**South-west**	**West**	**North-west**	**sum**
present	41.54	0.44	0.07	4.65	3.80	25.78	0.73	11.01	1.79	89.81
absent	30.61	0.32	0.05	3.43	2.80	18.99	0.54	8.11	1.32	66.17
sum	72.15	0.76	0.12	8.08	6.60	44.77	1.27	19.12	3.11	**155.98**

$\chi^2_{(8)}$ = 155.98, significant at the 0.1% level.

Chi-square analysis of habitat type with aspect categories (including slack data and level aspect category).

Observed	Aspect					
Habitat	**Level**	**North**	**East**	**South**	**West**	**sum**
Young dunes	23.00	63.00	6.00	14.00	4.00	110.00
Causeway dunes	13.00	1.00	1.00	14.00	1.00	30.00
Yellow dunes	193.00	94.00	59.00	180.00	57.00	583.00
Fixed dunes	179.00	113.00	75.00	114.00	47.00	528.00
Dune-slack transition	3.00	23.00	14.00	41.00	5.00	86.00
Slack	315.00	0.00	0.00	0.00	0.00	315.00
sum	726.00	294.00	155.00	363.00	114.00	1652.00
Expected						
Habitat	**Level**	**North**	**East**	**South**	**West**	**sum**
Young dunes	48.34	19.58	10.32	24.17	7.59	110.00
Causeway dunes	13.18	5.34	2.81	6.59	2.08	30.00
Yellow dunes	256.21	103.75	54.70	128.11	40.23	583.00
Fixed dunes	232.04	93.97	49.54	116.02	36.43	528.00
Dune-slack transition	37.80	15.31	8.07	18.89	5.93	86.00
Slack	138.43	56.05	29.56	69.22	21.74	315.00
sum	726.00	294.00	155.00	363.00	114.00	1652.00
Chi-square						
Habitat	**Level**	**North**	**East**	**South**	**West**	**sum**
Young dunes	13.28	96.32	1.81	4.28	1.70	117.39
Causeway dunes	0.01	3.53	1.17	8.32	0.55	13.58
Yellow dunes	15.59	0.92	0.34	21.02	6.99	44.86
Fixed dunes	12.12	3.86	13.08	0.04	3.06	32.16
Dune-slack transition	32.03	3.87	4.36	25.85	0.15	66.26
Slack	225.21	56.05	29.56	69.22	21.74	401.78
sum	298.24	164.55	50.32	128.73	34.19	**676.03**

$\chi^2_{(20)}$ = 676.03, significant at the 0.1% level.

Chi-square analysis of aspect categories with presence and absence of *Acaena* (excluding the level aspect category).

Observed	Aspect								
Acaena	**North**	**North-east**	**East**	**South-east**	**South**	**South-west**	**West**	**North-west**	**sum**
present	133.00	11.00	52.00	25.00	217.00	10.00	45.00	18.00	511.00
absent	163.00	13.00	39.00	15.00	146.00	8.00	20.00	13.00	417.00
sum	296.00	24.00	91.00	40.00	363.00	18.00	65.00	31.00	928.00
Expected									
Acaena	**North**	**North-east**	**East**	**South-east**	**South**	**South-west**	**West**	**North-west**	**sum**
present	162.99	13.22	50.11	22.03	199.88	9.91	35.79	17.07	511.00
absent	133.01	10.78	40.89	17.97	163.12	8.09	29.21	13.93	417.00
sum	296.00	24.00	91.00	40.00	363.00	18.00	65.00	31.00	928.00
Chi-sq									
Acaena	**North**	**North-east**	**East**	**South-east**	**South**	**South-west**	**West**	**North-west**	**sum**
present	5.52	0.37	0.07	0.40	1.47	0.00	2.37	0.05	10.25
absent	6.76	0.46	0.09	0.49	1.80	0.00	2.90	0.06	12.56
sum	12.28	0.83	0.16	0.89	3.27	0.00	5.27	0.11	**22.81**

$\chi^2_{(7)}$ = 22.81, significant at the 1% level.

Chi-square analysis of habitat type with aspect categories (excluding slack data and level aspect category).

Observed	**Aspect**				
Habitat	**North**	**East**	**South**	**West**	**sum**
Young dunes	63.00	6.00	14.00	4.00	87.00
Causeway dunes	1.00	1.00	14.00	1.00	17.00
Yellow dunes	94.00	59.00	180.00	57.00	390.00
Fixed dunes	113.00	75.00	114.00	47.00	349.00
Dune-slack transition	23.00	14.00	41.00	5.00	83.00
sum	294.00	155.00	363.00	114.00	926.00
Expected					
Habitat	**North**	**East**	**South**	**West**	**sum**
Young dunes	27.63	14.56	34.10	10.71	87.00
Causeway dunes	5.38	2.85	6.67	2.10	17.00
Yellow dunes	123.83	65.28	152.88	48.01	390.00
Fixed dunes	110.81	58.42	136.81	42.96	349.00
Dune-slack transition	26.35	13.89	32.54	10.22	83.00
sum	294.00	155.00	363.00	114.00	926.00
Chi-square					
Habitat	**North**	**East**	**South**	**West**	**sum**
Young dunes	45.31	5.04	11.85	4.20	66.40
Causeway dunes	3.58	1.20	8.08	0.57	13.43
Yellow dunes	7.18	0.60	4.81	1.68	14.27
Fixed dunes	0.04	4.71	3.80	0.38	8.93
Dune-slack transition	0.43	0.01	2.20	2.66	5.30
sum	56.54	11.56	30.74	9.49	**108.33**

$\chi^2_{(12)}$ = 108.33, significant at the 0.1% level.

Chi-square analysis of scaled categories of *Ammophila* with presence and absence of *Acaena* (including slack data).

Obs	***Ammophila (%)***											
Acaena	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
present	9.00	118.00	140.00	125.00	122.00	84.00	53.00	34.00	30.00	7.00	3.00	725.00
absent	386.00	170.00	82.00	58.00	79.00	56.00	49.00	33.00	39.00	20.00	12.00	984.00
sum	395.00	288.00	222.00	183.00	201.00	140.00	102.00	67.00	69.00	27.00	15.00	1709.00
Exp												
Acaena	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
present	167.57	122.18	94.18	77.63	85.27	59.39	43.27	28.42	29.27	11.45	6.37	725.00
absent	227.43	165.82	127.82	105.37	115.73	80.61	58.73	38.58	39.73	15.55	8.63	984.00
sum	395.00	288.00	222.00	183.00	201.00	140.00	102.00	67.00	69.00	27.00	15.00	1709.00
Chi-sq												
Acaena	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
present	150.05	0.14	22.29	28.90	15.82	10.20	2.19	1.09	0.02	1.73	1.78	234.21
absent	110.56	0.11	16.43	21.29	11.66	7.51	1.61	0.81	0.01	1.28	1.31	172.58
sum	260.61	0.25	38.72	50.19	27.48	17.71	3.80	1.90	0.03	3.01	3.09	**406.79**

$\chi^2_{(10)}$ = 406.79, significant at the 0.1% level.

Chi-square analysis of scaled categories of *Ammophila* with presence and absence of *Acaena* (excluding slack data).

Obs	*Ammophila (%)*											
Acaena	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
present	8.00	117.00	140.00	124.00	122.00	84.00	53.00	34.00	30.00	7.00	3.00	722.00
absent	45.00	147.00	79.00	57.00	78.00	55.00	50.00	33.00	39.00	20.00	12.00	615.00
sum	53.00	264.00	219.00	181.00	200.00	139.00	103.00	67.00	69.00	27.00	15.00	1337.00
Exp												
Acaena	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
present	28.62	142.56	118.26	97.74	108.01	75.06	55.62	36.18	37.27	14.58	8.10	722.00
absent	24.38	121.44	100.74	83.26	91.99	63.94	47.38	30.82	31.73	12.42	6.90	615.00
sum	53.00	264.00	219.00	181.00	200.00	139.00	103.00	67.00	69.00	27.00	15.00	1337.00
Chi-sq												
Acaena	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
present	14.86	4.58	3.99	7.05	1.82	1.06	0.12	0.13	1.42	3.94	3.21	42.18
absent	17.44	5.38	4.69	8.28	2.13	1.25	0.15	0.16	1.66	4.63	3.77	49.54
sum	32.30	9.96	8.68	15.33	3.95	2.31	0.27	0.29	3.08	8.57	6.98	**91.72**

$\chi^2_{(10)} = 91.72$, significant at the 0.1% level.

Chi-square analysis of scaled categories of *Ammophila* (where present only) with paths.

Observed	*Ammophila*										
Path	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
absent	201.00	153.00	127.00	155.00	114.00	85.00	54.00	57.00	27.00	15.00	988.00
present	67.00	67.00	54.00	45.00	26.00	17.00	13.00	12.00	0.00	0.00	301.00
sum	268.00	220.00	181.00	200.00	140.00	102.00	67.00	69.00	27.00	15.00	1289.00
Expected											
Path	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
absent	205.42	168.63	138.73	153.30	107.31	78.18	51.35	52.88	20.70	11.50	988.00
present	62.58	51.37	42.27	46.70	32.69	23.82	15.65	16.12	6.30	3.50	301.00
sum	268.00	220.00	181.00	200.00	140.00	102.00	67.00	69.00	27.00	15.00	1289.00
Chi-sq											
Path	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
absent	0.10	1.45	0.99	0.02	0.42	0.59	0.14	0.32	1.92	1.07	7.02
present	0.31	4.75	3.26	0.06	1.37	1.95	0.45	1.05	6.31	3.50	23.01
sum	0.41	6.20	4.25	0.08	1.79	2.54	0.59	1.37	8.23	4.57	**30.03**

$\chi^2_{(9)} = 30.03$, significant at the 0.1% level.

Chi-square analysis of scaled categories of *Ammophila* (where present only) with warrens.

Observed	*Ammophila*										
Warren	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
absent	158.00	125.00	124.00	156.00	124.00	101.00	65.00	68.00	27.00	15.00	963.00
present	110.00	95.00	57.00	44.00	16.00	1.00	2.00	1.00	0.00	0.00	326.00
sum	268.00	220.00	181.00	200.00	140.00	102.00	67.00	69.00	27.00	15.00	1289.00
Expected											
Warren	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
absent	200.22	164.36	135.22	149.42	104.59	76.20	50.06	51.55	20.17	11.21	963.00
present	67.78	55.64	45.78	50.58	35.41	25.80	16.94	17.45	6.83	3.79	326.00
sum	268.00	220.00	181.00	200.00	140.00	102.00	67.00	69.00	27.00	15.00	1289.00
Chi-sq											
Warren	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
absent	8.90	9.43	0.93	0.29	3.60	8.07	4.46	5.25	2.31	1.28	44.52
present	26.30	27.80	2.75	0.86	10.64	23.84	13.18	15.51	6.83	3.79	131.50
sum	35.20	37.23	3.68	1.15	14.24	31.91	17.64	20.76	9.14	5.07	**176.02**

$\chi^2_{(9)}$ = 176.02, significant at the 0.1% level.

Chi-square analysis of scaled categories of bare ground with presence and absence of *Acaena* (including slack data).

Obs	**Bare ground *(%)***											
Acaena	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
present	246.00	209.00	104.00	73.00	44.00	24.00	15.00	6.00	3.00	0.00	1.00	725.00
absent	466.00	179.00	59.00	45.00	57.00	43.00	36.00	22.00	15.00	15.00	47.00	984.00
sum	712.00	388.00	163.00	118.00	101.00	67.00	51.00	28.00	18.00	15.00	48.00	1709.00
Exp												
Acaena	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
present	302.05	164.60	69.15	50.06	42.85	28.42	21.63	11.88	7.64	6.36	20.36	725.00
absent	409.95	223.40	93.85	67.94	58.15	38.58	29.37	16.12	10.36	8.64	27.64	984.00
sum	712.00	388.00	163.00	118.00	101.00	67.00	51.00	28.00	18.00	15.00	48.00	1709.00
Chi-sq												
Acaena	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
present	10.40	11.98	17.57	10.51	0.03	0.69	2.04	2.91	2.81	6.36	18.41	83.71
absent	7.66	8.83	12.94	7.75	0.02	0.51	1.50	2.14	2.07	4.69	13.57	61.68
sum	18.06	20.81	30.51	18.26	0.05	1.20	3.54	5.05	4.88	11.05	31.98	**145.39**

$\chi^2_{(10)}$ = 145.39, significant at the 0.1% level.

Chi-square analysis of scaled categories of bare ground with p/a of *Acaena* (excluding slack data).

Observed	**Bare ground *(%)***											
Acaena	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
present	246.00	209.00	102.00	73.00	44.00	24.00	15.00	6.00	3.00	0.00	0.00	722.00
absent	239.00	124.00	53.00	39.00	49.00	39.00	31.00	16.00	10.00	6.00	8.00	614.00
sum	485.00	333.00	155.00	112.00	93.00	63.00	46.00	22.00	13.00	6.00	8.00	1336.00
Expected												
Acaena	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
present	262.10	179.96	83.76	60.53	50.26	34.05	24.86	11.89	7.03	3.24	4.32	722.00
absent	222.90	153.04	71.24	51.47	42.74	28.95	21.14	10.11	5.97	2.76	3.68	614.00
sum	485.00	333.00	155.00	112.00	93.00	63.00	46.00	22.00	13.00	6.00	8.00	1336.00
Chi-sq												
Acaena	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**sum**
present	0.99	4.69	3.97	2.57	0.78	2.96	3.91	2.92	2.31	3.24	4.32	32.66
absent	1.16	5.51	4.67	3.02	0.92	3.49	4.60	3.43	2.71	3.81	5.08	38.40
sum	2.15	10.20	8.64	5.59	1.70	6.45	8.51	6.35	5.02	7.05	9.40	**71.06**

$\chi^2_{(10)} = 71.06$, significant at the 0.1% level.

Chi-square analysis of scaled categories of bare ground with presence and absence of warrens.

Observed	**Bare ground**									
Warren	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-100**	**sum**
absent	624.00	271.00	112.00	93.00	78.00	49.00	41.00	23.00	33.00	1324.00
present	84.00	117.00	48.00	25.00	22.00	17.00	10.00	5.00	0.00	328.00
sum	708.00	388.00	160.00	118.00	100.00	66.00	51.00	28.00	33.00	1652.00
Expected										
Warren	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-100**	**sum**
absent	567.43	310.96	128.23	94.57	80.15	52.90	40.87	22.44	26.45	1324.00
present	140.57	77.04	31.77	23.43	19.85	13.10	10.13	5.56	6.55	328.00
sum	708.00	388.00	160.00	118.00	100.00	66.00	51.00	28.00	33.00	1652.00
Chi-sq										
Warren	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-100**	**sum**
absent	5.64	5.14	2.05	0.03	0.06	0.29	0.00	0.01	1.62	14.84
present	22.77	20.73	8.29	0.11	0.23	1.16	0.00	0.06	6.55	59.90
sum	28.41	25.87	10.34	0.14	0.29	1.45	0.00	0.07	8.17	**74.74**

$\chi^2_{(8)} = 74.74$, significant at the 0.1% level.

Chi-square analysis of scaled categories of bare ground with presence and absence of paths.

Observed	**Bare ground**									
Path	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-100**	**sum**
absent	604.00	294.00	121.00	85.00	87.00	53.00	43.00	26.00	27.00	1340.00
present	104.00	94.00	39.00	33.00	13.00	13.00	8.00	2.00	6.00	312.00
sum	708.00	388.00	160.00	118.00	100.00	66.00	51.00	28.00	33.00	1652.00
Expected										
Path	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-100**	**sum**
absent	574.29	314.72	129.78	95.71	81.11	53.54	41.37	22.71	26.77	1340.00
present	133.71	73.28	30.22	22.29	18.89	12.46	9.63	5.29	6.23	312.00
sum	708.00	388.00	160.00	118.00	100.00	66.00	51.00	28.00	33.00	1652.00
Chi-sq										
Path	**0**	**1-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-100**	**sum**
absent	1.54	1.36	0.59	1.20	0.43	0.01	0.06	0.48	0.01	5.68
present	6.60	5.86	2.55	5.15	1.83	0.02	0.28	2.04	0.01	24.34
sum	8.14	7.22	3.14	6.35	2.26	0.03	0.34	2.52	0.02	**30.02**

$\chi^2_{(8)} = 30.02$, significant at the 0.1% level.