A COMPARATIVE STUDY OF *CORYNEPHORUS CANESCENS* (L.) P.Beauv. COMMUNITIES OF INLAND SAND DUNES IN ENGLAND AND POLAND

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This work or any part thereof has not previously been presented in any form to the University or to any other body whether for the purposes of assessment, publication or for any other purpose (unless otherwise indicated). Save for any express acknowledgements, references and/or bibliographies cited in the work, I confirm that the intellectual content of the work is the result of my own efforts and of no other person.

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ABSTRACT

Inland sand dunes supporting Grey Hair-grass *Corynephorus canescens* are a declining European habitat designated for conservation under the EU's Habitats Directive. In Britain they are confined to a handful of sites in East Anglia and the West Midlands. This study investigated the relationships of the British populations to each other and to populations on five sites in Poland, where *C. canescens* is still widespread. It also conducted exploratory investigations into factors relevant to the conservation of this ecosystem, particularly in the West Midlands.

Data were collected chiefly from 1m^2 quadrat samples and direct sampling, which recorded the plants and animals present together with parameters such as vigour and fecundity in *C. canescens*, amounts of bare sand and litter, and measures of erosion and grazing. These data were variously analysed including by CANOCO multivariate analysis and, for the vegetation, TWINSPAN analysis.

153 taxa of plants and 251 of invertebrates were identified. Though strongly distributed on a regional basis, both flora and invertebrate fauna showed relationships particularly between Polish and West Midlands sites. Analysis of the vegetation suggested that West Midlands vegetation had some associations with *C. canescens* habitats in Europe and that East Anglian vegetation had links with British coastal *C. canescens* habitats. The invertebrate fauna showed some complex community relationships in Poland and the West Midlands but less so in East Anglia, while assemblages of invertebrates were associated with various vegetational and abiotic factors. Rabbits and hares were the only vertebrates regularly exploiting *C. canescens* habitats, which they grazed and, in the former case, produced sand disturbances for colonisation by *C. canescens*. Ants and to a lesser degree some other invertebrates also produced sand disturbances.

Observations made in a preliminary cultivation study in the West Midlands suggested that *C. canescens* may have a biennial phenology, high fecundity, low germination rates and limited dispersal powers in that region. A trampling investigation suggested that *C. canescens* may be very sensitive to heavy uncontrolled trampling and to vegetational succession under protection. Stages in succession of the *C. canescens* community were identified, and suggestions for further study and the conservation of *C. canescens* were drawn up.

CONTENTS

Chapter 1: Introduction

Chapter 2: Grey Hair-grass *Corynephorus canescens*: literature review

Chapter 3: The Study Sites

Chapter 4: General Methods

Chapter 5: Preliminary field investigations

Chapter 6: The *Corynephorus canescens* community (floral)

Chapter 7: The *Corynephorus canescens* community (faunal)

Page

Chapter 8: General conclusions and discussion

Page

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Plate 1: *Corynephorus canescens*

CHAPTER 1: INTRODUCTION

1.1 Background to this study

The foundations of this study were laid in 1986 when the author's brother, Michael Edwin Blunt, became Warden of the National Trust's property at Kinver Edge in south Staffordshire. This appointment coincided with a move by the Trust to integrate nature conservation values more fully into the management of Kinver Edge, which hitherto had been managed chiefly for its landscape, archaeological and amenity value.

Kinver Edge was notified as a Site of Special Scientific Interest (SSSI) by the Nature Conservancy in April 1968 and the notification was renewed in 1986, as an important link within a cluster of lowland heaths stretching between Cannock in Staffordshire and Hartlebury in northern Worcestershire. These heathland habitats have been characterised by Rodwell (1991) as falling chiefly within the National Vegetation Classification H9 *Calluna vulgaris*-*Deschampsia flexuosa* heath.

An apparent anomaly is the existence at Kinver Edge and two other nearby heathlands of small sand dune areas supporting colonies of Grey Hair-grass *Corynephorus canescens*. The Kinver Edge colony was the first to be discovered, by I. C. Trueman in 1977. Trueman reports (pers. comm.) that these discoveries led to speculation that the grass was recently introduced to the area, possibly originating from wartime tank-training exercises.

Being the rarest vascular plant species on Kinver Edge, Grey Hair-grass naturally became a priority species for conservation within the National Trust's management plan for the property, and field trials were conducted after 1986 to increase its population. These were instigated by M. E. Blunt and observed by the author, who thereby became familiar with *C. canescens* and its conservation at this site.

In June 1994 the author had an opportunity to visit Poland on a Socrates exchange programme with the University of Łódź. While there, he observed colonies of *C. canescens* widely on inland dunes and was intrigued by the possibility that study of these colonies might throw some light on the origins of those at Kinver Edge and neighbouring heaths. The visit also cemented close links with staff of the Department of Invertebrate Zoology and Hydrobiology at the University of Łódź, and in particular Dr (now Professor) Wojciech Jurasz. Further visits to Poland in 1995, 1997 and 1999 helped the author widen his experience of *C. canescens* there; an initial selection of sites for further study was made; and some data collection, principally invertebrate sampling, was carried out.

The publication of a comprehensive review of all extant U.K. populations of *C. canescens* by Trist (1998) prompted the author and M. E. Blunt to carry out a re-assessment of the size of the Kinver Edge populations resulting from the post-1986 management trials. This led to the publication of a Note in *Watsonia* (Blunt & Blunt, 2000). Trist's (*loc. cit.*) paper also showed the feasibility of a detailed study of all inland populations of the grass in the U.K., since these are restricted to two very localised areas – around Kidderminster in south-west Staffordshire and northern Worcestershire (including Kinver Edge and neighbouring heaths), and in Suffolk in the neighbouring parishes of Wangford and Lakenheath. Consequently, the author put a proposal to the University of Wolverhampton's Research Degrees Committee for a programme of study leading to the award of PhD, and this proposal was accepted with registration dated 1 June 2000.

1.2 Aims of the study

The study's aims follow directly from the author's interest in and experience of *C. canescens* habitats from 1986 to the present, as described above. They are:

- to seek evidence for the naturalness or otherwise of the West Midlands *C. canescens* populations by comparing their associated floral and faunal communities with those of other British inland *C. canescens* sites and Polish sites in the heart of the grass's native range;

- to establish key community relationships between and within the chosen *C. canescens* sites;

- to identify key factors with nature conservation implications for the British inland *C. canescens* populations.

1.3 Objectives of the study

In order to achieve the Aims of this study, the following Objectives were established:

- to review literature studies on the distribution and autecology of *C. canescens*, its relationships with other plants, animals and pathogens, and its conservation in both a British and European context;

- to establish criteria for the selection of study sites in Britain and Poland; to describe these sites in detail and to assess the advantages and limitations of this selection;

- to select methods of data collection and analysis for both vegetational and faunal elements of the *C. canescens* habitats of the study sites, and to assess the advantages and limitations of this selection;

- to extract from the literature factors which have implications for the conservation of British inland *C. canescens* populations; to select factors where further study may throw additional light on conservation measures particularly of the West Midlands populations; to explore those factors by carrying out preliminary field investigations, analysing results and formulating hypotheses for detailed experimental study;

- to investigate the plant communities of the selected sites; to analyse these communities by various means including multivariate analysis and community classification so as to explore relationships between sites, regions and countries; and to investigate the phytosociological relationships between these communities and established phytosociologies in both Britain and Poland;

- to investigate the invertebrate and vertebrate communities of the selected sites; to analyse these communities so as to explore similarities and differences between sites, regions and countries; to investigate the invertebrate fauna by various means including multivariate analysis so as to explore inter-relationships within the invertebrate fauna and relationships with selected vegetational and environmental parameters; and to investigate how the vertebrate and invertebrate fauna may impact directly on the *C. canescens* populations;

- to extract and discuss the key findings of the study in relation to its Aims, and to identify further issues for investigation arising from this study.

CHAPTER 2: GREY HAIR-GRASS *CORYNEPHORUS CANESCENS*: LITERATURE REVIEW

2.1 Species Description

A detailed description of Grey Hair-grass *Corynephorus canescens* (L.) P.Beauv. is given in the Biological Flora of the British Isles by J. K. Marshall (1967), and is drawn upon extensively by later authors in English such as Stace (1991) and Trist (1998). Marshall describes *C. canescens* as follows:

"A vertically growing, tufted, glaucous perennial of variable life-span, to 10(-30) cm tall with a finely-divided, fibrous root system and no rhizome. Leaf blades inrolled, setaceous, rigid, scabrid, pungent, erect to sub-erect, 3-6 cm long, 0.3-0.5 mm wide. Ligule acute, 2-4 mm. Leaf sheaths inflated, smooth, often purplish. Culms smooth or slightly rough, spreading to erect, slender with four to seven nodes, straw-coloured to variegated green/pink to pink. Panicle lanceolate to spreading at anthesis; culm erection sometimes coincides with anthesis. Panicles becoming dense in fruit, 1.5-8 cm long, 0.5-1.5 cm wide, variegated pale green and purple, or purple; branches short; pedicels 1-3 mm long. Spikelets two-flowered, lanceolate, compressed, 3-4 mm long, breaking up at maturity below each lemma. Glumes lanceolate, acuminate, nearly equal, slightly scabrid on keel, membranous with thinner white tips and margins, one-nerved. Lemma lanceolate, sub-obtuse, enclosed by glumes and with tuft of hairs at base, awned from base, 1.5-2 mm long. Awn equally divided, basal half orange to chestnut brown, twisted; upper half club-shaped, denticulate or papillate, geniculate, with short tuft of minute, stout hairs at the junction of the halves, the whole not exceeding the glumes, *c*. 2.5 mm. Palea slightly shorter than lemma, obtuse, two-nerved, both remaining in the closest association with the ovary when the caryopsis is shed. Lodicules two, anthers three, orange or purple, 1-1.5 mm long. Ovary globose with two very short, feathery stigmata. Caryopsis elliptical inside view, slightly compressed end-on, weighing in the order of 0.12 mg, oven-dry weight."

Some further details are added by Hubbard (1984), who gives a maximum tussock height of 35 cm and culms from 2- to 7-noded. He also specifies a flowering period of June - July and a chromosome number of 2n = 14. No chromosome races are given by British or Polish authors.

Marshall's account draws upon British, western European and Czech sources, but he cites no Polish authorities and makes no specific reference to Polish localities. For a description of the plant in Poland, therefore, we turn to Podbielkowski (1992), who says that it:

"forms close, compact, conjoined tussocks sometimes with long, thin tillers. It attains 30 cm in height. This grass is perennial, with numerous straight stems and rigid, slender, subulate leaves. The leaf-sheaths are blunt, infused with pink or crimson, a little swollen. The leaf ligule is about 3 mm long and ends bluntly. The whole plant is of a grey-green colour. The inflorescence is a spike-like, silvery-grey panicle enlarging a little at time of flowering. The spikelets are at first light greenish-grey, sometimes infused with pink; after flowering they adopt a silvery-grey colour. The glumes end in a sharp point and are twice as long as the lemmas. From near the bottom of the lower lemma arises the awn, which is brown below, white in the upper part and thickening into a club, furnished in the middle with a ring of short hairs. The anthers have a bluish-crimson or brown colour, rarely yellow. The flowers are pollinated by the wind. It flowers in July and August. The fruit is a seed longer than broad, closely surrounded by tightly-fitting lemmas."[1]

The shape of the awn is the key feature defining the genus (*Corynephorus* means "club-bearing" in Greek), and this is reflected in the French vernacular name for *C. canescens* – le Corynéphore; but it is the grass's characteristic silvery-grey hue with pinkish flush which accounts for its generic and many of its vernacular names: *canescens* ("growing grey") in Latin, silbergras ("silver grass") in German; szczotlicha siwa ("grey brush-grass") in Polish; and Grey Hair-grass in English. Besides the widely-used szczotlicha siwa, Rutkowski

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[1] Throughout this thesis translations are my own except where otherwise stated.

(1998) adds a further Polish vernacular name for this species – kozia bródka, meaning “goatee beard”. In the United States (where it is not a native species) *C. canescens* is variously referred to as Silvergrass, Grey Clubawn Grass or Clubgrass (Plate 1).

Besides *C. canescens* the genus includes four other species, all from the Mediterranean basin: *C. articulatus* (Desf.) P.Beauv., *C. divaricatus* (Pourret) Breistr., *C. fasciculatus* Boiss & Reuter and *C. macrantherus* Boiss. & Reuter.

2.2 Distribution

The native distribution of *C. canescens* occupies most of lowland central and western Europe, from Ukraine and Belarus in the east, through all countries bordering the southern Baltic, southern North Sea and the Atlantic Ocean as far south as Portugal (Figure 2.2a). The Carpathians and Alps act as boundaries to the species’ range extension in the south, except that there is an outlying population in the Hungarian plain between the rivers Danube and Tisza (Rychnovská, 1963). *C. canescens* also reaches the French Mediterranean coast of Languedoc, but is absent from much of Spain except for a spur in central Castille. Outside this core range there are scattered coastal populations in southern Norway and Sweden; the eastern Baltic as far north as Riga; Romania, Sardinia and possibly Corsica; plus a few inland sites in northern Italy and northern Morocco (Tutin *et al*., 1980). *C. canescens* has been variously interpreted as an Atlantic, sub-Atlantic, oceanic/suboceanic or European Southern-temperate species (Marshall, 1967; Preston *et al*., 2002; Danihelka, 2006).

For Poland, Podbielkowski (*loc. cit*.) describes *C. canescens* as “a very common lowland grass occurring on mobile dunes, sandy places and among light, dry pine scrub.” Its Polish distribution is mapped by Snowarski (2006) who shows it occurring almost ubiquitously except for the Tatras and neighbouring mountains of Poland’s southern border (Figure 2.2b).

Within the British Isles *C. canescens* is chiefly a plant of coastal dunes and tidal beaches, with the largest populations in East Anglia between Minsmere and Kessingland in Suffolk and Holme-next-the-Sea in Norfolk (Trist, 1998). It appears again on the south Lancashire coast at Ainsdale, a small relict of a formerly more widespread population. On the Scottish coast it grows in three widely-scattered places: Hedderwick near Dunbar (East Lothian); Lossiemouth (Moray); and Toigal near Morar, Arisaig (Highland), where a once-thriving colony is all but extinct (Trist, 1992). Further populations occur on the Jersey coast between St Brelade's Bay and Les Quennevais. Marshall (1967) and Stace (1991) also mention an extinct coastal site near Port Talbot, Glamorgan.

Inland within Britain *C. canescens* has two population centres. In the Breckland of East Anglia it occurs on parts of Lakenheath airfield, and nearby at Wangford Warren where the population is small and vulnerable. These are the recently rediscovered relicts of colonies found near Brandon and Lakenheath in 1883 (Hind, 1889; Trist, 1980).

The second inland population is in south-west Staffordshire and north Worcestershire, centred on Kidderminster: *C. canescens* is here found on heaths at Kinver Edge, the Devil's Spittleful/Rifle Range and Burlish Top. It has spread locally from the last two sites to embankments of the adjacent Severn Valley Railway. An investigation of these Kidderminster area populations was carried out by Hazlehurst (1992). The British distribution of *C. canescens* is shown in Figure 2.2c.

There has been some debate as to the origins of these U.K. populations. Writing before the discovery of the Kidderminster sites and rediscovery of the Breckland ones, Marshall considered only the coastal East Anglian and Jersey colonies truly native; those in Lancashire, Glamorgan and Moray were "doubtfully native" and the population near Arisaig was "certainly introduced" (Marshall, 1967). Subsequent authors (e.g. Stewart *et al*., 1994; Stace, 1997; Wiggington, 1999; Preston *et al*., 2002) have usually followed Marshall's view

Figure 2.2a: map showing the main areas of native distribution of *Corynephorus canescens* (adapted from Hazlehurst, 1992).

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Figure 2.2b: map of the distribution of *Corynephorus canescens* in Poland (adapted from Snowarski, 2006), showing the location of sites investigated in the present study.

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Figure 2.2c: map of the distribution of *Corynephorus canescens* in Britain (adapted from Stewart *et al*., 1994), showing the location of sites investigated in the present study.

Map removed from this electronic version to comply with copyright conditions for coastal sites[2], while the inland Breckland populations are usually treated as native and those around Kidderminster as introductions. Trist (1998), on the other hand, is more inclined to interpret all U.K. inland *C. canescens* sites as “relict areas which have resisted erosion”; while of the Kidderminster sites Hazlehurst (*loc. cit*. p. 69) says “there is therefore nothing to suggest that these recently discovered populations are not locally native, even though some of the locations in which they occur are to a certain extent artificial and have become modified due to varying degrees of disturbance.”

Beyond its native distribution, *C. canescens* occurs as a rare adventive in the New World in parts of Canada, north-east and north-west United States, Ecuador and Chile. It occurs there on sandy soils, waste ground and ballast dumps, but rarely persists. The related *Corynephorus fasciculatus* has been recorded as adventive in Argentina.

2.3 Autecology

Marshall (1967) and Rychnovská-Soudková (1961) are the starting point for autecological studies of this grass and are the principal authors drawn on in the following account, supplemented by others where indicated.

2.3.1 Soil properties

C. canescens occurs on disturbed or open sandy places, tolerating a wide pH range in both Britain and mainland Europe. The pH extremes quoted by Marshall (1967 Table 1) are: for Britain, from 4.1 (Norfolk) to 8.1 (Norfolk, Jersey); for Europe, from 3.7 (Germany) to 8.5 (northern France). Trist (1998) recorded maximum pH values at the Hedderwick site of 8.7, with one exceptional reading of 9.08. The majority of *C. canescens* sites, however, are on acidic soils, especially in the east of its range.

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[2] See Preston *et al*., 2002 for authors arguing a native status for colonies in Lancashire and Scotland.

In most analysed soil samples coarse sand (2.0 – 0.2 mm) predominated, regularly accounting for over 60% of a sample, and sometimes reaching 90%; fine sand (0.2 – 0.02 mm) accounted for no more than 58.5% and often less than 10%. Only in samples from Berlin analysed by Berger-Langfeldt & Sukopp (1965) did coarse sand range from 11.7% - 60.7% and fine sand from 36.5% - 85.4%. Marshall (1967) recorded the silt and clay (<0.02 mm) content mostly below 6% with a maximum value of 14.9%, and a pore space range from 38% to 60%. For Czech sites Rychnovská-Soudková (*loc. cit.*) observed a soil humus content of less than 1%, and found that *C. canescens* occupies substrates which are extremely low in mineral nutrients (N, P, K, Ca, Mg). The species does, however, exhibit some salt tolerance as it grows sporadically within the spring tidal spray zone of coastal sands, though its inability to withstand winter submergence by water excludes it from dune slacks and salt marshes (Marshall, 1967).

2.3.2 Temperature

Open sandy habitats are frequently subject to very high surface temperatures and large diurnal temperature fluctuations. Sand surface temperatures greater than 60°C have been recorded for England, and 70°C for the Upper Rhine dunes, though these values are exceptional, and more normal midsummer maxima at Winterton (Norfolk) fall between 30°C and 45°C. The diurnal temperature range at the same location is about 30°C, rarely 35°C. Soil moisture content is clearly affected by such conditions, though Marshall (1963) found that this effect operates only within the top 5 -10 cm of sand; below 10 cm moisture fluctuations are slight. Mature tussocks of *C. canescens* have a fibrous root system between 25 cm and 40 cm long (exceptionally 60 cm) and can normally cope with high temperature and transpiration levels; but seedling survival is badly affected by spring droughts when the depth of dry sand exceeds the root length of the young plant. In experiments, air-dried seed of *C. canescens* was found to retain its viability when exposed to temperatures of 80°C for three days; but 30°C was enough to reduce germination of imbibed seed. The grass also appears to be rather sensitive to winter and spring frosts (Marshall, 1967). Rychnovská-Soudková

(1961) considered the increasing incidence of summer droughts a range-limiting factor for this species in eastern Europe, with droughts in excess of 50 consecutive days being the critical level; while Marshall (1963) believed that temperature combined with a shorter growing period determines the species' northern range limits, by delaying the onset of germination and lessening the chance of seedling survival. *C. canescens* does not appear to reach its climatic limit in the British Isles, however, since the most northerly population at Lossiemouth is maintaining itself.

2.3.3 Sand erosion and accretion

Marshall (1963, 1965) and Rychnovská-Soudková (1961) showed that *C. canescens* tends to be self-eliminating under stable sand conditions, following the accumulation of humus which restricts the rate of the grass's root respiration and promotes conditions for the establishment of competitor species. Marshall (1967) concluded that *C. canescens* grows best where active sand accretion takes place: up to 10 cm of accretion per year provokes mature tussocks to elongate vegetatively from internodes low down on the stem. Individual clumps of *C. canescens* can in favourable conditions enlarge to 50 cm across, though between 2 cm and 25 cm is more usual. However, *C. canescens* cannot withstand complete burial by sand, and an accretion rate above 2 cm per year is enough to prevent the establishment of newly-germinated seedlings.

In Breckland Trist (1998) noted the reduction of sand storms and erosion following the extensive planting of conifers by the Forestry Commission in the 1920s. This protection from wind has halted sand erosion around the *C. canescens* colony at Wangford Warren, thereby reducing its vigour and necessitating conservation measures to produce sand accretion artificially. Wind is assumed by most authors to be the significant environmental factor promoting sand erosion at *C. canescens* sites, but Blunt & Blunt (2000) observed a significant local erosion at Kinver Edge produced by a heavy thunderstorm; and both they and Trist (*loc. cit.*) speculate that trampling by walkers may be a key factor influencing sand conditions at some *C. canescens* localities.

2.3.4 Reproduction, survival and longevity

According to Marshall (1967) and Böger (2006) *C. canescens* is wind-pollinated and its flowers are self-compatible. Anthesis is at a maximum in mid-July and continues up to October. Seed is set in abundance, with larger plants able to produce in theory as many as 36,000 viable caryopses; seed distribution is by wind and gravity, though some panicles may also be buried by sand accretion (Stoutjesdijk, 1959). Caryopses are shed from early August onwards, with the main dispersal period probably being early September. In laboratory conditions, air-dried seed retains a high level of viability for at least five years. Germination occurs abruptly following rain, provided that the sand surface layer remains moist long enough for imbibition. In field germination trials in Britain the highest proportion of seedlings produced was 65% of seed laid down; these field trials also demonstrated that seed set down between October and March failed to produce any seedlings capable of surviving winter frosts, spring droughts or sand accretion above 2 cm (Marshall, 1967).

In the continental climate of the Toruń Basin, Poland, Symonides (1979) conducted field observations of three populations of *C. canescens* over an eight-year period. She reported seed production and germination to be much lower than might be expected from studies such as Marshall’s. In her trials, similar-aged tussocks produced a similar number of panicles, increasing from 1-3 for a yearling plant to 18-23 for a four-year-old plant, by which age seed production had increased tenfold from its first flowering season. Symonides also recorded no more than about 1,150 caryopses produced per tussock, and a germination rate in the field ranging from a low value of 0.004% to a maximum of 16.25%; though in laboratory conditions she obtained germination rates from 62% to 68.5% for all three of her study populations. In the most hostile environmental conditions of her Site 1 (as defined by Symonides, *loc. cit.*), the greatest reproductive potential within the *C. canescens* population was contributed by two- to three-year-old tussocks; in less arid and more stable sand conditions the greatest contribution was made by three- to four-year-old plants. Tussocks lived for up to seven years but their seed production fell rapidly after their fourth or fifth season. In her study plots Symonides recorded consistently high seedling mortality, at least 80% dying within two months; and like Marshall earlier, she found that no seedling which germinated after mid-October survived the winter. More recently Jentsch (2001) and Jentsch & Beyschlag (2003) have reported an accumulation of *C. canescens* seeds up to 1,000 m^{-2} in the seed-bank of German sand dunes, but a very limited seed viability of no more than two or three years, with clear implications for the long-term viability of weakening *C. canescens* populations.

The response of this grass to sand accretion by producing tillers has been described in 2.3.3, and this response was considered by Marshall (1967) as essential for maintaining an individual tussock's vigour and longevity. Where sand remains unstable and regular accretion occurs, *C. canescens* is potentially a long-lived perennial. Trist (1998) further considered vegetative propagation rather than seed production to be the chief means whereby *C. canescens* maintains itself at Wangford Warren. Conversely, under stable sand conditions the life-span of individual plants is limited: Symonides (1979) assessed the average life span at her Polish site to be between seven and nine months, but for those plants which survived to flowering, a minimum of two growing seasons; other minimum values are, for Czechoslovakia 3-4 seasons, for Britain 2 seasons (but 5-6 seasons at Winterton, Norfolk) (Marshall, 1967); while for north-west Germany 2 growing seasons is regarded as the plant's normal life-span (Tüxen, quoted in Marshall, *loc. cit.*). Marshall also considered that, *pace* Trist's comments about the Wangford population, the long-term maintenance of a *C. canescens* community depends upon reproduction by seed. At Kinver Edge Blunt & Blunt (2000) found that seed production was overwhelmingly the means whereby *C. canescens* recolonised disturbed sand.

2.3.5 Response to competition

It is widely agreed that *C. canescens* is very sensitive to competition by other plant species and fails to maintain itself in stable soil conditions once competitors have become established. There are several ways in which the grass can be eliminated. On coastal dunes *Ammophila arenaria* tussocks may trap a greater depth of mobile sand than can be withstood by *C. canescens* seedlings (Marshall, 1967). Both Marshall (*loc. cit*.) and Trist (1998) record, for Winterton and Wangford respectively, encroachment by *Carex arenaria* leading to the demise of *C. canescens* plants through competition for moisture. In Germany an invasion of sand dunes by the alien grass *Cynodon dactylon* has displaced *C. canescens* from several sites (Biedermann *et al*., 2005); while in Poland Symonides (1979) found that the spread of *Polytrichum piliferum* on moister, cooler parts of dunes prevented the establishment and growth of seedlings of a range of species including *C. canescens*. When this happened the *C. canescens* population experienced fast changes in age structure, a population decrease, a decline in fertility and biomass, and ultimately the mass withering of tussocks. At Kinver Edge Blunt & Blunt (*loc. cit*.) also found that the arrival of *Polytrichum piliferum* led to a rapid succession, continuing with *Rumex acetosella*, *Deschampsia flexuosa*, *Festuca rubra* and *Hypochaeris radicata*, followed within three years by the appearance of seedlings of woody plants, notably *Calluna vulgaris* and *Ulex europaeus*. At this site a *C. canescens* population declined through the processes of succession within six years of its initial establishment.

Only rarely has *C. canescens* appeared to show better competitive powers than indicated above. In the most extreme habitat conditions on her Polish study area Symonides (*loc. cit.*) found some long-term stability of a *C. canescens* community throughout the eight years of her observations. On this site the vegetation consisted exclusively of two species*, C. canescens* and *Spergula morisonii (= vernalis)*; seedlings of four other species appeared during the study period but none survived longer than three months. During those eight years Symonides observed a 40-fold increase in the *C. canescens* population and a fourfold increase in that of *Spergula morisonii*; the latter species always outnumbered the former, but its proportion of the total biomass of the community fell from 36.7% in the first year to 1% in the final year, in inverse proportion to the biomass contribution of *C. canescens*. In controlled experiments on sand, Weigelt *et al*. (2002, 2004) found that *C. canescens* and *Festuca ovina* were the most competitive species in pair-wise competition plots in which *Deschampsia flexuosa*, *Carex arenaria*, *Hieracium pilosella* and *Jasione montana* were also trialled. The competitiveness of *C. canescens* was positively and significantly correlated with its biomass. However, these results were not replicated in either multi-species plots using the full suite of species or in field trials using *C. canescens*, *Hieracium pilosella* and *Carex arenaria*. The authors concluded that in pioneer vegetation of inland sand dunes a biomass advantage is crucial only for successful seedling establishment.

2.3.6 Grazers and pathogens

Rabbits and Brown Hares: *C. canescens* is an evergreen grass low in mineral nutrients (Rychnovská-Soudková, 1961). In Britain it is grazed by rabbits *Oryctolagus cuniculus* and brown hares *Lepus europaeus*, especially in winter and early spring, and an increase in populations of the grass at Blakeney Point, Norfolk, during the 1950s was attributed by White (1961) to a decline in rabbits following the onset of myxomatosis in 1954. At Wangford, however, Trist (1998) found that rabbit grazing was “confined to biting off a few inflorescences, which matters little as the loss of potential seed is probably of little account.” He further suggested that by grazing on young shoots of the vigorous competitor *Carex arenaria*, and disturbing sand through their burrowing activities, rabbits may be beneficial to the survival of *C. canescens* at this site. In Europe the effects of rabbit grazing on a vegetation mosaic including *C. canescens* have been studied by Oosterveld (1983) and Kuiters & Slim (2003) on abandoned agricultural land near the Dutch-Belgian border. They discovered that rabbits were significant grazers across the site in the early stages after abandonment, but as coarse grasses increased they preferentially grazed the *C. canescens* vegetation. Further discussion of rabbit grazing on *C. canescens* habitats is made in Chapter 7.4.2.

Domestic animals: studies of grazing by domestic animals on dunes supporting *C. canescens* have been carried out by Kuiters & Slim (*loc. cit*.), Kooijman & van der Meulen (1996) and Kooijman & Smit (2001) in the Netherlands, Peco *et al*. (2005) in Spain, and Tschöpe *et al*. (2002) in Germany. A general conclusion of these authors is that *C. canescens* grassland is not a preferential grazing habitat of large domestic herbivores. In Kooijman & van der Meulen's study, *C. canescens* cover decreased extensively (40% to 9%) over four years of grazing by cattle and ponies; while Peco *et al*. (*loc. cit*.) found that *C. canescens* was significantly linked ($P=0.019$) to the abandonment of grazing by cattle, sheep and goats. Kooijman & Smit (*loc. cit*.) recorded a shift of nutrients, with significantly reduced concentrations of potassium and nitrogen, in *C. canescens* communities as a result of cattle and pony grazing, but concentrations of phosphorus were unaffected.

Invertebrates: thirteen invertebrate species, from the Orders Lepidoptera and Hemiptera, are known or suspected to feed on *C. canescens* (Carvalho & Wagner, 1957; Gorczyca, 1994; Tuzov *et al*., 1997; University of York, 2001; Nickel & Remane, 2002; Viskens, 2004; Eliasson *et* al., 2005; Savela, 2006). None of these is monophagous on the grass, and for several species *C. canescens* is only a secondary pabulum. Two bugs, *Trigonotylus pulchellus* and *Neophilaenus minor*, appear to feed preferentially on *C. canescens*, and *N. minor* is of conservation concern, being Red Data Book listed in Germany (Nickel & Remane, 2002). Only one invertebrate species, *Anerastia lotella* (Lepidoptera: Pyralidae), has been associated with *C. canescens* in Britain (University of York, 2001). Further details and discussion of invertebrate herbivory on *C. canescens* are addressed in 7.3.3 and Table 7.3ii of the present study.

Pathogens and symbionts of *C. canescens* have been little studied. Marshall (1967) recorded parasitism of the gynoecium and anthers of *C. canescens* plants at Holme, Norfolk, by *Alternaria* sp., (the conidial state of the fungus *Pleospora* (Loculoascomycetes: Pleosporales)). In Poland Błaszkowski *et al*. (2004) found the arbuscular fungus *Glomus insculptum*

(Glomerales: Glomeromycota) in mycorrhizal association with *C. canescens* on inland dunes in Upper Silesia.

2.4 Conservation Issues

2.4.1 *Corynephorus canescens* in European legislation: the phytosociological framework

With the launch of the CORINE (Co-ordination of Information on the Environment) Biotopes Project in 1985 the European Economic Community (now styled the European Union) set about gathering data on ecosystems, habitat types and species as a basis for Community-wide environmental legislation. The CORINE Biotopes Manual was published in 1991 (Anon, 1991) and its classification of European habitats underpinned the Community's major piece of environmental legislation of the following year, widely referred to as the Habitats Directive (HD) (Anon, 1992). By this legislation member states are obliged to identify, and designate as Special Areas of Conservation (SACs), sites which are representative of habitat types listed in Annex 1 to the Habitats Directive. The Community's stated goal in the 1992 legislation is to establish across the continent a network of SACs under the title of *Natura 2000*; once designated, SACs are to be maintained in or restored to a "favourable conservation status" by the member countries concerned.

The HD Annex 1 designates as **habitat type number 2330** "inland dunes with open *Corynephorus* and *Agrostis* grasslands." A more detailed specification of the habitat was published in the EU's *Interpretation Manual* in 1996 and updated in 1999 (Anon, 1999), where habitat 2330 is described slightly differently as "open grassland with *Corynephorus* and *Agrostis* of continental dunes" and is identified with the phytosociological alliance **Corynephorion canescentis (Spergulo vernalis - Corynephoretum s.l.)**. However, the version of the *Interpretation Manual* now used (Anon, 2003a) omits this phytosociological identification and cross-refers Habitat 2330 to UK NVC and Nordic vegetation classifications (see below).

Complications in the process of identifying SACs arise because the CORINE Biotopes Project, and hence the HD Annex 1, draws heavily on the vegetational classifications developed in central Europe. Their application to countries outside that region is often problematical: habitat indicator species listed in the Interpretation Manual may be uncommon or absent; habitats elsewhere may involve geographical suites of species not present in “classic” central European phytosociologies; and many European countries have developed their own systems for classifying their vegetation types, which may sit uncomfortably with HD Annex 1 classifications (Ejrnaes *et al*., 2004).

The issue of identifying SACs in the British Isles well illustrates a number of these points. The Corynephorion canescentis key indicator species *Spergula morisonii* is absent, and *C. canescens* itself is rare (2.2; 2.4.3). The tension between HD Annex 1 and the National Vegetation Classification (NVC) as developed in and for Britain is felt by Rodwell (2000), who somewhat tentatively assigns his **NVC dune communities SD11** and **SD12** to the Corynephorion canescentis, even though *C. canescens* is a “rare species” in the former and not represented at all in the latter. In contrast, he assigns his **NVC community SD10** which includes *C. canescens* in British samples, and which is better represented in Breckland than SD11, to the Ammophilion arenariae. In selecting U.K. SACs the Joint Nature Conservation Committee considers Wangford Warren and Lakenheath SSSI as “the only occurrence in the U.K.” of habitat type 2330 (JNCC, 1999) whereas it treats coastal examples of the same NVC types (SD11 and SD12) as referable to **HD Annex 1 habitat 2130** (“fixed coastal dunes with herbaceous vegetation (‘grey dunes’)”) (JNCC, *loc. cit.*). Further conservation issues surrounding *C. canescens* in Britain are dealt with in 2.4.3 and 2.4.4 below.

Poland’s accession to the European Union on 1 May 2004 brought with it a need to establish a Polish *Natura 2000* network of SACs and to harmonise Polish nature conservation laws with EU legislation. The legal framework for this was set in motion by Poland’s Minister of the Environment with effect from 17 September 2001, and to date the main direction of Poland’s response to the Habitats Directive has been to update the phytosociologies of its native vegetation (Matuszkiewicz, 2001), to compile a register of Annex 1 habitat types represented in Poland, and to propose extensions to the habitats list in HD Annex 1. Habitat 2330 (inland dunes with *Corynephorus* and *Agrostis*) is fully recognised within the Polish register of key habitat types for conservation under the Habitats Directive (Dyduch-Falniowska *et al*., 2002). Habitat 2330 is treated by Polish phytosociologists as represented by one pioneer association: Spergulo morisonii-Corynephoretum canescentis (Czyżewska, 1992; Matuszkiewicz, 2001).

Some other European countries with inland dunes supporting *Corynephorus* and *Agrostis* (Habitat 2330) have now published national summaries, including France (ATEN, 2006), Portugal (ICN, 2006), Czech Republic (ISBE, 2006) and Germany (Anon, 2006). A feature of these publications is that the plant species given as typifying Habitat 2330 in one country differs in some degree from species listed for the habitat in other countries. Only in Germany does the suite of species of Habitat 2330 closely resemble that quoted in the EU *Interpretation Manual* (Anon, 2003a). The more extensive shifts in plant species composition of Habitat 2330 occur in the south-west of its range, through France and into Portugal, with the Portuguese *C. canescens* habitat being characterised by genera and species often very different from those of central Europe. Across its range, *C. canescens* occurs in assemblages which fall within a complex of vegetation classifications attributed to three classes, the details of which have been variously interpreted: Koelerio-Corynephoretea, Sedo-Scleranthetea and Helianthemetalia guttati (Rodwell *et al*., 2000; Rivas-Martínez *et al*., 2001, 2002; Chytrý & Tichý, 2003; Pérez Prieto & Font, 2005; Hövelmann *et al*., 2006). Section 6.4.2 of this thesis discusses these phytosociologies in more detail.

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2.4.2 *Corynephorus canescens* conservation in Europe

Since the EU's identification of inland dunes with *C. canescens* as a priority habitat for conservation several detailed studies of this habitat have been initiated, especially in Germany where working groups have been established in a number of universities. A further spur for this activity has been the realisation that dry acidic grasslands dominated by *C. canescens* are now more endangered than bogs or calcareous grasslands in central Europe (Bauernschmitt & Grebe, 1997; Jentsch & Beyschlag, 2003). Afforestation with *Pinus* spp. is the single greatest threat, with other land use changes such as urbanisation, plus the deposition of atmospheric nitrogen, as further major causes. Military training areas often constitute the last remaining large expanses of the habitat.

A response to this conservation problem has been the investigation of restoration techniques for inland dune ecosystems (Bank *et al*., 2002; Kirmer, 2004; Stroh, Kratochwil & Schwabe, 2004; Stroh, Storm & Schwabe, 2004; Böger, 2006; Hasse & Daniëls, 2006). Techniques of seed inoculation studied have included laying of mown material, raked material and sods from target plant communities. All methods produced vegetation types which developed in the direction of their target communities within three seasons. Inoculated plots showed significantly higher species numbers than the non-inoculated controls, which lacked nearly all target species over this period. The different inoculation methods produced only minor differences in vegetation composition, leading Stroh, Storm and Schwabe (*loc. cit.*) to conclude that a combination of mown and softly raked material is the most efficient inoculation technique. In the Netherlands Hasse & Daniëls (*loc. cit.*) implemented different treatments (sand deposition, litter deposition, nitrogen input and mechanical disturbance) to permanent plots representing different successional phases in *C. canescens* grassland. The effects were measured over two years, during which species composition hardly changed, though some individual species abundances responded significantly to particular treatments, with *C. canescens* and *Polytrichum piliferum* benefiting from sand deposition. The authors also measured responses to extreme weather conditions, finding that *Spergula morisonii* had the strongest negative response to drought, with *C. canescens* and *Polytrichum piliferum* less susceptible. Grazing experiments carried out on dune grassland have been discussed in 2.3.6 above. Other authors have studied the effects of trampling on sand dunes (e.g. Liddle & Greig-Smith, 1975; Hylgaard, 1980; Bowles & Mann, 1982), though these researches have focused chiefly on coastal sites, and none has specifically studied the effects of trampling on inland *C. canescens* populations. The effects of trampling on an inland *C. canescens* site is consequently investigated in section 5.3 of this thesis.

In parallel with these vegetational studies, several investigations have been carried out into the fauna of the *C. canescens* habitat. These will be discussed in detail in section 7.4 of the present study and are therefore simply summarised here. Most faunal studies have focused on specific invertebrate groups including spiders Araneae (Merkens, 2000; Mrzljak & Wiegleb, 2000; Rėlys, 2000; Kupryjanowicz, 2005); grasshoppers and crickets Orthoptera (Kindvall, 1995; Zehm, 1997a, b; Budrys et al., 2004); beetles Coleoptera (Schjøtz-Christensen, 1957, 1965; Lehmann *et al*., 2004; Hölscher *et al*., 2005); bugs Heteroptera (Gorczyca & Herczek, 1989; Gorczyca, 1994; Bröring & Wiegleb, 2005) and leafhoppers Hemiptera, Auchenorrhyncha (Szwedo, 1998; Nickel & Hildebrandt, 2003; Strauss & Biedermann, 2005; Biedermann *et al*., 2005). In addition, a range of invertebrate groups from different vegetation stands in Germany including *C. canescens* was studied by Bröring *et al*. (2005), while a detailed inventory of invertebrates associated with the Corynephoretum in Belgium is given by Zwaenepoel *et al*. (2002). Some inventory data are also available for several sites in this study, though these are not specifically related to the *C. canescens* habitat (Key *et al*., 1993, 1995; Marshall & Haes, 1988; English Nature, unpublished a, b; Kowalczyk & Szczepko, 2001a, b, c; Szczepko & Kowalczyk 2001, 2002; Kowalczyk *et al*., 2002). A feature of these studies is that the invertebrate species composition of the Corynephoretum varies considerably on a site-by-site basis, with only a few species occurring widely across Europe. Ants (Hymenoptera: Formicidae) are a key group for this habitat, and their impact on creating regular small-scale disturbance patches has been studied by Jentsch (2001) and Jentsch *et al*. (2002), who showed that these patches were frequently correlated with the presence of *C. canescens*.

Few vertebrate species have been studied in relation to the *C. canescens* habitat since none appears to be clearly associated with it. The sand lizard *Lacerta agilis* occurs on dunes across central Europe, and its scarcity has led to a number of autecological studies. However, *C. canescens* vegetation has been shown as only a marginal foraging habitat for this species within a mosaic of vegetation types (Märtens, 1999; Stumpel, 2004; Berglind, 2005). The importance of rabbits *Oryctolagus cuniculus* and brown hares *Lepus europaeus* in grazing this habitat has been addressed in section 2.3.6 above, and the work of Jentsch (2001) and Jentsch *et al*. (2002) on small-scale disturbances in the Corynephoretum has included the scratchings and excavations produced by rabbits, which they found to benefit *C. canescens* establishment in a similar way to ant disturbances.

2.4.3 *Corynephorus canescens* conservation in Britain

The original Atlas of the British Flora, which was published before the discovery of the West Midlands sites, maps the presence of *C. canescens* in eighteen 10-km squares after 1930 and a further seven squares for which only pre-1930 records exist (Perring & Walters, 1976). When Trist and his co-workers in the 1990s attempted to survey all surviving colonies of this grass, they found it in only sixteen 10-km squares in total, including those in the West Midlands (Trist, 1998 pp. 46-47). As discussed in 2.2, those authors whose work underpins vascular plant conservation policy in Britain have treated these populations as "alien" or "non-native" (Stewart *et al*., 1994; Wigginton, 1999; Preston *et al*., 2002). In the most recent edition of the British Red Data Book for vascular plants (Wigginton, *loc. cit*.), *C. canescens* is accorded the IUCN status of "Lower Risk – Near Threatened", which implies that the species could become threatened if further declines occur, but the risk of this is not considered high at present. Legally, *C. canescens* enjoys no specially protected status in Britain under the Wildlife & Countryside Act 1981 as later amended.

Several of the British *C. canescens* populations are, in fact, located on nature reserves or Sites of Special Scientific Interest (SSSIs), or else have sympathetic conservation management. Excepting the scattered locations along the Severn Valley Railway near Kidderminster (which have no public access but are otherwise unsafeguarded) all the inland populations of *C.*

canescens have some measure of conservation protection. In the West Midlands the Kinver Edge site is on land owned by the National Trust and active conservation measures are carried out to benefit this species (1.1; Blunt & Blunt, 2000); Burlish Top is a local nature reserve of the Wyre Forest District Council; and the Devil's Spittleful/Rifle Range complex is a SSSI managed partly by the Wyre Forest District Council and partly by the Worcestershire Wildlife Trust. In East Anglia, Wangford Warren is a nature reserve of the Suffolk Wildlife Trust. The Lakenheath airfield site is a SSSI on Ministry of Defence land with highly restricted access; its extensive floral and faunal interest is taken into account in site management. A few of the coastal colonies of *C. canescens* in Suffolk, Norfolk and Jersey are on or close to nature reserves (Minsmere Haven, Winterton Dunes, Blakeney Point, Holme-next-the-Sea, L'Ouaisné Common) but the majority of coastal sites have no specific protection and occur on beaches and dunes with open public access, on caravan parks, golf links and in a disused gravel pit (Trist, *loc. cit.*).

2.4.4 Case studies: Wangford Warren and Kinver Edge

Detailed descriptions of conservation measures taken to safeguard British inland colonies of *C. canescens* are given in Trist (1998) for Wangford Warren (referred to as Wangford Glebe in his account), and by Blunt & Blunt (2000) for Kinver Edge. The following section draws extensively on these two sources.

The colony at Wangford was rediscovered by Trist and M. G. Rutherford in January 1970. It occupies a small fixed dune of some 7 m x 9 m which lies above a line of underground spring water. In the 1970s this spring line was also marked by a few plants of *Juncus squarrosus* and *Juncus effusus*, while about 250 m away grew some old tussocks *of Carex paniculata* and a bed of *Calamagrostis canescens.* None of these plants could be found after about 1984, suggesting to Trist that the underground water supply was diminishing, probably through extraction by a deep bore pump within 1.5 km of the site. This loss of moisture has also in recent years encouraged the invasion by *Pteridium aquilinum*, *Deschampsia flexuosa* and *Carex arenaria* of the dune occupied by *Corynephorus canescens*, to the point at which the latter's colony has become vulnerable to elimination by competition.

When found in 1970 the *Corynephorus canescens* population at Wangford numbered 231 plants[3]. By 1975 it had halved to 112 plants, and it was noted that no natural sand accretion was taking place. In the autumn of that year, therefore, a wide trench was cut at the foot of the sand bank holding the colony to encourage wind disturbance of sand, while at the same time a "good covering" of sand was spread over the colony to stimulate vegetative growth. Applications of sand were again made in 1976, 1977 and 1978, after which Trist found 232 yearling plants out of a colony he initially assessed at 422 plants (Trist, 1980) but later revised to about 250 (Trist, 1998). No sand was spread and no population counts taken from then until 1992, when 226 plants were recorded and the area sanded again. This process was repeated in 1993, and annual counts from then until September 1996 revealed a fairly stable population of between 254 and 304 plants (Trist, 1998).

The problems at Kinver Edge and the conservation measures followed there are of a different nature. When discovered in 1977, about 550 plants occupied two areas some 300m apart near the National Trust property's south-eastern boundary; a few plants were additionally present in a private field beyond the boundary fence adjacent to the two main areas. These two main areas were subject to heavy trampling by walkers, which on Site KE1 (called Site 1 in Blunt & Blunt *loc. cit.*) had almost eliminated the grass from a sand bowl of 200 m^2. On this site just a few plants of *C. canescens* survived along the narrow rim of the bowl. Initial attempts in 1986 to protect these plants from further trampling by use of barriers constructed from pine brashings prevented deterioration of the existing tussocks but promoted no increase in the number of *C. canescens* plants. In the winter of 1989/90, therefore, more pine brashings were spread thinly across the whole of Site KE1, which effectively stopped further trampling of the area. *C. canescens* responded dramatically by covering the whole of Site KE1 with newly-germinated seedlings in the first

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[3] Trist (1980, 19992, 1998) does not define what he means by "plants", whether "ramets" or "genets" (*vide* Harper, 1977).

growing season, presumably from seed which had been lying dormant in the sand. Within six years at Kinver, however, a rapid succession of other species including *Polytrichum piliferum*, *Rumex acetosella*, *Deschampsia flexuosa*, *Festuca rubra* and *Hypochaeris radicata* led to a marked deterioration of the *C. canescens* colony through competition, so in the mid-1990s the whole of Site KE1 was ploughed with a Dutch harrow, effectively restoring the start of the succession and allowing *C. canescens* to re-seed itself vigorously across the entire site.

In 1994 a strip of bare, unvegetated sandy track measuring 30 m x 4 m and parallel to Site KE2 at Kinver Edge (Blunt & Blunt, *loc. cit.*) was fenced off to prevent further erosion and compaction through trampling by walkers. Pine brashings were laid across this area as described for Site KE1, with the similar result that seedlings of *C. canescens* covered the entire area in the first growing season. Also, in the early 1990s, ownership of the field adjacent to these *C. canescens* populations passed to the National Trust, and controlled light grazing by sheep and cattle was introduced to encourage the development of heathland communities. By 1997 it was evident that *C. canescens* was spreading in this field; therefore in summer of that year a count of *C. canescens* plants was made in the field, followed in July 1998 by a complete population census of all *C. canescens* localities at Kinver Edge, and a further assessment of the populations of the largest colonies in September 1998. These censuses led Blunt & Blunt (*loc. cit.*) to estimate that the size of the *C. canescens* population at Kinver Edge in the late 1990s was between 40,000 and 50,000 plants.

The management of other inland colonies of *C. canescens* in Britain has not been described in such detail, though Hazelhurst (1992) reported that some degree of erosion had been indirectly maintained at the Devil's Spittleful/Rifle Range site by the rotavation of a firebreak for several years; however, he concluded that this measure produced very little movement of the firmer sand around the *C. canescens* plants and appeared to have little effect in maintaining the population of the grass on this site.

The lessons that can be drawn from attempts to conserve *C. canescens* at Wangford Warren and Kinver Edge are that the poor powers of competition of this grass are a key element in the survival or demise of its populations. The factors which operate upon this poor competitiveness, however, vary greatly between the two sites: at Kinver Edge *C. canescens* suffers from both overtrampling and rapid vegetational succession, but responds remarkably well to management measures which reduce these factors; whereas at Wangford Warren the grass is subject to a much slower rate of vegetational succession but one which appears more difficult to halt, and management so far has barely succeeded in stabilising the *C. canescens* population.

Furthermore, Kinver Edge and Wangford Warren may not represent the extremes of the problem of conserving *C. canescens*. As Trist (*loc. cit*. p. 43) says by way of summary:

"The conservation of *C. canescens* is complicated. Some problems may be resolved while the solutions to others are impracticable and some not possible. The inland sites are subject to changes of their immediate surroundings by agriculture and other land uses. I agree with Marshall's (1967) conclusion that 'many of the present day European communities of *Corynephorus canescens* owe their existence to human interference' ……The coastal sites are at all times open to the threat of gales and tidal erosion."

CHAPTER 3: THE STUDY SITES

3.1 Selection of study sites

3.1.1 Criteria for selection of study sites

In order to meet the Aims of this study as given in 1.2 above, a number of sites in Britain and Poland were selected for investigation. The primary basis of selection was to try to encompass a representative sample of the inland *Corynephorus canescens* habitat in each country for the purposes of comparison. However, accessibility was a further necessary factor influencing site selection, especially in Poland where the author's time-frame for carrying out fieldwork was very restricted (3.1.2 below).

Site selection in Britain was a straightforward issue: as shown in 1.1, the number of inland communities of *C. canescens* in Britain is very small, consisting of two neighbouring localities in Breckland, East Anglia and three in the West Midlands around Kidderminster. In the latter region, scattered populations of the grass along the Severn Valley Railway in the vicinity of Burlish Top and the Devil's Spittleful/Rifle Range were considered by Hazlehurst (1992) to be an extension of those two sites, and an initial visit by the author endorsed this view; because of this and the hazard during fieldwork from trains passing along the Severn Valley Railway it was decided not to include the Severn Valley Railway colonies in this study.

With this exception the handful of inland U.K. study sites selected themselves, and the only issue to be settled was that of access. In the early stages of this research it was hoped that investigation of the Wangford site alone might give enough data for the East Anglian populations of *C. canescens*. As the study progressed, however, it became clear that inclusion of the much larger colony of the grass on Lakenheath SSSI would be desirable. Although this is on Ministry of Defence land with high security and very restricted access, permission was obtained to make two site visits there in 2002.

A major additional advantage of the Kinver Edge locality was the possibility, assisted by the National Trust Warden, of establishing a long-term fixed plot on site for preliminary field investigation on the effects of trampling on *C. canescens*.

In Poland this grass is common and widespread on sandy places in the lowlands (2.2) and site selection offered many options. Bromierzyk in Kampinos National Park, a locality first investigated by the author in 1994, was selected because this National Park has one of the best and most important inland dune systems in Europe (Herz, 1993), and also because of its accessibility and the availability of study facilities; the field station of the University of Łódź at Bromierzyk gave ready access to *C. canescens* dune habitats as well as overnight stay and laboratory facilities and was consequently adopted as a base. Three *C. canescens* colonies near the field station were selected to represent the range of conditions in which this grass grows at Bromierzyk: a stable, well-established population, a smaller population undergoing encroachment by forest, and a recovering population on the site of an abandoned dairy (see 3.2.3 and Appendix B.6 for details). The availability of data from other environmental studies carried out at Bromierzyk by the University of Łódź was an additional advantage in choosing this locality.

Further visits to Poland in the late 1990s showed that a *C. canescens* locality at Grabie in the Bolimów Landscape Park near Skierniewice, also first visited by the author in 1994, was being affected by increased vehicular traffic to a nearby house and by on-site tree-planting operations. This offered the possibility of studying a Polish *C. canescens* population subject to periodical human disturbance, and Bolimów was therefore chosen as a fourth Polish site. Finally, as investigations at Bromierzyk and Bolimów began to progress, it became evident that a fifth study site would be desirable to include elements of the Spergulo vernalis-Corynephoretum canescentis habitat which were not well represented at these localities. Consequently, with advice from Professor Siciński of the University of Łódź, the Ciosny Reserve at Rosanów near Łódź was selected in 2000. An enquiry was made at the same time to find a readily accessible Polish *C. canescens* locality on a *Calluna vulgaris* heath in order to provide further possible comparisons with the West Midlands sites in Britain, but no such site could be located.

3.1.2 Limitations imposed by selection of study sites

While the British and Polish sites chosen for this study conveyed many advantages for fulfilling its objectives, they also imposed some limitations to the studies which could be carried out. The chief ones were as follows:

Limited time-frame for studies. The author's work commitments made it feasible for him to visit the Polish study sites only in July and August, plus one visit in early June. In order to provide directly comparable data, therefore, fieldwork on the U.K. sites was mostly also carried out within the same time periods. Exceptions to this were the establishment of baseline vegetation data at Kinver Edge at the start of the trampling investigations in April 1999, and some direct observations of fauna during counts to assess the number of walkers trampling Site KE3 Area A between January and May 2002. A further consequence of this limited time-frame was that fieldwork could not be carried out on all sites in each year of the study.

Vulnerability of study sites. Excepting Lakenheath and perhaps Wangford Warren, all chosen study sites in both Britain and Poland are subject to regular public access. This factor made inadvisable the use of long-term monitoring equipment such as weatherstations and dataloggers designed to be left unattended *in situ* for weeks or months. In consequence, direct long-term monitoring of certain features such as climate was not possible. Moreover, fieldwork techniques employed throughout this study have had to be limited to equipment which the author could transport with him on site visits in Britain and Poland.

3.2 List of sites selected for this study

The sites selected for detailed investigation are listed below, along with their abbreviations as devised for and used throughout this study. A brief summary description is added. More detailed site descriptions and site diagrams are given in Appendix B, and photographs of some of the sites are shown on Plates 2, 3 and 4. The location of the main Sites are shown on the maps on page 10 (Figure 2.2b) and page 11 (Figure 2.2c).

3.2.1 Main East Anglian Sites

Site WW: Wangford Warren (Appendix B.1.1) (OS grid ref: TL 757 843)

A very small *C. canescens* population occupying some 5m^2 of a low dune system dominated by *Carex arenaria* and *Agrostis vinealis*.

Site LA: Lakenheath (Appendix B.1.2) (OS grid ref: TL 745 809)

Two *C. canescens* populations on a levelled dune system on either side of the main runway of an air-base close to Site WW. The populations exist in a species-rich turf kept constantly mown to a height of 4 cm.

3.2.2 Main West Midlands Sites

Site KE1: Kinver Edge Site 1 (Appendix B.2.1 and Plate 4)
Site KE2: Kinver Edge Site 2 (Appendix B.2.2)
Site KE3: Kinver Edge Site 3 (Appendix B.2.3 and Plates 3 and 4)

Three neighbouring sites (OS grid ref: SO 834 827 to 834 825) which together contain the great majority of *C. canescens* plants on this National Trust property. The Sites are surrounded by *Calluna vulgaris* - *Deschampsia flexuosa* heath and woodland dominated by *Quercus robur* and *Betula pendula*. A well-used footpath runs across Site KE3 and adjacent to Site KE1.

Site DS: Devil's Spittleful and Rifle Range (Appendix B.3.1 and Plate 2)
(OS grid ref: SO 808 746)

A small *C. canescens* population along a footpath between a railway embankment and *Calluna vulgaris* - *Deschampsia flexuosa* heath. Part of the Site is subject to encroachment by *Calluna vulgaris* and *Cytisus scoparius*.

Site BT: Burlish Top (Appendix B.4.1) (OS grid ref: SO 807 736)

The Site contains the great majority of *C. canescens* plants on the slope of a small sandstone plateau not far from Site DS. The *C. canescens* population is under heavy competition from a mixed acid heath vegetation.

3.2.3 Polish Sites

Site BR1: Bromierzyk Site 1 (Appendix B.6.1 and Plates 2 and 4)
Site BR2: Bromierzyk Site 2 (Appendix B.6.2 and Plate 2)
Site BR3: Bromierzyk Site 3 (Appendix B.6.3)

Three populations (co-ordinates 20° 23' E, 52° 18' N) on an ancient parabolic dune system close to the University of Łódź's field station in Kampinos National Park. They represent a stable, well-established *C. canescens* population (Site BR1); a smaller population undergoing encroachment by forest (Site BR2); and a recovering population on the site of an abandoned dairy (Site BR3).

Site BO: Bolimów Landscape Park (Appendix B.7.1)
(co-ordinates 20° 2' E 52° 0' N)

A *C. canescens* population among *Pinus sylvestris* plantations and subject to periodical disturbance by vehicles and tree-planting operations.

Site CR: Ciosny Reserve (Appendix B.8.1 and Plate 2)
(co-ordinates 19° 22' E 51° 55' N)

A small reserve near Łódź, mostly surrounded by houses and gardens. The *C. canescens* population lies within maturing *Juniperus communis* woodland.

3.2.4 Other Sites

In addition to these main study sites, the author set up in 1998 a small study plot in his garden in Alveley, Shropshire, transplanting from Kinver Edge, with National Trust permission, seven plants of *C. canescens* in order to study the phenology of this species in a closely monitored outdoor situation in the West Midlands. This is Site AL as described in Appendix B.5.1 and illustrated on Plate 3, and is the location of the investigation described in Chapter 5 section 5.2. It is located at OS grid reference: SO 762 845.

Although coastal *C. canescens* communities are not an integral part of the present study, opportunities became available to visit British coastal *C. canescens* sites at Caister-on-Sea (Norfolk) (OS grid ref: TG 528 118) on 12 July 2002 and at several points on the west coast of Jersey (around 49^{O} 10' N, 2^{O} 11' W) on 14 February 2003. Some data on the vegetation of these coastal sites were taken to examine whether they throw any light on the vegetation of inland British *C. canescens* communities. These data are used in some parts of the vegetational analysis in Chapter 6 as described there.

Plate 2: Examples of the situations associated with *Corynephorus canescens* in this study.

Left: heathland with *Calluna vulgaris*, *Cytisus scoparius* and *Betula pendula*. Site DS before erection of fence along right-hand side of path.

Right: stable Corynephoretum with saplings of *Pyrus communis* and a stand *of Calamagrostis epigejos* on right. Site BR1.

Left: open ground within *Juniperus communis* and *Pinus sylvestris* woodland. Site CR.

Right: Site BR2 showing encroachment by *Quercus robur*. The pale line running diagonally across the picture is an old vehicle track.

CHAPTER 4: GENERAL METHODS

4.1 Timing and nature of sampling

A summary of the fieldwork carried out during the study is given in Appendix C, which shows the dates and nature of observations made at each of the study sites. Additional visits to assess the trampling pressure on Kinver Edge Site KE3 are excluded from Appendix C but are detailed in Appendix A.

The annual time-frame for vegetation and faunal sampling is described in 3.1.2, and its limitations are discussed later in 4.4.3 and 8.5. Issues of practicability also dictated a need to restrict sampling to a diurnal time-frame between 10:00 and 16:00 hours, when invertebrate activity was at its height. On most study sites nocturnal sampling was ruled out because of difficulties of access and security, and so nocturnal visits were omitted from this study.

4.2 Authorities followed for identification, nomenclature, fieldwork methods and analytical methods

Authorities followed in the identification of taxa recorded in this study are given in Table 4.2i for British and Polish sites. The Table also indicates in bold type those authorities normally followed in the nomenclature of each group. The major nomenclatorial differences between the authors in this Table are addressed later in section 6.2 for plant species and section 7.2 for invertebrate species.

Table 4.2i: authorities followed in the identification and nomenclature of taxa recorded in this study.

Taxonomic group	**Britain**	**Poland**
Vascular plants (Tracheophyta)	Clapham, Tutin & Warburg (1962) **Stace** (1991, **1997**)	Podbielkowski (1992) **Rutkowski (1998)**
Lichens (Lichenes)	Dobson (1981) Duncan (1970) **Hodgetts (1992)**	**Hodgetts (1992)** Lipnicki & Wójciak (1995)
Mosses (Musci)	**Smith (1978)** Watson (1978)	Podbielkowski (1992) **Smith (1978)** Watson (1978)
Harvestmen (Opiliones)	**Jones (1983)**	[not applicable]
Spiders (Araneae)	Jones (1983) Jones-Walters (1989) **Roberts** (1993, **1995**)	Jones (1983) **Roberts** (1993, **1995**)
Insects (Coleoptera)	Britton (1956) Hodge & Jones (1995) Joy (1976) **Kloet & Hincks (1977)** Lindroth (1974) Majerus & Kearns (1989) Unwin (1984)	Chatenet (2000, 2002, 2005) Harde (1984) **Razowski (1991b)** Stebnicka (1978) Trautner & Geigenmüller (1987)
Insects (Diptera)	**Chandler (1998)** Colyer & Hammond (1968) Oldroyd (1969) Pape (1987) Stubbs (1996) Stubbs & Drake (2001) Stubbs & Falk (1983) Unwin (1981)	Geller-Grimm (2003) Pape (1987) **Razowski (1991a, 1997)** Trojan (1967, 1970)
Insects (Hemiptera)	Dolling (1991) Evans & Edmonson (2005) **Kloet & Hincks (1964)** Péricart (1998) Southwood & Leston (1959) Unwin (2001)	Lis (2000) Lis & Lis (1998) Péricart (1998) Pławilszczikow (1972) **Razowski (1990, 1997)**

continued…..

Table 4.2i continued…..

Taxonomic group	Britain	Poland
Insects (Hymenoptera)	Bolton & Collingwood (1975) Day (1988) Else (1999) Gauld & Bolton (1988) **Kloet & Hincks (1978)** Morgan (1984) Perkins (1919, 1922) Richards (1980) Skinner & Allen (1996) Willmer (1985) Yeo & Corbet (1983)	Banaszak & Romasenko (2001) Czechowski, Radchenko & Czechowska (2002) Dylewska (1974) Noskiewicz & Puławski (1958, 1960) Pesenko, Banaszak, Radchenko & Cierniak (2000) Pławilszczikow (1972) Puławski (1967) **Razowski (1997)** Willmer (1985) Zahradník (1999)
Insects (Lepidoptera)	Goater (1986) Skinner (1984) Thomas (1986) **Emmet (1991)**	Chinery (1989) Goater (1986) Novák (1998) **Razowski (1991a, 1997)**
Insects: other Orders (Orthoptera, Dictyoptera, Dermaptera, Planipennia, Psocoptera, Thysanoptera))	Chinery (1986) Kirk (1996) **Kloet & Hincks (1964)** Marshall & Haes (1988) New (1974)	Marshall & Haes (1988) **Razowski (1990, 1997)**
Reptiles (Reptilia)	**Arnold & Burton (1978)**	Arnold & Burton (1978) **Razowski (1991a)**
Birds (Aves)	Bang & Dahlstrom (1972) Bouchner (2000) **Bruun, Delin & Svensson (1992)**	Bang & Dahlstrom (1972) Bouchner (2000) Bruun, Delin & Svensson (1992) **Razowski (1991a, 1997)**
Mammals (Mammalia)	Bang & Dahlstrom (1972) Bouchner (2000) Corbet & Southern (1977) van den Brink (1967)	Bang & Dahlstrom (1972) Bouchner (2000) **Razowski (1991a)** van den Brink (1967)

Some Polish invertebrate material was identified from British authors as shown in the above Table. Identifications made throughout this study are primarily the author’s: translations of Polish identification keys were made by the author using technical glossaries in Rutkowski (1998) for vascular flora and Razowski (1996) for insects. Dr Michalska-Hejduk and Professor Siciński of the University of Łódź advised on Polish vascular plants, and Professor Czyżewska of the same University identified some lichen samples from Site BO. Advice on the Araneae and Hymenoptera of the Bromierzyk sites was given by Drs Bartos and Szczepko, also of the University of Łódź. Mr Robert Kemp of Shropshire, England identified a sample of Polish Odonata.

The main authorities consulted for the methodology adopted in this study are: for fieldwork methods, Southwood (1978), Williams (1991), Kent & Coker (1994), Rowell (1994), Sutherland (1996) and McGavin (1997); and for analytical methods, Hill (1979), ter Braak (1988, 1995), Chalmers & Parker (1989), Kent & Coker (1994), Stuttard (1994), Quinn & Keough (2002), and Lepš & Šmilauer (2003).

4.3 General methods: physical characteristics

In addition to basic general data on the location and orientation of all sites, which are given in the Site Descriptions in Chapter 3 and Appendix B, the following specific information was collected as elements within 1m^2 quadrat samples using the same methodology as for vegetational sampling (4.4.2)[4]:

4.3.1 ***bare sand*** was assessed in the same way and at the same time as the vegetation cover of a quadrat, as a percentage cover of the quadrat.

4.3.2 ***litter***, consisting mostly of plant debris (dead leaves, twigs, grass etc) with occasional other debris (stones, broken glass etc), assessed as a percentage cover.

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[4] i.e. the aggregation of percentage cover within 25 subdivisions of a 1m^2 quadrat.

4.3.3 *sand compaction*. This was measured on a three-point ordinal level scale:

Sand 1: completely loose sand
Sand 2: stable at the surface level only (i.e. to a depth of no more than 0.5cm)
Sand 3: completely compacted at and below the surface (to more than 0.5cm)

The sand compaction index of a quadrat was determined by probing the ground with a pencil or pen at several points within the quadrat and assessing the ease and the depth to which it could be pushed into the sand at each point. An estimate of the percentage of each level of compaction across the quadrat was then made and recorded for the quadrat.

4.3.4 *grazing impact.* This was assessed by examining the plants of *C. canescens* in a quadrat for direct evidence of nibbling, and by looking for the presence of a grazing herbivore via its droppings. The degree of grazing impact was measured on a four-point scale:

0 no grazing – no evidence of nibbling and no herbivore droppings present
1 minor grazing – nibbling of just one or two plants, or a very small amount of droppings present; grazing barely impacts on the quadrat vegetation
2 moderate grazing – nibbling of more than two plants, or a small to moderate amount of droppings present; grazing makes a small to moderate visual impact on the quadrat vegetation
3 extensive grazing – many plants nibbled, or abundant droppings present; grazing impacts extensively on the quadrat vegetation.

The assessed amount of grazing within a quadrat was recorded as one of these four scale points. The species of herbivore responsible for the grazing was also recorded where known.

Only the grazing impact of mammalian herbivores is monitored by this index; invertebrate herbivory, reported as very minor by Marshall (1967), was little observed in this study;

4.3.5 ***erosion impact.*** The impact within a quadrat was estimated for each of six causal agents: trampling (human); trampling (mammalian); rabbit excavations; insect excavations; rain; wind. This impact was assessed by observation of disturbances to the sand surface of a quadrat, and was recorded on a four-point ordinal scale:

0 no erosion – no evidence of erosion of the sand surface

1 minor erosion – barely impacts on the sand surface

2 moderate erosion – a small to moderate impact on the sand surface

3 extensive erosion – impacts extensively on the sand surface.

4.4 General methods: vegetation sampling

The vegetation of each site was assessed in two ways:

4.4.1 ***general inspection*** of the entire site.[5] The purpose of the general inspection was to assess by eye across the entire site the percentage foliage cover of plant species. The aim was to identify any species unrepresented in the quadrat samples plus species whose percentage foliage cover across the entire site was not well represented by quadrat sample data. Any such species were recorded on a Domin scale in “general” samples in the Disk Appendices.

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[5] i.e. within site boundaries as defined and shown in Appendix B.

4.4.2 *1m² quadrat samples* taken using a plastic frame of 1 m x 1 m, subdivided into 25 equal squares each with an area of 0.04 m². Estimates of the foliage ***cover abundance*** of all plant species in a quadrat were made by estimating the percentage cover of these elements within each of the 25 subdivisions and aggregating them. The results for all species were initially recorded as percentages and later transposed to a Domin scale.

The small size of some sites in the study (e.g. Sites BR2, BT, CR, WW) made it necessary to sample a large proportion of the *C. canescens* habitat of those sites in order to gain enough quadrat samples for meaningful analysis. This consideration effectively precluded the random placement of quadrats on those sites. Some other sites (e.g. Sites DS, KE3) were mostly linear in nature, again reducing options for random sampling using standard grid patterns. It was therefore decided to sample all sites similarly, by placing quadrats representatively so that they sampled proportionately each of the first three successional stages of the *C. canescens* habitat identified on the site, using the schema elaborated in 5.3.4. It is recognised that the non-random placement of quadrats introduced the possibility of unintentional bias in favouring some floral elements of a successional stage over others. The general inspections of vegetation on each site (4.4.1) were intended to act as at least a partial check on this.

As part of the quadrat data, measurements were also taken of vegetation height and number of *C. canescens* inflorescences to try to assess the vigour and fecundity of the vegetation under various conditions. These measurements were taken as follows:

4.4.2.1 *Vegetation height* measurements fall into three groups:

1) Sward height: the height of *C. canescens* tussocks excluding inflorescences; this was taken from ground level to the top of the longest leaves; in smaller plants this measurement was made directly, but larger and more spreading tussocks were grasped by hand into a tight bunch before measuring.

2) Inflorescence height: the height of *C. canescens* tussocks including inflorescences; this was taken after grasping the tussock into a tight bunch as described above.

3) Height of vegetation other than *C. canescens*. Measurements were taken of plants of other species abundant within a quadrat, as gauged from the cover abundance estimate. These plants might be measured directly from ground level to top (e.g. *Ulex europaeus*) or, if loose tussocks, after being constrained into a tight bunch (e.g. *Deschampsia flexuosa*).

4.4.2.2 The ***number of inflorescences*** was a direct count of the number of flowering culms on a flowering *C. canescens* plant.

The ***number of individual measurements*** of vegetation height and number of inflorescences taken for a particular quadrat were determined as follows: if there were few *C. canescens* plants within the quadrat (up to ten), the sward height, inflorescence height and number of inflorescences were normally measured for each plant. Where there were more than ten plants, normally 10-12 samples were taken to represent proportionately the range of *C. canescens* vegetation in the quadrat: i.e. for sward height, the relative proportions of small immature and larger, flowering plants was determined and represented in the samples; whereas for inflorescence height and number of inflorescences, the range of these parameters shown by flowering plants was determined and represented in the samples.

The number of measurements taken of the vegetation other than *C. canescens* in a quadrat was determined in the same way. Such measurements were only made when the other vegetation formed a dominant element within a quadrat.

The cover abundance of the individual plant species which made up the vegetation was assessed for every quadrat sample made during this study, but measurements of vegetation height and number of *C. canescens* inflorescences were made for only a selection of quadrats. This was partly because time limitations precluded the taking of a full range of measurements for every sample; and partly because, in the study's planning stage, the primary purpose of vegetational sampling was intended to be a comparison of the species composition of the Corynephoretum within and between sites. Only later did it become apparent that the vigour and fecundity of *C. canescens* might also provide useful comparative information.

4.4.3 Issues arising from vegetation sampling

Issues arising from the ***limited time-frame for sampling*** have been addressed in 3.1.2 and will be discussed more fully in 8.5 among issues for further study, but it may be observed here that the need to concentrate sampling into July-August may have led to winter annual species being unrepresented or under-represented in the vegetational samples.

Vegetational structure proved difficult to assess quantitatively. Vegetation height is clearly an important parameter; and as the grass obviously increases in height at anthesis (2.1) it was decided to measure the height of tussocks at both flowering and non-flowering stages. The method described in 4.4.2.1 was adopted after an alternative method - measuring the height from ground level of a cardboard disc lowered upon the tussock - was tried and rejected; in the latter case it was found that the flowering *C. canescens* tussock is too lax to support a disc at a height which meaningfully characterises the inflorescence height. Even so, the chosen method of measuring the longest shoot on a plant did not always express its true height above ground level; the longest shoot would sometimes be a side shoot (this was more frequent in flowering than non-flowering plants), so that a measure of "tussock height" might sometimes include an element of tussock spread. It is considered that this still gives a valid expression of tussock size which can be compared between individual plants and populations.

Counting the ***number of plants*** in a sample could also be problematical in wild populations of *C. canescens*, as it was sometimes difficult to determine whether a “plant” was merely a tiller of an adjacent tussock or a separate individual. The problem reflects the distinction between “ramets” and “genets” as defined by Harper (1977). In this study the count of individual plants of *C. canescens* was an attempt to count the number of genets, i.e. the number of individuals represented by original zygotes. The rarity and fragility of inland *C. canescens* populations in Britain precluded digging around tussocks to establish their true spread, and a “best guess” approach had to be adopted. This problem did not affect the study of *C. canescens* in cultivation as the short-lived tussocks failed to produce tillers for reasons which will be addressed in 5.2.3.

Throughout the present study the chosen measure of productivity is ***fecundity***, i.e. the number of inflorescences produced by the flowering *C. canescens* tussock. This single measure was adopted partly through time constraints but mainly because of the wide variability in the number of inflorescences per plant: the range given by Marshall (1967) is from 1 to 200, but this upper limit has been exceeded several times in the present study; for instance, three tussocks of *C. canescens* in cultivation had 257, 243 and 241 inflorescences (5.2.3). Both Marshall (*loc. cit.*) and Symonides (1979) additionally measured the number of caryopses per spikelet and number of spikelets per inflorescence. In their studies the former measure varied little, between 1.3 and 1.7; Marshall meanwhile quotes a maximum figure of 120 spikelets per panicle, while Symonides gives the range as between 25 and 100 (*loc. cit*. Fig. 12), this variation being attributed by her to tussock age. She also notes that the number of complex fruits and individual production of “biospores” (her term) are among the more constant features of this species. For present purposes an absolute value for the productivity of a *C. canescens* population is not deemed essential; and fecundity is considered to give the best single comparative measure, though this does assume that the number of caryopses and spikelets per panicle does not vary considerably in the vegetation sampled in this study.

4.5 General methods: faunal sampling

The restricted time-frame for faunal sampling in this study, the need to replicate methods in Poland and England, and the vulnerability of most sites to potential vandalism of equipment left *in situ*, all necessitated the use of faunal sampling techniques which were simple, easily transportable and which could yield viable data in a short period of time (3.1.2). The methodology adopted was therefore designed to meet these constraints. The use of a variety of techniques was further intended to offset the influence of biases inherent in any one of them. The rarity of *C. canescens* at most English sites precluded the possibility of removing tussocks for faunal investigation.

The fauna of the *C. canescens* habitat was sampled using the following methods:

4.5.1 ***direct search*** of the entire site. Each site was searched during each visit for evidence of vertebrate and invertebrate fauna. Vertebrates (birds, mammals and reptiles) were identified on site, except for some mammal footprints which were measured and drawn *in situ* for later identification. Searches for invertebrate fauna focused particularly on species which were not readily detected during quadrat sampling (4.5.2). A few invertebrates (e.g. butterflies) were identified on site, but most were determined by the capture of voucher specimens, which were either killed with ethyl acetate or preserved directly in 70% alcohol solution, and later identified in the laboratory.

4.5.2 ***1m² quadrat samples*** used the same 1 m x 1 m quadrat plots from which physical and vegetation data had been gathered (see 4.3 and 4.4). For faunal sampling the quadrats were delimited by sinking pegs in the sand at the four corners of the collapsible plastic frame used in vegetation sampling (4.4.2); the frame was then removed and string was stretched around the edge of the quadrat and held in place by the corner-pegs. The string was suspended at least five centimetres above the level of the sand to allow free passage of terrestrial invertebrates beneath. The quadrat was then left unattended for at least thirty minutes, until normal invertebrate activity was observed within it (e.g. resumption of activity by flying Hymenoptera), upon which a count was made of the number of individuals of each species observed in the quadrat during a timed period of fifteen minutes. Where necessary, specimens were retained for later determination of the species concerned.

4.5.3 ***cone traps.*** These consisted of sheets of thick, black artists' paper measuring 41.5 cm x 29.5 cm which completely excluded light (confirmed by viewing the sheet against a 100-watt lamp.) Each sheet was rolled transversely into a cone of approximately 30 cm height, sealed at the sides with tape and placed over a flowering tussock of *C. canescens* so as to include all the tussock within the cone. The base of the cone was surrounded by heaped sand to prevent the escape of invertebrates beneath it, and a clear glass or perspex collecting jar was inverted over the hole at the top of the cone and taped into place. The cones were left *in situ* for an hour, at the end of which they were examined and any invertebrates in the collecting jar or on the inner surface of the sheet were transferred to 70% alcohol. This method was devised to sample the small invertebrate fauna of the *C. canescens* tussock in lieu of techniques which necessitate uprooting the tussock (e.g. flotation and desiccation methods).

4.5.4 ***inflorescence samples*** taken by removing from four to six inflorescences of *C. canescens* from each site and carefully enclosing them in a sampling jar, into which a small amount of 70% alcohol solution was poured. The jars were then stoppered and shaken to dislodge any invertebrates present. Specimens collected in this way were then extracted by a fine brush into alcohol in a smaller collecting tube, and the inflorescence was discarded. Only a small number of inflorescences on a site were sampled in order to minimise the impact on the productivity of *C. canescens* in its most vulnerable sites. This method was intended to supplement the use of cone traps for sampling the small invertebrate fauna of the *C. canescens* tussock, an element which other methods in this study were expected to under-record.

4.5.5 Issues arising from faunal sampling

A number of issues arose from the methods described above, notably:

The adoption of ***quadrat sampling*** as a main method for sampling invertebrates conferred the great advantage of allowing faunal data to be correlated directly with the physical features and vegetation represented by the samples. However, it became evident that quadrat sampling was biased towards recording the more mobile and obvious invertebrates, while more cryptic fauna would be less well recorded by this method. The use of a fifteen-minute search period helped mitigate this bias somewhat, by allowing a very thorough search of the quadrat; but even so, it is felt that quadrat sampling under-recorded some elements of the invertebrate fauna.

The number of individuals of a species in a sample could sometimes be difficult to assess. In most samples a species would be represented by a single-figure count, and such low numbers could be accurately recorded; however, ants in particular occurred regularly in greater numbers, and the presence of an ants' nest near a quadrat would normally (but not invariably) lead to a high count for that sample, with a possibility that some individuals may have been missed. A further problem lay in the possibility of double-counting individuals. Invertebrates observed re-entering a quadrat were not counted again; however, it is likely that some re-entered the quadrat without being observed to do so, when they would be recorded as new individuals.

A further issue was the influence of the observer's presence on invertebrates. Both positive and negative influences were noted: some insects, mostly larger flying types such as butterflies, hoverflies and large Hymenoptera, were seen to be drawn towards the observer, apparently to investigate him; by contrast, some large and medium-sized Hymenoptera were seen to be deterred from entering a quadrat by the observer's presence. In the former case, the insects were treated as "transients" and dealt with as described in the following paragraph; in the latter case, the use of ***direct searches*** was considered sufficient to record most of the shy species regularly present on a site.

Another difficulty was that of distinguishing between invertebrates using the *C. canescens* habitat and those simply passing over or transient through it. As the purpose of faunal sampling was to study the characteristic fauna of the *C. canescens* habitat, it was decided to record only those invertebrates which were deemed to be “using” this habitat, determined as follows:

(a) those which settled on the soil or vegetation in the quadrat, or
(b) those considered to be investigating the soil or vegetation in the quadrat (for example, insects which circled low over it.)

With practice it became fairly easy to decide which invertebrates were “using” the quadrat. Those which were merely transient across an area normally formed a very low proportion of the observed fauna.

Cone traps and ***inflorescence sampling*** were devised by the author to overcome the problem of recording the fauna of the *C. canescens* tussock without uprooting and taking it away. Both were considered to be reasonably successful, though cone traps would clearly only capture invertebrate species which tended to gravitate to light. A problem arising from the design of the cone traps was that they could not be used on windy days, when they would be blown over. The inflorescence sampling technique allowed the extraction of probably all invertebrates in the samples taken. Both these methods normally allowed the recording of the fauna of only a very small proportion of *C. canescens* tussocks on site, and the results are therefore only indicative of the range of taxa present. Many more samples would be needed before meaningful statistical analysis could be given to this faunal element.

Other invertebrate sampling techniques were considered in the early stages of this study, but rejected for various reasons. Two were tried out:

(a) sweep-netting was found to be difficult in the low, sparse vegetation of much of the *C. canescens* habitat, catching few species which were not detected by the other methods used, and missing much of the terrestrial invertebrate fauna which was a key element in all *C. canescens* communities;

(b) the Baermann funnel method of extracting invertebrates from sand beneath a hot lamp was tried, but was found to require much more time than was available to process a sufficient number of samples.

Other methods considered but rejected included the use of pitfall traps (needed longer *in situ* placement than could be achieved at most sites); suction traps (equipment not available for Polish sites); and flight interception traps (i.e. Malaise traps) and water pan traps (both expected to sample too many transient insects).

Species identification presented a problem throughout this research, and many invertebrates were initially recorded in the data as “Species A” etc, to be identified later from samples taken at the time. As the study progressed the author gained greater confidence in identifying and recording invertebrates in the field at least to genus level, though wherever possible voucher specimens were always taken for later determination in the laboratory. However, it is possible that some closely related species may have been missed or misidentified, especially if specimens eluded capture, which happened regularly but on a small enough scale to suggest that identification errors do not significantly distort the data on this study.

A further gap in recording the range of invertebrates present on the sites undoubtedly arises through confining sampling to just a few months in the year. For example, Szwedo (1998) recorded several species of leafhopper (Homoptera, Auchenorrhyncha) in *C. canescens* sward in Upper Silesia, Poland, whereas few leafhoppers were recorded in the present investigation; one plausible reason given by Szwedo (*in litt.*) is that a large proportion of leafhoppers in his study were active in autumn (September – October) and would therefore be unlikely to feature in samples taken in mid-summer. Though the limited time-frame for sampling correlated well with emergence periods of many invertebrate groups in this study, spiders Araneae and ground beetles Coleoptera: Carabidae are other groups which may be particularly under-represented because of the time-frame adopted (8.5).

The visual observation methods on which this research is largely based are considered by Southwood (1978) as having the potential to produce estimates approaching the measurement of absolute populations. Results per unit effort are usually lower than can be achieved by mass trapping techniques, though in the present investigation the sampling methods produced adequate material for study. A feature of visual observation methods is that they rely heavily on the efficiency and skill of the observer; while there is no problem so long as the same observer takes all samples, this variable makes it difficult for replication of the research by other workers.

A major benefit of the methodology adopted for faunal sampling is that it uses mostly absolute methods, allowing invertebrate densities to be assessed and compared, in addition to species composition. A correlation of faunal data with the physical and vegetational elements of a site has already been noted as an important outcome of the adopted methodology. Moreover, the observational techniques employed make it possible to sample and analyse the fauna of the different stages of the *C. canescens* habitat more precisely than studies which use mass trapping techniques.

4.6 Analytical methods

A main approach in this study is to test the relationship between species data and a number of environmental variables in order to express the significance of those variables and whether the responses are local to certain sites or similar across sites. To achieve these aims two methods of data ordination have been used – CANOCO and TWINSPAN. These programs were chosen because they are appropriate to the objectives of this study, are widely used in ecological investigations and their outputs are widely understood.

4.6.1 Canonical correspondence analysis (CANOCO)

CANOCO is a suite of programs designed for the multivariate statistical analysis and modelling of ecological data (ter Braak 1988, 1995, ter Braak & Šmilauer 1998; Lepš & Šmilauer, 2003). These programs use multiple regression techniques to identify underlying trends in the data. CANOCO allows the ordination axes to be related to measured environmental parameters, and in certain circumstances the statistical significance of the relationship between the trends and environmental parameters can be tested. The use of standardised quadrats for sampling environmental, vegetation and invertebrate data in this study (4.3, 4.4.2, 4.5.2) allows a direct analysis of the relationship between species and environmental factors.

CANOCO incorporates two programs which compare the overall variation in the species content of a set of samples in conjunction with, but not constrained by, environmental variables: these are Principal Components Analysis (PCA) and Detrended Correspondence Analysis (DCA). These analyses extract the most important independent trends in the data. In DCA the second axis is detrended to eliminate its dependence on the first axis. The default method in CANOCO is “detrending by segments”, a process which simultaneously allows the data to be tested to see whether unimodal methods or linear methods are most appropriate. In the analysis the lengths of gradient associated with the segments are calculated: a gradient above 4.0 suggests that the data are unimodially distributed (i.e. samples are very different from each other) and DCA is the appropriate analysis; if below 4.0 the gradient suggests a linear model (i.e. the main difference is in quantities of each species) and PCA is the appropriate analysis (ter Braak, 1988). The level of significance of each trend in the data can be gauged by the calculation of eigenvalues (measures of how strong the axes are and how much of the data is involved in them). In PCA and DCA analyses axes are extracted in descending order of importance in terms of their contribution to the total variation of the data set. Species data are not constrained by the environmental variables and the analyses give a true picture of the strongest trends of differentiation between the samples based only on the species they contain.

CANOCO is also designed to allow a Redundancy Analysis (RDA) and a Canonical Correspondence Analysis (CCA) in which the species data are constrained by the environmental variables. These focus on that variation in species content between the samples which can be attributed to the environmental variables included in the analysis. In effect they isolate just that variation between samples which can be correlated with the environmental variables measured. CCA is designed for the analysis of unimodal data and RDA for the analysis of linear data. The validity of the outputs can be tested through Monte Carlo permutations, which randomise the data to produce patterns which can be compared with the pattern of relationships in the experimental data: a probability value above 0.05 suggests that the pattern is probably itself a random relationship, a value below 0.05 suggests the experimentally-determined relationship is unlikely to be random. The significance of a relationship can also be gauged from the F-ratio, which measures the relationship between the variance attributable to the relationship under test and the remaining variance in the sample: a F-ratio at 3.0 or above implies significance.

For data input a series of Microsoft Excel files (see Disk Appendices) was created containing all data collected for every sample in this study. Each column in these files represents a single sample and each row a single species or an environmental factor – either physical (such as sand stability or grazing scale), spatial (locality) or temporal (year). Prior to input the data set was modified to select one or more environmental factors relevant to the particular analysis being undertaken. Data were also log transformed if they were not already transformed through e.g. use of Domin scale values or nominal data sets. The resulting data were then input into CANOCO and tested initially through a DCA, in which the length of gradient produced was used as a guide to whether DCA or PCA would be the more suitable unconstrained ordination.

The outputs of a CANOCO analysis are diagrams in which two trends, typically the two strongest, are represented by axis 1 (horizontal) and axis 2 (vertical). Each species has a relationship with each axis: it will increase or decrease along each trend. In the output diagram the relationship is shown as a line or vector; its direction shows the trend in relation to the two axes chosen, and its length shows the strength of the relationship. In most output diagrams in this study a restriction has been used to filter out less informative species. For clarity of presentation species names have been abbreviated in the diagrams and a glossary of abbreviations incorporated. A detailed explanation of the input/output of CANOCO is given in ter Braak (1995).

4.6.2 Two-way Indicator Species Analysis (TWINSPAN)

TWINSPAN is a popular method for community classification. It produces a classification by dividing samples into two groups (identified as 0 and 1) on the basis of their position along the primary gradient, determined by DCA ordination. Re-ordination of each group then allows further divisions, each time into two groups, and in this way a hierarchy of divisions is achieved (Hill, 1979).

At each division ***indicator species*** are identified: these are species which have a strongly biased distribution towards one of the two groups of the division, and which are characteristic of the samples on one side of the division. An indicator species need not be entirely absent from the other side of the division to remain an indicator; nor need it be present in all samples of the group for which it is an indicator: it merely needs to be more frequently encountered on one side of the division than the other. The indicator value (I_j) of a species (j) is defined mathematically as

$$I_j = m_1/M_1 - m_2/M_2$$

where m_1 is the number of occurrences of species j in group 0 which contains M_1 stands, and m_2 is the number of occurrences in the other group 1 which consists of M_2 stands. The resulting association of indicator species with one of two groups in the division is useful in attempting to diagnose the ecological significance of each division.

TWINSPAN employs the idea of the “pseudospecies”, which is characterised by the presence of a species at predetermined levels of abundance. These abundance levels are then used in presence/absence form to make the classification (Kent & Coker, 1992). The version of TWINSPAN employed in this study uses the CANOCO species data input file, and the input plant species data in Chapter 6 uses the Domin scale of abundance. TWINSPAN “cut levels” which define the “pseudospecies” were therefore selected on the basis of the Domin scale levels appearing in the data sets.

The input file is derived from the same Microsoft Excel files used as the CANOCO input (4.6.1) but modified by deleting non-quadrat (ie “general”) data samples. The output is presented as a dendrogram which shows the classification resulting from the analysis.

CHAPTER 5: PRELIMINARY FIELD INVESTIGATIONS

5.1 Selection of preliminary field investigations, Aims and Objectives

This Chapter describes observations made during two preliminary field investigations which were established to support the third Aim of this study, i.e. to identify key factors which may have conservation implications for British inland *Corynephorus canescens* populations, principally the West Midlands populations (1.2).

From Chapter 2 it is apparent that many aspects of the ecology of *C. canescens* have already been well studied. In relation to its conservation, detailed studies exist of the response of *C. canescens* to soil properties, temperature, competition and grazing (2.3), and further investigation of these factors was not considered necessary in the present study. The key importance of sand erosion and accretion in producing suitable conditions for the growth and maintenance of vigour of *C. canescens* tussocks is recognised and has been well documented (2.3.3, 2.3.4); the use of sand deposition in the conservation of the Wangford Warren *C. canescens* population has been fully described (2.4.4); and this technique has also been adequately studied experimentally in the Netherlands (2.4.2). In view of these studies it was decided not to conduct an investigation into sand erosion and deposition in relation to the West Midlands *C. canescens* populations, though the potential importance of this factor in the conservation of these populations is acknowledged.

From the literature review, therefore, two factors were identified where potential implications for the conservation of *C. canescens* in its West Midlands sites suggested further investigation. These were the plant's phenology in this region, and the effects of trampling on a *C. canescens* population.

While several studies of the reproduction, growth and life-span of *C. canescens* already exist in both laboratory and field conditions in Britain, Poland and elsewhere in Europe, there is considerable variation between the findings of the various authors (2.3.4, 2.3.5). In particular, seed production, germination rates and life-span differ, notably between Polish (Symonides, 1979) and British (Marshall, 1967) studies. The dispersal of *C. canescens* has been little studied, and specifically in Polish field conditions (Symonides *loc. cit*.). There are further indications in the literature that results obtained in laboratory conditions e.g. for germination may be very different from those obtained in the field. It was consequently felt that the phenology of *C. canescens* in the West Midlands should be investigated, to inform an understanding of the growth, reproduction, life-span and dispersal of the species in this region.

A second factor identified for further investigation is the effect of trampling on a *C. canescens* population. All the West Midlands sites are adjacent to footpaths, while the Lakenheath site in East Anglia and Bolimów in Poland are subject to vehicular passage (Appendix B). Trampling is suggested by Trist (1998) and Blunt & Blunt (2000) to have potential for producing sand erosion and accretion on *C. canescens* sites. Several authors have studied the effects of trampling on heaths and coastal dunes (these will be reviewed in 5.3.3), but these studies are of limited relevance to the conservation of *C. canescens* in the West Midlands. Moreover, as will be discussed in 5.3.3, differences between methodologies employed in existing trampling studies limit their usefulness in drawing general conclusions from them. The effects of trampling on inland *C. canescens* populations have not been studied at all. For these reasons the effects of trampling on a West Midlands *C. canescens* site was selected for investigation. In view of the rarity of the species, the small size of the West Midlands sites and the impossibility of excluding the public these investigations have remained preliminary, but also have an objective of defining the parameters for possible future, more controlled experiments.

In summary, therefore, the following Objectives were set to achieve the Aims of this element of the research:

- to establish a small closed population of *C. canescens* in a West Midlands location totally isolated from other populations;

- to make observations and measurements over several years on growth, reproduction, life-span and dispersal in this *C. canescens* population;

- to monitor the effects of a path diversion and enclosure on an existing West Midlands *C. canescens* community;

- within the limits imposed by the small and linear nature of the site, and by its continuous use by the public, to superimpose a limited trampling investigation on the path diversion and enclosure;

- to estimate the trampling pressure on this site by direct counts and where necessary by extrapolation from such counts;

- to describe the plant species composition of the trampled site at the start, during and at the end of the investigation;

- to describe the effect of trampling on the substrate including sand compaction and the amount of bare sand and litter;

- to describe the effect of trampling on the abundance, vigour and fecundity of *C. canescens*;

- to analyse by multivariate analysis the relationship between plant species composition and trampling;

- to characterise the stages of ecological succession taking place in the vegetation at the *C. canescens* habitat;

- to compare the observations made from the phenological and trampling investigations with studies in the literature;

- to formulate from these preliminary investigations hypotheses for experimental testing.

5.2 Phenology of *Corynephorus canescens* in cultivation in the West Midlands

5.2.1 Methods

In August 1998 seven one-year-old tussocks of *C. canescens* were transplanted from Kinver Edge Site KE2 into the container at Site AL as described Appendix B.5.1. The permission obtained from the National Trust was to take young tussocks, as this was considered at the time to be less damaging to the *C. canescens* population than collection of the potentially large amounts of seed required by the very low germination rates in field conditions reported in the literature (Symonides, *loc. cit*.). One-year-old tussocks were taken as it was felt that they had a better chance of surviving transplantation than newly-germinated seedlings, a factor to be considered when dealing with a vulnerable species. The tussocks collected were all of the same age class (germinated in autumn 1997) and approximately the same size (60 mm). They had no inflorescences. They were planted around the inside edge of the container roughly equidistant from each other.

In July-August of the following four years (1999 to 2002) all *C. canescens* plants inside and outside the container were counted and measured, the measurements taken being sward height, inflorescence height and number of inflorescences per plant.[6] The location of plants in the container and the orientation and distances of individual plants growing outside the container were also recorded by mapping them each year on a sketch map of Site AL. During 1999-2002 an apparently regular pattern of growth, reproduction and dispersal was identified; but in July 2004 some anomalies in the normal

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[6] See 4.4 for methodology

reproductive pattern of *C. canescens* at Site AL were noticed, and it was therefore decided to take a further full series of data for 2004 to augment those already collected. Data analysed in 5.2.2 below, therefore, are from all years between 1998 and 2002 plus 2004.

In July 2001 it was found that the container consisted of 80% cover of *Rumex acetosella* and 10% *Pilosella officinarum*; the former arrived as seeds in the sand attached to the tussocks on transplantation, the latter self-seeded from nearby parts of Site AL. At this date the container was thoroughly weeded to remove these species. This apart, no intervention on the vegetation in the container was made. The surrounding garden was lightly weeded throughout this study, to control invasive species such as *Elytrigia repens*. In addition, dead tussocks of *C. canescens*, which were found to persist in the soil around the container for over a year, were routinely cleared away.

5.2.2 Results

The number of plants growing in the container (“Sand”) and surrounding garden (“Soil”) during the investigation are shown in Table 5.2i. In this Table plants are shown according to their period of germination, and the number surviving in each year from germination are indicated. The absence of data for 2003 means that plants from that year cannot be separated into their germination periods. “N/A” indicates that data are not available for the period concerned.

By recording and measuring individual plants in July-August of each year from 1999 to 2002 it was possible to follow them through their complete life cycles. It was observed that two periods of germination occurred - the first in late summer or autumn immediately after the setting of seed, and the second in spring of the following calendar year. This produced two cohorts of plants within each age class, which in July-August of their first year could normally be differentiated by sward height (autumn-germinated plants were between 60 and 95 mm high, spring-germinated ones from 20 to 45 mm high). It was

Table 5.2i: Number of *Corynephorus canescens* plants in cultivation by age class and growing medium for each year from 1998-2002 and 2004.

Growing medium	**When germinated**	**Number of plants surviving in each year from germination**		
		1st year	**2nd year**	**3rd year**
Sand	autumn 1997	7	7	6
	spring 1999	1	0	0
	autumn 1999	1	0	0
	spring 2000	11	0	0
	autumn 2000	0	0	0
	spring 2001	2	2	0
	autumn 2001	2	1	0
	spring 2002	19	0	0
	autumn 2002	1	N/A	0
	spring/autumn 2003	N/A	6	N/A
	spring 2004	10	N/A	N/A
	autumn 2004	46	N/A	N/A
Soil	spring 1999	0	0	0
	autumn 1999	0	0	0
	spring 2000	4	0	0
	autumn 2000	18	18	0
	spring 2001	1	0	0
	autumn 2001	4	4	0
	spring 2002	26	N/A	1*
	autumn 2002	9	N/A	1*
	spring/autumn 2003	N/A	6	N/A
	spring 2004	7	N/A	N/A
	autumn 2004	7	N/A	N/A

* this plant may have arisen from either spring or autumn 2002 germination

found, however, that sward height could not be used to distinguish between spring-germinated and autumn-germinated plants when they reached their second year; in practice, continuing differentiation into these separate age classes could only be achieved by tracking individual plants by mapping them as indicated above.

The data in Table 5.2i show that, when the number of seedlings germinating between 1999 and 2004 are totalled separately for spring and autumn germination periods, the totals are very similar (81 and 88 respectively). However, percentage survival was very different: between 1999 and 2002, 91% of autumn-germinated plants survived into their second year, whereas only 11% of spring-germinated plants did so. Of the original seven transplanted tussocks, six survived into their third year, after which they died; but only one plant which germinated in cultivation (in 2002) certainly reached its third year. Table 5.2i also indicates that, regardless of time of germination, survival was much better for plants which germinated in soil than for those in sand: between 1999 and 2002, 81% of plants in soil survived into their second year whereas only 18% of those in sand did so.

The fecundity of *C. canescens*, as defined in 4.4.3, was also recorded in this investigation and is shown in Table 5.2ii. This Table indicates the number of plants flowering in each year since germination, together with the percentage of the population of that age class represented by the flowering plants. The mean number of inflorescences per flowering plant is also shown. The data are given separately for the different germination periods.

The data in this Table show that within the very limited constraints of this investigation the reproductive pattern of *C. canescens* varied from year to year, but certain general patterns began to emerge. No spring-germinated plant flowered in its first year; but normally a small percentage of autumn-germinated plants did so, producing only a small number of inflorescences per plant. Table 5.2ii also indicates that normally all second year plants produced flowers, with only the plants of uncertain germination period (representing 2-year-old plants flowering in 2004) running counter to the general trend. In addition, second year plants normally produced a much higher mean number of inflorescences than did first year plants, though the range of means is considerable. The small number of plants which flowered in their first year normally survived to flower again in their second year. Of the seven plants which survived into their third year five flowered in that year.

Table 5.2ii: Number and percentages (in parentheses) of flowering plants and mean number of inflorescences produced by *Corynephorus canescens* plants in cultivation, by age class.

When germinated	**Measure of fecundity**	**Age of plant**		
		1st year	**2nd year**	**3rd year**
spring	no. (and %) of flowering plants	0 (-)	2 (100%)	0 (-)
	mean no. inflorescences per plant	-	15.0	-
autumn	no. (and %) of flowering plants	13 (13.7%)	30 (100%)	4 (67%)
	mean no. inflorescences per plant	10.0	54.0	31.8
uncertain	no. (and %) of flowering plants	0 (-)	3 (33%)	1 (100%)
	mean no. inflorescences per plant	-	112.7	243

Further measures of the vigour and fecundity of *C. canescens* in this investigation are shown in Table 5.2iii, which gives the means (to one decimal place) of sward height, inflorescence height and number of inflorescences per plant for each year of the experiment and for all years taken together. Table 5.2iii (a) gives these data for plants growing in sand, Table 5.2iii (b) for plants growing in soil, and Table 5.2iii (c) for all plants taken together. A dash (–)

indicates that no plants in that growing medium fell into that category in the year in question.

Table 5.2iii: Means of sward height, inflorescence height and number of inflorescences per plant of *Corynephorus canescens* in cultivation, by year and growing medium. Figures in parentheses are standard errors.

(a) Plants growing in sand

Mean	**Year**					**All Years**
	1999	**2000**	**2001**	**2002**	**2004**	
Sward height (mm)	81.1 (9.9)	71.9 (12.4)	30.0 (5.0)	48.0 (10.3)	33.5 (2.5)	43.8 (3.2)
Inflorescence height (mm)	328.6 (19.6)	233.8 (19.5)	–	338.8 (25.4)	90.0 (0)	306.0 (16.5)
Number of inflorescences per plant	30.3 (6.8)	31.8 (12.3)	–	20.3 (9.7)	4.5 (1.5)	25.2 (4.8)

(b) Plants growing in soil

Mean	**Year**					**All Years**
	1999	**2000**	**2001**	**2002**	**2004**	
Sward height (mm)	–	77.1 (11.3)	58.2 (15.6)	52.0 (5.7)	77.5 (10.7)	72.6 (5.9)
Inflorescence height (mm)	–	273.3 (20.9)	326.9 (41.3)	311.7 (18.1)	345.9 (53.7)	297.0 (18.4)
Number of inflorescences per plant	–	3.7 (1.2)	71.1 (28.5)	19.8 (4.6)	98.2 (47.3)	51.8 (15.0)

(c) All plants (sand plus soil)

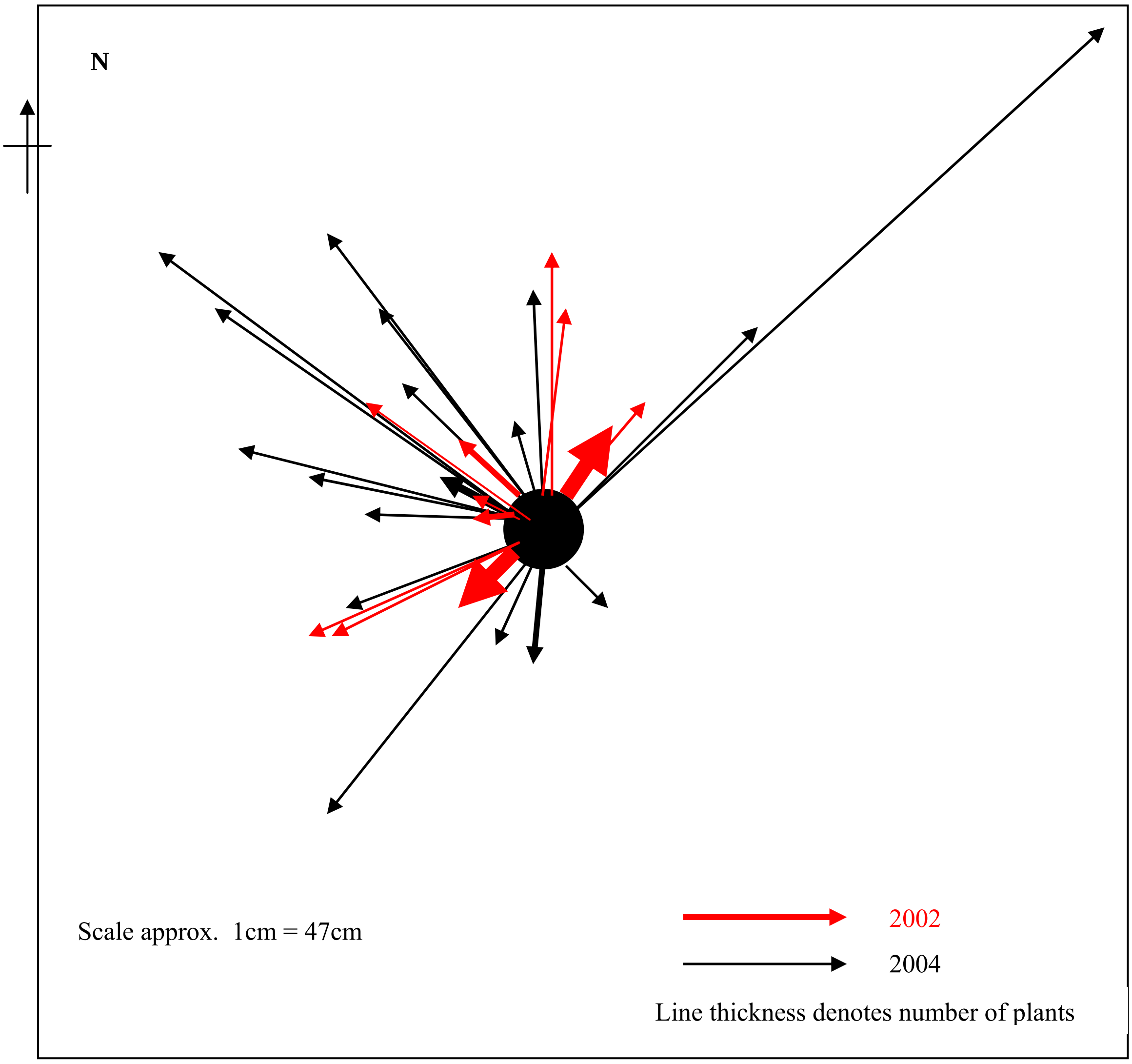
Mean	**Year**					**All Years**
	1999	**2000**	**2001**	**2002**	**2004**	
Sward height (mm)	81.1 (9.9)	75.2 (8.3)	48.8 (15.4)	51.0 (4.9)	47.0 (4.0)	54.5 (3.1)
Inflorescence height (mm)	328.6 (19.6)	250.7 (15.3)	326.9 (41.3)	320.0 (14.6)	281.9 (57.4)	304.8 (13.5)
Number of inflorescences per plant	30.3 (6.8)	19.7 (8.7)	71.1 (28.5)	19.9 (4.1)	74.8 (37.9)	41.3 (9.4)

In this Table the number of individual plants in one or other growing medium in some years was so small that it is probably best to consider the data for all plants taken together (Table 5.2iii(c)). This shows that mean inflorescence heights were reasonably consistent throughout this investigation despite the large variation in sizes of the different age classes in different years (see Table 5.2i). The mean sward height fell rather steeply between 2000 and 2001, after which it remained reasonably constant. This pattern is attributed to the original transplanted tussocks which survived until 2000 and led to a higher ratio of mature plants to seedlings in the earlier years of this study. The mean number of inflorescences per plant in Table 5.2iii varied quite widely from year to year and suggests a biennial cycle (higher fecundity in 1999 and 2001, lower in 2000 and 2002), though 2004 would appear not to fit this pattern. The Table also shows a greater vigour and higher fecundity of plants growing in soil compared with those in sand, as indicated by much higher means for sward height and number of inflorescences per plant.

The dispersal of plants away from the parent colony in the container was recorded in all years. In 2002 and 2004 mapping of the orientation of plants in relation to compass points was more precise than in 2000 and 2001 (i.e. to sixteen compass divisions rather than eight), and only data for 2002 and 2004 are therefore used to map the dispersal of plants from the parent colony in the container. These data are plotted in Figure 5.2a.

In this Figure the arrows plot the distance and orientation from the container of all plants growing outside the container in 2002 and 2004. The thickness of an arrow reflects the number of plants involved. This Figure reveals a similar dispersal pattern for both years: a majority of dispersed plants lies within 60 cm of the container, while individual plants seeded within the range 93 cm to 270 cm away, with one plant exceptionally 455 cm away. The great majority of dispersal occurred within the sector from north to south-west, and almost none between north-east and south. As the container is placed near the centre of Site AL and germination is possible at all compass points around it, the pattern shown in Figure 5.2a strongly suggests that a majority of seed is dropped close to the parent plants, and that those seeds which disperse to greater distances are normally wind-borne, as the funnelling effect of neighbouring houses produces the predominantly south-easterly winds implied by the Figure. Accidental dispersal on the author's boots remains a possibility for some seeds, though the dispersal pattern does not suggest that this is normally a factor: if it were so, we would expect to see a more even distribution around Site AL.

Figure 5.2a: Dispersal of self-seeded *Corynephorus canescens* plants in cultivation in 2002 and 2004.



5.2.3 Discussion

An objective of this cultivation study was to create a self-sustaining *C. canescens* population in a West Midlands location isolated from other populations. It appears from Table 5.2i that such a population was successfully established, allowing a series of measurements to be made which give information on growth, reproduction, life-span and dispersal in this population.

The study was initiated as a preliminary investigation into the phenology of *C. canescens* in the West Midlands, in order to make observations which may suggest hypotheses for formal experimental study. Because the investigation deals with a single population in isolation its results are essentially anecdotal and must be interpreted cautiously, and in particular conclusions based on direct comparison with the phenology of *C. canescens* in other regions cannot be sustained. It is, however, possible to ascertain where the observations made during this study reflect or do not reflect the findings of other studies.

The methodology described in 5.2.1 is considered sufficient to achieve the objectives of the investigation. Certain limitations which arise from it, however, need to be borne in mind when considering the results show in 5.2.2. One potential source area of error lies in ascribing plants to their age classes in Tables 5.2i and 5.2ii. Differentiation between autumn-germinated and spring-germinated *C. canescens* by means of sward height was feasible during the plant’s first year, though a very small number of plants showed a sward height between 45 mm and 60 mm, i.e. intermediate between the height ranges normally used to distinguish the two age classes. For example, in 2000 two first-year tussocks had sward heights of 50 mm and 55 mm; while in 2004 one plant had a sward height of 50 mm and two of 55 mm. All these were allocated to the “spring-germinated” age class since the seedlings with which they were most closely associated had sward heights which fell within the normal range for spring-germinated plants; it is assumed that these five somewhat taller specimens germinated earlier in spring than the majority of their neighbouring seedlings. Section 5.2.2 has also highlighted the problem of differentiating between autumn-germinated and spring-germinated plants when they reached their second season. Tracking plants individually from year to year by plotting them on a sketch map as described in 5.2.1 was normally sufficient to achieve this, but the close bunching effect often shown by seeding *C. canescens* (see Figure 5.2a) could occasionally inhibit the tracking of individual plants in this way. In hindsight these uncertainties could have been removed by marking individual plants rather than mapping them.

Despite these caveats, reasonable confidence in ascribing *C. canescens* plants to their age classes is given support by Symonides' (1979) findings that the size of tussocks of the same age is one of the least changing features of wild *C. canescens* populations. However, the picture given in Tables 5.2i and 5.2ii would potentially be affected by any age class distribution errors. It is believed that errors of this kind are few enough not to distort the overall picture shown in these Tables; but the total number of tussocks which survived to flower in this investigation was relatively small, and it is to be regretted therefore that no data are available for 2003. Such data might also throw further light on the apparently biennial cycle of fecundity suggested by Table 5.2iii. A study over a longer time period, or involving a larger number of plants, would be valuable in testing the observations made in this element of the investigation.

This study of *C. canescens* in cultivation encountered the same problems of measurement which arise in the study of wild populations (see 4.4), with one exception: in the present investigation there was never a difficulty in assessing the number of individual *C. canescens* plants, as the short-lived tussocks failed to enlarge through tillering, for reasons suggested below.

In 5.2.2 it was observed that under cultivation at Site AL *C. canescens* showed a tendency towards a biennial life history, with autumn-germinated plants surviving to flower, a few in their first year and normally all in their second year, after which all usually died. Six of the seven original transplants survived into their third year, but only one other tussock did so: it is suggested in this case that the act of transplanting delayed progress to maturity in the original plants. In 2.3.4 it was noted that *C. canescens* is considered by most authors to be a short-lived perennial surviving up to seven years, with maximum seed production in its second and third years. A two-year life cycle similar to that implied by this investigation, however, is not unknown and has been recorded in the field in Britain and Poland, while Tüxen (in Marshall, 1967) regarded two growing seasons to be the plant's normal life span in Germany. Given the importance attributed by various authors to sand accretion in prolonging the life of individual *C. canescens* tussocks by promoting tillering (2.3.3), the apparently biennial phenology of *C. canescens* observed in this study may be a response to a lack of tiller production in the absence of sand accretion.

An interesting observation from this investigation is the freedom with which *C. canescens* seeded itself into ordinary garden soil (Plate 3). This most frequently occurred in small patches of bare soil near the container, but some plants managed to germinate and survive in a close sward of *Thymus polytrichus*, one or two in a sward of *Herniaria glabra*, and a handful even seeded themselves into a tarmac drive-way (Plate 3). Although *C. canescens* is treated by all authors as a plant of sandy places, there is some evidence that it can occasionally occur on other substrates: on soils containing up to 14.9% silt plus clay (Berger-Landefeldt & Sukopp, 1965; Rychnovská-Soudková, 1961), on coarse gravel (Schøtz-Christensen, 1957); while elsewhere in this present study tussocks of *C. canescens* have been found seeding themselves into a humified layer of organic matter up to 19 mm thick overlying sand at Sites DS and BT (Appendix B.3.1, B.4.1). It is also interesting to note that at Site AL *C. canescens* showed much better survival, greater sward height and fecundity in garden soil than in sand. This may well be a response to the higher nutrient concentrations to be expected in the former growing medium; and the observation may also imply that *C. canescens* has a much wider potential than it normally exhibits in wild populations, where it is restricted by poor competitive powers rather than any inherently low fecundity.

Some patterns which are suggested by the data given in 5.2.2 are in line with previous authors' findings. For example, even taking Symonides' (*loc. cit.*) lowest values for numbers of caryopses per spikelet and spikelets per inflorescence would imply a yield of over 61,000 caryopses from the 1,889 inflorescences produced by Site AL plants between 1999 and 2002 (Table 5.2ii); so that the 169 seedlings recorded (Table 5.2i) represent a germination rate of 0.28% at best. This is much more in line with Symonides' germination rates for wild *C. canescens* populations than those she achieved in laboratory conditions (2.3.4). The poor survival of spring-germinated plants is also consistent with the findings of Marshall (1967) and Symonides (*loc. cit.*); but the survival rate of autumn-germinated plants in this investigation (92%) is much higher than that recorded by Symonides (20%). This high survival rate is almost entirely accounted for by plants germinating in soil (Table 5.2i), a growing medium not monitored by Symonides. Some climatic influences may also be possible here, for Symonides' *C. canescens* populations are likely to have encountered more severe winters with greater frost-heave in the continental Polish climate than would be experienced by plants in the more temperate Atlantic climate of the West Midlands.

Table 5.2iii gives means for inflorescence height which are consistent with the upper end of the range quoted by Hubbard (1984), Stace (1991) and Rutkowski (1998) of 100 mm to 350 mm. Eleven measurements of inflorescence height exceeded 350 mm; six of these were in excess of 400 mm, with a maximum of 460 mm. Plants growing in sand produced marginally taller inflorescences than those in soil, but fecundity, as measured by number of inflorescences, was much higher for plants growing in soil. This factor probably accounts for the high means for the number of inflorescences per plant, which mostly exceed the range recorded by Symonides for her most productive population (18 to 23). It is noteworthy that three tussocks of *C. canescens* in this investigation had 257, 243 and 241 inflorescences, exceeding the maximum figure of 200 given by Marshall (*loc. cit.*).

The dispersal pattern of *C. canescens* from the parent population in the container (Figure 5.2a) suggests that most seed fell and germinated close to their parents, though several seedlings germinated from seed dispersed up to 455 cm away. Symonides (*loc. cit.*) recorded a similar pattern of aggregation of seedlings close to parent plants, with only two new aggregations being formed during the eight years of her study. The dispersal pattern at Site AL strongly suggests that wind is normally the key means of dispersal. Elsewhere in this study, however, at Polish Sites BR1, BR2 and BO several individual tussocks of *C. canescens* were found growing up to 13.2 m inside neighbouring *Pinus sylvestris* plantations (see Appendix B.6.1, B.6.2, B.7.1), where wind-blow would be strongly reduced by the sheltering effect of the trees; and though wind-dispersal might account for these outlying plants, the possibility of animal-assisted dispersal or germination from long-buried seed (despite the assertion of Jentsch (2001) and Jentsch & Beyschlag (2003) that seed remains viable for only two or three years) cannot be ruled out.

This investigation into the growth, fecundity, life-span and dispersal of *C. canescens* has produced a number of observations which suggest that the species may in the West Midlands, at least under cultivation conditions, have a shorter life-span but greater potential in growth and fecundity than shown for other regions in the literature. These observations imply a wide amplitude between the grass's fundamental and realized niches (Harper, 1977), and are perhaps best reflected by the conclusion of Symonides from her Polish studies (*loc. cit.*, page 34):

> "It may be as well to note that exogenic factors, abiotic and biotic, to a large extent limited the realization of the tremendous biotic potential of *C. canescens* ……It may, therefore, be presumed that the ecological scale of *C. canescens* is much wider than indicated by the observation of its natural distribution."

5.2.4 Summary of observations from the preliminary investigation into the phenology of a small population of *Corynephorus canescens* in cultivation in the West Midlands

The following observations were made from this field investigation into the phenology of *C. canescens* in an isolated, introduced population in the West Midlands:

C. canescens appeared to have a normally biennial life history, with very few plants surviving into their third year;

Plants germinating in autumn survived much better than those germinating in spring;

Germination was very low and more consistent with germination in wild populations than in laboratory conditions as reported in the literature;

Flowering occurred in a plant's second year, with a small number of autumn-germinated plants flowering in their first year as well. Very few plants survived to flower in their third year;

Plants growing in soil had a better survival rate and higher fecundity than those growing in sand;

C. canescens vigour and fecundity in this investigation was rather higher than in other studies reported in the literature;

Dispersal from the parent population appeared to be largely wind-borne dispersal;

Dispersal mostly occurred within 60 cm of the parent population, and exceptionally up to 455 cm.

5.2.5 Suggestions for further study and conservation implications

The observations summarised above suggest a number of hypotheses for study by formal investigations, whose results may have implications for the conservation of *C. canescens*, particularly in the West Midlands. The following hypotheses should be tested using replicated and randomised plot experiments:

Hypothesis A: *that a normally biennial life-span of C. canescens is a result of the lack of sand accretion.*

This hypothesis may be tested by growing *C. canescens*, ideally from two or more regions, in one location in a replicated plot experiment. Each region's plants should be grown separately, and plots should have either treatment with sand accretion at a rate defined by Marshall (1967), or else no treatment (controls).

Hypothesis B: *that a normally biennial life-span of C. canescens is produced by the climatic conditions of the West Midlands*.

Plants from several regions including the West Midlands and regions where the life-span of *C. canescens* is normally longer than two years (see the literature summarised in 2.3.4) should be grown and monitored separately in a single West Midlands location.

Hypothesis C: *that C. canescens has greater seed production in soil than in sand.*

To be tested by growing *C. canescens* separately in sand and soil (in randomised, replicated plots).

Hypothesis D: *that the survival of spring-germinated C. canescens seedlings can be enhanced by protection, e.g. by the use of brashings (see Blunt & Blunt, 2000).*

To be tested by growing *C. canescens* in randomised, replicated plots some of which are treated by applying brashings and others are untreated controls.

These experiments have implications for the conservation of *C. canescens*, particularly in the West Midlands. For example, if the species is shown by formal experiment to have a normally biennial life-span in the West Midlands, a test of the main cause would clearly inform conservation measures. If sand accretion can be shown to extend the life of *C. canescens* tussocks in West Midlands populations, direct conservation measures can be developed accordingly; if, however, climatic factors largely determine life-span there, such measures would be ineffective.

The apparent potential of *C. canescens* for survival and attainment of high fecundity in garden soil also has implications for the conservation of this grass. The cultivation of tussocks in soil rather than sand may produce more caryopses for seeding into populations where natural seed production may need a boost, such as at Wangford Warren (Trist, 1998). Although not developed as a hypothesis above, it may also be possible to test experimentally whether *C. canescens* can survive to flowering in soils other than sand on a specific site in competition with the plant communities of that site. For example, the slow spread of *C. canescens* into a grassy field adjacent to Kinver Edge Sites 1 and 2 (Blunt & Blunt, *loc. cit.*) might be facilitiated by the findings of such an experiment.

A further observation from this preliminary investigation, that wind dispersal is the main means of dispersal in *C. canescens*, is difficult to test experimentally. However, its importance for the species' conservation is clear. If true, the natural foundation of new populations will to a large extent depend on the exposure of populations to prevailing winds. In the West Midlands all three Kinver Edge sites, along with Burlish Top, are currently open to the south, and removal of vegetation to increase their exposure to prevailing south-westerly winds would be easy to achieve. Besides better seed dispersal, *C. canescens* might also benefit at these sites from sand accretion consequent upon more exposure to prevailing winds if Hypothesis A above is confirmed. By contrast, the Devil's Spittleful / Rifle Range population lies at the foot of a steep railway embankment which effectively prevents exposure to south-westerly winds, and no such solution would be possible at that site.

5.3 Trampling investigation

5.3.1 Methods

A decision of the National Trust to divert the footpath across Site KE3 in mid-March 1999 provided an opportunity for preliminary investigation into the effects of trampling on *C. canescens*. The path diversion involved moving a fenced area by 2 metres as described in Appendix B.2.3. This action allowed the establishment of three different trampling treatments, as follows:

- a mature *C. canescens* population subjected to uncontrolled trampling at Site KE3 Area A (referred to as *Vegetated – Uncontrolled Trampling* in this section);
- a protected mature *C. canescens* population subjected to controlled trampling at Site KE3 Area B North (referred to as *Vegetated – Controlled Trampling*);
- a protected strip of bare sand subjected to controlled trampling at Site KE3 Area B South (referred to as *Bare – Controlled Trampling*).

The path diversion gave no opportunity to investigate uncontrolled trampling of bare sand, but Blunt & Blunt's (2000) studies showed that uncontrolled trampling of Sites KE1 and KE3, at the rates experienced at Kinver Edge, maintained bare sand in which *C. canescens* was unable to establish itself (see Plate 4).

5.3.1.1 Layout of the investigation

The path diversion resulted in the creation of a new enclosure measuring 30 m x 4 m in the week ending 13 March 1999. Within this were enclosed two parallel strips, one vegetated and one of bare sand (the previous position of the path). Along each strip a series of ten 2 m x 2 m plots were marked out using pegs and twine (Appendix B.2.3). These plots were numbered N1 to N10 along the vegetated strip and S1 to S10 along the bare strip.

As the literature on trampling experiments on dune and heathland vegetation (5.3.3) gave very few clues about the rate of trampling which *C. canescens* might sustain, and those experiments also adopted a wide variety of trampling methodologies, it was felt necessary to initiate an exploratory investigation with a range of trampling rates whose results might later be tested by formal experiment with replication. The rate of uncontrolled trampling on the new path was unknown at the start of this investigation, but was expected to be relatively heavy (Blunt & Blunt, *loc. cit.*). In consequence, it was decided to employ a progressive scale of relatively light trampling rates on individual plots in the enclosure. Three such trampling rates were selected, namely 100, 200 and 300 footfalls per month[7] (equivalent to 25, 50 and 75 footfalls/m^2/month respectively). It was also decided to estimate the rate of uncontrolled trampling along the new path outside the enclosure by extrapolation from a representative series of sample counts. It was hoped that this initial investigation might suggest hypotheses for formal experimental investigation at a later date.

Figure 5.3a gives the layout of the investigation. The enclosure is shown in relation to the new path. The latter, which is the *Vegetated – Uncontrolled Trampling* strip, is indicated in grey. Within the enclosure the *Vegetated – Controlled Trampling* strip is shown in green and the *Bare – Controlled Trampling* strip is shown in yellow. Plots within the enclosure are numbered, and the six trampled plots are shown in bold type, with their monthly rate of trampling (footfalls/month) given in parentheses. The remaining plots in the enclosure are untrampled controls.

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[7] a footfall is defined here as a single placing of a booted foot entirely within the plot.

Figure 5.3a: schematic diagram of Site KE3 trampling investigation (not to scale).

The exclusion of the public from the enclosure by means of a fence meant that a high degree of confidence can be placed in the accuracy of these rates of trampling. On one occasion in spring 1999 it was found that a member of the public had intruded into the enclosure and lightly trampled across plot S1; however this is believed to be the only such occurrence throughout the investigation and is considered to have had a negligible effect on the results.

The trampling regime within the enclosure began in March 1999 and continued for a total of 27 months up to and including May 2002. However, the national foot-and-mouth crisis of early 2001 meant that Kinver Edge was closed to all access for four months (February to May) and no trampling took place in those months. To compensate, the equivalent of four months' worth of trampling was made up later in 2001, but it should be borne in mind when interpreting the results of this investigation that the growth of vegetation in the enclosure was unchecked by trampling in early-mid spring 2001.

5.3.1.2 Determining the rate of uncontrolled trampling on the new path

The new path outside the enclosure exposed a 2 m wide strip of mature *C. canescens* vegetation to uncontrolled trampling by walkers across this part of Kinver Edge. Whereas the rates of trampling in the enclosure were controlled throughout the investigation, the trampling rate on the new path had to be ascertained. The use of a datalogger to make a direct count of walkers passing along the path was considered but rejected due to the high risk of theft or vandalism of the equipment. As an alternative, therefore, a series of hourly counts was made throughout 2002 of individuals using the new path, to allow a calculation of the total trampling pressure on the path by extrapolation. To reduce the possibility of bias, sample counts were made within nine time-frames formed from three types of day (weekdays, weekends and bank holidays) and three times of day (early, middle and late, the precise periods calculated by dividing the daylight hours into three, and varying according to the different day-lengths at different seasons). Counts were made throughout the year in both good and poor weather conditions. Within each of the nine time-frames from three to six sample counts were made across the year, except for the less frequent bank holidays, when either two or three sample counts were made in each time-frame. The number of samples taken in each time-frame is shown in Appendix A Table Aii. In this way the counts for each time-frame were repeated but no true replication could be achieved as each day must clearly be different from the rest. No counts were made at night as initial observations had shown that the number of walkers along the new path after dark were so few that they could be excluded without distorting the calculations.

The full schedule of counts and the calculations based on them are detailed in Appendix A, where it is estimated that the trampling pressure along the new path in 2002 was between 6,000 and 6,500 adult footfalls/m^2/month.

5.3.1.3 Quadrat sampling

The physical characteristics of each quadrat were recorded by the methods outlined in 4.3, and vegetational sampling was carried out as described in 4.4.

For **Site KE3 Area A (Vegetated – Uncontrolled Trampling)**, ten points were identified along the new path, each adjacent to ten plots (N1 to N10) in the enclosure (Area B). Because of limited time availability, five regular sampling points were selected adjacent to plots N1, N3, N5, N7 and N10, and one quadrat sample was taken at each of these points in 1999, 2000 and 2001. A second series of sampling points was identified contiguous with those above away from the fence, and a series of quadrat samples was taken at these second sampling points in 1999 and 2001. Finally, two contiguous quadrat samples across the path and orientated to each of the remaining plots (N2, N4, N6. N8, N9) were taken in 1999 only. This means that five quadrat locations were sampled in all three years, a further five locations in 1999 and 2001, and the remaining ten only in 1999. The timing of the samples also varied: in 1999 samples were taken in April so as to characterise the vegetation at the start of the investigation, but this meant measuring *C.*

canescens before its flowering period that year; in 2000 and 2001 measurements were taken in summer when *C. canescens* was in full flower.

Within the enclosure **Site KE3 Area B** nine of the twenty plots (i.e. the Bare – Controlled Trampling plots S1, S4, S6, S7, S10 plus the Vegetated – Controlled Trampling plots N1, N4, N7 and N10) were initially sampled in 1999, as it was felt that these would adequately characterise the vegetation of all plots at the start of the investigation. Subsequently, quadrat samples for all twenty plots were taken in July 2000, June 2002 (immediately after the end of trampling) and August 2004. One quadrat sample per plot was taken in each year, with a second, contiguous sample taken for N1, N4, N7 and N10 in 1999 and for all plots in 2002. Due to time constraints sampling during the flowering season was possible only in 2000, so sequential data on *C. canescens* inflorescence height and number of inflorescences are not available for Site KE3 Area B. The 2004 samples were made 27 months after the trampling exercise ceased, to investigate whether any continuing effects were apparent.

5.3.2 Results

Three analyses were carried out on the data for each of the areas in this investigation: the effects of trampling on the substrate, the effects of trampling on *C. canescens*, and the effects of trampling on plant species composition.

5.3.2.1 Site KE3 Area A (Vegetated – Uncontrolled Trampling)

Data on the ***changes in the substrate*** are shown in Table 5.3i, which gives the means and standard errors of percentages of bare sand, litter and each measure of sand compaction at the start of the investigation in 1999; in 2000; and at the end of the investigation in 2001.

Table 5.3i: Means and standard errors (SE) of percentages of bare sand, litter, and levels of sand compaction, Site KE3 Area A (Vegetated – Uncontrolled Trampling) in 1999, 2000 and 2001.

	1999		**2000**		**2001**	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
Bare sand	22.0	15.0	34.0	7.0	94.0	1.8
Litter	18.0	11.0	6.0	2.4	0.4	0.1
Sand compaction 1	0	0	10.0	3.5	92.0	2.7
Sand compaction 2	0	0	35.0	9.7	6.5	2.7
Sand compaction 3	100	0	55.0	12.3	1.5	1.5

This Table shows that at the start of the investigation the new path was fully compacted (sand compaction 3) with 22% bare sand and 18% litter. Over three years the sand surface became progressively opened up by trampling, until in 2001 almost all of the path's surface consisted of bare, loose sand, with hardly any compacted sand or litter remaining.

Data on ***changes in C. canescens*** over the three years of the investigation are shown in Table 5.3ii, which gives the means and standard errors of sward height, inflorescence height and number of inflorescences of *C. canescens* during the investigation.

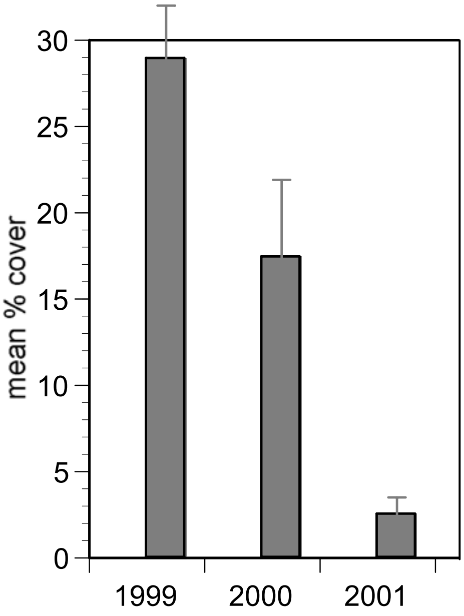
Table 5.3ii: Means and standard errors (SE) of sward height, inflorescence height and number of inflorescences of *Corynephorus canescens*, Site KE3 Area A (Vegetated – Uncontrolled Trampling) in 1999, 2000 and 2001.

	1999		**2000**		**2001**	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
Sward height (mm)	16.3	2.2	46.4	3.17	46.0	3.2
Inflorescence height (mm)	-	-	126.5	10.7	173.9	21.6
Number of inflorescences	-	-	3.6	0.5	11.9	3.4

This Table shows that mean sward height was only 16.3 mm at the start of the investigation but rose to approximately 46 mm in the following two years. To characterise the vegetation at the outset of this study the 1999 samples were taken in April (i.e. early in the growing season), and it is perhaps not unreasonable to expect mean *C. canescens* sward height to be less in that year than when sampled in July 2000 and September 2001. These sampling dates also mean that no data on *C. canescens* vigour and fecundity, as measured by inflorescence height and number of inflorescences, are available for 1999. Table 5.3ii shows that means for both these measures increased between 2000 and 2001, but even so fecundity remained much lower than the 18-23 inflorescences range recorded by Symonides (1979) for her most productive Polish populations.

A further indication of the impact of trampling on *C. canescens* is given by the percentage cover of this grass. Figure 5.3b shows the means and standard errors of *C. canescens* percentage cover for the new path over the three years of the investigation.

Figure 5.3b: Means and standard errors (error bars) of *Corynephorus canescens* percentage cover, Site KE3 Area A (Vegetated – Uncontrolled Trampling) in 1999, 2000 and 2001.



This Figure indicates that at the outset of the investigation the percentage cover of *C. canescens* on the new path was 28.9%, but fell dramatically to 17.4% in 2000 and 2.5% in 2001. This decline in percentage cover may be interpreted as a consequence of the progressive elimination of vegetation from the centre of the new path. In April 1999 the full width (2 m) of the path was vegetated, and *C. canescens* was distributed fairly evenly throughout. By July 2000, however, vegetation had become confined to a strip directly adjacent to the enclosure fence, the remainder of the path being bare sand. The mean width of ten measurements of this vegetated strip was 26.4 cm in 2000 and 35.2 cm in 2001. Within this strip *C. canescens* occupied a still narrower zone right against the fence, with a mean width of 19.8 cm in 2000 and 14.8 cm in 2001 (n=10). In other words, *C. canescens* showed less tolerance of the degree of trampling on the new path than other plant species, and was progressively reduced even when, in 2001, the other vegetation had managed to encroach a little more on the trampled area than in the previous year.

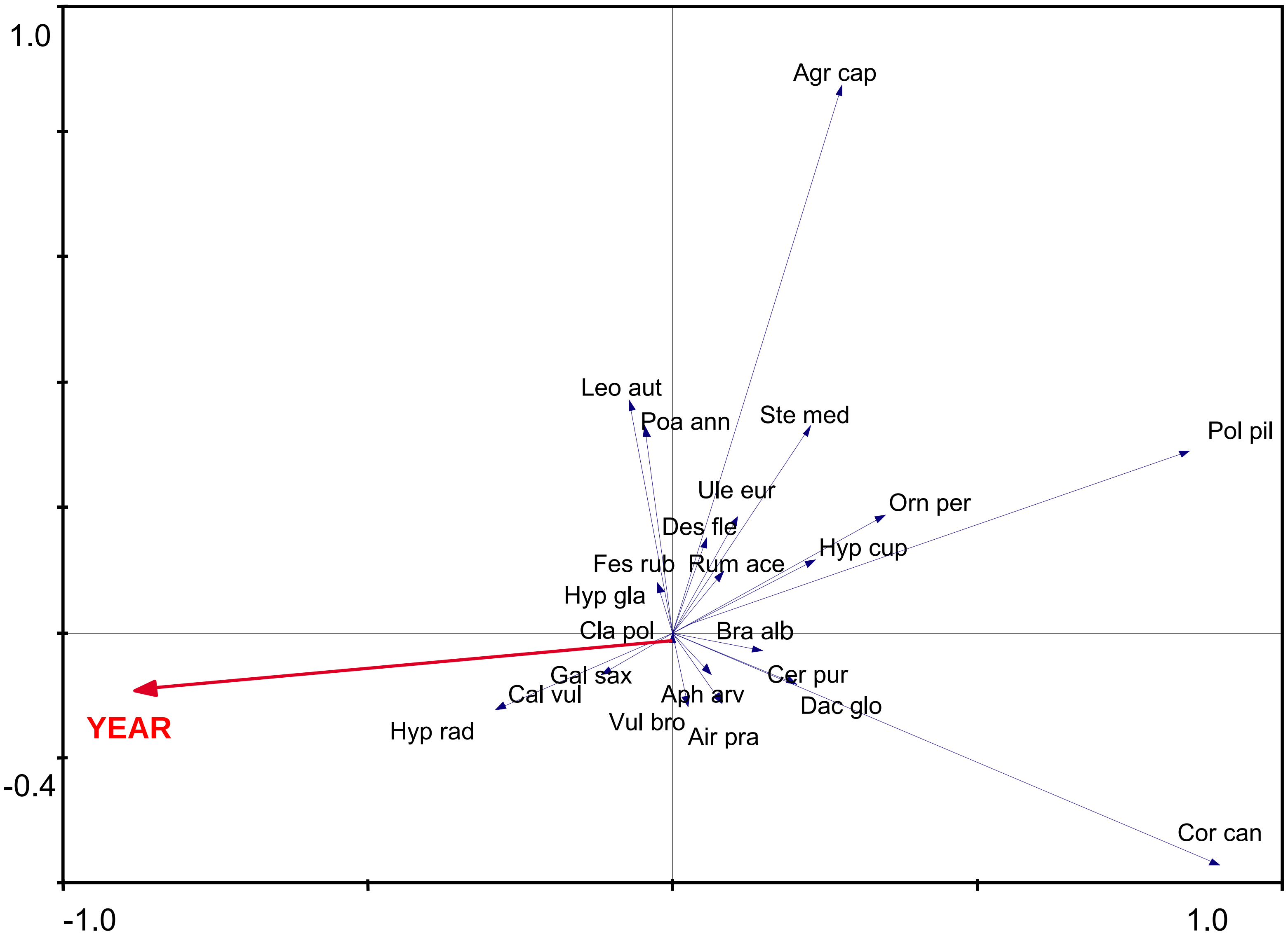
Changes in plant species composition on the new path were analysed by CANOCO, using Disk Appendix 1 as the baseline data from which the input files were derived. Plant species data were tested and showed a skewed distribution, and were therefore normalised by logarithmic transformation. The input covered 35 samples and 35 plant species with 205 occurrences. “Year” was input as the one available environmental variable that would give some measure of the progressive effects of trampling over the duration of this investigation, though effects of succession might potentially also be reflected in the analysis.

An exploratory DCA gave eigenvalues for axes 1 and 2 of 0.248 and 0.207 respectively. In this analysis the length of the longest gradient was 2.576, suggesting that the data best fit the linear model which is analysed by Principal Components Analysis (PCA). This gave an eigenvalue of 0.474 and a strong species-environment correlation of 0.882 for axis 1. The resulting species/environmental variable biplot is shown as Figure 5.3c. In this Figure the environmental variable “year” has been superimposed on the analysis (indirect gradient analysis) without affecting the trends in the species:sample matrix. Thus in Figure 5.3c the “year” vector merely reflects the distribution of the samples from different years on the species:sample trends.

In this Figure *C. canescens* and *Polytrichum piliferum* are the species most negatively correlated with year, suggesting that they disappear most quickly with time under heavy uncontrolled trampling, with three bryophytes (*Hypnum cupressiforme*, *Brachythecium albicans* and *Ceratodon purpureus*) plus *Ornithopus perpusillus* among the group of species next most affected by year. In contrast, *Hypochaeris radicata* and *Calluna vulgaris* are most positively correlated with this variable in the PCA. The first axis implies that *C. canescens*, *Ornithopus perpusillus, Polytrichum piliferum* and the other mosses were most susceptible to continuous heavy trampling on the new path. The second axis contrasts samples characterised by high levels of *Agrostis capillaris* with those containing a variety of species notably *Aira praecox*, *Aphanes arvensis* and *Vulpia bromoides*. These last three are all winter annual species: *Agrostis capillaris* on the other hand is a perennial grass. Possibly axis 2 reflects a trend between more stable, less drought-liable situations colonised by *Agrostis capillaris* and looser, less compacted substrates more liable to dry out in summer. This relationship does not appear to change from year to year and hence is not directly affected by opening up the vegetation to trampling.

A direct gradient analysis (RDA) was undertaken using the same data sets. Here the vegetation data are directly constrained by the environmental variable “year”. The principal axis eigenvalue of 0.377 and species-environment correlation of 0.899 show that the constraining axis overwhelmingly accounts for the variation within the data sets. Monte Carlo permutations give a P-value of 0.002 and F-ratio of 19.93, suggesting that the relationship between the environmental variable “year” and the changes in the vegetation shown in relation to axis 1 are not random. The resulting RDA diagram is shown in Figure 5.3d, which is very similar to Figure 5.3c and can be interpreted in the same way. The similarity suggests that ordination axis 1 in the PCA is satisfactorily explained by “year”. It serves to confirm that “year”

Figure 5.3c: Principal Components Analysis (PCA) showing relationship between plant species composition and duration of trampling, Kinver Edge Site KE3 Area A.

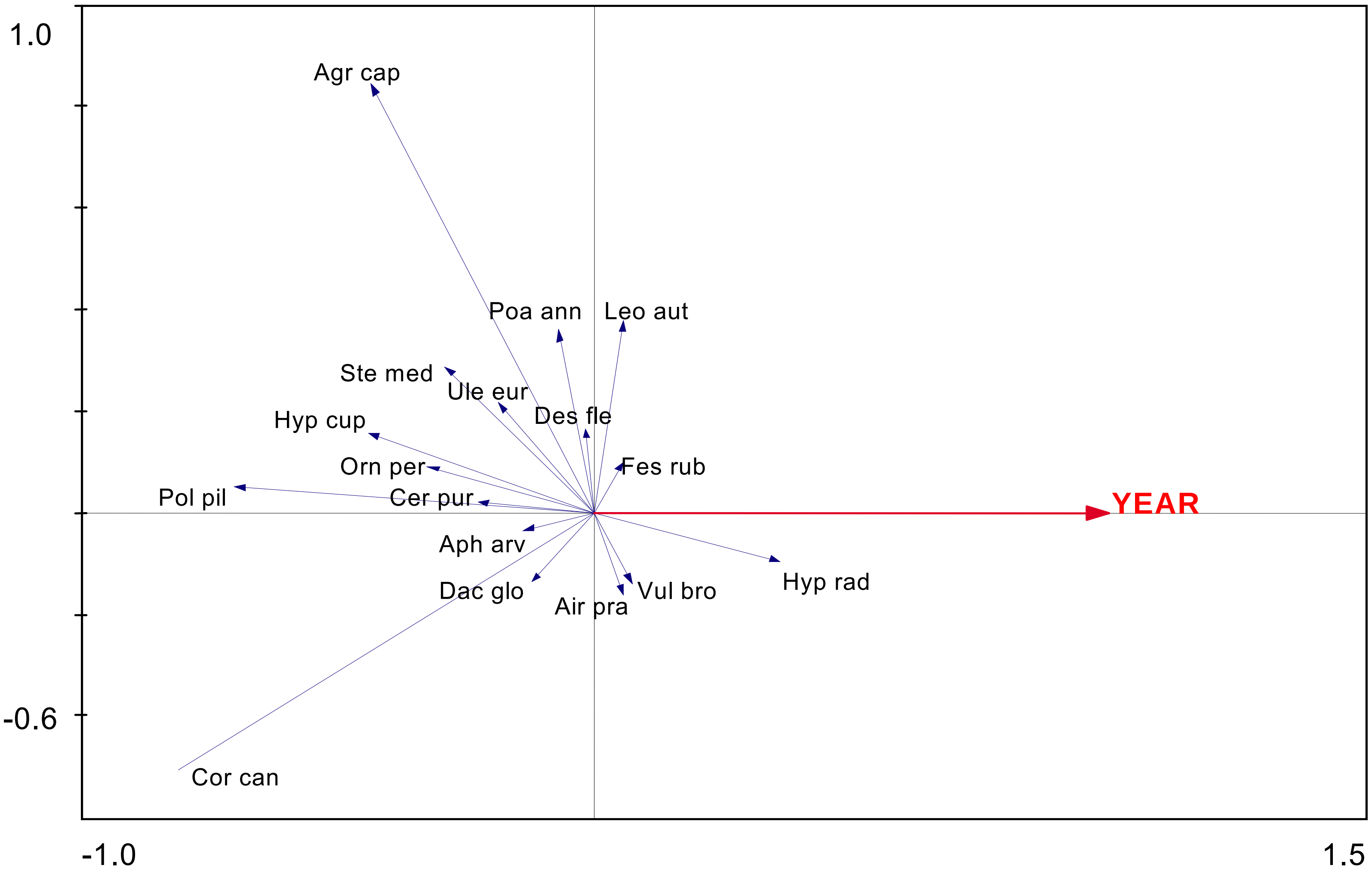


Key to abbreviations

Agr cap	*Agrostis capillaris*
Air pra	*Aira praecox*
Aph arv	*Aphanes arvensis*
Bra alb	*Brachythecium albicans*
Cal vul	*Calluna vulgaris*
Cer pur	*Ceratodon purpureus*
Cla pol	*Cladonia polydactyla*
Cor can	*Corynephorus canescens*
Dac glo	*Dactylis glomerata*
Des fle	*Deschampsia flexuosa*
Fes rub	*Festuca rubra*
Gal sax	*Galium saxatile*
Hyp cup	*Hypnum cupressiforme*
Hyp gla	*Hypochaeris glabra*
Hyp rad	*Hypochaeris radicata*
Leo aut	*Leontodon autumnalis*
Orn per	*Ornithopus perpusillus*
Poa ann	*Poa annua*
Pol pil	*Polytrichum piliferum*
Rum ace	*Rumex acetosella*
Ste med	*Stellaria media*
Ule eur	*Ulex europaeus*
Vul bro	*Vulpia bromoides*

	1	2	3	4
Eigenvalues	0.474	0.188	0.132	0.086
Spp-environment correlations	0.882	0.093	0.106	0.033
Cumulative % variance:				
of species data	47.4	66.2	79.4	87.9
of spp-environment relation	97.9	98.3	98.7	98.7

Figure 5.3d: Direct Gradient Analysis (RDA) showing relationship between plant species composition and duration of trampling, Kinver Edge Site KE3 Area A.



Key to abbreviations

Agr cap	*Agrostis capillaris*
Air pra	*Aira praecox*
Aph arv	*Aphanes arvensis*
Cer pur	*Ceratodon purpureus*
Cor can	*Corynephorus canescens*
Dac glo	*Dactylis glomerata*
Des fle	*Deschampsia flexuosa*
Fes rub	*Festuca rubra*
Hyp cup	*Hypnum cupressiforme*
Hyp rad	*Hypochaeris radicata*
Leo aut	*Leontodon autumnalis*
Orn per	*Ornithopus perpusillus*
Poa ann	*Poa annua*
Pol pil	*Polytrichum piliferum*
Ste med	*Stellaria media*
Ule eur	*Ulex europaeus*
Vul bro	*Vulpia bromoides*

	1	2	3	4
Eigenvalues	0.377	0.194	0.146	0.108
Spp-environment correlations	0.899	0.000	0.000	0.000
Cumulative % variance:				
of species data	37.7	57.1	71.7	82.5
of spp-environment relation	100.0	0.0	0.0	0.0

is the significant factor in the responses of plant species on the new path. As the main environmental effect associated with “year” is the sudden exposure of the new path to trampling it is reasonable to assume, but not provable, that these responses were largely the result of uncontrolled trampling.

5.3.2.2 Site KE3 Area B North (Vegetated – Controlled Trampling)

Data on ***the effects of trampling on the substrate*** are shown in Table 5.3iii, which gives the means and standard errors of percentages of bare sand, litter and each measure of sand compaction on the vegetated strip in the enclosure subjected to controlled trampling. No trampled plots were sampled in 1999 (5.3.1.3) so that data for that year are given only for untrampled plots.

Table 5.3iii: Means and standard errors (in parentheses) of percentages of bare sand, litter, and levels of sand compaction, Site KE3 Area B North (Vegetated – Controlled Trampling) in 1999, 2000 and 2002. Monthly trampling rates for the individual trampled plots are shown in red.

	1999	**2000**					**2002**				
	All untrampled	**Trampled**				**All untrampled**	**Trampled**				**All untrampled**
		N2 **100**	**N5** **20**	**N8** **300**	**All**		**N2** **10**	**N5** **200**	**N8** **300**	**All**	
Bare sand	1.6 (0.7)	0 (-)	2 (-)	1 (-)	1 (0.6)	7.1 (4.0)	0 (0)	17.5 (10.6)	8 (2.8)	8.5 (3.8)	0.4 (0.2)
Litter	2.9 (0.8)	10 (-)	3 (-)	2 (-)	2 (0.6)	8.7 (4.6)	10 (0)	15 (7.1)	8 (1.4)	11 (1.9)	7.3 (1.3)
Sand compaction 1	0 (0)	0 (-)	0 (-)	0 (-)	0 (-)	0.6 (0.6)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Sand compaction 2	0 (0)	0 (-)	1 (-)	0.5 (-)	0.5 (0.3)	16.1 (11.4)	0 (0)	12.5 (17.7)	0 (0)	4.2 (4.2)	25 (8.4)
Sand compaction 3	100 (0)	100 (-)	99 (-)	100 (-)	99.7 (0.3)	83.3 (11.3)	100 (0)	87.5 (17.7)	100 (0)	95.8 (4.2)	75 (8.4)

This Table suggests that the percentage of bare sand in the two more heavily trampled plots N5 and N8 increased between 2000 and 2002. The least trampled plot N2, however, had no bare sand in either year. The percentage of bare sand in untrampled plots appeared to increase between 1999 and 2000 then fall again to 2002.

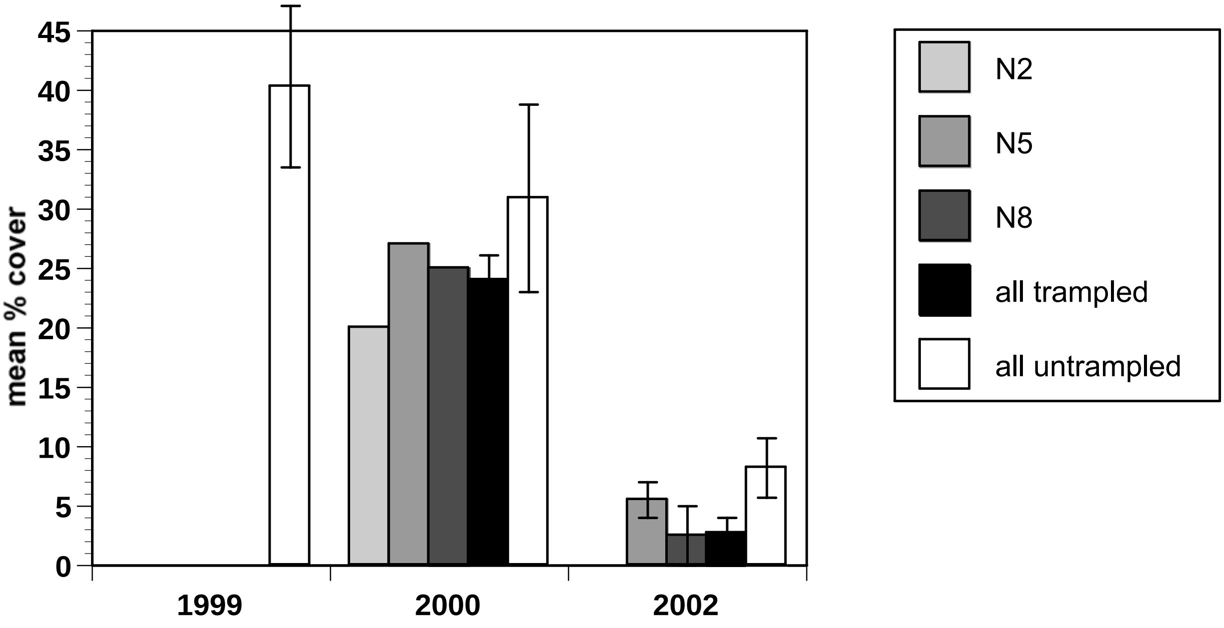
The Table additionally suggests that the amount of litter remained the same in the most lightly trampled plot N2 between 2000 and 2002 but increased in the more heavily trampled plots N5 and N8 between these years. The trend in untrampled plots appears to be an increase between 1999 and 2000 followed by a slight decrease to 2002.

Sand in the trampled plots remained almost completely compacted throughout this investigation, with the exception of the moderately trampled N5, where there appears to be some easing of heavily compacted sand (sand compaction 3) between 2000 and 2002. The trend in untrampled plots seems to be towards a progressive easing of compaction from 1999 to 2002. Almost no loose sand (sand compaction 1) was recorded on either trampled or untrampled plots in KE3 Area B North during this study.

In summary, this Table suggests some increase in bare sand and litter in trampled plots as the study progressed, but little easing of sand compaction. By contrast, untrampled plots appeared to show a progressive easing of sand compaction, while trends in percentages of bare sand and litter in untrampled plots were less clear and implied some increase between 1999 and 2000 followed by a decrease to 2002.

The ***effects of controlled trampling on C. canescens*** in an established vegetation may be evidenced by the percentage cover of this grass. Figure 5.3e shows the means and standard errors of *C. canescens* percentage cover for each trampled plot, all trampled plots taken together and all untrampled plots in KE3 Area B North between 1999 and 2002.

Figure 5.3e: Means and standard errors (error bars) of *Corynephorus canescens* percentage cover, Site KE3 Area B North (Vegetated – Controlled Trampling) in 1999, 2000 and 2002.



(zero value for N2 in 2002)

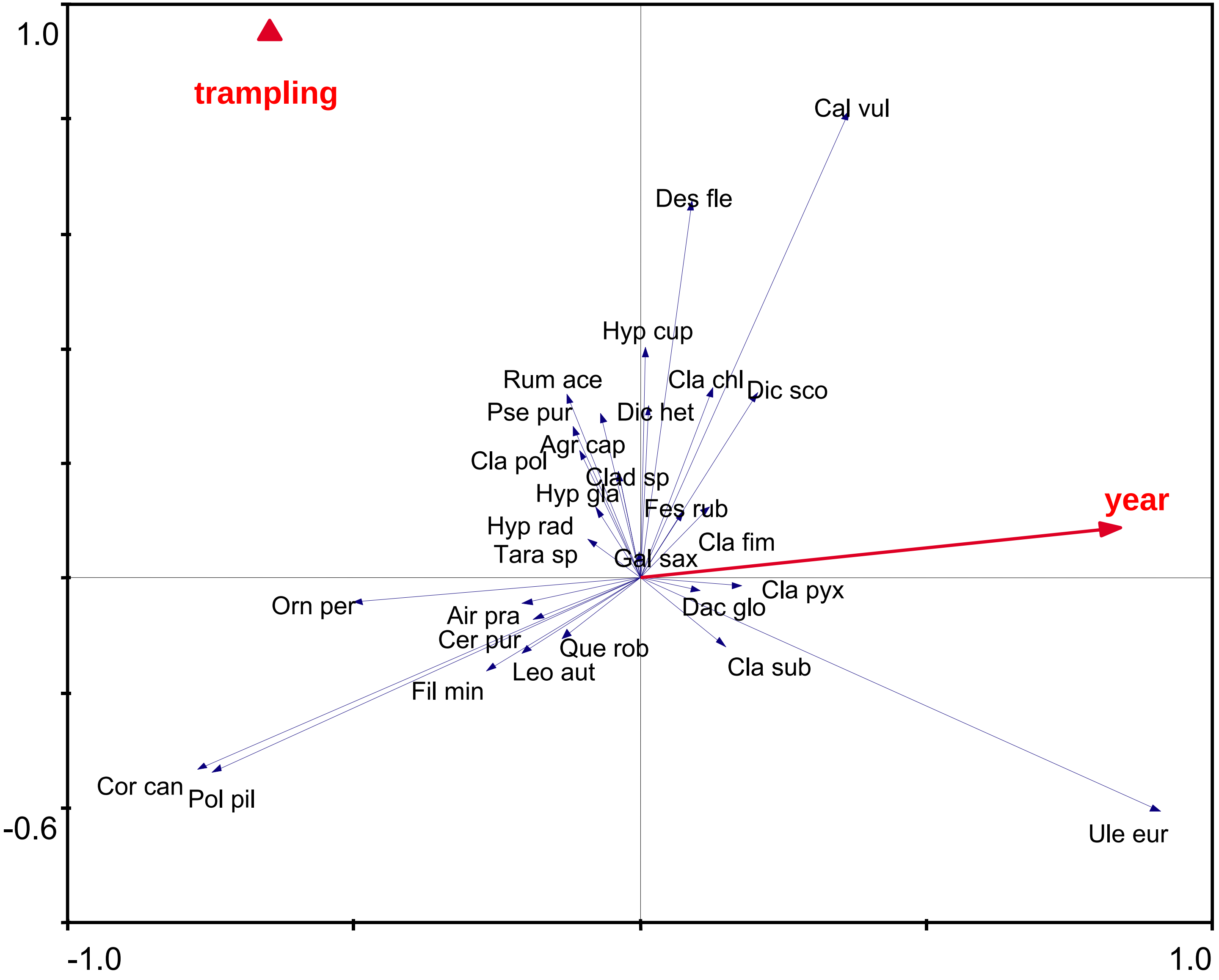
This Figure suggests a trend towards a progressive decrease in the mean cover of *C. canescens* in untrampled plots throughout the investigation. No data are available for trampled plots in 1999, but between 2000 and 2002 *C. canescens* appeared to suffer a large decline in trampled plots also, and no *C. canescens* was present in the least trampled plot N2 in 2002. Figure 5.3e does imply that trampled plots had less *C. canescens* than untrampled plots, but the difference is not great, and the trends shown by this Figure may perhaps be interpreted as a response by *C. canescens* to vegetational succession, which the imposition of trampling may have affected only a little if at all.

Figure 5.3e presents data covering the period of trampling from the outset in 1999 to the end of trampling in 2002. Further measurements of *C. canescens* percentage cover were made in August 2004, that is 27 months after the end of controlled trampling, and these may imply that trampling had a delayed or longer term effect. In that year *C. canescens* had all but disappeared from untrampled plots (0.4% cover), whereas in the three trampled plots the grass was recorded at 1% (N2), 15% (N5) and 10% (N8) cover, i.e. a greater percentage cover in each trampled plot than in 2002. By 2004 *Calluna vulgaris* and *Ulex europaeus* had become the dominant vegetation, accounting for 93.3% of the cover of untrampled plots and 74% of cover in all trampled plots taken together.

The ***effects of trampling on plant species composition*** on the Vegetated – Controlled Trampling plots was analysed by CANOCO, using Disk Appendix 1 as the baseline data. 48 samples incorporating 35 species and 366 occurrences were input; species data were logarithmically transformed; no species-weights or sample-weights were specified and no down-weighting of rare species was made. An exploratory DCA produced short gradients (2.982 for axis 1 and 1.669 for axis 2) suggesting that a PCA would be a more appropriate analysis. Initially trampling was input as three variables reflecting the three trampling levels imposed on plots N2, N5 and N8; “year” was the other variable tested in the analysis. No significance was obtained. The input file was therefore modified to treat trampling as a nominal + / - variable.

The resulting PCA had eigenvalues of 0.548 for axis 1 and 0.227 for axis 2, and these two axes together accounted for 92.1% of species-environment relationship. Figure 5.3f is the diagram of this PCA. In this Figure the strongest trend in the species data has *C. canescens* and *Polytrichum piliferum* (and to a lesser extent *Ornithopus perpusillus*) at one extreme and *Ulex europaeus* at the other. This suggests a distinction between *Ulex europaeus*-dominated stands on the right and stands with *C. canescens* and *Polytrichum piliferum*. Superimposition of the environmental variables “year” and “trampling” suggests that the latter species are associated with the early years and *Ulex europaeus* is associated with later years, especially where there is no trampling treatment. The second axis distinguishes a further set of species – *Calluna vulgaris* and *Deschampsia flexuosa*, the characteristic species of stable heathland. The positions of the environmental variables

Figure 5.3f: Principal Components Analysis (PCA) showing relationship between plant species composition and trampling, Kinver Edge Site KE3 Area B North.

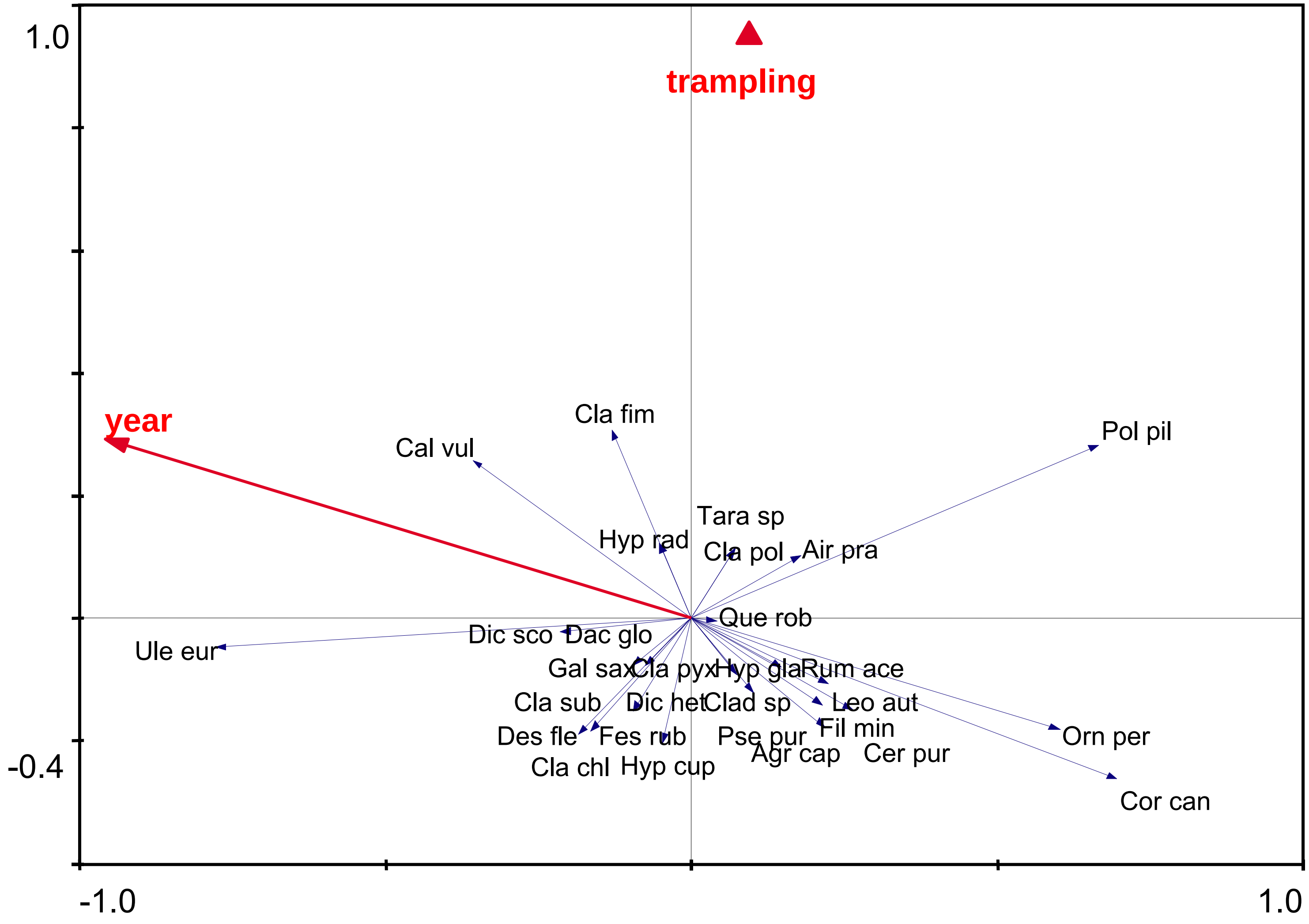


Key to abbreviations

Agr cap	*Agrostis capillaris*
Air pra	*Aira praecox*
Cal vul	*Calluna vulgaris*
Cer pur	*Ceratodon purpureus*
Cla chl	*Cladonia chlorophaea*
Cla fim	*Cladonia fimbriata*
Cla pol	*Cladonia polydactyla*
Cla pyx	*Cladonia pyxidata*
Clad sp	*Cladonia* species
Cla sub	*Cladonia subulata*
Cor can	*Corynephorus canescens*
Dac glo	*Dactylis glomerata*
Des fle	*Deschampsia flexuosa*
Dic het	*Dicranella heteromalla*
Dic sco	*Dicranum scoparium*
Fes rub	*Festuca rubra*
Fil min	*Filago minima*
Gal sax	*Galium saxatile*
Hyp cup	*Hypnum cupressiforme*
Hyp gla	*Hypochaeris glabra*
Hyp rad	*Hypochaeris radicata*
Leo aut	*Leontodon autumnalis*
Orn per	*Ornithopus perpusillus*
Pol pil	*Polytrichum piliferum*
Pse pur	*Pseudoscleropodium purum*
Que rob	*Quercus robur*
Rum ace	*Rumex acetosella*
Tara sp	*Taraxacum* species
Ule eur	*Ulex europaeus*

	1	2	3	4
Eigenvalues	0.548	0.227	0.100	0.072
Spp-environment correlations	0.878	0.149	0.574	0.183
Cumulative % variance:				
of species data	54.8	77.5	87.5	94.7
of spp-environment relation	91.0	92.1	99.2	99.7

Figure 5.3g: Direct Gradient Analysis (RDA) showing relationship between plant species composition and trampling, Kinver Edge Site KE3 Area B North.



Key to abbreviations

Agr cap	*Agrostis capillaris*
Air pra	*Aira praecox*
Cal vul	*Calluna vulgaris*
Cer pur	*Ceratodon purpureus*
Cla chl	*Cladonia chlorophaea*
Cla fim	*Cladonia fimbriata*
Cla pol	*Cladonia polydactyla*
Cla pyx	*Cladonia pyxidata*
Clad sp	*Cladonia* species
Cla sub	*Cladonia subulata*
Cor can	*Corynephorus canescens*
Dac glo	*Dactylis glomerata*
Des fle	*Deschampsia flexuosa*
Dic het	*Dicranella heteromalla*
Dic sco	*Dicranum scoparium*
Fes rub	*Festuca rubra*
Fil min	*Filago minima*
Gal sax	*Galium saxatile*
Hyp cup	*Hypnum cupressiforme*
Hyp gla	*Hypochaeris glabra*
Hyp rad	*Hypochaeris radicata*
Leo aut	*Leontodon autumnalis*
Orn per	*Ornithopus perpusillus*
Pol pil	*Polytrichum piliferum*
Pse pur	*Pseudoscleropodium purum*
Que rob	*Quercus robur*
Rum ace	*Rumex acetosella*
Tara sp	*Taraxacum* species
Ule eur	*Ulex europaeus*

	1	2	3	4
Eigenvalues	0.424	0.041	0.226	0.126
Spp-environment correlations	0.881	0.605	0.000	0.000
Cumulative % variance:				
of species data	42.4	46.4	69.0	81.6
of spp-environment relation	91.3	100.0	0.0	0.0

suggest that these species are neither decreasing nor increasing with year but may be encouraged by the trampling treatment.

In the RDA for North plots (Figure 5.3g) relationships between vegetational changes and the environmental variables are not random (tests by Monte Carlo permutations give for “year”: P-value = 0.0020, F-ratio = 29.58 and for “trampling”: P-value = 0.0020, F-ratio = 6.14). Eigenvalues are 0.424 for axis 1 and 0.041 for axis 2. In this Figure most species show a negative association with trampling, and no species is strongly associated with trampling. When compared with the PCA, *C. canescens* remains least associated with both variables, while the response of *Ornithopus perpusillus* is now more similar to that of *C. canescens*. In addition, *Polytrichum piliferum* remains poorly associated with year but now shows a somewhat positive association with trampling. *Ulex europaeus* and *Calluna vulgaris* react most positively to year. This RDA implies that when the data are constrained by the two environmental variables the main trend in the PCA is maintained and is associated with “year”. This is now subtracted from the “trampling” trend and under the circumstances *C. canescens* appears to respond negatively to trampling.

5.3.2.3 Site KE3 Area B South (Bare – Controlled Trampling)

Data on ***the effects of trampling on the substrate*** are shown in Table 5.3iv, which gives the means and standard errors of percentages of bare sand, litter and each measure of sand compaction on the enclosed bare strip subjected to controlled trampling. Since all sampled plots in 1999, both trampled and untrampled, consisted of 100% fully compacted and completely bare sand, the treatments are not differentiated in the Table for that year.

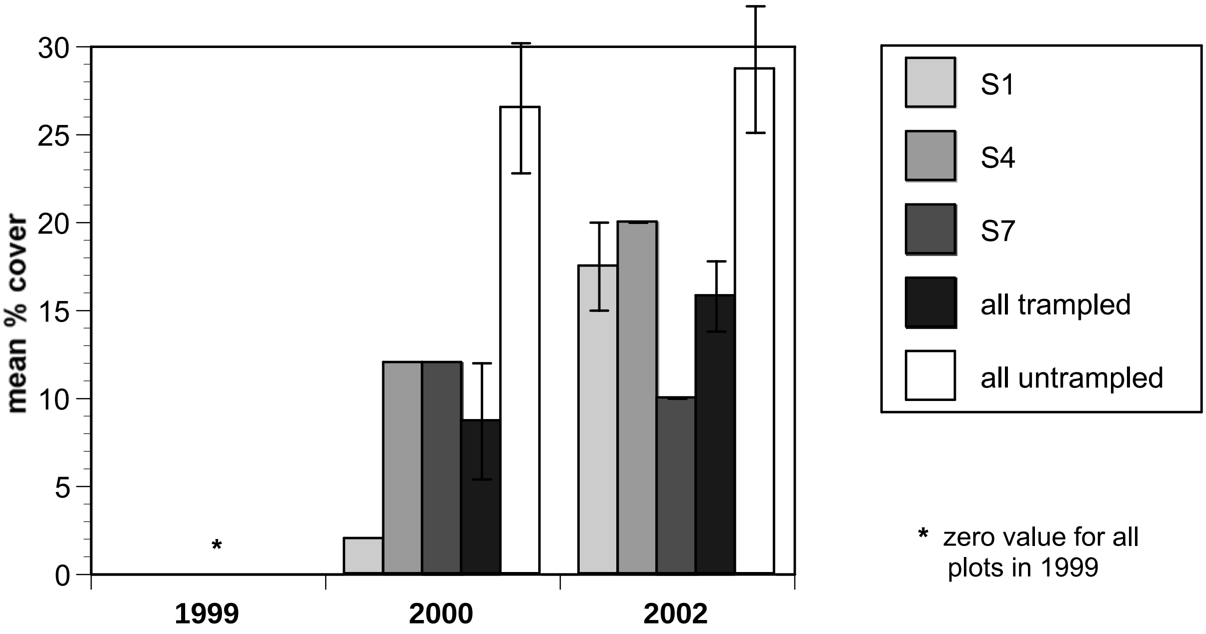
This Table indicates that during the course of this investigation all plots moved from 100% bare, fully compacted sand towards less bare sand and less compaction. The trend in reduction of bare sand is most marked in untrampled plots and least marked in the most trampled plot S7. Sand compaction also eased in both trampled and untrampled plots between 1999 and 2002. This trend appears to be stronger for trampled plots, with no fully compacted sand (sand compaction 3) recorded for 2002, whereas untrampled plots appeared to retain a reasonable amount of fully compacted sand at that date. The trend in percentage cover of litter appears to be a progressive increase in trampled plots throughout the study, whereas in untrampled plots the trend appears to be more variable - an increase to 2000 followed by a decrease to 2002.

Table 5.3iv: Means and standard errors (in parentheses) of percentages of bare sand, litter, and levels of sand compaction, Site KE3 Area B South (Bare – Controlled Trampling) in 1999, 2000 and 2002. Monthly trampling rates for individual trampled plots are shown in red.

	1999	**2000**					**2002**				
	All plots	**Trampled**				**All untrampled**	**Trampled**				**All untrampled**
		S1 **100**	**S4** **20**	**S7** **300**	**All**		**S1** **10**	**S4** **200**	**S7** **300**	**All**	
Bare sand	100 (0)	90 (-)	85 (-)	85 (-)	86.7 (1.7)	50.7 (13.0)	20 (15)	33.5 (11.5)	72.5 (2.5)	42 (11.1)	10 (3.3)
Litter	0 (0)	2 (-)	0 (-)	2 (-)	1.3 (0.7)	17 (7.6)	13 (12)	15.5 (9.5)	12.5 (2.5)	13.7 (4.0)	7.8 (1.5)
Sand compaction 1	0 (0)	0 (-)	1 (-)	3 (-)	1.3 (0.9)	0.7 (0.7)	0 (0)	0 (0)	25 (25)	8.3 (8.3)	0.4 (0.4)
Sand compaction 2	0 (0)	100 (-)	60 (-)	97 (-)	85.7 (12.9)	64.3 (16.3)	100 (0)	100 (0)	75 (25)	91.7 (8.3)	77.9 (9.0)
Sand compaction 3	100 (0)	0 (-)	39 (-)	0 (-)	13 (1.7)	35 (16.5)	0 (0)	0 (0)	0 (0)	0 (0)	21.8 (9.0)

An indication of the ***effects of controlled trampling on C. canescens*** in a vegetation recovering from bare sand is provided by the percentage cover of this grass. Figure 5.3h shows the means and standard errors of *C. canescens* percentage cover for each trampled plot, all trampled plots taken together and all untrampled plots for KE3 Area B South from the start of trampling in 1999 to its conclusion in 2002.

Figure 5.3h: Means and standard errors (error bars) of *Corynephorus canescens* percentage cover, Site KE3 Area B South (Bare – Controlled Trampling) in 1999, 2000 and 2002.



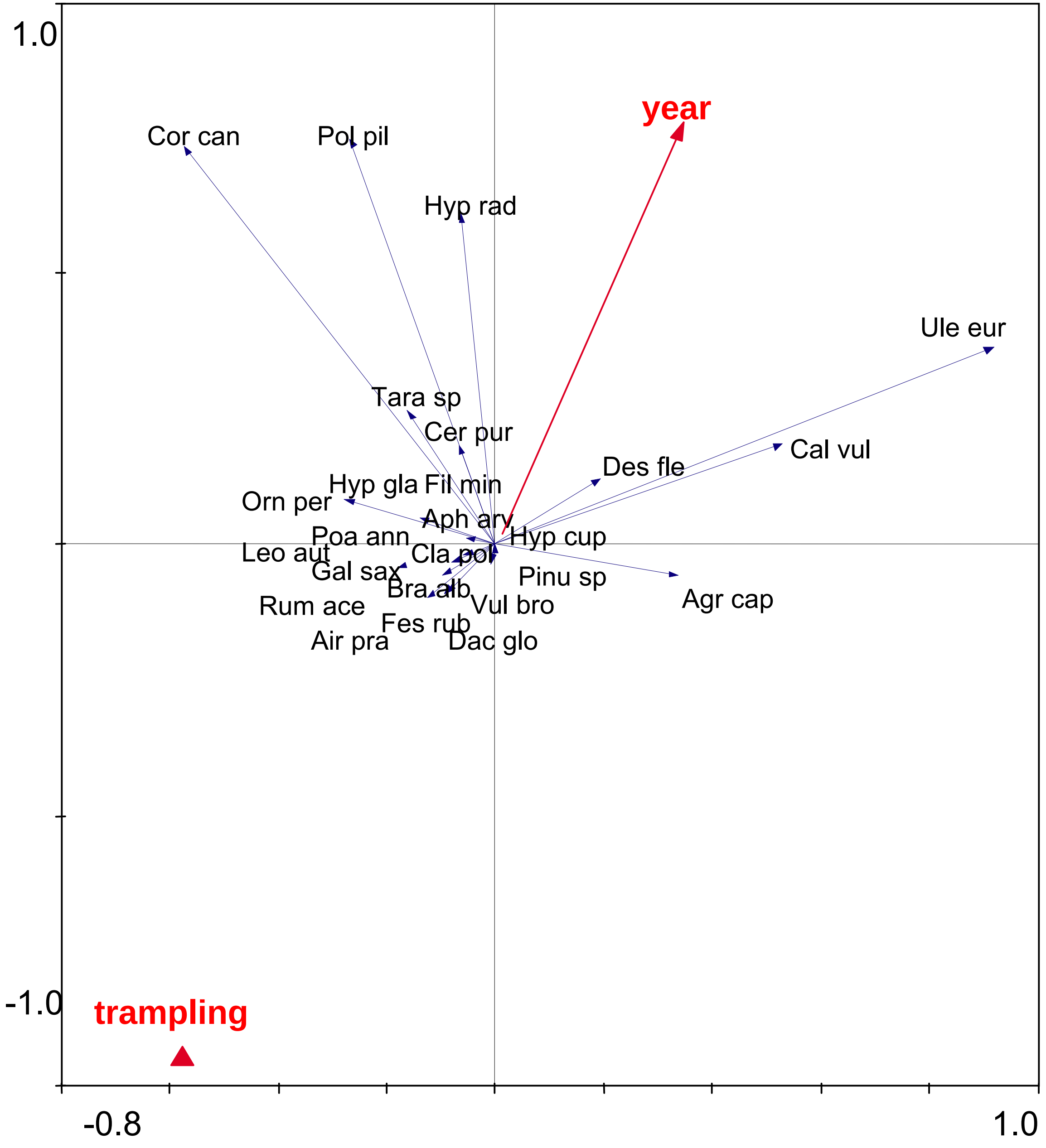
This Figure implies that *C. canescens* percentage cover increased progressively from zero in both trampled and untrampled plots throughout the investigation. There is a suggestion that the increase was greater in untrampled plots. This increasing trend appears not to have been sustained in the most trampled plot S7 where a small decrease was recorded between 2000 and the end of trampling in 2002. Further data are available for August 2004 and imply that the percentage cover of *C. canescens* continued to increase in trampled plots long after the end of trampling; at that date plot S1 had 40% cover and plots S4 and S7 each had 55% cover. In contrast, untrampled plots showed a decrease in the cover of *C. canescens* after the end of trampling, with a 10.2% cover being recorded for all untrampled plots together in August 2004.

The ***effects of trampling on plant species composition*** on the Bare – Controlled Trampling plots was analysed by CANOCO, using the baseline data in Disk Appendix 1. The input consisted of 45 samples and 35 species with 263 occurrences. Species data were treated as for the KE3 Area B North plots analysis above: “year” and “trampling” were included as the environmental variables, with trampling input as a nominal variable for the same reason as in the North plots (5.3.2.2).

The initial DCA produced gradients of 3.043 and 2.198 for the first two axes, therefore a PCA was undertaken, which gave eigenvalues of 0.425 (axis 1) and 0.260 (axis 2); these two axes accounted for 96.3% of species-environment relationship. The resulting diagram is Figure 5.3j which suggests three types of vegetation response not dissimilar to those in the North plots. The strongest trend is between quadrats containing a variety of species of open vegetation (e.g. the annuals *Aira praecox*, *Poa annua*, *Ornithopus perpusillus*) on the left and closed communities of *Calluna vulgaris* and *Ulex europaeus* on the right. The second strongest axis is between a vegetation consisting of *C. canescens*, *Polytrichum piliferum* and *Hypochaeris radicata* and the other species. When the environmental variables are superimposed the direction of “year” suggests that the *C. canescens* and *Calluna vulgaris* / *Ulex europaeus* communities increase with year and that the open vegetation complex is, perhaps weakly, associated with trampling.

In an RDA testing of the environmental variables by Monte Carlo permutations showed only the first variable (year) as having a non-random relationship with vegetational changes (P=0.0020, F-ratio = 11.67), nevertheless both variables were included in the analysis. Figure 5.3k is the resulting diagram, in which *C. canescens* shows a reasonably strong response to protection, not dissimilar to the response of *Hypochaeris radicata*, *Polytrichum piliferum*, *Ulex europaeus* and *Calluna vulgaris*. A weak positive (and not significant) response to trampling is suggested for *Taraxacum* spp., *Dactylis glomerata* and *Vulpia bromoides*. This Figure implies that the *C. canescens* / *Polytrichum piliferum* vegetation and *Calluna vulgaris* / *Ulex europaeus* vegetation which were differentiated in the PCA are both increasing in the bare area now protected by the fence, and that artificial trampling has had no significant effect on this development.

Figure 5.3j: Principal Components Analysis (PCA) showing relationship between plant species composition and trampling, Kinver Edge Site KE3 Area B South.

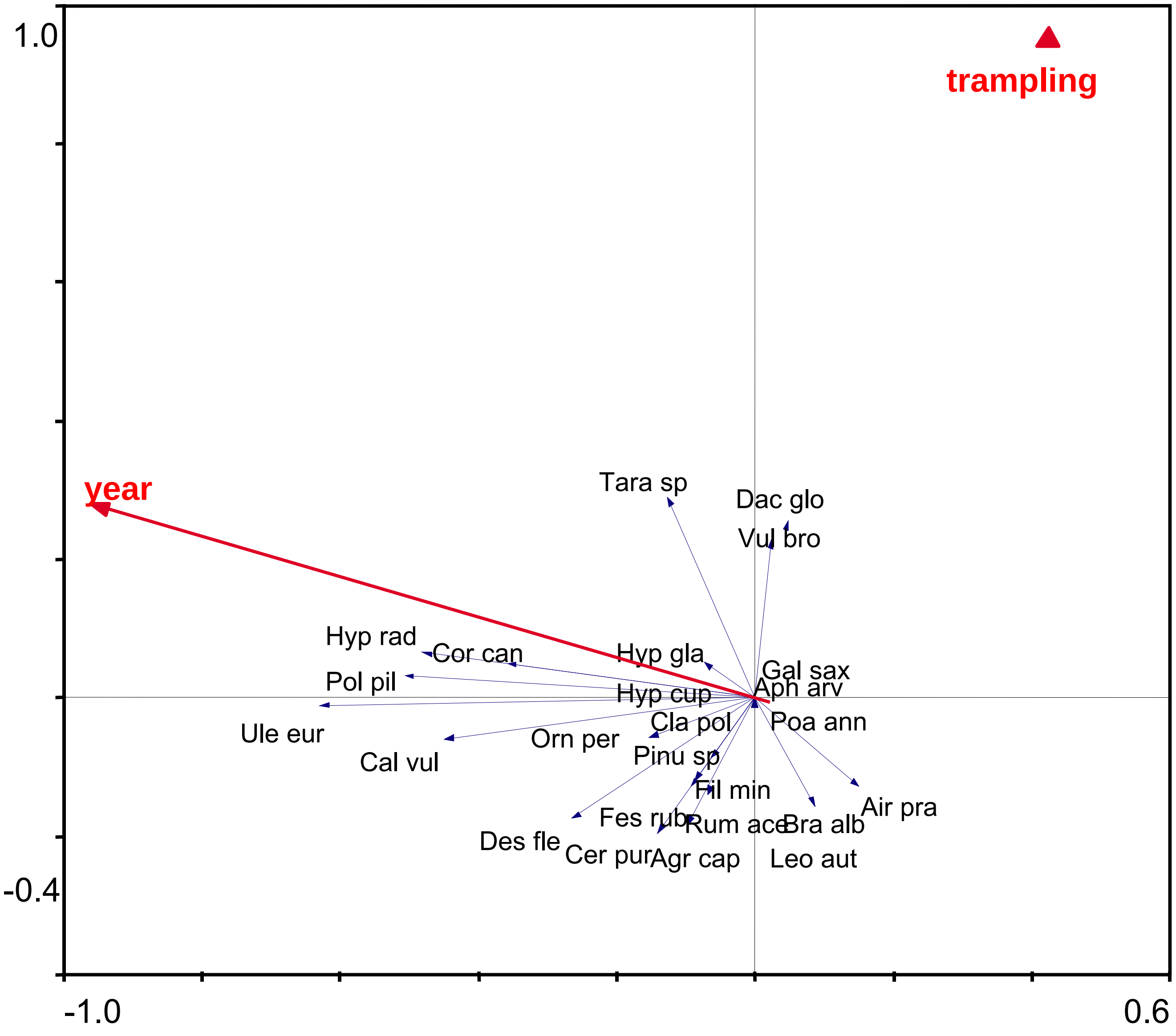


Key to abbreviations:

Agr cap	*Agrostis capillaris*
Air pra	*Aira praecox*
Aph arv	*Aphanes arvensis*
Bra alb	*Brachythecium albicans*
Cal vul	*Calluna vulgaris*
Cer pur	*Ceratodon purpureus*
Cla pol	*Cladonia polydactyla*
Cor can	*Corynephorus canescens*
Dac glo	*Dactylis glomerata*
Des fle	*Deschmpsia flexuosa*
Fes rub	*Festuca rubra*
Fil min	*Filago minima*
Gal sax	*Galium saxatile*
Hyp cup	*Hypnum cupressiforme*
Hyp gla	*Hypochaeris glabra*
Hyp rad	*Hypochaeris radicata*
Leo aut	*Leontodon autumnalis*
Orn per	*Ornithopus perpusillus*
Pinu sp	*Pinus* species seedling
Poa ann	*Poa annua*
Pol pil	*Polytrichum piliferum*
Rum ace	*Rumex acetosella*
Tara sp	*Taraxacum* species
Ule eur	*Ulex europaeus*
Vul bro	*Vulpia bromoides*

	1	2	3	4
Eigenvalues	0.425	0.260	0.099	0.088
Spp-environment correlations	0.372	0.801	0.184	0.056
Cumulative % variance:				
of species data	42.5	68.5	78.4	87.1
of spp-environment relation	25.1	96.3	97.7	97.9

Figure 5.3k: Direct Gradient Analysis (RDA) showing relationship between plant species composition and trampling, Kinver Edge Site KE3 Area B South.



Key to abbreviations:

Agr cap	*Agrostis capillaris*
Air pra	*Aira praecox*
Aph arv	*Aphanes arvensis*
Bra alb	*Brachythecium albicans*
Cal vul	*Calluna vulgaris*
Cer pur	*Ceratodon purpureus*
Cla pol	*Cladonia polydactyla*
Cor can	*Corynephorus canescens*
Dac glo	*Dactylis glomerata*
Des fle	*Deschampsia flexuosa*
Fes rub	*Festuca rubra*
Fil min	*Filago minima*
Gal sax	*Galium saxatile*
Hyp cup	*Hypnum cupressiforme*
Hyp gla	*Hypochaeris glabra*
Hyp rad	*Hypochaeris radicata*
Leo aut	*Leontodon autumnalis*
Orn per	*Ornithopus perpusillus*
Pinu sp	*Pinus* species seedling
Poa ann	*Poa annua*
Pol pil	*Polytrichum piliferum*
Rum ace	*Rumex acetosella*
Tara sp	*Taraxacum* species
Ule eur	*Ulex europaeus*
Vul bro	*Vulpia bromoides*

	1	2	3	4
Eigenvalues	0.231	0.003	0.398	0.110
Spp-environment correlations	0.882	0.179	0.000	0.000
Cumulative % variance:				
of species data	23.1	23.5	63.3	74.3
of spp-environment relation	98.5	100.0	0.0	0.0

5.3.3 Discussion

The methodology employed in this investigation was to a large extent dictated by the nature of the management changes made by the National Trust at Site KE3 in March 1999. The re-alignment of the path and fence led to the creation of three 30 x 2 m strips, differing from each other in their starting vegetation / lack of vegetation and protection / lack of protection. The dimensions and layout of the enclosure made it difficult to incorporate a formal experiment using replicated and randomised plots, for example a Latin square design. Moreover, the uncontrolled trampling on the new path could not be replicated as this was the only path across the site. It was therefore decided to treat the management changes at Site KE3 as an opportunity for a simple exploratory investigation into trampling of *C. canescens* vegetation moving in different directions with and without protection. In retrospect the design of the investigation could have been improved by duplicating each level of trampling in the enclosed strips, which would have given some replication but little scope for randomisation. Additional quadrat samples for each trampled plot in the enclosure would also have been desirable, as some of the observations made in this investigation are based on small data sets.

For the reasons set out above, the results of this investigation must be interpreted with care. They may indicate possible trends, but they cannot give any certainty. While it is feasible to consider trampling trends for all trampled plots along a strip taken together, as has been done in some elements of the analysis above (5.3.2), it should be borne in mind that these are pseudoreplications, not true replications, so cautious interpretation is again called for. In all cases in this investigation trends which appear to be important for the understanding and conservation of *C. canescens* would need to be verified by formal experiment. Some examples are identified in 5.3.6 below.

This investigation was instigated to explore whether trampling has a potential role in the conservation of *C. canescens*. With the above caveats, the results are not encouraging. They suggest that *C. canescens* is highly vulnerable to uncontrolled heavy trampling as it was one of the first species to be eliminated from the new path. It also appeared unable to exploit the creation of loose sand produced by heavy trampling. Under these circumstances it responded by surviving in a narrow, less trampled zone beside the path, where it had only a low level of fecundity (see Plate 3).

Another trend suggested by this investigation is that *C. canescens* is also eventually disfavoured by protection from trampling. Within the protection of the fence *C. canescens* in an established sward declined over the years of trampling, and the rates of trampling associated with plots N2, N5 and N8, which may have moved the vegetation away from *Ulex europaeus* and towards *Calluna vulgaris* heath, did not change the trend towards the loss of *C. canescens*. The protected bare sand initially led to extensive colonisation by *C. canescens*, but the sward also eventually moved through succession towards a dwarf shrub community. However, the investigation did suggest that succession might at least be delayed by light trampling. In this connection it is interesting to note elsewhere in this study that at Sites LA, BR1, BR2 and BO *C. canescens* appears to have some association with vehicle tracks and may possibly benefit from occasional vehicular passage across a site (Appendix B.1.2, B.6.1, B.6.2, B.7.1).

As noted in 5.3.1.1, literature studies on the effects of trampling on vegetation relevant to the vegetation of Site KE3 vary greatly in their methodologies[8], and their findings are therefore difficult to relate to the observations made in the present investigation. For instance, Burden & Randerson (1972) found that 7,500 "passages" (i.e. persons passing along a transect) per year would cause complete loss of vegetation in sand dunes: this figure may be about two times greater than the highest level of trampling imposed on KE3 Area B, but ten times smaller than the trampling pressure recorded for KE3 Area A; however, these measures of comparability are necessarily imprecise. In addition, a large number of studies (e.g. Bowles & Maun, 1982; Toullec *et al.*,

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[8] e.g. Lemauviel *et al.* (2003) used trampling levels of 75, 150 and 300 passages along trampled paths, whereas Gallet & Rozé (2001) used trampling levels of 100, 200, 500 and 750 times. Toullec *et al.* (1999) trampled at a rate of 10, 30 and 90 persons per day for four months.

1999; Gallet *et al*., 2004) focus on short-term trampling effects only, or trampling for an unknown period of time (Anderson, 1995), none of which is easy to relate to the long-term trampling regime (27 months) imposed on the enclosed plots in the present investigation.

Horne (1995) studied the impact of trampling on the vegetation of Kinver Edge. He investigated a number of heathland, grassland and woodland locations on this property, though none of the *C. canescens* sites was included in his study. Moreover, Horne monitored trampling pressure differently from the present study (he made half-hour counts at major path junctions on autumn weekends). His nearest monitoring locality to the *C. canescens* sites (his heathland sampling point 5) lies about 250 metres north of Site KE3, where he recorded a mean of 85 persons per hour (Horne, *loc. cit*. pp 31-32), possibly equating to twice the trampling pressure recorded for weekend counts in this study (Appendix A Table Aii).

Using TWINSPAN ordination, Horne found that high pedestrian levels eroded and enlarged pathways and produced vegetation zonation in which local vegetation communities were replaced by common, trampling-resistant plant species. In his “Heathland Community” he found that at minimal trampling levels (<1 person/hour) *Calluna vulgaris* was dominant at 90% cover, which reduced to 50% with higher trampling (150-200 persons/hour), at which point *Rumex acetosella* also occurred, at 3% cover. Where the path edge supported a grassland zone *Deschampsia flexuosa* was the only grass present, with 60% cover at trampling levels below 50 persons/hour. *Deschampsia flexuosa* progressively declined, and *Festuca rubra* and *Lolium perenne* arrived, under higher trampling pressures, until all three grasses formed about 10% cover at the highest trampling level of 150-200 persons/hour. *Agrostis capillaris* was also frequent at moderate trampling levels. Horne’s findings are reasonably consistent with the results of the present investigation, except that *Lolium perenne* occurred in this study at levels too low to show up in the CANOCO analyses.

Studies of trampling on Atlantic heaths include the recent investigations of Toullec *et al*. (1999), Gallet & Rozé (2001) and Gallet, Lemauviel & Rozé (2004) at Carnac, Brittany, where intensive visitor pressure has led to major habitat degradation. Toullec *et al*. (*loc. cit*.) carried out experiments at different intensities and at two times of year – summer and winter. They found that immediate and deferred responses of entire plant communities did not vary with trampling season, but at the intracommunity scale the responses of taxonomic groups differed according to the season of trampling: for instance, the resilience of *Ulex europaeus* and *Ulex gallii* was greater if trampled in winter than in summer. In addition, the recovery of vegetation after trampling differed according to the season when trampling had occurred. They also found no linear relationship between vegetation degradation and trampling intensity: degradation was produced at the lowest level of trampling (10 persons per day passing along a path 10 m long for four months), and heavier trampling did not increase degradation proportionately. Further studies on the same site found that the vegetation of dry heathland had a greater resistance to trampling than that of mesophilous heathland if trampling was carried out in dry conditions; under wet conditions the two heathland types showed no significant response difference (Gallet & Rozé, *loc. cit*.). These studies concluded that the resistance of heathland plant communities varies with season and weather conditions at time of trampling, and that the resistance of plant communities is the result of resistances of individual species in the community. In the present study trampling of Site KE3 Area B was always carried out in dry weather, and usually evenly throughout the year – except for the disrupted trampling in February-May 2001 and increase in trampling in some later months to compensate (5.3.1.1).

A number of trampling studies have focused on sand dunes, primarily coastal (e.g. Liddle & Greig-Smith, 1975; Hylgaard, 1980; Bowles & Mann, 1982) and heathland (e.g. Toullec *et al*., 1999; Gallet & Rozé, 2001; Gallet, Lemauviel & Rozé, 2004). Many such studies were initiated in response to an increase in tourism pressures on vulnerable sites (e.g. Boorman & Fuller, 1977; Meijer, 1992). However, the effects of trampling on inland dunes supporting *C. canescens* have not been addressed by previous studies.

The literature on trampling of sand dune communities has occasionally indicated some beneficial effects, for example by increasing water content through soil compaction (Liddle & Greig-Smith, *loc. cit.*; Boorman & Fuller, 1977); and diversity in dune habitats can sometimes be increased by moderate trampling (van der Maarel, 1971). However, trampling is more frequently harmful to dune communities, with both direct and indirect effects (Liddle, 1975a). Direct effects include mechanical damage to plants leading to death or damage from breakage and abrasion, especially severe on sandy soils (van der Maarel, *loc. cit.*). For example, Bowles & Anwar (1982) observed that a variety of dune species in Canada initiated new growth in the autumn following heavy trampling, but the shoots of almost all species failed to survive the winter. Indirect effects of trampling in plant ecosystems include soil compaction and water retention, reduction in soil organic matter, decrease of vegetation cover and biomass production, reduction in number of plant species and loss of biodiversity, interference in natural succession, creation of paths and erosion (Andersen, 1995), along with the modification of micro-environmental conditions within the plant cover (Kobayashi *et al.*, 1997). The indirect effects of trampling become apparent over a longer period than direct effects, and determine an ecosystem's resilience (Cole & Bayfield, 1993). The apparent long-term response of *C. canescens* in trampled plots in KE3 Area B in 2004 may perhaps be an example of this.

Most studies of dune trampling have focused on coastal dune communities containing suites of species unrepresented at Kinver Edge and few are likely to be relevant to the observations made in the present study. In his Denmark study Andersen (*loc. cit.*) found that “light” trampling (about one to two times the rate imposed upon the most trampled plots of Area B) created paths and reduced vegetation cover and species diversity in five coastal plant communities, with dunes in particular having a high proportion of sensitive species. Bryophytes and lichens were reduced by trampling in all vegetation types, while grass cover was most reduced in dune communities. Bowles & Maun (*loc. cit.*) recorded a similar and continued loss of lichen cover in trampled heath-grassland plots on dunes at Lake Huron. In the present study the effects of trampling on bryophytes, lichens and grasses are not so clear at the community level, though individual species do show specific responses in the CANOCO analyses.

In the present investigation the trampling levels imposed on both vegetated and bare plots in the enclosure were greater than those in some literature studies due to monthly repetition to give some comparison with the continued monthly trampling of the new path (Area A). A number of studies, such as those of Cole & Bayfield (1993), Toullec *et al*. (1999) and Harrison (1981) suggest that even light trampling rates (not exceeding 500 passages, i.e. persons passing along a transect) can be sustained only by the most resistant plant communities, while *Ulex europaeus*-dominated heathland and *Calluna vulgaris* are resistant at rates somewhat lower than this. The present study failed to suggest a trampling level which might be sustained by *C. canescens*, though the results of the investigation suggest that if such a level exists it is very light, and probably too light to prevent vegetational succession by more resistant species.

5.3.4 Characterising successional stages in the *Corynephorus canescens* habitat

This investigation of the effects of trampling has allowed observations to be made on the development of the *C. canescens* habitat in two opposite directions: progression from bare sand and from an existing *C. canescens*-rich sward. As a result, it has been possible to identify from the data collected in this investigation four successional stages of the *C. canescens* habitat using both physical and vegetational elements, which after some refinements to reflect the situation at the other study sites may be characterised as follows:

1 ***Pioneer Phase*** – sand surface mostly loose (“Sand 1”), with or without areas of surface stability (“Sand 2”) (occasionally Sand 1 may be more or less replaced by Sand 2); large areas of bare sand usually present; *C. canescens* represented by small, often even-aged tussocks, with no or very few inflorescences; vegetation other than *C. canescens*, if present, includes a

significant proportion of annual and/or biennial plant species; in droughted conditions dead plant material may be present;

2 ***Early Mature Phase*** – sand surface mostly with some surface stability (“Sand 2”), with or without areas of compacted sand (“Sand 3”); bare sand reduced to smaller areas between vegetation; usually little or no plant litter; *C. canescens* plants include some mature tussocks with several to many inflorescences; other vegetation may include small quantities of *Polytrichum piliferum* and/or *Cladonia* species; perennials may start to appear, but woody plants are mostly absent;

3 ***Late Mature Phase*** – sand stability with significant areas of compacted sand (“Sand 3”); few or no bare areas; some to much plant litter often present; *C. canescens* plants may consist mainly of mature tussocks with several to many inflorescences; tussocks may be producing tillers; other vegetation may include significant quantities of *Polytrichum piliferum* and/or *Cladonia* species; perennials now form a significant element in the vegetation; seedlings of woody plants may start to appear;

4 ***Transition Phase*** – sand almost entirely compacted (“Sand 3”); no areas of bare sand; *C. canescens* declining significantly in quantity and usually occurring as individual tussocks which occupy occasional gaps among the dominant vegetation; vegetation dominated by tall perennials, with few annuals or biennials; woody plant species present. This is the stage in which the *C. canescens* habitat passes to the next successional vegetation type.

In the trampling investigation this succession was well represented on KE3 Area B plots. Protection of bare sand in Area B South in 1999 led to colonisation by a pioneer *C. canescens* community which, by July 2000, had already reached the Early Mature Phase, in which *C. canescens* was producing abundant inflorescences, annuals such as *Ornithopus perpusillus* and *Poa annua* were still present but in small quantity, and small amounts of a range of perennials especially *Agrostis capillaris* and *Rumex acetosella* had started to appear. Bare sand was still fairly extensive in quadrats, the sand compaction index was largely 2 and 3, and litter was mostly absent. Even by July 2000 one or two quadrats in Area B South were showing evidence of the Late Mature Phase vegetation, with *Ulex europaeus* and *Calluna vulgaris* present in small quantity, much less bare sand, more compacted sand and a small amount of litter. By June 2002 all quadrats in Area B South were referrable to the Late Mature Phase. At this date Area B North plots supported extensive amounts of *Calluna vulgaris* and *Ulex europaeus* in a clearly Transition Phase vegetation.

The successional stages of the *C. canescens* habitat are less easy to identify for the new path (Area A) where uncontrolled heavy trampling affected all quadrats. A few species characteristic of the Late Mature Phase (e.g. *Calluna vulgaris*, *Hypochaeris radicata*) do appear to respond in a way consistent with succession (Figure 5.3c); on the other hand, the development of many characteristic elements of later successional stages (sand compaction, litter, cryptogams, *Ulex europaeus*) was arrested or even reversed. The analyses in 5.3.2.1 suggest that trampling had a much stronger impact on the new path than succession and therefore that the variable “year” in the CANOCO analyses gives a reasonable expression of the effects of heavy uncontrolled trampling there.

In studies of the floral and faunal *C. canescens* communities elaborated in Chapters 6 and 7 the stage of the *C. canescens* habitat represented by each quadrat was recorded and was also used to inform the siting of quadrats so as to measure the range of habitat stages represented on a site. Some quadrat data taken in the early years of this study before the above schema was developed, however, are not assigned to a stage of the *C. canescens* habitat.

5.3.5 Summary of observations from the trampling investigation

This field investigation was initiated to give preliminary indications of trends produced on *C. canescens* by three trampling treatments at a West Midlands site. As discussed above (5.3.3) the methodology employed does not allow any certain conclusions to be reached, but a number of observations have been made which may indicate trends. These remain to be tested by replicated experiments. The following are the main observations made from this study:

In an established sward subjected to uncontrolled heavy trampling over three years the substrate became less compacted, producing bare, loose sand, but *C. canescens* was unable to colonise;

Percentage cover of *C. canescens* in an established sward subjected to heavy uncontrolled trampling declined considerably over three years. *C. canescens*, *Polytrichum piliferum*, *Ornithopus perpusillus* and three moss species were the species most quickly eliminated under these conditions;

In an established sward subjected to heavy uncontrolled trampling over three years *C. canescens* survived only in a narrow zone of path-side vegetation where its vigour and fecundity increased, but fecundity remained low when compared with values given in the literature;

In an established vegetation under protection and subjected to light controlled trampling there was an increase in bare sand and litter in trampled plots but little easing of sand compaction;

An established vegetation under protection and subjected to light controlled trampling moved towards later successional stages dominated by *Ulex europaeus* and *Calluna vulgaris* in trampled and untrampled plots; the percentage cover of *C. canescens* declined sharply in trampled and untrampled plots, but partly recovered in trampled plots 27 months after the end of trampling;

In a sward recovering from bare sand the percentage cover of bare sand was reduced more in untrampled plots but sand compaction eased more in trampled plots;

In a sward recovering from bare sand both *C. canescens* and the later successional vegetation of *Calluna vulgaris* and *Ulex europaeus* responded positively to protection;

In a sward recovering from bare sand light trampling may have contributed towards a reduction of cover of *C. canescens* in the short term but may have delayed succession in the longer term.

5.3.6 Suggestions for further study

The observations summarised above suggest a number of hypotheses for study by formal experiments, of which the following may have the greater implications for the conservation of *C. canescens*, particularly in the West Midlands:

Hypothesis A: *that trampling leads to a decline in C. canescens percentage cover.*

Hypothesis B: *that trampling leads to a reduction of C. canescens vigour and fecundity;*

Hypothesis C: *that protection of a C. canescens population leads to its decline through vegetational succession*;

Hypothesis D: *that light controlled trampling followed by an easing of trampling delays succession in the vegetation and allows C. canescens partially to recover.*

Each of these hypotheses is best tested by a randomised, replicated plot experiment, e.g. in a Latin square design, and ideally at a West Midlands site. Such experiments would, however, require fairly extensive areas of *C. canescens* for division into sufficient plots to allow replicated and randomised treatments.

5.3.7 Potential conservation implications

The above discussion (5.3.3) expresses the view that the observations made in this study are not encouraging for the conservation of *C. canescens*. No trampling regime which might benefit this grass can be suggested from the study's results. A possibility does exist that such a regime might be identified experimentally, but this investigation suggests that, even if this were so, the control of successional vegetation would remain a major problem. Moreover, in practice it would be very difficult to manipulate public access to a *C. canescens* population so as to sustain a desired trampling rate. Occasional vehicular passage may offer a more practicable solution for conserving this grass: if an optimal rate of passage could be determined by experiment, it may be feasible to use mechanical means – for example, a lawn roller – to reproduce this level.

Observations made on the response of *C. canescens* to protection from trampling are ambivalent in their implications. If confirmed by experiment, they imply that protection from trampling may be a valuable conservation technique for establishing a *C. canescens* population, but it is not a viable solution to conserving this grass once established. This latter point may be exemplified in the West Midlands by Site DS, where exclusion of the public from part of the original *C. canescens* site by erection of a fence has led to the rapid near-elimination of the grass from the protected area by successional tall grassland and scrub communities (Appendix B.3.1). At this site re-opening of public access to the area formerly occupied by *C. canescens* is a desirable, and urgent, conservation measure.

Plate 3: Images from preliminary field investigations.

Left: *Corynephorus canescens* surviving on the rim of a heavily trampled path (Site KE3 Area A).

Right: Site KE3 Area B South four years after the end of trampling. *Corynephorus canescens* still flourishes in the most trampled plot.

Left: *Corynephorus canescens* growing in a tarmac driveway (Site AL).

Right: *Corynephorus canescens* growing in ordinary garden soil (Site AL).

CHAPTER 6: THE *CORYNEPHORUS CANESCENS* COMMUNITY (FLORAL)

6.1 Aims and Objectives

This Chapter seeks to characterise the plant communities in which *Corynephorus canescens* occurs on the study sites and to carry out analyses which inform the first Aim of this study, i.e. to seek evidence for the naturalness or otherwise of the West Midlands *C. canescens* populations (1.2). To achieve this Aim the Objectives of this element of the research are:

- to identify the plant community composition of the selected study sites by carrying out general inspections and quadrat sampling of each site;
- to compare the floristic composition of these communities so as to explore relationships between sites, regions and countries;
- to use ordination methods to analyse the similarities and differences between the study site communities;
- to investigate the phytosociological relationships between these communities and established phytosociologies in both Britain and Poland.

As indicated above, the Objectives of this Chapter focus directly on the first Aim of the study. An exploration of key relationships between the vegetation and invertebrate communities in pursuance of the second Aim of this study (1.2) is carried out in the faunal Chapter (see 7.3.3 and 7.4.2). This study of the floral communities of the *C. canescens* sites also has implications for the third Aim of the research (identifying factors with nature conservation implications for British inland *C. canescens* populations) insofar as it helps to clarify the phytosociological context for the conservation of this grass in the U.K.

6.2 Methods

At each study site the vegetation was sampled by general inspection and by the use of 1m^2 quadrat samples as described in 4.4 above. Estimates of cover abundance of each species within a quadrat and across the entire site were recorded as percentages, which were later transposed to a Domin scale for analysis. The baseline data file is appended as Disk Appendix 2. Species identifications were made using the authorities given in Table 4.2i. There are few significant differences in nomenclature between the authors, these being shown in Table 6.2i:

Table 6.2i: more important nomenclatorial differences for vegetation species in the literature consulted in the present study.

Nomenclature used in this study	**Synonyms in the literature**
Agrostis stolonifera	*Agrostis alba*
Agrostis vinealis	*Agrostis coarctata, A. canina montana*
Anisantha sterilis	*Bromus sterilis*
Chamerion angustifolium	*Epilobium angustifolium*
Elytrigia repens	*Elymus repens*
Filago minima	*Logfia minima*
Leontodon saxatilis	*Leontodon taraxacoides*
Pilosella officinarum	*Hieracium pilosella*
Spergula morisonii	*Spergula vernalis*
Cladonia mitis	*Cladina mitis*
Coelocaulon aculeatum	*Cornicularia aculeata*

Vegetation monitoring of the study sites was carried out according to the timetable shown in Appendix C. Additionally, visits were made to British coastal *C. canescens* sites at Caister-on-Sea (Norfolk) on 12 July 2002, and on Jersey (Channel Islands) at L’Ouaisné Common, La Pulente, La Carrière and Les Quennevais on 14 February 2003. A general record of the vegetation of these sites was made; and at Caister-on-Sea two representative quadrat samples of the *C. canescens* community were taken, including measurements of *C. canescens* sward height, inflorescence height and number of inflorescences. These Caister-on-Sea quadrat data are included in the TWINSPAN and CANOCO analyses to test whether they throw any light on the vegetation of inland British communities. These instances apart, the coastal sites do not form part of the present study.

6.3 Results

6.3.1 Taxonomic composition of the vegetation of the study sites

The vascular plants, bryophytes and lichens recorded on the study sites are shown in Table 6.3i. In this Table an X indicates that the species was recorded for that site, while a blank cell indicates the absence of that species from the site.

Table 6.3i: taxa of vascular plants, bryophytes and lichens recorded in this study, showing distribution between study sites.

Taxon	**British Sites**							**Polish Sites**				
	West Midlands					**East Anglia**						
	BT	**DS**	**KE1**	**KE2**	**KE3**	**LA**	**WW**	**BO**	**BR1**	**BR2**	**BR3**	**CR**
Acer negundo										X		
Achillea millefolium	X					X			X			
Agrostis capillaris	X	X	X	X	X							
Agrostis stolonifera								X	X	X	X	X
Agrostis vinealis						X	X					
Aira caryophyllea	X		X			X						
Aira praecox	X	X	X	X	X	X						
Anchusa arvensis							X					
Anisantha sterilis								X	X	X		
Anthoxanthum odoratum	X							X				
Aphanes arvensis			X		X	X						
Arrhenatherum elatius	X											
Artemisia campestris									X	X	X	
Artemisia vulgaris									X			
Berteroa incana									X	X	X	
Betula pendula	X	X	X					X	X		X	X
Bromus tectorum									X			
Calamagrostis epigejos									X		X	
Calluna vulgaris	X	X	X	X	X							
Carex arenaria						X	X					
Carex hirta											X	
Cerastium fontanum			X	X		X						
Cerastium glomeratum			X	X								
Cerastium semidecandrum									X			
Chamerion angustifolium	X											

continued…

Site Key: BT Burlish Top DS Devil's Spittleful / Rifle Range
KE1,2,3 Kinver Edge 1,2,3 LA Lakenheath WW Wangford Warren
BO Bolimów BR1,2,3 Bromierzyk 1,2,3 CR Ciosny Reserve

Table 6.3i continued…...

Taxon	**British Sites**							**Polish Sites**				
	West Midlands					**East Anglia**						
	BT	**DS**	**KE1**	**KE2**	**KE3**	**LA**	**WW**	**BO**	**BR1**	**BR2**	**BR3**	**CR**
Chenopodium album	X											X
Cochlearia danica		X										
Convolvulus arvensis									X	X		
Conyza canadensis									X	X	X	X
Corynephorus canescens	X	X	X	X	X	X	X	X	X	X	X	X
Crataegus monogyna	X	X										
Crepis capillaris						X						
Crepis tectorum											X	
Cytisus scoparius	X	X								X		
Dactylis glomerata			X	X	X							
Danthonia decumbens		X										
Deschampsia flexuosa	X	X	X	X	X							
Elymus caninus									X		X	
Elytrigia repens									X			
Erica cinerea					X							
Erodium cicutarium				X		X	X					
Fallopia convolvulus										X		
Festuca ovina	X	X				X		X		X		
Festuca rubra			X	X	X			X	X	X		X
Filago minima	X		X		X	X	X					
Galium saxatile			X	X	X							
Galium verum						X	X					
Helichrysum arenarium									X			
Herniaria glabra												X
Hieracium species		X										
Holcus lanatus	X											
Hypericum perforatum	X											
Hypochaeris glabra	X		X	X	X	X	X					
Hypochaeris radicata	X	X	X	X	X	X						
Jasione montana	X	X						X		X		
Juniperus communis								X				X
Lapsana communis	X											
Leontodon autumnalis		X	X	X	X							
Leontodon saxatilis						X	X					
Linaria vulgaris											X	
Linum catharticum		X										
Lolium perenne										X	X	
Luzula multiflora		X	X	X								
Medicago lupulina						X						
Myosotis ramosissima						X						
Oenothera biennis									X	X	X	
Ornithopus perpusillus	X	X	X	X	X	X						
Phleum arenarium						X				X		
Pilosella officinarum						X			X	X	X	X
Pinus species			X		X							
Pinus sylvestris							X	X	X	X	X	X
Plantago arenaria									X	X	X	X
Plantago coronopus						X						
Plantago lanceolata	X					X						

continued….

Table 6.3i continued…..

Taxon	**British Sites**							**Polish Sites**				
	West Midlands					**East Anglia**						
	BT	**DS**	**KE1**	**KE2**	**KE3**	**LA**	**WW**	**BO**	**BR1**	**BR2**	**BR3**	**CR**
Poa annua	X	X	X	X	X							
Polygonatum odoratum												X
Potentilla arenaria											X	
Potentilla argentea									X			
Prunus serotina												X
Pteridium aquilinum	X	X	X									
Pyrus communis									X		X	
Quercus robur		X	X		X			X	X	X	X	X
Quercus rubra												X
Rhamnus cathartica												X
Ribes species												X
Robinia pseudacacia									X	X	X	
Rubus fruticosus agg.	X	X	X									
Rumex acetosa									X	X	X	
Rumex acetosella	X	X	X	X	X	X	X	X	X	X		X
Sagina apetala				X	X				X			
Saponaria officinalis									X	X	X	
Scleranthus perennis								X				
Sedum acre						X	X					
Senecio erucifolius	X											
Senecio jacobaea	X						X					
Senecio sylvaticus	X	X					X					
Setaria viridis								X		X	X	
Silene latifolia										X	X	
Silene otites						X						
Solidago virgaurea									X			
Spergula arvensis	X											
Spergula morisonii								X	X	X	X	X
Stellaria graminea							X					
Stellaria media			X	X	X							
Syringa vulgaris											X	
Taraxacum species			X		X							
Teesdalia nudicaulis												X
Teucrium scorodonia		X										
Trifolium arvense	X					X						
Trifolium campestre						X						
Trifolium pratense	X											
Trifolium repens						X						
Ulex europaeus	X	X	X	X	X							
Veronica arvensis						X						
Veronica dillenii									X			X
Veronica species					X							
Viola arvensis							X		X	X		
Viola tricolor										X		
Vulpia bromoides	X		X	X	X							
Vulpia ciliata ambigua						X						
Brachythecium albicans			X		X							
Bryophyte species	X									X		

continued…

Table 6.3i continued…

Taxon	**British Sites**							**Polish Sites**				
	West Midlands					**East Anglia**						
	BT	**DS**	**KE1**	**KE2**	**KE3**	**LA**	**WW**	**BO**	**BR1**	**BR2**	**BR3**	**CR**
Bryum species				X								
Ceratodon purpureus		X	X		X			X	X	X	X	X
Dicranella heteromalla			X	X	X							
Dicranum scoparium			X	X	X							
Ditrichum heteromallum												X
Hypnum cupressiforme			X	X	X	X					X	X
Polytrichum juniperinum	X	X			X							
Polytrichum piliferum	X	X	X	X	X	X	X	X	X	X	X	X
Pseudoscleropodium purum			X	X	X							
Rhacomitrium canescens										X		
Tortula ruralis ruraliformis			X									
Cetraria ericetorum								X				
Cetraria islandica								X				
Cladonia arbuscula								X	X		X	
Cladonia cervicornis						X			X		X	
Cladonia chlorophaea			X		X				X			
Cladonia coccifera												X
Cladonia fimbriata			X		X							
Cladonia floerkeana			X								X	
Cladonia foliacea									X	X		
Cladonia furcata furcata									X	X	X	
Cladonia gracilis									X			
Cladonia mitis								X				X
Cladonia phyllophora											X	
Cladonia polydactyla			X		X				X		X	
Cladonia portentosa						X	X					
Cladonia pyxidata			X		X		X					
Cladonia subulata			X		X				X		X	
Cladonia uncinalis								X	X		X	
Cladonia species	X	X	X		X		X		X	X	X	
Coelocaulon aculeatum			X		X	X	X	X				X

From Table 6.3i it can be seen that totals of 120 taxa of flowering plants, 13 of bryophytes and 20 of lichens were recorded on the study sites, including 115, 11 and 19 respectively identified to species level. Besides *C. canescens* only one other species was recorded on all twelve study sites – the moss *Polytrichum piliferum*; while *Rumex acetosella* was recorded on eleven sites, being absent only from Bromierzyk Site BR3.

Of a total of 153 taxa, 99 (65%) were recorded on British sites and 81 (53%) on Polish sites; only 27 taxa (18%) were shared between the two countries. Within Britain, the Breckland sites held 44 taxa and the West Midlands sites 76 taxa, 22 being shared between these two regions. These relationships are shown in Figure 6.3a, where percentages of a region's flora which these numbers represent are given in italics, colour-coded by region.

Figure 6.3a: numbers and percentages of taxa in Poland, the West Midlands and East Anglia compared with the total number of taxa recorded in this study, and showing the numbers and percentages of taxa shared between these regions.

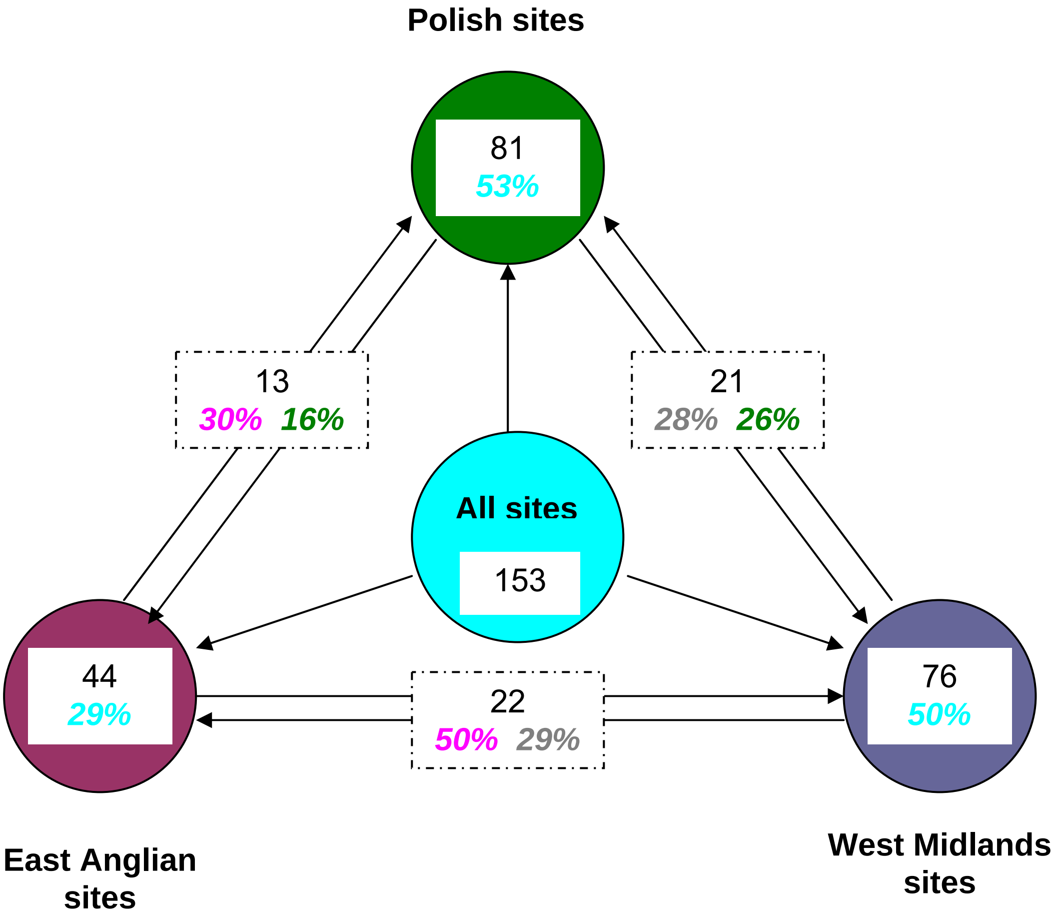

Figure 6.3a indicates that the plant species found on *C. canescens* sites in the three main geographical regions of this study (Poland, East Anglia, West Midlands) show considerable regionality, normally with 30% or less of species shared with any other region. The exceptional 50% of East Anglian species shared with West Midlands sites

may simply reflect the smaller size of the East Anglian flora rather than a stronger regional relationship, since the West Midlands flora has almost as many species and a similar proportion of its flora in common with Poland as with East Anglia.

The regional relationships apparent from Figure 6.3a were further tested through TWINSPAN and CANOCO analyses.

6.3.2 TWINSPAN analysis

A TWINSPAN indicator species analysis was made of 346 quadrat samples from all study sites plus Caister-on-Sea. Non-quadrat data derived from general inspection of the sites were excluded as not being comparable between sites. Four cut levels were applied at 0, 2, 4 and 7, since inspection of the input data showed these as the most natural Domin groupings in the samples. Hardly any data sets contained species abundances at the highest Domin levels (9 and 10) so a fifth cut level to differentiate between these was considered unnecessary. The results are shown in Figure 6.3b as an annotated dendrogram in which the indicator species at each division are given up to the third division. Eigenvalues and sample sizes are shown for each division.

The first division produces a **Group 0** which is indicated by a cluster of species characteristic of Atlantic dwarf shrub heathland and acidic grassland – *Calluna vulgaris*, *Ulex europaeus*, *Deschampsia flexuosa* and *Agrostis capillaris* – along with *Ornithopus perpusillus* and *Rumex acetosella* which are typical of sparse, open vegetation particularly on sandy soils. The opposite group in this division, **Group 1**, has only one indicator species – *Spergula morisonii* – which is a spring annual of inland sand dunes widespread in Poland but absent from Britain. *Spergula morisonii* is given as an indicator at cut level 1 with 50 samples, while the other three positive preferentials for this division include *Spergula morisonii* at level 2 with 30 samples[9].

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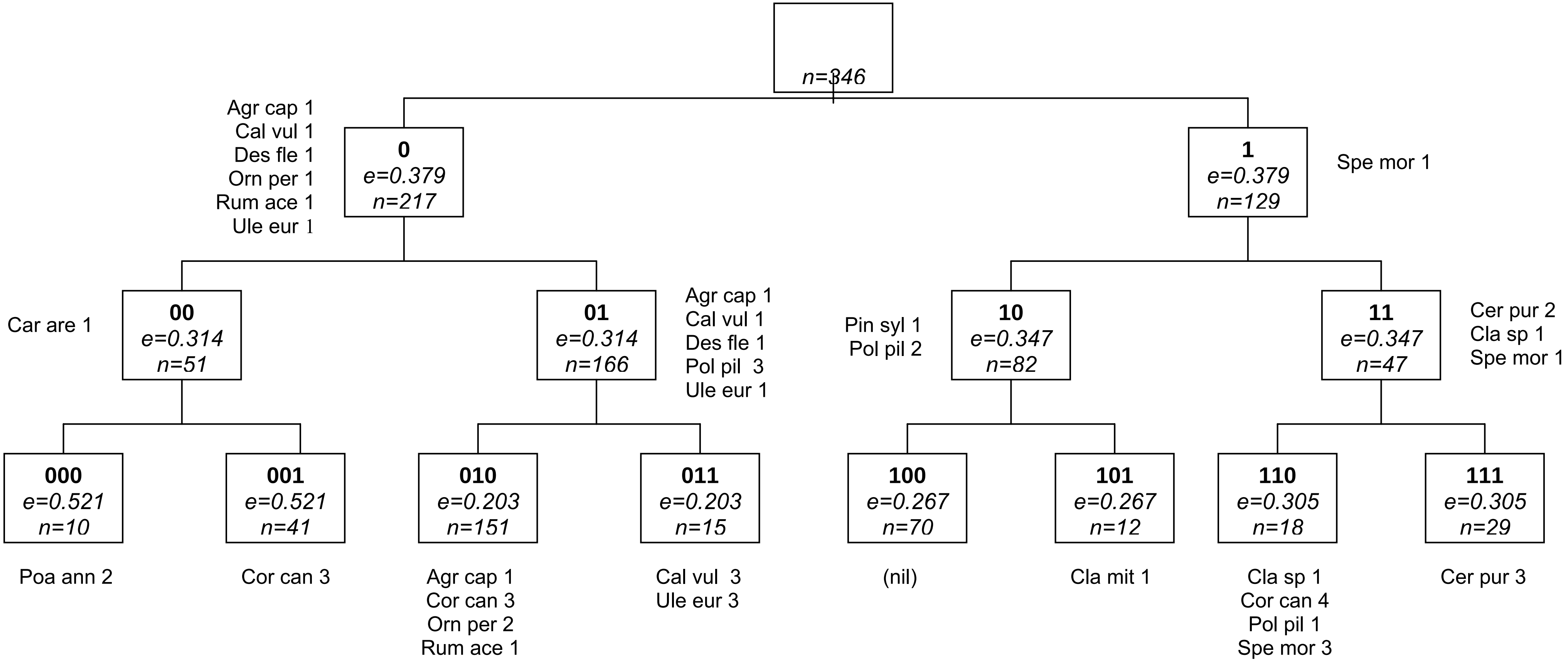
[9] plus *Cladonia* sp. at level 1 (with 2- and 26+ samples) and *Ceratodon purpureus* at level 2 (15- and 29+ samples)

Figure 6.3b: TWINSPAN indicator species analysis of vegetation in 346 quadrat samples in Britain and Poland, showing indicators at each level of division.



Key to abbreviations:

Agr cap	*Agrostis capillaris*
Cal vul	*Calluna vulgaris*
Car are	*Carex arenaria*
Cer pur	*Ceratodon purpureus*
Cla mit	*Cladonia mitis*
Cla sp	*Cladonia* species
Cor can	*Corynephorus canescens*
Des fle	*Deschampsia flexuosa*
Orn per	*Ornithopus perpusillus*
Pin syl	*Pinus sylvestris*
Poa ann	*Poa annua*
Pol pil	*Polytrichum piliferum*
Rum ace	*Rumex acetosella*
Spe mor	*Spergula morisonii*
Ule eur	*Ulex europaeus*

e = eigenvalues for each division

n = number of samples in division

numbers 1 to 4 after the species indicate abundance levels according to the four cut levels: see text for details

The division clearly separates British from Polish sites. All samples in Group 0 are spread across all British sites, except for a single Polish sample – number 126 from Site CR, perhaps placed here because it contains an untypically large amount of *Festuca rubra* for Polish samples. Group 1 contains largely Polish samples with a few from Kinver Edge and one (sample 106) from Site WW. The latter may be placed here because it contains the positive preferential *Cladonia* species, but it is less apparent why the Kinver samples should appear here: perhaps their particular mix of bryophyte species abundances may be a factor.

Dividing Group 0 produces Group 00, with 51 stands, and Group 01 with 166 stands. **Group 01**'s indicator species are similar to those for Group 0 – *Agrostis capillaris*, *Calluna vulgaris*, *Deschampsia flexuosa* and *Ulex europaeus* are again given, along with *Polytrichum piliferum* at level 3, though *Ornithopus perpusillus* and *Rumex acetosella* do not feature in this division either as indicators or preferentials. All 166 samples in this group belong to Kinver Edge where the *Deschampsia flexuosa* – *Calluna vulgaris* heathland is best represented among the study sites. Just one species is given as an indicator of **Group 00**, namely *Carex arenaria* at level 1, and it appears in the list of preferentials also at levels 2 and 3. This sedge is a frequent associate of *C. canescens* on the two Breckland sites and at Caister-on-Sea, but it was found nowhere else in this study. It has a chiefly coastal distribution in Britain and is very local inland (Stace, 1991), where it is mainly confined to wind-disturbed sand and sandy brown soils in Breckland and Lincolnshire (Rodwell, 2000). The other preferentials for Group 00 include *Agrostis vinealis* at levels 1, 2 and 3, which was also found only on the Breckland sites and Caister-on-Sea in this study. This Group contains all East Anglian stands (except the untypical sample 106 – see above) but is also represented by 27 samples from Kinver Edge, many of which contain winter annuals such as *Aira praecox* and *Vulpia bromoides* typical of looser substrates. This division therefore appears to separate the stable acidic heathland vegetation widely represented on Kinver Edge with vegetation more associated with drought-liable sands which are characteristic of the East Anglian sites but which are also represented at Kinver.

The division of Group 1 gives **Group 10**, indicated by *Pinus sylvestris* and *Polytrichum piliferum* (at level 2), and **Group 11**, indicated by *Spergula morisonii*, along with

Ceratodon purpureus (level 2) and *Cladonia* species. In this study *Pinus sylvestris* occurs only as a plantation tree which seeds into neighbouring *C. canescens* sites, and its presence in this division cannot be related to any natural vegetation type. The preferential species for Group 10 are *Polytrichum piliferum* at levels 1, 2 and 3, while the preferentials for Group 11 include *Ceratodon purpureus* at levels 1, 2 and 3 plus *Spergula morisonii* at levels 1 and 2. Group 11 consists entirely of samples from Bromierzyk sites, whereas Group 10 is largely made up of samples from Sites CR and BO, but with some samples from Bromierzyk and 18 from Kinver Edge. Interpretation of this division is complicated, not least because a key species, *Ceratodon purpureus*, has a very wide ecological range (Smith, 1978; Watson, 1978). With the exception of *Pinus sylvestris*, all species on both sides of this division are typical of the Polish Corynephoretalia (see 6.4.2.2). From the distribution of stands, it seems that this division mainly reflects a difference between vegetation represented on the Bromierzyk sites and that on the other Polish sites; but associated with the latter group are also some elements of the Bromierzyk vegetation and some of the Kinver Edge vegetation.

The division of Group 00 leads to **Group 000**, indicated by *Poa annua* at level 2, and **Group 001**, with *C. canescens* at level 3 as the sole indicator species. The eigenvalue for this division – 0.521 – is particularly strong. The negative preferentials are *Poa annua* at levels 1, 2 and 3, while the positive preferentials include *C. canescens* at all levels to level 4, plus ten other species. Even though the negative indicator *Poa annua* was recorded only at Kinver Edge and Burlish Top in this study, this division is clearly not a simple reflection of geography, since the positive preferentials include species which are shared between the West Midlands and East Anglian sites (e.g. *Aira praecox*, *Filago minima*), others which occur only in East Anglia (*Agrostis vinealis*, *Sedum acre*) and others which are found on both British and Polish sites (*C. canescens* itself, *Polytrichum piliferum*, *Hypnum cupressiforme*). The distribution of stands shows that Group 000 is entirely made up of Kinver Edge samples while Group 001 consists of most East Anglian samples plus 17 from Kinver Edge. A possible interpretation is that this division reflects sand compaction, since *Poa annua* is among the plant species most resistant to trampling, while *C. canescens* appears to be susceptible to trampling (5.3.3) and some other species among the positive preferentials (*Filago minima*, *Carex arenaria*, *Aira praecox*, *Ornithopus perpusillus*) are typical of looser substrates.

The division of Group 01 yields **Group 010**, indicated by *C. canescens* at level 3 plus *Agrostis capillaris*, *Ornithopus perpusillus* (level 2) and *Rumex acetosella*, mirroring the non-woody indicator species seen at earlier divisions on the negative side of this analysis. In contrast, **Group 011** has *Calluna vulgaris* and *Ulex europaeus* as indicators, with the positive preferentials being *Calluna vulgaris* at levels 3 and 4 plus *Ulex europaeus* at levels 2, 3 and 4. All samples in Group 011 are from Site KE3 while those of Group 010 are from all West Midlands sites, including some on Site KE3. This division apparently differentiates the Transition Phase (5.3.4) of the *C. canescens* habitat on the West Midlands sites from the earlier phases of the habitat as expressed on the same sites.

Arising from Group 10 are Groups 100 and 101, represented by 70 and 12 stands respectively. *Cladonia mitis* is the sole indicator species for **Group 101**; it also appears among the list of preferentials at all levels from 1 to 4, along with *Hypnum cupressiforme* at levels 1 and 2 and *Pinus sylvestris* and *Rumex acetosella* at level 1. There is no indicator species for **Group 100**, and the only preferential species for this group is *C. canescens* at level 4. In the absence of indicators of the negative group this is a difficult division to interpret: *Cladonia mitis* was recorded only in Poland, at Bolimów and Ciosny but not the Bromierzyk sites[10]. *C. canescens* level 4 is representative of the Early Mature Phase of the Corynephoretum (5.3.4) when this grass is at its most prolific. Eighteen of the 70 stands in Group 100 are on British sites (17 on Kinver Edge); the remainder are Polish, scattered across all sites. Group 101, however, is entirely made up of stands from Site CR except for one sample with abundant *Cladonia mitis* from Site BO. This division may possibly be separating out examples of the subassociation *Cladinetosum mitis* of the *Spergulo morisonii-Corynephoretum canescentis* (Czyżewska, 1992). Although not included as an indicator or preferential species for Group 101, the lichen *Coelocaulon aculeatum* is a

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[10] It is rare in Britain and absent from the West Midlands and East Anglia (Duncan, 1970; Dobson, 1981)

constant for this subassociation, and in this study was similarly recorded in Poland at Bolimów and Ciosny but not Bromierzyk.

The division of Group 11 produces Group 110 with 18 stands and Group 111 with 29 stands. The indicators for **Group 110** are *Cladonia* species and *Polytrichum piliferum* at level 1, *Spergula morisonii* at level 3 and *C. canescens* at level 4. **Group 111** is indicated by one species, *Ceratodon purpureus* at level 3, with a second species – *Cladonia foliacea* – shown as a preferential. All stands on both sides of this division occur on the three Bromierzyk sites. With *C. canescens* level 4 occurring on one side of this division, it may be interpreted as a differentiation between two phases of the Corynephoretum on the same sites – though this interpretation perhaps implies that the greatest abundance of *Ceratodon purpureus* occurs at a more mature phase on Polish sites than it may do on British sites (5.3.2.1).

In summary, this interpretation of the TWINSPAN analysis clearly separates British sites on the negative side of the analysis, as apart from the single sample 126 no Polish stands appear anywhere on this side as far as the analysis has been carried through. Further negative divisions separate stable acidic heathland communities characteristic of Kinver Edge from more drought-resistant vegetation represented on British sites including parts of Kinver Edge. The East Anglian sites are also well differentiated in this part of the analysis, with just one sample (number 106 from Wangford Warren) appearing anomalous. The positive side of the analysis is largely about Polish sites; at the second level of division there is some differentiation between Bromierzyk sites and the other Polish sites; and at the third division Ciosny Reserve is also differentiated, on an apparently phytosociological basis. An important outcome of this analysis is that, while a strong regional trend is apparent within the same three regions identified above (Figure 6.3a), some Kinver Edge samples are not so clearly differentiated, and elements of the vegetation of Kinver Edge can be associated with both Polish and East Anglian samples in several parts of this analysis. No other inter-relationship between regions is so clearly apparent from this TWINSPAN analysis.

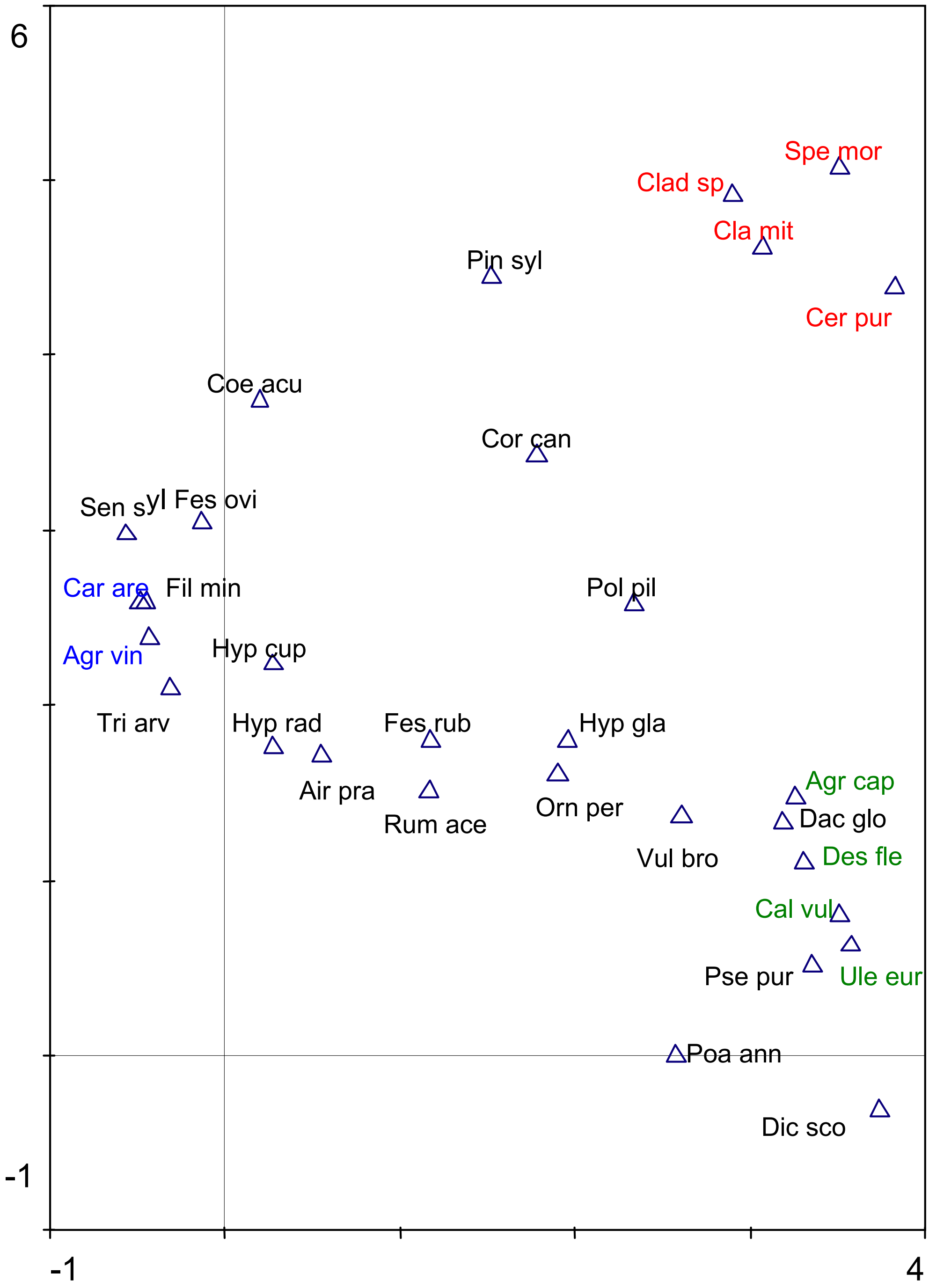
Further insights into some elements of this TWINSPAN classification might be given by applying ecological or functional strategies for vascular plants, such as Ellenberg’s indicator values or Grime’s C-S-R strategies, to analyse indicator and preferential species: examples might include the apparently anomalous samples 106 and 126, and those Kinver Edge samples which are located with either Polish or East Anglian samples. However, the dominance of bryophytes and lichens as indicators and preferentials on the positive side of the classification would present limitations to analysing the entire classification using strategies devised for vascular plants.

6.3.3 CANOCO analysis

The same input data file used in the TWINSPAN analysis was further analysed using CANOCO. As the data were already logarithmically transformed by using Domin values, no further transformation was deemed necessary. The exploratory Detrended Correspondence Analysis (DCA) produced quite long gradients (3.905 for axis 1, 4.872 for axis 2) which are borderline but probably indicative that DCA is the more useful analysis. The eigenvalues were very high throughout (axis 1 – 0.557; axis 2 – 0.497; axis 3 – 0.418; axis 4 – 0.322). This analysis accounted for 15% of the variation in the species data.

The output diagrams are shown as Figures 6.3c and 6.3d. Figure 6.3c shows the distribution along the first two axes of 30 species with a weighting of 1% or above. It is possible to identify species groupings similar to those in the TWINSPAN analysis (6.3.2): positive indicators from that analysis (i.e. *Spergula morisonii*, *Ceratodon purpureus*, *Cladonia mitis*, *Cladonia* species) appear as a cluster in Figure 6.3c, and the dominant East Anglian species *Carex arenaria* and *Agrostis vinealis* lie at the opposite end of axis 1 to the typical West Midlands vegetation characterised by *Calluna vulgaris*, *Ulex europaeus*, *Agrostis capillaris* and *Deschampsia flexuosa*. *Poa annua* lies much nearer to this last group than to the East Anglian group, perhaps reinforcing the interpretation of TWINSPAN Groups 000 and 001 above as a response to soil compaction on the more heavily trampled West Midlands sites. While Figure 6.3c shows elements of species grouping into three regions (Poland, East Anglia, West Midlands), several species seem to be distributed differently: *Senecio sylvaticus*, *Trifolium arvense, Filago minima* and *Festuca ovina* occurred in both East Anglia and the West Midlands (but mostly at Site BT in the latter region), while *Hypnum cupressiforme* was equally distributed across British and Polish sites.

Figure 6.3c: Detrended Correspondence Analysis (DCA) of vegetation samples showing distribution of species along the first two axes.

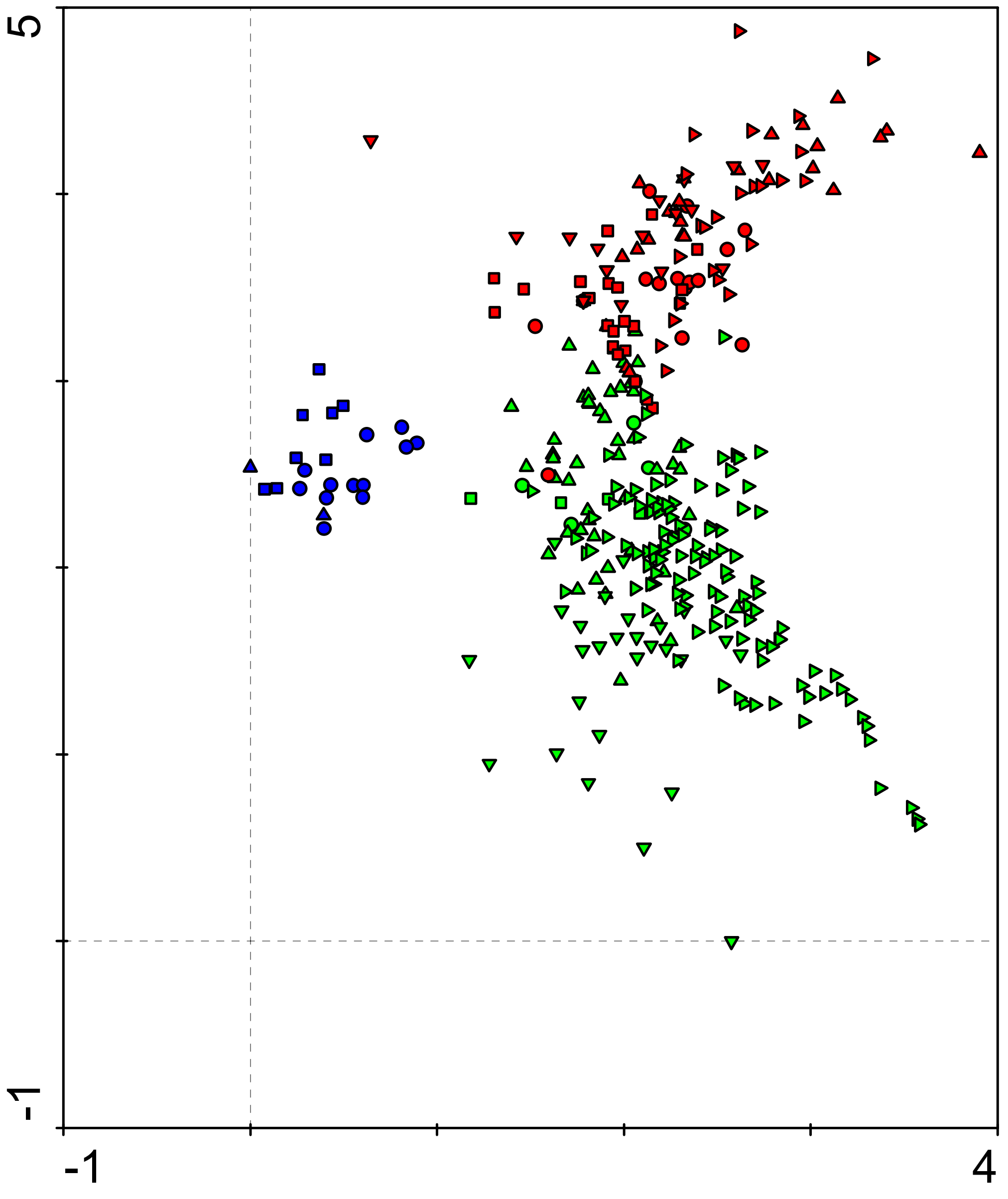


Key to abbreviations:
Agr cap *Agrostis capillaris* Agr vin *Agrostis vinealis* Air pra *Aira praecox* Cal vul *Calluna vulgaris*
Car are *Carex arenaria* Clad sp *Cladonia* species Cla mit *Cladonia mitis*
Coe acu *Coelocaulon aculeatum* Cor can *Corynephorus canescens* Dac glo *Dactylis glomerata*
Des fle *Deschampsia flexuosa* Dic sco *Dicranum scoparium* Fes ovi *Festuca ovina*
Fes rub *Festuca rubra* Fil min *Filago minima* Hyp cup *Hypnum cupressiforme*
Hyp gla *Hypochaeris glabra* Hyp rad *Hypochaeris radicata* Orn per *Ornithopus perpusillus*
Poa ann *Poa annua* Pin syl *Pinus sylvestris* Pol pil *Polytrichum piliferum*
Pse pur *Pseudoscleropodium purum* Rum ace *Rumex acetosella* Sen syl *Senecio sylvaticus*
Spe mor *Spergula morisonii* Tri arv *Trifolium arvense* Ule eur *Ulex europaeus*
Vul bro *Vulpia bromoides*

	1	2	3	4
Eigenvalues	0.557	0.497	0.418	0.322
Lengths of gradient	3.905	4.872	3.080	2.837
Cumulative % variance of species data	4.7	9.0	12.5	15.3

Blue = species strongly associated with East Anglian sites
Red = species strongly associated with Polish sites
Green = species strongly associated with West Midlands sites

Figure 6.3d: Detrended Correspondence Analysis (DCA) of vegetation samples showing the distribution of 346 quadrats along the first two axes.



	1	2	3	4
Eigenvalues	0.557	0.497	0.418	0.322
Lengths of gradient	3.905	4.872	3.080	2.837
Cumulative % variance of species data	4.7	9.0	12.5	15.3

Site Key:

BO	Bolimow
BR1	Bromierzyk Site 1
BR2	Bromierzyk Site 2
BR3	Bromierzyk Site 3
BT	Burlish Top
COS	Coastal East Anglia
CR	Ciosny Reserve
DS	Devil's Spittleful / Rifle Range
KE1	Kinver Edge Site 1
KE2	Kinver Edge Site 2
KE3	Kinver Edge Site 3
LA	Lakenheath
WW	Wangford Warren

Blue = East Anglian sites

Green = West Midlands sites

Red = Polish sites

Figure 6.3d shows the distribution of quadrats along the first two axes of the DCA analysis. A cluster of quadrats is clearly segregated along axis 1, and these quadrats are almost all East Anglian ones including those form Caister-on-Sea). In the main grouping of quadrats it is possible to identify clusters for Polish sites and West Midlands sites, but there is some overlap between these two regions. This Figure clearly suggests that the West Midlands sites and Polish sites are nearer to each other than either is to the East Anglian sites, and that the Breckland vegetation has its closest affinities with the coastal *C. canescens* community at Caister-on-Sea. The loose scatter of Site KE2 quadrats which lie a little away from the main grouping are all from 1999, at a time when the site was just beginning to recover from scrub clearance following extensive encroachment by *Ulex europaeus* (Blunt & Blunt, 2000).

6.4 Discussion

6.4.1 Taxonomic composition of the vegetation of the study sites

Of the plant species recorded in this study (Table 6.3i) the great majority are considered to be nationally widespread in suitable habitats within a British (Stace, 1997) or a Polish (Rutkowski, 1998) context. Only one of the plant species recorded on the Polish sites in this study is included in the List of Threatened Plants in Poland (Zarzycki, Wojewoda & Heinrich, 1992) as a species of conservation importance: this is the lichen *Cetraria islandica*, which occurs as a local constituent of the vegetation of Site BO (Appendix B.7.1). Within Britain, three species qualify for Red Data Book status in the most recent revision (Cheffings & Farrell, 2005): these are *C. canescens* itself, which is categorised as Near Threatened; *Silene otites* which is Endangered; and *Hypochaeris glabra*, which is Vulnerable.

A feature of this study is the high proportion of taxa which occur infrequently in the samples. Both the quadrat samples and general vegetation data contain 72% of taxa at less than 1% frequency. Moreover, many of the infrequent taxa are nationally widespread in both Britain and Poland, and therefore potentially available to many more sites and samples. This situation may well arise from the small or very small size of *C. canescens* populations on many sites in this study, which is likely to inhibit the expression of the full vegetational potential of the community and make communities more vulnerable to regular incursion by species from other neighbouring vegetation types.

6.4.2 Phytosociological analysis

6.4.2.1 Syntaxonomies including *Corynephorus canescens*

Work on the taxonomies of plant communities has been carried out in Europe since the 1920s, leading to the evolution of a hierarchical taxonomy[11] and the publication of numerous papers covering particular vegetation types in regional or national contexts. In 1992 a European Vegetation Survey was launched to develop a unified phytosociological syntaxonomy drawing on work already in progress in many countries including Britain and Poland (Dierschke, 1992). In the project's test phase it was proposed to focus on clarifying relationships between selected plant communities including the complex Koelerio-Corynephoretea / Sedo-Scleranthetea / Helianthemetalia guttati within which *C. canescens* communities are placed. From the outset Polish vegetation taxonomies have followed the European taxonomical system (e.g. Matuszkiewicz, 1984, 2001), but in Britain the National Vegetation Classification (NVC) uses its own non-hierarchical nomenclature, though it has recently been correlated with European taxonomies (Rodwell, 2000).

A problem encountered in all phytosociological systems is that species assemblages change more or less continuously if a geographically widespread community is sampled throughout its range (Mueller-Dombois & Ellenberg, 1974). This has led to regional differences in interpretation of certain vegetation assemblages, including *C. canescens* communities. In central and north-west Europe these communities have traditionally been placed within two closely-related classes, the Sedo-Scleranthetea and Koelerio-Corynephoretea, and this arrangement continues to be accepted by some authors (e.g. Chytrý & Tichý, 2003), though a treatment of the Sedo-

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[11] see Barkman, Moravec & Rauschert (1986) for a recent conspectus

Scleranthetalia as subsumed within the Koeleria-Corynephoretea[12] is gaining ground on the continent (e.g. Hövelmann *et al*., 2006). In Britain Rodwell *et al*. (2000) treat the Sedo-Scleranthetalia as a parallel order to the Corynephoretalia canescentis within the class Koelerio-Corynephoretea, differentiating it as occurring in “closed swards of calcareous to acidic, drought prone soils on rock outcrops.” In the south-western part of its European range, in France, Portugal and Spain, *C. canescens* occurs in communities characterised by species with a Sub-Atlantic-Mediterranean distribution, including *Helianthemum guttatum* (= *Tuberaria guttata*). These communities are typically placed by Iberian phytosociologists within the class Helianthemetea guttati (Tuberarietea guttatae), a parallel class to both the Koelerio-Corynephoretea and Sedo-Scleranthetea (Rivas-Martínez *et al*., 2001, 2002; Pérez Prieto & Font, 2005).

To aid comparison of data from the present study with current vegetation classifications a Constancy Table has been constructed for each of the three main site groupings (Poland, East Anglia, West Midlands). The constancy with which a species occurs in samples for a site is shown in capital Roman numerals on a five-point scale:

V = occurs in 81 – 100% of samples (often called “constant” species)
IV = occurs in 61 – 80% of samples (“ “ “ “ “)
III = occurs in 41 – 60% of samples (often called “common” or “frequent” species)
II = occurs in 21 – 40% of samples
I = occurs in up to 20% of samples

The measure of frequency of a species is independent of its abundance: the abundance range of a species in the samples is shown in parentheses using the Domin scale. The Constancy Tables itemise every species which occurred at a category III or higher on at least one site. Each site is shown separately, and the data are then aggregated for each of the geographical groups of sites – i.e. Poland, East Anglia, West Midlands. This aggregation of geographically connected sites is felt to be validated by the results of the TWINSPAN and CANOCO analyses above, and is

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[12] Dengler *et al*. (2003) treat Sedo-Scleranthenea and Koelerio-Corynephorenea as parallel subclasses within Koelerio-Corynephoretea

made to counteract any skew which may appear for the smallest sites where only small data sets could be taken. The results are shown in Table 6.4i, in which a dash (-) means that the species did not appear in the samples for that site. Species with a frequency of I or II on all sites in the geographical region are not listed but can be adduced from Table 6.3i.

Table 6.4i: frequencies and abundance ranges (in parentheses) of the most frequent species within each geographical group of sites.

(a) Polish sites

Species	**Site**					
	BO	**BR1**	**BR2**	**BR3**	**CR**	**All**
Corynephorus canescens	V (4-8)	V (4-9)	V (4-8)	V (4-8)	V (1-7)	V (1-9)
Polytrichum piliferum	V (2-8)	II (1-4)	I (2-5)	III (1-8)	IV (2-7)	III (1-8)
Spergula morisonii	II (1-2)	III (1-3)	II (1-4)	V (1-5)	II (1-2)	III (1-5)
Ceratodon purpureus	-	II (2-8)	II (2-3)	III (1-4)	II (1-4)	II (1-8)
Cladonia mitis	1 (1)	-	-	-	IV (1-8)	I (1-8)
Pinus sylvestris	III (1-2)	1 (2-3)	1 (1)	-	II (1-4)	I (1-4)
Number of remaining taxa with frequency II or I	13	37	21	23	14	

(b) East Anglian sites

Species	**Site**		
	LA	**WW**	**Both**
Corynephorus canescens	V (4-8)	V (1-7)	V (1-8)
Carex arenaria	IV (1-4)	V (5-7)	V (1-7)
Agrostis vinealis	V (1-7)	IV (4-7)	IV (1-7)
Polytrichum piliferum	III (2-6)	IV (1-2)	IV (1-6)
Rumex acetosella	IV (1-5)	V (1-4)	IV (1-5)
Filago minima	-	V (2-5)	III (2-5)
Hypnum cupressiforme	V (1-4)	-	III (1-4)
Hypochaeris radicata	V (1-4)	-	III (1-4)
Ornithopus perpusillus	V (1-5)	-	III (1-5)
Aira praecox	III (1-5)	-	II (1-5)
Cladonia cervinalis	III (1-2)	-	II (1-2)
Cladonia pyxidata	-	III (1-2)	II (1-2)
Crepis capillaris	III (1-2)	-	II (1-2)
Festuca ovina	III (5-7)	-	II (5-7)
Sedum acre	IV (1-3)	-	II (1-3)
Senecio sylvaticus	-	IV (1-5)	II (1-5)
Silene otites	III (1-4)	-	II (1-4)
Trifolium arvense	IV (1-5)	-	II (1-5)
Number of remaining taxa	15	8	

continued…..

Table 6.4i continued…..

with frequency II or I			

(c) West Midlands sites

Species	**Site**					
	BT	**DS**	**KE1**	**KE2**	**KE3**	**All**
Corynephorus canescens	V (4-8)	V (4-8)	V (2-9)	IV (1-7)	V (2-8)	V (1-9)
Polytrichum piliferum	III (4-7)	V (3-7)	IV (2-8)	II (1-5)	IV (2-8)	IV (1-8)
Rumex acetosella	III (1-2)	II (2-4)	IV (1-8)	IV (1-7)	IV (1-7)	IV (1-8)
Aira praecox	IV (1-4)	I (1)	II (1-5)	III (1-5)	I (1-2)	III (1-7)
Ornithopus perpusillus	II (1)	II (1)	I (1-4)	III (1-6)	IV (1-5)	III (1-6)
Poa annua	I (2)	I (2)	I (1-4)	IV (1-8)	I (1-2)	II (1-8)
Ulex europaeus	IV (1-2)	-	I (1-2)	II (1-4)	III (1-4)	II (1-4)
Agrostis capillaris	I (5)	-	I (1-5)	II (2-5)	IV (1-7)	II (1-7)
Calluna vulgaris	I (2)	II (2-5)	I (1-4)	II (1-7)	III (1-7)	II (1-7)
Deschampsia flexuosa	V (1-4)	III (1-2)	I (2-5)	II (1-5)	III (1-4)	II (1-5)
Hypochaeris radicata	IV (2-6)	III (1-5)	I (1-2)	I (1-3)	I (1-2)	I (1-6)
Jasione montana	I (3)	III (1-2)	-	-	-	I (1-3)
Number of remaining taxa with frequency II or I	18	6	21	16	16	

6.4.2.2 Polish sites

Matuszkiewicz (2001) has produced the latest guide to Polish phytosociology, with the following syntaxonomy for the order Corynephoretalia canescentis:

KOELERIO GLAUCAE-CORYNEPHORETEA CANESCENTIS Klika in Klika & Novák 1941
CORYNEPHORETALIA CANESCENTIS R.Tx.1937
  Corynephorion canescentis Klika 1934
    Spergulo morisonii-Corynephoretum canescentis (R.Tx. 1928) Libb. 1933
    Corniculario-Cladonietum mitis Kreiger 1937 ex Kródska & Tobolewski 1978
    Polytricho piliferi-Stereocauletum condensati (Zieliński 1967) Głowacki 1981
    Agrostietum coarctatae (vinealis) Kobendza 1930

Three further alliances (*Koelerion albescentis* R.Tx 1937; *Vicio lathyroidi-Potentillion argenteae* Brzeg in Brzeg & M. Wojt. 1996; *Koelerion glaucae* (Volk 1931) Klika 1935) are included within the Corynephoretalia in Poland but are not elaborated here. Polish inland psammophilous grasslands on acid sands are considered to support only one pioneer association: Spergulo morisonii-Corynephoretum canescentis (Czyżewska, 1992).

Matuszkiewicz (*loc. cit.*) gives the following plant species as characteristic of the order and alliance in Poland. The queries are Matuszkiewicz's own, indicating some doubt whether the species concerned belong here:

Order Corynephoretalia canescentis

Agrostis vinealis, Brachythecium albicans, Carex ligerica *(?)*, Cerastium semidecandrum, Ceratodon purpureus, Cladonia foliacea, C. furcata var. palarnaea, C. subulata, Corynephorus canescens, Festuca ovina, Filago minima, Helichrysum arenarium, Jasione montana, Myosotis ramosissima, Polytrichum piliferum, Potentilla collina, Rhacomitrium canescens, Rumex acetosella, R. tenuifolius, Scleranthus perennis, Sedum acre, S. sexangulare *(?)*, Thymus serpyllum, Trifolium arvense, T. campestre, Veronica dillenii.

Alliance Corynephorion canescentis

Cephaloziella starkei, Cladonia mitis, C. cervicornis ssp. verticillata, C. coccifera, C. floerkeana, C. macilenta, C. pleurota, C. uncialis, Coelocaulon aculeatum, C. muricatum, Spergula morisonii, S. pentandra *(?)*, Stereocaulon condensatum, S. incrustatum, S. tomentosum, Teesdalia nudicaulis.

Table 6.4i (a) indicates that *Spergula morisonii* and *Polytrichum piliferum* occurred as frequent species on Polish sites, the former more abundant on the Bromierzyk sites and the latter more abundant at Bolimów and Ciosny. The timing of most sampling in July – August (3.1.2) may be expected to produce an under-representation of the Polish spring annual community in the samples – *Spergula morisonii* in particular, along with *Cerastium semidecandrum* and *Veronica dillenii* – as plants of these species die before mid-summer. Nevertheless, the species recorded on the Polish sites (Table 6.3i) and the pattern of their frequency (Table 6.4i (a)) are consistent with the standard interpretation of the alliance Corynephorion canescentis in Poland (Czyżewska, 1992; Matuszkiewicz, 2001). The main difference is the scarcity in this study of the indicator species *Teesdalia nudicaulis*, which occurred infrequently at Ciosny and not on the other sites. Of the associations within this alliance, as elaborated by Czyżewska (*loc. cit*.), Ciosny (Site CR) appears to fall into the Spergulo-Corynephoretum cladinetosum mitis, (Corniculario-Cladonietum mitis *sensu* Matuszkiewicz *loc. cit*.) since *Cladonia mitis* is both frequent and abundant here, and *Coelocaulon aculeatum* is present but in smaller quantity. The site lies within a stable, maturing *Juniperus communis* woodland (3.2.3). Czyżewska places Polish pioneer communities typically within the association Spergulo morisonii – Corynephoretum canescentis, and despite the absence of *Teesdalia nudicaulis*, Sites BR1 and BR3 appear to fall comfortably within this association. Sites BR2 and BO fit less well into this association, though they may indeed belong there. They are the study sites most affected by neighbouring *Pinus sylvestris* plantation and *Quercus robur* woodland, which may have led to a modification of habitats through shelter and shading.

In considering the analyses of the vegetation data for Polish sites it may be noted that the picture which emerges from the TWINSPAN and CANOCO analyses, together with the frequency table, is both internally consistent and relates well to the standard Polish phytosociology of the Corynephoretum. Moreover, the aggregation of data across all Polish sites (the ”All” column in Table 6.4i (a)) has evened out the frequency of *Pinus sylvestris* to demote this alien plantation species from the higher frequency categories so that it does not distort the emerging picture.

6.4.2.3 East Anglian sites

The Constancy Table for the East Anglian sites (Table 6.4i (b)) shows over twice as many species in the higher frequency categories (III – V) than is the case for either Polish or West Midlands sites: in fact, 50% of the species recorded on each of the two sites fall into these categories. The constants for both sites taken together include *Agrostis vinealis*, *Carex arenaria*, *Polytrichum piliferum* and *Rumex acetosella*, and the frequent species are *Filago minima*, *Hypnum cupressiforme*, *Hypochaeris radicata* and *Ornithopus perpusillus*.

Rodwell (2000) has described in detail British sand dune communities dominated by *Carex arenaria*. This sedge is seldom found inland in this country, and all such communities identified by Rodwell lie in East Anglia (*loc. cit*. p. 200). His analysis places Breckland *Carex arenaria* vegetation in two NVC classifications – SD10 *Carex arenaria* dune community and SD11 *Carex arenaria – Cornicularia aculeata* dune community. SD10 occurs around the British coast and inland in Breckland and Lincolnshire; SD11 is found mainly on the British east coast, with a *Festuca ovina* sub-community extending inland to Breckland, and it is this sub-community which is linked by Rodwell to the Breckland *C. canescens* sites. Treating *Carex arenaria* as characteristic of the Corynephorion, Rodwell identifies SD11 with the association Spergulo morisonii – Corynephoretum canescentis on the grounds of a strongly overlapping range of lichens plus some shared herbaceous species (*Rumex acetosella*, *Filago minima* and *Teesdalia nudicaulis* in addition to *C. canescens* and *Carex arenaria*).

There are some intriguing differences between Rodwell's account for SD11, including his Floristic Table (*loc. cit*. pp 206-207), and the present study's data for the Breckland *C. canescens* communities. Nowhere does Rodwell mention *Agrostis vinealis*, *Trifolium arvense*, *Silene otites*, *Ornithopus perpusillus* or *Senecio sylvaticus* as associated with SD11, though in this study they occurred frequently in samples on one or both Breckland sites (Table 6.4i (b)), which comprise a high proportion of the Breckland *C. canescens* population. In addition, SD11 appears to be much richer in lichen species than is recorded here (Table 6.3i). The omission of *Agrostis vinealis* is the most telling[13], as this study found it strongly represented on the Breckland sites, and it is a characteristic species of *C. canescens* communities in western and central Europe (Bohn *et al*., 2000; Matuszkiewicz 1984, 2001), where it gives its name to the association Agrostietum coarctatae (vinealis) (Kobendza 1930) Tx. in Dierssen 1972, treated variously as belonging within the Corynephorion canescentis (Bohn *et al*., *loc. cit*.) or the closely-related alliance Thero-Airion (University of Bonn, 2006). Equally interesting is the constant presence of *Ornithopus perpusillus* in the Lakenheath samples, for according to Stankevičiūtė (2002) "all described communities with *O. perpusillus* belong to the …..Thero-Airion R. Tx. 1951 alliance." These differences between the present study and the National Vegetation Classification may possibly be a consequence of the different sample sizes used – 1m^2 in this study, 4m^2 in the

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[13] The *Agrostis* species which Rodwell ascribes to SD11 is *Agrostis capillaris*

NVC – which may have produced different numbers of species and frequency measures: but this is considered unlikely, since the Wangford Warren *C. canescens* population occupies only about 5m^2 in any case (Appendix B.1.1). It is more likely that either the NVC uses data for the Wangford site as a whole rather than just the *C. canescens* population there[14] or that the Breckland *C. canescens* populations were not specifically sampled in the NVC survey[15].

The Breckland *C. canescens* communities are, in fact, difficult to analyse in terms of their phytosociological alliances. The size of the Wangford Warren population is so small that very few samples can be taken without overlap. Lakenheath has a much larger population, but its regular management by close mowing (Appendix B.1.2) means that it is now part of a closed turf where it exists in stasis, protected from competitive elimination by the weakening of its competitors but unable to propagate itself from seed, though vegetative propagation through tillers remains possible. The Lakenheath population is thus unlike any other investigated in this study, and the species-richness of individual samples is also untypical. The TWINSPAN and CANOCO analyses clearly suggest that the Breckland sites are different from both West Midlands and Polish sites, and Figure 6.3d associates them most with the East Anglian coastal vegetation. Rodwell's (*loc. cit.*) own analysis of the *Carex arenaria* communities of Breckland indicates a strong relationship with the vegetation of the East Anglian coast.

6.4.2.4 West Midlands sites

The constancy data are shown in Table 6.4i (c). In forming this Table a number of stands from the protected Site KE3 Area B were omitted where succession had transformed the *C. canescens* community to a *Ulex*-dominated shrub heath. The Table shows *Polytrichum piliferum* and *Rumex acetosella* as constants for the West Midlands sites, plus *Aira praecox* and *Ornithopus perpusillus* as frequent species. A further seven species occurred at the higher frequency levels (III or above) at one or more sites. The chief difference between sites is the occurrence of *Deschampsia*

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[14] Rodwell's account appears to draw heavily on Malloch (1985) for Wangford Warren data

[15] Rodwell seems unaware of the Lakenheath population, as he writes of *C. canescens* as "remaining now at only a single inland station." (*loc. cit*. p. 204)

flexuosa and *Hypochaeris radicata* as frequent species on Sites BT and DS but at a much lower level of frequency at the three Kinver Edge sites. *Jasione montana* shows a similar pattern, except that it is frequent only at the Devil's Spittleful and completely absent from Kinver Edge.

Hazlehurst (1992) analysed 185 1m^2 stands from the West Midlands sites using TWINSPAN and VESPAN II. His analysis grouped the vegetation of these sites into four subdivisions which he considered were differentiated chiefly by degree of disturbance. Three of his four subdivisions (Groups 00, 01 and 10 in his designation) give a similar picture to that which arises from the present study: his fourth subdivision (Group 11) measures a ruderal weed community including *Arabidopsis thaliana*, *Poa pratensis*, *Stellaria media*, *Cardamine hirsuta* and *Verbascum thapsus* at high frequency levels, which was not encountered in the present study. Hazlehurst analysed his data through the MATCH program on VESPAN II to give a fit for his subdivisions to the National Vegetation Classification. All subdivisions produced a highest match for the NVC U1 community, *Festuca ovina-Agrostis capillaris-Rumex acetosella* grassland, with coefficients of 51.5, 51.5 and 41.3 and 34.9 for Groups 00, 01,10 and 11 respectively. In addition, the first three groups produced a lesser match for NVC community SD11 (coefficients 31.3, 34.8 and 25.3). Hazlehurst concluded that the West Midlands *C. canescens* communities could reasonably be ascribed to the NVC U1 community, but may also show some affinities with the Breckland sites.

Rodwell (1992) describes the NVC U1 *Festuca ovina-Agrostis capillaris-Rumex acetosella* as a very diverse but distinctive grassland type which is "characteristic of base-poor, oligotrophic and summer-parched soils in the warm and dry lowlands of southern Britain, with grazing and disturbance often very important contributory factors in maintaining the typical aspect of the vegetation." *Festuca ovina* (occasionally replaced by *Festuca rubra*) and *Agrostis capillaris* are constants. Among other grasses which appear in this community without normally playing an important role in the vegetation are *Deschampsia flexuosa* (especially in areas of higher rainfall) and *Anthoxanthum odoratum* and *Holcus lanatus* (on less parched soils). Among herbs, *Rumex acetosella* is the only constant of the community; *Hypochaeris radicata* is diagnostic of one sub-community but does not play a main part in the typical sub-community; and other rosette species such as *Plantago lanceolata*, *Plantago coronopus* and *Taraxacum* spp. may occur. A number of ephemerals make a contribution, notably *Poa annua*, *Aira praecox*, *Teesdalia nudicaulis*, *Aphanes arvensis*, *Erodium cicutarium*, *Myosotis ramosissima* and *Veronica arvensis*. *Calluna vulgaris*, *Ulex* spp. and, on less impoverished soils, *Rubus fruticosus* agg. often spread into this community, and *Pteridium aquilinum* is also very common. The cryptogam element is represented chiefly by *Polytrichum piliferum*, with, more occasionally, *Polytrichum juniperinum*, *Ceratodon purpureus*, *Dicranum scoparium*, *Brachythecium albicans*, *Hypnum cupressiform*e, *Pseudoscleropodium purum* and *Rhytidiadelphus squarrosus*. *Coelocaulon aculeatum* and *Cladonia arbuscula* are early colonists in some stands, with other *Cladonia* species appearing and persisting in closed swards.

The similarity of this description of NVC U1 to the vegetation of the West Midlands sites as shown both in the present study (Tables 6.3i and 6.4i (c)) and by Hazlehurst (*loc. cit*.) is immediately apparent, though in the present study *Festuca* spp. are not frequent in the community and *Festuca rubra* partly replaces *Festuca ovina* on Kinver Edge. Hazlehurst's attribution of the West Midlands *C. canescens* communities to the U1 grassland type is, therefore, considered reasonable. The data presented in Table 6.4i (c) further suggest that the Burlish Top vegetation (and possibly the Devil's Spittleful too) might be referrable to the *Hypochaeris radicata* sub-community, and this matches Hazlehurst's interpretation of his Group 10.

Rodwell's (*loc. cit*.) account notes that the *Festuca ovina-Agrostis capillaris-Rumex acetosella* grassland type was initially described in the Breckland, and is a characteristic vegetation of that region. *Agrostis vinealis* was formerly common and sometimes abundant there, but seems to have declined after myxomatosis. The rare species *Silene otites* is also encountered within this grassland type in Breckland. The data for Lakenheath shown in Tables 6.3i and 6.4i (b) suggest that the *C. canescens* community there might be better interpreted as lying within a U1 community rather than SD11.

Rodwell (1992) initially aligned the U1 community of the southern half of England with the Thero-Airion alliance in the Corynephoretalia canescentis, on account of the part played by *Aira praecox*, *Filago minima*, *Ornithopus perpusillus* and *Teesdalia nudicaulis*. Later, however, he placed U1 in the Plantagini-Festucion ovinae Passarge 1964 within the Sedo-Scleranthetalia (Rodwell, 2000). Either interpretation would associate the NVC U1 vegetation, and therefore that of the West Midlands *C. canescens* sites, with continental vegetation associated to some extent with *C. canescens*.

An issue throughout this analysis has been the very small sizes of *C. canescens* populations being studied. To enable sufficient samples to be made, this study has adopted plot sizes of 1m^2. In most modern phytosociological studies larger relevé plot sizes are used for grassland and other vegetation sampling, though there is considerable variation in practice. There is also evidence that vegetation sampling in differently sized plots may yield different classifications (Fekete & Szöks, 1974) or different vegetation-environment correlations (Palmer, 1990; Reed *et al*., 1993). In recent years Chytrý & Otýpyková (2003) have investigated this effect and suggested a standardised plot size of 4m^2 for low-growing herbaceous vegetation of the type being investigated here. While use of this plot size would be impracticable for several sites (Sites WW, BT, DS, CR and BR2 would yield too few data sets on this sampling scale), it is felt that the methodology adopted here yields results which are consistent with other studies of this vegetation type. A further outcome of the small size of many *C. canescens* populations is that it proved possible to measure a large proportion of the vegetation of most sites, thereby reducing the bias towards selecting species-rich plots which is inherent in many phytosociological studies (Chytrý, 2001).

While the TWINSPAN and CANOCO analyses appear to differentiate the vegetation on a regional basis, the phytosociological analysis suggests that the sites across all three regions do retain some common elements. In reviewing the wider European scene, Rodwell *et al*. (2000) noted that certain vegetation types that are clearly defined in neighbouring parts of Europe tend to lose their integrity in the UK, and this may be the case for inland sand dunes. Nonetheless, this study has shown that all the British inland *C. canescens* sites, including the West Midlands sites treated as introductions by many authors (2.4.3), do have recognisable links with continental dune vegetation types, though the size of the sites make their allocation to European syntaxonomies somewhat tentative. It is felt that the Breckland sites are perhaps more in need of further review than the West Midlands ones, as their attribution to the Spergulo morisonii – Corynephoretum canescentis appears difficult to sustain from the data presented in this study. There is a conservation issue here, for as long as the Joint Nature Conservation Committee continue to treat Wangford and Lakenheath as the only occurrence in the U.K. of CORINE habitat 2330 (2.4.1) the West Midlands sites will continue to be undervalued.

6.4.3 Summary of conclusions from the investigation of the floral community of *Corynephorus canescens* sites

The main conclusions from this investigation are:

153 taxa of flowering plants and cryptogams were identified on the study sites but only a handful of these taxa are of conservation importance in Britain or Poland;

A high proportion (72%) of taxa appeared infrequently in the samples; this was interpreted as a function of the small size of several study sites;

The taxa showed a tendency to be distributed into three regions – Poland, East Anglia, West Midlands – with mostly 30% or fewer taxa shared between any two regions;

In TWINSPAN analysis the first division largely separated British from Polish samples on the negative and positive sides of the ordination respectively;

Later divisions of the TWINSPAN analysis were further interpreted as differentiating between the following elements:
stable acidic heathland and drought-resistant vegetation (– side of ordination)
trampled and loose substrates “
early and late phases of the *C. canescens* habitats “
different stages and subassociations of the Corynephoretum (+ side of ordination)

In the TWINSPAN analysis various samples from Kinver Edge were associated with other West Midlands and East Anglian samples at all divisions on the negative side, and with some Polish samples at the first two divisions on the positive side. Kinver Edge sites were the only sites clearly showing relationships with the vegetation across all three regions;

The CANOCO DCA analyses showed some groupings of plant species along similar lines to the TWINSPAN analysis. The CANOCO analyses also suggested that:

- inland East Anglian *C. canescens* stands had their closest affinities with coastal East Anglian stands
- the vegetation of the Polish and West Midlands sites is nearer to each other than either is to the East Anglian sites;

In a phytosociological analysis conducted on a regional basis the following conclusions were reached:

- Polish sites fitted well into the Corynephorion canescentis alliance as described by Polish authors;
- on the basis of their species composition East Anglian sites did not fit particularly well into the NVC classification SD11 as described by and into which they have been placed by British authors, notably Rodwell (2000). Some doubt was raised whether the East Anglian *C. canescens* populations were specifically sampled by those authors;
- within East Anglia the vegetation of Site LA was heavily influenced by its management regime and its plant species composition showed some elements of similarity with NVC vegetation type U1;
- West Midlands sites could be ascribed to the NVC U1 classification which has links with continental dune vegetation types in orders within which *C. canescens* occurs.

6.4.4 Suggestions for further study

As indicated in 6.1, the Aims and Objectives of this Chapter do not include an exploration of key relationships within and between the *C. canescens* communities of the study sites. Relationships between the vegetation and invertebrate communities will be addressed in the following Chapter (7.3.3, 7.4.2). In addition, analysis of relationships between the floral communities of the study sites using systems for classifying and describing vegetation such as those elaborated by Ellenberg and Grime present the attractive possibility of answering the problem of comparing very different floras by reducing them to their functions. In a series of publications Ellenberg (1979, 1988) and Ellenberg *et al*. (1991) devised indicator values for vascular plants of central Europe based on their ecological requirements on seven major scales: Temperature, Continentality, Light, Moisture, Reaction, Nitrogen and Salt. Each scale is represented by a gradient of values, and plant species are given a value score for each scale. Ellenberg indicator values have been used in several ways including environmental monitoring, the interpretation of ordinations (Hill *et al*., 1999), and the analysis of differences between vegetational composition (Hill & Carey, 1997). However, not all plant species are constant in their ecological requirements across their range, and many species which have a wide ecological amplitude in central Europe do not behave similarly in Britain (Hill *et al*., *loc. cit*.), factors which clearly imply some limitations on the use of Ellenberg's indicator values to compare British and Polish vegetation samples.

Grime's (1974, 1977, 2002) classification identifies three key strategies in vascular plants – Competitors, Stress Tolerators, Ruderals – commonly referred to as C-S-R strategies. Plant species are characterised according to how they respond to high or low stress and disturbance. In addition to classifying plant communities, the C-S-R model has been used to predict changes or resilience in vegetation (Grime, Hodgson & Hunt, 1988), to explain mechanisms controlling rarity and abundance (Hodgson 1986a, b), and to distinguish between vegetational responses to grassland management techniques (Moog, Kahmen & Poschlod, 2005). However, gaps in our current knowledge of plant ecology, and other factors such as a species' genetic variation over its geographical or habitat range, pose some limitations on the use of the C-S-R model (Grime, Hodgson & Hunt, *loc. cit*.).

CHAPTER 7: THE *CORYNEPHORUS CANESCENS* COMMUNITY (FAUNAL)

7.1 Aims and Objectives

This Chapter investigates the invertebrate and vertebrate fauna of the *Corynephorus canescens* habitat on the study sites and carries out analyses aimed at informing all three Aims of this study (1.2), i.e. seeking evidence for the naturalness or otherwise of the West Midlands *C. canescens* populations; exploring key community relationships; and identifying factors which may have conservation implications for *C. canescens* populations. To achieve these Aims the Objectives of this Chapter are:

- to characterise the invertebrate communities of the selected sites through sampling by general inspections of each site, quadrats, cone traps and inflorescence samples;

- to characterise the vertebrate communities of the selected sites through sampling by general inspections of each site and by quadrat data on grazing and soil disturbance;

- to analyse the faunistic composition of these communities so as to explore relationships between sites, regions and countries;

- to use ordination methods to analyse the similarities and differences between the study site communities and to attempt to relate these to physical and vegetational environmental factors;

- to explore relationships between the invertebrate fauna and selected vegetational and environmental parameters;

- to explore selected inter-relationships within the invertebrate communities and compare these across the three regions of this study;

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- to investigate how the vertebrate and invertebrate fauna may impact directly on *C. canescens* populations through grazing and the creation of sand disturbances, and to address the conservation implications.

7.2 Methods

The invertebrate fauna was sampled using the methods described in 4.5. Some identifications were made during sampling, but in the majority of cases voucher specimens of species encountered during faunal sampling were retained for laboratory determination (see Table 4.2i for authorities followed). Some direct observations of invertebrate activity were also made during site visits, and some measurements of sand erosion and accretion resulting from invertebrate activity were also made. Data on the vertebrate fauna of the sites were obtained by direct observation of animals and their signs during general searches of each site.

For detailed faunal analysis data relating only to those invertebrates identified to species or genus level were used. Because it was not possible to obtain Polish keys to all groups of fauna sampled on the Polish sites, identifications of some specimens were made using keys for neighbouring countries, e.g. Asilidae (key for Germany) and Sarcophagidae (key for Scandinavia) or, in a few instances (e.g. Pompilidae), from keys relating to the British fauna. In the case of spiders (Araneae) determinations were made from works which cover Poland but do not include all species found in that country (Table 4.2i). Determinations made from such works were cross-referred to the check-list of Polish species (Razowski 1990, 1991a, 1991b, 1997) in order to assess the likely validity of an identification (except that no Polish check-list was obtainable for Araneae). The following procedure was then applied:

(a) where the available keys reasonably covered the Polish fauna within a genus and a specimen could be determined to species level, it was recorded as that species;

(b) where the keys did not adequately cover the Polish fauna within a genus but a specimen could still be keyed out to a species, it was recorded thus: *Evagetes aff crassicornis* etc;

(c) where a specimen could only be ascertained to genus level, it was recorded thus: *Amara* species A etc.

(d) closely-related species which could not be separated were recorded thus: *Nysius thymi / ericae* etc.

The main differences in the literature in nomenclature of species and genera recorded in this study are shown in Table 7.2i.

Table 7.2i: more important nomenclatorial differences for invertebrate species and genera in the literature consulted in the present study.

Nomenclature used in this study	**Synonyms in the literature**
Chorthippus brunneus	*Glyptobothrus brunneus*
Chrysolina sturmi	*Chrysolina goettingensis, C. violacea*
Corymbia rubra	*Leptura rubra*
Ectemnius continuus	*Crabro continuus*
Evylaeus spp	*Lasioglossum spp*
Lycaena tityrus	*Heodes tityrus*
Macronychia spp	*Moschusa spp*
Metopia campestris	*Anicia campestris*
Micraspis 16-punctata	*Tytthaspis 16-punctata*
Psen spp.	*Mimesa spp., Mimumesa spp.*

Invertebrate data were loaded into two Microsoft Excel files (Disk Appendices 3A and 3B) in which each column represents either a single quadrat sample or a general search of a site conducted on a single visit. The files include the number of individuals of each species recorded in each sample. Every quadrat sample also includes some physical and vegetation data taken as described in 4.3 and 4.4. For further analysis these Excel files were subdivided into four sheets, two in Appendix 3A and two in Appendix 3B, in which all invertebrate data are included along with various combinations of quadrat and non-quadrat, vegetation and environmental data.

7.3 Results

7.3.1 Taxonomic composition of the invertebrate fauna

Invertebrates identified to species or genus level are shown in Table 7.3i, in which taxa recorded for each site are indicated by an X.

Table 7.3i: invertebrates identified to genus or species level in the study.

Species	British Sites							Polish Sites				
	West Midlands					East Anglia						
	BT	DS	KE1	KE2	KE3	LA	WW	BO	BR1	BR2	BR3	CR
Araneae												
Aelurillus v-insignitus							X	X	X			
Agelena labyrinthica	X				X				X			
Arctosa perita			X	X								
Enoplognatha ovata						X						
Euophrys aequipes			X		X						X	
Evarcha species A									X			
Heliophanus flavipes											X	
Heliophanus species A									X	X		
Mangora acalypha					X							
Micaria pulicaria			X		X		X					
Neon species A										X		
Neoscona adianta										X		
Pisaura mirabilis			X		X							
Runcinia grammica								X				
Salticus scenicus				X								
Salticus species A								X		X		
Steatoda phalerata									X			
Tetragnatha pinicola			X									
Theridion bimaculatum					X				X			X
Theridion sisyphium					X							
Tibellus species A									X		X	
Xysticus erraticus									X			
Yllenus arenarius								X	X		X	
Zelotes electus							X			X		

Site Key: BT Burlish Top DS Devil's Spittleful / Rifle Range
KE1,2,3 Kinver Edge 1,2,3 LA Lakenheath WW Wangford Warren
BO Bolimów BR1,2,3 Bromierzyk 1,2,3 CR Ciosny Reserve

continued…

Table 7.3i continued…

Species	**British Sites**							**Polish Sites**				
	West Midlands					**East Anglia**						
	BT	**DS**	**KE1**	**KE2**	**KE3**	**LA**	**WW**	**BO**	**BR1**	**BR2**	**BR3**	**CR**
Coleoptera												
Adonia variegata				X	X				X		X	
Amalus scortillum			X	X	X		X					
Amara aenea						X	X					
Amara tibialis			X		X		X					
Amara species A							X					
Amara species B									X			
Apion tenue					X							
Calathus fuscipes					X							
Cetonia aurata											X	
Chrysolina sturmi										X		
Cicindela campestris			X									
Cicindela hybrida								X	X	X	X	X
Cleonus piger								X				
Clivina fossor							X	X				
Coccinella 7-punctata	X	X		X		X	X	X	X	X	X	X
Corymbia rubra										X		
Crypticus quisquilius						X	X	X	X		X	
Cryptocephalus fulvus		X	X	X		X	X					
Dyschirius species A												X
Glischrochilus hortensis		X										
Harpalus anxius						X						
Harpalus latus								X				
Harpalus neglectus											X	
Harpalus picipennis								X				
Harpalus rubripes					X		X					
Harpalus rufipes		X				X						
Harpalus rufitarsis							X					
Melanimon tibialis			X					X	X	X		
Metabletus foveatus		X	X									
Micraspis 16-punctata			X		X				X			
Micrelus ericae					X							
Notoxus monocerus							X					
Olibrus corticalis		X										
Onthophagus ovatus							X					
Otiorrhynchus sulcatus		X										
Oulema melanopus								X				X
Philopedon plagiatus							X					
Phyllopertha horticola						X	X	X	X			
Potosia metallica								X				
Pterostichus melanarius					X							
Rhagonycha fulva						X						
Scymnus frontalis											X	
Sitona striatellus		X										
Strophosomus capitatus										X		
Thea 22-punctata											X	
Typhaeus typhoeus					X							
Crustacea												
Armadillidium species A										X		

continued…

Table 7.3i continued…

Species	British Sites							Polish Sites				
	West Midlands					East Anglia						
	BT	DS	KE1	KE2	KE3	LA	WW	BO	BR1	BR2	BR3	CR
Dermaptera												
Forficula auricularia					X	X						
Dictyoptera												
Ectobius lapponicus										X		
Diptera												
Acrosathe annulata							X					
Anthrax varia								X	X	X	X	
Antipalus varipes								X	X	X		
Chalarus species A										X		
Chrysotoxum bicinctum									X			
Dialineura anilis											X	
Dysmachus trigonus			X	X	X		X					
Eristalis species A								X				
Helophilus pendulus					X							
Holopogon fumipennis									X	X		
Leptarthrus vitripennis									X			
Machimus atricapillus												X
Machimus cingulatus		X		X								
Macronychia griseola									X			
Macronychia polyodon				X	X							
Metopia campestris							X			X		X
Micropeza lateralis		X										
Miltogramma punctata		X										X
Oebalia cylindrica	X									X	X	
Oebalia sachtlebeni										X		
Philonicus albiceps							X					
Piezura boletorum												X
Platycheirus aff fulviventris								X				
Pterella species A									X			
Sarcophaga species A						X						
Senotainia conica	X	X	X									
Syrphus ribesii								X				
Tachina fera					X							
Thereva nobilitata			X		X							
Tolmerus atricapillus / pyragra								X				
Hemiptera												
Adelphocoris lineolatus	X											
Aelia acuminata								X		X		
Alydus calcaratus		X								X		
Cercopis vulnerata				X								
Chorosoma schillingi							X					
Coranus subapterus							X					
Drymus ryeii									X			
Elasmostethus interstinctus			X									
Eurydema oleracea											X	

continued…

Table 7.3i continued…

Species	**British Sites**							**Polish Sites**				
	West Midlands					**East Anglia**						
	BT	**DS**	**KE1**	**KE2**	**KE3**	**LA**	**WW**	**BO**	**BR1**	**BR2**	**BR3**	**CR**
Hemiptera continued…												
Eurygaster maura									X			
Eurygaster testudinaria								X		X		
Heterogaster urticae			X	X								
Ischnocoris angustulus		X										
Macrodema micropterum		X										
Megalonotus sabulicola											X	
Nabis pseudoferus										X		
Neophilaenus minor									X		X	
Notostira species A									X			
Nysius thymi / ericae			X					X	X		X	X
Ortholomus punctipennis							X					
Peritrechus geniculatus									X		X	
Phimodera humeralis									X			
Prostemma aff guttula									X	X		
Pyrrhocoris apterus									X	X	X	
Rhyparochromus vulgaris									X			
Sciocoris cursitans									X	X		
Scolopostethus decoratus									X			
Stenodema calcaratum		X										
Stenodema laevigatum	X								X	X		
Stenodema virens										X		
Stygnocoris fuligineus							X					
Trapezonotus arenarius	X	X	X		X				X	X		
Trigonotylus ruficornis/pulchellus								X	X	X		X
Trigonotylus species A									X			
Hymenoptera												
Ammophila pubescens	X		X		X			X				X
Ammophila sabulosa	X	X	X		X			X	X	X	X	X
Andrena humilis			X									
Andrena labialis					X							
Andrena species A					X							
Andrena (Cnemiandrena) species B								X				
Andrena species C		X										
Anoplius aff infuscatus									X		X	
Apis mellifera		X										
Argygorytes mystaceus			X									
Astata boops												X
Aulacus striatus					X							
Bembix species A									X	X		
Bombus lapidarius						X						
Brachygaster minuta										X		
Cerceris arenaria	X	X			X			X	X			
Cerceris cunicularia												X
Cerceris ruficornis			X		X							
Cerceris rybyensis		X						X				

continued…

Table 7.3i continued…

Species	British Sites							Polish Sites				
	West Midlands					East Anglia						
	BT	DS	KE1	KE2	KE3	LA	WW	BO	BR1	BR2	BR3	CR
Hymenoptera continued..												
Chrysura species A											X	
Crabro peltarius										X		
Crabro scutellatus							X		X			
Crossocerus anxius										X		
Crossocerus imitans												X
Crossocerus wesmaeli	X				X				X	X		
Dasypoda altercator								X			X	
Diodontus minutus					X							
Ectemnius continuus									X		X	
Ectemnius sexcinctus										X		
Elampus panzeri			X		X							
Epeolus cruciger			X									X
Evagetes crassicornis							X	X				
Evagetes aff pectinipes									X	X	X	
Evylaeus brevicornis								X				
Evylaeus lucidulus									X		X	
Evylaeus parvulus								X				
Evylaeus semilucens										X		
Formica cinerea								X	X	X	X	X
Formica cunicularia								X	X	X		
Formica fusca		X	X	X	X							
Formica sanguinea									X			
Gorytes quadrifasciatus											X	
Gorytes quinquecinctus									X			
Gorytes tumidus					X							
Halictus rubicundus									X			
Halictus sexcinctus											X	
Halictus tumulorum					X							
Hedychridium ardens					X		X					
Hedychrum nobile								X	X			
Hedychrum rutilans									X		X	
Lasioglossum punctatissimum					X							
Lasioglossum species A				X	X							
Lasius alienus	X						X	X	X			X
Lasius brunneus					X							
Lasius flavus		X			X	X	X		X		X	X
Lasius niger		X	X		X		X					
Leptothorax crassispinus										X		
Megachile leachella							X					
Megachile maritima	X	X	X	X	X							
Miscophus ater										X		
Myrmica ruginodis			X									
Myrmosa atra atra			X									
Nomada rufipes		X										
Nomada species A									X			
Omalus aeneus									X		X	

continued…

Table 7.3i continued…

Species	**British Sites**							**Polish Sites**				
	West Midlands					**East Anglia**						
	BT	**DS**	**KE1**	**KE2**	**KE3**	**LA**	**WW**	**BO**	**BR1**	**BR2**	**BR3**	**CR**
Hymenoptera continued..												
Oxybelus argentatus						X						
Oxybelus bipunctatus												X
Oxybelus mandibularis										X	X	X
Oxybelus uniglumis	X	X	X	X	X							
Philanthus triangulum										X		
Podalonia affinis							X					
Pompilus cinereus				X	X				X		X	
Ponera coarctata									X			
Priocnemis parvula							X					
Psen equestris				X	X							
Psen lutarius							X					
Psen spooneri							X					
Smicromyrme rufipes								X	X	X	X	
Sphecodes monilicornis		X			X							
Sphecodes aff rufiventris									X	X		
Sphecodes aff spinulosus									X			
Sphecodes species A									X			
Sphecodes species B								X				
Tachysphex obscuripennis									X		X	X
Tachysphex pompiliformis										X		
Tetramorium caespitum			X					X	X	X	X	
Lepidoptera												
Agriphila aff inquinatella									X		X	
Anarsia spartiella					X							
Aphantopus hyperantus									X	X		
Coenonympha pamphilus							X	X	X	X	X	
Cucullia umbratica					X							
Eilema lutarella								X	X			
Eupithecia aff icterata											X	
Glaucopsyche alexis									X			
Issoria lathonia								X				
Lycaena phlaeas	X	X	X				X	X				
Lycaena tityrus										X		
Maniola jurtina					X			X				
Pediasia fascelinella								X				
Phytometra viridaria								X	X		X	
Polyommatus icarus								X				
Pyronia tithonus					X							
Synaphe punctalis								X			X	
Thymelicus sylvestris	X											
Odonata												
Sympetrum striolatum										X		

continued…

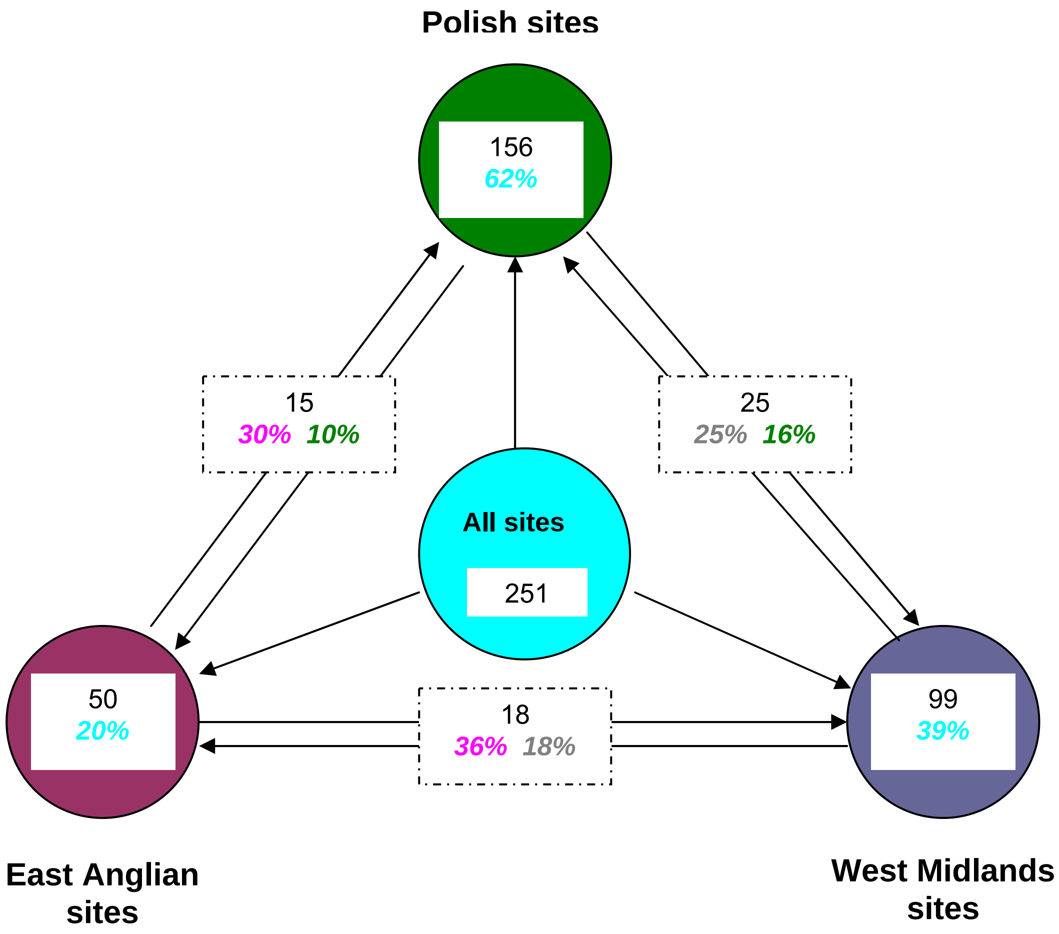
Table 7.3i continued…

Species	British Sites							Polish Sites				
	West Midlands					East Anglia						
	BT	DS	KE1	KE2	KE3	LA	WW	BO	BR1	BR2	BR3	CR
Opiliones												
Opilio saxatilis				X								
Phalangium opilio		X	X		X							
Rilaena triangularis			X									
Orthoptera												
Chorthippus brunneus		X	X	X	X		X	X	X	X		X
Chorthippus parallelus	X		X		X		X	X				
Myrmeleotettix maculatus		X	X	X	X	X	X	X	X	X	X	
Oedipoda coerulescens								X	X	X	X	X
Planipennia												
Myrmeleon formicarius								X	X	X	X	X
Psocoptera												
Stenopsocus aff stigmaticus							X					

Table 7.3i shows a total of 251 taxa distributed among 14 Orders. Of these, 156 taxa were recorded on Polish sites and 131 on British sites. The numbers of taxa shared between the main regions in this study (Poland, West Midlands, East Anglia) are shown in black type in Figure 7.3a, where percentages of a region's fauna which these numbers represent are given in italics, colour-coded by region.

Table 7.3i and Figure 7.3a together suggest that the fauna falls into three distinctly regional elements in much the same way as the flora does (cf Figure 6.3a). Polish sites contain a higher proportion of the total number of invertebrate species than they do of plant species, and the converse is true of the East Anglian and West Midlands regions. Smaller proportions of invertebrate species than plant species are shared between regions, except that the percentage of East Anglian species shared with Poland is the same for both invertebrates and plants (30%).

Figure 7.3a: numbers and percentages of taxa in Poland, the West Midlands and East Anglia compared with the total number of taxa recorded in this study, and showing the numbers and percentages of taxa shared between these regions.



Species of conservation importance: within Britain several species in Table 7.3i are primarily coastal and found in few inland localities[16]: others, especially among the Hymenoptera, have a distinctly southern or south-eastern distributional bias[17] (Edwards, 1997, 1998; Edwards & Telfer, 2001, 2002; Edwards & Broad, 2005). For a number of these species the West Midlands heaths form an isolated extension to their known inland ranges and the findings of the present study give regionally important range extensions. These include *Megachile maritima*, *Cerceris arenaria*, *Cerceris*

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[16] e.g. *Acrosathe annulata*, *Chorosoma schillingi*, *Philonicus albiceps*, *Podalonia affinis*

[17] e.g. *Ammophila pubescens*, *Cerceris* spp., *Crabro scutellatus*, *Megachile maritima*, *Psen spooneri*

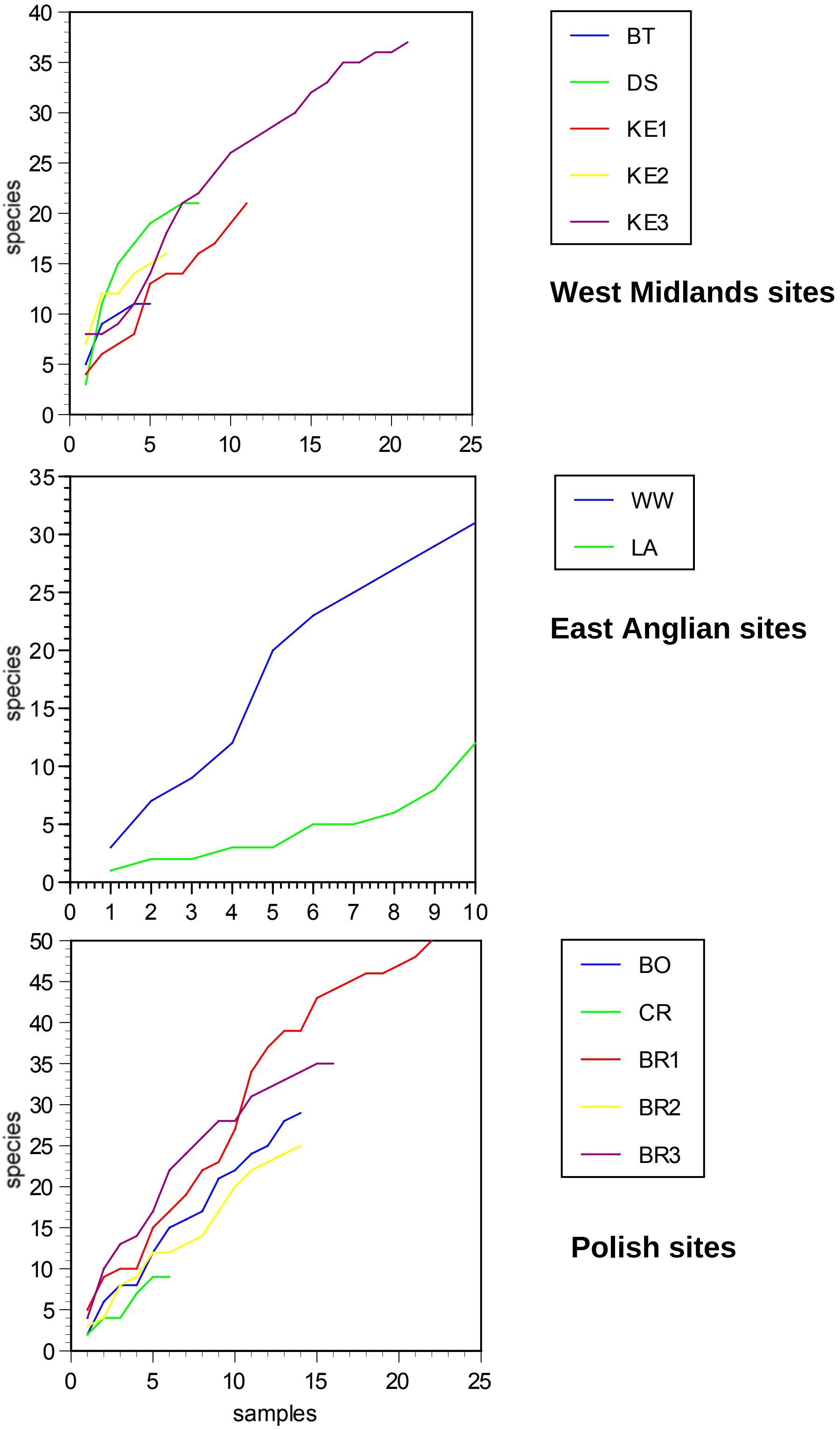
rybyensis and *Ammophila pubescens*; the study sites also consolidate the northernmost distribution range of *Lasius brunneus*; and both *Tetramorium caespitum* and *Cerceris ruficornis* are entirely new records for the West Midlands region. The Brecklands area is well-known as a refugium for many rare and local British invertebrates, and several were recorded in this study: *Chorosoma schillingi*, *Psen spooneri*, *Podalonia affinis*, *Zelotes electus* and *Anisantha annulata* on Wangford Warren, plus *Oxybelus argentatus* at Lakenheath. *Crabro scutellatus* appears to be a new Breckland record. *Crabro scutellatus* is British Red Data Book listed, together with *Lasius brunneus*, *Oxybelus argentatus*, *Podalonia affinis*, *Psen spooneri*, *Megachile leachella* and *Micropeza lateralis* (Falk 1991a, 1991b).

Where distribution and status are given in the literature consulted, most of the Polish invertebrates in Table 7.3i are widespread in that country, though *Crossocerus anxius* and *Crossocerus imitans* appear to be rare species (Noskiewicz & Puławski, 1960). In a wider European context *Neophilaenus minor* is a species of conservation concern, being Red Data Book listed in Germany (Remane *et al*., 1998).

Sampling efficiency: the data in Table 7.3i are derived from several techniques but chiefly from quadrat samples and direct searches (4.5). To evaluate the results of invertebrate sampling it is helpful to know the efficiency of these techniques in assessing a site's fauna. For quadrat sampling, therefore, species-accumulation curves were plotted following Longino (2000). The results are given in Figure 7.3b.

In Figure 7.3b the raw species-accumulation curves are shown for quadrat-only data for all sites, grouped regionally. Quadrat samples were entered chronologically and any new species for a site were added to the running tally of species from previous samples for that site. The results show that quadrat data samples alone do not exhaustively sample the invertebrate fauna, though the graphs produce acceptable trends for all sites except Lakenheath (Site LA). In this case the curve could suggest a highly undersampled fauna (Longino, *loc. cit*.), though the result is more likely to be a

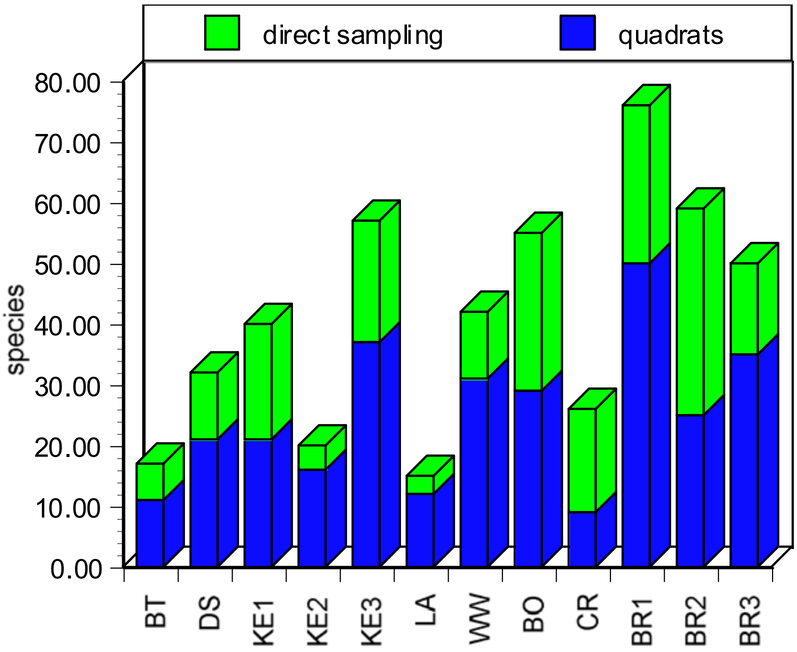
Figure 7.3b: species-accumulation curves for quadrat samples.



consequence of environmental and management factors unique to that site which create conditions inhospitable to invertebrates (Appendix B.1.2).

An indication of the relative contribution of quadrat sampling and direct searches in producing site species inventories is given in Figure 7.3c. In this Figure, "quadrats" shows the number of species for a site recorded by quadrat sampling, irrespective of whether those species also occurred in non-quadrat samples; whereas "direct sampling" shows those additional species only present in non-quadrat samples. A site's invertebrate species total is the sum of the two.

Figure 7.3c: number of species recorded by quadrat sampling and direct sampling for each site.



In this Figure considerable variation between sites is apparent. For Sites KE2 and LA quadrat samples include a high proportion of the total site fauna, and this result favours the above interpretation of the species-accumulation curve for Lakenheath in Figure 7.3b. Quadrat samples also include a reasonably high proportion of the total fauna of Sites BT, DS, WW and BR3, but for the other sites quadrat sampling efficiency is more limited, and for Site CR quadrat samples represent only 35% of the site's invertebrate species richness. It is interesting to note that the tiny *C. canescens* population on Site WW, the smallest in this study, produced the second-highest species total (42) among British sites and sixth highest overall.

These results are instructive. Quadrat sampling was adopted principally to enable the correlation of invertebrate data with vegetation and environmental factors, and not to provide a faunal inventory for the study sites (4.5.5). However, results obtained through such correlations need to be interpreted in the context of how representative those data are for the sites concerned. Comparisons of the data with other faunal studies on *C. canescens* habitats and xerothermic grasslands also need to bear in mind those authors' aims and methodologies.

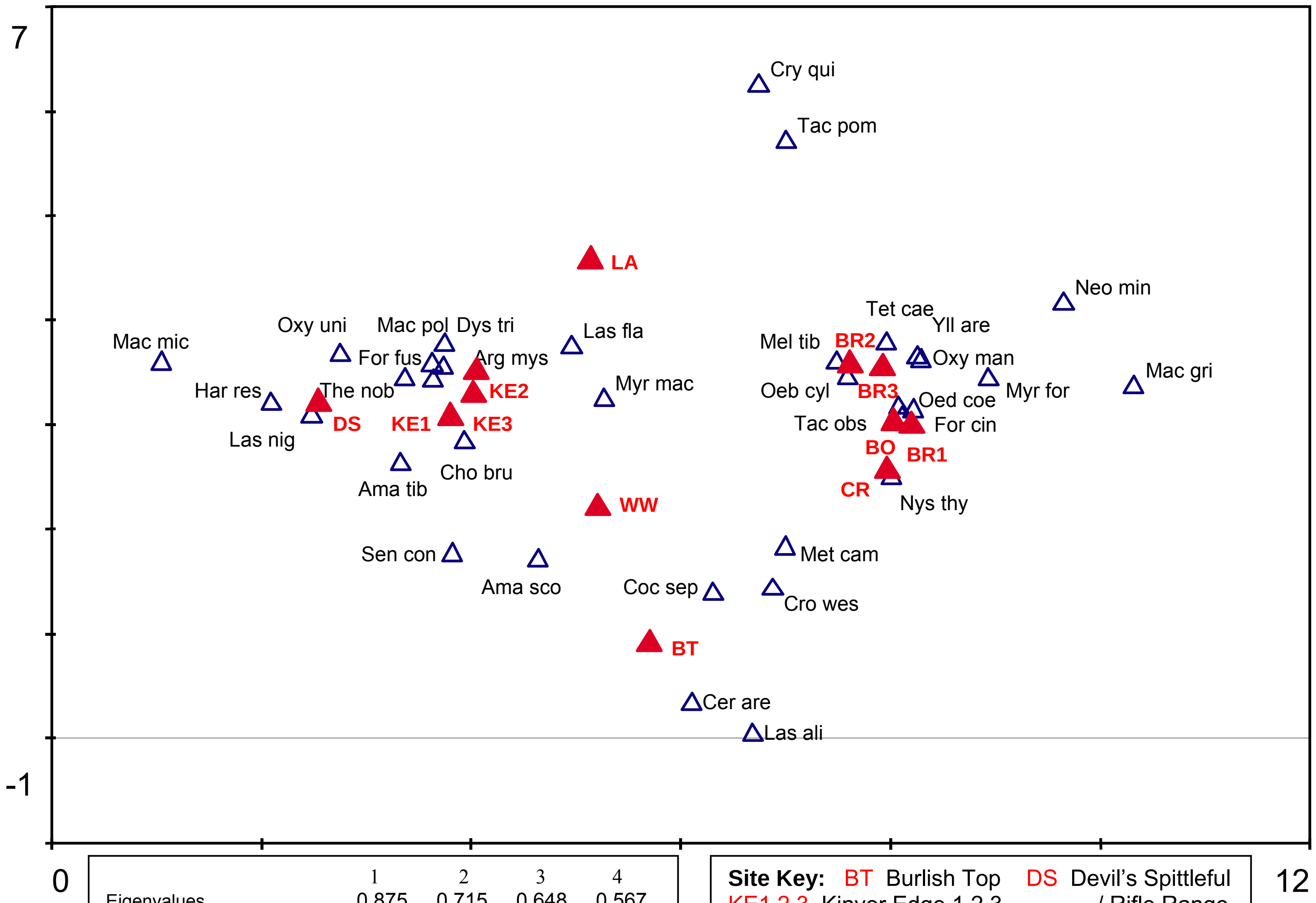
7.3.2 Relationship of the invertebrate fauna to sites

The foregoing discussion of sampling efficiency touches directly upon the relationship of invertebrate species to sites. To test this relationship a CANOCO analysis was carried out. Using the input file Disk Appendix 3B Sheet 1 the data were transformed (Y = log (1xY+1) and all species included in an exploratory DCA analysis. This initially produced one sample (no. 104) which was exceptionally different from all others (eigenvalue 1.000, gradient 0.000), probably because it contained just a single invertebrate species (*Heliophanus* species A): this species was found in no other sample. This sample was therefore deleted, leaving 125 samples and 251 species in the analysis. The twelve study sites were input as environmental data. The resulting log gave very long gradients (9.621, 7.307, 7.747 and 7.848 for axes 1 to 4) suggesting that the data were unimodially distributed and that DCA was the appropriate analysis.

The output diagram is Figure 7.3d, which shows the 34 species produced by applying a 4% fit. In this diagram the five Polish sites are clustered together at one end of the first axis, with Kinver Edge sites and Devil's Spittleful at the opposite end; Lakenheath, Wangford Warren and Burlish Top are placed more centrally and are differentiated along the second axis. The distribution of invertebrate species along the axes is for the most part strongly correlated with the sites or regions of their greatest abundance: for example *Macrodema micropterum*, which lies at one end of the first axis, was found only at site DS but appeared in some numbers in quadrat samples there; and *Macronychia griseola* showed a similar pattern at Site BR1. Other invertebrates characteristic of West Midlands sites (*Oxybelus uniglumis*, *Macronychia polyodon*, *Lasius niger*, *Harpalus rufipes*, *Thereva nobilitata* etc) and of Polish sites (*Neophilaenus minor*, *Myrmeleon formicarius*, *Oedipoda coerulescens*, *Formica cinerea* etc) are placed accordingly, and species found with equal abundance across two or three regions tend to be centrally placed (*Coccinella 7-punctata*, *Cerceris arenaria*, *Myrmeleotettix maculata*, *Lasius flavus* etc). The analysis is not entirely about sites, however, for one or two species do not fit this pattern: *Tachysphex pompiliformis* and *Crypticus quisquilius* do not share a similar site distribution but are associated in Figure 7.3d towards one end of the second axis. These species apart, however, much in this Figure suggests a strong correlation between species and sites on the first axis, and a lesser but still clear correlation on the second axis. The Figure appears to indicate which are the main invertebrate species responding to site influence. Why *Crypticus quisquilius* and *Tachysphex pompiliformis* are placed together at the top of the diagram is unclear, as they occupy very different ecological niches: *Crypticus quisquilius* is a detritivorous beetle of the ground layer and *Tachysphex pompiliformis* a predator on grasshoppers.

Figure 7.3d was produced from quadrat only samples. A further analysis of quadrat plus non-quadrat data from Disk Appendix 3A Sheet 1 (DCA analysis) gave a very similar picture to Figure 7.3d, continuing to separate British from Polish sites and to distribute species according to their regions of greatest abundance. Its similarity to Figure 7.3d implies that the general (i.e. non-quadrat) data were not affecting the analyses and that the invertebrate data

Figure 7.3d: Detrended Correspondence Analysis (DCA) showing relationship of invertebrate species to sites.



	1	2	3	4
Eigenvalues	0.875	0.715	0.648	0.567
Spp-environment correlations	0.960	0.701	0.507	0.571
Cumulative % variance				
of species data	3.4	6.1	8.6	10.8
of spp- environment relation	17.0	23.1	0.0	0.0

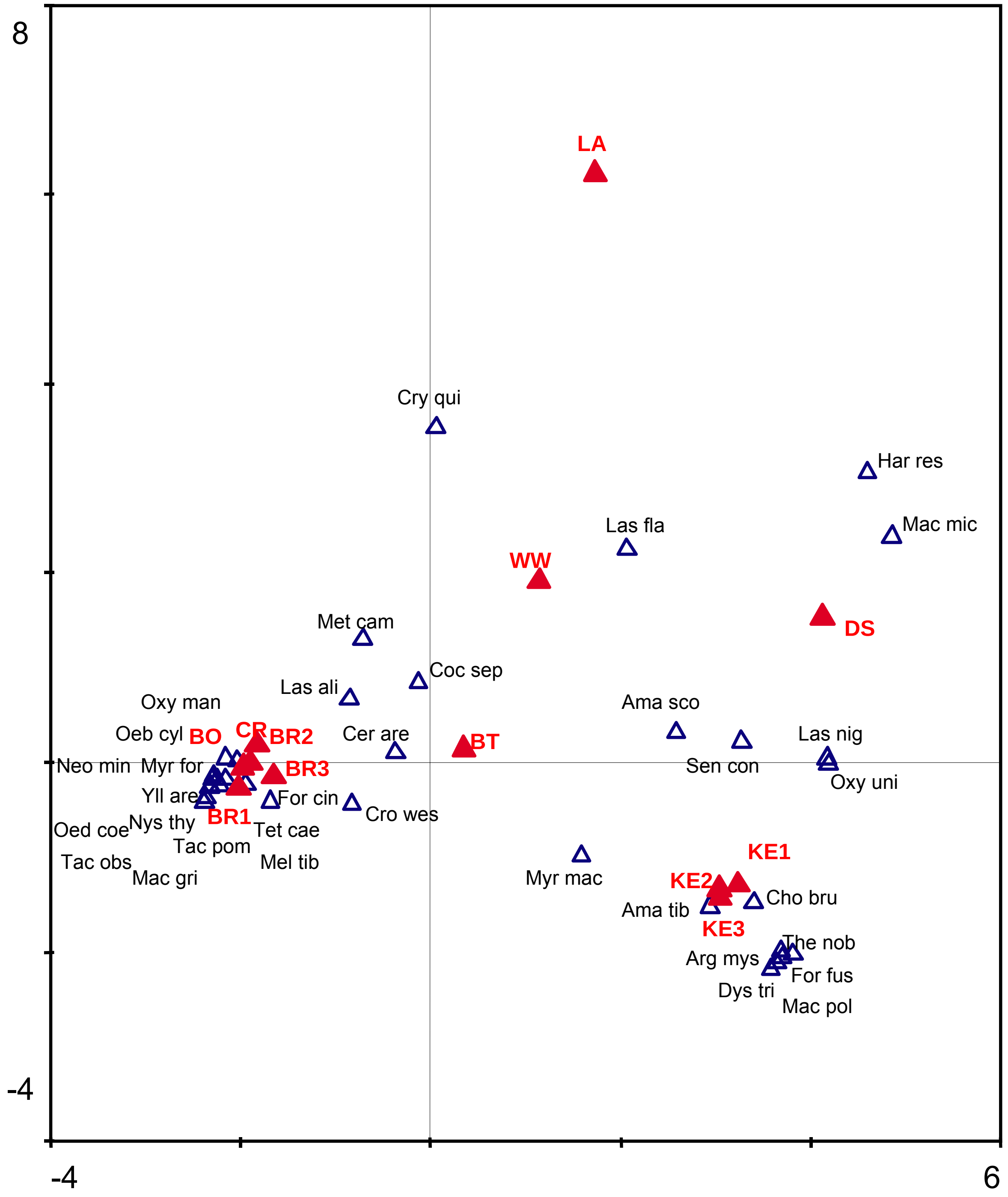
Site Key:

BT	Burlish Top	DS	Devil's Spittleful / Rifle Range
KE1,2,3	Kinver Edge 1,2,3		
LA	Lakenheath	WW	Wangford Warren
BO	Bolimów	BR1,2,3	Bromierzyk 1,2,3
CR	Ciosny Reserve		

Key to abbreviations:

Ama sco	*Amalus scortillum*
Ama tib	*Amara tibialis*
Arg mys	*Argygorytes mystaceus*
Cer are	*Cerceris arenaria*
Cho bru	*Chorthippus brunneus*
Coc sep	*Coccinella 7-punctata*
Cro wes	*Crossocerus wesmaeli*
Cry qui	*Crypticus quisquilius*
Dys tri	*Dysmachus trigonus*
For cin	*Formica cinerea*
For fus	*Formica fusca*
Har res	*Harpalus rufipes*
Las ali	*Lasius alienus*
Las fla	*Lasius flavus*
Las nig	*Lasius niger*
Mac gri	*Macronychia griseola*
Mac mic	*Macrodema micropterum*
Mac pol	*Macronychia polyodon*
Mel tib	*Melanimon tibialis*
Met cam	*Metopia campestris*
Myr for	*Myrmeleon formicarius*
Myr mac	*Myrmeleotettix maculatus*
Neo min	*Neophilaenus minor*
Nys thy	*Nysius thymi/ericae*
Oeb cyl	*Oebalia cylindrica*
Oed coe	*Oedipoda coerulescens*
Oxy man	*Oxybelus mandibularis*
Oxy uni	*Oxybelus uniglumis*
Sen con	*Senotainia conica*
Tac obs	*Tachysphex obscuripennis*
Tac pom	*Tachysphex pompiliformis*
Tet cae	*Tetramorium caespitum*
The nob	*Thereva nobilitata*
Yll are	*Yllenus arenarius*

Figure 7.3e: Canonical Correspondence Analysis (CCA) of quadrat only data showing invertebrates constrained by site with no elimination of regional effect.



Key to abbreviations: Ama sco *Amalus scortillum* Ama tib *Amara tibialis* Arg mys *Argygorytes mystaceus*
Cer are *Cerceris arenaria* Cho bru *Chorthippus brunneus* Coc sep *Coccinella 7-punctata*
Cro wes *Crossocerus wesmaeli* Cry qui *Crypticus quisquilius* Dys tri *Dysmachus trigonus*
For cin *Formica cinerea* For fus *Formica fusca* Har res *Harpalus rufipes* Las ali *Lasius alienus*
Las fla *Lasius flavus* Las nig *Lasius niger* Mac gri *Macronychia griseola* Mac mic *Macrodema micropterum*
Mac pol *Macronychis polyodon* Mel tib *Melanimon tibialis* Met cam *Metopia campestris*
Myr for *Myrmeleon formicarius* Myr mac *Myrmeleotettix maculatus* Neo min *Neophilaenus minor*
Nys thy *Nysius thymi/ericae* Oeb cyl *Oebalia cylindrica* Oed coe *Oedipoda coerulescens*
Oxy man *Oxybelus mandibularis* Oxy uni *Oxybelus uniglumis* Sen con *Senotaenia conica*
Tac obs *Tachysphex obscuripennis* Tac pom *Tachysphex pompiliformis* Tet cae *Tetramorium caespitum*
The nob *Thereva nobilitata* Yll are *Yllenus arenarius*

	1	2	3	4
Eigenvalues	0.850	0.640	0.597	0.510
Spp-environment correlations	0.990	0.953	0.956	0.933
Cumulative % variance				
of species data	3.3	5.7	8.1	10.0
of spp-environment relation	18.2	32.0	44.8	55.7

Site Key: BT Burlish Top DS Devil's Spittleful
KE1,2,3 Kinver Edge 1,2,3 / Rifle Range
LA Lakenheath WW Wangford Warren
BO Bolimów BR1,2,3 Bronierzyk 1,2,3
CR Ciosny Reserve

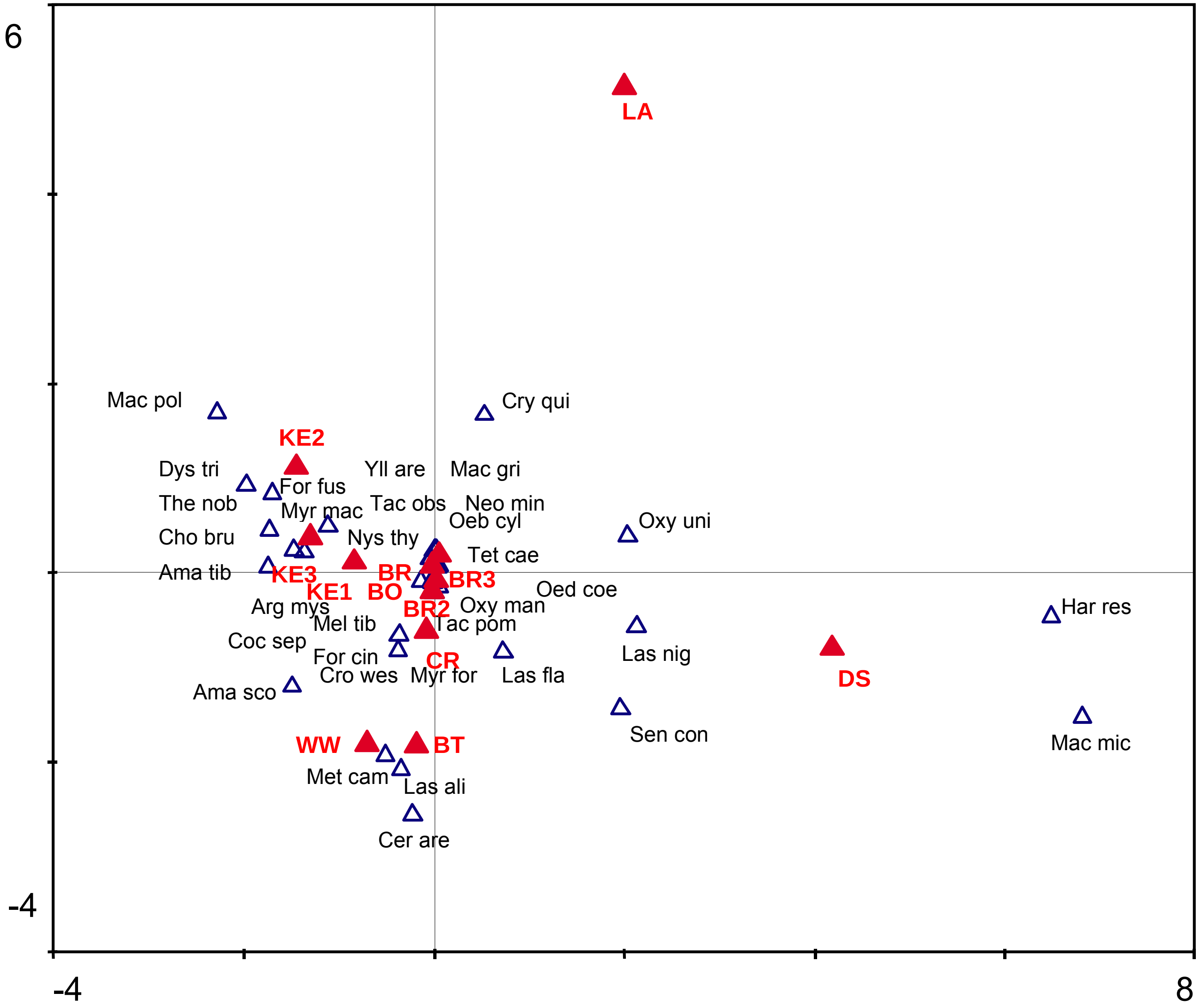
were sufficiently represented by the quadrat only data; this despite the reasonably high proportion of species not occurring in quadrats (Figure 7.3c).

Using Disk Appendix 3B Sheet 1 a further investigation was made to discover how the invertebrate data are constrained by sites by direct gradient analysis. Sample 104 was again found to be exceptionally different from the rest and was omitted. In the first instance a CCA was produced in which all sites were input, though four did not produce significance when tested in Monte Carlo permutations (Sites BR2, BR3, CR, B0, producing F-values of 1.62 and lower). The output diagram is Figure 7.3e, in which Polish sites form one cluster and Kinver Edge sites a second cluster, with the remaining four sites scattered along axis 1, and Site BT showing some tendency towards the Polish sites. The distribution of the invertebrate fauna has a similar rationale to that of the DCA (Figure 7.3d), with some centrally placed species being distributed equally across two or three regions (*Crypticus quisquilius*, *Myrmeleotettix maculatus*, *Amalus scortillum*). In this diagram *Crypticus quisquilius* is no longer associated with *Tachysphex pompiliformis*.

A further analysis of the same input data was made with the three regions input as covariables in an attempt to eliminate regional influence. The partial CCA is shown in Figure 7.3f. In this the Polish and Kinver Edge sites lie close together; Sites WW and BT show some relationship with each other; Site DS is separated along the first axis; and Site LA lies at the opposite end of the second axis to Site WW, its Breckland neighbour. The groupings of invertebrate species again largely follow their sites of greatest abundance, with the same species as before located towards the ends of the two axes (*Macrodema micropterum*, *Harpalus rufipes*, *Cerceris arenaria*, *Lasius alienus*, *Crypticus quisquilius*). Figure 7.3f reflects Figure 7.3a in suggesting that Kinver Edge sites may have more in common with the Polish sites than with East Anglian sites in terms of their invertebrate fauna.

These analyses of the relationship between invertebrates and sites consistently produce two site clusters, comprising the three Kinver Edge sites and the five Polish sites. The remaining sites (BT, DS, WW and LA) are

Figure 7.3f: partial Canonical Correspondence Analysis (CCA) showing invertebrates quadrat data constrained by site, with regional effect as a covariable.



Key to abbreviations:

Ama sco	*Amalus scortillum*
Ama tib	*Amara tibialis*
Arg mys	*Argygorytes mystaceus*
Cer are	*Cerceris arenaria*
Cho bru	*Chorthippus brunneus*
Coc sep	*Coccinella 7-punctata*
Cro wes	*Crossocerus wesmaeli*
Cry qui	*Crypticus quisquilius*
Dys tri	*Dysmachus trigonus*
For cin	*Formica cinerea*
For fus	*Formica fusca*
Har res	*Harpalus rufipes*
Las ali	*Lasius alienus*
Las fla	*Lasius flavus*
Las nig	*Lasius niger*
Mac gri	*Macronychia griseola*
Mac mic	*Macrodema micropterum*
Mac pol	*Macronychis polyodon*
Mel tib	*Melanimon tibialis*
Met cam	*Metopia campestris*
Myr for	*Myrmeleon formicarius*
Myr mac	*Myrmeleotettix maculatus*
Neo min	*Neophilaenus minor*
Nys thy	*Nysius thymi/ericae*
Oeb cyl	*Oebalia cylindrica*
Oed coe	*Oedipoda coerulescens*
Oxy man	*Oxybelus mandibularis*
Oxy uni	*Oxybelus uniglumis*
Sen con	*Senotaenia conica*
Tac obs	*Tachysphex obscuripennis*
Tac pom	*Tachysphex pompiliformis*
Tet cae	*Tetramorium caespitum*
The nob	*Thereva nobilitata*
Yll are	*Yllenus arenarius*

	1	2	3	4
Eigenvalues	0.614	0.523	0.474	0.353
Spp-environment correlations	0.951	0.936	0.910	0.913
Cumulative % variance:				
of species data	2.5	4.6	6.6	8.0
of spp-environment relation	19.0	35.2	49.8	60.7

Site Key: BT Burlish Top DS Devil’s Spittleful / Rifle Range
KE1,2,3 Kinver Edge 1,2,3
LA Lakenheath WW Wangford Warren
BO Bolimów BR1,2,3 Bromierzyk 1,2,3
CR Ciosny Reserve

variously distributed, with the two East Anglian sites (WW and LA) showing little relationship with each other. This distributional pattern might be a product of less complete data sets for these smaller sites – though Figures 7.3b and 7.3c suggest that, with the possible exception of Site LA, they are not very undersampled. Site LA is notable in remaining quite different from the other sites in this analysis, a result which reflects the vegetational analysis in Chapter 6. Figures 7.3d to 7.3f produce clusters of invertebrate species which are difficult to analyse in terms of their ecological relationships: further analyses to seek to clarify such relationships are therefore carried out in the following sections.

7.3.3 Relationship of the invertebrate fauna to vegetation

From the literature it appears that *C. canescens* provides a pabulum for few invertebrate species, and a summary of known or suspected associations is shown in Table 7.3ii.

This Table largely represents European data, as only *Anerastia lotella* is recorded as feeding on *C. canescens* in a British context (University of York, 2001): the site of this record is not stated and may be coastal. None of the species in Table 7.3ii is monophagous on *C. canescens*, and all utilise other grasses, especially *Agrostis* spp and *Festuca* spp. In the present study *Coenonympha pamphilus* and *Neophilaenus minor* were recorded on *C. canescens* sites, and *Trigonotylus pulchellus* probably so, though specimens could not be separated from *Trigonotylus ruficornis* with the available literature. On one occasion a specimen of *Trigonotylus pulchellus / ruficornis* was observed feeding on the sap of a *C. canescens* culm on Site BR3.

Table 7.3ii: invertebrate species recorded or suspected as feeding upon *Corynephorus canescens* in the literature.

Species	**Order**	**Family**	**Method**	**Authority**
Coenonympha pamphilus	Lepidoptera	Nymphalidae Satyrinae	Larva on leaves	Eliasson *et al.*, 2005
Hipparchia semele	“	“	“	Tuzov *et al.*, 1997
Elachista bifasciella	“	Elachistidae	Larva within shoots	Savela, 2006
Elachista dispilella	“	“	“	“
Elachista gregori?	“	“	“	“
Crambus ericellus	“	Pyralidae	Larva on roots & stems	“
Anerastia lotella	“	“	“	University of York (2001)
Trigonotylus pulchellus	Hemiptera Heteroptera	Miridae	Larva and adult on leaf tissue, seeds and flowers	Carvalho & Wagner, 1957; Viskens, 2004
Amblytylus albidus	“	“	As above?	Gorczyca, 1994
Neophilaenus minor	Hemiptera Homoptera	Cercopidae	Larva (and adult?) on xylem sap of culms	Nickel & Romane (2002)
Recilia horvathi?	“	Cicadellidae	Larva (and adult?) on phloem sap?	“
Psammotettix albomarginatus?	“	“	“	“
Psammotettix excisus	“	“	“	“

A few other phytophagous invertebrates recorded in this study are strongly associated with the characteristic plant species of the *C. canescens* habitat as identified in Chapter 6. These include *Lycaena phlaeas, Lycaena tityrus* and *Ortholomus punctipennis* (larval foodplant = *Rumex acetosella*) and *Eilema lutarella* (larval foodplant = *Cladonia* spp.): in this study *Lycaena phlaeas* was observed ovipositing on *Rumex acetosella* on Sites KE1 and BO. *Polytrichum piliferum* was the probable foodplant of *Synaphe punctalis* on Site BR3. One species which occurred regularly on

British sites, the distinctive weevil *Amalus scortillum*, may well prove to be associated with *Rumex acetosella*, though the literature gives *Polygonum* spp. as its typical pabulum (Cooter, 1991): no *Polygonum* species was present on any of the study sites.

Some larval foodplants which are lesser components of the *C. canescens* habitat were found in this study with typical herbivores (e.g. *Olibrus corticalis* on *Senecio* spp.); and a number of species associated with plants of later successional and transitional habitat stages also occurred, e.g. *Strophosomus capitatus* (foodplant = *Betula* spp.), *Micrelus ericae* (foodplant = *Calluna vulgaris*), and *Sitona striatellus* and *Anarsia spartiella* (foodplants = *Ulex* spp.*, Cytisus scoparius*). Another group of species in Table 7.3i are polyphagous[18], including several Hemiptera which are seed-eaters[19]. These were typically found foraging on the ground layer, though *Nysius thymi / ericae* was not infrequently taken on *C. canescens* inflorescences. This group of generalist seed-eaters was much more frequent on Polish than on British sites.

To explore the relationship between the invertebrate fauna and plant species composition of the sites CANOCO analyses were carried out on two data sets: nominal non-quadrat data (Disk Appendix 3A Sheet 2) containing all species recorded for each site, and quantitative quadrat data (Disk Appendix 3B Sheet 1) containing only those species recorded in quadrat samples.

The ***non-quadrat data*** input file comprises twelve samples (one per site),152 plant taxa (i.e. all taxa except the unidentified bryophyte sp.) and 251 invertebrate taxa. No data transformation was made as the input data are nominal. Because of the great imbalance between number of species and number of samples a very high degree of collinearity resulted from the exploratory DCA and PCA analyses. Several attempts were made to reduce collinearity: first by thinning the data to 49 plant taxa (input as the environmental variable) and 53 invertebrate taxa (input as species data) by

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[18] e.g. *Chorthippus* spp., *Otiorrhynchus sulcatus*, *Phyllopertha horticola*

[19] e.g. *Eurydema oleracea*, *Nysius* spp., *Stenodema* spp., *Trapezonotus arenarius*.

applying a 25% fit; then by using Monte Carlo permutations in a CCA, which reduced the number of significant plant species to three but still produced high levels of collinearity; then by removing all collinear species and selecting six plant species common to all three regions studied. Both DCA and CCA analyses were tried inputting the selected six plant species as environmental variables; in the latter case the testing of significance through Monte Carlo permutations gave only *Coelocaulon aculeatum* as significant. It was finally concluded that no satisfactory analysis could be carried out on the non-quadrat input data file.

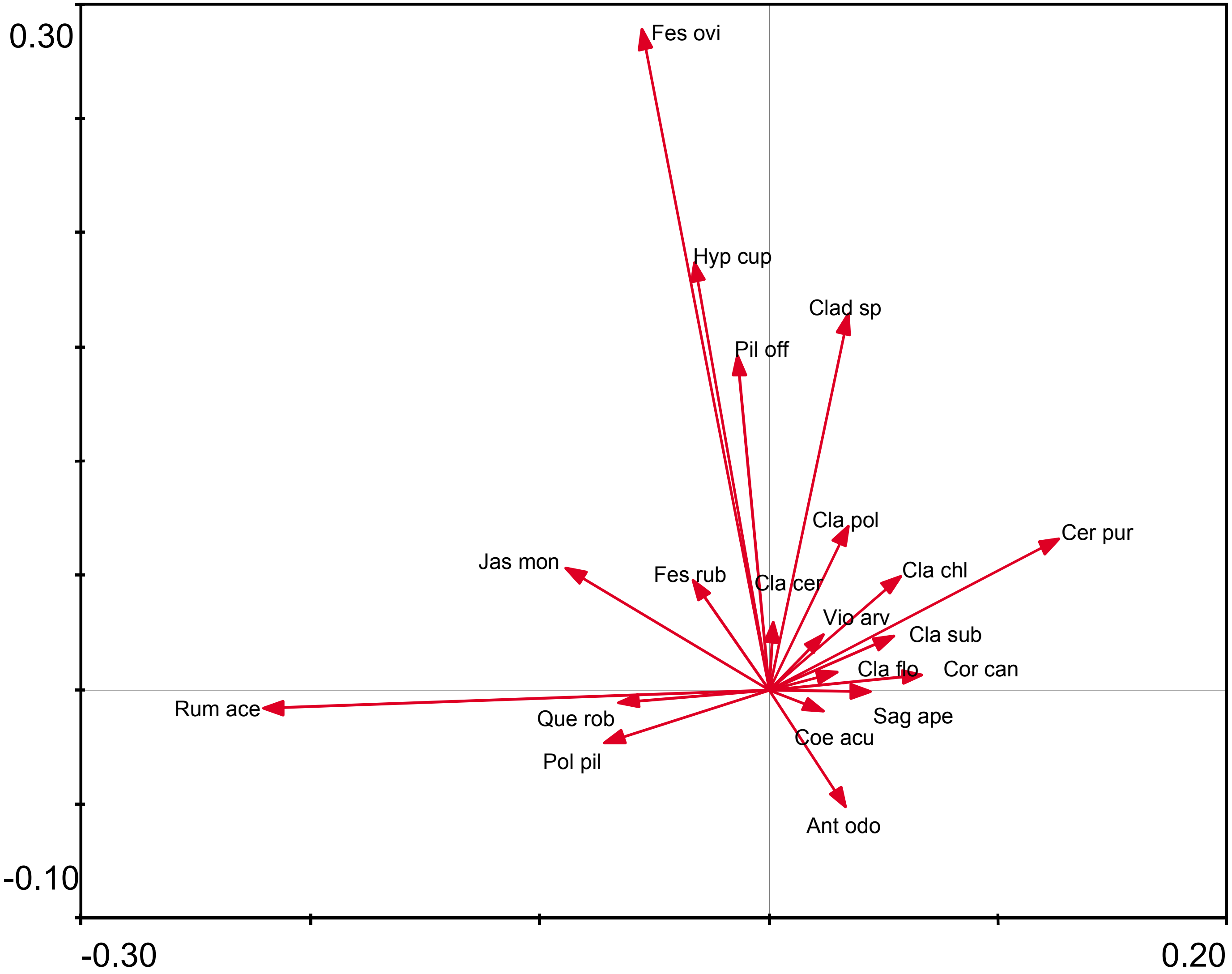
The relationship of invertebrates and plants in ***quadrat samples*** was made using Disk Appendix 3B Sheet 1. To try to nullify the strong influence of the three regions a limited number of plant species was sought; and as only 6 species were common to all three regions, a selection was made of 20 species common to Britain and Poland, i.e. all plant species found in both countries except *Cytisus scoparius* (deemed to be associated with the transition phase of the habitat) and an undetermined bryophyte species. Invertebrate data were log transformed, and after the exploratory DCA threw up the same exceptionally different sample (no. 104) as in earlier analyses (7.3.2) this was deleted to leave 125 samples. The data sets resulting from these procedures were then used for the following analyses.

To explore the ***relationship between invertebrate species and plant species*** an initial DCA was produced with the invertebrate data and the selected 20 plant species input. The gradients for axes 1 to 3 were long – 9.621, 7.307, 7.747 – suggesting that DCA was the appropriate analysis. Although sites were not part of this analysis and plant data were selected to reduce regional effect the resulting diagram still showed a distribution of invertebrate species very similar to that in Figure 7.3d. The selected plant species were next tested via a DCA analysis to investigate how they are distributed according to the invertebrate data. The output diagram is Figure 7.3g, in which invertebrate data are not shown but affect the analysis. The Figure represents the first two axes in a DCA of the invertebrate data. The diagram shows the vectors for the 20 selected plant species treated as environmental variables in an indirect gradient analysis. Thus *Rumex acetosella* is associated with low scores on the invertebrate axis 1 and *C. canescens* is associated with high scores on this axis. *Festuca ovina*, *Hypnum cupressiforme*, *Pilosella officinarum* and *Cladonia* species are associated with high scores on the second invertebrate axis. This Figure may be interpreted together with Figure 7.3d, which is the DCA from the same data and shows the distribution of the invertebrate species. By inspecting these two Figures together the plant species on the left of the first axis in Figure 7.3g (*Rumex acetosella*, *Quercus robur*, *Polytrichum piliferum* and *Jasione montana*) appear to be associated with the invertebrates interpreted as linked to West Midlands sites (7.3.2), while *C. canescens* and *Ceratodon purpureus* are associated with invertebrates linked to Polish sites. The oddly placed invertebrates in Figure 7.3d – *Crypticus quisquilius* and *Tachysphex pompiliformis* – are associated with *Festuca ovina*, *Hypnum cupressiforme*, *Pilosella officinarum* and *Cladonia* species, while *Cerceris arenaria* and *Lasius alienus* are associated with *Anthoxanthum odoratum*. This analysis does link *Neophilaenus minor* to its pabulum *C. canescens* (Table 7.3ii) as well as to Polish sites, and the position of *Amalus scortillum* suggests a relationship with *Rumex acetosella* as speculated above. Few invertebrates in Figure 7.3d are herbivores, however, and this limits the possibility of direct associations between invertebrates and plant species in the analysis. The anomalous position of *Crypticus quisquilius* and *Tachysphex pompiliformis* in Figure 7.3d is still not easily explained, nor are *Cerceris arenaria* and *Lasius alienus* known from the literature to have a relationship with *Anthoxanthum odoratum*. It is felt, therefore, that relationships between invertebrates and plant species implied by a comparison of Figures 7.3d and 7.3g are indirect ones, relating more to other features represented by the vegetation (e.g. sward height or the stage of the *C. canescens* habitat) than to the plant species themselves.

The analysis then proceeded to explore how the invertebrate data are directly constrained by the plant species data in a CCA. A Monte Carlo permutations test was used to identify those plant species showing a significant relationship with the entomological data. Four plant species – *Festuca ovina*, *Hypnum cupressiforme*, *Cladonia* species and *Rumex acetosella* – showed a significant relationship. The analysis produced high species-environment correlations and cumulative percentage variance of species-environment relations.

The output diagram is Figure 7.3h. In a CCA analysis the trends in the data are directly attributable to the environmental variable, and though some elements of regionality may still appear in the distribution of the invertebrates the constraining influence is that of the four chosen plant species. In Figure 7.3h the first axis shows that the strongest trend attributable to the plant species is associated with an increase or decrease in *Festuca ovina* and *Hypnum cupressiforme*. Most of the invertebrates in the diagram decrease with an increase in *Festuca ovina* and *Hypnum cupressiforme*, but *Crypticus quisquilius* and to a lesser extent *Oxybelus uniglumis* and *Lasius flavus* increase. The next strongest trend is associated with an increase in *Cladonia* species and a decrease in *Rumex acetosella*. *Cladonia* species probably represents the most open vegetation type (it appears in the second phase of the Corynephoretum as defined in 5.3.4) as the associated invertebrates include several typically found in bare areas still present in the second stage of the Corynephoretum (e.g. *Oedipoda coerulescens*, *Tetramorium caespitum*, *Myrmeleon formicarius*, *Oebalia cylindrica*). The association of *Crypticus quisquilius* and *Lasius flavus* with the development of a grassy *Festuca ovina* sward is consistent with the ecology of these species, though *Oxybelus uniglumis* would not seem to fit as well into this interpretation. *Rumex acetosella* probably represents a further trend in vegetation development as it is most abundant in the third stage of the Corynephoretum in somewhat less fertile conditions than *Festuca ovina*. Several of the invertebrates most associated with *Rumex acetosella* in Figure 7.3h might be expected from their known ecology to appear in the later mature stage of the *C. canescens* habitat (e.g. *Coccinella 7-punctata*, *Chorthippus brunneus*, *Formica fusca*, *Thereva nobiliata*), but the relationship of other species in this diagram with a more closed vegetation type is less certain from the literature. In this analysis *Amalus scortillum* again shows a clear relationship with *Rumex acetosella*.

Figure 7.3g: Detrended Correspondence Analysis (DCA) of invertebrate quadrat data showing the distribution of key plant species associated with the invertebrate data in indirect gradient analysis.

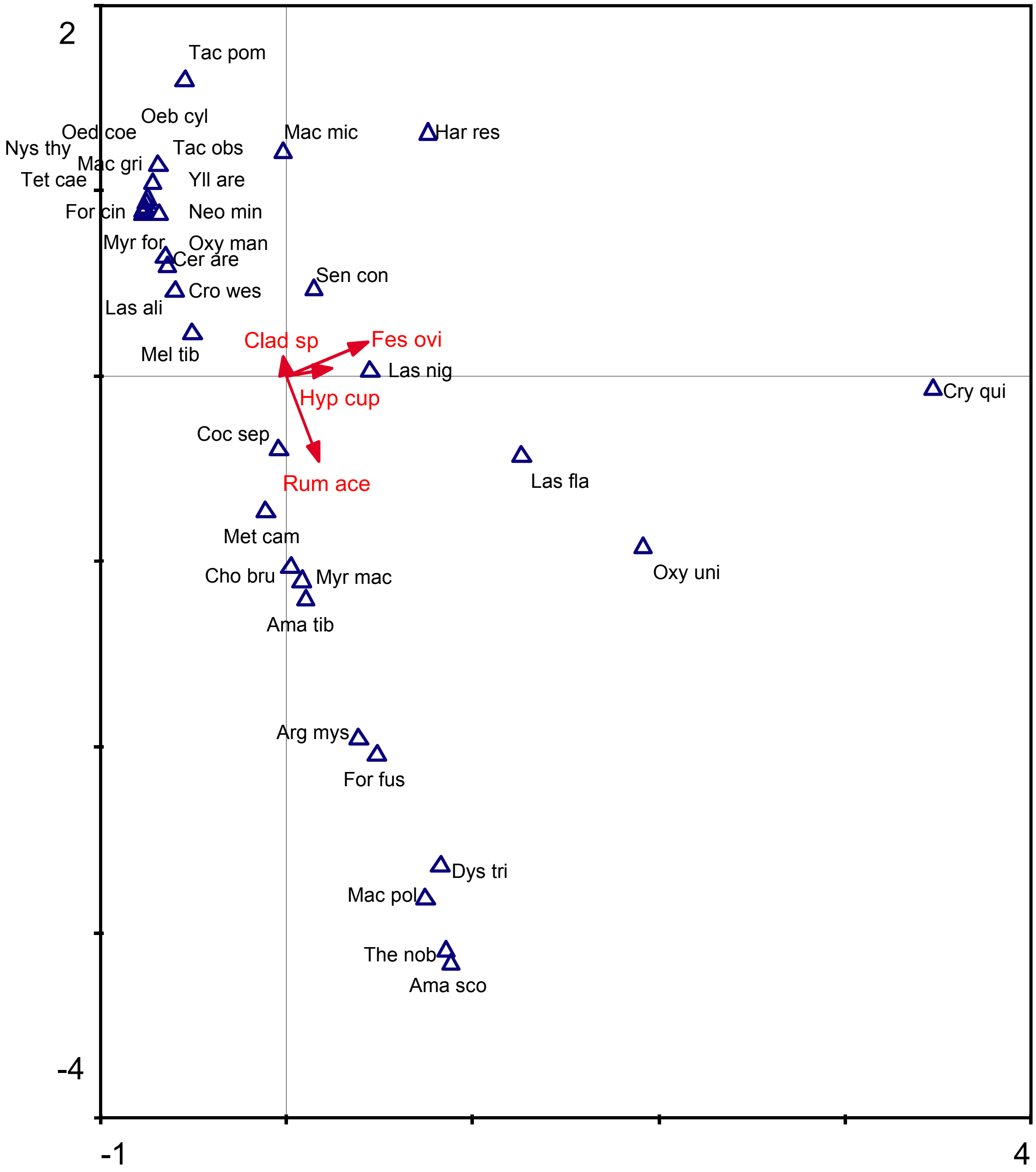


Key to abbreviations:

Ant odo	*Anthoxanthum odoratum*
Cer pur	*Ceratodon purpureus*
Cla cer	*Cladonia cervicornis*
Cla chl	*Cladonia chlorophaea*
Clad sp	*Cladonia* species
Cla flo	*Cladonia floerkeana*
Cla pol	*Cladonia polydactyla*
Cla sub	*Cladonia subulata*
Coe acu	*Coelacaulon aculeatum*
Cor can	*Corynephorus canescens*
Fes ovi	*Festuca ovina*
Fes rub	*Festuca rubra*
Hyp cup	*Hypnum cupressiforme*
Jas mon	*Jasione montana*
Pil off	*Pilosella officinarum*
Pol pil	*Polytrichum piliferum*
Que rob	*Quercus robur*
Rum ace	*Rumex acetosella*
Sag ape	*Sagina apetala*
Vio arv	*Viola arvensis*

	1	2	3	4
Eigenvalues	0.875	0.715	0.648	0.567
Spp-environment correlations	0.960	0.701	0.507	0.571
Cumulative % variance:				
of species data	3.4	6.1	8.6	10.8
of spp-environment relation	17.0	23.1	0.0	0.0

Figure 7.3h: Canonical Correspondence Analysis (CCA) of invertebrate quadrat data constrained by selected significant plant species.



Key to abbreviations: Ama sco *Amalus scortillum* Ama tib *Amara tibialis*
Arg mys *Argygorytes mystaceus* Cer are *Cerceris arenaria* Cho bru *Chorthippus brunneus*
Coc sep *Coccinella 7-punctata* Cro wes *Crossocerus wesmaeli* Cry qui *Crypticus quisquilius*
Dys tri *Dysmachus trigonus* For cin *Formica cinerea* For fus *Formica fusca*
Har res *Harpalus rufipes* Las ali *Lasius* alienus Las fla *Lasius flavus* Las nig *Lasius niger*
Mac gri *Macronychia griseola* Mac mic *Macrodema micropterum* Mac pol *Macronychia polyodon*
Mel tib *Melanimon tibialis* Met cam *Metopia campestris* Myr for *Myrmeleotettix formicarius*
Myr mac *Myrmeleotettix maculatus* Neo min *Neophilaenus minor* Nys thy *Nysius thymi/ericae*
Oed coe *Oedipoda coerulescens* Oeb cyl *Oebalia cylindrica* Oxy man *Oxybelus mandibularis*
Oxy uni *Oxybelus uniglumis* Sen con *Senotainia conica* Tac obs *Tachyspex obscuripennis*
Tac pom *Tachysphex pompiliformis* Tet cae *Tetramorium caespitum* The nob *Thereva nobilitata*
Yll are *Yllenus arenaria*
Clad sp *Cladonia* species Fes ovi *Festuca ovina* Hyp cup *Hypnum cupressiforme*
Rum ace *Rumex acetosella*

	1	2	3	4		1	2	3	4
Eigenvalues	0.636	0.535	0.377	0.353	Cumulative % variance				
Spp-environment correlations	0.920	0.872	0.851	0.822	of species data	2.5	4.5	6.0	7.3
					of spp-environment relation	33.5	61.6	81.4	100.0

The final analysis of the relationship between invertebrates and plants explored the importance of ***vegetation structure***. For each quadrat sample sward heights measured as described in 4.4.2.1 were reduced to six classes:

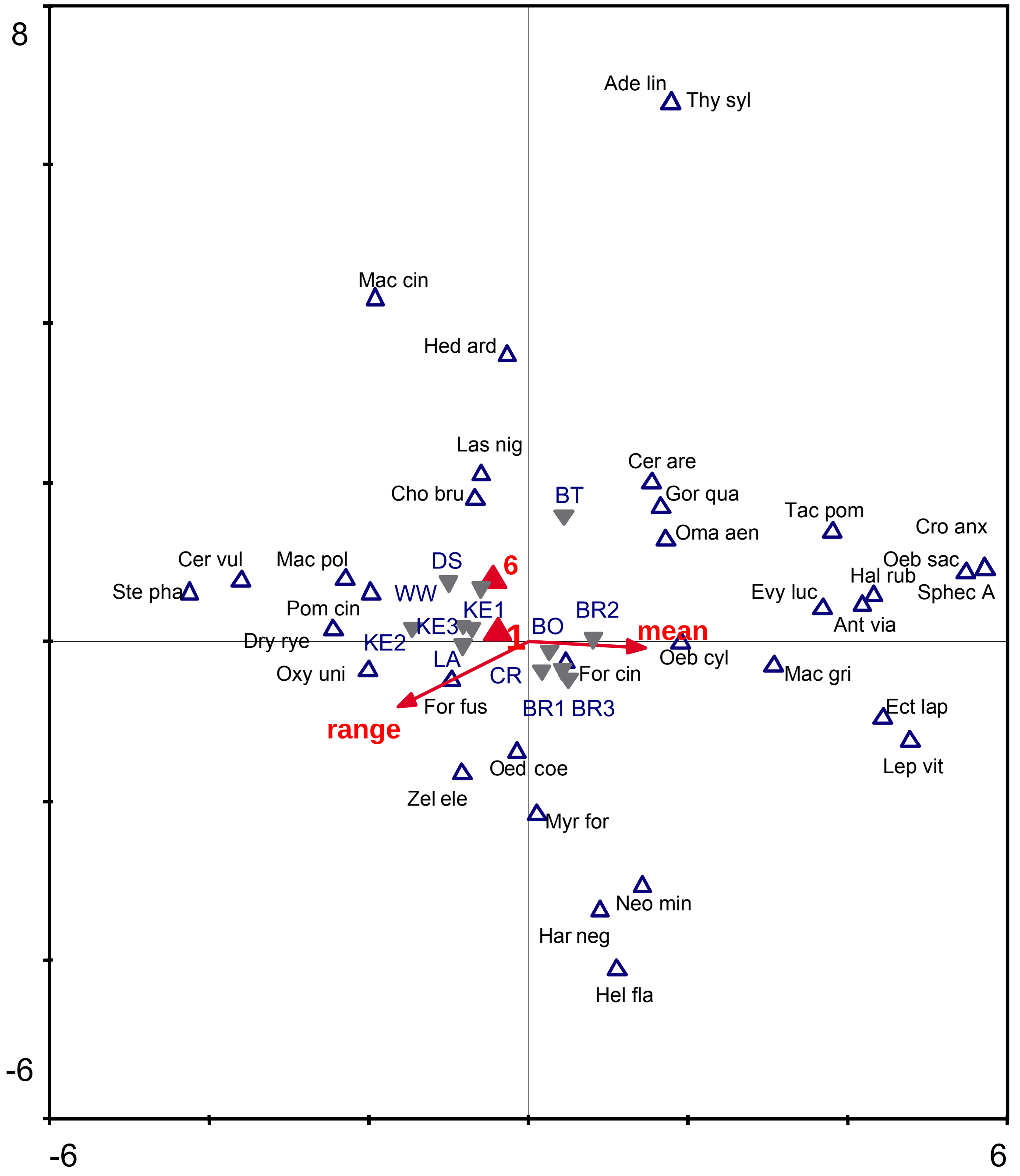
Class 1 = 5-50mm
Class 2 = 55-90mm
Class 3 = 95-145mm
Class 4 = 150-220mm
Class 5 = 225-295mm
Class 6 = 300+mm

Each class represented in a sample was input as nominal data (Disk Appendix 3B Sheet 1); the number of classes represented was entered as “range”; the highest class in a sample was included as “max”; and the mean of all sward height measurements in a sample was entered as “mean” (in millimetres). These data were then input as non-constraining environmental variables along with the invertebrate quadrat data and analysed via an indirect DCA. This produced vectors for “mean” and “range” of sward height at opposite ends of axis 1. The constraining effect of sward height was then tested via a CCA, in which the sward height classes 1 and 6, the mean height and the range in height were found to be significant by Monte Carlo permutations and were therefore selected as the environmental variables. The sites were input as non-constraining covariables. The resulting log gave less strong eigenvalues than other CANOCO analyses in this section, but very high species-environment correlations and cumulative percentage variance.

Figure 7.3j is the output diagram, in which the invertebrates were reduced to 34 species by applying a 4% fit. The invertebrate species involved in this analysis have many differences from those seen in the other Figures, with 18 species not figuring in previous analyses. The diagram shows a group of invertebrates on the left associated with vegetation with a low mean height and a wide range in height, while those on the right are associated with vegetation taller on average and which varies in height much less. The cluster of invertebrate species to the left of this diagram includes two – *Cercopis vulnerata* and *Steatoda phalerata* – which typically live in taller swards and two – *Macronychia polyodon* and *Oxybelus uniglumis* – which favour areas with low vegetation, where *Macronychia polyodon* is a parasite in *Oxybelus* species nests in loose sand (Pape, 1987). The ecology of two further invertebrates in this part of the diagram – *Pompilus cinereus* and *Drymus ryeii* – is less clear-cut, as both seem to favour more open vegetation but are also able to forage in taller sward. A group of species to the right of axis 1 includes several which typically nest in sand (*Crossocerus anxius*, *Halictus rubicundus*, *Evylaeus lucidulus*, *Tachysphex pompiliformis*) plus nest parasites on these or related species (*Oebalia sachtlebeni*, *Anthrax varia*, *Macronychia griseola*), all of which were found only on Polish sites in this study. Also to the right of axis 1 in Figure 7.3j are *Ectobius lapponicus* and *Leptarthrus vitripennis*, which again were found only on Polish sites. Their ecology might suggest an association with somewhat taller vegetation than the other invertebrates with which they are associated; their position in the diagram implies they prefer vegetation of relatively tall, uniform height.

The second axis in Figure 7.3j has both the tallest and shortest vegetation on the positive side of the axis. This suggests that the invertebrates above the line are associated with the presence of both very tall and very short vegetation, while those below the line are associated with vegetation lacking those extreme types. In the former group of species are *Adelphocoris lineolatus* and *Thymelicus sylvestris* which in this study were found associated with *Holcus lanatus* (the preferred larval foodplant of *Thymelicus sylvestris*) in a sward of very varied height on Site BT. *Machimus cingulatus* would also appear to be well placed according to this interpretation, as it inhabits long grass as an adult but requires open sandy soil for its larva (Stubbs & Drake, 2001). A similar relationship with very different sward heights, however, does not appear to be established for *Hedychridium ardens* in the literature. On the negative side of the second axis *Oedipoda coerulescens*, *Zelotes electus* and *Myrmeleon formicarius* would appear to fit well with this analysis, as the first two species typically inhabit open dunes with low vegetation while *Myrmeleon formicarius* lives as a larva in pits in open sand. Figure 7.3j further implies that the *C. canescens*-feeding *Neophilaenus minor* is most associated with uniform stands of this grass.

Figure 7.3j: Canonical Correspondence Analysis (CCA) showing invertebrate data constrained by sward height, with sites superimposed as supplementary variables.



Key to abbreviations:

Ade lin	*Adelphocoris lineolatus*	Ant via	*Anthrax varia*	Cer are	*Cerceris arenaria*
Cer vul	*Cercopis vulnerata*	Cho bru	*Chorthippus brunneus*	Cro anx	*Crossocerus anxius*
Dry rye	*Drymus ryeii*	Ect lap	*Ectobius lapponicus*	Evy luc	*Evylaeus lucidulus*
For cin	*Formica cinerea*	For fus	*Formica fusca*	Gor qua	*Gorytes quadrifasciatus*
Hal rub	*Halictus rubicundus*	Har neg	*Harpalus neglectus*	Hed ard	*Hedychridium ardens*
Hel fla	*Heliophanus flavipes*	Las nig	*Lasius niger*	Lep vit	*Leptarthrus vitripennis*
Mac cin	*Machimus cingulatus*	Mac gri	*Machronychia griseola*	Mac pol	*Machronychia polyodon*
Myr for	*Myrmeleon formicarius*	Neo min	*Neophilaenus minor*	Oeb cyl	*Oebalia cylindrica*
Oeb sac	*Oebalia sachtlebeni*	Oed coe	*Oedipoda coerulescens*	Oma aen	*Omalus aeneus*
Oxy uni	*Oxybelus uniglumis*	Pom cin	*Pompilus cinereus*	Sphec A	*Sphecodes* species A
Ste pha	*Steatoda phalerata*	Tac pom	*Tachysphex pompiliformis*		
Thy syl	*Thymelicus sylvestris*	Zel ele	*Zelotes electus*		

	1	2	3	4
Eigenvalues	0.387	0.289	0.223	0.192
Spp-environment correlations	0.813	0.765	0.748	0.715

Cumulative % variance	1	2	3	4
of species data	1.5	2.6	3.5	4.2
of spp-environment relation	35.5	61.9	82.4	100.0

In fieldwork for this study some invertebrates in Figure 7.3j were observed to have habitat preferences which are reflected in the diagram as described in the preceding paragraph. For many species in this analysis, however, no clear niche preferences are known from the literature and the Figure may therefore be providing useful insights. Moreover, the superimposed sites imply that there is a subtle difference in vegetation structure between British and Polish sites, with the latter having higher sward height means and less variability in sward height. This may be a climatically related phenomenon, as Polish sites were found to be much more frequently droughted in summer than British sites. Drought led to the death of a large proportion of the vegetation on Polish sites, including *C. canescens* itself, followed by extensive germination of *C. canescens* plants. This phenomenon produced a relatively even sward height, which under the relaxation of drought led to the maturity of *C. canescens* tussocks *en masse*. The data presented in Figure 7.3j also suggest that there are assemblages of invertebrates in both Britain and Poland which are associated with different vegetation structures in the *C. canescens* habitat.

7.3.4 Relationship of the invertebrate fauna to environmental factors

During fieldwork it became evident that the activities of invertebrates have a clear effect on ***sand erosion and accretion***. In the present study some measurements and general observations of this process were made and are summarised in Table 7.3iii.

Table 7.3iii: summary of measurements and general observations of sand erosion caused by invertebrate activities.

Species	Site	Year	Measurements	Observations
Formica cinerea	BR1, 2 & 3	2000	Measurements of nest mounds (n = 20): length mean 26.4cm “ range 9cm -100cm width mean 21.1cm “ range 7.5cm - 80cm depth mean 2.5cm “ range 0.4cm - 15cm	Nests often at base of *C. canescens* tussocks. Older mounds colonised by *C. canescens* (up to 25 seedlings per nest), *Agrostis alba*, *Berteroa incana*, *Artemisia vulgaris*, *Pilosella officinalis*.
Formica cinerea	BR1	2000	Forage trail measurements: length 227cm width range 0.5cm to 5.5cm depth range 0cm to 3.4cm	Trail ran underground for two stretches of 9cm and 48cm.
Formica cinerea	BR3	2000	Forage trail measurements: length 645cm width range 0.4cm to 3.8cm depth range 0cm to 2.4cm	Trail underground for several short stretches. Trail extant between 1997 and 2001 but not present 2003.
Tetramorium caespitum	BR1	2000	Measurements of nest mounds (n = 10): diameter mean 4.6cm “ range 3.2cm - 6.6cm depth mean 0.6cm “ range 0.3cm - 1cm Up to 18 nests per m^2.	Nests are only in open ground and do not support any vegetation.
Lasius alienus	BT	2000	Sand depths produced by nests (n = 4): mean 2.3cm range 1.4cm to 3cm. (No definable length and width of nests)	Nests mostly underground but throwing up surface sand at base of *C. canescens* tussocks.
Cerceris ruficornis	KE3 Area B	1999	Density of nest holes in ten $4m^2$ bare plots: mean 3.3 per m^2 range 1.0 to 8.3 per m^2 Only one nest in ten $4m^2$ well-vegetated plots	*Cerceris* spp. nest holes produce small casts of loose sand, (no measurements made.) Nests may be placed at base of *C. canescens* tussock or in open ground.

continued…

Table 7.3iii continued…

Species	Site	Year	Measurements	Observations
Cerceris ruficornis	KE3 Area B	2002	Mean density of nest holes in two most heavily trampled 4m^2 bare plots = 8.1 per m^2.	
Myrmeleon formicarius	BR3	2002	Larval pits cause minor erosion affecting up 1%of a m^2 quadrat.	
Typhaeus typhoeus	KE3 Area B	2002	Mean = 0.6 per m^2. Max = 3.0 per m^2 (n = 42)	Adult emergence holes.

The data taken in this study indicate that ants are the invertebrates most involved in the process of sand erosion, and particularly *Formica cinerea*, the dominant species on the Polish study sites. This ant was found typically to begin its foundation nests in the early stages of the *C. canescens* habitat, when it would often site them at the bases of *C. canescens* tussocks. At Bromierzyk some *Formica cinerea* nests clearly survived for several years. The largest were associated with the late mature phase of the habitat (cf Plate 4): at Sites BR1 and BR3 the largest mounds were situated in taller marginal grassland vegetation, while those nests in the middle of the sites (in the pioneer and early mature phases of the habitat) were underground with little or no surface mound. In some instances where ant excavations had thrown up large amounts of sand around *C. canescens* tussocks these plants were found to be dead, but it is not known if the ant activity was the cause of death. As well as on the Bromierzyk sites, *Formica cinerea* also produced some large surface mounds at Ciosny reserve; but at Bolimów this ant appeared to live in entirely underground nests.

Two other ant species in this study had an influence on sand erosion and disturbance, though to a much lesser degree. In Poland *Tetramorium caespitum* nested regularly in areas of bare sand, and its small circular nest mounds were frequently observed. Unlike *Formica cinerea*, however, it did not site its nests at the base of *C. canescens* or other plants. Its nests were much smaller and involved the excavation of smaller volumes of sand (Table 7.3iii).

In Britain no single ant species was dominant in the *C. canescens* habitat, and only *Lasius alienus* was found to produce sand accretions similar to those of *Formica cinerea*, and only at Burlish Top. *Tetramorium caespitum* was taken on Site KE1, but is apparently rare there and its nests were not observed. Although the well-known ant-hill species *Lasius flavus* was recorded on several sites, none of its nests was found and it was thought to be only foraging in the *C. canescens* habitat. In a similar way *Formica cunicularia* foraged on some Polish sites, though the nearest nest found (on Site BO) was inside the forest edge twelve metres from open *C. canescens* habitat.

Several other invertebrate species were observed causing sand disturbances in this study. Nests of *Cerceris arenaria*, *Cerceris rybyensis*, *Crossocerus wesmaeli*, *Megachile maritima* and *Formica fusca* were all found sited at the base of *C. canescens* tussocks, and *Ammophila sabulosa*, *Pompilus cinereus*, *Oxybelus uniglumis* and *Evagetes aff. pectinicornis* were observed excavating in open sand, but the volume of sand disturbed by the activities of all these species was on a very small scale only, and hardly measurable. Three species – *Cerceris ruficornis*, *Myrmeleon formicarius* and *Typhaeus typhoeus* – occurred locally in sufficient densities to produce measurable erosion, which for each species reached a maximum of 1% per m^2.

During this study other environmental data were recorded in quadrat samples, notably the percentage cover of ***bare sand and litter*** (4.3.1, 4.3.2) and the ***stage of Corynephoretum*** represented by the samples (5.3.4). Using Disk Appendix 3B Sheet 2 an investigation was undertaken to test how the invertebrates responded to these three data sets, which were input as explanatory variables, with invertebrate quadrat data input as response variables. All invertebrate data were log transformed.

The exploratory DCA produced one sample (number 116) which was exceptionally different from the rest and was therefore deleted[20], leaving 138 samples in the analysis. Sites were included as supplementary variables. The

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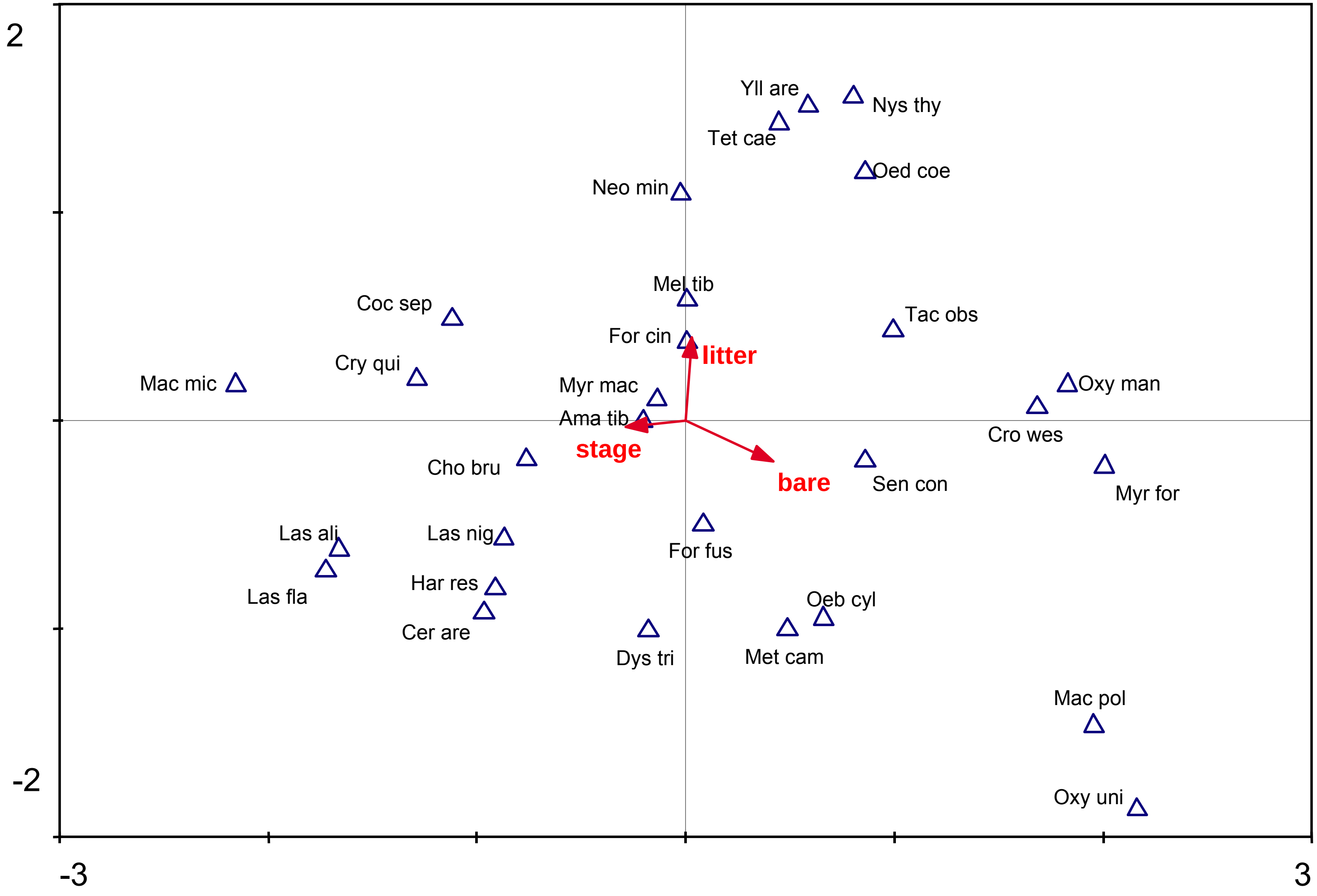
[20] this is the same sample as no. 104 in earlier analyses using a different input file (7.3.2)

output diagram for this DCA showed basically the same distribution of species and sites as Figure 7.3d, with “bare” and “litter” producing opposite trends along the first axis and “bare” and “stage” showing differentiation along the second axis. The main purpose of this analysis, however, was to investigate how the invertebrate data are constrained by the three selected environmental variables, and a CCA was therefore produced from the same data inputs. When tested for significance via Monte Carlo permutations “bare” and “litter” were found to be significant (P = 0.0020 and 0.0020 respectively), and “stage” showed a degree of significance even after elimination of the other two variables (P = 0.0280): all were therefore kept in the analysis. The log gave a low cumulative percentage variance of species data but high species-environment correlations.

The output diagram is Figure 7.3k, which shows the distribution of 29 species selected by applying a 4% fit. In this Figure invertebrate species are distributed very differently from the typical site-influenced pattern seen in Figure 7.3d. The first axis has “stage” and “bare” producing trends in almost opposite directions, a not unexpected result given that a strong reduction in the amount of bare sand characterises the successional development of the Corynephoretum (5.3.4). A cluster of species associated in this Figure with the later successional stages includes *Macrodema micropterum*, which feeds on *Calluna vulgaris*, the aphidivore *Coccinella septempunctata* and the detritivore *Crypticus quisquilius*, each of which might be expected to find their pabulum more abundantly in the later stages of the habitat. These three species also show a small positive relationship with litter along the second axis.

A further group of species is associated in the diagram with later successional stages but has a negative association with litter. In this group are three *Lasius* spp. ants, the grasshopper *Chorthippus brunneus*, the solitary wasp *Cerceris arenaria* and the carabid beetle *Harpalus rufipes*. As with the previous group of species, better foraging opportunities in the more developed habitat stages may be a key factor in this association: for example, although *Cerceris arenaria* nests in open sandy areas it preys on weevils Curculionidae which

Figure 7.3k: Canonical Correspondence Analysis (CCA) showing invertebrates species constrained by the amount of bare sand and litter and the stage of the *Corynephorus canescens* habitat.



Key to abbreviations:

Ama tib	*Amara tibialis*
Cer are	*Cerceris arenaria*
Cho bru	*Chorthippus brunneus*
Coc sep	*Coccinella 7-punctata*
Cro wes	*Crossocerus wesmaeli*
Cry qui	*Crypticus quisquilius*
Dys tri	*Dysmachus trigonus*
For cin	*Formica cinerea*
For fus	*Formica fusca*
Las ali	*Lasius alienus*
Las fla	*Lasius flavus*
Las nig	*Lasius niger*
Har res	*Harpalus rufipes*
Mac mic	*Macrodema micropterum*
Mac pol	*Macronychia polyodon*
Mel tib	*Melanimon tibialis*
Met cam	*Metopia campestris*
Myr for	*Myrmeleon formicarius*
Myr mac	*Myrmeleotettix maculatus*
Neo min	*Neophilaenus minor*
Nys thy	*Nysius thymi/ericae*
Oeb cyl	*Oebalia cylindrica*
Oed coe	*Oedipoda coerulescens*
Oxy man	*Oxybelus mandibularis*
Oxy uni	*Oxybelus uniglumis*
Sen con	*Senotainia conica*
Tac obs	*Tachysphex obscuripennis*
Tet cae	*Tetramorium caespitum*
Yll are	*Yllenus arenarius*

	1	2	3	4
Eigenvalues	0.372	0.262	0.252	0.836
Spp-environment correlations	0.820	0.725	0.788	0.000
Cumulative % variance:				
of species data	1.3	2.3	3.2	6.2
of spp-environment relation	42.0	71.6	100.0	0.0

are typically found on herbaceous and woody plants in mature grasslands, woodland and scrub. The cluster of *Lasius* spp. ants in this quartile may also reflect the longevity of their colonies, which is particularly a feature of *Lasius flavus*; this explanation, however, would not explain the distribution of other ant species (*Lasius cinerea*, *Formica fusca*, *Tetramorium caespitum*) in different parts of the diagram. The association of this last species with bare sand matches its observed nesting preferences; the relationship of this ant and *Formica cinerea* with litter is less obvious from their known biology, unless the requirement of *Tetramorium caespitum* for plant seeds is a factor (Czechowski *et al*., 2002). It may be relevant that another granivore, *Nysius thymi/ericae*, lies near *Tetramorium caespitum* in Figure 7.3k.

A further group of species showing a positive correlation with bare sand and a neutral or negative one with litter consists of the ant-lion *Myrmeleon formicarius* whose larvae form pits in loose open sand, together with three small sphecid wasps which nest in similar places (*Oxybelus mandibularis*, *Oxybelus uniglumis*, *Crossocerus wesmaeli*) and their dipterous parasitoids (*Metopia campestris*, *Oebalia cylindrica*, *Senotainia conica* and *Macronychia polyodon*). The closely interrelated group of species in this quartile may be interpreted as representing the invertebrate community of the pioneer stage of the Corynephoretum, which is characterised by extensive areas of loose, bare sand (5.3.4).

The second axis in Figure 7.3k is largely about “litter” and partly about “bare”. As these are measures of percentage cover within a quadrat it is not surprising that they show related but opposite trends. However, a greater abundance of litter is not invariably correlated with the later stages of the *C. canescens* habitat, since even in the pioneer stage plant material from dead spring annuals such as *Spergula morisonii* and from *C. canescens* itself in very droughted conditions was not infrequent. A group of invertebrates differentiated more clearly along this axis than axis 1 include two *Formica* spp. ants, the robbberfly *Dysmachus trigonus*, the detritivore *Melanimon tibialis* and the sap-feeding *Neophilaenus minor*, one of the herbivores recorded on *C. canescens* (Table 7.3ii). The spider *Yllenus arenarius* also shows a strong relationship with litter in this analysis. Its predatory habits have been studied on the Bromierzyk sites and elsewhere by Bartos (2000a, 2000b), who found that *Yllenus arenarius* hunted a wide variety of prey items by stalking them at ground level (favouring Diptera, Homoptera, Orthoptera, Thysanoptera and larvae of Lepidoptera). This hunting strategy is very different to that of *Dysmachus trigonus*, which captures its prey (mostly Diptera and Hymenoptera) in flight (Stubbs & Drake, 2001). The differentiation of these two species at opposite ends of the second axis may well reflect these differences in hunting strategy, since litter would provide food and shelter for the prey of *Yllenus arenarius* as well as stalking cover for the spider itself; but litter would have less value as a habitat for prey of *Dysmachus trigonus* and instead could offer escape opportunities from the capture-dart forays of this robberfly.

A final observation from Figure 7.3k is the different environmental preferences of the three grasshoppers *Oedipoda coerulescens*, *Myrmeleotettix maculatus* and *Chorthippus brunneus*. These are differentiated chiefly in their response to the degree of bareness and successional stage of the Corynephoretum, with *Oedipoda coerulescens* favouring the former and *Chorthippus brunneus* the latter, and *Myrmeleotettix maculatu*s placed in the middle. This pattern neatly reflects the known ecology of these species (Marshall & Haes, 1988), though the additional association of *Oedipoda coerulescens* with litter is possibly new.

In summary, the constraining influences of the three important environmental variables of bareness, litter and stage of the Corynephoretum correlate well with the ecologies of some of the invertebrate species involved where these are relatively well known. For others species, whose ecology is not so well known, the analysis may be providing useful new information, particularly in the response of some species to the amount of litter on the sand surface as discussed above.

7.3.5 Interrelationships among the invertebrate fauna

In the fieldwork for this study several direct observations were made of invertebrates interacting with other invertebrates. A summary of these observations is given in Table 7.3iv.

Table 7.3iv: observations of invertebrate interactions made in the present study.

Species	Site	Date	Observation
Cerceris arenaria and *Otiorrhynchus sulcatus*	DS	16.7.97	*Cerceris arenarius* carrying *Otiorrhynchus sulcatus* as prey
Megachile leachella, Psen lutarius, Crabro scutellatus	WW	20.7.98	All three species nesting together in bank at mouth of rabbit burrow.
Pompilus cinereus and *Yllenus arenarius*	BR1	22.7.99	*Pompilus cinereus* seen chasing but not catching *Yllenus arenarius*
Oxybelus uniglumis and *Senotainia conica*; unspecified small Diptera	DS	21.8.99	*Senotainia conica* frequently shadowed *Oxybelus uniglumis* carrying Diptera prey
Cicindela campestris and unspecified Lygaeidae	KE1	28.8.99	*Cicindela campestris* devoured small Lygaeid bug
Machimus cingulatus and *Heterogaster urticae*	KE2	28.8.99	*Machimus cingulatus* chased but failed to catch *Heterogaster urticae*
Machimus cingulatus and *Lasius* sp.	KE2	28.8.99	*Machimus cingulatus* devoured ant (possibly *Lasius flavus*)
Pompilus cinereus and unspecified spider	KE3 Area B	16.7.00	*Pompilus cinereus* tried to bury spider in compacted sand but gave up after several attempts and dragged prey away
Formica cinerea and *Sphecodes aff rufiventris*	BR1	22.7.00	*Sphecodes aff rufiventris* being dragged into entrance of *Formica cinerea* nest
Cicindela hybrida and *Formica cinerea*	BR1	23.7.00	*Cicindela hybrida* caught and ate an alate *Formica cinerea*
Hedychrum rutilans and *Bembix* sp.	BR1	23.7.00	*Hedychrum rutilans* shadowing *Bembix* sp. at mouth of burrow

continued…

Table 7.3iv continued…

Species	**Site**	**Date**	**Observation**
Formica cinerea and unspecified aphid	BR1	23.7.00	Aphid tended by alate *Formica cinerea*
Cicindela hybrida and *Oedipoda coerulescens*	BR3	23.7.00	*Cicindela hybrida* stalked *Oedipoda coerulescens* but did not attack
Cicindela hybrida and *Formica cinerea*	BR3	23.7.00	*Cicindela hybrida* caught and ate an alate *Formica cinerea*, but released immediately a worker of the same species it also caught. Worker ran round in circles for several seconds
Miltogramma punctata, Ectemnius continuus, Sphecodes aff rufiventris	BR3	23.7.00	*Miltogramma punctata* in groups of 2-3 followed *Ectemnius continuus* and *Sphecodes aff rufiventris* around site
Yllenus arenarius and unspecified Diptera	BR3	23.7.00	*Yllenus arenarius* observed hunting, targeted prey being mostly small Diptera
Cicindela hybrida and Formica cinerea	BR1	24.7.00	On approach of *Cicindela hybrida*, two *Formica cinerea* ran in circles causing *Cicindela hybrida* to flee
Tetramorium caespitum and unspecified lepidopteran	BR2	25.7.00	Several *Tetramorium caespitum* attacking a small lepidopteran larva at nest
Evagetes aff pectinicornis and *Formica cinerea*	BR2	25.7.00	*Evagetes aff pectinicornis* fled on approach of *Formica cinerea*
Formica cinerea and *Tetramorium caespitum*	BR2	6.6.01	*Formica cinerea* seized *Tetramorium caespitum* but released it immediately
Myrmeleon formicarius and ?*Synaphe punctalis*	BR3	6.6.01	Larva possibly of *Synaphe punctalis* fell into *Myrmeleon formicarius* larval pit and was devoured
Cerceris rybyensis and unspecified Syrphidae	DS	25.7.01	*Cerceris rybyensis* observed with syrphid prey
Macronychia polyodon and *Crossocerus wesmaeli*	KE3	4.6.02	*Macronychia polyodon* observed shadowing *Crossocerus wesmaeli*

The observations in this Table are unsystematic, but they do give some insights into the relationships of the fauna on the sites. From these observations and information on life histories in the literature (Table 4.2i supplemented by Stubbs & Chandler (1978), Yarrow (1986) and Cooter (1991)), it is possible to construct simplified food webs showing the main niches of the invertebrate taxa recorded in this study. Figures 7.3l, m and n present these food webs for the three main regions. In these Figures the *C. canescens* habitat is represented in stylised form, and the genera utilising its different niches are derived from the species/site lists in Table 7.3i. The Figures use almost all the genera recorded in each region, omitting only a very small number for which the literature offers insufficient ecological information, or which may simply be transients through the sites. Those genera which appear to be associated chiefly with later successional habitats are shown in boxes labelled "OFF-SITE", though they may have an occasional foraging niche within the Corynephoretum. A genus is represented more than once if it utilises the habitat in more than one way. Major interrelationships between invertebrates and plants, and invertebrates and other invertebrates, are colour-coded, while the direction of the arrows indicates relationships such as predation and parasitism rather than energy flow. The thickness of the arrows is intended to represent the strength of relationships; this measure is derived from the product of the number of taxa involved in a particular relationship, modified by an assessment of the number of other options for those taxa, including off-site options. For example, all sites were visited by invertebrates seeking nectar sources, though those sources were often better represented in nearby off-site habitats: the directional arrows therefore indicate both these options, with off-site nectaring as the stronger. A few higher taxa (Families) recorded from the sites are also shown on the diagrams where they contribute to an understanding of community interrelationships.

From these Figures it is apparent that the Polish sites represent the most complex and the East Anglian sites the simplest invertebrate community structures, with the West Midlands sites intermediate between the two. This may be just a product of the size of the species lists for each region. However,

Figure 7.3l: associations between invertebrate fauna within key habitat elements, Polish sites.

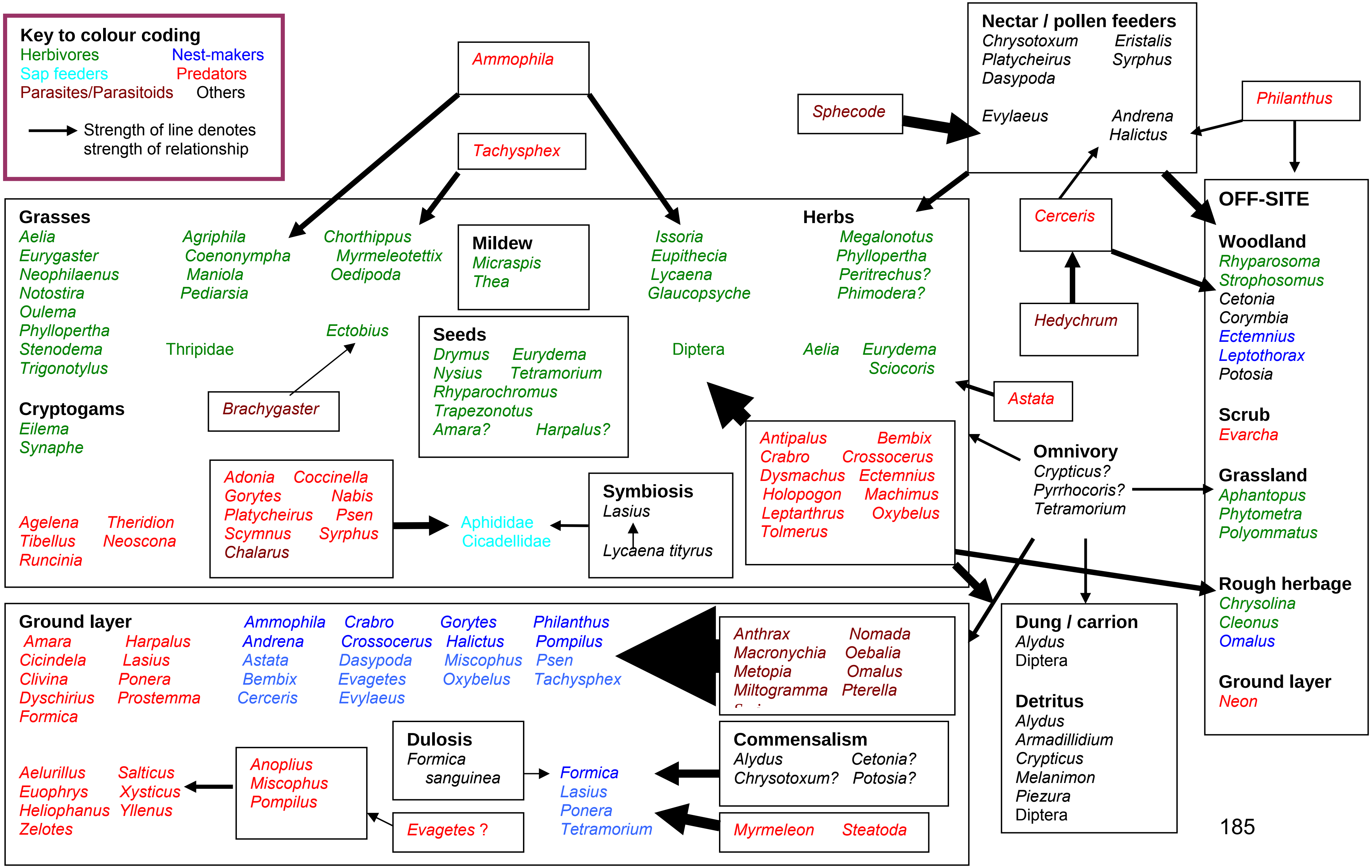


Figure 7.3m: associations between invertebrate fauna within key habitat elements, West Midlands sites.

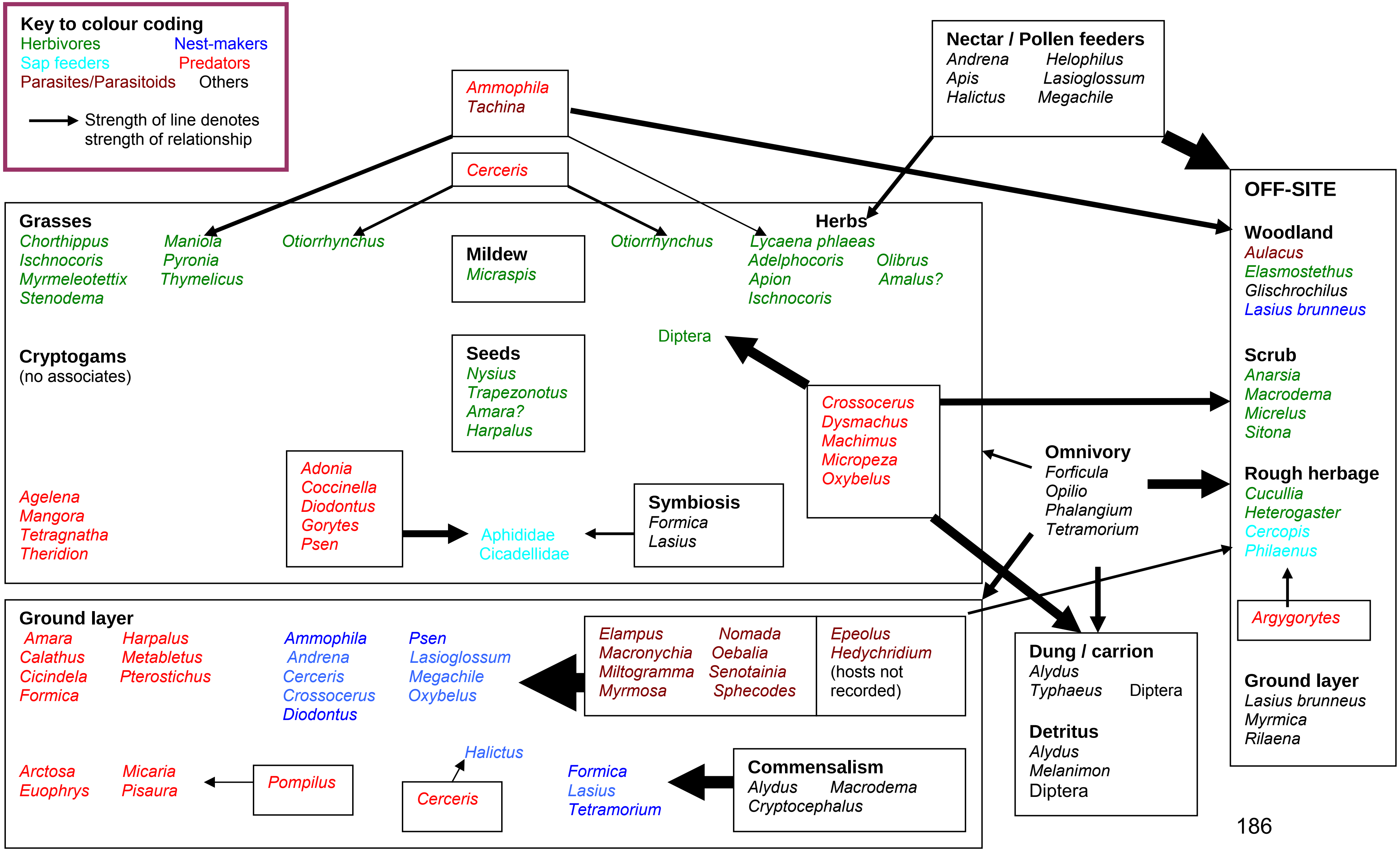
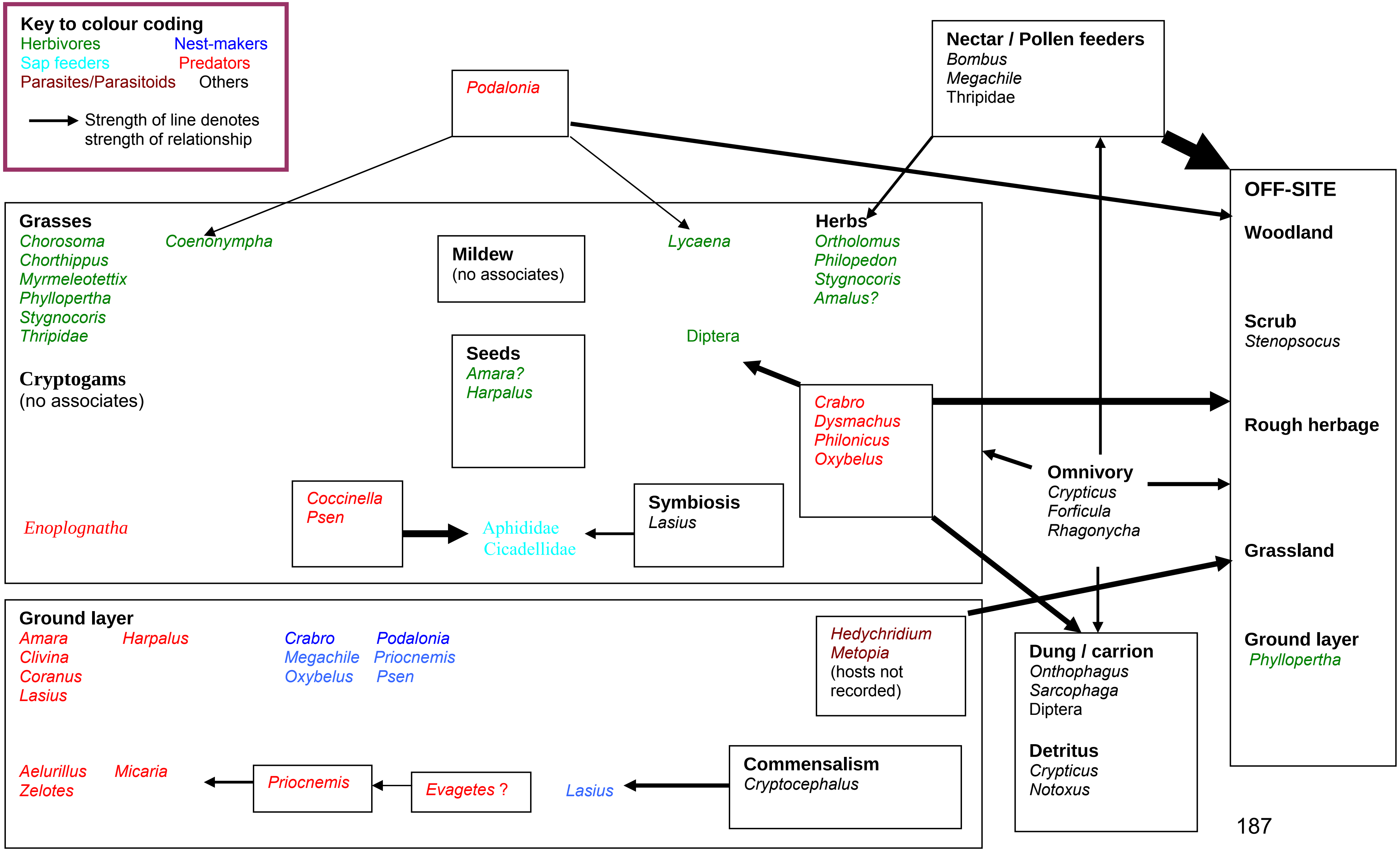


Figure 7.3n: associations between invertebrate fauna within key habitat elements, East Anglian sites.



this faunal simplification is not even across all invertebrate niches: the East Anglian sites have only half the number of taxa recorded on West Midlands sites yet hold almost as many omnivores, detritivores, dung and carrion feeders and predators on Diptera, while the number of herbivore taxa is not much smaller. It is evident from Figures 7.3l, m and n that faunal simplification is most marked in the more specialised relationships – oligophagous predation, parasitism and social relationships such as commensalism and dulosis. Among the communities feeding on plant materials the granivore, mildew-feeder and cryptogam-feeder elements simplify more than grass- and herb-feeding communities. Compared with Poland the West Midlands sites retain many of these more specialised elements reasonably intact within the *C. canescens* habitat, and have a particularly good representation of parasitoids of ground-nesting Hymenoptera; in East Anglia these parasitoids have all but disappeared from the *C. canescens* habitat. A reasonable explanation of what we observe in Figures 7.3l, m and n is that the typical invertebrate communities of this habitat tend to break down where sites become small and isolated.

A further way of testing this hypothesis is to look at the extent of mimicry present in the invertebrate faunas of the three regions, on the assumption that mimicry is a feature of more complex and interrelated community structures. Four main mimicry rings can be identified from the faunal data – black-and-yellow wasps; black-and-red wasps; bee mimics; and ant mimics. These complexes are largely Müllerian and most species involved belong to the Hymenoptera, though some Batesian elements may be present among the associated Diptera (*Eristalis*, *Helophilus*, *Platycheirus*, *Syrphus*) and possibly Hemiptera (*Cercopis* and *Alydus*).[21] Table 7.3v shows how these mimicry rings are represented in the three regions.

Alydus calcaratus forms separate mimicry relationships in its nymphal and adult states, and these are tallied separately in the site totals. This Table

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[21] Batesian mimicry – an unpalatable model is mimicked by palatable species. Müllerian mimicry – several unpalatable species share the same mimicry pattern.

Table 7.3v: composition of invertebrate mimicry rings identified on Polish, West Midlands and East Anglian sites.

Mimicry ring	Poland	West Midlands	East Anglia
Ant mimics	*Alydus* (nymph) *Formica* (3 spp.) *Lasius* (2 spp.) *Leptothorax* *Ponera* *Smicromyrme* *Steatoda* *Miscophus* ?	*Alydus* (nymph) *Formica* *Lasius* (4 spp.) *Micaria* *Myrmica* *Myrmosa*	*Lasius* (3 spp.) *Micaria*
Hive bee mimics	*Andrena* *Dasypoda* *Halictus* (2 spp.)	*Andrena* (4 spp.) *Apis* *Eristalis* *Halictus* *Megachile*	*Megachile*
Black-&-yellow wasp mimics	*Bembix* *Cerceris* (3 spp.) *Chrysotoxum* *Cicindela* *Crabro* (2 spp.) *Ectemnius* (2 spp.) *Gorytes* (2 spp.) *Nomada* *Philanthus* *Platycheirus* *Syrphus*	*Argygorytes* *Cerceris* (3 spp.) *Helophilus* *Nomada*	*Crabro*
Black-&-red wasp mimics	*Alydus* (adult) *Ammophila* (2 spp.) *Anoplius* *Astata* *Evagetes* (2 spp.) *Prostemma* *Pyrrhocoris* *Sphecodes* (4 spp.) *Tachysphex* (2 spp.)	*Alydus* (adult) *Ammophila* (2 spp.) *Cercopis* *Gorytes* *Psen* *Sphecodes*	*Evagetes* *Podalonia* *Psen* (*lutarius* only)
Total number of mimicry relationships	46	30	9

shows that the ratio of mimicry relationships between Polish: West Midlands: East Anglian sites is approximately 9:5:2 compared with ratios of 3:2:1 for the total of all invertebrate species in these regions (Figure 7.3a). Omitted from this Table are Coccinellidae with similar aposematic colours but lacking the patterns or shapes of the models in Table 7.3v; if included, however, they would slightly alter the ratio between sites to 9:6:2 in terms of number of relationships within the mimicry rings. This analysis reinforces the interpretation of Figures 7.3l, m and n that the invertebrate fauna of the West Midlands sites, while smaller than that of the Polish sites, retains a recognisably similar community structure; in East Anglia, however, that community structure has simplified considerably and may be tending towards disintegration.

7.3.6 The vertebrate fauna

The vertebrates recorded on each site are shown by an X in Table 7.3vi.

Five species in this Table – the yellowhammer *Emberiza citrinella*, yellow wagtail *Motacilla flava*, common redstart *Phoenicurus phoenicurus*, sand lizard *Lacerta agilis* and brown hare *Lepus europaeus* (once on Site BO) – were directly observed during fieldwork for this study, but most vertebrates were detected from their footprints, dung or feeding signs.

Vertebrate species were normally infrequent visitors to the *C. canescens* habitat and were typically recorded in this study only once per site. The chief exceptions were the rabbit *Oryctolagus cuniculus* and brown hare. Rabbits occurred on all British sites, and grazing signs were common. Brown hares replaced rabbits as the main grazer of this habitat on the Polish sites. Other vertebrates which were recorded more than once per site were common redstart, which was seen on each visit to Site CR, and the hedgehog *Erinaceus europaeus*, whose droppings were found twice at Site KE3.

Table 7.3vi: vertebrates recorded for each site in the study.

Species	British Sites							Polish Sites				
	BT	**DS**	**KE1**	**KE2**	**KE3**	**LA**	**WW**	**BO**	**BR1**	**BR2**	**BR3**	**CR**
Aves												
Emberiza citrinella					X							
Motacilla flava								X				
Phoenicurus phoenicurus												X
Picus viridis/canus									X			
Phasianidae									X			
Mammalia												
Alces alces									X			
Capreolus capreolus										X		
Erinaceus europaeus			X		X							
Lepus europaeus								X	X		X	X
Oryctolagus cuniculus	X	X	X	X	X	X	X					
Sus scrofa									X			
Vulpes vulpes							X		X	X		X
Arvicolidae									X			
Cervidae											X	
Mustelidae										X		
Sauria												
Lacerta agilis								X	X			

The location of Bromierzyk within large expanses of forest and meadow with little human disturbance meant that large herbivores were in the vicinity and occasionally visited the *C. canescens* sites. Footprints of elk *Alces alces*, roe deer *Capreolus capreolus*, an unidentified deer species (Cervidae), and a small family of wild boar *Sus scrofa*, were found once each on various sites at Bromierzyk as shown in Table 7.3vi; however, there was no evidence of any of these species attempting to feed there and they are thought simply to have passed across the sites on their way to and from other feeding grounds.

With these exceptions, most species appeared to use the *C. canescens* habitat as an occasional part of their feeding territories. A yellowhammer was searching for plant seeds on the ground, and a common redstart was observed picking up terrestrial invertebrates. On Site BR1 signs were present of a woodpecker *Picus viridis* or *Picus canus* – probably the former – feeding on ants. Hedgehog droppings containing Coleoptera remains were found on two Kinver Edge sites. Footprints and faecal evidence of fox *Vulpes vulpes* on four sites, a member of the Mustelidae on Site BR2 and a game bird (Phasianidae) on Site BR1 suggest that these animals occasionally foraged over the *C. canescens* habitat. From Table 7.3vi it is evident that the fox is the carnivore most associated with this habitat, probably attracted by the regular presence of lagomorphs on nearly all sites. At Site WW footprints and scratchings showed that a fox had clearly investigated a rabbit burrow within the *C. canescens* population. On Site BR1 scratchings in the sand suggested that a fox had been searching for voles (Arvicolidae); fox dung on that site contained part of the jaw of a vole *Arvicola* / *Clethrionomys* species, though the time required for digestion makes it likely that this prey item was caught off-site. Sand lizards *Lacerta agilis* were recorded twice: once on Site BO, where a mature animal was disturbed from mixed vegetation in the transition zone between the *C. canescens* habitat and forest edge; and once on Site BR1 when 3-4 young sand lizards were disturbed from beneath *C. canescens* tussocks; but it was not possible to observe whether they were seeking prey or shelter within the *C. canescens* habitat.

For all study sites an assessment of grazing impact and sand erosion caused by wild mammals was made during quadrat sampling (4.3.4, 4.3.5). The results are shown in Table 7.3vii.

In this Table the “impact scale mean” and “impact scale range” follow the scales given in 4.3.4 and 4.3.5, and are calculated only for affected quadrats, not all quadrats. The results for rabbit and hare grazing are very similar: mostly light grazing affecting about a third of quadrat samples. Rabbits also caused sand erosion in nearly 9% of quadrat samples, their impact ranging from minor to extensive. Fox scratchings causing sand erosion are included for Site WW (at scale level 3) but not for Site BR1 as the latter were not part of a quadrat sample.

Table 7.3vii: grazing impact and sand erosion caused by wild mammals

Site	**Agent**	**Grazing**					**Sand erosion**				
		total no. quadrats	**no. quadrats affected**	**% quadrats affected**	**impact scale mean**	**impact scale range**	**total no. quadrats**	**no. quadrats affected**	**% quadrats affected**	**impact scale mean**	**impact scale range**
BT	rabbit	5	0	-	-	-	5	1	20.0	2.0	2
DS	“	6	3	50.0	2.7	2-3	6	0	-	-	-
KE1	“	56	18	32.1	1.2	1-2	54	3	5.6	1.3	1-2
KE2	“	11	11	100	1.9	1-3	11	1	9.1	3.0	3
KE3	“	75	20	26.7	1.2	1-3	75	5	6.7	1.0	1
LA	“	11	3	27.3	1.0	1	11	1	9.1	2.0	2
WW	rabbit / fox	10	9	90.0	1.4	1-2	6	4	66.7	2.0	1-3
BO	brown hare	17	2	11.8	1.0	1	17	0	-	-	-
CR	“	17	10	58.8	1.8	1-2	17	0	-	-	-
BR1	“	27	10	37.0	1.2	1-2	27	0	-	-	-
BR2	“	16	1	6.3	1.0	1	16	0	-	-	-
BR3	“	21	9	42.9	1.0	1	21	0	-	-	-
Total rabbit		174	64	36.8	1.4	1-3	168	15	8.9	1.6	1-3
Total hare		98	32	32.7	1.3	1-2	98	0	-	-	-
Total		272	96	35.3	1.4	1-3	266	15	5.6	1.6	1-3

7.4 Discussion

7.4.1 Faunal composition of *Corynephorus canescens* sites

Data on various invertebrate groups have been gathered by several authors for a number of sites in this study: for Lakenheath and Wangford Warren (Key *et al.*, 1993, 1995; Marshall & Haes, 1988; English Nature, unpublished b); for Kinver Edge and the Devil’s Spittleful (English Nature, unpublished a); and for sites at the University of Łódź field station at Bromierzyk (Kowalczyk &

Szczepko, 2001a, b, c; Szczepko & Kowalczyk 2001, 2002; Kowalczyk *et al.*, 2002). All these studies are faunal inventory surveys; those for the British sites cover a wide range of Orders, while the Polish publications deal with various families of Hymenoptera. They use a range of collection techniques (sweep netting, D-Vac suction sampling, Moericke traps, direct searching), all but the last of which were not employed in the present study; and they cover a wide range of habitats within the areas of survey. It is certain from the published reports that none of the Lakenheath data are from the *C. canescens* habitats on that site, while the data for the other British sites were assembled largely, perhaps entirely, from habitats other than the *C. canescens* populations. Some of the studies carried out at Bromierzyk describe the habitat types which were sampled in the present study; those defined as sand dunes and xerothermic grasslands may include *C. canescens* habitats though precise identification of these locations is difficult from the published data.

The large differences in purpose and methodologies limit the comparability of these data with the present study. Nonetheless, exactly half (25) of species from the two East Anglian sites in Table 7.3i were also recorded in non-*C. canescens* habitats on these sites by Key *et al*. (1993, 1995), Marshall & Haes (1988) and English Nature (unpublished b): examples include rare and local species such as *Podalonia affinis*, *Oxybelus argentatus*, *Crypticus quisquilius*, *Megachile leachella* and *Zelotes electus*. In contrast not one of the species recorded for the West Midlands sites in Table 7.3i is included in the English Nature database for these sites (English Nature unpublished a), which largely consists of Lepidoptera records. While little can be made of the latter data sets, the fact that so many of the East Anglian species also occur in non-*C. canescens* habitats may be evidence that the presence of *C. canescens* has little influence on the invertebrate communities there.

None of the above information for the British sites is quantitative, but quantitative data are available for habitats within 3 km of Bromierzyk field station (Kowalczyk & Szczepko, 2001c; Szczepko & Kowalczyk, 2001; Kowalczyk *et al.*, 2002). These authors discovered that sand dunes and xerothermic grasslands held consistently fewer species and number of individuals of the hymenopteran families Chrysididae and Sphecidae than did willow scrub, pine forest, abandoned fields and farm outbuildings in the same vicinity. The species which they recorded in sand dunes and xerothermic grasslands correlate reasonably well with the present study, with *Ammophila sabulosa*, *Tachysphex obscuripennis*, *Crabro scutellatus* and *Omalus aeneus* being among the most frequently encountered Sphecidae and Chrysididae; though four other species recorded in some numbers by Kowalczyk and his fellow workers – *Harpactus elegans*, *Tachysphex helveticus*, *Oxybelus bidentatus*, *Bembecinus tridens* – were not encountered at all in the present study.

Other *C. canescens* localities and xerothermic grasslands in Europe have been the subject of several studies focussed on specific invertebrate groups, including spiders Araneae (Merkens, 2000; Mrzljak & Wiegleb, 2000; Rėlys, 2000; Kupryjanowicz, 2005); grasshoppers and crickets Orthoptera (Kindvall, 1995; Zehm, 1997a, b; Budrys et al., 2004); beetles Coleoptera (Schjøtz-Christensen, 1957, 1965; Lehmann *et al*., 2004; Hölscher *et al*., 2005); bugs Heteroptera (Gorczyca & Herczek, 1989; Gorczyca, 1994; Bröring & Wiegleb, 2005) and leafhoppers Hemiptera, Auchenorrhyncha (Szwedo, 1998; Nickel & Hildebrandt, 2003; Strauss & Biedermann, 2005; Biedermann *et al*., 2005). In addition, a range of invertebrate groups from different vegetation stands in Germany including *C. canescens* was studied by Bröring *et al*. (2005), while a detailed inventory of invertebrates associated with the Corynephoretum in Belgium is given by Zwaenepoel *et al*. (2002).

From these authors it is possible to identify the major invertebrate groups[22], and within these a few key species, which occur frequently in the *C. canescens* habitat across Europe. However, there are also many species in all larger invertebrate Orders studied whose association with this habitat is highly localised to a site or region. This pattern may arise from variations in

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[22] e.g. Araneae, Salticidae; Coleoptera, Carabidae; Diptera, Asilidae; Hemiptera, Lygaeidae; Hymenoptera, Chrysididae, Halictidae, Pompilidae & Sphecidae; Orthoptera, Acrididae

sampling methodology used by the different authors (for example, only those which employed pitfall trapping are likely to have sampled species which are both epigeic and nocturnally active); but it may also indicate that much of the invertebrate faunal composition of *C. canescens* sites is dependent on local features rather than those generally typifying the Corynephoretum. For example, the ground bug *Macrodema micropterum* is identified in the present study (Figure 7.3d) as being strongly site-associated, specifically with Site DS; it is also associated with "*Corynephorus canescens* with afforestation" and "heather" in eastern Germany (Bröring & Wiegleb, 2005); but is absent from Spergulo vernalis-Corynephoretum associations in south-central Poland (Gorczyca & Herczek, 1989; Gorczyca, 1994).

These studies therefore prompt the question, is there a specific invertebrate fauna of inland sand dunes supporting *C. canescens*? Merkens (2000) explored this in relation to spiders, and through DCA analyses concluded that the spider communities of inland dunes in northern Germany can generally be distinguished from the spider communities of the neighbouring habitats, but that there is no uniform species community which is characteristic and unique to open inland dunes. "The concrete vegetation and environmental factors of the site and its surroundings determine the species composition of the spider community" (Merkens, *loc. cit.*). The further question of similarity between inland and coastal invertebrate communities seems to have been little addressed, though some assessment is possible from lists of Coleoptera taken on *C. canescens* sites on the Norfolk coast provided by Collier *in litt*. (2000). Of 26 species which Collier considers typical of sandy sites on the Norfolk coast, two (*Philopedon plagiatus*, *Crypticus quisquilius*) occurred in this study on the East Anglian sites, and a further two (*Melanimon tibialis*, *Cleonus piger*) on other study sites. This seems to be a very low level of association, though there is nothing else with which to compare.

From the foregoing studies a typical invertebrate fauna of *C. canescens* sites can be constructed at least to higher taxonomic levels, and these are reflected very well by the fauna identified in the present study. Two groups of species in Table 7.3i which are seldom mentioned in the literature for *C. canescens* habitats are the parasitic flies Sarcophagidae[23] and the harvestmen Opiliones. The former are identified in this study as characteristic of more complex faunal communities (Figures 7.3l, m and n) and appear as significant components in several CANOCO analyses, especially in relation to bare sand in the earlier successional stage of the Corynephoretum (Figure 7.3k). The relationship of these Sarcophagidae to the Hymenoptera species found regularly in the *C. canescens* habitat is well established by Pape (1987) and Stubbs & Chandler (1978), and their absence from European faunal studies of this habitat probably indicates a lack of attention rather than a main difference between the literature and the present study. The Opiliones, on the contrary, were seldom encountered in this study and only on West Midlands sites. They are omnivores, though chiefly carnivorous, and they require humid surroundings at all times (Cloudsley-Thompson, 1958; Sankey & Savory, 1974) even when associated with sand dunes, such as *Opilio saxatilis*. It is suspected that there are climatic differences between the regions which make the West Midlands sites alone suitable for this group to forage in the *C. canescens* sites, but even there it is still a marginal habitat for them.

At species level the current study compares reasonably well with other published works on the European Corynephoretum fauna, and perhaps best with the communities represented in Belgium (Zwaenepoel, *loc. cit.*) and Denmark (Schøtz-Christensen, 1957). It is at species level that the greatest differences between *C. canescens* sites are found in the literature, and these may well be a function of site-specific or regional features such as Merkens (*loc. cit.*) found for spider communities in Germany. The strong relationship of the fauna to sites and regions which underlies many of the CANOCO analyses above (e.g. Figures 7.3d, e, f, j) also reflects this finding. In general the present study records fewer species in each of the main taxonomic groups than do more specialised studies of each group, which frequently use mass-collecting techniques over many more months of the year. It is clear, however, that the invertebrate fauna of the study sites as reflected particularly in Figures 7.3l, m and n is very recognisable as a typical *C. canescens* fauna.

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[23] genera *Macronychia*, *Metopia*, *Miltogramma*, *Oebalia*, *Pterella*, *Senotainia* in Table 7.3i

7.4.2 Relationship of the fauna to vegetational and environmental factors

Several studies in the literature investigate the relationship of the *C. canescens* and xerothermic grassland faunas to a number of vegetational and environmental factors. One of the earliest is Schøtz-Christensen's (1957) enquiry into the beetle Coleoptera fauna of the Mols laboratory grounds in Denmark. Carrying out analyses of soil properties, temperature and plant density in four study plots, Schøtz-Christensen found that beetle communities in the plots varied less in species composition than in the relative abundance of species. He concluded that differences in beetle communities were predominantly due to the degree of plant cover, with lowest beetle densities found in open areas of sparse vegetation. Several key species showed adaptations in their phenology to avoid temperature extremes, with *Amara infima*, *Opatrum sabulosum* and *Cardiophorus asellus* hibernating through the winter as adults and becoming active in early spring, producing larvae which survived the summer beneath the sand surface. In a later study of the population dynamics of ground beetles Carabidae at the same locality, Schøtz-Christensen (1965) found a very different response to increasing plant cover. Populations of most species were highest immediately after the creation of open sandy areas through clearance of *Calluna vulgaris* heath; as coverage of *C. canescens* became denser with time only three species – *Harpalus anxius*, *Harpalus neglectus* and *Harpalus smaragdinus* – remained in significant numbers, and these declined as *Calluna vulgaris* reinvaded the study plots. *Bradycellus collaris* began to colonise the Corynephoretum as *Calluna vulgaris* started to appear, while *Amara infima* had the widest tolerance of different vegetation cover. Schøtz-Christensen concluded that only the three *Harpalus* species were truly restricted to the Corynephoretum.

Using CANOCO to ordinate the carabid fauna of open, sandy areas in northern Germany, Hölscher *et al*. (2005) identified groups of species correlated with various elements of the vegetation. Eight species showed a significant positive correlation with the cover of lichens, and four were similarly correlated with the cover of herbaceous plants: two species, *Calathus* *fuscipes* and *Harpalus tardus*, showed both relationships. A weakly negative correlation with the cover of herbs, lichens and grasses was found for *Harpalus neglectus*, *Cicindela hybrida* and five other species, while four more had a similar negative correlation with lichen cover only. The species involved in these relationships are not among those found to be significant by Schøtz-Christensen (*loc. cit.*) or those recorded in the present study (Table 7.3i), and these regional differences therefore make comparability difficult.

The effect of vegetation structure on the communities of grasshoppers Orthoptera in sandy areas of the upper Rhine plain has been studied by Zehm (1997a). Using computer analysis he concluded that a direct relationship could be made between vegetation structure and grasshopper colonisation. The pioneer Corynephoretum proved to be poor in species and characterised by *Myrmeleotettix maculatus* in particular, with *Oedipoda coerulescens*, *Chorthippus mollis* and *Oecanthus pelluscens* also associated. The greatest abundance of Orthoptera could be found in dense but not totally closed vegetation, whereas a completely different grasshopper coenosis was found in dominant stands of grasses. In a study of plant species eaten by Orthoptera Zehm (1997b) found that *Myrmeleotettix maculatus* and *Chorthippus mollis* intensively grazed *Berteroa incana*, *Lolium perenne* and *Carex hirta* while *Oedipoda coerulescens* preferred *Medicago minima*, *Centaurea rhenana* and *Hypnum cupressiforme*; no grasshopper grazed *C. canescens*. In the present study *Oedipoda coerulescens* appears to be positively associated with *Cladonia* species but negatively with *Hypnum cupressiforme* (Figure 7.3h); and a specimen was observed browsing on dead lichen propagules on Site BR3 on one occasion.

The importance of vegetation structure on many invertebrate communities is further corroborated by work on abandoned coal mining sites in Germany (Bröring et al., 2005; Bröring & Wiegleb, 2005). Colonisation of newly-available sites by a range of invertebrate groups was rapid and extensive, with generally little difference in colonisation rates between phytophagous and zoophagous species. The subsequent changes in species assemblages were due to a combination of factors, of which developing vegetation structure and some soil parameters (pH, water capacity, nitrogen and phosphate content, heat output of substratum) were the most important. Vegetation structure tended to be more crucial for herbivore communities and soil parameters for zoophagous species, but these differences were not great. For Heteroptera the development of plant species composition and SO_4 content of the soil were additional important factors. Differentiation between vegetation types was unimportant for spiders Araneae, which responded most to vegetation architecture and spatial nearness between sites (Mrzljak & Wiegleb, 2000). Studying other habitats Usher (1992) and Wheater *et al*. (2000) achieved similar results showing the influence of vegetation structure for spiders. Usher's studies of arthropods in *Calluna vulgaris* heathlands additionally found a wet-dry gradient influence. Edaphic factors were also suspected to be more significant than any vegetation parameters for carabids in Scottish sand dunes (Blake *et al*., 2003).

A somewhat different result to the above studies of spiders was achieved by Merkens (2000) for spiders on German inland sand dunes. Using DCA analysis and calculated correlation coefficients she identified three species groups: one positively correlated with lichen cover, one positively correlated with cover of mosses and herbs, and a small third group correlated negatively with vegetation cover. *Aelurillus v-insignitus* was among the group exclusively found on sites with lichen cover, while *Arctosa perita*, *Oedothorax apicatus*, *Archaeodictyna ammophila* and *Yllenus arenarius* were restricted to the initial stage of the Spergulo-Corynephoretum where they lived on open sand. Merkens' results appear to conflict with Figures 7.3h and 7.3k where *Yllenus arenarius* is positively correlated with *Cladonia* spp. and plant litter. However, Merkens also found evidence that even within Germany a regional effect could be detected in habitat niche preferences, as several species were found regularly in dune habitats in western Germany which they typically did not occupy in the east of the country, a situation which she attributed to climatic differences. Whether there are regional or site specific factors operating for the habitat choice of *Yllenus arenarius* in Poland is not demonstrable in the present study, but the possibility cannot be ruled out.

Section 7.3.6 concluded that very few vertebrate species are regularly associated with the *C. canescens* habitat except rabbits and brown hares. A study of rabbit grazing on an inland *C. canescens* site on former agricultural land near the Dutch-Belgian border was carried out by Oosterveld (1983) and Kuiters & Slim (2003). The former author found that rabbits were significant grazers in the early stages after abandonment in 1972, when they completely prevented tree regeneration. However, rabbit densities across the site declined sharply as coarse grassland developed, so that by 2000 the highest densities of rabbits remained on patches of *C. canescens* grassland with densities up to 8 animals/ha when the mean across all habitats was <1 (Kuiters & Slim, *loc. cit.*). These findings mirror those of Ranwell (1960) and Zeevalking & Fresco (1977) that rabbits normally contribute effectively to grazing in open dune grasslands, as well as those of Anderson & Romeril (1992), that rabbits tend to avoid tall, dense grass swards. Kuiters & Slim (*loc. cit.*) simultaneously studied pony grazing on the same reserve and found that these animals under-exploited *C. canescens* grassland in favour of other grassland types. Further studies of grazing by domestic animals – cattle, sheep, ponies, goats – confirm that they do not find *C. canescens* very palatable and the grass declines under such grazing regimes (Kooijman & van der Meulen, 1996; Kooijman & Smit, 2001; Peco *et al.*, 2005) (cf Plate 4). Grazing by brown hares does not seem to have been addressed in the literature, but from the present study it would appear to have a similar impact on *C. canescens* grassland to rabbit grazing.

The other vertebrate species which has been studied in relationship to this habitat is the sand lizard *Lacerta agilis* (Märtens, 1999; Stumpel, 2004; Berglind, 2005), a scarce species across much of its range in central Europe and one which is vulnerable to increasing habitat fragmentation. From Märtens (*loc. cit.*) it appears that, while sand lizards occur on *C. canescens* habitats, these are the least frequented of seven vegetation types studied. In the Netherlands Stumpel (*loc. cit.*) found this lizard in six different habitat types but overwhelmingly in young conifer plantations with open areas containing abundant *Calluna vulgaris* and *Deschampsia flexuosa*; breeding took place almost exclusively in this habitat. In Sweden the restoration of open sandy areas with a structurally complex microhabitat consisting of open patches of bare sand with *Polytrichum piliferum* and a dense field layer of *Calluna vulgaris* led to the long-term recovery of sand lizard populations, though population growth was very slow. Both Berglind and Stumpel concluded that sand lizards require habitat diversity and large sites for their survival. The few observations made in the present study (7.3.6) are consistent with the findings of these studies.

7.4.3 Impact of the fauna on sand erosion and accretion

Six ant species are frequent associates of dry acidic grasslands in central Europe (Boomsma & van Loom, 1982; Boomsma, van der Lee & van der Have, 1982; Seifert, 1996; Soerensen, 1999), three of which - *Lasius niger*, *Formica cinerea* and *Tetramorium caespitum* - were recorded on the study sites. Monitoring of the effects of ants on sand erosion and accretion in early successional communities of the Spergulo morisonii- Corynephoretum canescentis has been carried out in southern Germany by Jentsch (2001) and Jentsch *et al*. (2002). These authors found that patches deriving from ant disturbances covered from 1% to 3% of the pioneer habitat stage, causing superficial but repeated sand burial of the matrix vegetation (mainly consisting of cryptogams) on a scale similar to that occurring on the Bromierzyk sites (7.3.4). Disturbance patches were often closely correlated with the occurrence of *C. canescens* which, along with *Spergula morisonii* and *Teesdalia nudicaulis*, had a significantly higher seedling establishment on disturbed plots than on undisturbed controls. Disturbances were generally short-lived and showed a seasonal pattern, decreasing in winter when vegetation cover, particularly of mosses, expanded. *Polytrichum piliferum* was a dominant recoloniser of disturbance patches, showing a main vegetative growth in autumn when it grew rapidly through sand dumped by ants, resulting in the loss of patches for colonisation by other species (King, 1997; Jentsch, 2001; Jentsch et al., 2002). *Polytrichum piliferum* has been shown to inhibit the germination of forbs and grasses (Rice, 1984; Putnam & Tang, 1986; van Tooren, 1990; Bechtel *et al*., 1998) through allelopathy and the induction of seed dormancy (Keizer *et al*., 1985; van Tooren *et al*., 1987; van Tooren, 1990). This reflects the present study's finding that *Polytrichum piliferum* is a keystone species in the succession of the *C. canescens* habitat (5.3.4). In a further study Martinez & Maun (1999) showed that *Ceratodon purpureus* was also very resistant to burial by sand and could emerge from depths equivalent to 35 times its height.

Jentsch (2001) and Jentsch *et al*. (2002) studied the pioneer phase of the Corynephoretum in which ants produced sand surface disturbance only and did not create ant-hills – again mirroring the pattern shown at Bromierzyk, where *Formica cinerea* characteristically produced mounds in the later successional stages (7.3.4). In the United States Baxter & Hole (1966) studied the mound-building operations of *Formica cinerea* in prairie soil and estimated that they moved 7.4 metric tonnes per hectare every year. Soil movement was localised near the nest, many nests were short-lived and over the longer term much of the habitat could be affected. Other studies of ant activities in dry grasslands include those of Dean *et al*. (1997) on set-aside meadows in Germany, where nest-mounds of *Lasius flavus* and *Lasius alienus* had significantly less plant cover and mean number of plant species than the surrounding grassland; only a few plant species, notably *Calluna vulgaris*, *Thymus serpyllum* and *Cerastium arvense*, had a higher occurrence and cover on the mounds. The authors concluded that ant nest-mounds may favour plant species that cannot compete with tall grasses in this habitat.

Ants have a greater impact on grassland habitats than simply the creation of disturbance patches. Dean *et al*. (*loc. cit*.) noted that soils of nest-mounds had a different chemical composition (more Na and K, less P and N) than the surrounding soils; pH was also significantly higher; but these effects were not mirrored by differences in plant species growing on or off mounds. Ants are also regular distributors of seeds (Düll & Kutzelnigg, 1986; Oostermeijer, 1989). In the maintenance of the Corynephoretum, however, it is ants' creation of small-scale, frequent disturbances which appear to be the key factor (Jentsch, 2001).

In addition to the effects of ant disturbances on dry acidic grasslands Jentsch (*loc. cit.*) and Jentsch *et al*. (2002) studied the impact of rabbit disturbances. They found that rabbits create similar patches of free substrate to those of ants, though their disturbances tend to be of greater longevity and magnitude (affecting up to 15% of the habitat). They exhibited similar seasonal patterns, with increased activity between February and October, and similar clumped spatial patterns of distribution. The response of typical pioneer plant species of the Corynephoretum to rabbit disturbances mirrored their response to ant disturbances, with *C. canescens* showing even better seedling establishment on rabbit (40% presence) than on ant (24% presence) disturbances.

Further studies have been carried out on the impact of disturbances by small burrowing mammals on xerothermic grasslands (e.g. Platt, 1975; Hansell, 1993; Hoobs & Mooney, 1995), of animal tracks (Fischer et al., 1996), wind and water erosion (Bowers, 1982) and human activities (Cordes et al., 1997; Demarais *et al*., 1999). The impact of other fossorial invertebrates such as observed in 7.3.4, however, appears still to be thoroughly investigated.

7.4.4 Summary of conclusions from the investigation of the faunal community of *Corynephorus canescens* sites

The following conclusions have been reached from the study of the fauna:

251 taxa of invertebrates from 14 Orders were recorded on the study sites;

The invertebrate fauna showed a regional distribution into Polish, East Anglian and West Midlands sites in a similar same way to the flora, but with generally smaller proportions of invertebrate species than plant species shared between regions;

Both East Anglian and West Midlands sites contained species of conservation importance in Britain; the West Midlands sites acted as a refugium for several species with a coastal or southern / south-eastern British distribution;

Only a handful of invertebrates on Polish sites appeared to be of conservation importance in central Europe;

The invertebrate fauna of the study sites correlated well at the higher taxonomic levels (Order and Family) with other studies in the literature; at species level correlations were lower. This was compared with the literature which implied that the species composition of *C. canescens* habitats is localised and often site-specific;

The present study established relationships of parasitic flies (Diptera: Sarcophagidae) and harvestmen (Opiliones) with the *C. canescens* habitat. These relationships have been poorly studied in the literature;

The quadrat sampling methodology did not exhaustively sample the invertebrate fauna, but quadrat samples did appear sufficiently to characterise the fauna in CANOCO analyses;

CANOCO analysis of the effect of sites on the invertebrates suggested that:

- a strong relationship existed between species and sites;
- species associated with Kinver Edge sites and Polish sites consistently formed two groups; species associated with other West Midlands sites and East Anglian sites had less consistent associations;
- the Kinver Edge sites appeared to have more in common with Polish sites than East Anglian sites in terms of their fauna;

Lakenheath consistently appeared to be very different from other sites in several analyses. This was attributed to the specific management of the site;

Few invertebrates fed directly on *C. canescens*, but several were associated with other plant species appearing in various phases of the Corynephoretum;

in CANOCO analyses assemblages of invertebrate species appeared to be associated with:

- three vegetation types – a *Cladonia*-rich habitat, a maturing *Rumex acetosella* habitat and a *Festuca ovina – Hypnum cupressiforme* sward, but fewest species were associated with *Festuca ovina – Hypnum cupressiforme* vegetation;
- various sward height parameters – sward containing very tall and very short vegetation; a fairly tall sward with more uniform height; a shorter sward with very varied height structure; and a sward lacking extremes of height;
- various amounts of litter, of bare sand, and the stages of the *C. canescens* habitat;

The faunal analysis implied that Polish sites had a different vegetation structure to British sites;

Assemblages of invertebrate species associated with various vegetational and edaphic factors implied some relationships which had not previously been identified in the literature;

Polish sites were found to support a complex invertebrate community with a wide range of trophic and social relationships;

West Midlands sites supported communities comparable with those of Polish sites, with many but not all complex relationships represented;

East Anglian sites showed a simplification of faunal community structures, in particular through the thinning or disappearance of more complex trophic and social elements e.g. mimicry rings;

A handful of invertebrates, and particularly the ant *Formica cinerea* on Polish sites, produced sand erosion and deposition through their nesting habits.

Such erosion appeared to have positive benefits for the conservation of *C. canescens* populations;

Among vertebrates only rabbits and brown hares were regularly associated with the *C. canescens* habitat. A few other vertebrate species occasionally foraged over this habitat;

Rabbits benefited *C. canescens* populations by grazing and creating small-scale sand disturbances.

Plate 4: impact of man and animals on the *Corynephorus canescens* habitat.

Left: *Corynephorus canescens* tussock uprooted and discarded by grazing cattle, Site KE1.

Right: heavily trampled path and fenced paddock, Site KE3 (1994 enclosure). *Corynephorus canescens* is flourishing under protection.

Right: nest mound of ant *Formica cinerea* showing sand deposition around *Corynephorus canescens* plants. Site BR1.

CHAPTER 8: GENERAL CONCLUSIONS AND DISCUSSION

8.1 Extent to which the Aims of this study are realised

At the outset of this study three Aims were identified (1.2). The extent to which these have been realised is as follows:

Aim 1: to seek evidence for the naturalness or otherwise of the West Midlands Corynephorus canescens populations by comparing their associated floral and faunal communities with those of other British inland C. canescens sites and Polish sites in the heart of the grass's native range.

Twelve study sites were selected in the West Midlands, East Anglia and Poland (Chapter 3 and Appendix B) and data collected on the physical characteristics, vegetation, invertebrate and vertebrate fauna of these sites using the methodologies described in Chapter 4. The resulting data are given in the Tables and Figures of Chapters 5-7 and in the Disc Appendices.

The data were variously analysed to compare the floral and faunal communities of all sites. Taxonomic similarities and differences between sites were analysed in detail in 6.3.1 for the vegetation and 7.3.1 for the invertebrate fauna. Data on the vertebrate fauna were given in 7.3.6, but a detailed taxonomic comparison between sites was not carried out for the vertebrate fauna as most vertebrate species were infrequent visitors to *C. canescens* sites.

Further comparisons of the floral communities of the study sites were carried out by a TWINSPAN analysis of quadrat data (6.3.2), a CANOCO analysis of the same data (6.3.3), and a phytosociological analysis which compared the vegetation of the study sites with published phytosociologies for Britain and Poland (6.4.2). Further comparisons of the faunal communities of the study sites was carried out by CANOCO analysis (7.3.2). Some analyses of the invertebrate fauna carried out under Aim 2 are also relevant to Aim 1, particularly the inter-relationships between the invertebrate fauna (7.3.5).

The similarities and differences between sites and regions was discussed in detail in 6.4.1 and 6.4.2 for the vegetation and 7.4.1 for the invertebrate fauna.

By making comparisons between data for the different sites in this study, the analyses summarised above provide a cumulative body of evidence which is directly relevant to an assessment of the naturalness or otherwise of the West Midlands *C. canescens* populations. To this extent the study succeeds in fulfilling Aim 1. Further potentially relevant investigations beyond the scope of this study can be identified. For example, a cytological investigation of the *C. canescens* populations of the study sites may throw additional light on this problem though it cannot give a definitive answer. Additional lines of study which are potentially relevant to this Aim are detailed in 8.5 below.

Aim 2: to establish key community relationships between and within the chosen C. canescens sites

The analyses of the vegetational data by TWINSPAN and CANOCO (6.3.2, 6.3.3) and the phytosociological analysis (6.4.2) helped to clarify relationships between the vegetational elements of the study sites. The successional stages of the *C. canescens* habitat were identified and described (5.3.4) and the resulting schema was used in interpreting the analysis of the plants and invertebrates quadrat samples.

The relationships between plant species, vegetation structure and the invertebrate fauna were analysed including by CANOCO in 7.3.3 and discussed in 7.4.2. CANOCO was also used to analyse relationships of the invertebrate fauna to site-specific environmental factors such as the amounts of bare sand and litter, and to the successional stage of the *C. canescens* habitat (7.3.4) and these analyses were discussed in 7.4.2 and 7.4.3. Complex inter-relationships among the invertebrate fauna were explored via mimicry rings and food webs (7.3.5). Figures 7.3l, m and n express diagrammatically the relationships between the various taxa of invertebrate fauna and between the invertebrate fauna and flora of *C. canescens* habitats in the three regions.

It is felt that the above analyses successfully fulfil Aim 2 by exploring key community relationships in some depth for both flora and fauna, and most extensively for the invertebrate fauna. Still further exploration is possible by additional analyses beyond the present study, particularly for the flora; for example, characterising the vegetation in terms of ecological or functional strategies may allow further elaboration of relationships in the plant community.

Aim 3: to identify key factors with nature conservation implications for the British inland C. canescens populations.

A review of the literature on *C. canescens* (Chapter 2) identified factors relevant to the conservation of this grass, arising from its autecology (2.3), from recent studies in Europe (2.4.2), and from conservation measures taken at UK inland sites (2.4.3, 2.4.4). The conservation status of *C. canescens* in Britain and Europe was also addressed in detail (2.4.1).

Chapter 5 identified two factors (the phenology of *C. canescens* in the West Midlands and the effects of trampling on inland *C. canescens* populations) not covered by the literature and which may have conservation implications for British inland populations (5.1). Preliminary investigations were carried out and observations made on the phenology of *C. canescens* in cultivation and the response of *C. canescens* to trampling in three different situations in the West Midlands. Possible implications for the conservation of *C. canescens* were suggested (5.2.5, 5.3.7). Methodological issues limited the interpretation of the data (5.2.3, 5.3.3) and validation of the results remains to be carried out by formal replicated experiments. Hypotheses for testing by such experiments were drawn up (5.2.5, 5.3.6).

The faunal study quantified sand disturbances caused by rabbits *Oryctolagus cuniculus*, ants and other invertebrates and explored their relevance for the conservation of *C. canescens* (7.3.4, 7.3.6, 7.4.3).

The phytosociological analysis in 6.4.2 tested British inland *C. canescens* populations against syntaxonomies which underpin the conservation framework of these populations in UK and EU legislation. The results suggested that the conservation status of British populations needs revision.

In fulfilling Aim 3 this study successfully identifies and discusses some of the key factors for the conservation of *C. canescens*, including the importance of sand accretion and deposition and the role of vertebrate and invertebrate fauna in producing this. It also successfully explores the conservation framework of this grass in Britain. It is partly successful in exploring two factors potentially relevant to the conservation of *C. canescens* in the West Midlands, but this element of the study requires further experimental elaboration before firm conclusions can be reached. The study is also successful insofar as it allows information from its various elements to be collated into a management prescription for the conservation of *C. canescens* in Britain (8.4.2).

8.2 Some main conclusions from this study

Observations and conclusions reached from this study have been discussed in detail in Chapters 5, 6 and 7 and summarised in 5.2.4, 5.3.5, 6.4.3 and 7.4.4. The following paragraphs extract the main elements.

The ***preliminary field investigations*** in Chapter 5 suggest that *C. canescens* may have a wide amplitude between its fundamental and realised niches. A cultivation study in the West Midlands implied a phenology different in some respects from that realised in other field studies, and produced hypotheses for testing the differences and their main causes. A trampling investigation suggested that *C. canescens* may be disfavoured by both heavy uncontrolled trampling and protection from trampling. If verified by formal experiment, these findings could imply that *C. canescens* flourishes within a narrow set of environmental parameters and is competitively weak. The implications for conservation of this grass are treated in more detail below (8.4.2).

This investigation allowed the identification of four stages in the development of the *C. canescens* habitat, characterised by a mixture of physical and vegetational features: a pioneer phase; an early mature phase; a late mature phase; and a transition phase in which the *C. canescens* habitat passes to the next successional vegetation type.

An investigation of the ***vegetation of the C. canescens community*** in Chapter 6 showed that a number of associated plant species were quite strongly distributed on a regional basis, within three regions – Poland, East Anglia and the West Midlands. A relatively high proportion of species occurred infrequently in the samples, which was interpreted as a product of the small size of many sites in this study. A comparison of the suites of species represented on the study sites with British and European phytosociologies led to the conclusion that, while the Polish sites relate well to the typical Polish Corynephorion canescentis community, the classification of the British sites is more problematical. The East Anglian sites show some relationship with coastal *C. canescens* habitats; the West Midlands sites may be referrable to the NVC U1 community which may have some associations with continental vegetation types in which *C. canescens* occurs (6.4.2.4).

Chapter 7 investigated the ***faunal community of C. canescens sites*** and found that they were regionally divided along the same lines as the plant community. A number of invertebrate species are of conservation importance, particularly on British sites, and the West Midlands sites appear to act as a refugium for several species with a predominantly south-eastern or coastal British distribution. Very few invertebrate herbivores are directly associated with *C. canescens*. However, the *C. canescens* habitat is shown to support a complex invertebrate community, which is well developed in Poland, reasonably well developed in the West Midlands, and poorly developed on East Anglian sites. The analysis of invertebrate species against vegetational and environmental factors also highlighted a number of invertebrate relationships especially to vegetation structure and composition and the amount of bare sand and litter present (7.3.3, 7.3.4). In contrast to the invertebrate fauna, few vertebrates are strongly associated with the *C. canescens* habitat, with only rabbits and brown hares frequently recorded. Both are regular grazers of this habitat, and rabbits, along with ants and a few other invertebrates, are creators of small-scale sand disturbances which may influence seedling establishment and micro-scale distribution of *C. canescens*.

8.3 Is *Corynephorus canescens* native in its West Midlands sites?

A key motivation for this study was to explore whether *C. canescens* is native in its West Midlands sites (1.1, 2.2). Most authors have treated this grass as an introduction to these sites, with tank movements during the Second World War proposed as a possible mechanism (Trueman, pers. comm.). Evidence to support this view is that *C. canescens* is occasionally adventive well beyond its native range (2.2) and that it occurs on military sites in western Europe (Tschöpe *et al*., 2002; Jentsch & Beyschlag, 2003; Friedrich *et al*., 2004) and on a former tank training ground at Hedderwick, Scotland (Trist, 1998).

In the Second World War several locations around Kidderminster were occupied by US troop divisions between November 1943 and May 1944. The largest camp was at Site BT, known as “Camp Bewdley”, where tanks and artillery were stationed. Turley & Turley (2000) give a detailed history of Camp Bewdley, showing that US army units arrived via ports at Liverpool and Glasgow and remained in camp until May 1944, when they were moved south to take part in the Normandy landings. From June 1944 to July 1945 Camp Bewdley was converted to a field hospital for wounded soldiers repatriated from Normandy. Thirteen further localities near Kidderminster were occupied by US army units, but these did not include the Devil’s Spittleful / Rifle Range site or Kinver Edge: during the war the former was used for small arms practice and the latter by a local Home Guard unit (Turley & Turley, *loc. cit*.; M. E. Blunt, pers. comm.). The history of Camp Bewdley shows that it is very unlikely that troops and artillery using Site BT came into contact with populations of this grass, especially as Normandy falls outside the distribution range of *C. canescens* in France (Figure 2.2a; de Ruffray *et al*., 2002). The presence of *C. canescens* on the Devil's Spittleful / Rifle Range and Kinver Edge is also unlikely to be attributable to wartime military activities for reasons advanced above. If human agency is indeed responsible for the introduction of *C. canescens* to the West Midlands sites then transportation by itinerant farm workers, such as is attested for Site BT (Appendix B.4.1), seems a likelier explanation.

However, the findings of the present study suggest that a native origin for these *C. canescens* populations is certainly possible. By comparing the vegetation of the West Midlands sites with Polish and East Anglian sites, it is suggested that the two former groups of sites have plant communities which are more similar to each other than they are to the East Anglian sites (6.3.3), and that in the West Midlands *C. canescens* is located in vegetation types and suites of species which have some associations with the grass's known alliances in a European context (6.4.2). The faunal study further suggests that the West Midlands sites retain invertebrate community structures which have more in common with those of Polish than of East Anglian sites (7.3.2, 7.3.5). The present author therefore concludes that *C. canescens* occurs in a very natural context in its West Midlands sites and there is consequently no compelling reason to doubt that it is native there.

8.4 Conservation implications

8.4.1 The classification of Habitat 2330 in Britain

In Chapter 6 it was argued that, in relation to some other European countries, the JNCC has interpreted CORINE Habitat 2330 ("inland dunes with open *Corynephorus* and *Agrostis* grasslands") too narrowly within a UK context. Their interpretation aligns Habitat 2330 with the Spergulo morisonii-Corynephoretum canescentis association and treats the Breckland sites as the sole British examples (Rodwell, 2000). However, the EU Interpretation

Manual does not specifically identify Habitat 2330 with the Spergulo morisonii-Corynephoretum canescentis (Anon, 2003a), and several countries have aligned their inland *C. canescens* communities with Habitat 2330 even though their plant species assemblages are very different from the “classic” Corynephoretum (2.4.1). In Germany Habitat 2330 has been interpreted as represented by both the Corynephorion canescentis and Thero-Airion (Anon, 2006). On this basis there seems a case for arguing the inclusion of the West Midlands sites as further British examples of Habitat 2330. If accepted, this designation would bring the West Midlands sites fully within the conservation measures for Habitat 2330 required by the EU Habitats Directive.

8.4.2 Practical conservation measures for *Corynephorus canescens*: a prescription

The findings of the present study endorse Trist’s (1998) comments on the complexities of conserving *C. canescens* populations. In most sites the regular movement of sand appears to be the key element in maintaining early pioneer stages of open dune vegetation in which *C. canescens* may, however briefly, have a competitive edge (2.3.5). Factors producing sand movement which have been studied in the literature include:

wind action
mammal (especially rabbit) excavations
invertebrate (especially ant) excavations
trampling by humans and / or grazing herbivores
direct interventions e.g. rotavation, sand deposition, seed inoculation

In addition, it was observed in the present study that vehicle activity may have an influence on the local distribution of *C. canescens* plants on some sites (5.3.7); while the possibility that rain action may produce important sand movements (Blunt & Blunt, 2000) is still to be fully investigated.

As extensive afforestation of sand dunes in Europe has greatly modified the main natural process producing sand movement – i.e. wind action – other processes must therefore assume greater importance. Rabbits and ants are clearly effective in producing small-scale disturbances which favour the germination and longevity of *C. canescens* plants, and grazing by rabbits may also benefit *C. canescens* by reducing the vigour of plant competitors (2.3.6, 7.3.6, 7.4.2). However, it is uncertain whether rabbit and ant activities would be sufficient to maintain a *C. canescens* population over the long term. Studies in the literature of grazing by domestic animals (2.3.6, 7.4.2) imply that this management technique is of very limited value for *C. canescens*, while the trampling investigation in the present study suggests that trampling is unlikely to be a practicable measure for conserving *C. canescens* populations, though controlled light rolling might have more potential (5.3.7). Much is therefore left to direct interventions – sand deposition, rotavation, seed inoculation – to preserve or recreate specific *C. canescens* populations (2.4). Fortunately, *C. canescens* can respond well to such treatment, and interventions need only be on a small scale to produce favourable results.

A further natural process which may favour the longevity of a *C. canescens* community is the incidence of summer droughts, which may benefit the grass by preventing the establishment of competitor species (2.3.2, 2.3.5). This factor needs further study (see 8.5 below), but is only likely to impact significantly on populations in the east of its range: for example, in the present study droughted conditions were observed only on Polish Sites BR1, BR3 and BO in some years.

To summarise, the conservation of *C. canescens* populations needs to be assessed on a site-by-site basis. A conservation prescription may include restoring natural processes as far as possible, supplemented where necessary by interventions. An example may be:

- enhancing the influence of natural climatic processes, i.e. wind action (by removing barriers which act as wind-breaks) and drought (by removing shading vegetation)

- maintaining conditions favourable to rabbits and ants (e.g. marginal dwarf shrubs for the former, well insolated areas for the latter)

- controlling public access by footpath rotation

- assessing the value of interventions, e.g. rotavation, sand deposition, rolling, occasional vehicular passage, seed inoculation, and, where desirable, implementing them.

In 5.2.5 it was suggested that growing *C. canescens* in soil rather than sand in controlled conditions may be a short-term measure for producing large amounts of seed for inoculation in recovering sites. Long-term conservation success, however, is most likely to be dependent on the success with which vigorous wind action on open sand can be restored to a site.

8.5 Issues for further study

The conclusions from this research have suggested further issues whose investigation may throw valuable light on the ecology and conservation of *C. canescens* (e.g. 5.2.5, 5.3.6, 6.4.4). Further examples are:

How do climatological factors influence C. canescens communities?
The response of *C. canescens* itself to temperature has been addressed in the literature (2.3.2), but the effects of climate on the composition and population dynamics of *C. canescens* communities require further study. Differences between the continental climate of Poland (typified by more summer droughts and lower winter temperatures) and the Atlantic climate of Britain and western Europe (wetter summers and milder winters with rainfall throughout the year) may be a significant factor in competition and succession within the vegetation. The species composition of the invertebrate fauna may also be expected to respond to climatic differences at regional, local and site levels, and a possible example has been detected in the present study (Opiliones on West Midlands sites, 7.4.1). The influence of rainfall in

producing sand erosion has been briefly addressed in the literature (2.3.3) and initial data are available from the present study (4.3.5), but a more thorough investigation is merited.

How would an extended time-frame for sampling affect the results? As indicated in 3.1.2 and 4.1 sampling in this study was necessarily confined to the summer months and the hours either side of mid-day. This may have led to some under-recording of a few elements in the vegetation (e.g. winter and spring annuals), and more elements in the faunal communities (e.g. nocturnal invertebrates and those whose imagines occur early or late in the year)(4.5.5). An investigation of these elements would be desirable for a more complete understanding of *C. canescens* communities, and to assess whether the conclusions of this present study would need modification in consequence.

How are the British inland C. canescens communities associated with those of south-west Europe? From Chapter 6 it is evident that the interpretation of sand dune vegetation is a complex issue. Some findings from this study suggest that we may need to look even more widely at the European picture than our current NVC classifications appear to do. For example, over forty years ago Clapham, Tutin and Warberg (1962) described the annual *Hypochaeris glabra* as "a characteristic plant of open communities on non-calcareous sand, on dunes with *Corynephorus canescens* and *Jasione montana* ……etc." This plant was found on all British sites in this study except Site DS but, although widespread in Europe, it hardly features in phytosociologies or site descriptions for north-west European *C. canescens* habitats. In France, however, Julve (2005) described it as a characteristic species of the Violo caninae var. dunensis-Corynephoretum canescentis Westhoff (1943), where it is associated with abundant *Aira praecox* and *Jasione montana* (two other species which appear to play little part in north-west European *C. canescens* communities). In Iberia *Hypochaeris glabra* has been treated as typical of the Thero-Airion (Tüxen & Oberdorfer, 1958) along with a range of species including *Filago minima* and *Vulpia bromoides*. More recently it has been placed in the Helianthemenion guttati, in which it forms an association Hypochoerido glabrae-Tuberarietum guttatae Rivas-Martínez *et* *al*. 1993, (Rivas-Martínez *et al*., 2001). Associations involving *Aira praecox* are also included in the Helianthemenion guttati; while a current interpretation of Thero-Airion in Iberia includes an association Filagini minimae-Airetum praecocis Wattez, Géhu & De Foucault 1978. Rodwell's (2000) synthesis of British dune vegetation types with continental syntaxonomies appears to draw largely on a north-western European tradition; but it is suggested from the present study that relationships between the vegetation of British inland *C. canescens* sites and those of south-west Europe deserve more exploration.

Is there a typical invertebrate fauna of inland C. canescens habitats? In 7.4.1 it was argued from the findings of the present study that a typical fauna can be constructed at higher taxonomic levels (Order, Family), but this result does not seem to hold good at species level. Studying spiders, Merkens (2000) concluded that there is no characteristic species community of this habitat, and that the species composition of her sites largely depended on site-specific factors. This conclusion may also be implied by other site or regional accounts in the literature, which have few species in common. To test this hypothesis, three further studies are suggested for comparing the invertebrate fauna of inland *C. canescens* habitats with:

- other sandy habitats without *C. canescens* on the same sites
- coastal *C. canescens* habitats
- other habitat types (e.g. calcareous grassland) across a series of sites in the same geographical regions as the *C. canescens* habitats studied

This third study is suggested to test whether any site-specificity of the invertebrate fauna is an inherent quality of invertebrate communities in general or a particular feature of *C. canescens* communities. Even if the invertebrate fauna of inland *C. canescens* habitats cannot be defined as effectively as their plant communities, this study has shown that it may be a richly complex one sometimes involving rare and vulnerable species. Their conservation needs are as important to the maintenance of biodiversity within EU Habitat 2330 as the plant community itself.

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APPENDIX A: CALCULATION OF TRAMPLING PRESSURE ON SITE KE3 AREA A

Table Ai presents the raw data obtained from the counts made in 2002, as described in 5.3.2.1. The data show the number of individuals (adults, children, dogs, adults on bicycles, and push-chairs) which passed across Site KE3 Area A during each of 38 hours of observation spread across the year. By extrapolation from these data a calculation has been obtained of the trampling pressure per square metre per month, and this calculation is shown in Table Aii. It has been achieved by the following stages:

(1) every count detailed in Table Ai has been allocated to one of nine separate time periods (weekdays, bank holidays and weekends, each subdivided into early, middle or late times of day). The number of hourly samples which fall into each of these nine time periods is shown in column 3 of Table Aii;

(2) the number of individuals counted in each time period is aggregated and a mean is obtained for each category of individual by dividing by the number of samples shown in column 3. These means are shown in columns 4-8;

(3) the total number of daylight hours available to walkers in each of these nine time periods across the year has been calculated and is shown in column 9. The number of daylight hours has been reduced for the early periods of the day since the National Trust Warden’s observations suggest that virtually no walkers use the very early daylight hours in late spring and summer;

(4) columns 10-14 multiply the mean values for each category of individual by the number of available daylight hours to obtain the total number of individuals expected to pass across Area A during a calendar year;

(5) the different categories of individual are then converted to “adult equivalents” by weighting them according to a broad assessment of their differential impact on the sand surface (based mainly on their estimated

relative body weights): thus adults, adults on bicycles, and push-chairs all have a weighting of 1; children are weighted 0.5; and dogs are weighted 0.3. The sums of these weighted numbers are shown in column 15 as the “total adult equivalents” for the year.

In Table Aii a figure of 76,124 has been reached as the annual total of “adult equivalents” passing across KE3 Area A. By experimental observation of two male and one female adults walking 10 metres each it has been ascertained that one adult makes roughly two footfalls per metre when walking in a straight line. Since Area A is two metres in width, then the trampling pressure on it per month can be readily calculated as follows:

$$\frac{\textit{Total adult equivalents per year} \times \textit{number of footfalls per metre}}{\textit{Width of Area A in metres} \times \textit{number of months in year}}$$

Which is:

$$\frac{76{,}124 \times 2}{2 \times 12} = 6{,}344$$

It may be deduced, therefore, that the trampling pressure on Site KE3 Area A is broadly between 6,000 and 6,500 adult footfalls per m² per month.

Table Ai: Number of individuals passing across Site KE3 Area A during one-hour sample counts in 2002

Date (2002)	Day	Period of day	Weather conditions	Number of individuals				
				A	C	D	B	P
17 Feb	Sun	L (	dry, cool	112	20	20	0	3
“	“	L (						
25 Feb	Mon	E	drizzle	7	0	4	0	0
“	“	M	light rain	7	0	5	0	0
“	“	L	heavy rain	8	0	7	0	0
26 Feb	Tues	E	warm, windy	13	0	15	0	0
“	“	M	“	17	0	12	0	0
“	“	L	rain, clearing	13	0	11	0	0
3 Mar	Sun	E	dry, mild	41	0	26	0	0
“	“	M	“	71	11	17	0	0
24 Mar	Sun	E	dry, mild	35	2	17	0	0
“	“	M	dry, cool	28	3	10	0	0
1 Apr	Mon (BH)	E	dull, mild	18	0	13	0	0
“	“	M	drizzle, clearing	11	2	0	6	0
“	“	L	showers, windy	8	1	3	0	0
6 May	Mon (BH)	M	dull, cool	17	0	8	0	0
“	“	M	“	34	8	15	0	1
“	“	L	dull, warm	16	2	1	0	0
“	“	L	“	9	1	7	0	0
31 May	Fri	M	warm, sunny	5	0	2	0	0
“	“	M	“	6	2	8	0	0
“	“	L	“	7	0	6	0	0
“	“	L	“	1	0	0	0	0
1 June	Sat	M	hot, sunny	11	0	3	0	0
“	“	M	“	13	0	6	0	0
18 July	Thurs	E	dry	0	0	0	0	0
“	“	E	“	6	0	5	0	0
27 July	Sat	E	cloudy, warm	8	0	5	0	0
11 Aug	Sun	L	cloudy, warm, rain later	25	0	13	0	0
“	“	L	rain, clearing	9	0	6	0	0
25 Aug	Mon (BH)	E	dry, weak sun	8	0	4	0	0
25 Oct	Sat	L	mild, sunny	30	4	8	0	0
“	“	L	mild, dull	23	1	9	1	0
3 Nov	Sun	M	sunny, breezy	63	18	19	0	1
“	“	M	“	42	4	11	0	0
19 Nov	Tues	M	mild, dull	11	0	3	0	0
“	“	L	“	8	0	4	0	0
“	“	L	“	6	0	5	0	0

Key: A = adults B = adults on bicycles BH = Bank Holiday C = children
D = dogs E = early M = middle L = late P = push-chairs

Table Aii: Mean number of individuals recorded per hour and estimated total number of individuals per year crossing Site KE3 Area A in 2002

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Day	**Time of day**	**No. of samples**	**Mean number of individuals recorded per hour**					**Est. hours / year**	**Estimated total number of individuals per year**					**Total adult equiv-alents/year**
			A	**C**	**D**	**B**	**P**		**A**	**C**	**D**	**B**	**P**	
Week-day	E	4	6.5	0	6.0	0	0	847	5506	0	5082	0	0	7200
	M	5	9.2	0.4	6.0	0	0	1016	9347	406	6096	0	0	11582
	L	6	7.2	0	5.5	0	0	1016	7315	0	5588	0	0	9178
Bank Holiday	E	2	13.0	9	8.5	0	0	24	312	0	204	0	0	380
	M	3	20.7	3.3	7.7	2.0	0.3	32	662	106	246	64	10	871
	L	3	11.0	1.3	3.7	0	0	32	352	42	118	0	0	412
Week-end	E	3	28.0	0.7	16.0	0	0	346	9688	242	5536	0	0	11654
	M	6	38.0	6.0	11.0	0	0	416	15808	2496	4576	0	0	18581
	L	6	33.2	4.2	9.3	0.2	0.5	416	13811	1747	3869	83	208	16266
Annual Total								4145	62801	5039	31315	147	218	76124

Key: A = adults B = adults on bicycles C = children D = dogs E = early M = middle L = late P = push-chairs

APPENDIX B: DETAILED DESCRIPTIONS OF SITES CHOSEN FOR THIS STUDY

The following sections give detailed information on the location, conservation status, general description and history of the sites chosen for this study. Schematic diagrams show (in light yellow) the location of the *Corynephorus canescens* populations on the sites. The main distribution of *C. canescens* is shown; patchiness within the population is not expressed diagramatically but is referred to in the text where recorded. Isolated tussocks which lie outside site boundaries are not shown but are also referred to in the text. Main features mentioned in the text are also plotted.

B.1 East Anglian sites: general information

Co-ordinates: 0^{o} 35' east, 52^{o} 25' north
Ordnance Survey grid reference: TL 757 843
Altitude: about 10 metres above sea level
Location: The two East Anglian sites lie in the adjacent parishes of Lakenheath and Wangford between the towns of Mildenhall and Brandon in west Suffolk. They are respectively about 6 km and 3.5 km south-west of Brandon.

Conservation status: Both localities are Sites of Special Scientific Interest (SSSIs) designated most recently under the Wildlife and Countryside Act 1981. Wangford Warren (also known as Wangford Glebe) is a Nature Reserve of the Suffolk Wildlife Trust, which owns the site. Lakenheath SSSI is on an air-base owned by the Ministry of Defence and public access is prohibited without special permission. There is liaison between designated personnel on the air-base and English Nature's Peterborough office over conservation issues on this SSSI.

General description and historical information: Information in the following paragraphs is largely drawn from Trist (1998), Webb (1986) and Williamson (2000). This area of East Anglia is known as the Brecklands and covers some 1,000 km² of agriculturally marginal land, with an average rainfall, at 558 mm, one of the lowest in Britain. Its light acidic sands lie above porous chalk and were formed by leaching at the end of the earlier Ice Ages. The region has been cultivated from about 4,000 BC when forest clearance was begun by Neolithic farmers, and it has been continuously exploited by man since then, though populations have fluctuated at various times. Sheep were grazed on the Brecklands from the Roman period into the 20th century, with a peak in the Middle Ages when vast flocks were pastured on heathlands by day and folded onto arable land by night. Rabbits *Oryctolagus cuniculus* were introduced in the 12th century and warrens were established on many heaths: that on Lakenheath Warren is thought to have existed for 700 years. In periods of prosperity marginal heathlands were often ploughed and cultivated for a few years, after which they were allowed to revert back to heath: these are the “break lands” after which this Brecklands region is named.

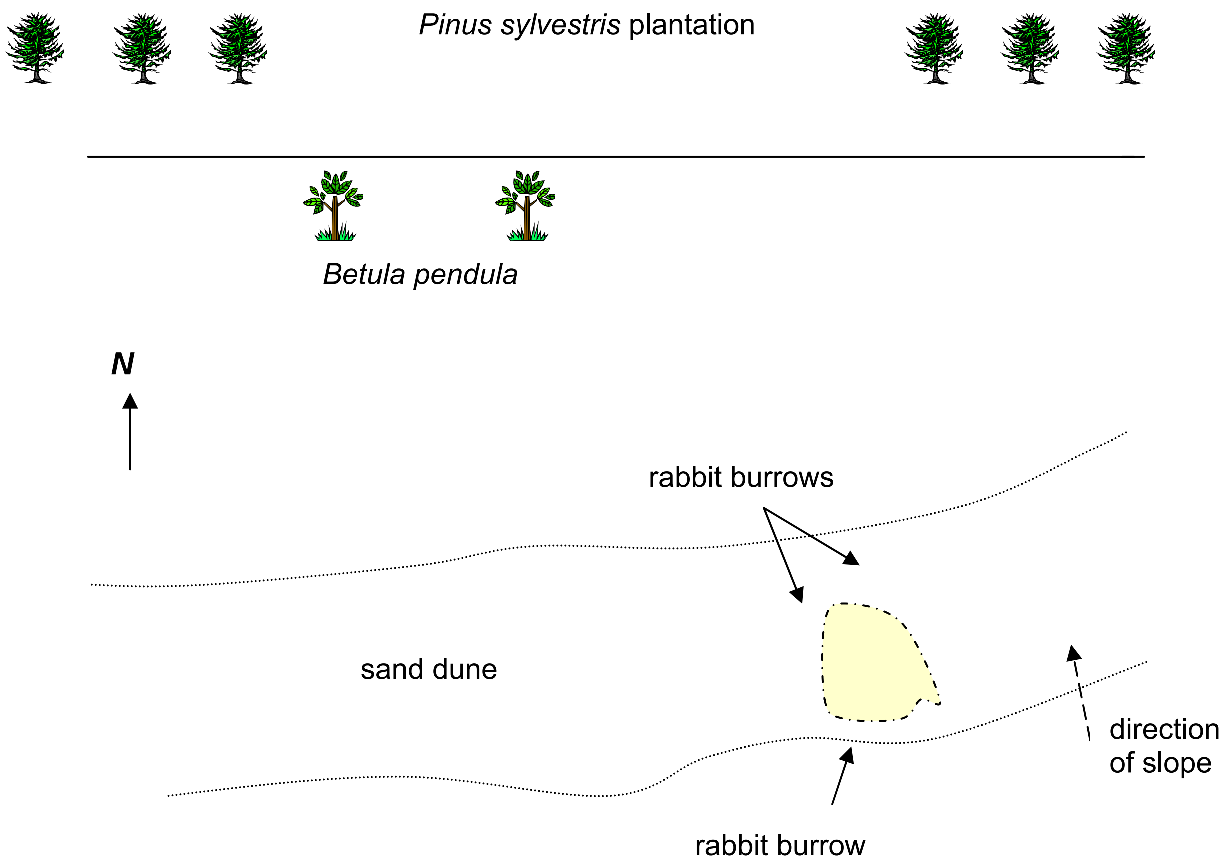
This combination of climate, soil and grazing produced large areas of thinly vegetated land subject to frequent disturbance by wind-storms, some of which could be severe. Lakenheath Warren was among the largest dune systems in the region, extending over 280 hectares, with dunes up to 1 km wide and 6 metres high. From the 1920s, however, huge areas of the Brecklands were acquired by the Forestry Commission and planted up with *Pinus sylvestris* and *Pinus nigra*; the plantations around Brandon and Mildenhall close to the study sites date from the late 1930s. In 1942 Lakenheath Warren was commissioned as an airfield and its entire dune system was bulldozed flat. A particular consequence of the planting of conifer shelter-belts has been a marked decline in frequency and severity of wind erosion and sand deposition; this in turn has reduced the formerly large areas of open mobile dunes to small remaining fragments, of which Wangford Warren is the best surviving example.

Descriptions of the two East Anglian study sites are given in B.1.1 and B.1.2 below.

B.1.1 Wangford Warren (Site WW)

Description of study site: A brief description of the site of the *C. canescens* colony at Wangford Warren in the years following its rediscovery there is given in 2.4.4. When first visited by the author in July 1998 the colony was found to occupy an area of about 5 m^2 on the south-facing slope of a small dune rising about 1.5 metres above the neighbouring ground. At the foot of the dune immediately to the south of the colony, and again on the crest of the dune immediately to the north, are extensive excavations caused by rabbits, though the grass was not found on these areas of fresh rabbit activity. The open sand on the dune is extensively colonised by sand sedge *Carex arenaria* and brown bent *Agrostis vinealis*, forming a sparse sward about 30 cm in height; *Senecio sylvaticus* and *Filago minima* are also frequent associates in this area, and *Pteridium aquilinum* is encroaching within a few metres on the northern slope of the dune. Away from the immediate vicinity of the *C. canescens* colony Wangford Warren consists chiefly of an open area of well-developed, dry lichen heath where *Carex arenaria* and *Agrostis vinealis* are again the dominant higher plants. As Trist (1998) observed, little lichen survives around the *C. canescens* plants due to the effects of spreading sand there to encourage growth of this grass. Forty metres to the north of the *C. canescens* colony is a mature plantation of *Pinus sylvestris* extending the full width of the reserve along its northern boundary, and just within the boundary fence close to the *C. canescens* population are two large *Betula pendula*.

Figure B.1a: schematic diagram of Site WW (not to scale).



B.1.2 Lakenheath (Site LA)

Description of study site: Because of the military nature of this site only a written description of the area immediately surrounding the *C. canescens* populations is given here, without a diagram. In June 2002 a thorough search was made of all locations on Lakenheath SSSI where this grass has been recorded in the past, based on information in Trist (1998) and held by A. Cunningham on the air-base. As a result of these searches *C. canescens* was found in three localities: two by the main runway and a third in the northern sector of the air-base just inside the perimeter fence. Only two plants of the grass were present in this third location and these form no further part of this study. Three other locations where the grass formerly grew were searched without success; the habitat still appears to be suitable at two of these, but the “smaller area” referred to in Trist (*loc. cit.*) has been built over. Consequently, this study of *C. canescens* at Lakenheath SSSI concentrates on the two main surviving locations which are designated here as Area A and Area B.

Area A lies about 150 metres north of the main runway and some 300 metres south-west of Wangford Farm. It extends in a broad band parallel to the runway for a length of about 400 metres and a width of 100 metres. *C. canescens* is patchily distributed within this area, forming three more or less discrete colonies; the smallest, at the northern end of Area A, holds perhaps 200 plants, while the other two have several thousand plants each; however it is difficult to judge both the boundaries and size of these populations because the turf in which they grow is kept constantly mown to a height of no more than 4 cm. Area A is flat and featureless, yet although exposed to strong winds and turbulence there is hardly any evidence here for sand movement; on the contrary, the sand is stable and covered by an almost completely closed sward. There is some indication that *C. canescens* grows most profusely in parallel bands, perhaps implying that the movement of wheeled vehicles may play a part in its local distribution in Area A.

Across the main runway to the south of Area A lies Area B. Its appearance is very similar to the foregoing, consisting of a featureless, flat, closely-mown area of about 200 m^2. *C. canescens* is thinly scattered in three small patches, together totalling no more than 100 plants. Within Area B is a small hollow about 2.5 m^2 in area containing loose, wind-blown sand; being below the level of the surrounding terrain, the vegetation within the hollow is not affected by mowing and *C. canescens* forms normal flowering tussocks there.

The turf in Areas A and B is dominated by *Festuca ovina*, with *Agrostis vinealis* also frequent. There is a rich assemblage of other species which are fully described in the appropriate sections of Chapter 6.

B.2 Kinver Edge: general information

Co-ordinates: 2° 15’ west 52° 26’ north
Ordnance Survey grid reference: SO 834 827
Altitude: about 125 metres above sea level
Location: Kinver Edge lies immediately south-west of the village of Kinver, just within the south-western boundary of Staffordshire. It is 6.25 km due north of the town of Kidderminster. The three study sites are located close to the south-eastern boundary of the National Trust property.

Conservation status: Land on Kinver Edge was donated to the National Trust in 1917 and is managed by the Trust, advised by a local committee of Kinver residents including the National Trust Warden. It is a Site of Special Scientific Interest (SSSI) and is being managed to restore areas of *Calluna vugaris* heathland and conserve its characteristic landscape, flora and fauna (Anon, 2003b).

General description and historical information: Much of the information in the following paragraphs is taken from Anon (1974), Hazlehurst (1992) and Horne (1995). Kinver Edge covers an area of about 246 hectares of which 141 ha are the property of the National Trust. It consists of a ridge of Lower Mottled Sandstone of Triassic origin, orientated NE-SW and reaching 165 metres above sea level at its highest point. The soft sandstone rock has a loosely-cemented cap, and is overlain by Bunter Pebble Beds which outcrop on the dip slope of the Edge. The sandstone is very free-draining, which results in a leached acidic soil supporting a *Calluna vulgaris* - *Deschampsia flexuosa* heathland vegetation. Woodland consisting largely of *Quercus robur* and *Betula pendula* grows extensively on and below the escarpment.

An Iron Age hill fort at the north-eastern end of the ridge attests human settlement on Kinver Edge from an early period. A series of caves in the scarp slope may also have been occupied from ancient times, and these caves remained as dwellings until the 1960s; one has recently been restored and re-occupied by the National Trust. The later land use of Kinver Edge is not well evidenced, though between about AD 1100 and 1300 it was almost certainly managed under forest law as part of the Royal Forest of Kinver, administered from Stourton Castle on the outskirts of the village. Extensive deforestation occurred between the 14th and 17th centuries, probably linked to the rise of the iron industry in Kinver. From then to the 20th century the dip slope of Kinver Edge was grazed by sheep and large numbers of rabbits; the removal of the former in the course of the 20th century, and a huge decline in the latter through myxomatosis in the 1950s, brought about a rapid succession of the heathland to deciduous woodland; this was almost complete by 1986 when a programme of heathland restoration was initiated by the National Trust (Anon, 2003b).

Descriptions of the three Kinver Edge study sites are given in B.2.1, B.2.2 and B.2.3 below.

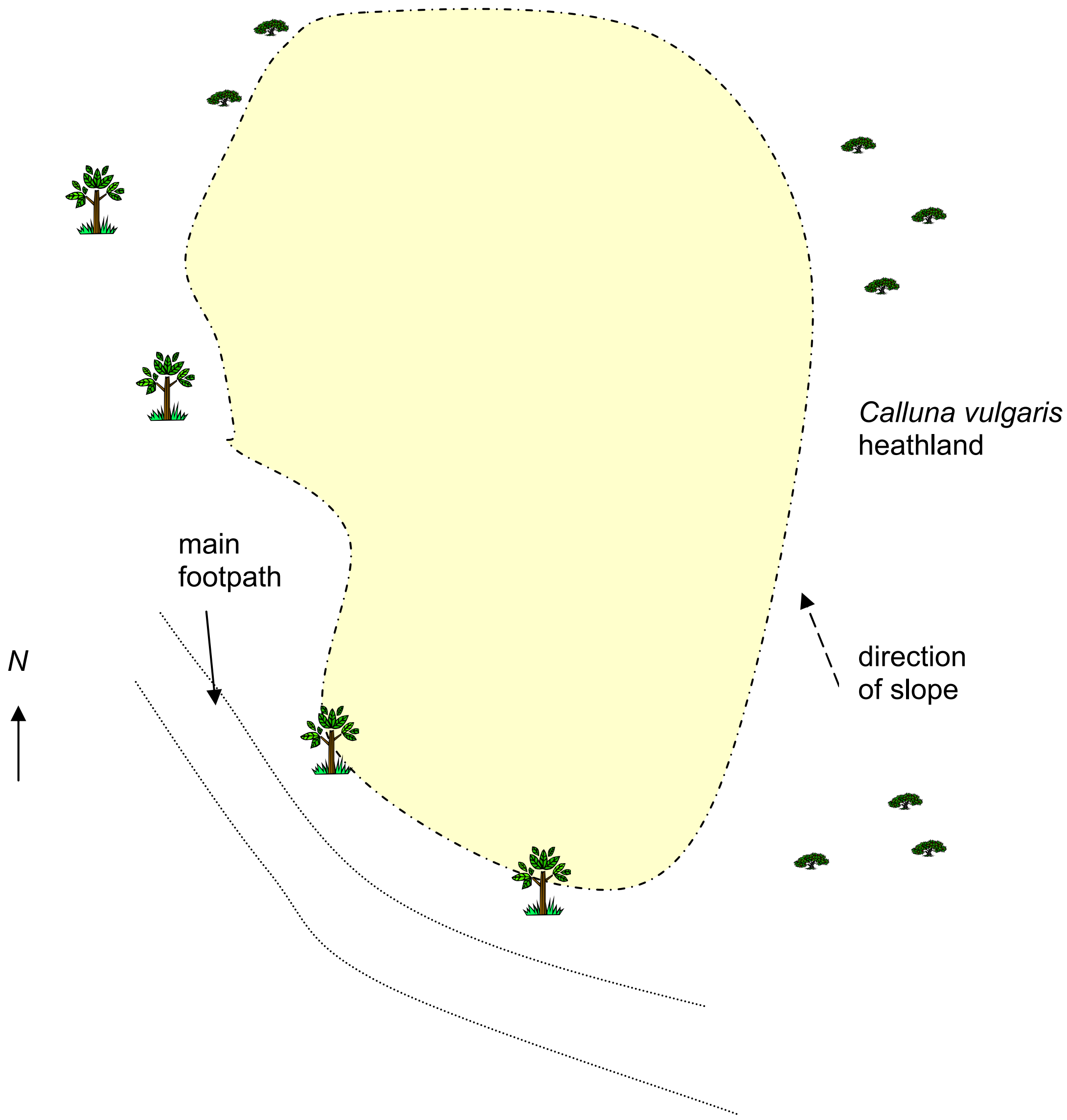
B.2.1 Kinver Edge Site 1 (Site KE1)

Description of study site: Kinver Edge Site 1 as defined by Blunt & Blunt (2000) is exactly the same as Site KE1 as defined in this present study. A description of this site from its discovery in 1977 up to 1998 is given in section 2.4.4; a more recent description follows here:

Site KE1 is a S/SE-facing slope of fairly open sand, loose in places and subject to movement as a result of rainfall. It measures 23 metres from top to bottom and 11 metres at its greatest width; the general shape is oval and it covers an area of roughly 200 m^2. Immediately above and below the slope run tracks used by the public, the lower being the main footpath around this part of the National Trust property. Beside the lower footpath and encroaching a little onto Site KE1 are two *Betula pendula* growing to 5 metres. On its other sides Site KE1 is bounded by heathland dominated by *Calluna vulgaris* and

Ulex europaeus, with seedlings of *Quercus robur* and *Betula pendula* and a patch of *Pteridium aquilinum*. A fairly well developed lichen heath exists in parts of the surrounding vegetation and a little of it encroaches onto the site itself. The main vegetation of Site KE1, however, consists of *C. canescens*, *Polytrichum piliferum* and *Rumex acetosella*, and both *Calluna vulgaris* and *Ulex europaeus* seed themselves freely into the semi-open sand. The site is grazed by rabbits, and since 1997 by cattle (Plate 4).

Figure B.2a: schematic diagram of Site KE1 (not to scale).

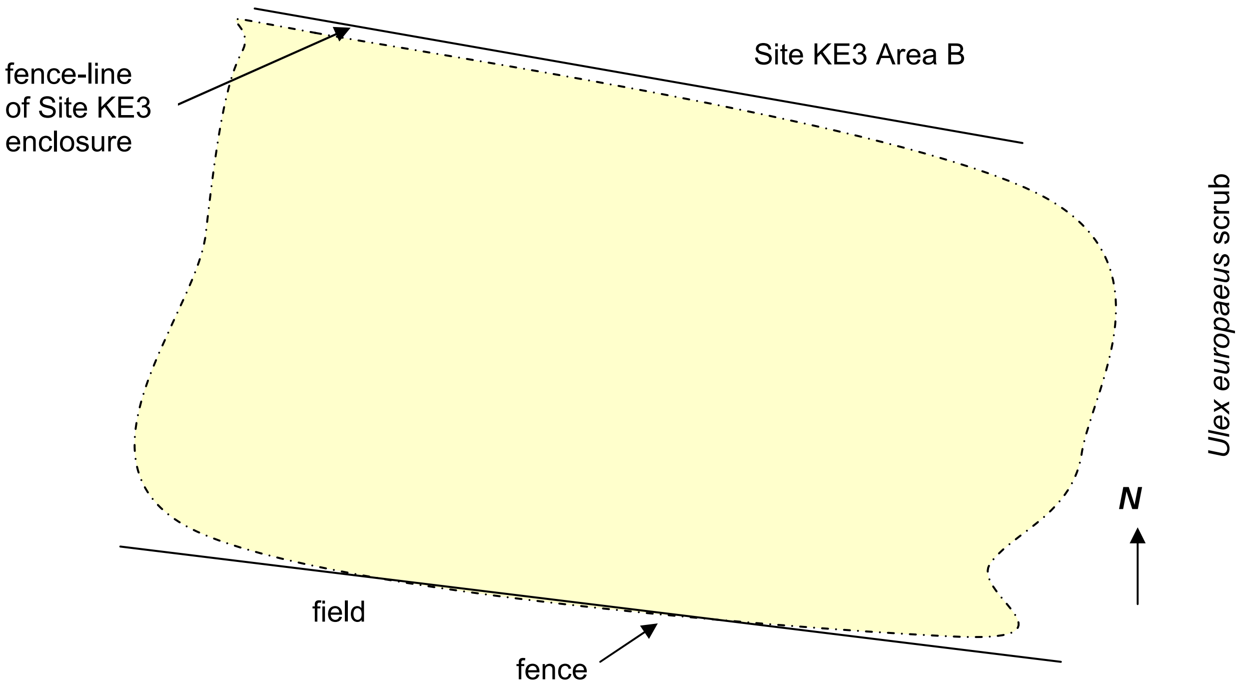


B.2.2 Kinver Edge Site 2 (Site KE2)

Description of study site: Section 2.4.4 describes this site as it existed up to 1998, at which point it was being overrun with *Ulex europaeus* scrub. Kinver Site 2 as defined by Blunt & Blunt (2000) and addressed in 2.4.4 is almost the same as Site KE2 as defined in this present study.

The site lies about 300 metres to the south-west of Site KE1 and separated from it by *Quercus robur* woodland. It butts upon the old boundary fence of the National Trust property and covers a rectangular flat area of about 179 m² (as measured by Blunt & Blunt, *loc. cit.*). Its eastern point is delimited by a *Ulex europaeus* thicket, and this same species also encroaches heavily at its western point, where the sand is shallowly undulating. In January 2001 the *Ulex europaeus* scrub at the western end of Site KE2 was cut down and removed. The site's northern boundary is the fence-line which delimits Site KE3 Area B (see B.2.3 below). The vegetation of Site KE2 consists chiefly of *C. canescens*, *Polytrichum piliferum* and *Rumex acetosella*, with *Vulpia bromoides* and *Deschampsia flexuosa* more locally. Both *Ulex europaeus* and *Calluna vulgaris* seedlings are scattered across the site.

Figure B.2b: schematic diagram of Site KE2 (not to scale).



There is frequent rabbit activity on site in the form of grazing and sand disturbance. Cattle grazing has also occurred during the summer months since 1997 and the site is also subject to light trampling by walkers, though the great majority of these use the track designated Site KE3 Area A in B.2.3 below.

B.2.3 Kinver Edge Site 3 (Site KE3)

Description of study site: Blunt & Blunt (2000) described Kinver Site 3 as an enclosure measuring 30 metres x 4 metres parallel to Kinver Site 2. This enclosure was fenced off in 1994 to prevent further footpath erosion by walkers, and when it was constructed the enclosed ground consisted entirely of bare sand. As a result of these measures, by 1998 about 11,000 plants of *C. canescens* were estimated to be growing in the enclosure.

To prevent further footpath erosion the boundaries of the fenced area were moved in March 1999 by 2 metres to the south of their previous location, leaving a 2-metre wide strip of *C. canescens* habitat from the 1994 enclosure as the new footpath. This footpath is designated in the present study as Site KE3 Area A.

Site KE3 Area B, as defined for the present study, is this 1999 enclosure which comprises an area of 30 metres x 4 metres. It directly adjoins Site KE2. It is enclosed by stock-proof fencing but is accessible to rabbits. Within this enclosure are two parallel strips, each measuring 30 m x 2 m, the northern one starting in 1999 as a well-developed *C. canescens* habitat and the southern one as bare, trampled sand. In March 1999 the author marked out with pegs and twine twenty study plots, each measuring 2 metres x 2 metres, ten along the *C. canescens* strip (designated Plots N1 to N10) and ten along the bare strip (designated Plots S1 to S10).

In this study Site KE3 has served as the location for a trampling investigation which is described in full in Chapter 5 section 5.3. Figure 5.3a is a schematic diagram of Site KE3 (see also Plates 3 and 4).

Although the above sites contain the major *C. canescens* populations on Kinver Edge, Blunt & Blunt (*loc. cit.*) identified three other places where this grass grows on the property, and since their publication a few other tussocks have been located in a fourth spot. These additional locations do not form a part of the present study.

B.3.1 Devil's Spittleful and Rifle Range (Site DS)

Co-ordinates: 2° 17' west 52° 22' north
Ordnance Survey grid reference: SO 808 746
Altitude: about 35 metres above sea level
Location: The Devil's Spittleful and Rifle Range complex lies immediately south-west of the town of Kidderminster in north Worcestershire, and about 3.5 km from the town centre. The Severn Valley Railway forms the southern and south-western boundary of the site, and the *C. canescens* population is adjacent to the railway.

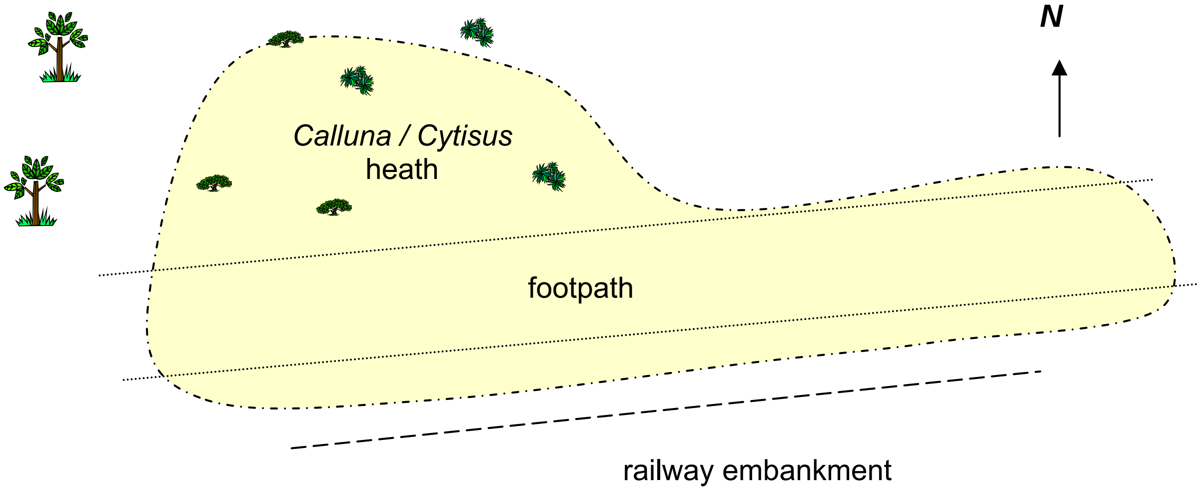
Conservation status: The Devil's Spittleful and Rifle Range together form a Site of Special Scientific Interest (SSSI) as a single site in dual ownership: the Devil's Spittleful is a reserve of the Worcestershire Wildlife Trust and the Rifle Range is a reserve of the Wyre Forest District Council. Habitats on these two areas merge into each other and the actual boundaries of each reserve are not obvious on the ground; it appears, however, that the *C. canescens* locality lies just within the Rifle Range part of the complex.

General description and historical information: The site comprises 60.7 ha of which about 12 ha is *Calluna vulgaris* heath and the remainder mostly deciduous woodland dominated by *Quercus robur* and *Betula pendula*. The north Worcestershire heathlands are generally restricted to sandstone substrates and are considered to be an extension of those of Staffordshire. It is thought that heathlands were once distributed across a broad swathe of north Worcestershire, but little evidence of their former extent and the process of habitat loss is available; it is estimated, however, that less than 10% of the area of heathland present in Worcestershire in 1775 is now left (Worcestershire County Council, 2006). What remains is subject to severe encroachment by woodland, scrub and *Pteridium aquilinum* following the cessation of grazing. The opening of the Severn Valley Railway in 1878 also brought with it a threat of fire from passing steam locomotives, a threat which persists today as the line continues to operate as a steam railway. During World War II military activities were carried out on the site of the Rifle Range reserve, and the vegetation there shows signs of disturbance in contrast to the adjacent, relatively undisturbed Devil's Spittleful (Hazlehurst, 1992).

Description of study site: The site lies along a 30-metre stretch of footpath orientated east-west on the northern side of the Severn Valley Railway. The railway embankment rises steeply within 2 metres of the footpath and bears a dense vegetation dominated by *Pteridium aquilinum*, *Cytisus scoparius*, *Rubus* spp. and *Agrostis capillaris*. Between this vegetation and the edge of the footpath is a flat area of no greater width than 55 cm where a few isolated plants of *C. canescens* survive. The footpath itself consists of mostly compressed sand kept bare by trampling, and varies in width between 70 cm and 185 cm. *C. canescens* grows most profusely along the northern edge of the footpath in a belt of vegetation up to 530 cm wide where, partly through management by fire and partly through occasional trampling by walkers, encroachment of *Calluna vulgaris* heath is suppressed enough to allow the population of *C. canescens* to maintain itself. The sand here is overlain with a thin humified crust varying in thickness from 3.0 mm to 10.5 mm, and the commonest plant associates are *Rumex acetosella*, *Senecio sylvaticus*, *Deschampsia flexuosa*, *Jasione montana* and *Hypochaeris radicata*. Beyond this zone of vegetation, and merging into it, is a further 10 metres of flat open ground where *C. canescens* recently grew as well-spaced single plants. The vegetation here is typical of *Calluna vulgaris – Deschampsia flexuosa* heath, with these two species dominating along with *Pteridium aquilinum* and *Cytisus scoparius* and regenerating *Quercus robur* and *Betula pendula* scrub (see Plate 2). A fence erected about 2000 along the northern side of the footpath effectively cut the main colony of *C. canescens* in two, and by 2003 this grass had largely been eliminated from within the fenced area by tall *Deschampsia flexuosa* sward and *Cytisus scoparius* scrub. As a result, *C. canescens* is now largely confined to the sides of the footpath.

Three further very small patches of *C. canescens* located by Hazlehurst (1992) along woodland tracks away from this main colony could not be re-found in 1998 and had presumably died out in the meantime through vegetational encroachment.

Figure B.3a: schematic diagram of Site DS (not to scale).



B.4.1 Burlish Top (Site BT)

Co-ordinates: 2° 17’ west 52° 21’ north

Ordnance Survey grid reference: SO 807 736

Altitude: about 75 metres above sea level

Location: Burlish Top is situated on the northern edge of the town of Stourport-on-Severn about 2 km NNW of the town centre. It lies 1 km south-east of the Devil’s Spittleful / Rifle Range *C. canescens* location.

Conservation status: Burlish Top is owned by and is a Local Nature Reserve of the Wyre Forest District Council. It does not have SSSI status but is a Special Wildlife Site as designated by Worcestershire County Council (2006).

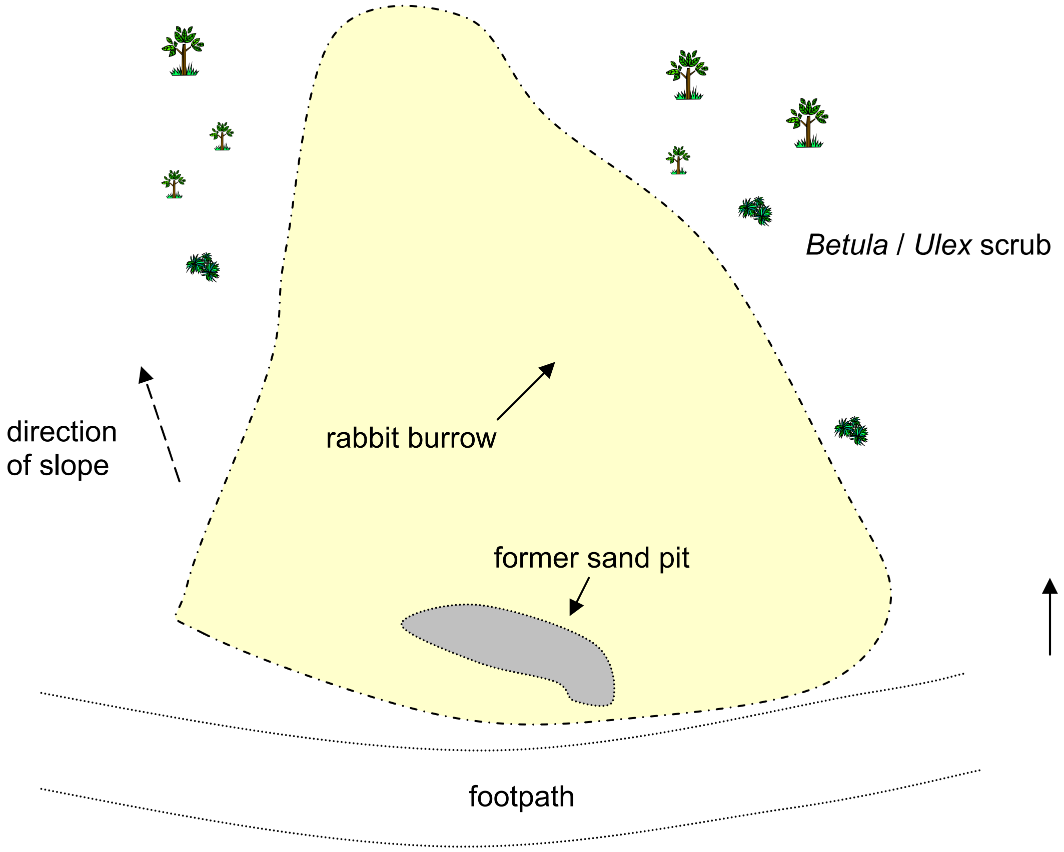
General description and historical information: Burlish Top reserve comprises a small sandstone plateau and its north-facing slope. It covers 35 ha of which about 12 ha is heathland. The soils are acidic and thin due to the underlying Bunter Sandstone, though where organic matter has accumulated is found a mosaic of secondary woodland and scrub, consisting chiefly of *Quercus robur*, *Betula pendula*, *Ulex* spp., *Cytisus scoparius* and *Pteridium aquilinum* (Hazlehurst, 1992). In the mid-20th century Burlish Top was a much more open habitat with few trees, heavily grazed by the horses of gypsies who camped there while working on local farms during the harvest. A small colliery also existed at the bottom of the slope (J. Anderson, pers. comm.). In the Second World War a military camp was established on the plateau and tanks were billeted there; remains of this camp are still visible on the ground today.

Description of study site: The main *C. canescens* colony is found about a third of the way down the slope below the plateau; a second, smaller population is at the foot of the slope, and a few scattered plants occur along paths radiating from the largest colony. All appear to be scattered relics of a single continuous population now much obliterated by tall vegetation and scrub. Only the largest area forms a part of the present study. It is located on a gentle slope and its dimensions are 17.5 metres on the NW-SE axis running down the slope and 9 metres on the NE-SW axis running across the slope at the lowest and broadest part of the site. It is somewhat bell-shaped with the narrowest part at the NW end and the broadest at the E/SE end. The surface of the ground is undulating, and at its south-eastern point there was until levelled in 2003 a deep, fresh sand-pit, completely unvegetated and measuring 4.2 metres long (E-W) and 45 cm deep, with a width varying between 0.8 metres and 2.1 metres. This pit (shown in grey on the diagram) was next to the footpath which defines the lowest edge of the site.

Vegetation surrounding the main *C. canescens* site includes: on the N and E sides, a thick scrub of *Ulex europaeus* to 2 metres in height, with some *Betula pendula* saplings to 3 metres; on its NW side *Betula pendula*, *Cytisus scoparius* and *Ulex europaeus* to 1.5 metres; and on its W and SW sides patches of *Pteridium aquilinum* and *Calluna vulgaris* with several low *Cytisus scoparius* bushes, a single *Crataegus monogyna* to 1.2 metres, and grassland dominated by *Holcus lanatus* with some *Deschampsia flexuosa*.

The vegetation within the site includes much *C. canescens, Polytrichum piliferum, Agrostis capillaris, Aira praecox* and *Hypochaeris radicata*; *Calluna vulgaris* and *Ulex europaeus* are also seeding well in places. In a few spots the sand is covered by a humified crust to 19 mm depth. Apart from the former pit there is little open sand, most of the site being well vegetated; and though fruiting and seeding quite well, *C. canescens* is under heavy competition. There is a rabbit burrow on site and in a few places ant-hills have created accretions of sand at the base of *C. canescens* tussocks to a maximum depth of 30 mm.

Figure B.4a: schematic diagram of Site BT (not to scale).



The remaining small populations of *C. canescens* at Burlish Top grow along path-sides, one of which is mown. The vegetation on and surrounding these populations is very similar to that of the main site, with *Arrhenatherum elatius* and *Rubus* spp. in addition.

B.5.1 Alveley Experimental Plot (Site AL)

Co-ordinates: 2° 21’ west 52° 27’ north
Altitude: about 105 metres above sea level
Location: in the village of Alveley, Shropshire, about 7.5 km WNW of the Kinver Edge colonies.

Conservation status: nil. The Experimental Plot is in the author’s private garden.

Description of study site: The Experimental Plot consists of a round wooden container with inner dimensions of 32 cm depth and 57 cm diameter and an internal area of about 2,550 cm^2. It has drainage holes in the bottom and was filled to a depth of 15 cm with pebbles and covered by 15 cm of sand, of unknown origin, obtained from a builders’ merchant. The container was sunk into garden soil to a depth of 18 cm. Vegetation surrounding the container consists of carpets of *Thymus polytrichus* and *Herniaria glabra*, together with a variety of specimen garden plants. The Experimental Plot was created by the author in August 1998, when 7 one-year-old tussocks of *C. canescens*, with small quantities of sand around their roots, were transplanted there from Kinver Edge Site KE2.

B.6 Bromierzyk sites: general information

Co-ordinates: 20° 23’ east 52° 18’ north
Altitude: about 80 metres above sea level
Location: Bromierzyk lies near the south-western boundary of Kampinos National Park in central Poland close to Warsaw. The nearest town is Sochaczew, about 14 km to the south-west. Bromierzyk was formerly a village consisting of scattered farmsteads along a dirt track which runs eastwards into the Park from its boundary at Famułki Brochowskie. Following re-purchase of land by the Park authorities only a few tenanted farms remain and Bromierzyk no longer exists as a village. Its former school building was during the period of this study used by the University of Łódź as a field station.

Conservation status: Much of the information for this and the following paragraphs is taken from Herz (1993) and Sobotkowska & Sobotkowski (1999). Kampinos National Park covers 35,721 ha and was designated in 1959. It incorporates a number of Strict Reserves (Rezerwaty ścisłe), Partial Reserves (Rezerwaty częściowe), Nature Monuments (Pomniki przyrody) plus other land in public ownership. In 1993 about 13% of the Park was private property, but this is steadily reducing through the policy of re-purchase. The Bromierzyk study sites lie close to a parabolic dune system known as the Hill of St Theresa (Góra koło św. Teresy), so called after a small chapel which stands close to the field station. The area has Partial Reserve status, which indicates that a primary conservation aim is the restoration of natural ecosystems on land degraded by farming activity.

General description and historical information: In the heart of Kampinos National Park lies the ancient river valley of the Vistula (Wisła) as it existed at the end of the last Ice Age, the so-called Upper Płoński Glaciation. On each side of the valley stretch parallel dunes which mark the river’s former banks and which form one of the finest inland dune systems in Europe; they rise to 35 metres above the surrounding landscape in the northern dunes, and to 20 metres in the southern dunes where Bromierzyk is located. The dunes are of several types, the commonest being parabolic dunes which were shaped through the movement and deposition of sand by the prevailing westerly post-glacial winds. Over several thousand years the Kampinos area developed a vegetational complex of pine, deciduous and mixed forest on drier ground with wet *Alnus* spp. woodland, marshes and peat bogs along the ancient course of the Vistula and its tributaries. This original woodland cover is referred to as the Ancient Kampinos Forest (Puszcza Kampinoska). From the 11th century AD settlers began to clear lands along the river valley, and from the 15th century clearances extended within the forest itself, a process which peaked in the 19th century. The idea of conserving the forest was first mooted in 1906, the first reserves were created in 1936 and 1937, and the Kampinos National Park finally came into being in 1959. In September 1939 the forest was the site of fierce large-scale fighting between Polish and German armies, and after the fall of Warsaw brigades of partisans operated from bases in the forest for the rest of the Second World War.

The area around Bromierzyk is dominated by the Hill of St Theresa, which today is covered with recent plantations of *Pinus* spp. over acidic soils. Here and there a few older deciduous trees survive. The field station and study sites are located at the western foot of this parabolic dune system, in the basin created by scouring wind action during the deposition of the dune.

Descriptions of the three Bromierzyk study sites are given in B.6.1, B.6.2 and B.6.3 below.

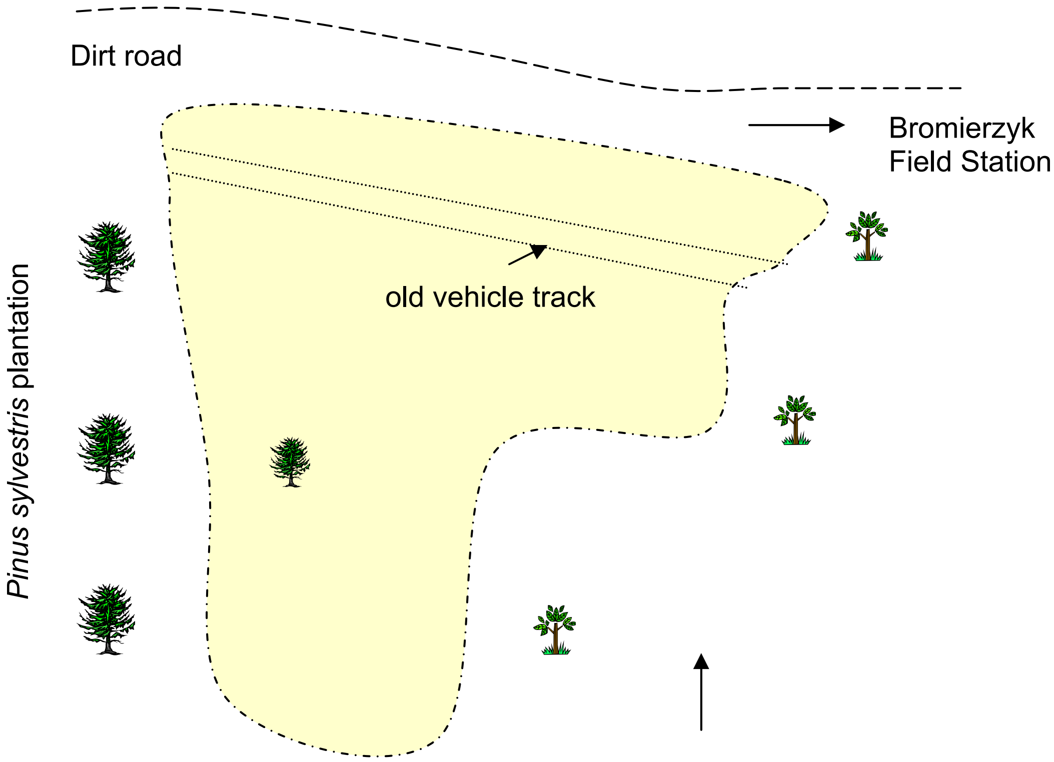
B.6.1 Bromierzyk Site 1 (Site BR1)

Description of study site: The site is an open, flat terrain just to the west of the field station and bounded along its northern edge by the dirt road through Bromierzyk. Its entire western side is bounded by a dense *Pinus sylvestris* plantation, with trees up to 9 metres tall in 1999. The site occupies 265 m², and resembles a rectangle whose sides at their greatest dimensions measure 19 metres (E-W axis) and 17.5 metres (N-S axis), but whose south-eastern section has been taken over by invading tall grassland and *Betula pendula* scrub. The areas of more open sand are situated towards the dirt road and these support a thin vegetational cover with *Spergula morisonii* and *Berteroa incana* as regular associates of *C. canescens*. An old vehicle track runs along the northern edge of the *C. canescens* habitat, forming the only small undulation on the otherwise flat terrain, and acting as a line of demarcation between Site BR1 and the surrounding vegetation. Lichens *Cladonia* spp. occur sparingly in the more open parts of the site and increase in frequency in its south-western corner, which is partly shaded by the neighbouring plantation. A solitary young *Pinus sylvestris* grows in the western part of Site BR1 and by 2003 this had reached a height of 4.5 metres.

On three of its sides the site grades into tall herbage in which *Agrostis stolonifera*, *Elymus repens* and *Calamagrostis epigejos* dominate, along with a variety of herbaceous species such as *Rumex acetosa* and *Oenothera biennis*; saplings of *Betula pendula*, *Pyrus communis* and *Robinia pseudacacia* regenerate freely among this taller herbage, and one or two small *Pyrus communis* saplings also invade the *C. canescens* habitat at its eastern edge (see Plate 2). Individual tussocks of *C. canescens* are occasionally found within this zone of taller vegetation up to 575 cm from the edge of the open Corynephoretum. Along its western side Site BR1 has no transitional zone of taller grassland but ends abruptly at the edge of the conifer plantation. The low overhanging branches cast heavy shade here, yet a handful of *C. canescens* tussocks grow beneath them, from 80 cm to 450 cm inside the plantation (mean of four measurements = 215 cm).

In July 2003 it was found that a wheeled vehicle had recently attempted to cut across Site BR1 in a south-easterly direction from the dirt road and had left two deep ruts of loose, soft sand, which were devoid of vegetation at that date.

Figure B.6a: schematic diagram of Site BR1 (not to scale).



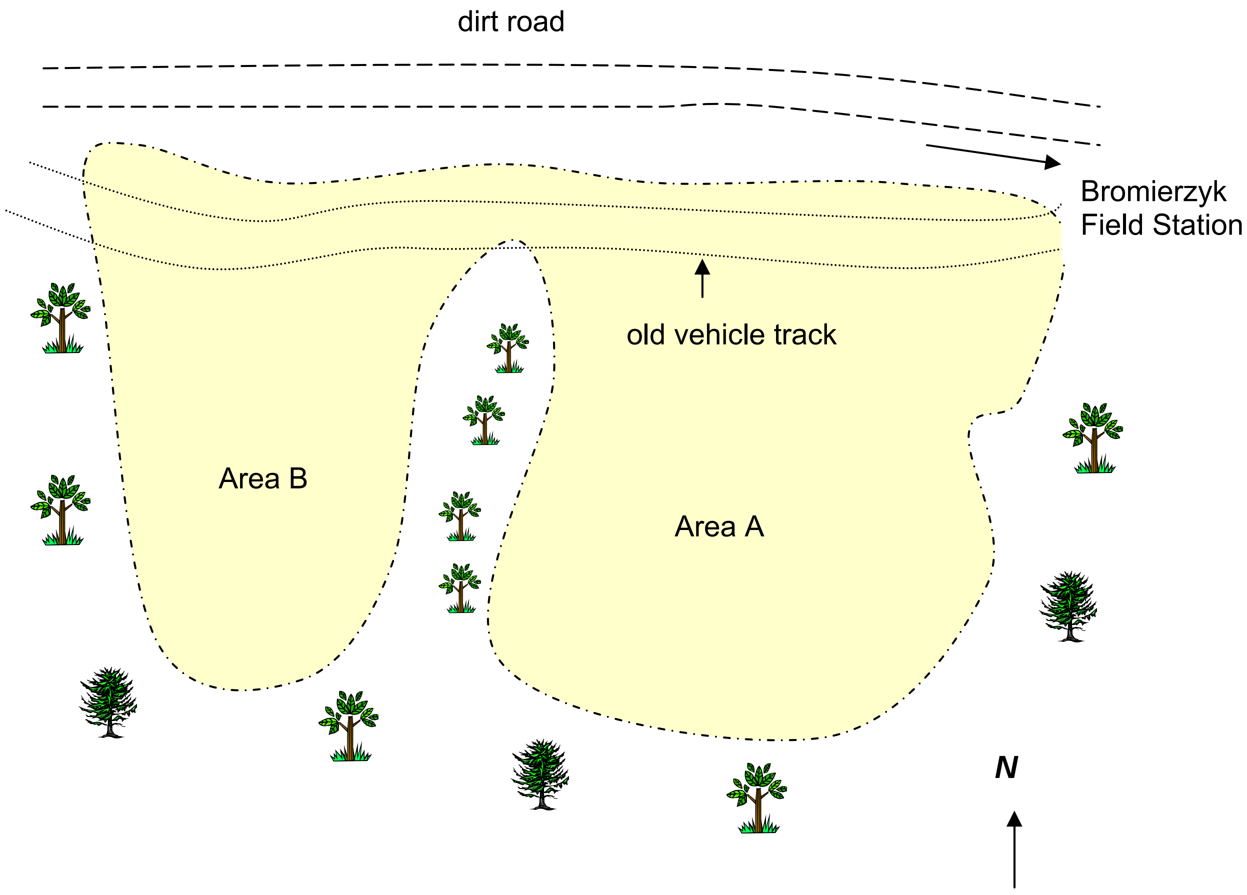
B.6.2 Bromierzyk Site 2 (Site BR2)

Description of study site: Site BR2 lies approximately 385 metres due west of Site BR1 and immediately south of the dirt road leading to Bromierzyk field station. It consists of two small clearings, the larger (eastern) one occupying about 90 m² and the smaller about 35 m², separated by a single line of *Quercus robur* to 4 metres tall. The site is surrounded by young woodland and scrub consisting largely of *Quercus robur*, *Pinus sylvestris* and *Robinia pseudacacia* and reaching a maximum height of 5.5 metres. Some saplings of these species are also at present invading the main *C. canescens* colony. An old track made by a wheeled vehicle marks the northern boundary of the site and separates the *C. canescens* habitat from a fringe of taller grassland next to the road; the ridges and ruts of this track also provide the largest area of open, thinly-vegetated sand on the site (see Plate 2).

For the purposes of this study the two clearings are designated Area A (larger clearing) and Area B (smaller clearing). *C. canescens* grows throughout these clearings as fairly tall, scattered tussocks among a thick leaf litter composed chiefly of dead *Quercus robur* leaves. Other plant species are not frequent and the best expression of the variety of plants in this habitat is in the northern and north-western edges of Area A, where the main *C. canescens* habitat grades transitionally into a taller herbage; associates here include *Convolvulus arvensis*, *Artemisia campestris*, *Berteroa incana* and *Agrostis stolonifera*.

As in Sites BR1 (above) and BO Area A (see B.7.1), individual *C. canescens* tussocks can be found within the neighbouring forest, here up to a maximum distance of 645 cm (mean of 17 measurements = 220 cm). In July 2000 the *C. canescens* colony of Site BR2 was estimated at about 300 plants in total.

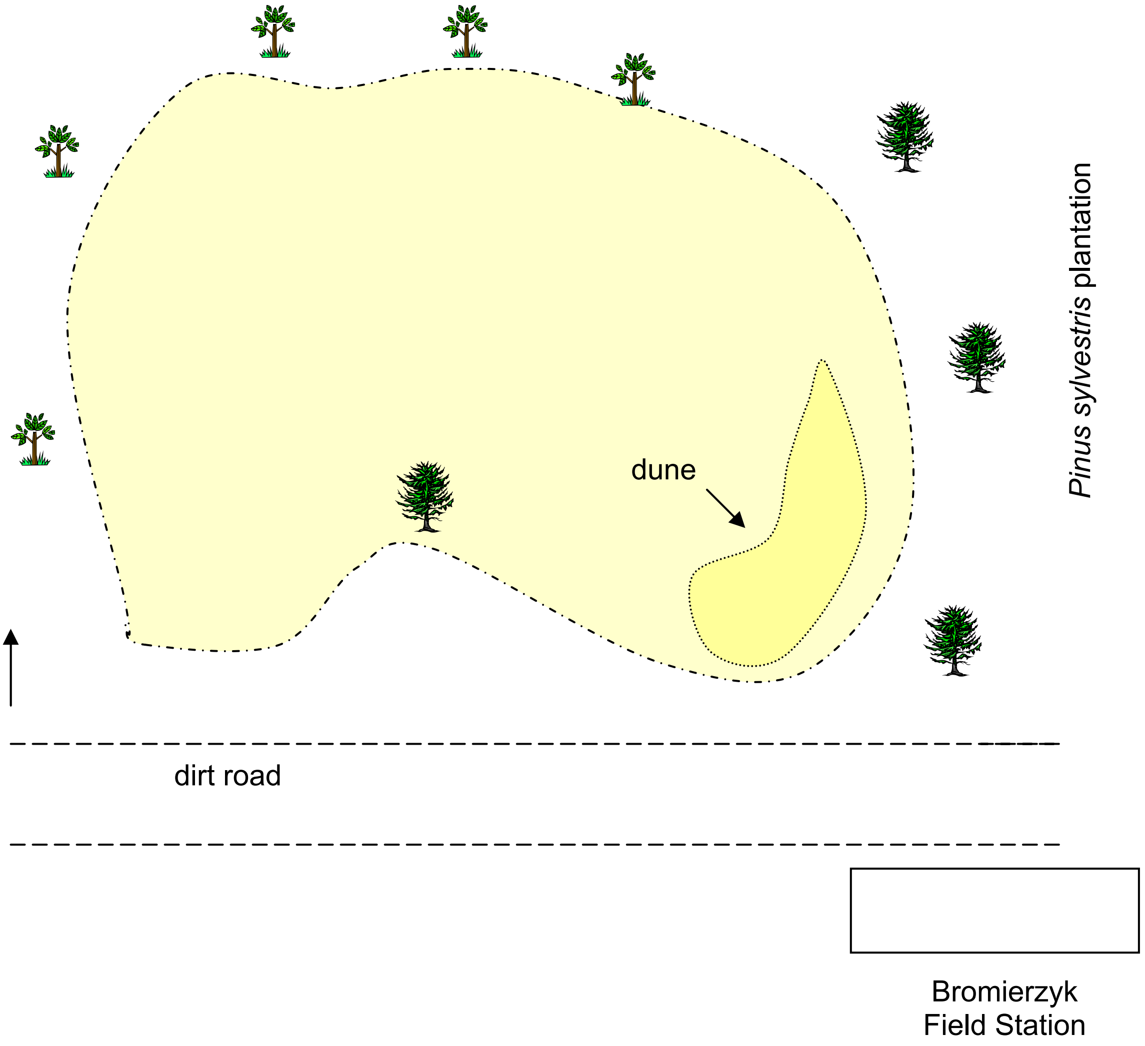
Figure B.6b: schematic diagram of Site BR2 (not to scale).



B.6.3 Bromierzyk Site 3 (Site BR3)

Description of study site: Site BR3 lies to the north of the dirt road through Bromierzyk and immediately across the road from the field station. It consists of a flattened depression with a gently undulating surface, and rising on its eastern flank to a dune some 1.3 metres higher than the surrounding ground level. The total area of Site BR3 is about 450 m^2; its maximum dimensions are 28 metres along its E-W axis and 18 metres along its N-S axis. The habitat is fairly uniform open sand with *C. canescens* common throughout, though in the centre of the site the vegetation cover becomes thin. There is a small *Cladonia* heath on the north-eastern edge of the site. On three sides the *C. canescens* habitat ends quite abruptly at woodland and scrub: a *Pinus sylvestris* plantation (height 9 metres) to the east; dense *Betula pendula* scrub to the north; and equally dense *Robinia pseudacacia* scrub to the south. A single 5-metre tall *Pinus sylvestris* grows just within the southern boundary of the site and shades an area around it. Only on its western edge does the *C. canescens* habitat grade into a transition zone of taller grassland consisting of *Calamagrostis epigejos*, *Agrostis stolonifera* and *Elymus caninus*, with a single mature lilac *Syringa vulgaris* on the forest edge as a relic from previous cultivation. Site BR3 was formerly the location of Bromierzyk's dairy; there are still small patches of asphalt on the dune in the south-eastern corner of the site, and a scattering of broken glass and domestic waste attesting to its former purpose can become exposed in the sand anywhere on the site.

Figure B.6c: schematic diagram of Site BR3 (not to scale).



B.7.1 Bolimów Landscape Park (Site BO)

Bolimowski Park Krajobrazowy

Co-ordinates: 20° 2' east 52° 0' north

Altitude: about 105 metres above sea level

Location: Bolimów Landscape Park lies about half-way between Łódź and Warsaw, just to the north-east of the town of Skierniewice in the Province of Łódź (Województwo łódzkie). The study site is at Grabie close to Leśnictwo (Forest District) Prochowy Młynek, about 8 km north-east of Skierniewice centre. It is about 0.3 km from the River Rawka.

Conservation status: The Bolimów Landscape Park, some 23,130 ha in area, was declared a protected zone in 1986. The study site is on private farmland within the Park.

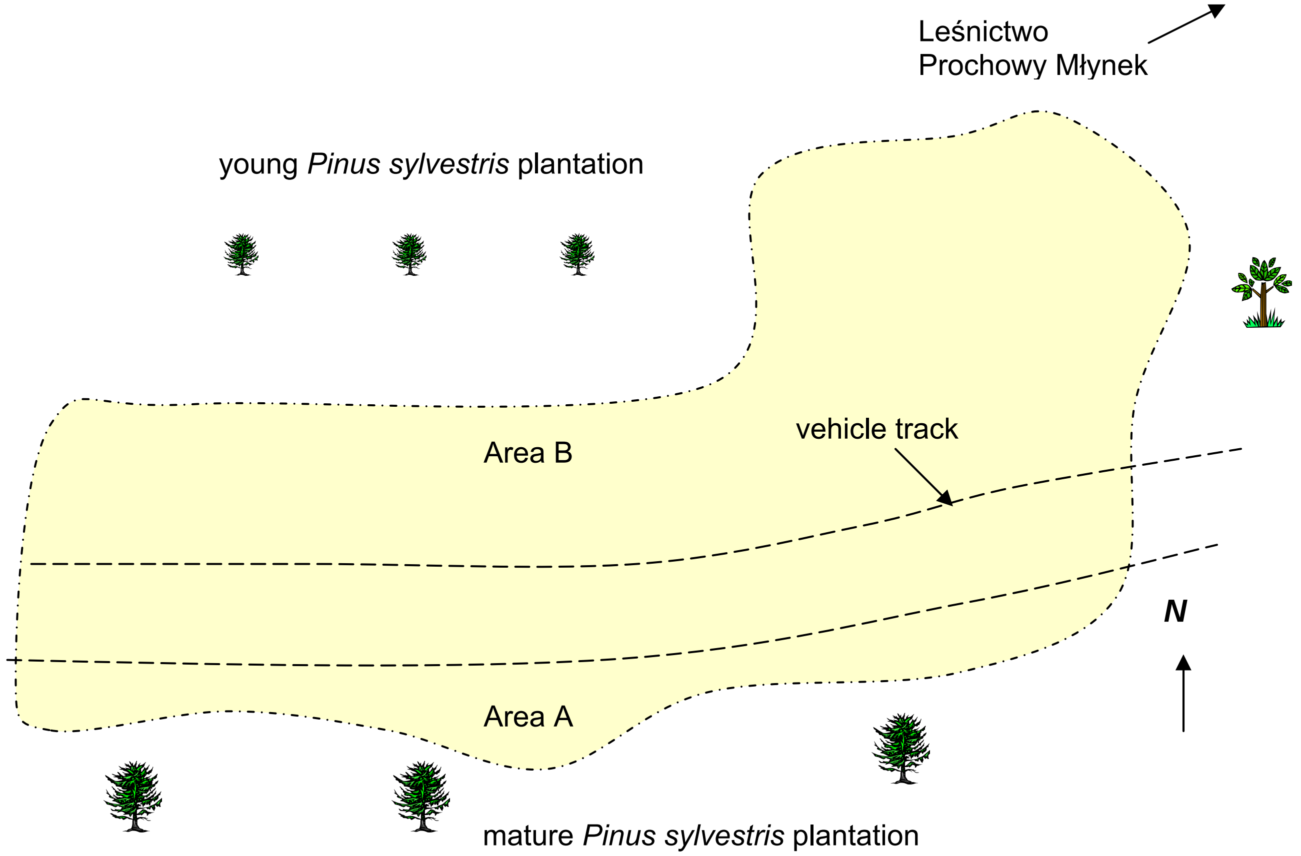
General description and historical information: Bolimów Landscape Park is the last remaining stretch of a once much larger forest complex. At its core runs the River Rawka and its tributaries, flanked by lush marshy meadow-lands, pastures and riverine thickets of *Alnus* spp. The valley is dotted with numerous pools and there is a series of oxbow lakes close to the study site. Away from the vicinity of the R. Rawka the Park is marked by poor, sandy soils which support woodlands dominated by *Pinus* spp., *Betula* spp. and *Populus tremula*, and containing specimen trees of *Quercus* spp., *Tilia* spp., *Acer* spp. and *Carpinus betulus*. Bolimów forest was the scene of fighting during the First World War; cemeteries are to be found throughout the forest and trenches from this war still exist within a kilometre of the study site.

Description of study site: The site occupies an area beside a 75-metre length of sandy track which runs east-west and is 2.6 metres wide, allowing vehicles to approach a homestead, farmland, young forestry plantation and an oxbow lake, all of which lie close to the study area. Access to the site is through a small *Pinus sylvestris – Quercus robur* woodland from the main dirt road almost opposite Leśnictwo Prochowy Młynek.

To the south of the sandy track rises a dense *Pinus sylvestris* plantation to 6 metres in height, confining *C. canescens* very largely to a narrow margin of track-side open ground. The largest area here is a patch of lichen heath measuring 5.5 metres x 4 metres, with *Cetraria islandica* and several tussocks of *C. canescens*; this is Site BO Area A. Isolated plants of *C. canescens* appear able to germinate within the plantation where even very small gaps in the canopy let in enough light: thirteen measurements taken from the edge of the track into the plantation located *C. canescens* plants at between 40 cm and 1,320 cm, with a mean distance of 540 cm.

To the north of the track is the main colony of *C. canescens*, designated Area B, and consisting partly of a flat open space measuring 14 metres (N-S) by 7.5 metres (E-W) with mature lichen heath and much *C. canescens*. It is backed to the east and north by forest consisting of mature *Pinus sylvestris, Quercus robur* and *Betula pendula*, with a single *Juniperus communis* some 2 metres high on the forest edge. Area B continues as a flat margin, about 4 metres wide, running on the northern side of the sandy track for about 67.5 metres to the west. The sand here is fairly compact and less vegetated with very little lichen or moss. At its western end the vegetation grades rapidly into taller grassland dominated by *Agrostis stolonifera*, and on its northern side it is bounded by a large area of ploughed and furrowed sandy ground planted in the early 1990s with rows of *Pinus sylvestris* interspersed with occasional rows of *Betula pendula*. By 2000 some of these saplings had reached 2 metres in height, though most were scarcely over 1 metre. There are traces of former vehicle tracks and parallel plough marks across the whole of Area B, showing that Site BO has been intermittently disturbed in the recent past.

Figure B.7a: schematic diagram of Site BO (not to scale).



B.8.1 Ciosny Reserve (Site CR)

Rezerwat Ciosny

Co-ordinates: 19° 22’ east 51° 55’ north
Altitude: about 140 metres above sea level
Location: At the village of Rosanów in the municipality of Zgierz (gmina Zgierz) in the Province of Łódź (Województwo łódzkie). The reserve lies about 16 km NNW of the centre of Łódź. Its entrance is at the end of Rowan Street (ulica Jarzębinowa), just north of the dirt road running through Rosanów towards the hamlet of Ciosny.

Conservation status: Much of the following information is taken from Kurowski (1996). Ciosny is a small reserve of 2.4 ha designated in 1971 within the administration of the Minister of Forestry and Wood Industry (Minister Leśnictwa i Przemysłu Drzewnego). The reserve was created to protect its large numbers of *Juniperus communis*.

General description and historical information: Ciosny Reserve is shaped like an irregular polygon with a maximum width of 135 metres and length (north-south) of 260 metres; it is surrounded by a fence beyond which lie the gardens and allotments attached to local houses and weekend bungalows. The reserve covers a small area of parabolic dunes which probably came into being at the end of the last Ice Age through the action of frosts and aeolian winds. There is almost no information about the development of vegetation on the reserve site, but it is thought that a partial woodland cover was retained when the surrounding area was settled and farmed. How grazing and wood-cutting affected growth and succession on the site can be gauged from the response of *Juniperus communis* after the creation of the reserve. In 1969, two years before reserve status was designated, only 148 *Juniperus communis* could be found there with a trunk diameter above 5 cm; by 1991 this number had increased to around 600; while today around 1,300 reach this dimension from a total population of 8,000. These trees exhibit a wide morphological variety, from broad spreading clumps to columnar specimens up to 6 metres tall. *C. canescens* grows, rather sparsely, in the southern half of the reserve.

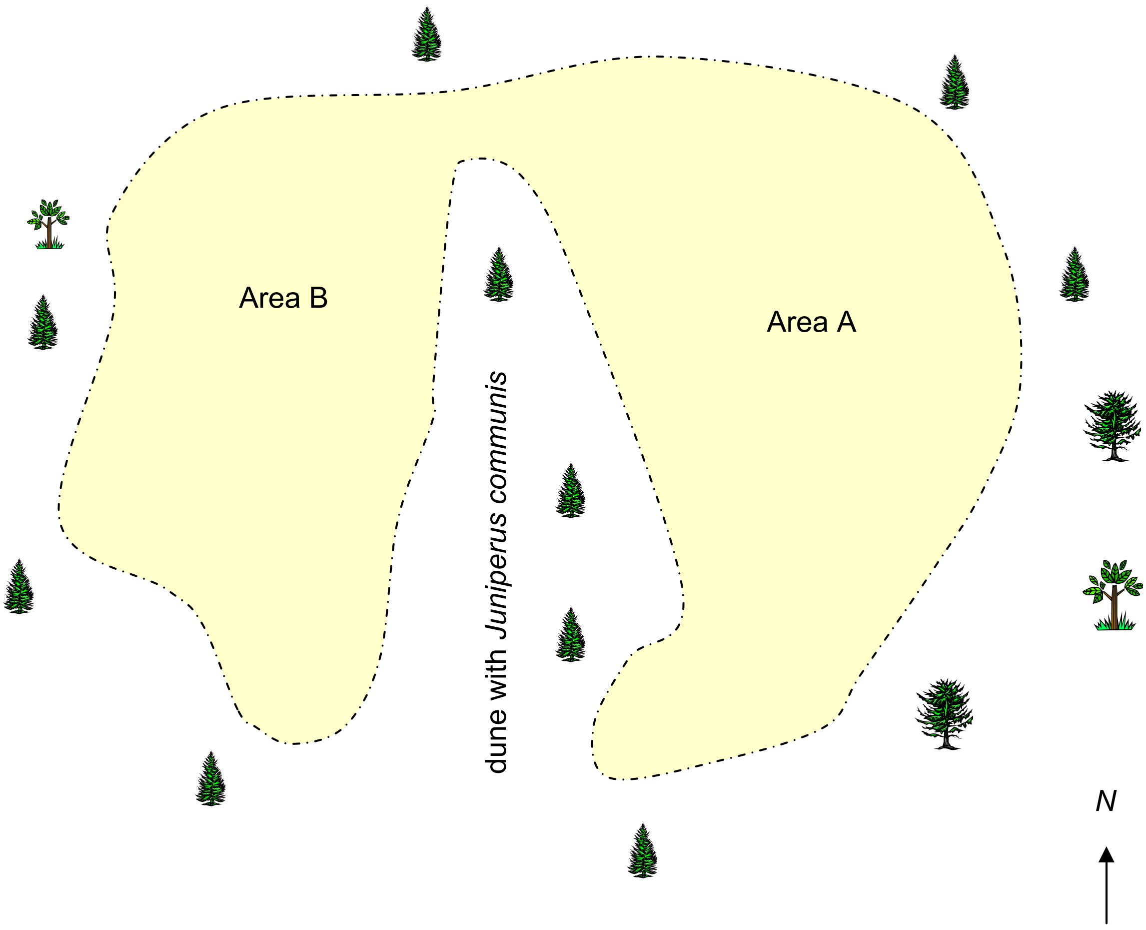
Because of its small size and nearness to human habitation, Ciosny Reserve suffers a number of conservation problems. The boundary fence has been unofficially cut open, allowing frequent access by the public and their dogs, and litter is an issue. More serious, however, is the invasion of the reserve by alien trees from neighbouring gardens, notably *Prunus serotina* and *Quercus rubra*, which seed themselves vigorously at the expense of native vegetation.

Description of study site: The chosen site consists of a small population of *C. canescens* on flat ground almost bisected by a narrow ridge of dunes rising 1 metre above the surrounding ground level and supporting a single line of *Juniperus communis* bushes to a height of 1.5 metres. The two resulting areas are designated Area A and Area B for the purposes of this study.

Area A is orientated NE-SW and measures 12 metres by 5 metres. It terminates in juniper scrub to 3.5 metres high at its NE end, and by a specimen of *Pinus sylvestris* to 6 metres at its SW end. The southern and eastern sides consist of *Juniperus communis* and *Pinus sylvestris* woodland, with a single *Quercus robur* approximately 6 metres high; while on the western side the open terrain is bounded by the central ridge of *Juniperus communis* bushes (Plate 2). Area A slopes very gently from SE to NW and consists of *C. canescens* along with *Polytrichum piliferum* and well-developed patches of *Cladonia mitis*. A few seedlings of *Pinus sylvestris* are also present; and a patch of *Polygonatum odoratum* grows by the central ridge.

Area B lies to the west of the central ridge and is connected with Area A at the NE end of the ridge. Area B is also orientated NE-SW and measures 15.5 metres in length, with a width varying between 3.0 metres and 6.5 metres. The centre of Area B consists largely of open sand with very sparse *C. canescens* and *Polytrichum piliferum* and hardly any other vegetation; though the slope in the lee of the central ridge also holds a little *Cladonia mitis* and *Rumex acetosella.* Area B is almost surrounded by *Juniperus communis* scrub to a maximum height of 3 metres, with a single *Quercus robur* sapling to 1.5 metres.

Figure B.8a: schematic diagram of Site CR (not to scale)



APPENDIX C: SUMMARY OF FIELDWORK CARRIED OUT DURING THE STUDY

Region	Site	Year & Date	Nature of observations			
			General observations	Vegetation monitoring	Faunal monitoring	Investigation data collection
West Midlands	**Burlish Top (BT)**	**2000** 30 July	√	√		
		2001 26-27 July	√	√	√	
		2004 07 August	√		√	
	Devil's Spittleful (DS)	**1998** 16 July	√	√	√	
		1999 21 August	√		√	
		2001 25-26 July	√	√	√	
		2004 07 August	√		√	
	Kinver Edge 1 (KE1)	**1998** 14, 18 July	√	√	√	
		1999 13 June		√		
		28-30 August		√	√	
		2000 02, 07 & 09 July	√	√		
		2002 31 May		√	√	
		17 July		√		
	Kinver Edge 2 (KE2)	**1999** 29 April		√		
		09 June		√		
		28 August		√	√	
		2000 09 July		√		
		2001 07 January	√			
		2002 05 & 23 June	√	√	√	
		07 July		√	√	
		2004 07 August	√	√	√	

continued…

Region	Site	Year & Date	Nature of observations			
			General observations	**Vegetation monitoring**	**Faunal monitoring**	**Investigation data collection**
West Midlands (continued)	**Kinver Edge 3 (KE3)**	**1998** 18 July			√	
		1999 08 & 11 April & 10 June		√		√
		11 July			√	
		2000 08 & 09 July	√	√		√
		16-17 July	√	√		√
		2001 07 January	√			
		04 September		√		
		2002 21 January	√		√	
		01, 04 & 05 June	√	√	√	√
		17 July		√	√	
		31 August			√	
		2004 07 August	√	√	√	√
	Alveley (AL)	**1999** 21 August				√
		2000 18 July				√
		2001 25 July				√
		2002 23 & 25 July				√
		2004 21 August				√
East Anglia	**Lakenheath (LA)**	**2002** 09 June	√	√	√	
		14 July	√	√	√	
	Wangford Warren (WW)	**1998** 20 July	√	√	√	
		2002 08 June	√	√	√	
		13 July	√	√	√	

continued…

Region	Site	Year & Date	Nature of observations			
			General observations	Vegetation monitoring	Faunal monitoring	Investigation data collection
Poland	**Bolimów (BO)**	**1997** 14 July	√	√	√	
		1999 24 July	√	√		
		2000 26 July	√	√	√	
		2001 09 June	√	√	√	
		2003 30 July			√	
	Bromierzyk 1 (BR1)	**1997** 16-17 July	√	√	√	
		1999 22-23 July	√	√	√	
		2000 22-25 July	√	√	√	
		2001 07-08 June	√	√	√	
		2003 29 July	√		√	
	Bromierzyk 2 (BR2)	**1997** 16 July	√	√	√	
		1999 22-23 July	√	√	√	
		2000 22, 23 & 25 July	√	√	√	
		2001 06 June	√	√	√	
		2003 28 July	√		√	
	Bromierzyk 3 (BR3)	**1997** 17 July	√	√	√	
		1999 22-23 July	√	√	√	
		2000 23-24 July	√	√	√	
		2001 06-07 June	√	√	√	
		2003 28-29 July	√		√	
	Ciosny Reserve (CR)	**1999** 27 July	√	√		
		2000 20 July		√		
		2001 05 June	√		√	
		2003 27 July			√	