# POST-FELLING VEGETATION CHANGES ON THREE AFFORESTED SAND-DUNE SYSTEMS

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by Peter William Sturgess.
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## Summary

Several nature reserves on dune systems include areas of pine plantation which have little conservation value. Some are currently being removed in an attempt to restore a more natural sand-dune habitat.

This project describes vegetation and soil changes observed following tree clearance at Ainsdale, Whiteford and Tentsmuir National Nature Reserves.

TWINSPAN is used to describe the vegetation communities of felled sites. DECORANA is used to find trends in community structure in relation to time after felling, woodland age, soil properties and exposure. Successional processes are discussed, with reference to studies of soil changes and seedbanks.

A common response to clear-felling is the rapid establishment of a weed community characterised by *Senecio* spp and *Chamaenerion angustifolium*, and also including plants still present below the pines. This is associated with vigorous growth and increased levels of available nutrients.

In the youngest and smallest woodlands this community was gradually invaded and replaced by typical dune species. In older plantations with more litter the weed flora was later replaced with a bryophyte and lichen community, with a tendency towards pine regeneration and invasion by *Betula* spp.. The perennial species *C.angustifolium* and *Carex arenaria* were locally dominant, favoured by their efficient use of nutrients and vegetative colonisation. This was associated with a phase of nutrient immobilisation.

One of the major influences on the vegetation of clear-felled sites is the layer of accumulated needle litter. This greatly modifies the sand-dune soil, holding large amounts of nutrients, sometimes leading to a long-term increase in soil fertility. Litter can inhibit germination from the sand-dune seed-bank and is an unsuitable substrate for the growth of many calcicolous dune plants. It may contain a seed-bank of ruderal species.

Although it may not be possible to restore the original dune flora following clear-felling a dune plantation, it may be feasible to create one which is very similar, or even to create a vegetation type not previously present at the site but still with greater value for conservation than a plantation.

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# POST-FELLING VEGETATION CHANGES ON THREE AFFORESTED SAND-DUNE SYSTEMS

## CHAPTER ONE: INTRODUCTION

### 1.1 Preamble

This study is an attempt to describe and understand the effects of clear-felling pine plantations on the biological environment of sand-dune systems. Areas on many British dune systems have been afforested with coniferous trees since the end of the nineteenth century, but conservationists are becoming increasingly concerned about the detrimental effects upon wildlife caused by plantations. There are now several places in Great Britain where conifers have been removed for conservation reasons, which will be examined in the present work.

Both sand-dune systems and clear-felling operations have been widely investigated (eg. Ranwell, 1972; Hill et al, 1984) but until recently the felling of dune forest has received little attention.

Ranwell (1972) wrote of the subject:"If the study of the ecology of dune scrub is in its infancy, that of the afforested dunes has scarcely yet begun and it offers challenging opportunities for work relating to the changing communities associated with fire and felling recovery sequences of considerable practical interest ". This study begins to meet that challenge.

## 1.2 Sand Dune Plantations

British dune systems containing areas of conifer plantation include Culbin Sands (Ovington, 1950), Tentsmuir Point (Ovington, 1951), Whiteford Burrows (Davies *et al*, 1985), Ainsdale (Gresswell, 1953) and Holkham (Ball & Williams, 1974). Most date from the first half of the twentieth century, although older plantations exist; for example, 1839 at Culbin Sands, and 1887 on the Sefton Coast (Macdonald, 1954). Planting continues to the present day: it has been estimated that 8000ha of dunes were afforested in the last 50 years (Doody, 1989).

In Britain pines are the most commonly used trees for dune plantations. They are ideally suited for growth on sandy soils of poor fertility due to their tight cycling of nutrients (Miller *et al*, 1979). They are also effective at preventing erosion, by forming a dense and fairly uniform obstacle to wind currents, and by forming litter in abundance (Lehotsky, 1941). The most widely planted species in Britain is *Pinus nigra* ssp *laricio*: other species include *P.sylvestris*, *P.pinaster*, and often in wetter areas, *P.contorta*.

Afforestation may occur for a number of reasons; sand stabilisation, timber production, or amenity value. Protection from sand movement is often of prime importance if the dune is near a developed area, road or railway; a cover of pine trees achieves stabilisation quickly and effectively. Lehotsky (1941, 1972) describes how planting of pines on the Grand Haven Dune Project, Michigan, USA, was able to stabilise over 8000 acres of blowing sand in less than 30 years. Shelter belts of conifers may be planted to protect agricultural areas inland.

The tree crop from dune plantations can be very great, although this is only in the larger forests where the influence of wind and salt spray on the main crop can be reduced by a margin of poor quality, deformed trees on the seaward side (Ranwell, 1972). A problem often associated with plantations on dunes is nutrient deficiency, especially of nitrogen, causing a declining growth rate during the middle age of the trees (Williams, 1972).

Planting pine trees for enhancing the scenic value of dunes accounts for many of the smaller plantations. They are often well liked by the general public, creating a degree of shelter, providing landmarks, and adding diversity to the landscape.

The trees are planted on a stable sand surface. On fixed dunes this presents no problem. However, where there are large quantities of mobile sand lacking vegetation cover the sand must be stabilised first. Planting Ammophila arenaria is the traditional method for fixing mobile dunes, although an increasingly popular method is thatching the sand with pine or birch branches (Agate, 1986).

A shelter crop such as Hippophae rhamnoides or Acer pseudoplatanus may be planted to the seaward side of the young conifers, and in some cases (eg. Newborough Warren) a new dune ridge has been built to protect a plantation (Blackstock, 1985).

Spacing of the trees is variable. They are planted close together to give one another mutual shelter prior to being thinned. At Ainsdale trees were planted approximately one metre apart; subsequent neglect and lack of thinning in some areas has led to an unhealthy canopy density. This has caused the development of weakened, disease-susceptible trees; 'whips' which damage other trees by hitting them, and many 'wolf' trees with too many broad spreading branches (Brown, 1955). In the well managed areas of Ainsdale the timber is of good quality (D.Wheeler, pers.comm.).

Dune systems are rarely afforested completely. The seaward edge of the system will be much more exposed to saltladen winds and blowing sand, so the landward dunes are preferred for planting. Tree-planting in the slacks is prevented by winter flooding. Slacks are sometimes planted a few years after the surrounding dunes, as the water table is often sufficiently lowered by the transpiration of large numbers of well-rooted trees (Macdonald, 1954). The highest crests of dunes may not support the growth of trees, mainly because of the greater degree of exposure, and increased water stress on the young trees. Sometimes trees die as a result of fires, pest attack or disease; this also causes a degree of variation within the population structure.

### 1.3 Effects of Afforestation

Accounts of the changes caused by afforestation on British dune systems include studies at Newborough (Hill & Wallace, 1989), Tentsmuir (Ovington, 1951), and Culbin (Ovington, 1950, 1951; Wright, 1955, 1956).

Changes to the physical environment include shade, shelter from wind and salt spray and increased evapotranspiration leading to a lowering of the water table.

The shelter effect is an important reason for tree planting; the trees can effectively reduce wind speeds for distances up to 25 times their height (Ranwell & Boar, 1986). A healthy plantation will prevent any movement of the sand surface below its canopy. Other microclimatic changes include the moderating influence on the temperature range and the humidity.

The tree canopy reduces the rainfall reaching the ground while transpiration from the dunes is increased; as a consequence the level of the watertable of several dune systems has fallen following afforestation, including Ainsdale (R.K.Pegg, pers.comm), Newborough (J.Ratcliffe, pers.comm.) and on the island of Amrum, Germany (H.Kuhbier, pers.comm). Bakker (1990) has recorded a 1 metre fall in the water level following afforestation in the Netherlands, with an increase in evapotranspiration from 360 to 550 mm per year. This has caused problems in unplanted dune slacks, which often become colonised by birch and willow scrub when the watertable is too low for the slacks to flood in winter.

Changes to the biological environment are very great. The dunes prior to planting usually support grassland or heath, and few plant or animal species of such low vegetation are able to live in the woodlands. Light-demanding plants are shaded out and only a few species, mainly bryophytes and orchids, are to be found in a dark plantation. A greater diversity of plant species can be found in older woodlands, at wood edges, where management has opened up the canopy by thinning, and in secondary replanted woodlands. These plants are not dune specialists; they are woodland species adapted to the woodland habitat provided by afforestation (Hill & Wallace, 1989).

Following the planting of pines the dune surface becomes carpeted by a layer of pine needles, leading to the formation of mor humus (Handley, 1954). Pine needles are slow to decay for a number of reasons; they have a high cellulose content but a low nitrogen content (Heal et al, 1982), their cuticular waxes reduce leaching (Nykvist, 1959; Millar, 1974), and polyphenol compounds hold proteins in forms resistant to microbial decay (Davies et al, 1964a & b). The pine needles fall faster than they decay, resulting in an accumulation to depths of up to 20cm (pers.obs.). The organic layer can change the dune soil characteristics markedly: Zinke (1962) found that around a single 45 year-old Pinus contorta tree on a coastal dune soil in California, the surface sand became increasingly acidic with a higher total nitrogen content nearer to the trunk, where the needle litter was deepest.

Trees gradually increase the organic content of the dune soil, and this is reflected by an enormous increase in the microbial biomass of the dune (Eastwood et al, 1950). Most of these organisms are present in the organic surface layers, although fungal hyphae may extend into the mineral soil and even help to aggregate the sand (Thornton et al, 1956). The majority of the fungi of the unplanted dunes are Deuteromycetes (Brown, 1958), but following afforestation there is a change in species composition with a great increase in the number of Basidiomycetes (Blanchard, 1952).

The overall long-term effect of plantations on sand dunes is analogous to a rapid acceleration of the natural succession towards dune woodland. Although there is little natural dune woodland in Britain, the ground-flora of the older plantations, and especially those in their second or subsequent rotations, is increasingly similar to that of the natural dune woodlands on the Dutch coast (pers.obs.). The major irregularities with this view are that pine and mor humus would not usually be present in a natural British dune woodland, and that there would not naturally be such a marked loss of species diversity as occurs in the youngest plantations. A better description might be 'deflected succession' (Godwin, 1929) since it is human interference which has altered the natural vegetation sequence.

## 1.4 Clear-felling Dune Plantations

There are no detailed accounts of woodland clearance from a dune system. However, clear-felling operations studied elsewhere may give useful insights into changes which might be expected after the clear-felling of a dune plantation. Table 1.1 summarises the effects of felling upland conifer plantations:

Table 1.1 Inter-relationships between causes and effects, direct and indirect, following clear-felling. (Hill *et al*, 1984).

| Causes | Effects | |
|---|---|---|
| | 0 | Clear-felling operations |
| 0 | 1 | Removal of tree canopy |
| 0 | 2 | Local compaction of soil |
| 0 | 3 | Local disturbance of litter layer |
| 0 | 4 | Input of brash to forest floor |
| 1 | 5 | More light on forest floor |
| 1 | 6 | Greater temperature variation |
| 1 | 7 | More water reaches forest floor |
| 1 | 8 | Stumps and roots begin to die |
| 1 | 9 | Litterfall ceases |
| 1 | 10 | Tree roots cease to absorb water |
| 8 | 11 | Tree roots cease to absorb nutrients |
| 3,5,6 | 12 | Buried seeds germinate |
| 2,7,10 | 13 | Soil wetter, at least in winter |
| 7,10 | 14 | Run-off and/or percolation increase |
| 6,13 | 15 | Rate of decomposition changes |
| 9 | 16 | Forest floor loses mass |
| 11,16 | 17 | Mineralised nutrients dissolve |
| 17 | 18 | Nutrient redistribution or loss |
| 5,12 | 19 | Ground vegetation re-establishes |
| 19 | 20 | Voles increase |

The removal of the canopy will allow sunlight to penetrate to the forest floor, once again allowing growth of light-demanding plants. Diurnal temperature could vary almost as widely as on an unplanted dune, although the brash will continue to insulate the mineral soil to some extent.

Both interception of rainfall and transpiration by the canopy cease after clear-felling. Pierce (1969) showed that the stream-flow from a deforested river basin in the Hubbard Brook experimental forest increased by up to five times following deforestation. It is likely that the amount of water percolating through the sand will increase after tree clearance from a sand dune; this may have important consequences for the amount of nutrients leaching from the system. Surface water flow is not a common phenomenon on dunes but may occur on hydrophobic sand, where the sand has an organic coating causing it to repel water (Dekker & Jungerius, 1990). If the increase in soil organic matter has increased the water repellency of the sand then surface water flow may be seen on some clear-felled sites.

There are changes in the amount and distribution of nutrients within the ecosystem following clear-felling. Some nutrients are removed as the timber is taken away, but there is an addition of nutrients to the forest floor in the form of needles and brash. The breakdown of organic material is complex as nutrients are held in several forms. Fresh material with a high nitrogen content has a potentially higher rate of decomposition and nutrient release (Newell & Heal, 1982), with the needles decomposing before branches or bark (Fogel & Cromack, 1977). Wright (1955) showed that a surface layer of brushwood on dunes at Culbin could maintain a higher soil moisture content; this together with the increased ground temperatures of a clear-felled site would enable microbial litter decomposition to continue at a faster rate than observed in the uncut woodland (Bormann & Likens, 1979). Temperature and soil moisture have been positively correlated with microbial carbon dioxide production (Witkamp, 1966 a & b).

Stumps and large roots left after felling may act as a 'nutrient sink' (Newell & Heal, 1982). They are large and initially poor in nutrients, with a carbon:nitrogen ratio of about 1000; but they may act as a site for accumulation and slow turn-over of nutrients, while the needles are a site for rapid release. Plant nutrients could be translocated from adjacent sources to the stumps by fungi, nitrogen would remain in the microbial biomass while carbon would be lost through respiration.

Before the re-establishment of vegetation and uptake of nutrients a great deal may be lost by leaching. Likens et al (1977) demonstrated this by using herbicides to prevent regrowth of a clear-felled forest; the treatment resulted in increased losses of most major plant nutrients from the system.

The clear-felled dune soil has a much higher nutrient status and organic content than an unplanted dune, and the seedbank will have been modified by the length of time under woodland conditions (Granstrom, 1987). It is therefore unlikely that the post-felling vegetation will be the same as it would have been if the trees had not been planted. In many studies of secondary succession the first vegetation response is the rapid establishment of ruderal species adapted for copious production of small, aerially dispersed seeds (for example: Dyrness, 1973; West & Chilcote, 1968) . Blanchard (1952) described several sites in the Ainsdale pinewoods, clear-felled 10 years previously, indicating Chamaenerion angustifolium as the most important colonist. C.angustifolium with Senecio sylvaticus are the primary colonists of clear-felled sites in the North Holland Dune Reserve (Van Andel, 1975).

Blanchard (1952) suggested that Carex arenaria and Salix repens would become the dominant species at the Ainsdale clear-felled sites after the ruderal phase. Hill and Wallace (1989) found that C.arenaria made up a large part of the ground flora and seed-bank at Newborough Forest and predicted that it would be an important constituent of the post-felling vegetation, together with C.angustifolium, Rubus fruticosus, R.caesius and grasses. In addition to these, Betula regeneration is also common on clear-fell sites (Hill, 1979c) and so may be expected to occur where dune woodlands are removed.

## 1.5 Management Considerations

The aim of the removal of pinewoods is to create areas of greater conservation value. Several reasons have been given for removing areas of plantation at Ainsdale (Wheeler, 1987; Rothwell, 1985; M.Garbett, pers.comm.):

1. The shade and acid litter below the pines eliminate most of the indigenous flora and fauna.
2. The plantations create shelter, which encourages scrub growth, causing the disappearance of grassland plants and animals.
3. The lowering of the water-table causes drying of dune slacks, resulting in a loss of rare plants and development of scrub.
4. Pine seedlings are common around mature plantations. Their control is a constant drain on resources.
5. The removal of pinewoods could provide scope for increasing the amount of yellow-dune.
6. The cost of managing a woodland on an exposed coastal site may be greater than the value of the timber.

Despite these factors there are several reasons for leaving the plantations unfelled (Wheeler, 1987; M.Davies pers.comm.; P.Kinnear pers.comm.; Pers.obs.; and Atkinson & Sturgess, 1991):

1. Woodlands were often planted to stabilise sand. Removal of the trees may result in a renewal of erosion, especially if the stumps are removed.
2. Plantations are important landscape features in areas with few other woodlands. They are very popular with the public for recreation and large-scale felling may meet local opposition.
3. Some plantations contain rare and protected species; for example, the rare orchid Epipactis dunensis, and the red squirrel (Sciurus vulgaris) occur throughout the plantations on the Sefton coast.
4. There is no guarantee that the post-felling environment will support a typical dune flora and fauna. Further management problems may arise if unwanted weeds or scrub colonise the clear-fell site, or if pine regenerates from seed.
5. Most plantations are less than 100 years old. Over a longer time scale the plantations may develop a more diverse woodland flora and fauna, of greater conservation value.
6. It may not be economical to fell the trees if the value of timber is not high.
7. The pulse of nutrients released from a recently felled site will drain to the water-table. This may cause eutrophication problems in dune slacks.

Reasons for and against felling plantations must be balanced by the dune manager according to the requirements for the site. There is an element of risk involved; several of the reasons listed are purely hypothetical and still require testing. The outcome of clear-felling dune plantations, therefore, is still unclear. However, the following chapters describe studies of the three first deliberate attempts to restore dune vegetation from afforested dunes in Britain. It is hoped that these case studies may help in the decision-making at other dune systems.

## 1.6 Study Locations

This project is based on research at three British National Nature Reserves (N.N.R.s), on three sand-dune systems; Ainsdale Sand Dunes N.N.R., on the Sefton Coast, Merseyside; Whiteford Burrows N.N.R., West Glamorgan; and Tentsmuir Point N.N.R., Fife. The locations of these reserves are shown in figure 1.1. Although the majority of the work was conducted on the Ainsdale N.N.R. on the Sefton Coast areas other dunes were included in order to reduce research problems associated with local effects. The National Trust reserve at Formby Point, situated immediately south of Ainsdale N.N.R. provided additional data from the Sefton Coast, and is also described in this section.

Climate data from the three study areas is given in table 1.2.

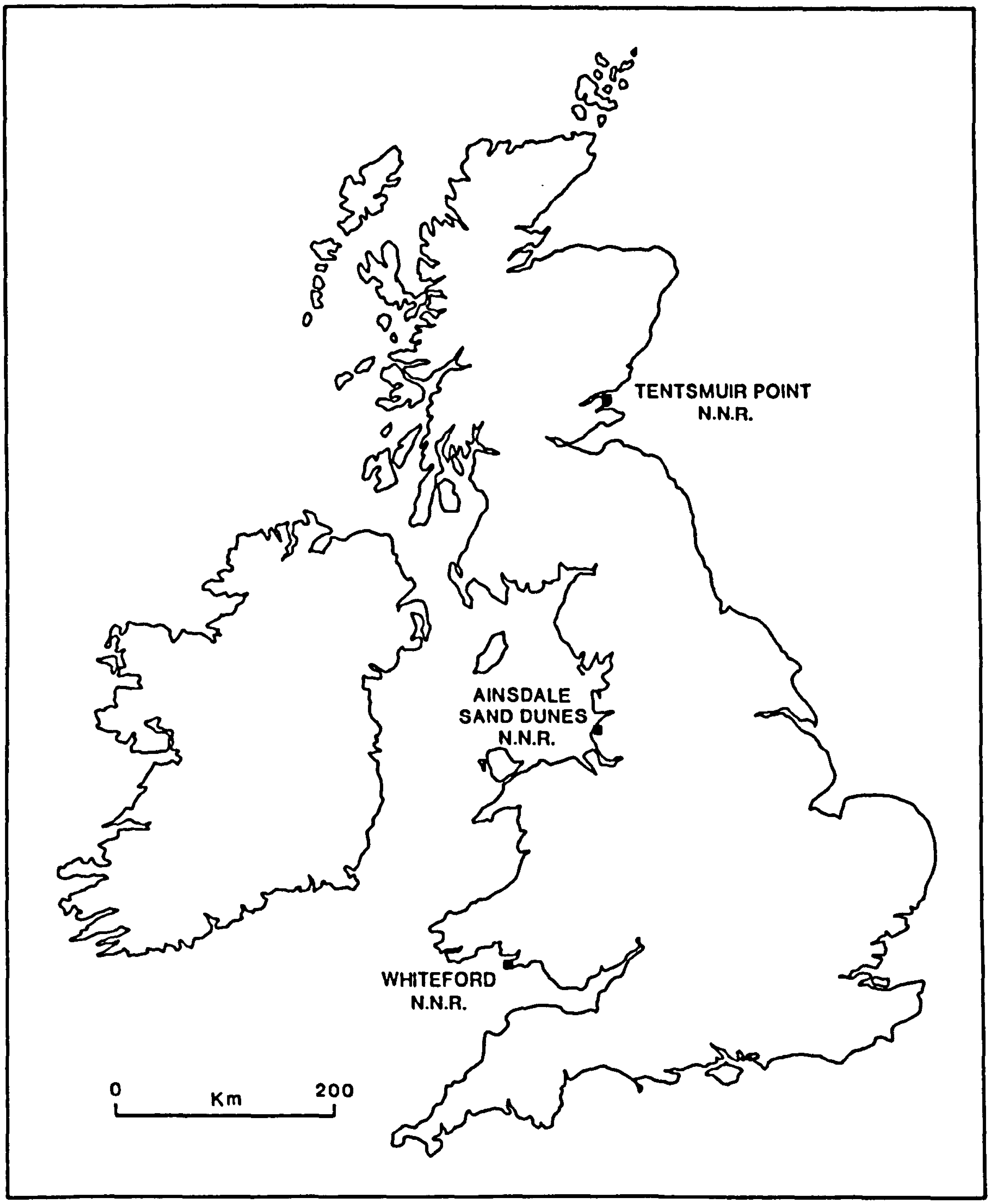



Figure 1.1 Location of study sites

Table 1.2 Climate data from the three study areas. Rainfall is given in millimetres. Temperatures are given in degrees Centigrade.

| | Total annual rainfall | Mean January temperature min. | max. | Mean July temperature min. | max. |
|---|---|---|---|---|---|
| Whiteford 1960 to 1984 (Penmaen) | 1207.7 | 2.6 | 7.0 | 12.1 | 19.4 |
| Ainsdale 1941 to 1970 (Southport) | 836.0 | 0.8 | 6.1 | 12.1 | 18.9 |
| Tentsmuir 1921 to 1950 (Leuchars) | 773.4 | 1.1 | 5.7 | 10.7 | 18.7 |

### 1.6.1 Ainsdale Sand Dunes National Nature Reserve

Ainsdale Sand Dunes N.N.R. occupies 492 hectares of the Sefton Coast dune system, Merseyside (National Grid Reference SD 289094 to SD 302115). A map of the reserve is given in figure 1.2 (also see plates 1-3, 7-9 and 17). Estimates of the age of the dunes vary considerably but the oldest dunes are probably in the region of 300 to 400 years old (Salisbury, 1925; Pearsall, 1934). The first planting of pine trees in the area was in 1895, as an attempt to prevent sand from blowing onto the Liverpool to Southport railway line (NCC, 1986). Planting continued until 1960, by which time nearly one third of the reserve was afforested. This was mostly of *Pinus nigra* ssp *laricio*, but also including some *P.sylvestris* and *P.pinaster*, and later, *P.contorta*. The edges of the young plantations were sometimes sheltered by belts of *Hippophae rhamnoides*, *Populus* spp or *Acer pseudoplatanus*; these species are still present and in some areas are a serious problem. The trees were primarily intended for sand stabilisation and amenity purposes and so little woodland management was carried out. A thinning programme was introduced following Ainsdale's designation as a National Nature Reserve in 1965.

Woodland clearance operations in the Ainsdale pinewoods have been undertaken over a number of years, providing a useful time sequence for the study of a post-felling vegetation succession.

The earliest fellings were carried out during the Second World War (Gresswell, 1953), but most of these areas were replanted with pine trees, and the others are not representative of a natural succession. One of the clearings used for asparagus farming now supports a rank grassland community, and another has been successfully planted with native, broad-leaved trees (see section 4.5).

Between 1977 and 1982 three fire-breaks were cut through the landward pinewoods. This involved clear-felling belts of trees, up to 150 metres wide and 500 metres long (figure 1.2). Most of the timber was removed from these areas, but from that time until the present no further management work has been done (D.Wheeler, pers.comm.). The fire-break vegetation is the natural secondary succession on this site, and so formed an important part of this study. In 1989 a small area of the seaward dunes was clear-felled in order to study the process of revegetation before felling a larger area of similar woodland.

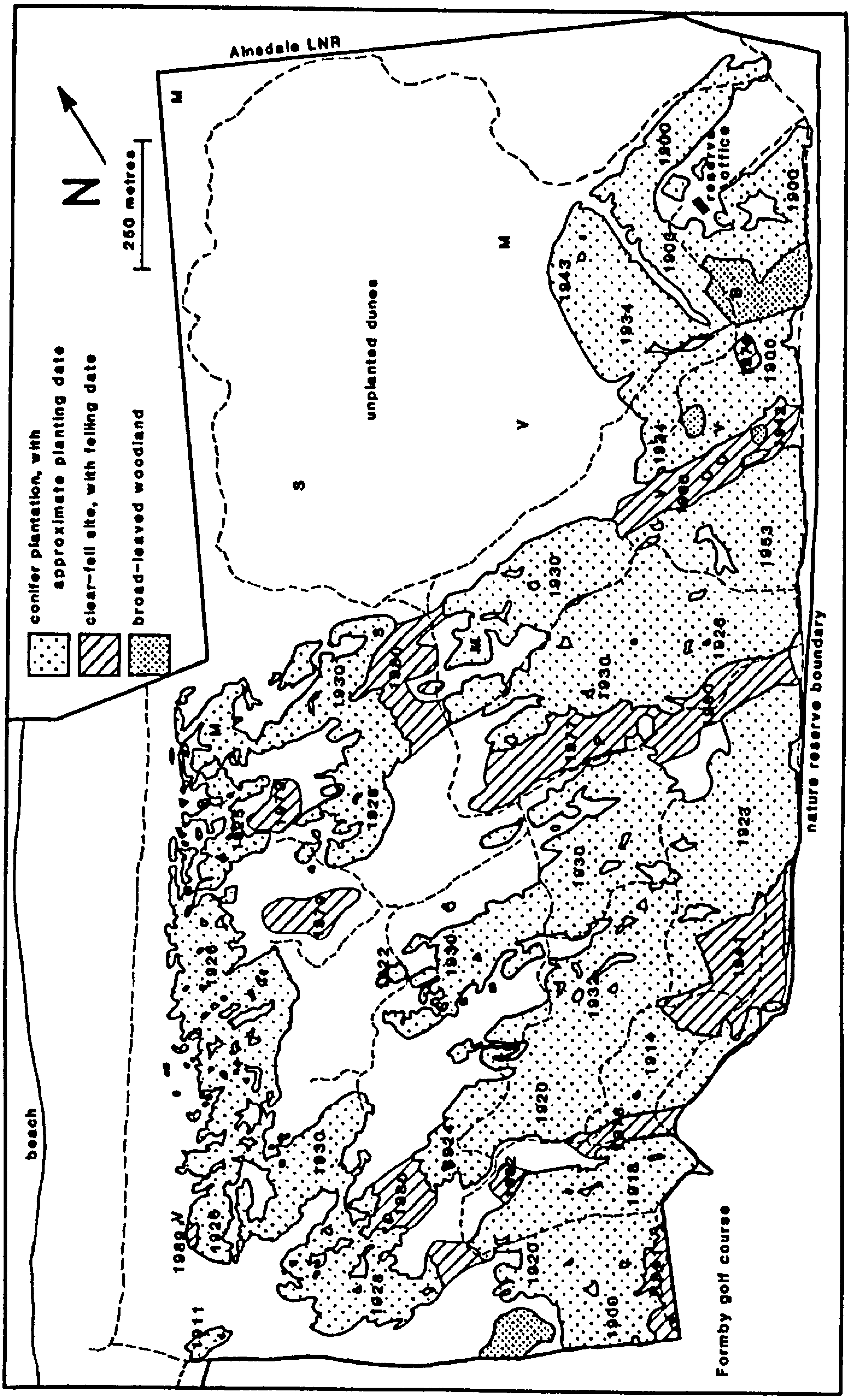



Figure 1.2 Ainsdale Sand Dunes National Nature Reserve.
B = site replanted with broad-leaved trees (section 4.6).
D = sites in decomposition study (section 2.4).
M = sites used in mineral weathering studies (section 2.3.5).
S = sites used in seed-bank study (section 3.4).
V = sites used in vesicular arbuscular mycorrhiza study (section 3.5).
P = site used for pine regeneration study (section 3.6).

### 1.6.2 Whiteford National Nature Reserve

Whiteford N.N.R. lies to the north of the Gower peninsula, West Glamorgan, at the mouth of the Loughour estuary (National Grid Reference: SS 433940 to SS 442968). The land is owned by the National Trust and was leased to the Nature Conservancy Council in 1967. The sand dunes, known as Whiteford Burrows, occupy about 120 hectares of the reserve. A map of the area is given in figure 1.3 (also see plates 10-15).

The history of the plantations at Whiteford has been described by Hughes (1978). Between 1955 and 1964 some 42.5 acres were planted with conifers. Most of this consisted of _Pinus nigra_ spp _laricio_, with some _P.sylvestris_, _P.pinaster_, _P.contorta_, _Picea abies_ and _Chamaecyparis_ sp. In 1972 it was decided to fell five of the youngest, smallest plantations (A, B, L, M, and O (figure 1.3); amounting to 3.25 acres). The National Trust sold the timber of four further plantations (F, G, I, and K) to the NCC, in order that they be progressively removed. The oldest and largest plantations are being left to grow to maturity (Hughes, 1978).

The clear-felling operations so far have completely removed the plantations A, B, L, M and O in 1973, plantation G between 1981 and 1983, and plantation F in 1983. Plantation K was thinned by 50% between 1975 and 1977. Felling in plantations I and K has been conducted by gradually enlarging gaps, the largest clearings were created between 1984 and 1985. In all of these areas the timber was removed from the site, branches were gathered

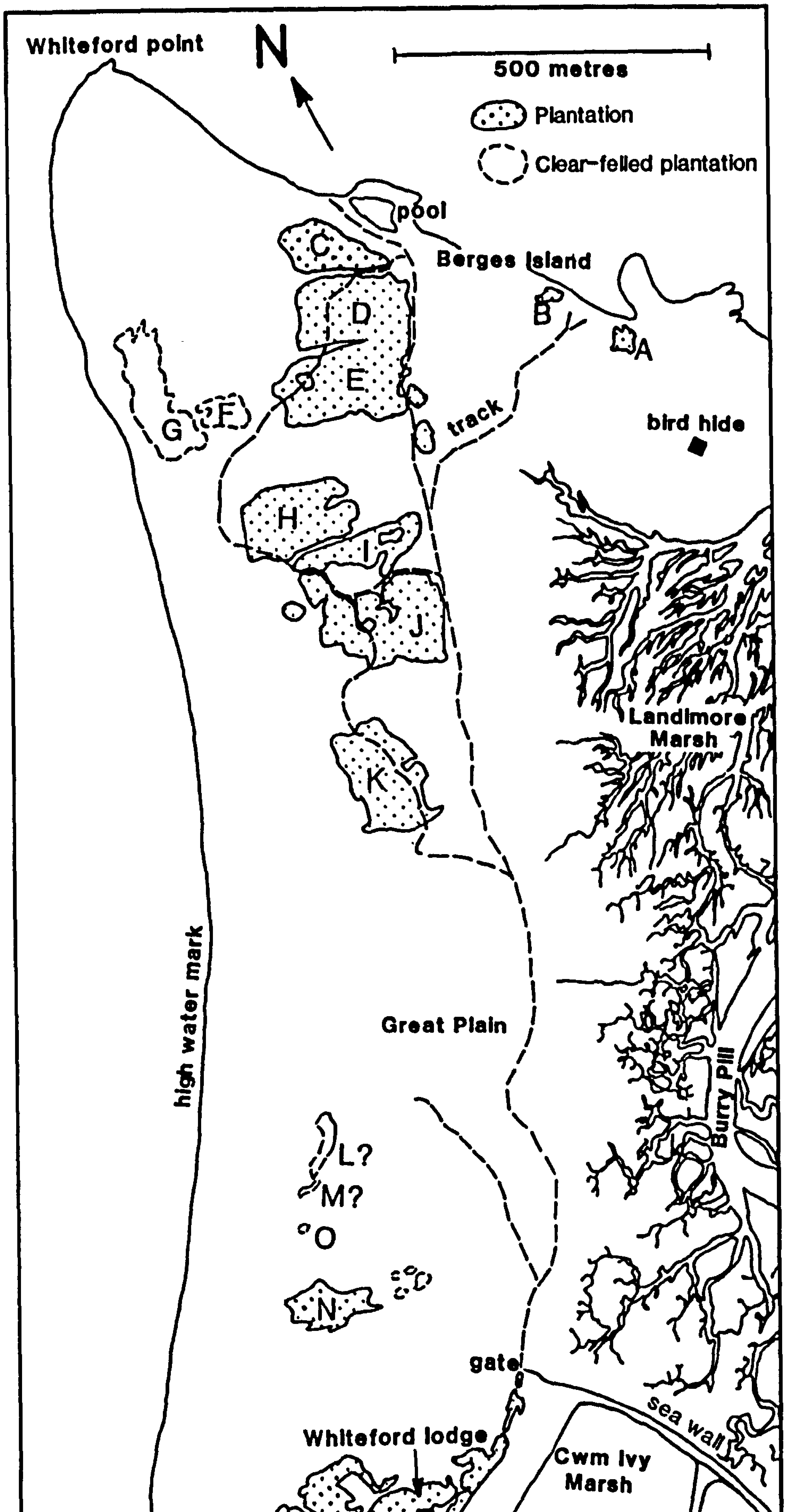



Figure 1.3 Whiteford National Nature Reserve

into heaps and burned, and stumps and needle litter were left in place.

Plantation K has been managed with the intention of restoring ground vegetation before the trees are felled. This has involved the thinning of trees, and setting up permanent quadrats (see section 3.2). Two areas at the edge of plantation K were felled by me in November 1988 (see figure 3.1), in order to study the immediate responses to clear-felling in more detail.

### 1.6.3 Tentsmuir Point National Nature Reserve

Tentsmuir Point N.N.R. is situated south of the Tay estuary on the east coast of Scotland (National Grid Reference NO 452294 to NO 502249). A map of the reserve is given in figure 1.4 (also see plates 4-6).

Unlike the eroding systems at Ainsdale and Whiteford, Tentsmuir Point is a rapidly accreting dune system; the area occupied by the reserve is less than 200 years old (Deskmukh, 1974). However, this system is the least calcareous of those studied in this project, because the major sand source is sediment from the river Tay (Crawford, in press).

Much of the dune system adjacent to the reserve is used for commercial forestry, and forms one of Britain's largest dune forests with a total area of 604 ha (Doody, 1989b). Following a reduction in rabbit grazing after the outbreak of myxomatosis in 1956, seeding from the neighbouring plantations led to areas of the unforested reserve becoming colonised by pine trees. These were mostly

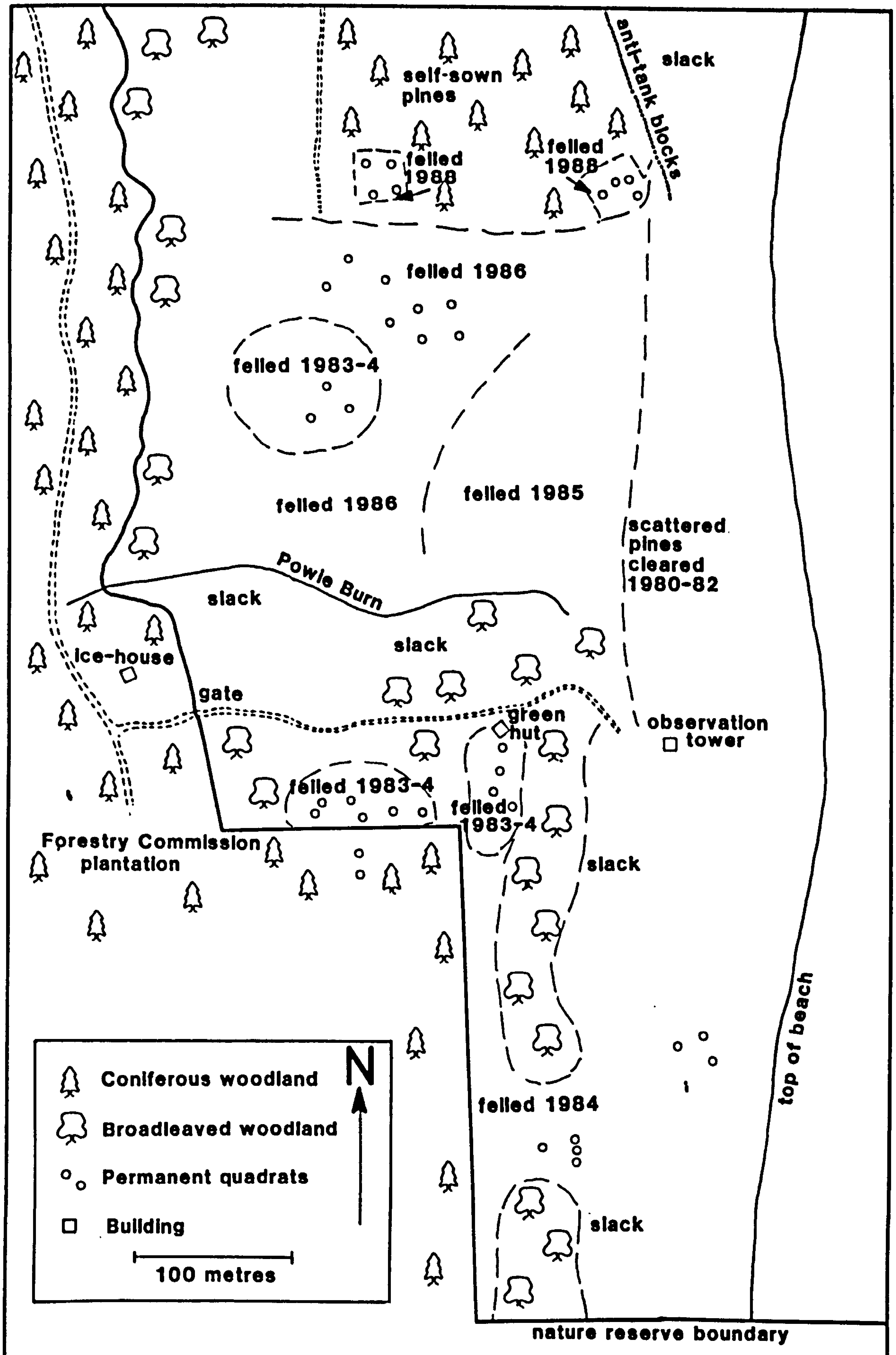



Figure 1.4 Tentsmuir National Nature Reserve

Pinus sylvestris, but also P. contorta, P. nigra, Picea sitchensis and Larix sp. For over 20 years this was allowed to continue, and by 1978 pines were well established over about one half of the landward area of the N.N.R. (Leach & Kinnear, 1985). The oldest pines were up to 40 years old. Due to the loss of 'natural' dune habitat a management programme of conifer removal was introduced. The dates that areas were cleared of pine trees are indicated on figure 1.4.

Perhaps the most important difference between this site and the other two study areas is that the woodland at Tentsmuir N.N.R. is self-sown. This has resulted in an uneven canopy structure with many gaps of varying sizes still supporting dune vegetation.

Other major management problems at Tentsmuir are invasions by Hippophae rhamnoides and Betula sp. H.rhamnoides has been successfully eradicated from most areas, although the development of Betula scrub is continuing. As a result of the drainage and high evapotranspiration in the adjacent plantations there is currently no regular winter flooding on the reserve. This has enabled Betula colonisation of slacks, with seedlings now also abundant on some areas cleared of pine trees.

### 1.6.4 Formby Point National Trust Reserve

The National Trust owns 200.2 hectares of coastal dunes to the west of Formby on the Sefton coast, Merseyside (National grid reference from SD 269069 to SD 274093). Of this, 64.9 hectares are afforested and managed as amenity woodland. This site is the most visited of the study areas, with over 250,000 visitors during 1990 (M.Garbett, pers.comm.). The pinewoods are very popular with the public, particularly because of their large population of red squirrels (*Sciurus vulgaris*).

Tree planting at Formby began in 1895, with most of the plantations being established by 1903 (National Trust, unpublished data). Subsequent planting has been on a smaller scale, with new trees being planted during each decade to the present (M.Garbett, pers.comm.). The majority of the trees are Scots Pine (*Pinus sylvestris*) and Corsican Pine (*P.nigra* ssp *laricio*), with areas of broad-leaved coppice (sycamore, birch and alder) in the lower areas (M.Garbett, pers.comm.). The Formby Point woodland is included in this study primarily because it contains several afforested areas which were clear-felled in about 1942. These sites have not been replanted or farmed since their clearance, and present a valuable opportunity for studying the results of plant and soil development over the last 45 years.

Clear-felling work prior to replanting of areas is now undertaken as part of the National Trust's woodland management plan. Two of these small clear-felled sites were studied in order to make a comparison between woodlands clear-felled for different lengths of time.

## CHAPTER TWO: SOIL CHANGES FOLLOWING CLEAR FELLING

### 2.1 Introduction

The composition of the sand dune soil is changed considerably following afforestation, especially due to the increased stability and the accumulation of an acidic layer of mor humus. The sand below a dune plantation can become acidified at the surface (Moriarty, 1978), and may develop into a 'micropodzol' with an acid A horizon and a weakly developed B horizon which may contain iron mottles and concretions (James, 1985; also see plate 8). A micropodzol may develop less than 21 years after tree planting (James & Wharfe, 1989) although the podzolisation is progressive and intensifies with depth of accumulated pine litter (Ball & Williams, 1974).

Following the removal of the pine canopy the soil will be subjected to a different set of soil-forming factors. There may be physical disturbance during the felling operation, the supply of pine litter ceases, effective rainfall increases, the ground is exposed to wider temperature range, and the flora will change with the increase in the amount of light.

This study aims to investigate the fate of the dune woodland soils after a clear-felling operation, particularly in relation to plant nutrients and organic matter. Nitrogen and phosphorus were chosen for analysis as they are the main limiting nutrients in dunes (Willis, 1963, 1989).

A variety of sites were sampled, varying in the length of time since felling, the age of woodland before felling and the pH of the pre-woodland dune soil. Study sites were chosen to try to minimise other variables, such as distance from the sea, but this proved difficult in practice, adding complications to the interpretation of results.

To try and assess the rate of breakdown and the changes in composition of the organic material from the woodland floor a study of litter decomposition was carried out at Ainsdale, following the fate of litter samples in litter-bags; this is described in section 2.4.

The fertility of a variety of dune, woodland and clear-felled soils was tested by bioassay under greenhouse conditions; this is described in section 2.5.

## 2.2 Methods

Soil and litter samples were collected from all of the study sites and brought back to the laboratory for analysis. There were a total of 278 samples, taken from 104 soil profiles.

This section describes the methods used to analyse the following soil properties: pH, organic matter, total nitrogen, inorganic nitrogen and extractable phosphate.

At all times during collection and analysis care was taken to avoid contamination of samples. Dry soil was stored in sealed bags to avoid spillages and to keep it dust-free. Skin contact with the soil was avoided. All glassware used in the analyses was acid-washed and rinsed with distilled water. All dilutions of samples and reagents were performed using distilled water; double distilled water was used for the phosphate analysis.

Several replicate samples were usually taken from each site but the analyses of each sample were generally not replicated, as this study is primarily to give a very general description of the soils for their botanical rather than pedological implications. pH and phosphate analyses were performed twice, and the results presented are mean values. Some of the nitrogen tests were repeated, but showed good reproducibility; usually with less than 5% variation.

### 2.2.1 Soil Collection and Storage

A vertically-sided profile pit, usually about 30 x 30cm wide and 30cm deep, was dug at each sampling site. Two sides of the pit were scraped clear with a trowel to allow the description of soil horizons. None of the woodland sampling sites supported a well developed ground flora, although a few exploratory soil pits were excavated while undertaking vegetation surveys in well vegetated parts of the plantations.

Soil was collected from different depths of the profile using a trowel. In pinewoods and clear-felled soils the organic horizons were collected separately as litter layer (L), fermentation layer (F), and humus layer (H); occasionally combining F and H horizons where there was no visible distinction. Samples from mineral horizons and non-forested areas were collected according to depth; depths usually being 0-5cm, 5-15cm, and 15-25cm from the surface. A sample of the soil at 0-1cm depth was occasionally taken when there was no pine litter layer. Fewer samples were taken below 15cm as the deeper sands are not greatly affected by soil-forming processes.

Each sample was collected from more than one face of the soil pit and contained approximately 300cm$^3$ of soil. This was put into a labelled polythene bag, sealed and brought to the laboratory within 24 hours. The pH of the field-moist soil was determined immediately after returning to the laboratory, using about 20cm$^3$ of the sample. The remainder was air-dried at approximately 25$^\circ$ C. The drying was necessary to prevent any microbial activity from altering the chemical composition of the soil, particularly of nitrogen compounds (A.D. Bradshaw, pers. comm.).

The air-dried soil was passed through a 2mm sieve. This removed large sticks, pine cones and most plant roots, which were not included in the soil tests. Sticks and pine cones were ground and analysed separately for the litter-bag study. Pine needles were broken up using scissors until they could pass through the mesh. The sieving was done in a fume-cupboard to avoid dust contamination between samples. After sieving, the soils were stored in sealed polythene bags until required for further testing.

### 2.2.2 pH

Approximately 20cm$^3$ of fresh soil was placed in a 100ml beaker and mixed with 50ml of distilled water to produce a cloudy suspension. This was allowed to settle for about 20 minutes, after which the pH of the supernatant liquid was measured using a glass-calomel electrode pH meter.

### 2.2.3 Loss On Ignition

The organic matter content of the soils was estimated as being the fraction of the soil released during combustion. This method follows Allen et al (1974).

Approximately 3g of air-dried soil was put into a weighed, dry porcelain crucible. This was reweighed to determine the exact weight of air-dried soil. A loose fitting lid was put on the crucible and it was left overnight in an oven at 105°C. After removal from the oven the crucible was allowed to cool to room temperature in a desiccator, and weighed again. This ensured that water loss did not influence the weight difference following combustion. It also allowed the calculation of the moisture content of the air-dried soil, to be used later as a correction factor for other tests involving air-dried soil.

The crucible was placed in a muffle furnace and ignited at a temperature of 450°C for four hours. It was then removed and allowed to cool in a desiccator before reweighing. The weight loss after ignition was calculated as a percentage of weight of oven dry soil.

There were some problems with this method, and results can only be regarded as an approximate indication of the organic matter present. In several cases, particularly samples from litter horizons, there were still traces of carbon present after ignition. This incomplete combustion is likely to have caused an underestimation of the carbon content of the more organic soils. An alternative method, igniting at 850°C for 30 minutes (Allen et al, 1974), was used for litter samples from the decomposition study (section 2.4), where loss of calcium carbonate was not a complicating factor.

### 2.2.4 Total Nitrogen

The total nitrogen content of soil samples was analysed using a Kjeldahl digest after a pretreatment to include inorganic nitrogen. The method follows Johnson (1981).

A 1g sample (0.5g for organic soils) was put into a digestion tube, to which 3ml of salicylic acid in sulphuric acid ($34gl^{-1}$) was added. This was then left to stand overnight before adding 0.5g of sodium thiosulphate powder. Nitrates and nitrites are converted to nitro compounds by the salicylic acid mixture, these are then reduced to amino compounds by the sodium thiosulphate (Hesse, 1971).

The digestion tube was put into a heating block, and the sample digested by 5ml of concentrated sulphuric acid, in the presence of a Kjeldahl catalyst tablet (containing 1.0g of potassium sulphate and 0.1g copper sulphate). The first part of the digestion was at 150°C for one hour. During this period several of the more organic samples reacted very strongly: where organic material was lost from the top of the tube the analysis was repeated using less soil (0.5g) and allowing more time for a slower digestion before adding the catalyst. After the first hour the temperature was raised to 350°C for approximately 3 hours, the digestion being complete after the contents of the tube had lost its brown, organic colour, sometimes becoming completely clear.

The tube was removed from the heating block and allowed to cool to room temperature. 10ml of distilled water was added and shaken gently to dissolve the solidified digest. This was then made up to 100ml with distilled water, by filtering several washes of the tube into a volumetric flask.

Approximately 15ml of the diluted solution was transferred to a 20ml plastic bottle and kept frozen until needed for the next part of the analysis. At the end of the digestion any nitrogen present in the sample was converted to ammonium nitrogen.

The amount of ammonium in solution was determined using a Technicon Autoanalyser. This uses a reaction between ammonium nitrogen and an alkaline phenate solution followed by 1.5% sodium hypochlorite to produce a green coloured indophenol compound; this is measured colorimetrically and the results are plotted by a chart recorder. Copper interference is prevented by using a solution containing EDTA.

A stock solution of $1000mgl^{-1}$ of ammonium nitrogen was made by dissolving 4.7162g ammonium sulphate in 1l of 0.5M sulphuric acid. From this working standards from 30 to $0.5mgl^{-1}$ (80 to $5mgl^{-1}$ for litter samples) were prepared, also in 0.5M sulphuric acid. These standards were used to plot a calibration curve from which the concentration of ammonium nitrogen in each of the samples could be determined. This was then calculated back to find the total nitrogen content of the original soil samples. Results are expressed as $mgg^{-1}$.

### 2.2.5 Inorganic nitrogen

Nitrate, nitrite and ammonium nitrogen can be determined after a single extraction by potassium chloride solution. The procedure follows Johnson (1981).

Five grams of air-dried soil were weighed into a 150ml jar and shaken with 25ml of 2M potassium chloride solution for 1 hour. For more organic samples 50 or 75ml of potassium chloride solution were used. The liquid was filtered into 20ml plastic bottles through Whatman 42 filter paper, and kept frozen until required for further analysis.

Ideally the extraction of inorganic nitrogen would be done using fresh soil. This was not possible for this project due to availability of equipment.

Subsequent analysis of the extracts was carried out using a Technicon Autoanalyser. The procedure for ammonium nitrogen is similar to that described in section 2.2.4, however the sensitivity of the reaction is increased by the inclusion of sodium nitroprusside in the sodium hypochlorite solution. Standard solutions from 0.02 to $1.00mgl^{-1}$ were prepared using a $1000mgl^{-1}$ stock solution made up of 4.7162g ammonium chloride in 1l of 2M potassium chloride.

Nitrate and nitrite nitrogen were analysed together using another module of the Technicon Autoanalyser. In this test the nitrate is first reduced to nitrite by hydrazine sulphate under alkaline conditions, using copper as a catalyst. Nitrite then reacts with sulphanilamide under acid conditions to form a diazo compound. This compound couples with N-1-naphthylethylenediamine dihydrochloride to form a reddish-purple azo dye which is measured colorimetrically at 520nm. Standards were prepared from 1 to 50mg$l^{-1}$ from a 1000mg$l^{-1}$ stock solution of 7.221g potassium nitrate in 1l of potassium chloride solution.

In both cases the standard solutions were used to plot calibration curves from which the nitrate and nitrite and ammonium nitrogen concentrations of the sample extracts could be determined. It was then possible to calculate back to find the amount present in the soil. Results are expressed as mgN100$g^{-1}$ oven-dried soil.

2.2.6 Acid-extractable phosphate

An indication of the amount of phosphate available to plants can be measured after a simple extraction in dilute sulphuric acid. The concentration of the extract can be determined colorimetrically following a vanadomolybdate reaction. The method is based on Allen et al (1986) and Johnson (1981).

Ten grams of air-dried soil was weighed into a 150ml glass jar, and shaken for 30 minutes with 25ml 0.001M sulphuric acid, which had been buffered at pH3. 0.2g of Darco-G-60 carbon black was added to clear the extract while it was shaking. The liquid was filtered into 20ml plastic bottles through Whatman 42 filter paper and kept frozen until needed for analysis.

An aliquot of 1ml of the extract was put into a 25ml volumetric flask and mixed with 5ml of B.D.H. vanadomolybdate reagent 19184. This was made up to 25ml with 0.001M sulphuric acid. The solution was left for about 30 minutes while the colour developed. Phosphate ions react with an acid solution of ammonium vanadate and ammonium molybdate to form a yellow complex. Absorption at 400nm was read from the spectrophotometer. Standard solutions from 0.2 to 1.0mgl$^{-1}$ were prepared from a 1000mgl$^{-1}$ stock solution made up of 0.1757g of potassium dihydrogen phosphate in 1l of double distilled water. The standards were used to plot a calibration curve from which the concentrations of phosphate in each extract could be determined, this could be calculated back to find the amount of available phosphate in the original soil samples. Results are expressed in mg100g$^{-1}$.

2.3 Results

The results of most of the soil analyses are summarised in figures 2.1, 2.2 and 2.3. These diagrams are not records of individual profiles, but are intended to show very general trends. Points shown are means of values taken from several soil pits, standard errors are shown where they are greater than 5% of the range.

$NO_3$, $NH_4$ and $PO_4$ show N and P measured on an elemental basis. $NO_3$ N etc...

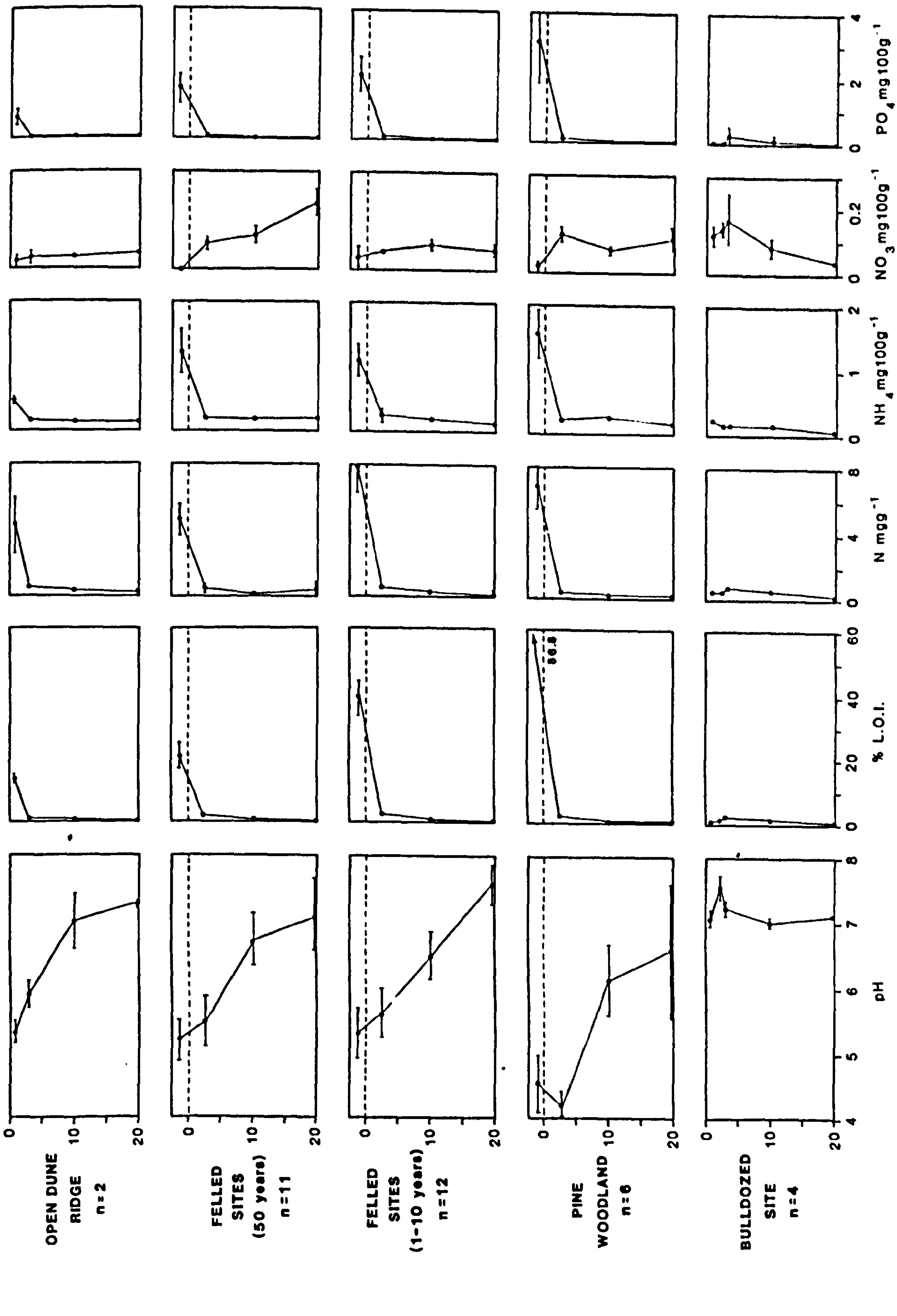
Legends for figures on pages 40-42:

Figure 2.1 Summary of results of soil analyses for samples from Ainsdale and Formby. Page 40.

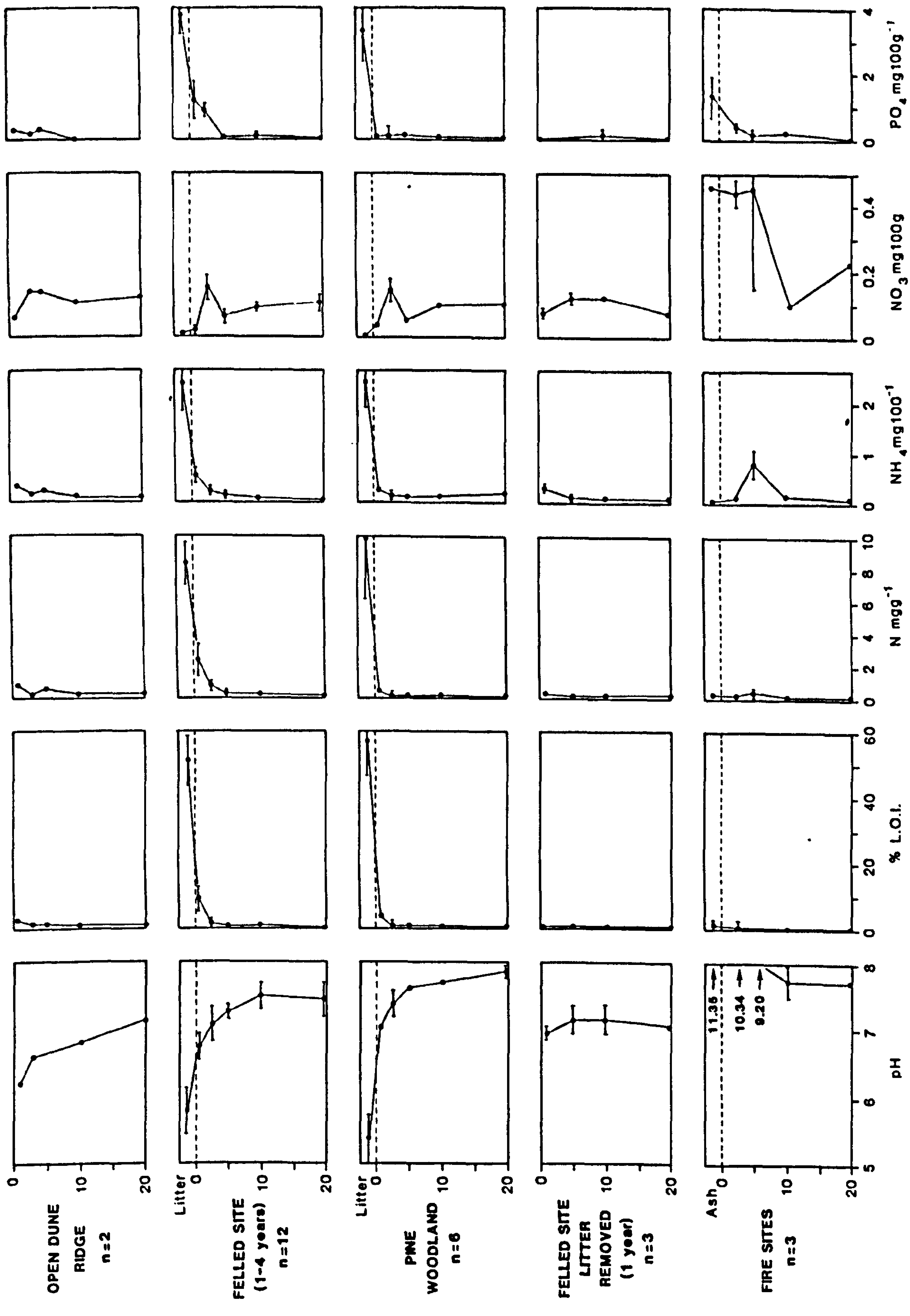
Figure 2.2. Summary of results of soil analyses for samples from Whiteford. Page 41.

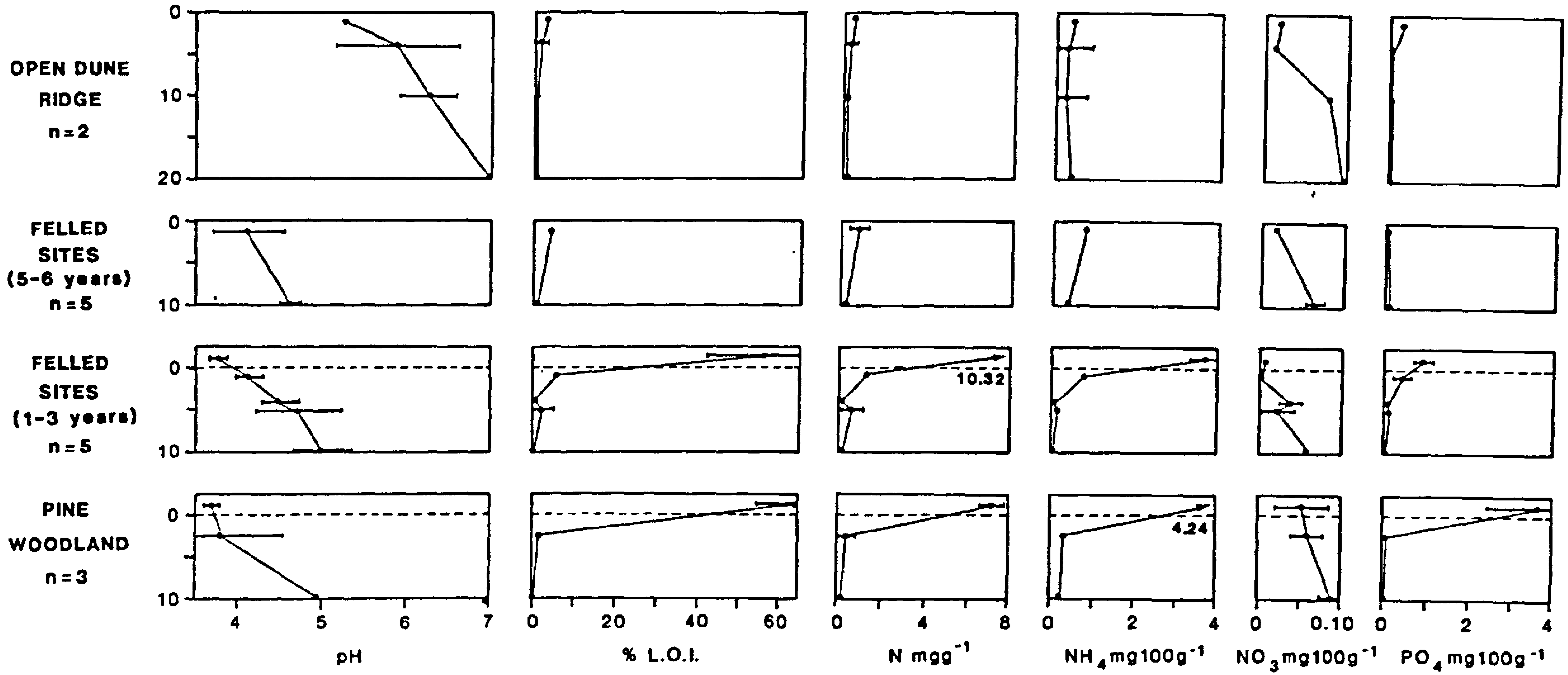
Figure 2.3. Summary of results of soil analyses for samples from Tentsmuir. Page 42.

In all three figures the vertical scale shows soil depth in centimetres. Organic horizons (and ash, in figure 2.2) are shown above the dotted line.



OPEN DUNE RIDGE n=2
FELLED SITES (50 years) n=11
FELLED SITES (1-10 years) n=12
PINE WOODLAND n=6
BULLDOZED SITE n=4
pH
% L.O.I.
N mgg-1
NH4 mg100g-1
NO3 mg100g-1
PO4 mg100g-1
56.8


OPEN DUNE RIDGE n=2
FELLED SITE (1-4 years) n=12
PINE WOODLAND n=6
FELLED SITE LITTER REMOVED (1 year) n=3
FIRE SITES n=3
Litter
Ash
0
10
20
pH
5
6
7
8
11.36
10.34
9.20
% L.O.I.
0
20
40
60
N mgg-1
0
2
4
6
8
10
NH4 mg100-1
0
1
2
NO3 mg100g
0
0.2
0.4
PO4 mg100g-1
0
2
4


OPEN DUNE
RIDGE
n=2
FELLED
SITES
(5-6 years)
n=5
FELLED
SITES
(1-3 years)
n=5
PINE
WOODLAND
n=3
pH
% L.O.I.
N mgg-1
NH4 mg100g-1
NO3 mg100g-1
PO4 mg100g-1
10.32
4.24

### 2.3.1 Unplanted dunes

The soil pits from the unplanted dunes at each site were all dug at sites of similar distance from the sea. The soils can be described as sand pararendzinas (James, in press) with little definition of soil horizons, but they are not identical at all three sites. The dunes at Ainsdale and Whiteford are both formed from calcareous sand and are similar to one another at 20cm below the surface, however the Whiteford system does not have such well developed soil. The pH profiles show that the surface sand at Whiteford is about 1 pH unit higher than at Ainsdale. The Tentsmuir dunes are the most recently formed, but the sand here has a lower pH than the other sites, even 20cm below the surface the sand is about 0.5 pH units lower than at Ainsdale. This is because of different origin of the parent sand (see section 1.6.3).

The unplanted dunes do not contain high concentrations of any of the nutrients measured, although there has been some incorporation of plant material close to the soil surface.

### 2.3.2 Woodlands

In most of the woodland profiles the differences between the organic layers derived from needle litter and the mineral soil are very clear, showing little incorporation of organic matter into the sand. This is shown particularly well by the loss-on-ignition data. The organic horizons have a lower pH, and higher total and ammonium nitrogen, and available phosphate than the mineral soil. The interaction between pH and nitrate and ammonium nitrogen (Rorison & Robinson, 1986) results in little or no nitrate nitrogen being found in the organic horizons: nitrate nitrogen tends to increase with depth, generally increasing with pH (spearman rank correlation coefficient 0.459, d.f.= 267, $p<0.0005$). The highest concentration of nitrate nitrogen in the pinewood soils at Ainsdale and Whiteford is about 5cm below the soil surface: this possibly represents the depth at which the pH results in the mineralization of ammonium nitrogen to nitrate.

The mineral soil below the needle layer seems to vary in its response to afforestation. Soils at Whiteford are apparently unchanged by 32 years under plantation conditions, while at Tentsmuir there is a drop of nearly 2 pH units in about the same length of time under self-sown pine trees. At Ainsdale and Formby there is a reduction in the pH of surface sand below the woodlands, with many of the profiles showing evidence of podzolisation. Even so, the changes appear to be mostly limited to the top 5cm. The capacity for leaching may be greatly reduced below a dense pine canopy. However, woodland microclimates were not examined in detail in this study.

Acidification may be related to the age of the dunes within the study area prior to planting (Hill & Wallace, 1989). To test this, pH profiles from planted and unplanted dunes at Ainsdale aged about 150-200 years old were compared with planted and unplanted dunes from the main study area in older dunes, formed about 250-300 years ago (ages are approximate, based on dates of dune ridge formation; Gresswell, 1953). The results are shown in figure 2.4. Both woodlands were 65 years old but soil acidification was more advanced on the older dune. These differences may be due to calcium carbonate content or other base minerals in the sand. This could provide a larger buffering effect on the acidity of dunes at Whiteford and Ainsdale than at Tentsmuir. Unfortunately, calcium carbonate was not measured in this analysis. Hill & Wallace (1989) reported that there was no significant difference between the calcium carbonate content of soils from planted and unplanted dunes of the same age at Newborough, Anglesey, although the pH at 5cm depth was significantly lower in the woodland than the unplanted dunes. The results from figure 2.4, although based only on individual profiles, also suggest that the reduction in pH of the surface mineral soil caused by 65 years of afforestation is almost twice that caused by 100 years of natural dune weathering.

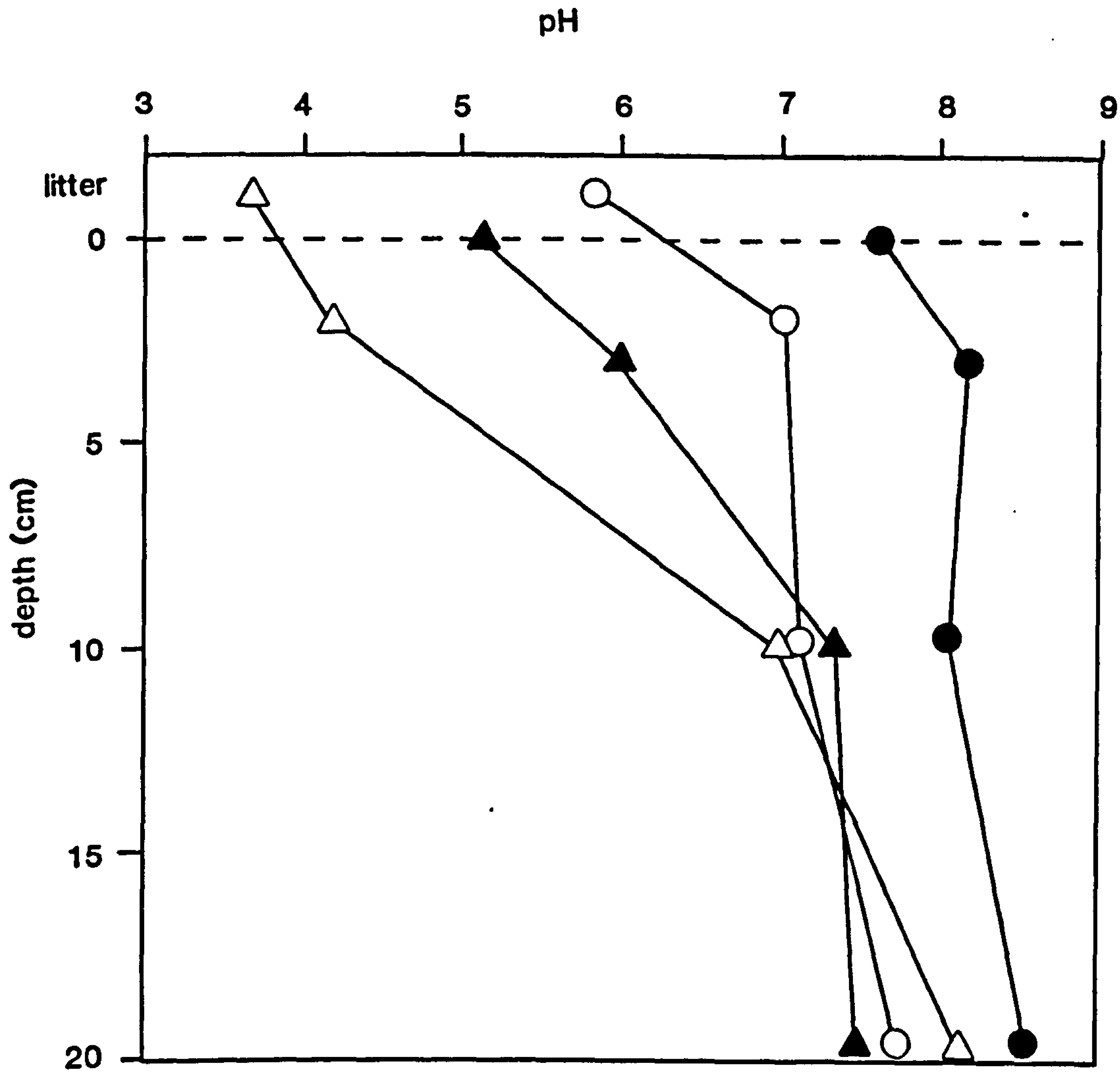



Figure 2.4 pH profiles of four sites along the plantation boundary at Ainsdale N.N.R.. Shaded symbols are from dunes aged about 150 to 200 years, open symbols show dunes aged about 250 to 300 years old. Triangles were woodland sites. Circles were from unplanted dunes.

### 2.3.3 Felled sites

Soil profiles from felled areas vary between the study sites and with time after felling. At Whiteford and Tentsmuir most soil characteristics do not show any significant differences from the woodlands after three years, although there is a reduction in organic matter content and a slight increase in nitrogen concentration in the organic surface horizons (see section 2.4). At Ainsdale sites felled for 50 years have a surface organic matter and total nitrogen content very similar to the unplanted dunes, although the levels of ammonium nitrogen and phosphate are as high as the woodland. Sites felled for up to 10 years show a reduction of the organic matter and a slight increase in total nitrogen concentration in the litter layer, when compared with the woodland soil (also see plate 9, and section 2.4). The pH profiles from sites at Ainsdale felled 50 years ago are more similar to the unplanted dunes than the woodlands: this may be partly because the woodland soil development was not very far advanced when the trees were felled at around 20 years old (Moriarty, 1978; James & Wharfe, 1989) and partly due to plant growth and animal activity redistributing soil material during the 50 years following felling.

The soil change following stump-removal by bulldozer was investigated at Ainsdale (figure 2.1). The micropodzol is completely broken up, leaving the soil profile closer to that of the grey, or even mobile dunes, as the organic material is buried and unaltered calcareous sand is brought to the surface.

### 2.3.4 Fire sites

Local effects of burning brash at small fire sites were studied at Whiteford. Figure 2.2 shows that organic matter and total nitrogen are almost eliminated from the woodland soil after burning, while pH and nitrate concentration are very high in the ash. Acid-extractable phosphate probably gives a low estimate of available phosphate in this situation. Under such alkaline conditions an extraction by sodium bicarbonate may have been more useful (P.A.James, pers.comm).

### 2.3.5 Mineral weathering

With the increase in acidity of the sand below the pinewoods, at least in the Ea horizon, an increase in mineral weathering may be expected. No laboratory analysis was undertaken as part of this study, but two unpublished reports of mineralogy at Ainsdale N.N.R. allow comparison of soils of woodlands and unplanted dunes (Minton, 1985; Rimmer, 1989). The studies are not completely compatible although data from some analyses can be re-examined. Experimental differences between the two workers is minimised by choosing study sites which are close together (see figure 1.2) and supporting woodland of similar age.

The percentage (by weight) of soil material passing through a 125μm mesh, and the percentage (by counting) of quartz and feldspar grains (those most resistant to weathering) in the 125-250μm fraction, are shown for four soil profiles in figure 2.5.

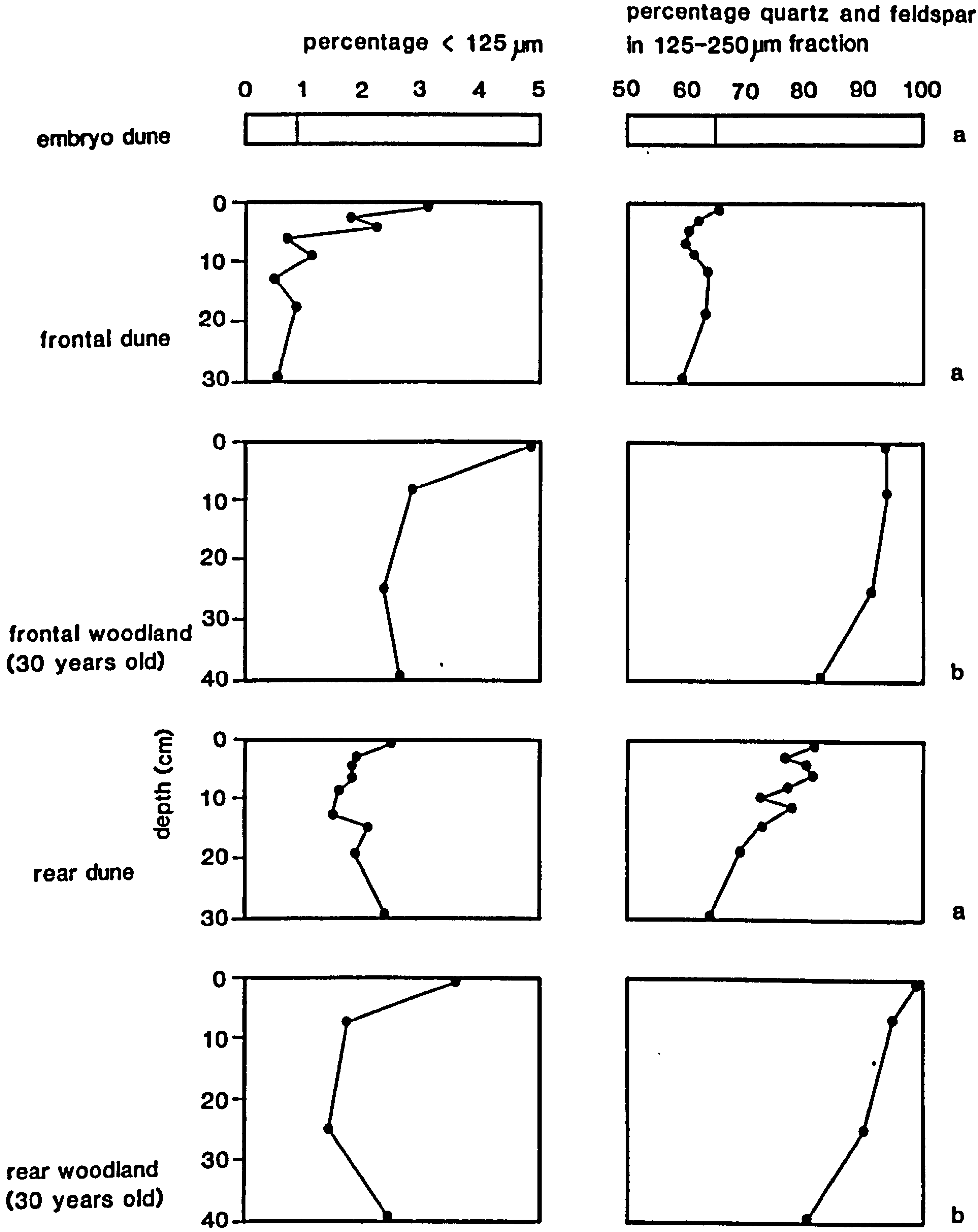



Figure 2.5. A comparison of selected mineralogical data from five sites at Ainsdale N.N.R.. a: Data from Minton (1985); b: data from Rimmer (1989).

The proportion of quartz and feldspar decreased with depth in all profiles. This suggests that mineral weathering has progressed further in the surface horizons, where relatively unstable minerals such as calcite have broken down by hydrolysis in the more acid conditions, leaving the more resistant grains.

The particle size distributions show several distinctions between the profiles. The proportion of fine material at the surface is higher in the woodlands than in the unplanted dunes, which may be as a result of weathering. Minton reports a more weathered appearance to the grains from the older soils when examined in thin section. This is reflected in the percentage counts for quartz and feldspar grains which are higher at the surface of the unplanted grey dune than the yellow dune. Rimmer shows a higher proportion of these resistant minerals in the woodlands, with almost 100% quartz and feldspar in the surface sand of an afforested grey dune.

## 2.4 Decomposition Study

One of the most important changes brought about by the pinewoods is the production of needle litter, which often carpets the ground as a thick layer. Klimo and Grunda (1989) observed a 46% increase in the supply of material to the forest floor after clear-felling a Norway Spruce stand. The extra material due to the felling was mostly needles, current year's twigs and small branches. This study examines the rate of litter decomposition following clear-felling, and the rate at which nitrogen is released. The decomposition of weighed samples of different types of litter under post-felling conditions is monitored using a 'litter-bag' method, noting changes in dry weight, loss on ignition and organic nitrogen content. The results are compared with field data from section 2.3.

### 2.4.1 Methods

Pine cones, twigs and three types of litter were collected from a 70 year old stand of <u>Pinus nigra</u> ssp <u>laricio</u> at Ainsdale. The site was adjacent to a fire-break clear-felled 10 years previously (see figure 1.2). The plant material was air-dried for two weeks before sub-sampling into 15 x 15 cm bags of 1mm nylon mesh. Each bag was weighed before being loosely filled with litter, then sewn up and reweighed. The number and contents of the litter-bags is described in table 2.1.

Table 2.1 Litter-bag experiment, started August, 1989.

| Litter Type | Number | Description |
|---|---|---|
| Green litter | 40 | Needles taken from live branches |
| Brown litter | 40 | Recently fallen needles |
| Humus | 40 | Partially decomposed litter |
| Twigs | 10 | 10cm x 10-20mm diameter twigs |
| Cones | 10 | Recently fallen cones |

The weighed bags were placed at two sites within the fire-break on August 21st, 1989. At each site post-felling conditions were simulated by removing all vegetation regrowth and surface litter, and replacing it with litter from the woodland. The new litter was laid down as found naturally, with the most recent at the surface, and trampled down to a depth of about 10cm. The litter-bags were placed in this litter with the humus buried deepest, the brown litter, cones and twigs 4cm below the surface and the green litter 2cm below the surface.

The bags were divided between two sites within the fire-break as a precaution against vandalism. The sites were chosen because they were very similar and only 20 metres apart. Other precautions taken were to bury the samples and to dye the nylon brown.

Collections of bags were made on March 28th, 1990, October 10th, 1990, and May 18th, 1991. Five bags each of green litter, brown litter and humus were taken from each site at each collection. The cones and twigs were brought back on the third collection.

The bags were air-dried in the laboratory and weighed, then opened. The contents of four bags of each litter type from each collection were analysed for moisture content, loss on ignition and total organic nitrogen, as described in sections 2.2.2 and 2.2.3. The organic carbon content of the each sample was estimated from the total organic matter using the following regression equation:

$$y = 0.476x - 1.87$$

where y is organic carbon and x is loss on ignition (Hesse, 1971).

### 2.4.2 Results and discussion

The results of the laboratory analysis are summarised in table 2.2. Weight loss and net changes in nitrogen content are shown in figures 2.6 and 2.7.

Table 2.2 Carbon and nitrogen content in litter. Each figure is derived from four replicate samples.

| Litter | Collection | Carbon (%) Mean | Carbon (%) SE | Nitrogen (%) Mean | Nitrogen (%) SE | C/N |
|---|---|---|---|---|---|---|
| Green | 0 | 44.6 | 0.03 | 0.92 | 0.01 | 48.5 |
| | 1 | 43.9 | 0.15 | 1.08 | 0.07 | 40.8 |
| | 2 | 43.2 | 0.30 | 1.11 | 0.11 | 39.1 |
| | 3 | 43.3 | 0.31 | 1.48 | 0.05 | 29.2 |
| Brown | 0 | 45.0 | 0.02 | 0.61 | 0.05 | 73.5 |
| | 1 | 44.8 | 0.05 | 0.53 | 0.14 | 84.9 |
| | 2 | 44.4 | 0.19 | 0.89 | 0.08 | 50.0 |
| | 3 | 43.9 | 0.30 | 0.83 | 0.05 | 53.0 |
| Humus | 0 | 29.2 | 1.60 | 0.74 | 0.06 | 39.5 |
| | 1 | 41.5 | 0.32 | 1.01 | 0.07 | 41.1 |
| | 2 | 40.3 | 0.36 | 1.13 | 0.04 | 35.6 |
| | 3 | 41.4 | 0.28 | 1.06 | 0.06 | 39.1 |
| Cone | 0 | 45.6 | 0.02 | 0.30 | 0.02 | 150.9 |
| | 3 | 45.1 | 0.23 | 0.47 | 0.34 | 125.6 |
| Twigs | 0 | 44.8 | 0.05 | 0.29 | 0.03 | 153.5 |
| | 3 | 44.4 | 0.21 | 0.39 | 0.06 | 114.9 |

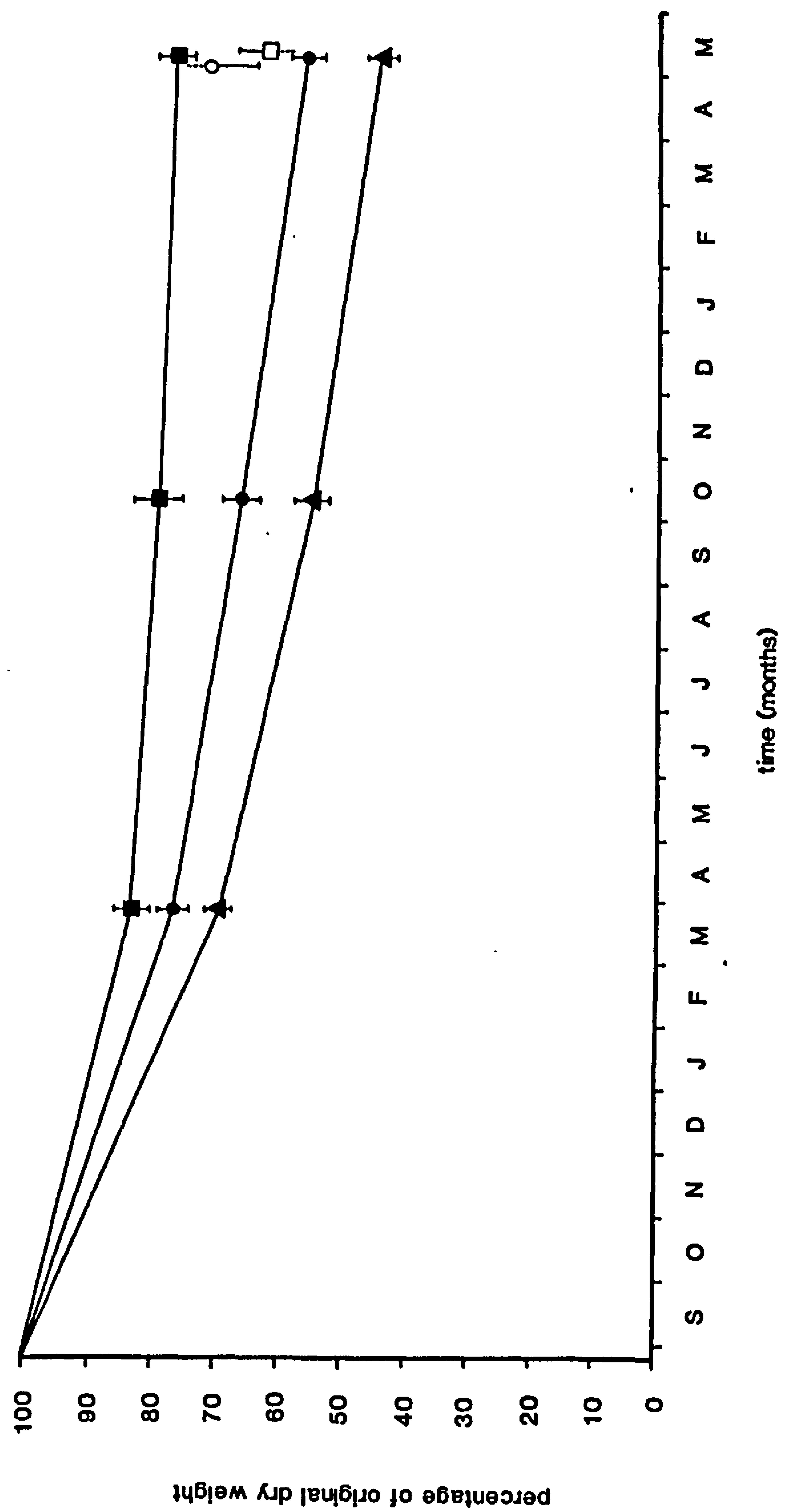



Figure 2.6 Changes in dry weight of litter bags in a simulated clear-felling environment at Ainsdale N.N.R.. Mean values are given, with standard error bars. Symbols are as follows: ▲ green litter, ● brown litter, ■ humus, O pine cone, □ sticks.

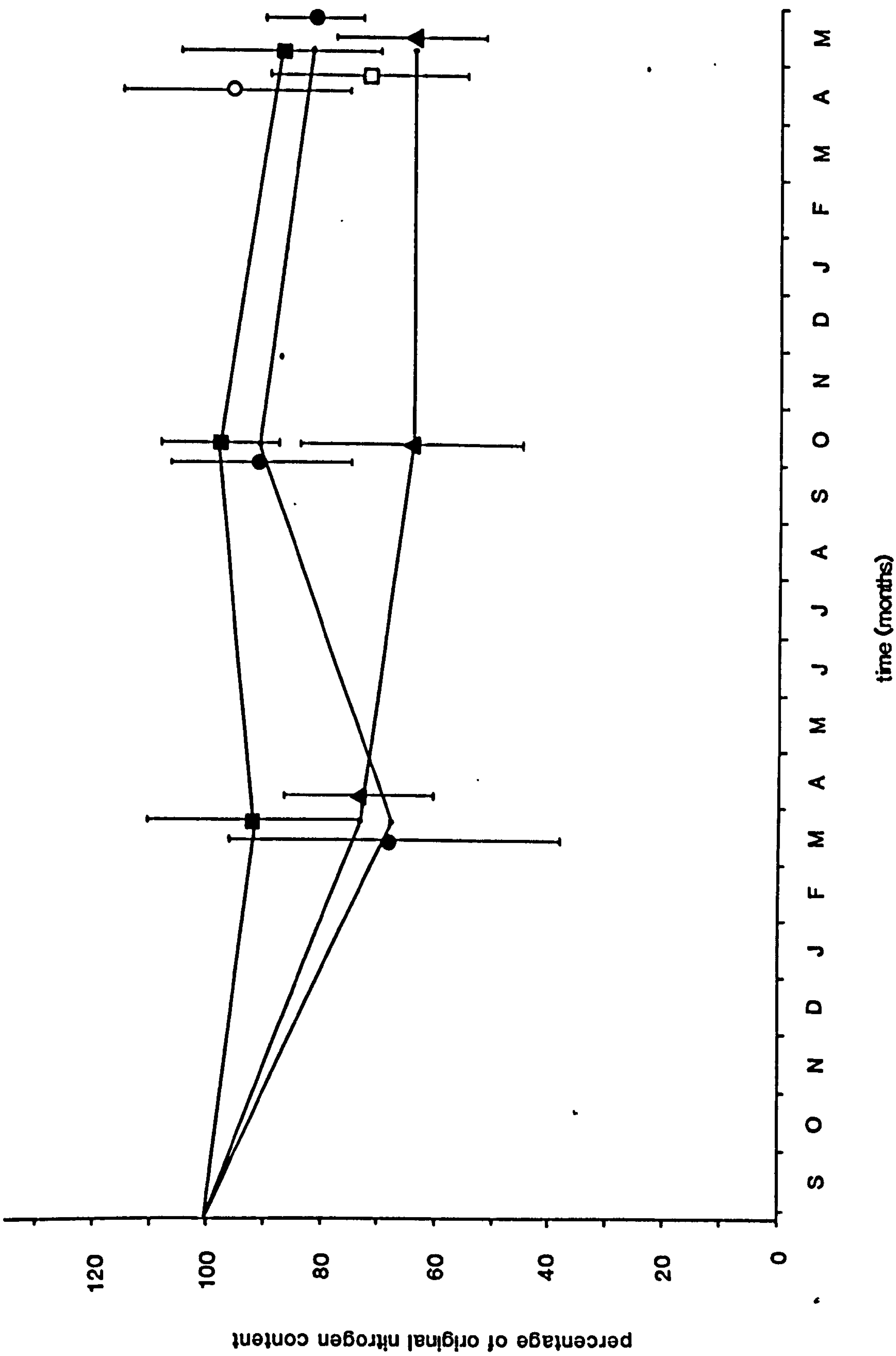



Figure 2.7 Percentage changes in total nitrogen content of litter bags in a simulated clear-felling environment at Ainsdale N.N.R.. Mean values are given, with standard error bars. Symbols are as follows: ▲ green litter, ● brown litter, ■ humus, ○ pine cone, □ sticks.

Figure 2.6 shows that the woody materials and humus lost weight more slowly than the green and brown litter. The rate of humus decomposition may be artificially slow due to a relatively high sand content.

The differential weight losses may depend upon the nutrient status of the litter. C/N ratio is often used as a measure of the degree of decomposition of organic material in soil. The general trend in this study is an increase in the percentage nitrogen content with time, and a decrease in C/N ratio.

Berg (1986) has suggested a two-phase model for decomposing pine litter; in the first phase soluble nutrients and non-lignified carbohydrates are decomposed, with the rate of mass-loss determined by the concentrations of nutrients which limit microbial activity, such as nitrogen, phosphorus and sulphur. The second phase begins after the easily degraded compounds have been broken down, leaving behind mostly lignin and lignified carbohydrates. The second phase is slower, being regulated by the rate of mass-loss of lignin. In this study the green and brown litter bags lost weight more quickly than the humus, perhaps because they contained a greater proportion of soluble organic compounds and nutrients. The brown litter would have had a lower concentration of nitrogen than the green litter as much nitrogen is reabsorbed from needles before they fall naturally (Staaf & Berg, 1981). The rate of nitrogen-loss from the humus samples, which were already partially decomposed, may have been slower as they were in the second phase of decomposition and dependent on the rate of lignin breakdown.

The highest C/N ratio was seen in the cones. These were slow to decay, again possibly because of the high lignin content. The nitrogen content of the cones was initially low, and like the humus showed only a slight decrease over the 20 month study period. Nitrogen may be retained by microorganisms while the amount of carbon is progressively reduced through respiration (Gosz et al, 1973), but this cannot explain the absolute increase seen in some litter bags. Vitousek and Melillo (1979) have suggested that fungi may transport large quantities of nitrogen and other minerals into decomposing logs, and Newell and Heal (1982) have described tree stumps as nutrient-sinks, into which nutrients are translocated by decomposer fungi from adjacent sources, such as needles. In the same way other high C/N materials may accumulate nutrients in a clear-felled environment. Berg and Staaf (1981) found that nitrogen accumulation is dependent on the nitrogen concentration of the litter, with accumulation occurring when the C/N ratio is greater than about 36-170, varying with the system. They found that nitrogen would continue to increase until a critical level was reached. This also varies with the system.

The twigs had a high C/N ratio but they decayed relatively quickly. This may be because they were very fresh (taken from a live branch) at the start of the study, and might have had higher proportions of nutrients and soluble carbohydrates, at least in their bark. Sollins et al (1987) have found C/N ratios of over 250:1, and Newell and Heap (1982) ratios of about 1000:1 for conifer heartwood and so the twigs chosen for this study do not give a typical representation of decay rates for wood. The small size of the twigs also means that there is a proportionally greater surface area for microbial attack.

Nitrogen was the only nutrient measured in this study, but others are known to influence litter decomposition. Staaf and Berg (1982) examined the retention of several other elements during litter breakdown since 'nutrients limiting microbial growth could be expected to be retained or accumulated to a minimum concentration, and thereafter be released at the same rate as organic matter weight loss, while elements in nonlimiting concentrations are released during the whole period of decomposition'. They suggested that phosphorus was the most limiting element for microbial activity during the first phase, with nitrogen and sulphur also being accumulated. Manganese, calcium, potassium and magnesium were all released from the beginning of the incubation.

The immobilisation of nutrients in the litter affects the rate of decomposition, but also has implications for plant recolonisation following clear-felling. The amount of nutrients available for uptake by plants may be temporarily large if there is an initial leaching phase (Berg & Staaf, 1981), however most of the nutrients remain chemically bound within the litter (Berg, 1986). Berg (1988) observed a considerable turnover of $^{15}N$ in decomposing pine litter, but this was not reflected in the total nitrogen analysis because for any release there was usually a simultaneous uptake into the litter. Vitousek (1981) found that in low nutrient systems, such as coniferous forests, with a C/N greater than 20-25:1, all of the nitrogen could be in an immobilised form. This study shows that the litter bags in the fire-breaks at Ainsdale have a higher C/N ratio (29-153 after 20 months), suggesting that although the percentage of total nitrogen in the litter is considerably higher than that of the grey dunes, the available nitrogen may be much less. The availability of nitrogen in dune sand has been found to be higher in young, mobile dunes than in older, grey dunes, although total nitrogen increases through time (Fay & Jeffrey, in press; P.Fay, pers.comm.).

To compare these experimental findings with the field situation the Ainsdale N.N.R. soil data (section 2.3) from organic horizons from soil pits near to the fire-break have been reanalysed (table 2.3) to show how the C/N ratio changes with time after felling.

Table 2.3 Carbon and nitrogen data from organic horizons of some soils at Ainsdale N.N.R.. Mean values are given, with standard error shown in brackets.

| Years Afforested | Years Felled | n | Carbon (%) | Nitrogen (%) | C/N |
|---|---|---|---|---|---|
| 0 | 0 | 2 | 6.3 (0.02) | 0.41 (0.14) | 15.5 |
| 20 | 50 | 4 | 6.5 (1.41) | 0.33 (0.06) | 19.7 |
| 50 | 10 | 5 | 23.9 (2.77) | 0.78 (0.16) | 30.7 |
| 60 | 0 | 4 | 26.3 (7.18) | 0.63 (0.23) | 41.7 |

The data show that the C/N ratio falls with time after felling. The high value for the fire-break sites felled 10 years previously suggests that there is very little nitrogen release. This is reflected in the vegetation, which is dominated by mosses and perennial species such as Chamaenerion angustifolium which established very soon after felling and are well adapted to internal nutrient cycling (Van Andel & Nelissen, 1979). Colonies of C.angustifolium have survived on clear-felled sites at Ainsdale for 50 years (Blanchard, 1952; pers.obs). The ratio for the site felled 50 years ago is much closer to that of the unplanted dune, suggesting that this soil has a higher proportion of its nitrogen available to plants. The vegetation of this site, dominated by tall Carex arenaria, Festuca rubra, Poa pratensis and Dactylis glomerata, is consistent with this suggestion. However, since the site had only been afforested for about 20 years, there may also be other reasons for differences in vegetation; these are discussed in chapter 3.

## 2.5 Bioassay of Soil Fertility

Levels of mineral nutrients, particularly nitrogen, phosphorus and potassium are known to be limiting in many dune systems (Willis, 1989). The deficiency of nutrients and consequent low plant productivity is largely responsible for the high species diversity of sand dune grassland, preventing dominance by any single species. Addition of fertiliser to dune grassland at Braunton Burrows increased vegetation height and biomass, with the grasses Festuca rubra and Agrostis stolonifera becoming strongly dominant (Willis & Yemm, 1961; Willis, 1963). Section 2.3 has shown that there is an increase in total and ammonium nitrogen at the soil surface following accumulation of needle litter in dune plantations; after clear-felling this may result in a soil fertility too great to support a diverse and typical dune flora.

To try to assess the suitability of the soil for plant growth following clear-felling, seedlings of Festuca rubra were grown in soil samples taken from unplanted dunes, woodlands and clear-fell sites of different ages. The method is based on that used by Hodgkin (1984).

## 2.5.1 Methods

Soil samples were taken from the top 10cm (including litter) of five 20 x 20cm soil pits at Ainsdale N.N.R., in unplanted dunes, woodlands and clear-felled sites. Samples were only taken from south-facing slopes (10-15°). None of the woodland sites had a well developed ground flora. The soil was sieved and mixed thoroughly with an equal volume of sterile silver sand (to reduce physical differences between samples, such as drainage, and to emphasise differences in soil fertility by making nutrients more limiting).

Ten 10cm pots were filled with each soil mixture and four seedlings of Festuca rubra were planted into each. The seedlings were all seven days old and had been germinated in sterile vermiculite. The pots were kept in a heated glasshouse and watered with distilled water. The plants were harvested after 5 months.

## 2.5.2 Results

The results are summarized in figure 2.8. An analysis of variance with Scheffé's multiple range test was used to test for differences between treatments ($p > 0.05$, df= 9,86, F= 25.73).

Soil from the two most recently felled sites gave significantly the greatest yields. The mobile and grey dune sand gave low yields although not significantly different from one another. Few significant differences were shown in the data.

Table 2.4 Spearman's Rank Correlation Coefficients. ** = $p<0.001$, * = $p<0.05$, NS = not significant

| | pH | L.O.I. | Total N | $NH_4$ N | $NO_3$ N | $PO_4$ |
|---|---|---|---|---|---|---|
| Yield | -0.339<br>** | 0.542<br>** | 0.541<br>** | 0.197<br>* | 0.144<br>NS | 0.418<br>** |

Table 2.4 shows that higher yields correlate with lower pH, and larger amounts of organic matter (L.O.I.), total nitrogen, ammonium nitrogen and phosphate; that is, from deeper organic soils. The unfelled woodland soils were mostly less fertile than clear-felled sites, possibly because the litter decomposition was not so advanced (see section 2.4) with nutrients being held in unavailable forms (Williams, 1972). The highest yield was from the most recently cleared site, probably a result of rapid nutrient mineralisation during the first few months following felling (Berg & Staaf, 1981; Vitousek, 1981). The reason for the high yield from the site felled for 10 years is unclear since a high C:N ratio would theoretically result in poor yields. It is possible that over 5 months under the warm, well watered and aerated conditions of the glasshouse

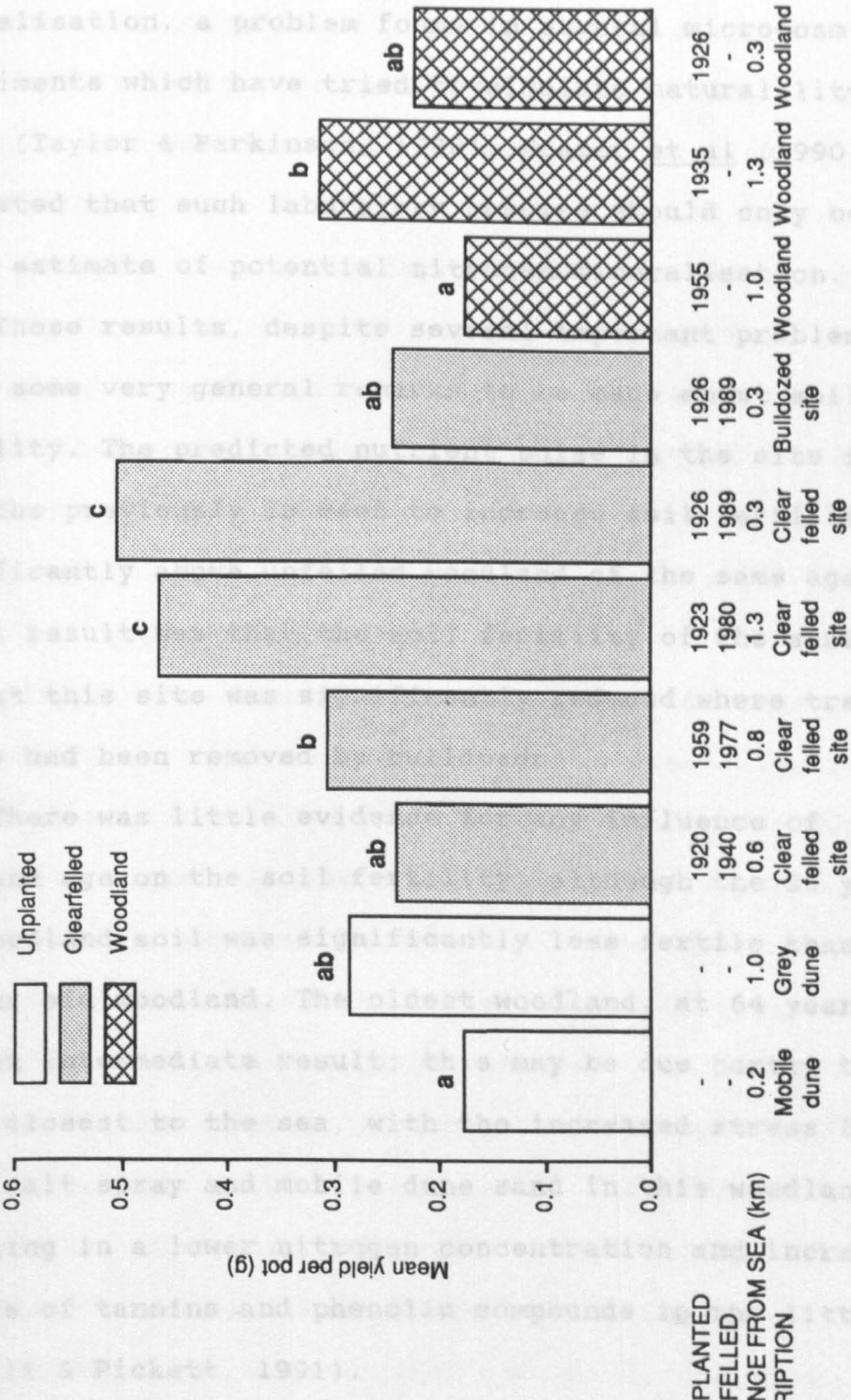



Figure 2.8 Results of the bioassay experiment. Columns sharing the same letter are not significantly different from one another ($p > 0.05$).

could have accelerated decomposition and nitrogen mineralisation, a problem found in several microcosm experiments which have tried to simulate natural litter decay (Taylor & Parkinson, 1988). Frazer et al (1990) have suggested that such laboratory results should only be used as an estimate of potential nitrogen mineralisation.

These results, despite several important problems, do allow some very general remarks to be made about soil fertility. The predicted nutrient pulse in the site felled 6 months previously is seen to increase soil fertility significantly above unfelled woodland of the same age. One useful result was that the soil fertility of the surface sand at this site was significantly reduced where tree stumps had been removed by bulldozer.

There was little evidence for any influence of woodland age on the soil fertility, although the 35 year old woodland soil was significantly less fertile than the 55 year old woodland. The oldest woodland, at 64 years old, gave an intermediate result; this may be due partly to it being closest to the sea, with the increased stress from wind, salt spray and mobile dune sand in this woodland resulting in a lower nitrogen concentration and increased amounts of tannins and phenolic compounds in the litter (Facelli & Pickett, 1991).

The length of time following felling is apparently correlated with a decrease in soil fertility. However, this may also be a consequence of the length of time under forested conditions. Fifty years after a 20 year old plantation was clear-felled, the soil fertility was not significantly different from that of a former 18 year old woodland felled 13 years previously, and neither of them was significantly different from the fertility of grey dunes. Clear-felling older plantations resulted in significantly more fertile soil after 10 and 0.5 years. This suggests that the older a plantation is, the greater the enrichment of the soil may be; although the experimental conditions do not allow any accurate estimate of the time scale for nutrient mineralisation or loss under normal temperature and rainfall.

## 2.6 General Discussion

The various investigations described in this chapter have confirmed that the changes to the dune soils following afforestation are largely a consequence of the accumulation of needle litter. In the young plantations at Whiteford the afforestation appeared to have had only a small effect on the mineral soil below the litter. However, greater changes were evident in plantations at Ainsdale and Tentsmuir.

The development of a micropodzolised soil profile is not always seen in dune plantations. The process is, to some extent, dependent on time (James & Wharfe, 1989), but site conditions may have an over-riding influence. The ground flora, the base-mineral content of the sand, and the microclimate are particularly important.

A well developed, herbaceous ground flora can lead to a more easily decomposed, base-rich litter; with more active cycling of nutrients by plant roots and a larger soil fauna. Root death can also increase the transfer of organic material deeper down the soil profile. In this case a brown earth profile may form, as seen in some of the older woodland at Ainsdale (pers.obs.) and in dune plantations at Newborough (J.Ratcliffe, pers.comm.). The same effect is seen when a post-felling flora develops, with the boundary between the mineral and organic horizons becoming very indistinct.

Another important factor is the base content of the sand: Ball and Williams (1974) studied soil development below pines at Holkham, Norfolk, on dunes formed from quartz sand containing less than 2% calcium carbonate, observing that '...morphological and chemical changes due to pedogenesis occur during a relatively short time on dune sand of low calcium content...'. The afforested fore-dunes at Ainsdale are not podzolised, while those on the older dunes are. Some afforested calcareous dunes in Northern Ireland do not show any evidence of podzolisation even 60 years after planting (P.Wilson, pers.comm.). This has implications for dune managers wishing to clear-fell plantations and restore the area to a near-original state. On a very calcareous dune system which has only been afforested for a short time, it may be much easier to restore a soil profile after removing the litter horizons, than on a more acid system where the surface sand will have been influenced by the pines to a greater extent.

Although not investigated in this study, the influence of salt may result in differences between soil development between different dune plantations. Salt-spray deposition is greater on taller vegetation than grassland, especially nearer to the sea (Malloch, 1972, Etherington, 1967). The deposited salt will eventually reach the soil; McLoughlin (1988) reported a negative correlation between soil cation content and distance from the sea, within the Ainsdale plantations. Salt may affect the soil by replacing hydrogen ions on cation exchange sites, offsetting the acidity of the needle litter, this helps to explain why the highest pH of the L and F horizons at Ainsdale, 7.0, was from the soil pit nearest to the sea. Salinity may also influence the decomposition of pine litter. Laura (1974) found that nitrification in decomposing Delonix regia leaves was inhibited by salt concentrations between 0.6 and 0.9%, however, carbon and nitrogen loss increased at higher salinities. Laura's hypothesis (1976) was that although salt may inhibit microbial decomposition, the protolytic action of water increases in alkaline and saline conditions, thereby increasing the mineralisation of organic matter. This may be important in sand-dune plantations and further investigations would be useful.

The soils of the recently clear-felled sites were more similar in appearance to those of the woodlands than those of the unplanted dunes due to the continued presence of the organic material. Unless it is physically removed, or greatly disturbed during felling, this litter can remain for several years; some areas within the 10 year-old Ainsdale fire-breaks still have compacted layers of organic material over 10cm deep (pers.obs., and plate 9). The main reason for its slow decay may be its high carbon:nitrogen ratio. The litter which remains for the longest time tends to be the woody cone and stick material, but of the needle-based litter the F and H horizons last longest.

In young plantations, such as those felled 17 years ago at Whiteford, the majority of the litter may consist of a loose layer of recently fallen needles which can decompose quickly. This poses little difficulty to dune restoration. However, an older plantation will have a thicker F and H horizon which after felling can form a compact layer which may reduce the infiltration of rainfall and suppress germination from the buried seed-bank (see chapter 3). Vegetation recovery on such a substrate will be very unlike that of the unplanted dunes. Organic mats of decomposing needle material were seen on felled sites at all three study sites, invariably supporting a community dominated by bryophytes (particularly *Dicranum scoparium*, *Hypnum cupressiforme* and *Campylopus introflexus*) and *Chamaenerion angustifolium*. *Betula* and *Pinus* appeared able to regenerate particularly well on this surface. Thin organic crusts at Whiteford and Tentsmuir became cracked after dry periods, exposing some of the sand below the litter.

The release of nitrogen and phosphorus from the decaying litter is of particular importance to vegetation recovery. There may be a pulse of nutrients, such as nitrates, released immediately after felling as non-lignified carbohydrates are decomposed; this period of most rapid weight- and nitrogen-loss lasted for less than 7 months in the litter-bag study at Ainsdale (figures 2.6 and 2.7). Nutrients released during this phase may be taken up by plants, but if no plants are present they can be leached from the system, assisted by the increased effective rainfall. The study of nutrient losses from the soil could be monitored much more closely by the use of suction-plate lysimeters (A.D.Bradshaw, pers.comm.). At all of the study sites the plants present immediately after felling grew vigorously, suggesting an unusual abundance of available nutrients. Particularly note-worthy observations included strong growth of _Urtica dioica_ together with _Cirsium vulgare_ which reached a height of 2 metres on a site felled for 6 months at Ainsdale (although _Hippophae rhamnoides_ was possibly present on this site several years previously (NCC, unpublished data), and may also have enriched the soil). At Whiteford the normally biennial _Oenothera parviflora_ was seen to germinate and flower within 6 months of clear-felling. The latter species is common in sites clear-felled for 4, 5 and 6 years at Whiteford, but almost exclusively as basal-leaf rosettes surviving year after year without flowering. This may be a symptom of nutrient deficiency, which would be very easy to test by supplying some of the plants with nitrogen and/or phosphorus as a foliar feed. Nutrient deficiency should be expected after the initially rapid phase of decay, as nutrients are retained in lignified tissues and in the microbial community (see section 2.4).

The removal of the timber crop represents a net loss of nutrients from the system. Heal _et al_ (1982) have suggested that this may result in phosphorus becoming more limiting after harvesting at some sites. The phosphorus content of 20 year old pines at Whiteford was investigated in 1975 (J.R.Etherington, unpublished). It was shown that the plantation had utilised all of the easily available phosphorus from the soil organic pool, although there was sufficient total insoluble calcium phosphate in the soil to replace this loss.

The sites felled 50 years ago at Ainsdale often support a scrub or mesotrophic grassland vegetation (see section 3.3), suggesting that they have a greater soil fertility than the unplanted dunes. The total amount of nitrogen held in the litter of the woodland floor is much higher than in the rooting zone of most plants on the unplanted dunes (Jenkins, in preparation). Theoretically, if the gradually released nutrients are retained by plants then their artificially high concentration at the soil surface will be maintained, resulting in nutrient levels too high to support a natural flora. However, observations on dunes at Drigg, Cumbria, where a long established colony of black-headed gulls has recently deserted the site, suggest that large amounts of nutrients can, in fact, be leached from a closed dune grassland in a very short time. Nutrient enrichment over several decades had resulted in a nitrophilous flora locally dominated by _Urtica dioica_ and _Arctium minus_. Less than 10 years after the gulls' leaving, the vegetation has more or less returned to typical dune grassland vegetation. Unlike the soil of the clear-felled woodlands the soil at this site had not built up a deep organic layer (D.Simpson, pers.comm.).

If nutrients can be leached quickly from dune vegetation then the reason for the prolonged increase in soil fertility 50 years after felling cannot be simply a response to a high nutrient content. There must be a mechanism (or mechanisms) for holding nutrients within the system. A long-term slow release from tree stumps and other woody components in litter has been shown to provide a slow turn-over of nutrients after felling (Newell & Heal, 1982). The presence of organic material can also increase the cation exchange capacity of the soil, slowing nutrient losses, particularly where a low pH results in inorganic nitrogen existing primarily as ammonium ions. Factors such as increased water retention by the decomposing litter may lead to better plant growth, with a greater proportion of nutrients held in living tissues. A large plant biomass, as in rank grassland or scrub, may be able to cycle nutrients and even build up new litter horizons almost as efficiently as the plantation. Some species, such as Chamaenerion angustifolium, are particularly well adapted for internal nutrient cycling (Van Andel & Vera, 1977).

Any sand dune manager wishing to restore typical dune vegetation on the site of a clear-felled plantation must pay particular attention to the soil. The organic litter horizons from the woodland are an atypical growth medium for most dune plants. If organic material is left in situ it may take several years to decay, initially encouraging the development of a weed and scrub flora. The immobilisation of nutrients in the decomposing litter may result in a phase of nutrient deficiency. However, this is only temporary and if retained in the ecosystem the eventual total nutrient release may be greater than in a typical dune grassland.

## CHAPTER THREE: POST-FELLING CHANGES TO THE PLANT COMMUNITY

### 3.1 Introduction

Vegetation change following felling is the central aspect of this study since the aim of the tree clearance is to restore a plant community similar to the original dune flora. The study sites all possess unplanted dunes which may be used for comparison with the clear-felled areas; if the vegetation of the felled woodlands is indistinguishable from the unplanted dunes then the clearance can be judged successful in conservation terms.

The methods used to examine the plant communities are based on quadrat sampling; the computer package VESPAN II (Malloch, 1988) was used to process the survey results. The classification program TWINSPAN (Two-way Indicator Species Analysis) (Hill, 1979a) was used to establish which quadrats are most similar to one another, grouping them into vegetation types. The ordination program DECORANA (Detrended Correspondence Analysis) (Hill, 1979b) was used to identify the main trends in vegetation quality within the data. With the quadrat data arranged along ordination axes, variables such as soil and time factors were correlated with these trends, allowing possible causes of the changes to be recognised. The main ordination analysis was limited to a three-year study period. However, a smaller survey at Whiteford provided data for a ten-year period.

Associated studies of vegetation change were also made: these include investigations into the differences between the seedbanks of unplanted dunes and woodlands, and the vesicular arbuscular mycorrhizal floras of four different habitats at Ainsdale.

## 3.2 Permanent Quadrat Study 1978-1988, Whiteford

Plantation K at Whiteford N.N.R. contains a mixture of *Pinus sylvestris* and *P. nigra* ssp *laricio*, planted in 1959. Since its purchase by the Nature Conservancy Council in 1972 the plantation has been managed with the intention of encouraging the development of a ground flora prior to clear-felling the trees. An even, 50% thinning, mostly of the poorer trees, was carried out from late 1975 to mid 1978, and the remaining trees brashed to head-height. The cut trees and brashings were removed or burnt on site.

In 1978 a vegetation survey was conducted, and quadrats marked with stakes (Hughes, 1978). Between 1983 and 1984 five areas within the plantation were clear-felled, the timber was removed and the branches burned on site (Davies, 1985). Thirty-six of the the stakes from the original survey were still present in 1988, some still below the tree canopy, and some now in cleared areas. This presents a valuable opportunity to compare woodland and clear-felled vegetation types, and to assess the effects of the various treatments used.

### 3.2.1 Methods

Four transect lines (A-D) were set up in the plantation by students of University College, Cardiff. Each line was marked by thirteen posts at 10 metre intervals, forming a survey grid of 52 posts as shown in figure 3.1.

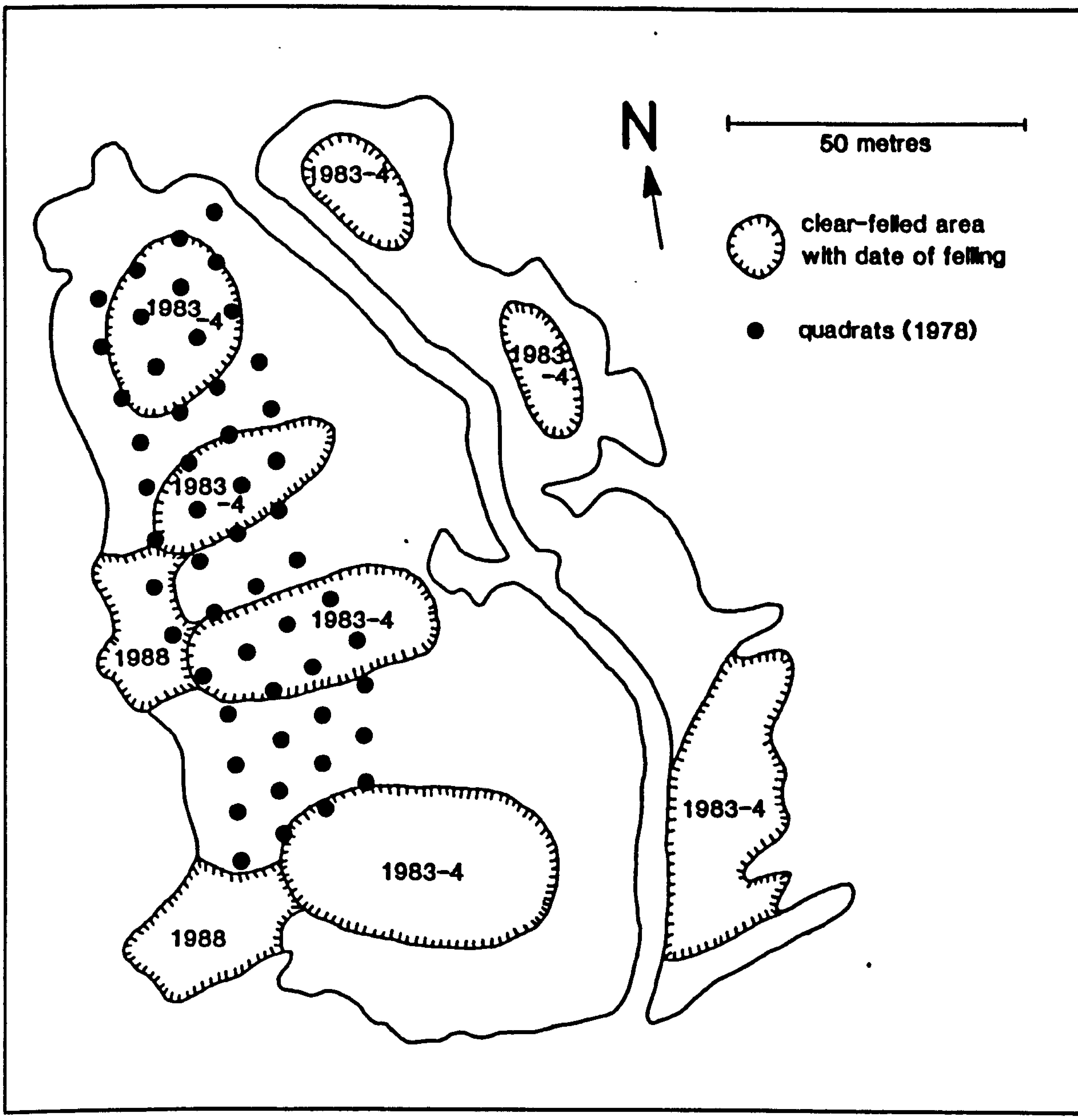



Figure 3.1 Layout of permanent quadrats in plantation K, Whiteford. Based on Hughes, (1978).

The vegetation was surveyed on 15th August, 1978. A 1x1m square quadrat was placed over each post, with the post in the centre of each quadrat. Within each quadrat an estimate of percentage cover was made for each of the species present. A series of photographs was also taken (Hughes, 1978). On 4th September 1988 the 36 remaining posts were resurveyed by me. Some of the sites were photographed from the same positions as before.

Data from the 1978 and 1988 surveys were analysed together using DECORANA and TWINSPAN. Because of the very small sample size, species occurring in only one quadrat were excluded from the analysis completely, and rare species were downweighted in the DECORANA run (as described by Malloch, 1988).

### 3.2.2 Results

DECORANA arranges the species along ordination axes. The species ordination is shown in figure 3.2. The quadrat data are then arranged along the same axes with the ordination score for each quadrat being the mean of the scores for the species occurring in them. The quadrat ordination along DECORANA axes 1 and 2 is shown in figure 3.3. The approximate positions of the first two TWINSPAN divisions are also drawn onto the diagram.

The 1978 data from the newly thinned woodland are mostly clustered together indicating a fairly uniform floristic composition. The first TWINSPAN division groups them all together, with a few similar 1988 woodland quadrats. 1988 quadrats from the clear-felled area are

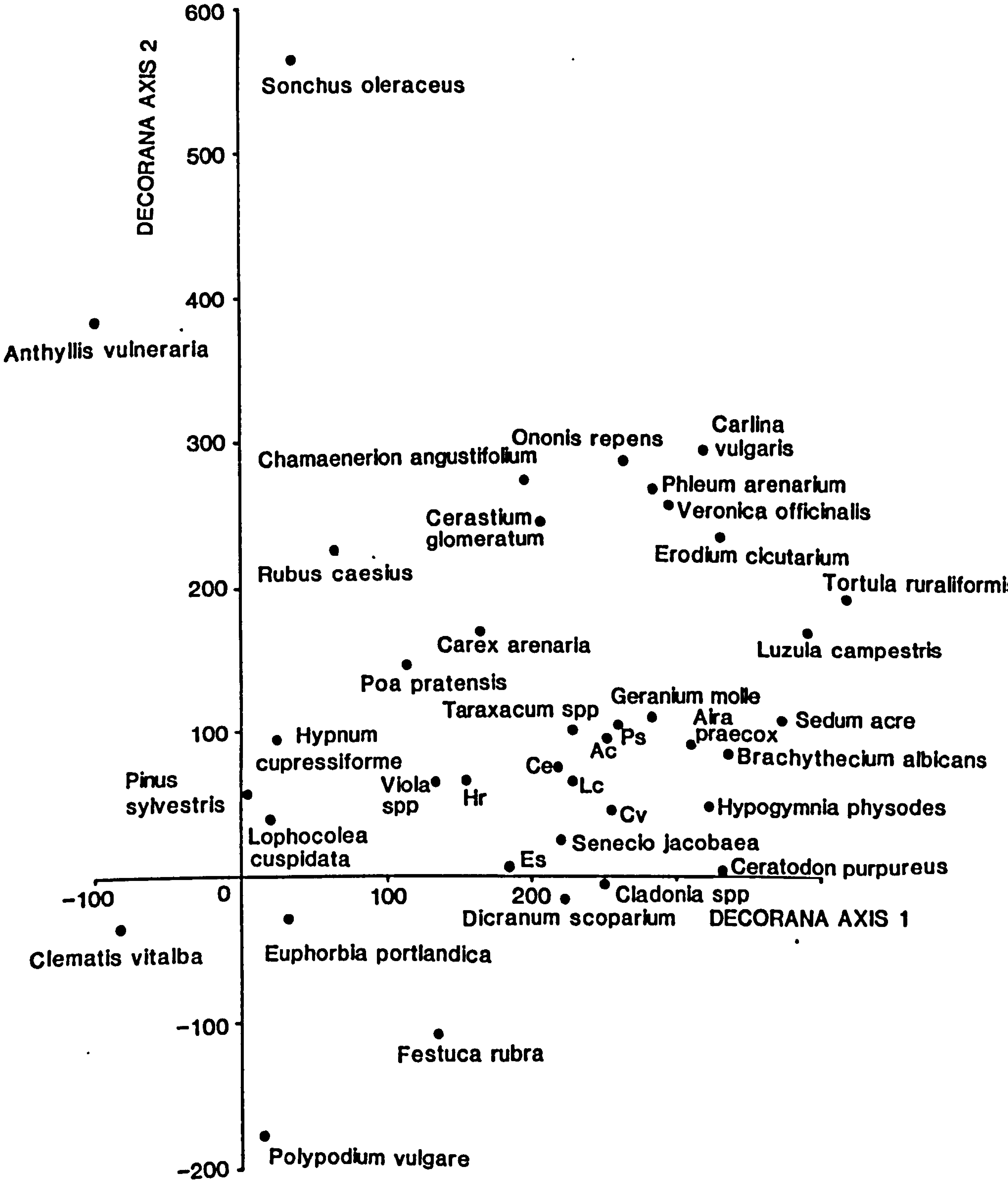



Figure 3.2 Whiteford permanent quadrats. 1978-1988. DECORANA species ordination.

Abbreviations:

Ce = Centaurium erythraea
Es = Epilobium spp.
Lc = Lotus corniculatus
Ac = Agrostis capillaris
Cv = Cirsium vulgare
Hr = Hypochoeris radicata
Ps = Peltigera spp.

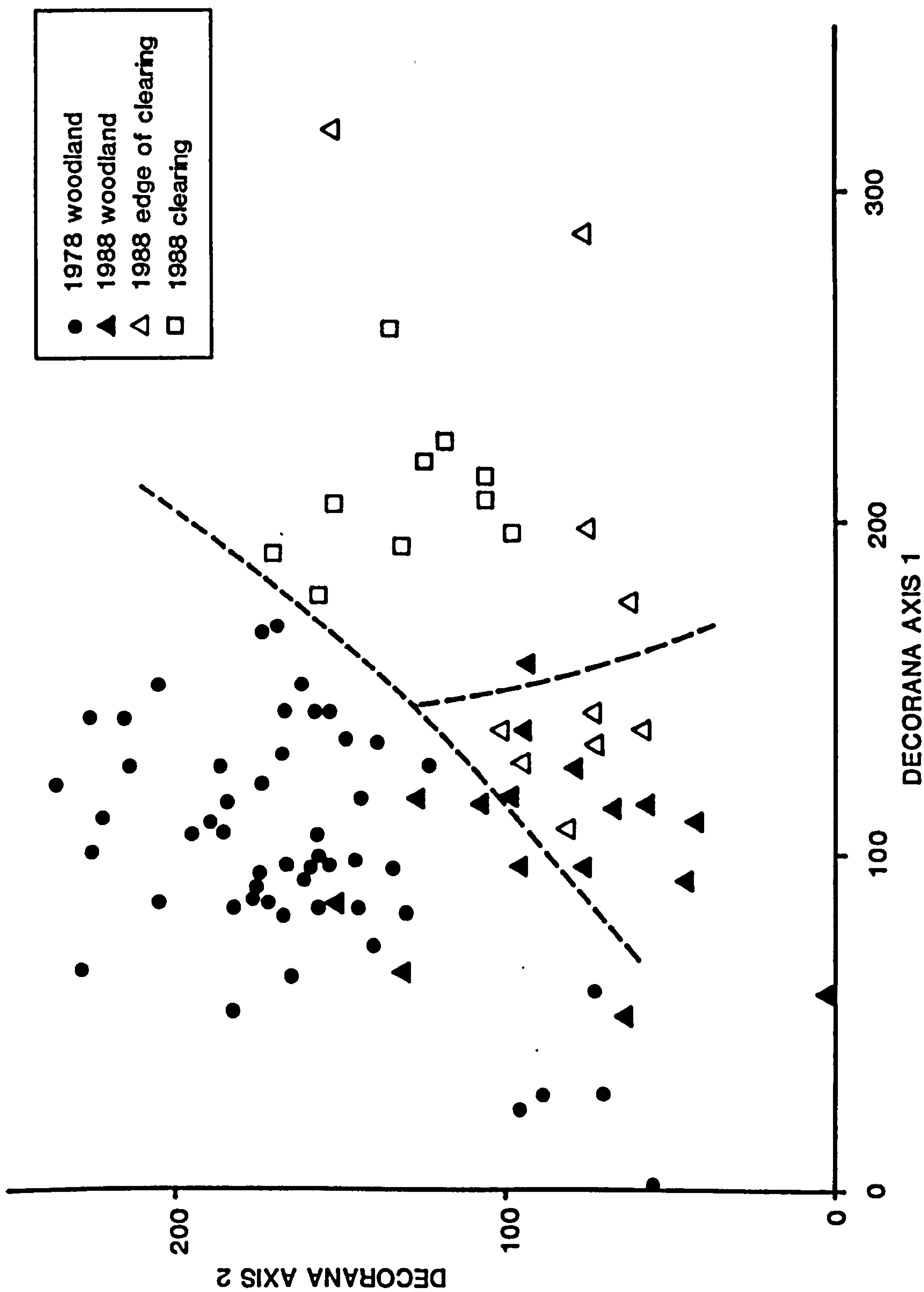



Figure 3.3 Whiteford permanent quadrats, 1978-1988. DECORANA quadrat ordination.

grouped into a cluster with higher scores along axis 1 than they had before, showing that the tree clearance has probably the most significant effect on the vegetation. Comparing 1988 woodland quadrats with those of 1978, they have generally changed their position along axis 2, showing either that there has been vegetation change without further woodland management, or that there have been differences between observers, or both. The latter two options are unlikely (M. Hughes, pers.comm.)

Some reasonable assumptions about the meaning of DECORANA axes 1 and 2 may be made by correlating the axes with some of the measured variables and examining the species present. Table 3.1 shows the Spearman's rank correlation statistics for some of the variables.

Table 3.1 Spearman's rank correlation coefficients for DECORANA axes 1 and 2 with variables measured during the Whiteford 1978-1988 permanent quadrat study. (With 80 degrees of freedom;
** = P<0.005, * = P<0.05, NS = Not significant).

| Variable | AXIS 1 | | AXIS 2 | |
|---|---|---|---|---|
| Total number of species | 0.467 | ** | -0.271 | * |
| Total plant cover % | 0.411 | ** | -0.067 | NS |
| Bryophyte cover % | -0.036 | NS | -0.374 | ** |
| % Bare sand | -0.020 | NS | 0.245 | * |

Axis 1 is apparently related to shade, suggested by the distribution of the open and shaded quadrats (figure 3.3), and also the correlation with percentage plant cover and species diversity. Positions of quadrats from the edge of the clearings will be affected by whether or not they are in the shadow of the trees during the daytime.

Axis 2 correlates positively with bare sand, and negatively with the amount of bryophytes. The woodlands appear to have increased their bryophyte cover considerably during the 10 year period (mostly with Hypnum cupressiforme and Lophocolea cuspidata) , while the amount of bare sand has decreased. The disturbance created by the thinning operation in 1978 could account for a greater amount of bare sand, while the resulting increase in light reaching the woodland floor may explain the increased moss cover in 1988. The position of Sonchus oleraceus high on axis 2 would also suggest that disturbance was an important factor operating at the time of the first survey; this is one of the species quickest to colonise disturbed ground in this plantation (see section 3.3, and plate 11). Conversely, Polypodium vulgare, a more typical woodland species, occupies the lowest position on axis 2; this was only found in the woodland in the 1988 survey.

Changes in the ground flora of young upland pine plantations have been described by Hill (1979c). He recorded an initial rapid decline in cover by vascular plants through the first 10-15 years as the canopy closes. This is followed by a slow increase as a woodland flora develops. The plantation at Whiteford was about 20 years old in 1978, and the closed canopy had excluded most of the original ground flora. Using Hill's timescale, an increase in both vascular plants and bryophytes could be expected during the 10 year study period; table 3.2 shows that this is in fact the case.

Table 3.2 Mean percentage cover by vascular plants and bryophytes in woodland and clearfelled quadrats in 1978 and 1988. Standard error is shown in parentheses. Woodland edge quadrats are not included.

| | 1978 Woodland | 1988 Woodland | 1988 Clearing |
|---|---|---|---|
| Vascular plants | 11.4 (1.6) | 22.0 (3.4) | 61.3 (8.4) |
| Bryophytes | 7.6 (2.1) | 18.5 (6.1) | 18.9 (5.0) |

The percentage cover by vascular plants in the felled areas is considerably higher than in the woodland. The species composition of the cleared sites was not directly compared with the natural dune vegetation in this study: however, a comparison with the two woodland surveys reveals some interesting differences. It is clear that several species common in the surrounding dunes had colonised the felled area during the 5 years since felling. Table 3.3 shows a list of species found in this quadrat study.

Table 3.3 Percentage frequencies for species recorded in the 1978-1988 quadrat study, Whiteford N.N.R.. All species reaching a percentage frequency of 10% at least once have been included. Woodland edge quadrats are not included.

| Species | 1978 woodland n=52 | 1988 woodland n=16 | 1988 Clearing n=12 |
|---|---|---|---|
| Agrostis capillaris | 10 | 13 | 67 |
| Aira praecox | 0 | 0 | 17 |
| Anthyllis vulneraria | 17 | 6 | 0 |
| Carex arenaria | 65 | 56 | 83 |
| Carlina vulgaris | 0 | 0 | 17 |
| Cerastium spp. | 63 | 13 | 92 |
| Chamaenerion angustifolium | 12 | 6 | 33 |
| Clematis vitalba | 10 | 19 | 0 |
| Erodium cicutarium | 0 | 0 | 25 |
| Euphorbia portlandica | 15 | 50 | 25 |
| Festuca rubra | 6 | 25 | 8 |
| Geranium molle | 0 | 13 | 50 |
| Hieracium pilosella | 2 | 13 | 0 |
| Holcus lanatus | 2 | 6 | 17 |
| Hypochoeris radicata | 29 | 31 | 67 |
| Leontodon spp. | 29 | 13 | 75 |
| Lotus corniculatus | 13 | 0 | 42 |
| Luzula campestris | 0 | 13 | 8 |
| Ononis repens | 15 | 0 | 58 |
| Phleum arenarium | 4 | 0 | 25 |
| Poa pratensis | 0 | 19 | 8 |
| Polygala vulgaris | 2 | 44 | 33 |
| Polypodium vulgare | 0 | 50 | 0 |
| Rubus caesius | 87 | 81 | 83 |
| Senecio jacobaea | 4 | 75 | 75 |
| Taraxacum spp. | 4 | 31 | 42 |
| Veronica officinalis | 0 | 0 | 25 |
| Viola spp. | 29 | 38 | 67 |
| | | | |
| Brachythecium albicans | 0 | 0 | 58 |
| Brachythecium rutabulum | 0 | 38 | 8 |
| Ceratodon purpureus | 0 | 13 | 67 |
| Hypnum cupressiforme | 77 | 63 | 58 |
| Lophocolea cuspidata | 0 | 44 | 17 |
| Tortula ruraliformis | 0 | 0 | 50 |
| | | | |
| Cladonia spp. | 0 | 50 | 75 |
| Peltigera spp. | 21 | 13 | 67 |

A total of 25 species were recorded in the 1978 woodland survey. In 1988 this had increased to 32 species, and 38 species were found in the clear-felled quadrats. The 1988 surveys may have underestimated the total numbers because of the smaller number of quadrats remaining, however the results do show that both the older woodland and the clear-felled site have a greater species diversity than the woodland in 1978.

An examination of table 3.3 reveals that several species, usually common on sand dunes, such as Anthyllis vulneraria, Cerastium spp., Leontodon spp., Peltigera spp. and Ononis repens have apparently declined in the woodland during the study period. These species were probably only present in the woods as residual populations left over from the original dune flora, possibly temporarily favoured by the thinning operation which would create patches of bare sand and reduce the amount of shade. Species which have increased in the woodland include the typically woodland species Clematis vitalba and Polypodium vulgare, Lophocolea cuspidata and Brachythecium rutabulum, but also several unexpected species such as Euphorbia portlandica, Hieracium pilosella, Geranium molle, Luzula campestris, Poa pratensis, Polygala vulgaris and Senecio jacobaea. These unlikely increases may be due to the opening up of the plantation by the clearings, allowing light into the wood from the clearing edges; the clearings may also increase the seed supply of some species to the inside of the plantation.

The clearings have the greatest percentage plant cover, and the greatest number of species. Species occurring in the clearings which were not seen in the woodland include Aira praecox, Carlina vulgaris, Erodium cicutarium, Veronica officinalis, Brachythecium albicans and Tortula *ruraliformis*. All of the species in the clearings occur on the surrounding unplanted dunes and would have existed on the site prior to afforestation. Some, such as *Rubus caesius* and *Carex arenaria*, have maintained a population under the trees, but others must have recolonised either from buried seedbank or from seeds reaching the site from the surrounding dunes.

The species composition of the clearings at Whiteford is discussed further in section 3.3.3

## 3.3 Quadrat Survey 1988-1990

In order to examine the effects of clear-felling over a wider area and to enable comparison between the different sand dune systems another quadrat study was undertaken between June and September in 1988, 1989 and 1990. National Vegetation Classification techniques were used to ensure that the results would be compatible with surveys at other sites. Habitat types sampled at the three study areas are summarised in table 3.4.

Table 3.4 Summary of areas surveyed.

| Site | Habitat type | Number of Quadrats |
|---|---|---|
| Ainsdale | Unplanted dunes | 89 |
| | Clear-felled sites | 118 |
| | Woodland | 103 |
| | Total | 310 |
| Whiteford | Unplanted dunes | 58 |
| | Clear-felled sites | 166 |
| | Woodland | 103 |
| | Total | 287 |
| Tentsmuir | Unplanted dunes | 58 |
| | Clear-felled sites | 142 |
| | Woodland | 40 |
| | Total | 240 |

### 3.3.1 Methods

Vegetation data were collected using National Vegetation Classification techniques (Malloch, 1985). Samples of woodland, unplanted dunes and clear-felled sites were examined using 2x2 metre quadrats. No quadrats were taken in dune slacks. The abundance of species present was recorded using DOMIN values; these are shown in table 3.5.

Table 3.5 The DOMIN scale for estimation of plant species abundance.

| Percentage Cover | DOMIN Value |
|---|---|
| 91-100 | 10 |
| 76-90 | 9 |
| 51-75 | 8 |
| 34-50 | 7 |
| 26-33 | 6 |
| 11-25 | 5 |
| 4-10 | 4 |
| < 4 Frequent | 3 |
| < 4 Occasional | 2 |
| < 4 Rare | 1 |

Several plants, including Ranunculus, Sonchus and Vicia species, were very common as seedlings at the time of the survey and could not be separated to species level at this stage. The following, also difficult to distinguish to species level, included:

Betula spp.

Cladonia spp. (put into broad categories 'squamules', 'fimbriata' and 'rangiformis'.)

Epilobium spp. (vegetative)

Festuca rubra/ovina (vegetative)

Hieracium spp. (sometimes put into sub-groups)

Leontodon taraxacoides/hispidus

Lophocolea spp.

Oenothera spp.

Peltigera spp. (non-fruiting)

Salix spp.

Taraxacum spp.

Usnea spp.

Viola riviniana/canina (vegetative)

The following site characteristics were also estimated in each quadrat. Slope to the nearest 5°, aspect, mean vegetation height to the nearest 5cm (from measurements at each corner and in the centre of the quadrat), total percentage cover by live vegetation (not including needle litter) and by bare sand and the depth of the organic layers at the soil surface. Shade by the pine canopy was noted, with quadrats being put into one of three broad categories: unshaded, below a pine canopy, or at a woodland edge (not directly below a canopy, but still (at least partly) shaded by the trees; this sometimes included quadrats from well thinned pinewoods).

Trends within the quadrat data were examined using DECORANA, with TWINSPAN being used to identify vegetation types at each site. TWINSPAN divisions were made until either there were 5 or less in a group, or the groups of quadrats could not easily be separated by eye on the plot of DECORANA axes 1 and 2. Each TWINSPAN vegetation type is numbered, with the numbering relating approximately to the position along DECORANA axis 1. Species ordinations are not shown because there are so many species; instead a simplified TWINSPAN summary diagram is given. This shows the approximate position of each TWINSPAN group on the ordination diagram, listing the indicator species used to define the group with their TWINSPAN constancy values.

Each species is assigned a constancy value within each group it occurs in. Constancy values relate to percentage frequency as shown in table 3.6.

Table 3.6 Constancy values for species in TWINSPAN groups.

| Percentage frequency | Constancy value |
|---|---|
| 1 - 20 | I |
| 21 - 40 | II |
| 41 - 60 | III |
| 61 - 80 | IV |
| 81 - 100 | V |

Each site is described separately using the TWINSPAN vegetation types as units for description and comparison with environmental variables. Each vegetation type is described, listing its species composition and showing comparative frequency diagrams for the different variables. Some of the variables are shown on ordination axes to assist interpretation.

### 3.3.2 Results: Ainsdale

The results of the DECORANA analysis are presented in figures 3.4 to 3.8. TWINSPAN vegetation types are described in table 3.8, with percentage frequency diagrams comparing measured site variables between the groups in figures 3.9 to 3.15.

Legends for figures 3.4 to 3.8: DECORANA analysis of the Ainsdale quadrat data.

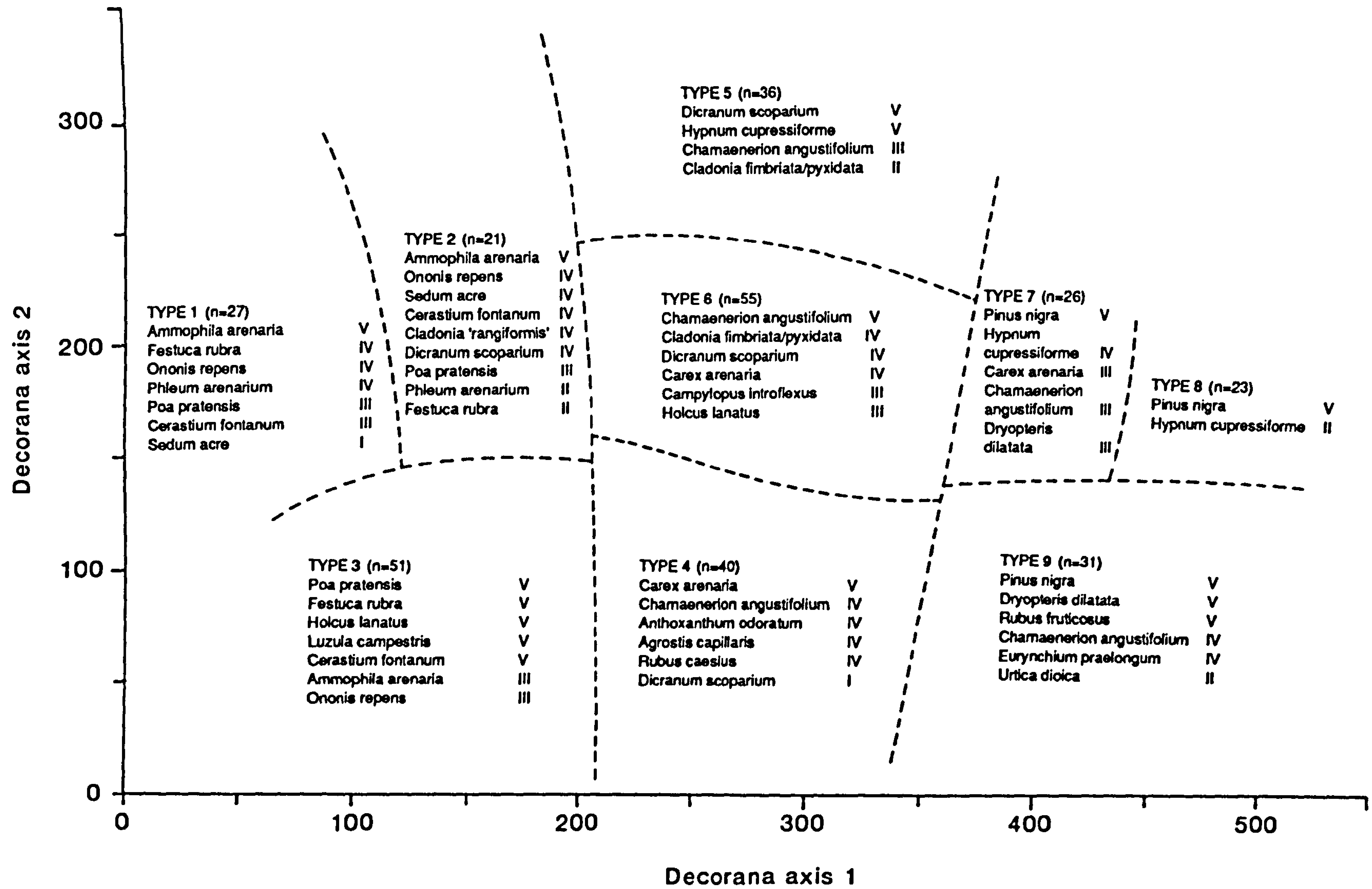
Figure 3.4. (page 89). TWINSPAN summary diagram. Positions of boundaries are approximate.

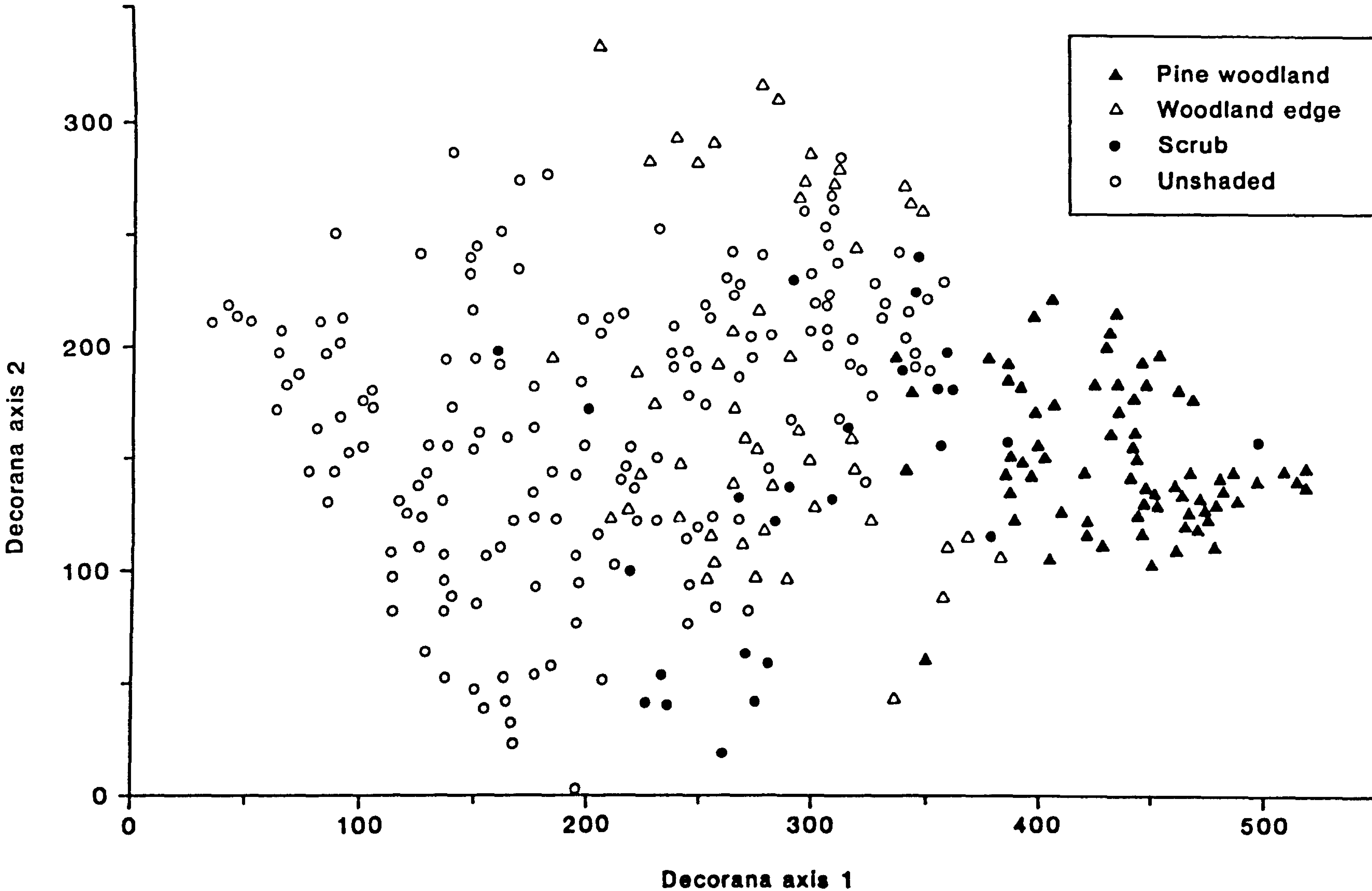
Figure 3.5. (page 90). Variation with shade.

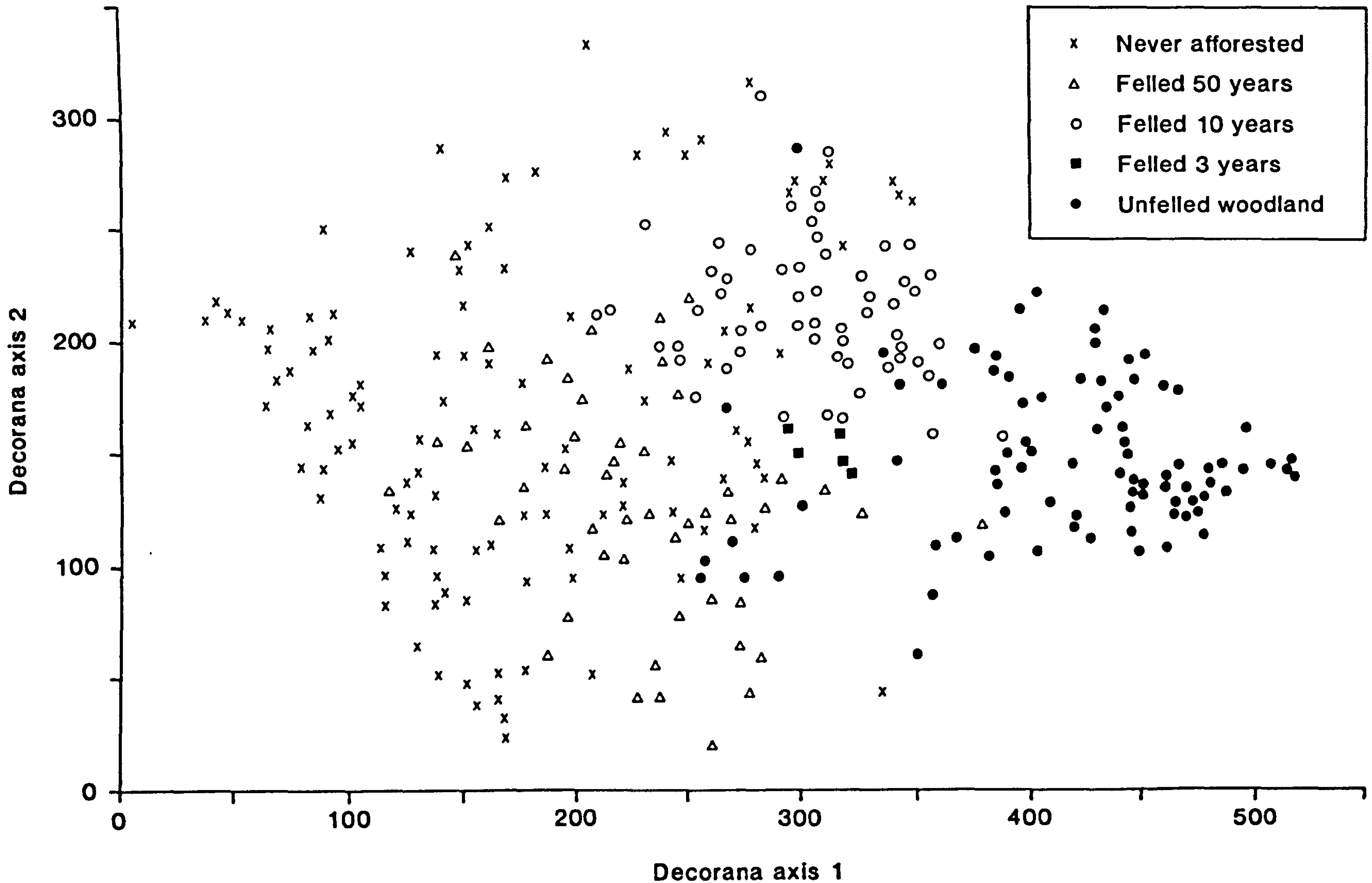
Figure 3.6. (page 91). Time after felling.

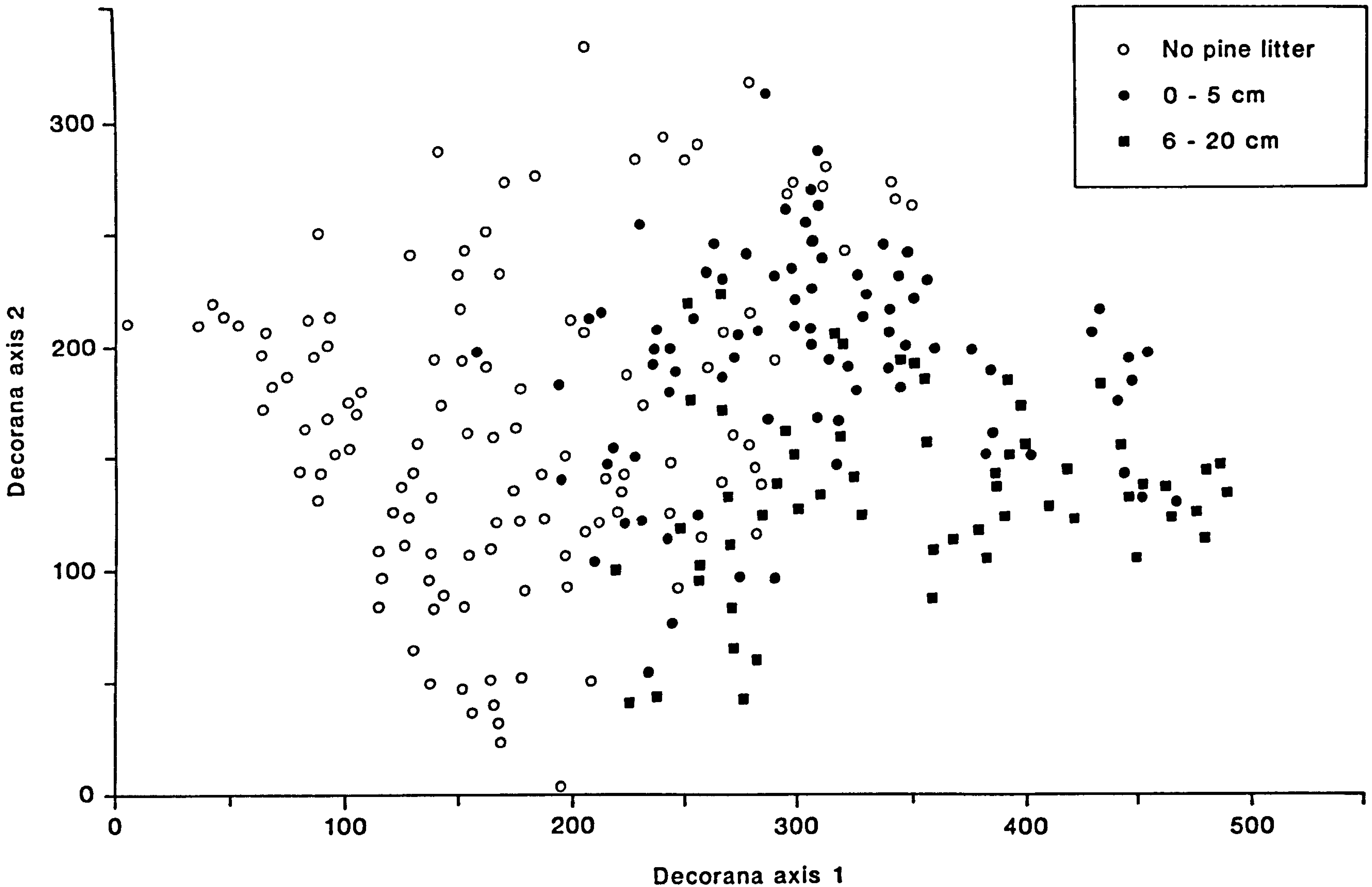
Figure 3.7. (page 92). Depth of pine needle material.

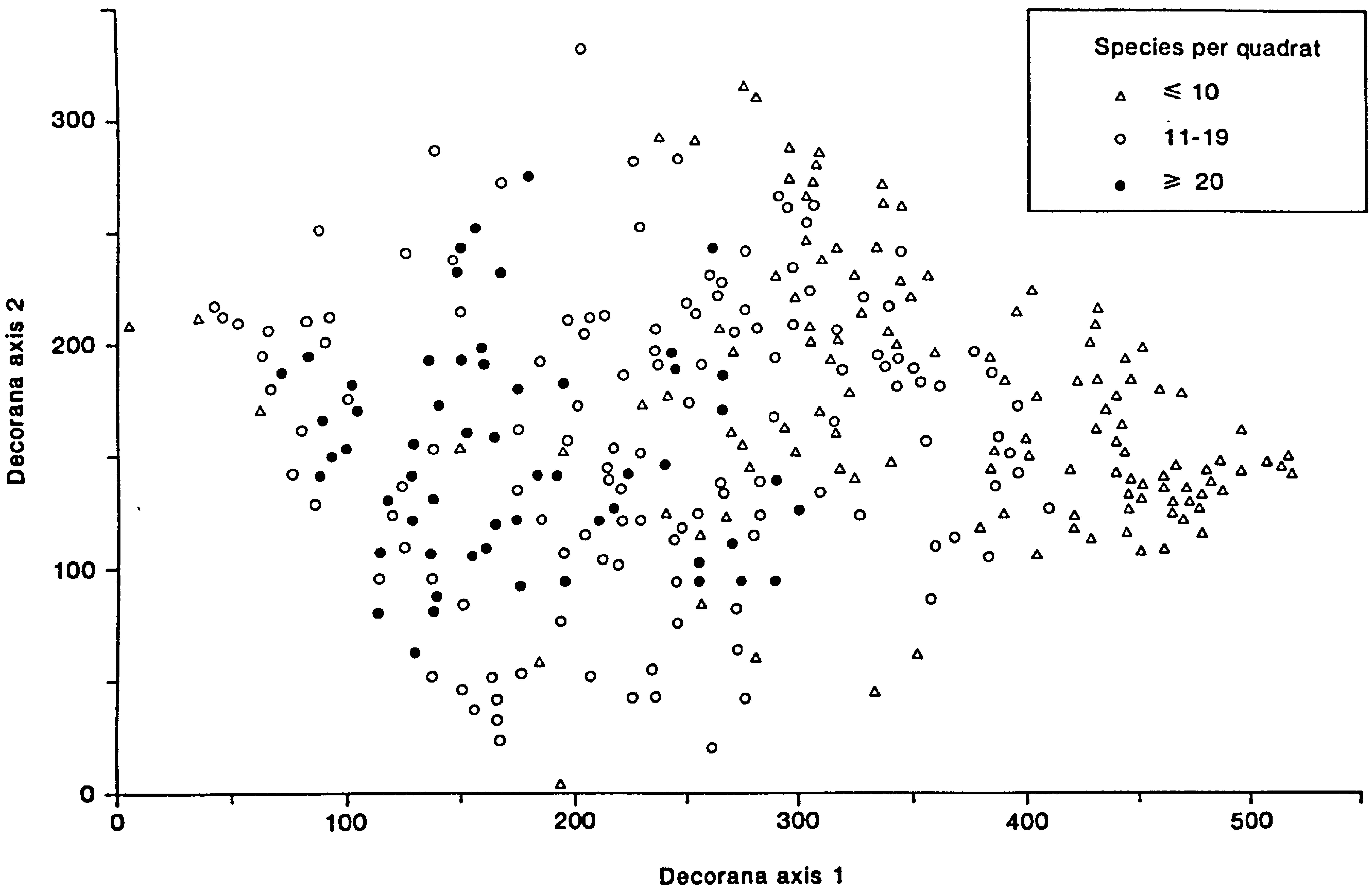
Figure 3.8. (page 93). Numbers of species per quadrat.


TYPE 1 (n=27)
Ammophila arenaria V
Festuca rubra IV
Ononis repens IV
Phleum arenarium IV
Poa pratensis III
Cerastium fontanum III
Sedum acre I
TYPE 2 (n=21)
Ammophila arenaria V
Ononis repens IV
Sedum acre IV
Cerastium fontanum IV
Cladonia 'rangiformis' IV
Dicranum scoparium IV
Poa pratensis III
Phleum arenarium II
Festuca rubra II
TYPE 3 (n=51)
Poa pratensis V
Festuca rubra V
Holcus lanatus V
Luzula campestris V
Cerastium fontanum V
Ammophila arenaria III
Ononis repens III
TYPE 4 (n=40)
Carex arenaria V
Chamaenerion angustifolium IV
Anthoxanthum odoratum IV
Agrostis capillaris IV
Rubus caesius IV
Dicranum scoparium I
TYPE 5 (n=36)
Dicranum scoparium V
Hypnum cupressiforme V
Chamaenerion angustifolium III
Cladonia fimbriata/pyxidata II
TYPE 6 (n=55)
Chamaenerion angustifolium V
Cladonia fimbriata/pyxidata IV
Dicranum scoparium IV
Carex arenaria IV
Campylopus introflexus III
Holcus lanatus III
TYPE 7 (n=26)
Pinus nigra V
Hypnum cupressiforme IV
Carex arenaria III
Chamaenerion angustifolium III
Dryopteris dilatata III
TYPE 8 (n=23)
Pinus nigra V
Hypnum cupressiforme II
TYPE 9 (n=31)
Pinus nigra V
Dryopteris dilatata V
Rubus fruticosus V
Chamaenerion angustifolium IV
Eurynchium praelongum IV
Urtica dioica II
Decorana axis 2
Decorana axis 1
0
100
200
300
400
500


Pine woodland
Woodland edge
Scrub
Unshaded
Decorana axis 2
Decorana axis 1
0
100
200
300
400
500


Never afforested
Felled 50 years
Felled 10 years
Felled 3 years
Unfelled woodland
Decorana axis 2
Decorana axis 1
0
100
200
300
400
500


No pine litter
0 - 5 cm
6 - 20 cm
Decorana axis 2
Decorana axis 1
0
100
200
300
400
500


Species per quadrat
≤ 10
11-19
≥ 20
300
200
100
0
100
200
300
400
500
Decorana axis 2
Decorana axis 1

DECORANA axes 1 and 2, representing the two most important trends within the vegetation, are correlated with several measured variables in table 3.7. From this it is apparent that axis 1 is related to the tree-cover, with higher values given to quadrats with older woodland, with a deeper organic soil, low species diversity and low percentage ground vegetation cover. On Axis 2 high values are given to quadrats with a shallow organic soil and a relatively high number of lichen and moss species, and a high percentage of bare sand. Low values are given to quadrats with deeper soil and taller vegetation. This may be related to soil fertility.

Table 3.7 Ainsdale: Linear regression statistics for DECORANA axes 1 and 2, with recorded variables. Percentage data have been arcsine transformed.
** = $p<0.005$, * = $p<0.05$, NS = not significant.

| Variable | AXIS 1 | | | | AXIS 2 | | | |
|---|---|---|---|---|---|---|---|---|
| | t | $R^2$ | df | p | t | $R^2$ | df | p |
| Woodland age | 22.9 | .630 | 308 | ** | 3.4 | .035 | 308 | ** |
| Years felled | -2.6 | .021 | 308 | * | -2.7 | .023 | 308 | * |
| Organic Soil depth | 6.5 | .208 | 158 | ** | -5.3 | .151 | 158 | ** |
| Percent cover | -8.6 | .261 | 208 | ** | -1.2 | .006 | 208 | NS |
| Percent sand | -4.3 | .071 | 244 | ** | 5.0 | .092 | 244 | ** |
| Mean height | 3.9 | .057 | 255 | ** | -2.7 | .029 | 255 | * |
| Total species | -14.6 | .410 | 308 | ** | -2.4 | .018 | 308 | * |
| Total mosses | 5.4 | .087 | 308 | ** | 6.5 | .121 | 308 | ** |
| Total lichens | -1.6 | .009 | 308 | NS | 12.2 | .326 | 308 | ** |
| Slope | -4.2 | .066 | 253 | ** | -1.0 | .004 | 253 | NS |

Figure 3.6 shows that quadrats from recently felled wooodlands occupy an intermediate position along DECORANA axis 1 between the woodlands and the unplanted dunes. The five quadrats from the site felled three years ago are

plotted nearer to the unfelled woodland than the majority of quadrats from sites felled 10 and 50 years ago. The quadrats from the fire-breaks, felled 10 years ago, are seen to form a cluster high on axis 2, while the sites felled during the Second World War tend to have much lower scores for axis 2. Many of the quadrats from sites felled for 50 years are seen to have low scores on axis 1, and appear to be no different from many of the quadrats which have never been forested. Some quadrats from unplanted dune sites are plotted very close to woodland quadrats and those felled for 10 years, however these tend to be the ones taken at woodland edges (see figure 3.5), and are not representative of a typical unplanted dune vegetation.

The three main TWINSPAN divisions, shown in figure 3.4, appear broadly to separate the data into unplanted dune, clear-felled and woodland quadrats. Within each of these groups three further divisions were made. All of the end groups contained at least 20 quadrats.

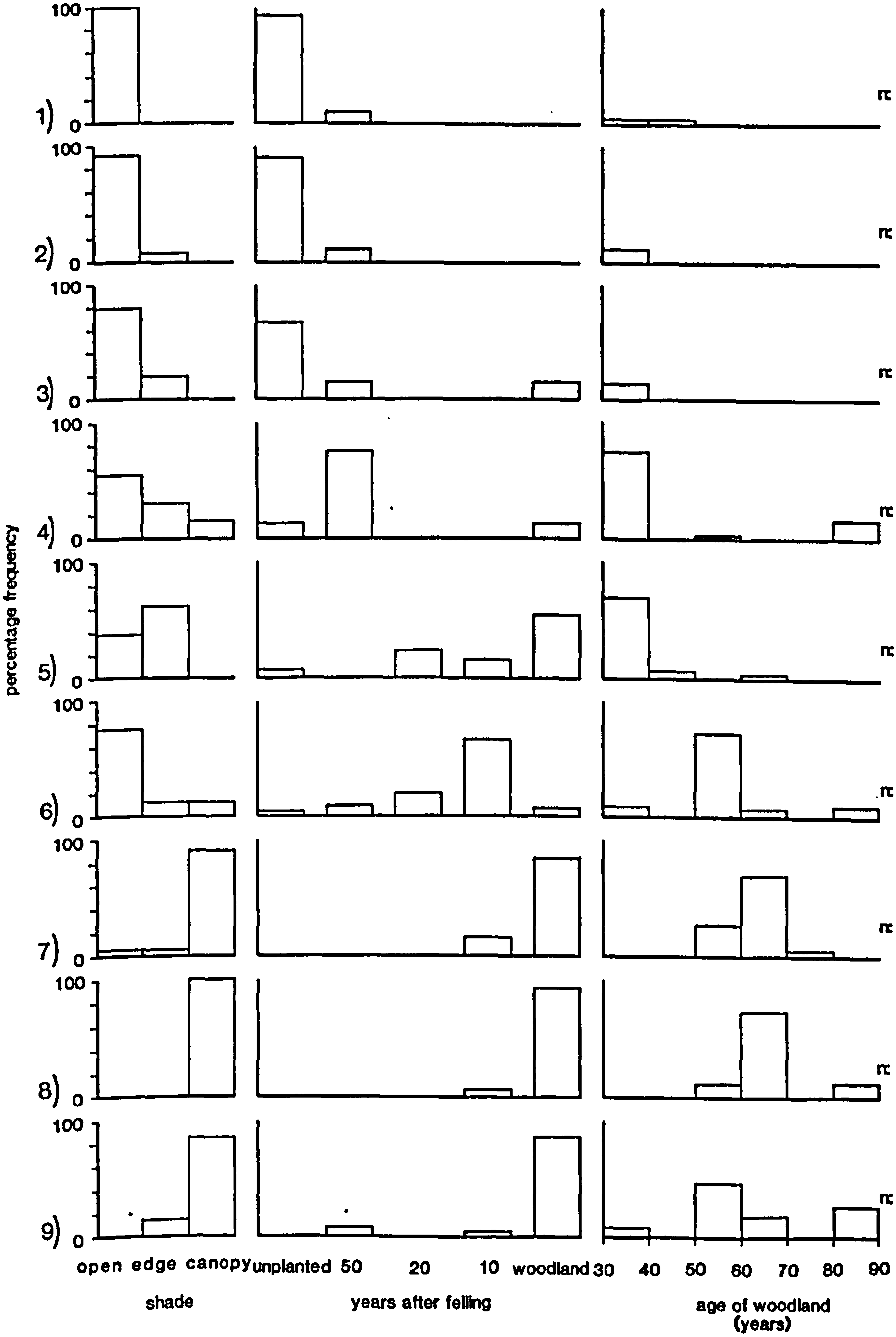



Figure 3.9 Shade, time after felling and age of woodland. Percentage frequencies for TWINSPAN vegetation types 1 to 9 at Ainsdale. n = number of quadrats.

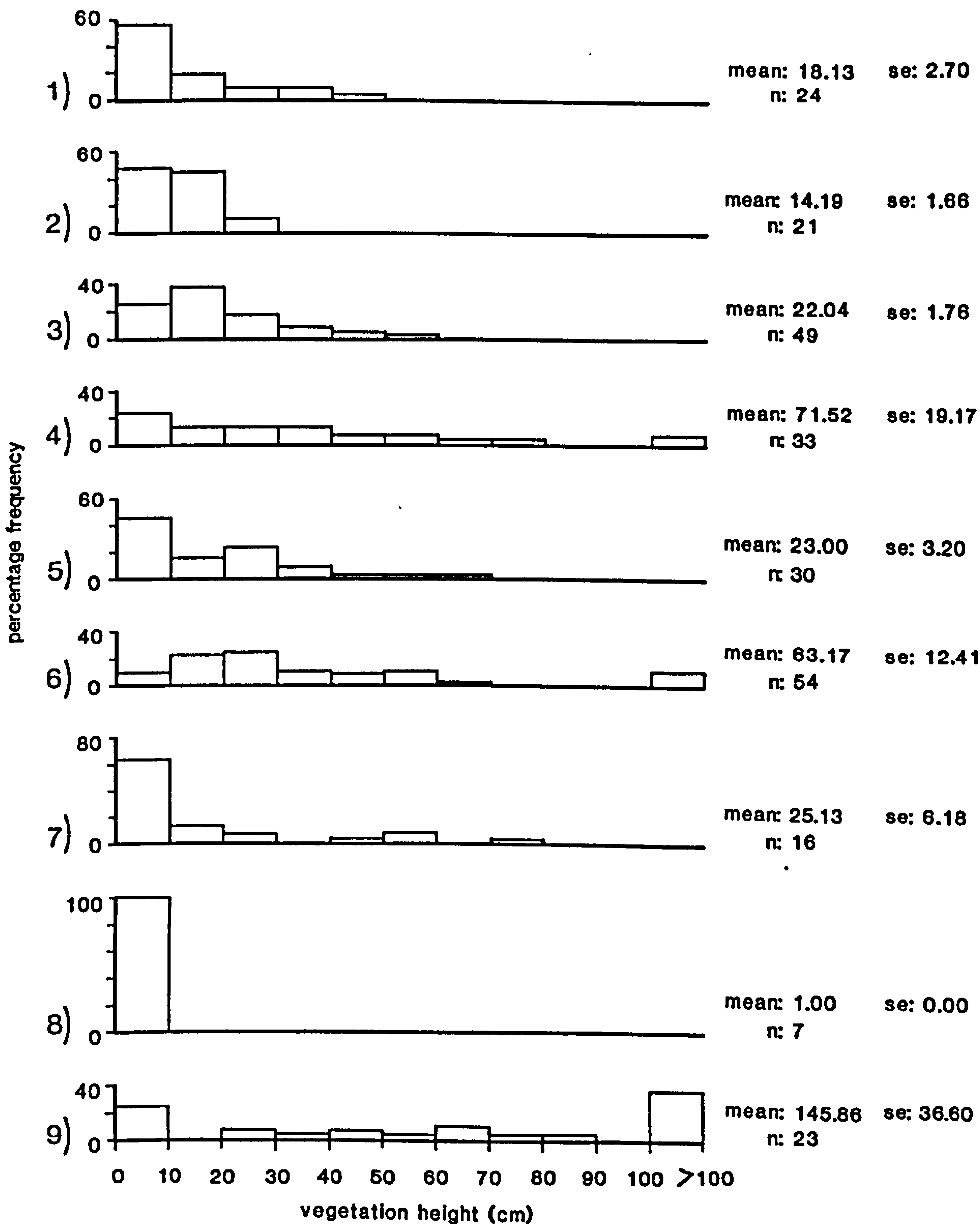



Figure 3.10 Mean vegetation height. Percentage frequencies for TWINSPAN vegetation types 1 to 9 at Ainsdale. n = number of quadrats. se = standard error.

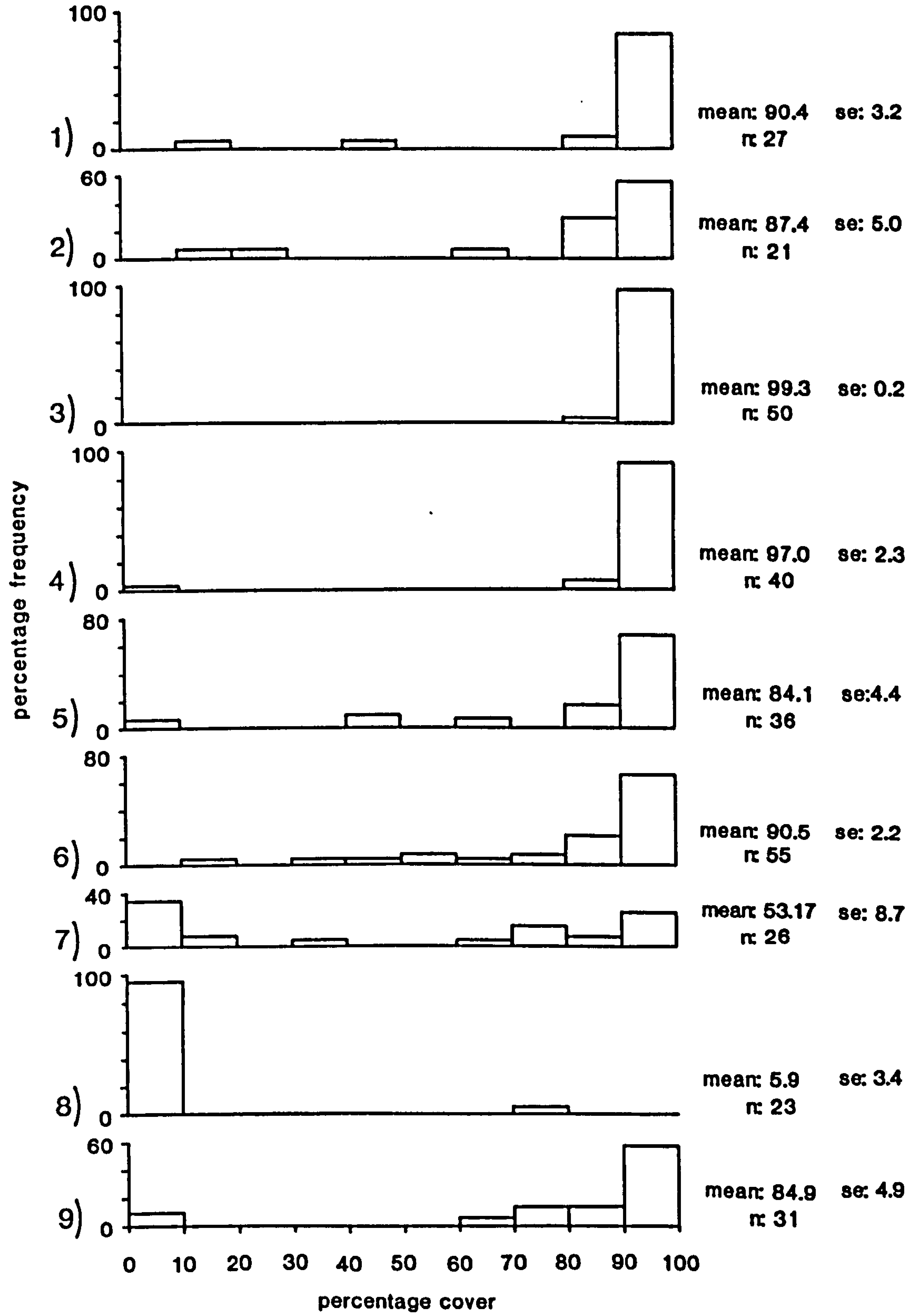



Figure 3.11 Percentage vegetation cover. Percentage frequencies for TWINSPAN vegetation types 1 to 9 at Ainsdale. n = number of quadrats. se = standard error.

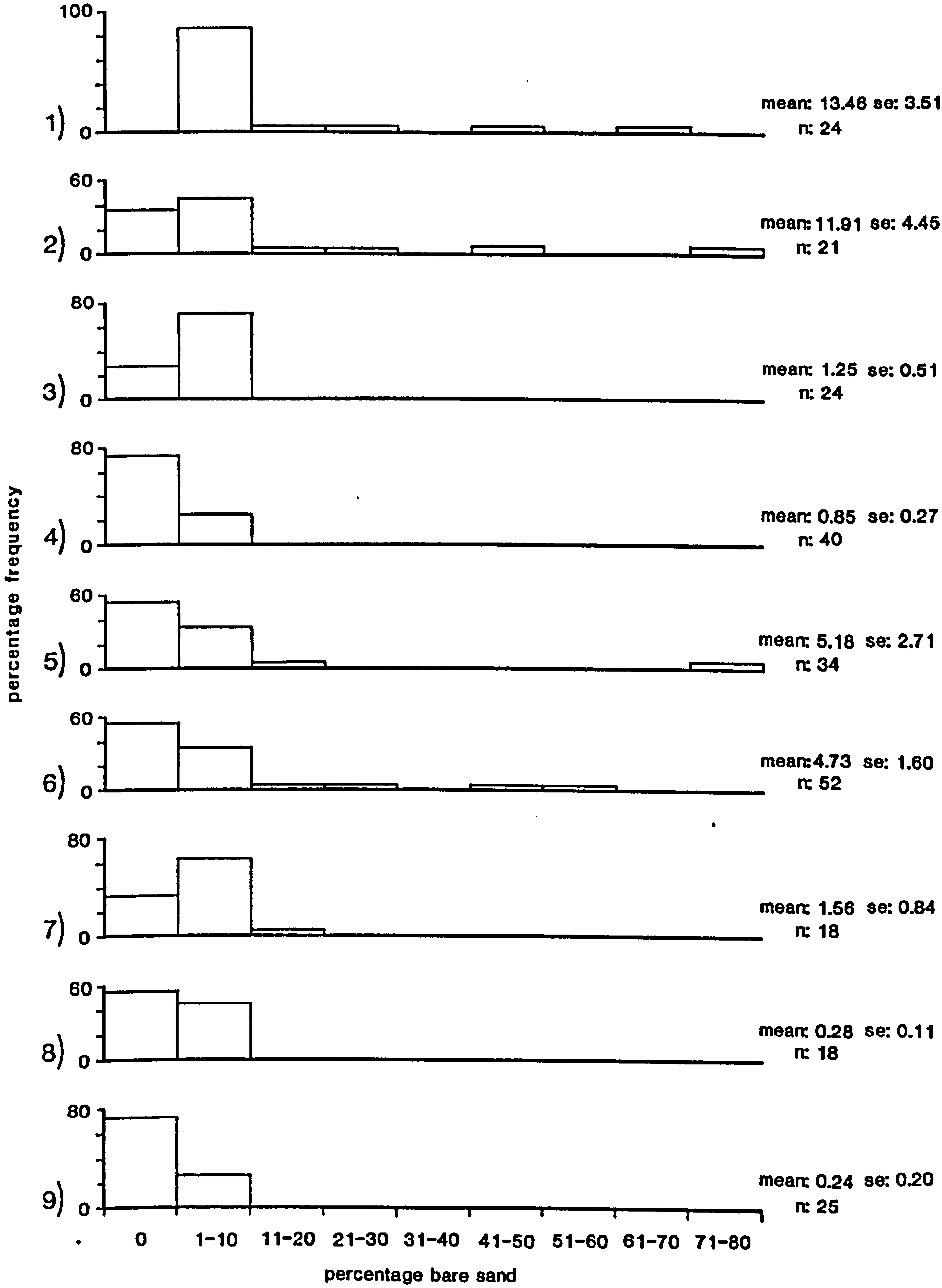



Figure 3.12 Percentage bare sand. Percentage frequencies for TWINSPAN vegetation types 1 to 9 at Ainsdale. n = number of quadrats. se = standard error.

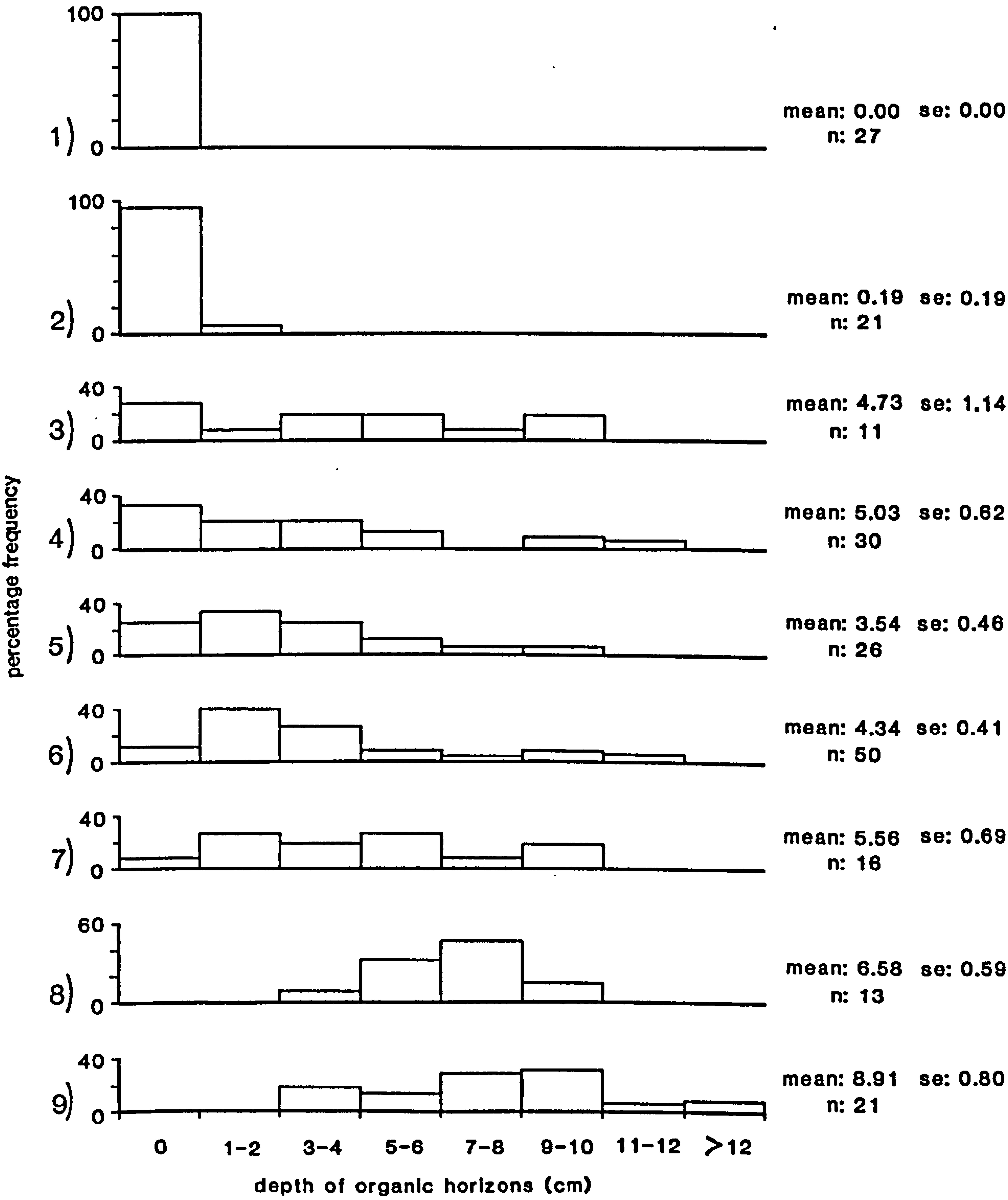



Figure 3.13 Depth of organic soil horizons. Percentage frequencies for TWINSPAN vegetation types 1 to 9 at Ainsdale. n = number of quadrats. se = standard error.

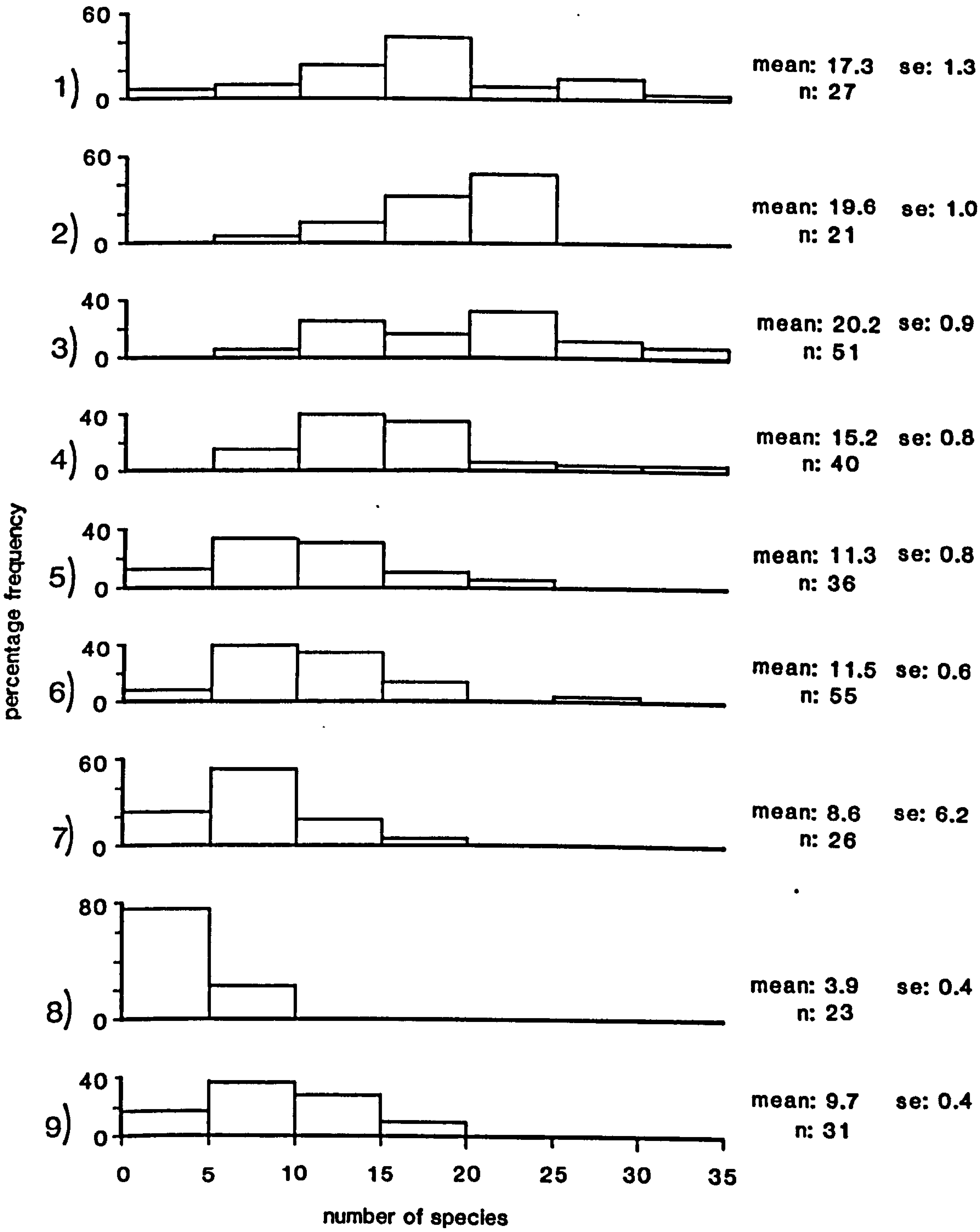



Figure 3.14 Number of species per quadrat. Percentage frequencies for TWINSPAN vegetation types 1 to 9 at Ainsdale. n = number of quadrats. se = standard error.

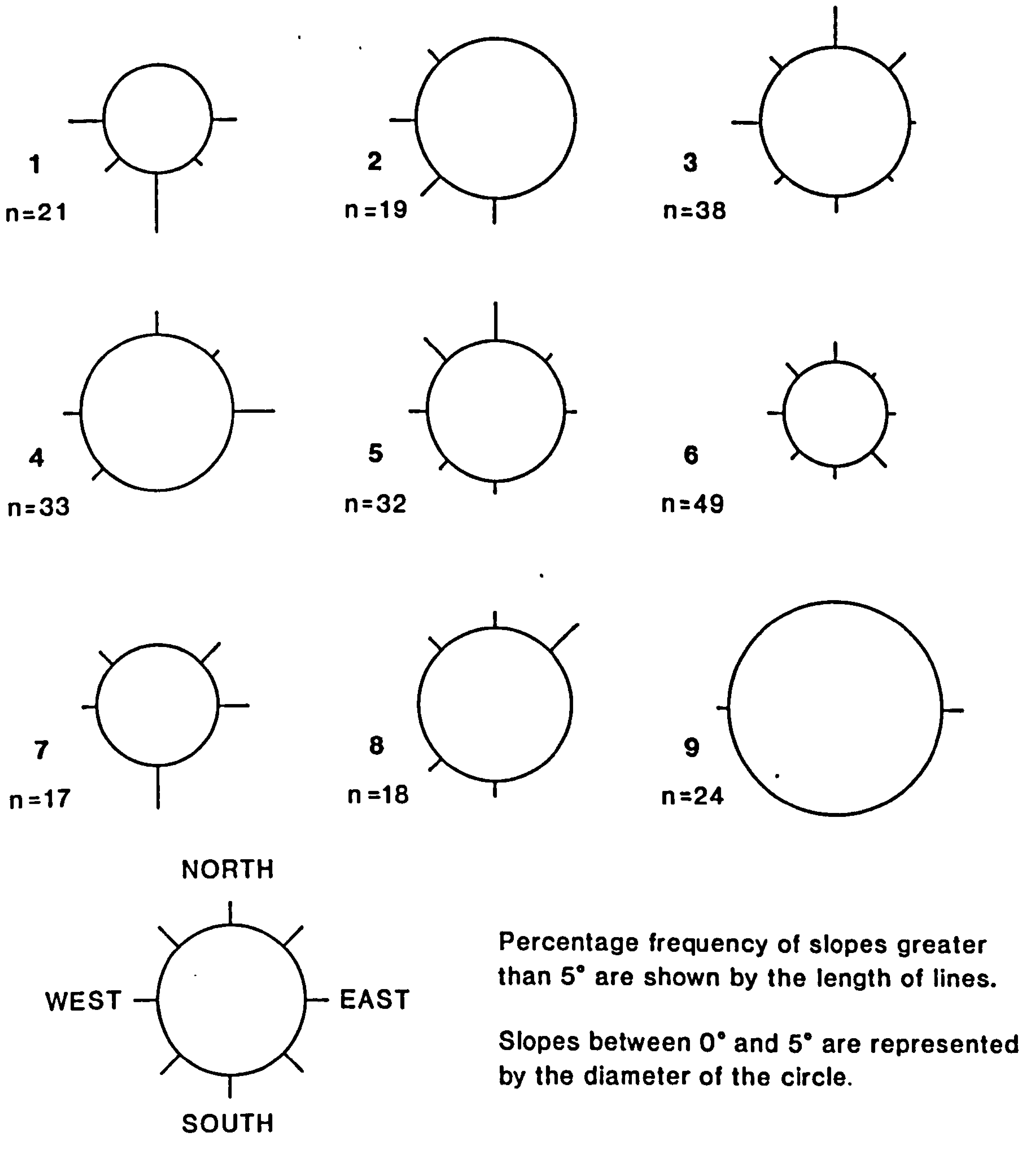



Figure 3.15 Slope and aspect. Percentage frequencies for TWINSPAN vegetation types 1 to 9 at Ainsdale. n = number of quadrats.

Table 3.8 TWINSPAN vegetation types studied at Ainsdale. For each community the species are grouped into frequency classes. Species with a constancy value of I are not shown. Species order within the frequency classes is determined by the TWINSPAN program.
DOMIN scores are summarised, giving the median value for each species, followed by the range of recorded values in brackets.

TYPE 1:
Number of quadrats 27
Mean number of species per quadrat 17.3 (SE = 1.3)

| Species | Constancy | Score |
|---|---|---|
| Ammophila arenaria | V | 5 (1-9) |
| Cerastium semidecandrum | V | 2 (1-3) |
| Leontodon spp. | V | 2 (1-4) |
| | | |
| Arenaria serpyllifolia | IV | 2 (1-3) |
| Cerastium glomeratum | IV | 2 (1-3) |
| Festuca rubra | IV | 5 (1-8) |
| Myosotis arvensis | IV | 1 (1-2) |
| Ononis repens | IV | 5 (1-8) |
| Phleum arenarium | IV | 2 (1-5) |
| Sedum acre | IV | 4 (1-5) |
| Carex arenaria | IV | 4 (1-5) |
| | | |
| Cerastium fontanum | III | 1 (1-4) |
| Erodium cicutarium | III | 3 (1-3) |
| Erophila verna | III | 2 (1-3) |
| Hieracium sp. | III | 1 (1-4) |
| Poa pratensis | III | 2 (1-4) |
| Viola spp. | III | 2 (1-4) |
| Aira praecox | III | 2 (1-3) |
| Hypochoeris radicata | III | 1 (1-4) |
| Senecio jacobaea | III | 2 (1-4) |
| Rubus caesius | III | 2 (1-7) |
| | | |
| Lotus corniculatus | II | 2 (1-6) |
| Polygala vulgaris | II | 2 (1-3) |
| Vicia lathyroides | II | 2 (1-3) |
| Ranunculus spp. | II | 2 (1-4) |
| Luzula campestris | II | 2 (1-4) |

TYPE 2:
Number of quadrats 21
Mean number of species per quadrat 19.6 (SE = 1.0)

| Species | Constancy | Score |
|---|---|---|
| Ammophila arenaria | V | 2 (1-4) |
| Leontodon spp. | V | 2 (1-3) |
| Senecio jacobaea | V | 3 (1-4) |
| Carex arenaria | V | 3 (2-7) |
| Cerastium fontanum | IV | 2 (1-3) |
| Erodium cicutarium | IV | 2 (1-3) |
| Ononis repens | IV | 7 (3-9) |
| Sedum acre | IV | 2 (1-3) |
| Viola spp. | IV | 2 (1-3) |
| Cladonia 'squamules' | IV | 2 (1-4) |
| Dicranum scoparium | IV | 5 (1-8) |
| Cladonia 'rangiformis' | IV | 1 (1-8) |
| Rubus caesius | IV | 4 (1-7) |
| Cerastium glomeratum | III | 1 (1-2) |
| Euphorbia paralias | III | 1 (1-2) |
| Poa pratensis | III | 1 (1-5) |
| Aira praecox | III | 2 (1-3) |
| Hypnum cupressiforme | III | 2 (1-7) |
| Arenaria serpyllifolia | II | 3 (1-3) |
| Cynoglossum officinale | II | 1 (1-2) |
| Festuca rubra | II | 1 (1-5) |
| Phleum arenarium | II | 1 (1-3) |
| Hieraceum pilosella | II | 2 (1-3) |
| Polygala vulgaris | II | 1 (1-2) |
| Salix repens | II | 5 (1-5) |
| Tortula ruraliformis | II | 2 (1-7) |
| Peltigera spp. | II | 1 (1-3) |
| Hypochoeris radicata | II | 1 (1-2) |
| Veronica officinalis | II | 2 (1-2) |
| Vicia sp. | II | 1 |
| Cladonia fimbriata | II | 1 (1-2) |
| Hieraceum umbellatum | II | 1 (1-2) |
| Holcus lanatus | II | 1 (1-2) |

TYPE 3:
Number of quadrats 51
Mean number of species per quadrat 20.2 (SE = 0.9)

| Species | Constancy | Score |
|---|---|---|
| Cerastium fontanum | V | 2 (1-4) |
| Festuca rubra | V | 4 (1-8) |
| Poa pratensis | V | 3 (1-7) |
| Luzula campestris | V | 3 (1-6) |
| Holcus lanatus | V | 4 (1-8) |
| Senecio jacobaea | IV | 2 (1-4) |
| Carex arenaria | IV | 3 (1-8) |
| Rubus caesius | IV | 4 (1-8) |
| Ammophila arenaria | III | 2 (1-8) |
| Leontodon spp. | III | 2 (1-4) |
| Lotus corniculatus | III | 2 (1-7) |
| Ononis repens | III | 3 (1-8) |
| Polygala vulgaris | III | 2 (1-3) |
| Salix repens | III | 3 (1-6) |
| Anthoxanthum odoratum | III | 3 (1-7) |
| Hypochoeris radicata | III | 2 (1-6) |
| Taraxacum spp. | III | 1 (1-2) |
| Centaurium erythraea | II | 1 (1-3) |
| Cirsium arvense | II | 2 (1-3) |
| Hieraceum pilosella | II | 2 (1-5) |
| Sedum acre | II | 2 (2-3) |
| Trifolium repens | II | 2 (1-3) |
| Vicia lathyroides | II | 2 (1-3) |
| Ranunculus spp. | II | 1 (1-7) |
| Viola spp. | II | 2 (1-3) |
| Aira praecox | II | 2 (1-3) |
| Vicia spp. | II | 1 (1-2) |
| Agrostis capillaris | II | 4 (1-7) |
| Dicranum scoparium | II | 1 (1-8) |
| Hypnum cupressiforme | II | 1 (1-6) |

TYPE 4:
Number of quadrats 40
Mean number of species per quadrat 15.2 (SE = 0.8)

| Species | Constancy | Score |
|---|---|---|
| Carex arenaria | V | 7 (1-8) |
| | | |
| Anthoxanthum odoratum | IV | 3 (1-7) |
| Agrostis capillaris | IV | 3 (1-8) |
| Rubus caesius | IV | 4 (1-6) |
| Chamaenerion angustifolium | IV | 3 (1-7) |
| Hypnum cupressiforme | IV | 4 (1-8) |
| | | |
| Festuca rubra/ovina | III | 4 (1-7) |
| Luzula campertris | III | 2 (1-4) |
| Hypochoeris radicata | III | 2 (1-4) |
| Vicia sp. | III | 1 (1-3) |
| Holcus lanatus | III | 2 (1-6) |
| | | |
| Lotus corniculatus | II | 2 (1-7) |
| Hieracium pilosella | II | 2 (1-3) |
| Poa pratensis | II | 2 (1-6) |
| Viola spp. | II | 2 (1-3) |
| Hieracium umbellatum | II | 1 (1-3) |
| Cladonia rangiformis | II | 2 (1-7) |
| Polytrichum spp. | II | 2 (1-5) |
| Betula sp. | II | 1 (1-10) |

TYPE 5:
Number of Quadrats 36
Mean number of species per quadrat 11.3 (SE = 0.8)

| Species | Constancy | Score |
|---|---|---|
| Dicranum scoparium | V | 5 (1-9) |
| Hypnum cupressiforme | V | 9 (1-10) |
| Cladonia rangiformis | III | 4 (1-8) |
| Polytrichum spp. | III | 2 (1-8) |
| Carex arenaria | III | 4 (2-9) |
| Chamaenerion angustifolium | III | 4 (1-6) |
| Pinus nigra (s) | III | 1 (1-2) |
| Lophocolea spp. | III | 2 (1-4) |
| Festuca rubra/ovina | II | 1 (1-7) |
| Leontodon spp. | II | 1 (1-3) |
| Poa pratensis | II | 1 (1-3) |
| Luzula campestris | II | 2 (1-3) |
| Viola spp. | II | 1 (1-3) |
| Aira praecox | II | 1 (1-2) |
| Hypochoeris radicata | II | 1 (1-2) |
| Cladonia fimbriata | II | 2 (1-2) |
| Senecio jacobaea | II | 2 (1-3) |
| Cladonia 'squamules' | II | 1 (1-4) |
| Campylopus introflexus | II | 4 (1-9) |
| Betula sp. | II | 2 (1-4) |
| Dryopteris dilatata | II | 1 (1-3) |
| Rubus fruticosus | II | 4 (1-5) |

TYPE 6:
Number of quadrats 55
Mean number of species per quadrat 11.5 (SE = 0.6)

| Species | Constancy | Score |
|---|---|---|
| Chamaenerion angustifolium | V | 5 (1-6) |
| Cladonia fimbriata | IV | 2 (1-4) |
| Dicranum scoparium | IV | 5 (1-9) |
| Carex arenaria | IV | 9 (1-10) |
| Aira praecox | III | 1 (1-3) |
| Hypochoeris radicata | III | 1 (1-2) |
| Senecio jacobaea | III | 1 (1-3) |
| Campylopus introflexus | III | 4 (1-9) |
| Holcus lanatus | III | 2 (1-5) |
| Hypnum cupressiforme | III | 1 (1-8) |
| Rubus fruticosus | III | 1 (1-4) |
| Leontodon spp. | II | 1 (1-2) |
| Cladonia rangiformis | II | 1 (1-3) |
| Polytrichum spp. | II | 2 (1-6) |
| Betula sp. | II | 1 (1-9) |
| Pinus nigra (s) | II | 1 (1-8) |
| Dryopteris dilatata | II | 1 (1-4) |

TYPE 7:
Number of quadrats 26
Mean number of species per quadrat 8.6 (SE = 6.2)

| Species | Constancy | Score |
|---|---|---|
| Pinus nigra (c) | V | 7 (2-9) |
| Hypnum cupressiforme | IV | 7 (1-10) |
| Lophocolea spp. | IV | 2 (1-8) |
| Dicranum scoparium | III | 2 (1-5) |
| Carex arenaria | III | 2 (1-10) |
| Chamaenerion angustifolium | III | 2 (1-10) |
| Pinus nigra (s) | III | 1 (1-2) |
| Dryopteris dilatata | III | 1 (1-9) |
| Rubus fruticosus | III | 2 (1-3) |
| Holcus lanatus | II | 1 (1-2) |
| Dicranella heteromalla | II | 1 (1-3) |

TYPE 8:

Number of quadrats 23

Mean number of species per quadrat 3.9 (SE = 0.4)

| Species | Constancy | Score |
| --- | --- | --- |
| Pinus nigra (c) | V | 9 (7-10) |
| Senecio jacobaea | II | 1 |
| Rubus caesius | II | 1 (1-2) |
| Hypnum cupressiforme | II | 2 (2-8) |
| Brachythecium rutabulum | II | 1 (1-4) |

TYPE 9:

Number of quadrats 31

Mean number of species per quadrat 9.7 (SE = 0.4)

| Species | Constancy | Score |
| --- | --- | --- |
| Dryopteris dilatata | V | 9 (1-10) |
| Rubus fruticosus | V | 4 (1-10) |
| Pinus nigra (c) | V | 8 (4-9) |
| Chamaenerion angustifolium | IV | 2 (1-9) |
| Eurynchium praelongum | IV | 2 (1-6) |
| Lophocolea spp. | IV | 2 (1-3) |
| Carex arenaria | III | 4 (1-10) |
| Holcus lanatus | II | 2 (1-10) |
| Rubus caesius | II | 2 (1-5) |
| Betula sp. | II | 3 (1-9) |
| Hypnum cupressiforme | II | 1 (1-3) |
| Urtica dioica | II | 1 (1-3) |

Groups 1,2 and 3 include very few quadrats from clear-felled or woodland sites (figure 3.9). Those quadrats from clear-felled sites which are classified in these groups were from the plantations felled 50 years ago, rather than the more recently felled fire-breaks. The three divisions within this 'seminatural' vegetation correlate approximately with the variations identified by the National Vegetation Classification for the area (Edmondson *et al*, 1988/89), where vegetation type 1 equates with an '*Ammophila arenaria* - *Phleum arenarium* dune' community (Malloch, 1985), type 2 with an '*Ammophila arenaria* - *Ononis repens* dune' community and type 3 with an '*Ammophila arenaria* - *Ononis repens* dune *Hypnum cupressiforme* sub-community'. A mosaic of these communities was found over much of the unplanted dune area. Figure 3.15 shows that vegetation type 1 tends to occur on south-facing slopes, while type 2 is found on less steep dunes. Type 3 is not readily explained by slope or aspect, however it may be related to a more stable dune surface, with taller vegetation (figure 3.10) and less bare sand (figure 3.12) than the other two groups.

The total numbers of species present in these three communities was greater than in any other community. Species occurring in these communities but absent from the other, mainly clear-felled and afforested vegetation types included:

| | |
|---|---|
| Anthyllis vulneraria | Aphanes microcarpa |
| Arabidopsis thaliana | Bellis perennis |
| Cynoglossum officinale | Erigeron acer |
| Erophila verna | Euphorbia paralias |
| Euphorbia portlandica | Galium verum |
| Gentianella campestris | Inula conyza |

| | |
|---|---|
| Lathyrus pratensis | Linaria vulgaris |
| Linum catharticum | Oenothera x fallax |
| Ornithopus perpusillus | Pastinaca sativa |
| Phleum arenarium | Rumex crispus |
| Saxifraga tridactylites | Teesdalia nudicaulis |
| Tortula ruraliformis | Trifolium dubium |
| Valerianella locusta | Veronica arvensis |
| Viola tricolor ssp curtisii | Vulpia fasciculata |

Vegetation type 4 is made up largely of quadrats from sites felled 50 years ago, with just a few others from unplanted and woodland sites (figure 3.9). These clear-felled sites have not returned to one of the typical unplanted dune communities, 1 to 3, although species composition includes many species of the unplanted dunes. The National Vegetation Classification identified some of these communities as 'Carex arenaria dune - Dicranum scoparium sub-community','Carex arenaria - Cladonia spp. dune' or 'Mesotrophic grassland', while others were not assigned to any recognisable community.

There are fewer species per quadrat in group 4 than in the unplanted dune communities (figure 3.14), with the vegetation dominated by Carex arenaria and grasses. Several quadrats are dominated by Betula sp. and Populus spp. scrub (figure 3.5), and the vegetation is generally taller than in groups 1 to 3 (figure 3.10), suggesting either that the soil 50 years after felling is better for plant growth, or perhaps less intensively grazed or trampled. Figure 3.13 shows that the organic soil horizons are deeper than in the unplanted dunes even 50 years after felling.

The following species were present in vegetation types 1-4, but absent from types 5-9 which were mainly in woodland and on sites felled less than 20 years ago.

| | |
|---|---|
| Arrhenatherum elatius | Bromus hordeaceus |
| Calluna vulgaris | Campanula rotundifolia |
| Carex flacca | Cornicularia aculeata |
| Crepis capillaris | Dactylis glomerata |
| Daucus carota | Galium verum |
| Geranium molle | Lapsana communis |
| Lolium perenne | Ononis repens |
| Plantago lanceolata | Populus alba |
| Sieglingia decumbens | Trifolium arvense |

The list includes several light-demanding sand-dune species, such as Galium verum, Campanula rotundifolia and Ononis repens which would probably not have survived long under woodland conditions, and therefore have probably recolonised during the 50 years since felling. Species such as Arrhenatherum elatius, Plantago lanceolata, Lolium perenne and Daucus carota are typical mesotrophic grassland species, more common in type 4, again suggesting that the soil fertility has increased in comparison with the unplanted dunes of the same age (see section 2.5). Some of the species, including Sieglingia decumbens, Calluna vulgaris and Cornicularia aculeata are usually found on the oldest, most acid dunes at Ainsdale. Their presence on clear-felled sites could be related to an increase in acidity of the soil following afforestation (see Chapter 2).

Vegetation type 5 consists mostly of quadrats taken at woodland edges (figure 3.9), with a few from recently felled sites. This community tends to occur on the north-facing edges of the plantations, and in rides and small clearings which are shaded from direct sunlight (pers. obs.; Soutar et al in preparation). The dominant species are mosses and Cladonia lichens, which may form extensive patches. Vascular plants are scarce: Carex arenaria and Chamaenerion angustifolium are often the only species present. This community is present where the trees cast some shade, but not under heavy shade or where there is thick needle litter, or where a dense canopy might intercept the majority of the rainfall. The mean depth of the organic soil horizons is intermediate between the unplanted dunes and the afforested and clear-felled sites (figure 3.13). Vegetation type 5 has a high diversity of bryophytes and lichens, including:

<u>Mosses</u>

| | |
|---|---|
| Aulacomnium androgynum | Aulacomnium palustre |
| Brachythecium rutabulum | Calliergon cuspidatum |
| Campylopus introflexus | Ceratodon purpureus |
| Dicranella heteromalla | Dicranum bonjeanii |
| Dicranum scoparium | (Dicranum majus?) |
| Drepanocladus aduncus | Hypnum cupressiforme |
| Leucobryum glaucum | Mnium hornum |
| Plagiothecium undulatum | Pleurozium schreberi |
| Pohlia nutans | Polytrichum formosum |
| Pseudoscleropodium purum | Rhizomnium punctatum |
| Rhytidiadelphus squarrosus | Thuidium tamariscinum |

<u>Liverworts</u>

| | |
|---|---|
| Lepidozia reptans | Lophocolea cuspidata |
| Lophocolea heterophylla | Ptilidium ciliare |

<u>Lichens</u>

| | |
|---|---|
| Cladonia arbuscula | Cladonia chlorophaea |
| Cladonia coccifera | Cladonia coniocraea |
| Cladonia cervicornis | Cladonia fimbriata |
| ssp. verticillata | Cladonia foliacea |
| (Cladonia furcata?) | Cladonia gracilis |
| Cladonia macilenta | Cladonia portentosa |
| Cladonia pyxidata | Cladonia rangiformis |
| (Cladonia squamosa?) | Peltigera canina |
| Peltigera horizontalis | Peltigera polydactyla |

Vegetation type 6 is almost entirely made up from quadrats from clear-felled sites, mostly from the fire-breaks felled 10 to 20 years ago (figure 3.9). The most constant species in these sites is <u>Chamaenerion angustifolium</u>, with <u>Carex arenaria</u>, <u>Cladonia fimbriata</u> and <u>Dicranum scoparium</u> present in 60-80% of quadrats. <u>Betula</u> and <u>Rubus fruticosus</u> are present in over 20% of the quadrats recorded but form a continuous scrub cover over a very large part of the fire-break area (plate 7). The ground flora is virtually indistinguishable from the rest of the fire-break community although this may change as the scrub matures. Figure 3.11 shows that there is a low percentage vegetation cover in comparison with the other unshaded communities; this reflects the large amount of uncolonised litter at the site, and also the rabbit activity which maintains areas of bare sand.

The Ainsdale fire-break vegetation includes several species of patch-forming mosses: Dicranum scoparium, Campylopus introflexus and Hypnum cupressiforme are locally dominant, with Ceratodon purpureus, Polytrichum juniperinum, P.formosum and Pseudoscleropodium purum also common. Cladonia lichens, especially C.fimbriata and C.rangiformis often encrust bare sand and woody materials.

The higher plants in the fire-break community tend to be either those which are present in the woodlands, such as Chamaenerion angustifolium, Carex arenaria and Dryopteris dilatata, or those with light, wind-dispersed seeds which can colonise quickly, such as Senecio jacobaea, Leontodon taraxacoides and Betula spp.. Few species from the unplanted dune communities are common in vegetation type 6 although several are present in very small numbers. The following unplanted dune species were found in quadrats in type 6:

| | |
|---|---|
| Aira praecox | Ammophila arenaria |
| Anthoxanthum odoratum | Asparagus officinalis |
| Brachythecium albicans | Carex arenaria |
| Centaurium erythraea | Cerastium fontanum |
| Cerastium glomeratum | Cerastium semidecandrum |

| | |
|---|---|
| Ceratodon purpureus | Chamaenerion angustifolium |
| Cladonia fimbriata | Dicranum scoparium |
| Cladonia rangiformis | Festuca rubra |
| Erodium cicutarium | Holcus lanatus |
| Hieracium pilosella | Hypnum cupressiforme |
| Homalothecium lutescens | Leontodon taraxacoides |
| Hypochoeris radicata | Luzula campestris |
| Lotus corniculatus | Poa trivialis |
| Poa pratensis | Polytrichum juniperinum |
| Polygala vulgaris | Rubus caesius |
| Pseudoscleropodium purum | Trifolium repens |
| Senecio jacobaea | |

Vegetation types 7, 8 and 9 are all woodland communities (figure 3.9). TWINSPAN separates these from the other types in its first division using the constant Pinus nigra canopy as an indicator species. Subsequent divisions identify three broad categories within the woodland vegetation, these are associated with the age and management of the trees.

Type 7 is closely related to type 5 but tends to be associated with edges which allow sunlight to penetrate beneath the canopy, especially south-facing edges, and replanted or recently thinned woodland. The community does not have such a high mean percentage cover as type 5, probably due to disturbance and needle-fall, in addition to the shade. The most constant species are Hypnum cupressiforme and Lophocolea cuspidata although the vascular plants Carex arenaria, Chamaenerion angustifolium and Dryopteris dilatata are locally dominant. Pine seedlings are often present.

Vegetation type 8 is possibly the most common woodland community, found throughout the first rotation plantations, and where the canopy is most dense (plate 1). This is a floristically poor community, with an average of less than

4 species per quadrat (including the Pinus nigra canopy), dominated by bare needle litter. The only plant appearing to be growing well under the shaded conditions was Epipactis dunensis. Species present in this community were mostly either shade-tolerant species or weed seedlings. The full list of species recorded in quadrats is as follows:

| | |
|---|---|
| Asparagus officinalis | Brachythecium rutabulum |
| Carex arenaria | Chamaenerion angustifolium |
| Cirsium vulgare | Dicranum scoparium |
| Cladonia rangiformis | Epipactis dunensis |
| Epilobium montanum | Galium aparine |
| Eurynchium praelongum | Hypnum cupressiforme |
| Holcus lanatus | Poa pratensis |
| Lophocolea cuspidata | Rosa canina |
| Pinus nigra (seedling) | Rubus fruticosus |
| Rubus caesius | Senecio jacobaea |
| Sambucus nigra | Sonchus sp. |
| Solanum dulcamara | Taraxacum sp. |
| Stellaria media | |
| Urtica dioica | |

Vegetation type 9 is seen where the tree canopy is more open, and especially in older and second rotation woodlands on the older dunes. The ground flora is dominated by Dryopteris dilatata and Rubus fruticosus, often with Chamaenerion angustifolium (Plate 2). Many species usually present in native woodlands are present in this community, it can in fact be classified as a Quercus robur - Pteridium aquilinum - Rubus fruticosus community in the National Vegetation Classification (Rodwell, 1991). Woodland plants from the group 9 quadrats include:

| | |
|---|---|
| Acer pseudoplatanus | Aulacomnium androgynum |
| Betula sp. | Brachypodium sylvaticum |
| Brachythecium rutabulum | Corydalis claviculata |
| Crataegus monogyna | Dicranella heteromalla |
| Dryopteris borreri | Dryopteris dilatata |
| Dryopteris filix-mas | Eurynchium praelongum |
| Fagus sylvatica | Fraxinus excelsior |
| Hedera helix | Hypnum cupressiforme |
| Ilex aquifolium | Ligustrum vulgare |
| Lonicera periclymenum | Lophocolea cuspidata |

| | |
|---|---|
| Mnium hornum | Plagiomnium rostratum |
| Plagiothecium undulatum | Polypodium vulgare |
| Polytrichum formosum | Rosa canina |
| Rubus fruticosus | Sambucus nigra |
| Solanum dulcamara | Urtica dioica |
| Viola riviniana | |

The significance of these findings is discussed further in section 3.6.

### 3.3.3 Results: Whiteford

The results of the DECORANA analysis are presented in figures 3.16 to 3.21. TWINSPAN vegetation types are described in table 3.10, with percentage frequency diagrams comparing measured site variables between the groups in figures 3.22 to 3.28.

Legends for figures 3.16 to 3.21. DECORANA analysis for Whiteford quadrat data.

Figure 3.16. (page 118). TWINSPAN summary diagram. Positions of boundaries are approximate.

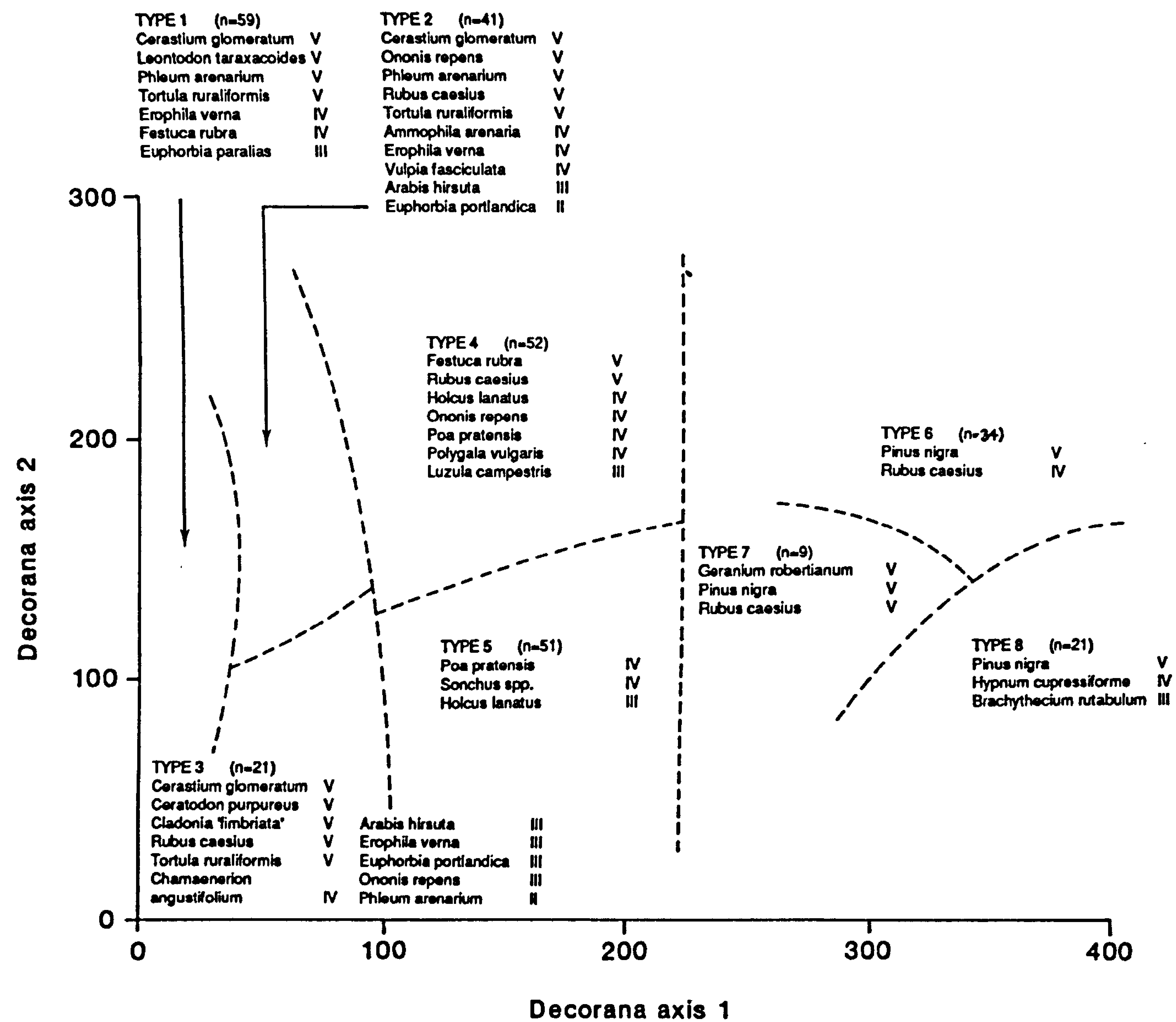
Figure 3.17. (page 119). Variation in shade.

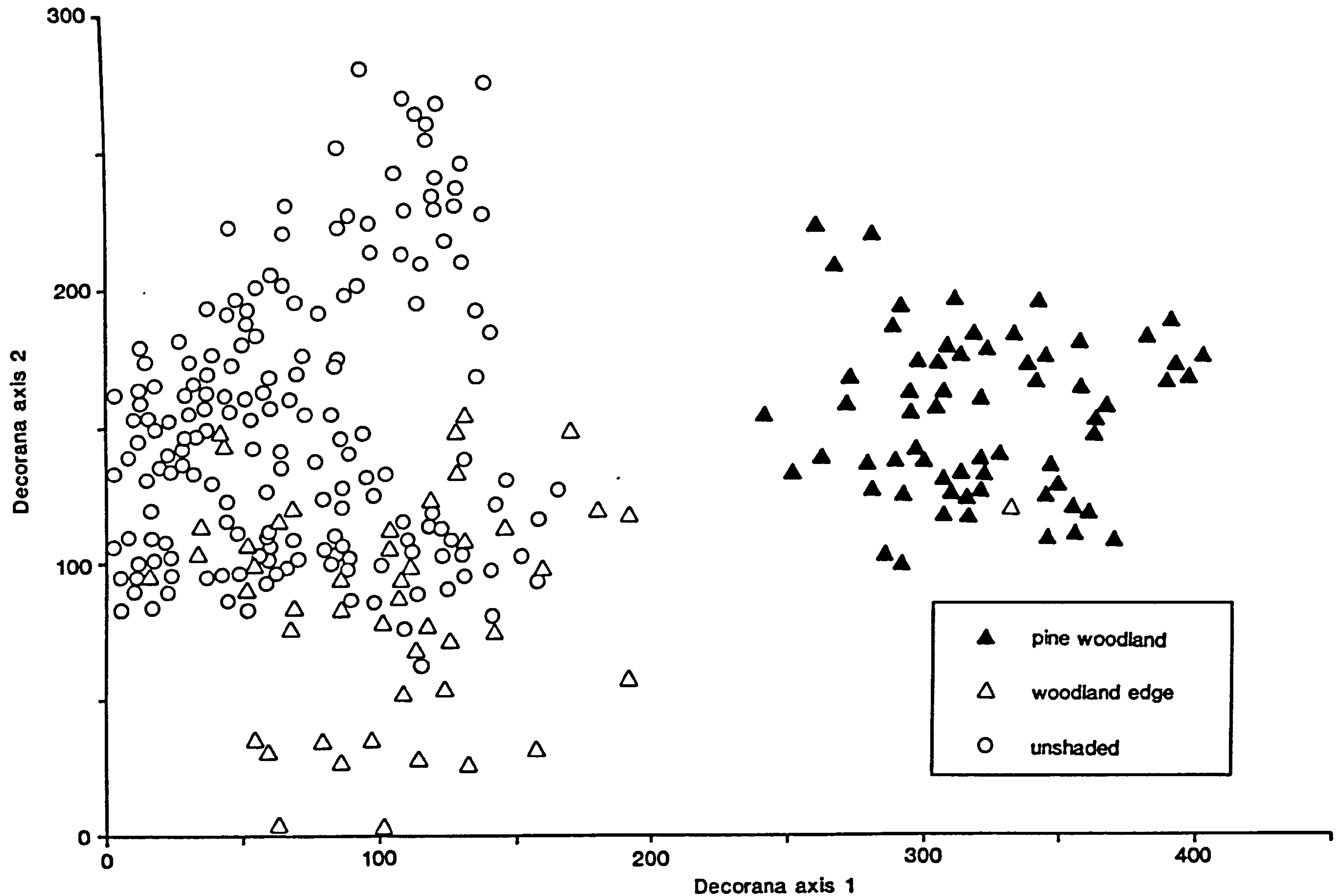
Figure 3.18. (page 120). Time after felling.

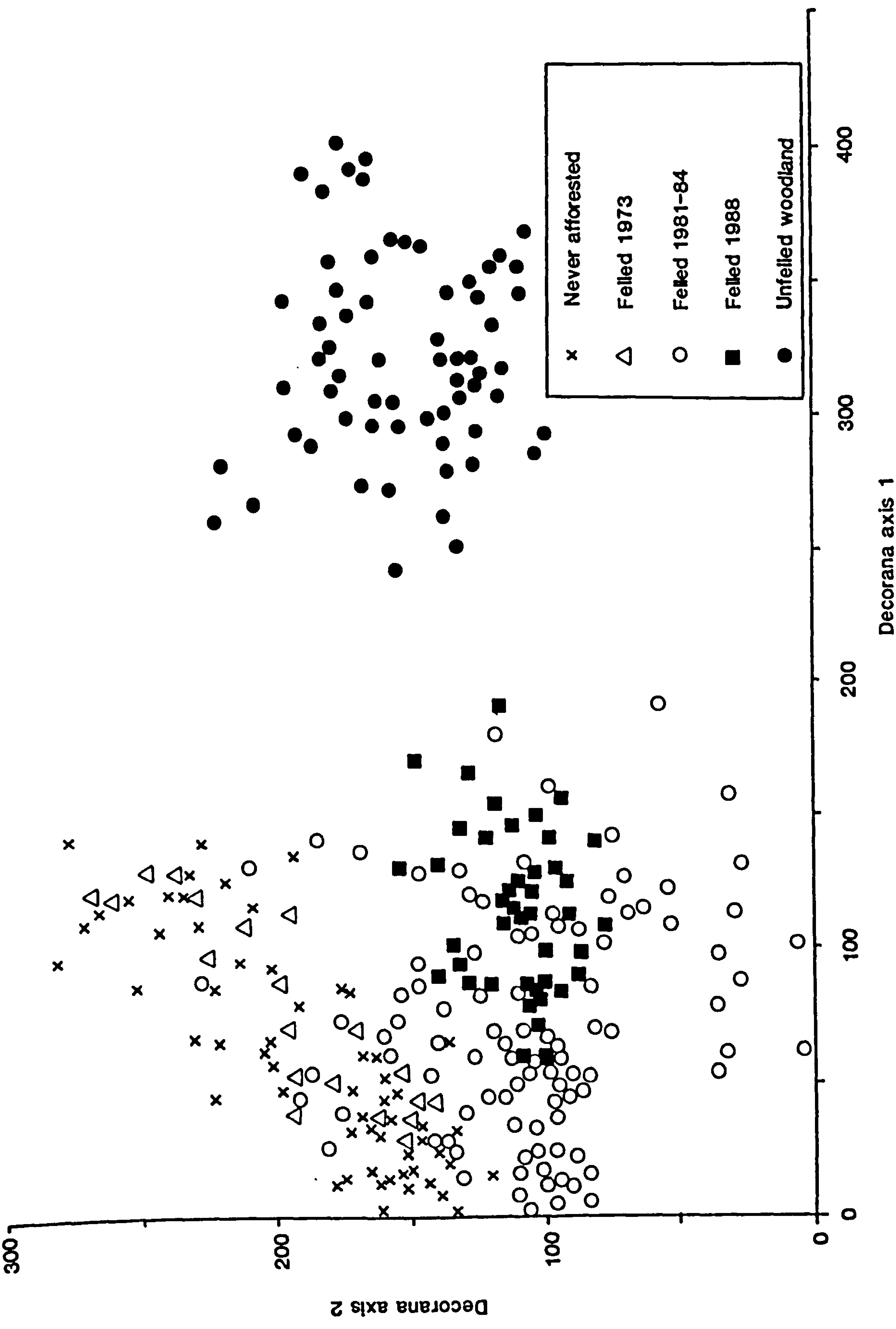
Figure 3.19. (page 121). Depth of pine needle material.

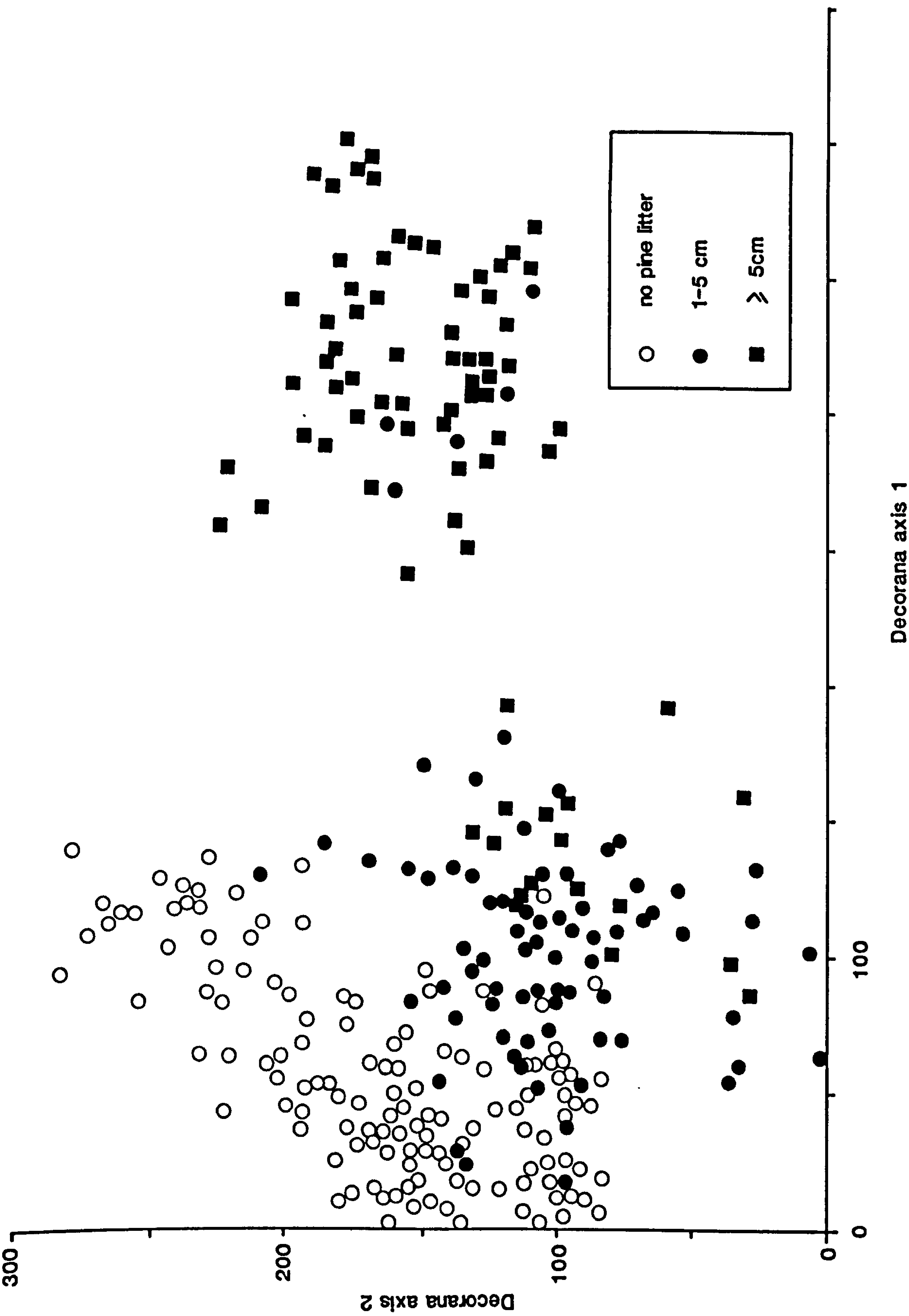
Figure 3.20. (page 122). Number of species per quadrat.

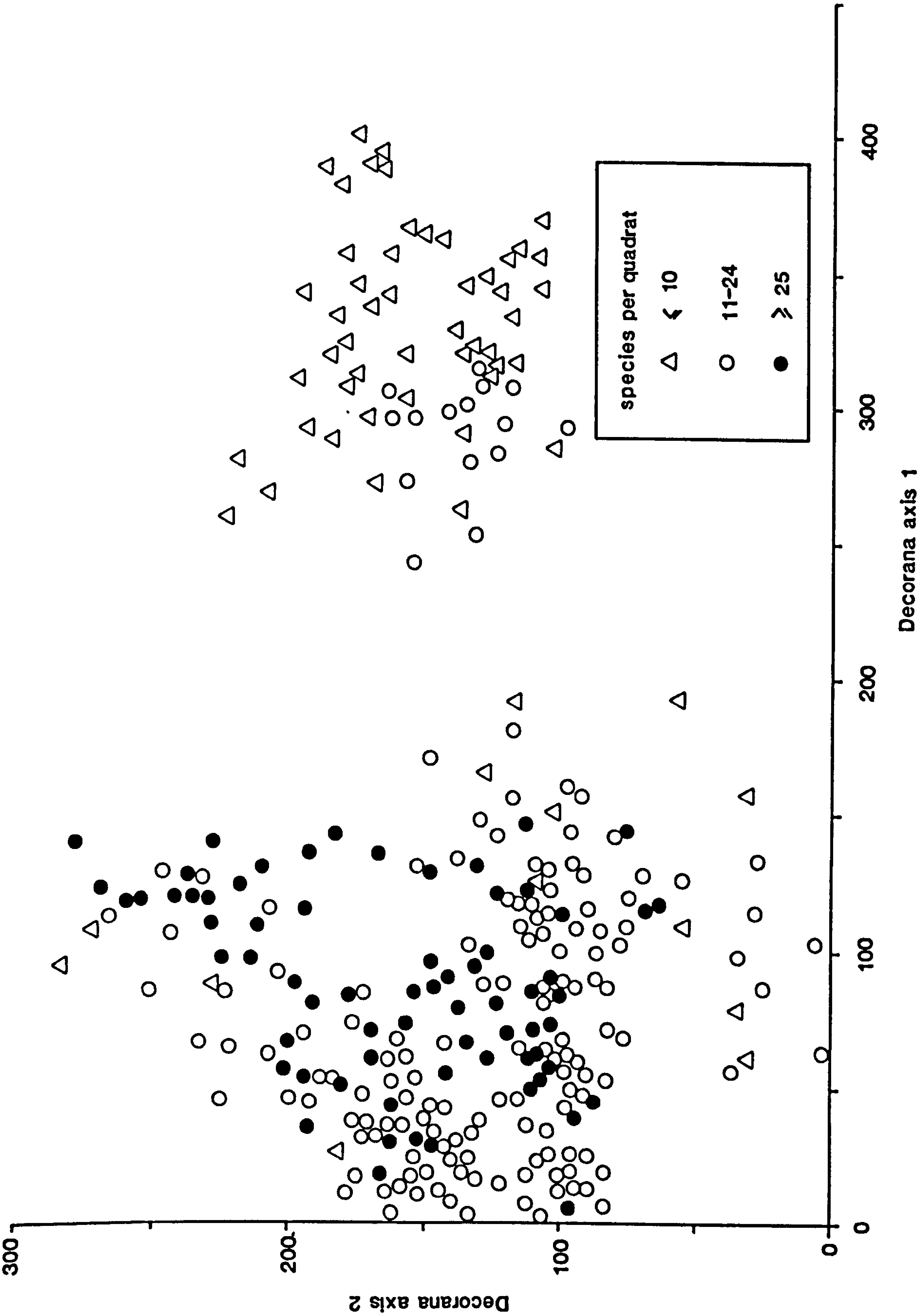
Figure 3.21. (page 123). Changes in the positions of permanent quadrats at Whiteford, between 1988 and 1990. See text for explanation.

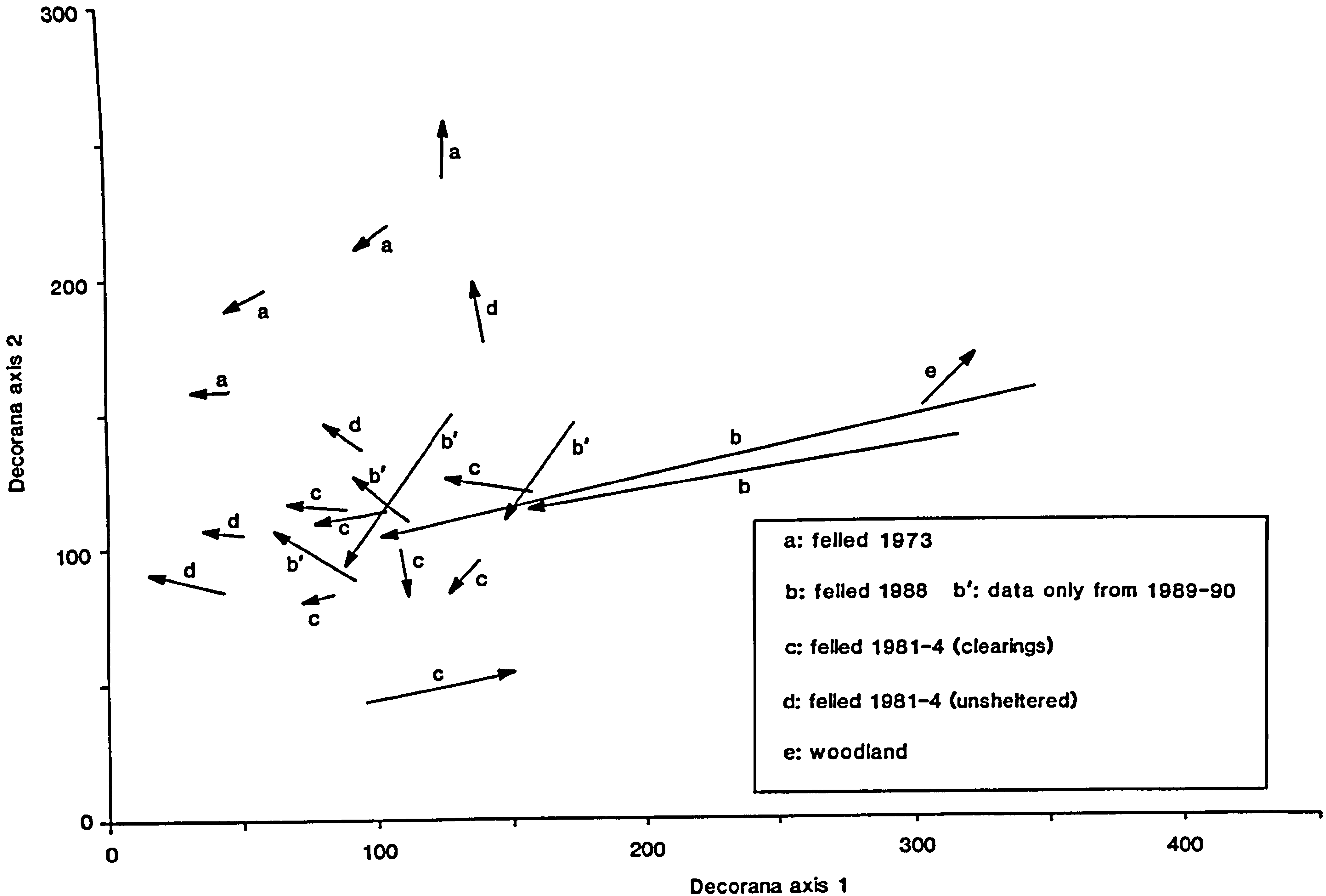

TYPE 1 (n=59)
Cerastium glomeratum V
Leontodon taraxacoides V
Phleum arenarium V
Tortula ruraliformis V
Erophila verna IV
Festuca rubra IV
Euphorbia paralias III
TYPE 2 (n=41)
Cerastium glomeratum V
Ononis repens V
Phleum arenarium V
Rubus caesius V
Tortula ruraliformis V
Ammophila arenaria IV
Erophila verna IV
Vulpia fasciculata IV
Arabis hirsuta III
Euphorbia portlandica II
TYPE 3 (n=21)
Cerastium glomeratum V
Ceratodon purpureus V
Cladonia 'fimbriata' V
Rubus caesius V
Tortula ruraliformis V
Chamaenerion angustifolium IV
Arabis hirsuta III
Erophila verna III
Euphorbia portlandica III
Ononis repens III
Phleum arenarium II
TYPE 4 (n=52)
Festuca rubra V
Rubus caesius V
Holcus lanatus IV
Ononis repens IV
Poa pratensis IV
Polygala vulgaris IV
Luzula campestris III
TYPE 5 (n=51)
Poa pratensis IV
Sonchus spp. IV
Holcus lanatus III
TYPE 6 (n=34)
Pinus nigra V
Rubus caesius IV
TYPE 7 (n=9)
Geranium robertianum V
Pinus nigra V
Rubus caesius V
TYPE 8 (n=21)
Pinus nigra V
Hypnum cupressiforme IV
Brachythecium rutabulum III
Decorana axis 2
Decorana axis 1
300
200
100
0
0
100
200
300
400


300
200
100
0
0
100
200
300
400
Decorana axis 2
Decorana axis 1
pine woodland
woodland edge
unshaded


Never afforested
Felled 1973
Felled 1981-84
Felled 1988
Unfelled woodland
Decorana axis 1
Decorana axis 2
0
100
200
300
400
0
100
200
300


no pine litter
1–5 cm
≥ 5cm
Decorana axis 1
Decorana axis 2
0
100
200
300


species per quadrat
≤ 10
11–24
≥ 25
Decorana axis 1
0
100
200
300
400
Decorana axis 2
0
100
200
300



300
200
100
0
Decorana axis 2
0
100
200
300
400
Decorana axis 1
a
a
a
a
b
b
b'
b'
b'
b'
c
c
c
c
c
c
c
c
d
d
d
d
d
e
a: felled 1973
b: felled 1988 b': data only from 1989-90
c: felled 1981-4 (clearings)
d: felled 1981-4 (unsheltered)
e: woodland

The DECORANA analysis of the Whiteford data makes a very obvious distinction between woodland and non-woodland quadrats along axis 1 (figure 3.17). This shows that the presence of pine trees accounts for the greatest variation within the data. Table 3.9 shows clearly that the woodland has the greatest significant influence over axis 1, with woodland quadrats having high scores, being associated with a lower percentage cover by vegetation, deeper litter, less bare sand, and fewer species per quadrat than the non-woodland quadrats (figures 3.18 to 3.20). There is a significant negative correlation between slope and position on axis 1 (table 3.9), this is probably because tree-planting was concentrated on the older, flatter, more sheltered dunes, leaving the steeper, seaward dunes unplanted.

Table 3.9. Whiteford: Linear regression statistics for DECORANA axes 1 and 2, with recorded variables. Percentage data have been arcsine transformed.
** = p<0.005, * = p<0.05, NS = not significant.

| Variable | AXIS 1 | | | | AXIS 2 | | | |
|---|---|---|---|---|---|---|---|---|
| | t | $R^2$ | df | p | t | $R^2$ | df | p |
| Woodland age | 11.0 | .298 | 286 | ** | -9.1 | .226 | 286 | ** |
| Years felled | -8.3 | .195 | 285 | ** | -2.2 | .017 | 285 | * |
| organic Soil depth | 20.3 | .646 | 225 | ** | 1.4 | .009 | 225 | NS |
| Percent cover | -10.9 | .295 | 286 | ** | 9.2 | .228 | 286 | ** |
| Percent sand | -4.9 | .076 | 285 | ** | -4.1 | .057 | 285 | ** |
| Mean height | 1.3 | .006 | 286 | NS | 4.8 | .074 | 286 | ** |
| Total species | -15.8 | .464 | 286 | ** | 1.7 | .009 | 286 | NS |
| Total mosses | -3.1 | .033 | 286 | ** | -2.9 | .029 | 286 | ** |
| Total lichens | -5.7 | .102 | 286 | ** | -4.5 | .067 | 286 | ** |
| Slope | -1.6 | .009 | 286 | ** | 1.3 | .006 | 286 | NS |

Position on axis 2 is positively correlated with percentage vegetation cover and vegetation height, and negatively correlated with woodland age, percentage of bare sand, and numbers of moss and lichen species (table 3.9). This may be linked with nutrient availability, (as described at Ainsdale), or disturbance. Although they have the deepest needle litter (figure 3.19) quadrats with low scores on DECORANA axis 2 appear to have a low soil fertility, possibly due to nutrient immobilisation (see chapter 2); they have shorter vegetation with more mosses and lichens than the quadrats with high scores, which appear to be more fertile, with taller vegetation.

Figure 3.17 shows that shade may also be important in accounting for the variation along DECORANA axis 2, with higher numbers of mosses and lichens present in the woodland edge habitat (as seen at Ainsdale). Much of the felling between 1981 and 1984 was undertaken to create small clearings within the plantations. However, plantations G and F were felled completely and now have no shade or shelter effects (figure 1.3). Although they are nearer to the sea they can be used for a comparison with the more sheltered clearings. The quadrats taken from plantations G and F now have higher scores on axis 2 than those from the clearings (pers.obs. and see figure 3.17). They also have lower scores on axis 1, suggesting a much better recovery following clear-felling.

The length of time following felling and the age of the woodland before clear-felling are related to the vegetation composition (figure 3.18). The woodlands felled in 1973 were the youngest woodlands (about 12 years old) and they have had the longest time for recovery. They are now only distinguishable from the unplanted dunes by the presence of stumps, some of which are regenerating (pers.obs.). Their DECORANA scores are similar on both axes. Quadrats from woodlands felled between 1981 and 1984 are scattered widely over DECORANA axis 2; this is probably due to the effects of shade and shelter in different clear-fell sites, as already mentioned, with the more open sites now supporting vegetation most similar to the unplanted dunes. The most recently felled areas had supported trees for about 32 years. Quadrats from these sites form a cluster on the DECORANA diagram, showing that they all share a very similar species composition, which is different from the unplanted dunes.

Permanent quadrats in different clear-felled areas are shown on figure 3.21. In order to reduce the influence of distorting factors such as slight variations in sampling date over the three year study period the end points of each arrow represent the mean DECORANA scores for each quadrat in 1988 and 1989, and in 1989 and 1990, except where there are only data for two years. The data show a general trend for a lower score on DECORANA axis 1 in 1990 than in 1988, indicating that the vegetation is becoming more like the unplanted dunes than the woodland. The only two exceptions to this were in the woodland and a site felled in 1984 which was still shaded by trees. Despite the limitations of the timescale this suggests that there is a gradual, directional change in the flora towards a more natural state, and this may still be continuing at some sites nearly 20 years after felling.

The first TWINSPAN division splits the woodland quadrats from the non-woodland quadrats. Subsequent divisions of the non-woodland quadrats are roughly parallel with DECORANA axis 1 and then axis 2. All of the non-woodland vegetation types have over 20 quadrats, but two of the woodland types have only 6 and 9.

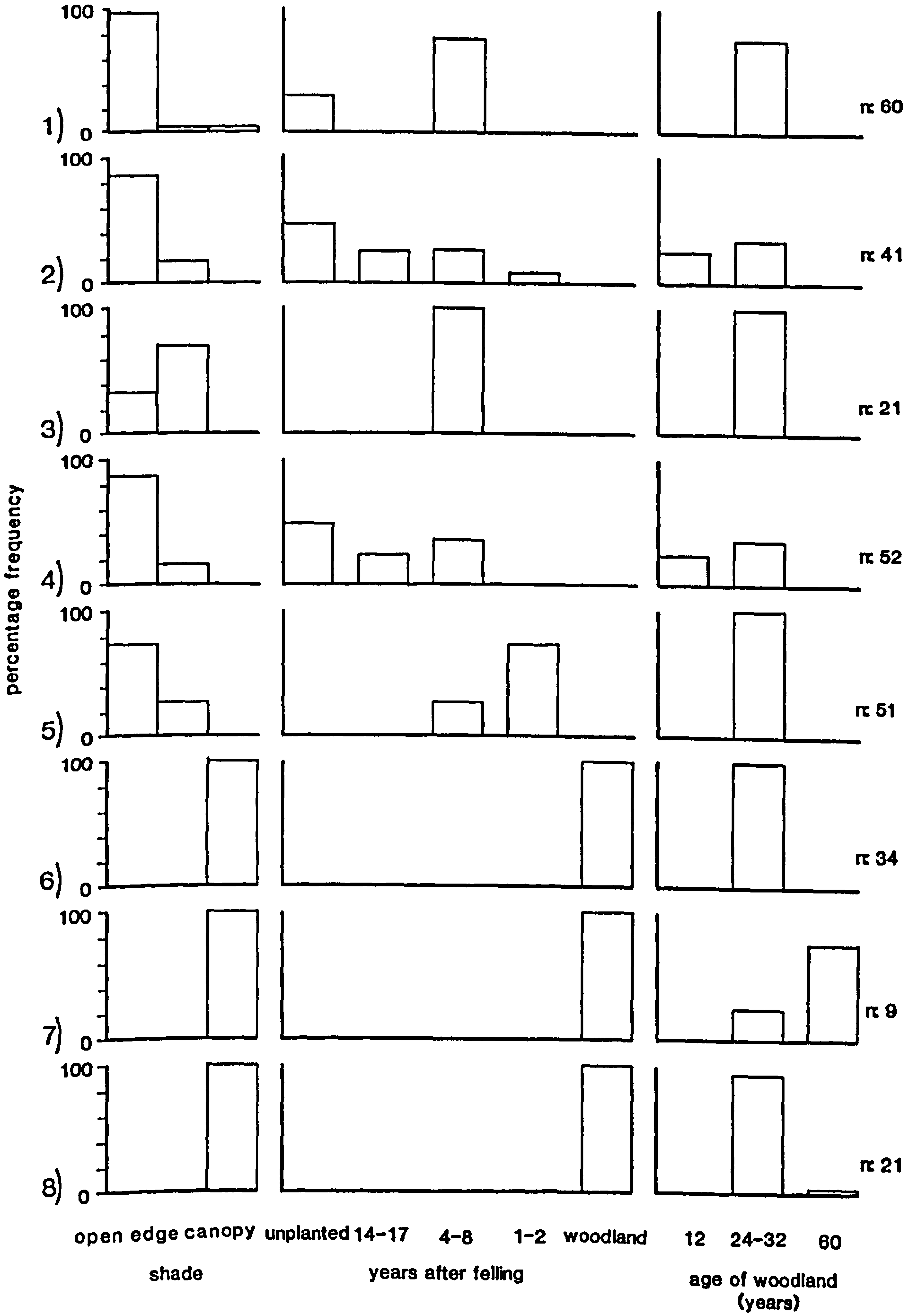



Figure 3.22 Shade, time after felling and age of woodland. Percentage frequencies for TWINSPAN vegetation types 1-8 at Whiteford. n= number of quadrats.

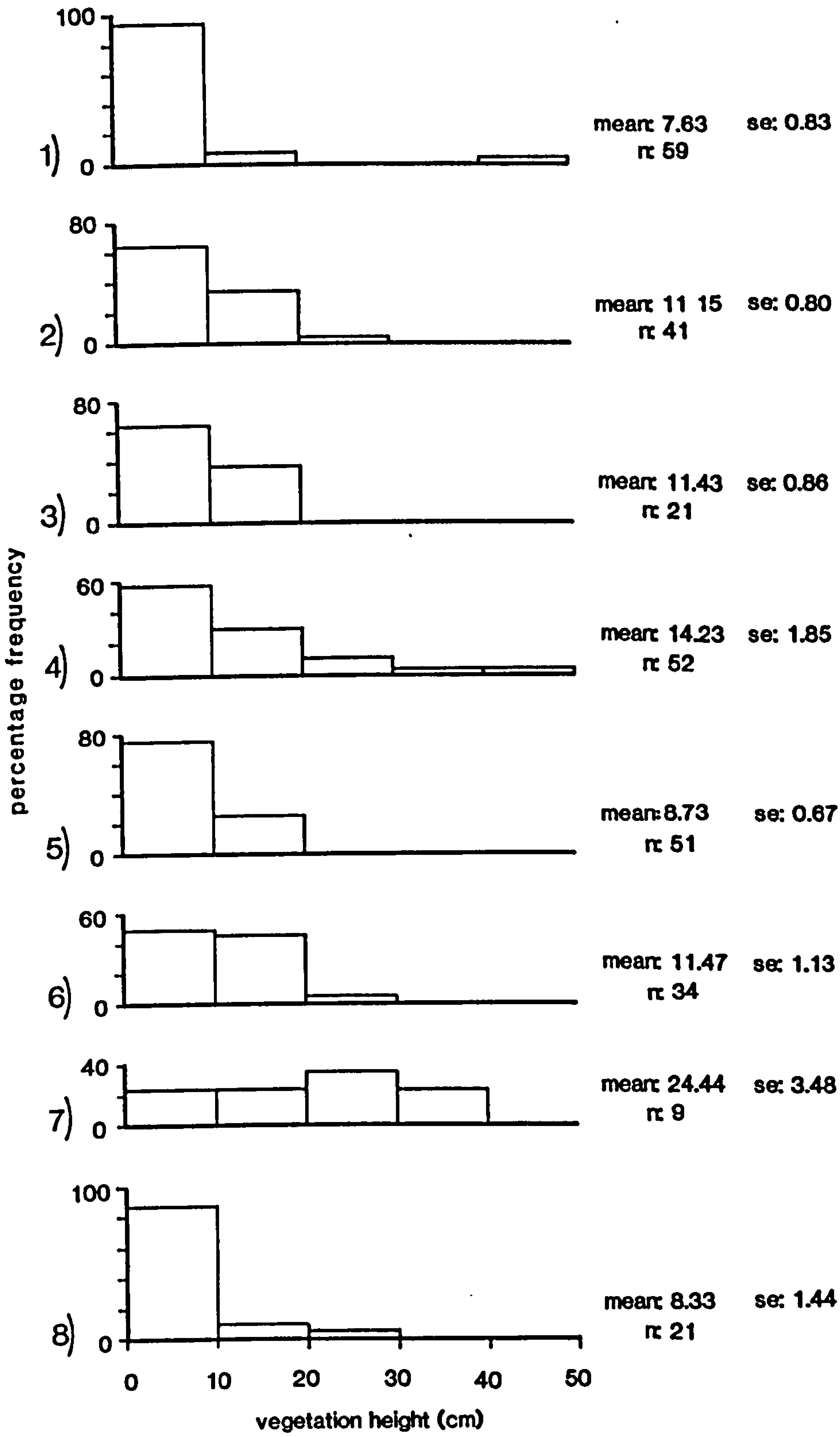



Figure 3.23 Vegetation height. Percentage frequencies for TWINSPAN vegetation types 1-8 at Whiteford. n= number of quadrats. se= standard error.

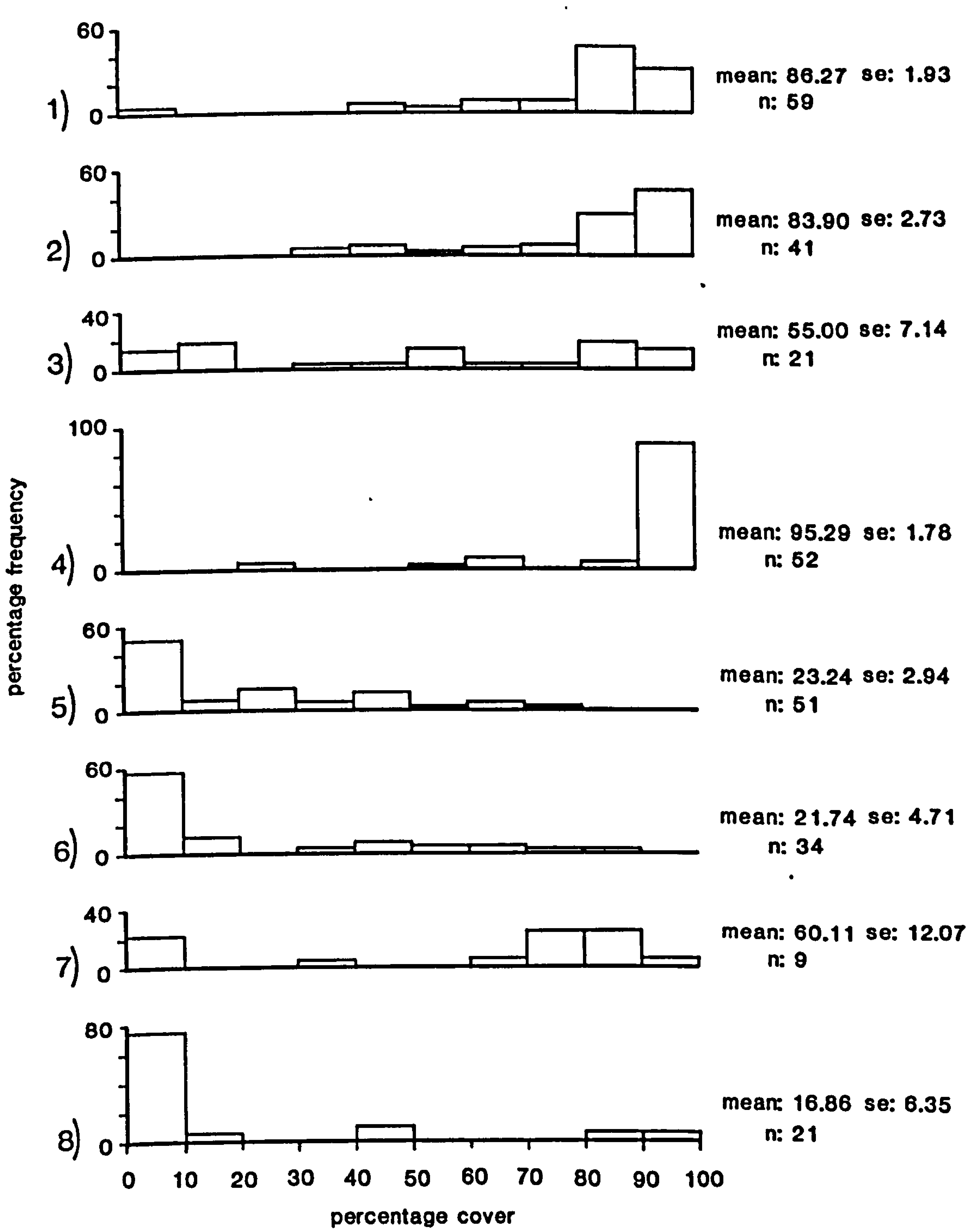



Figure 3.24 Percentage cover. Percentage frequencies for TWINSPAN vegetation types 1-8 at Whiteford. n= number of quadrats. se= standard error.

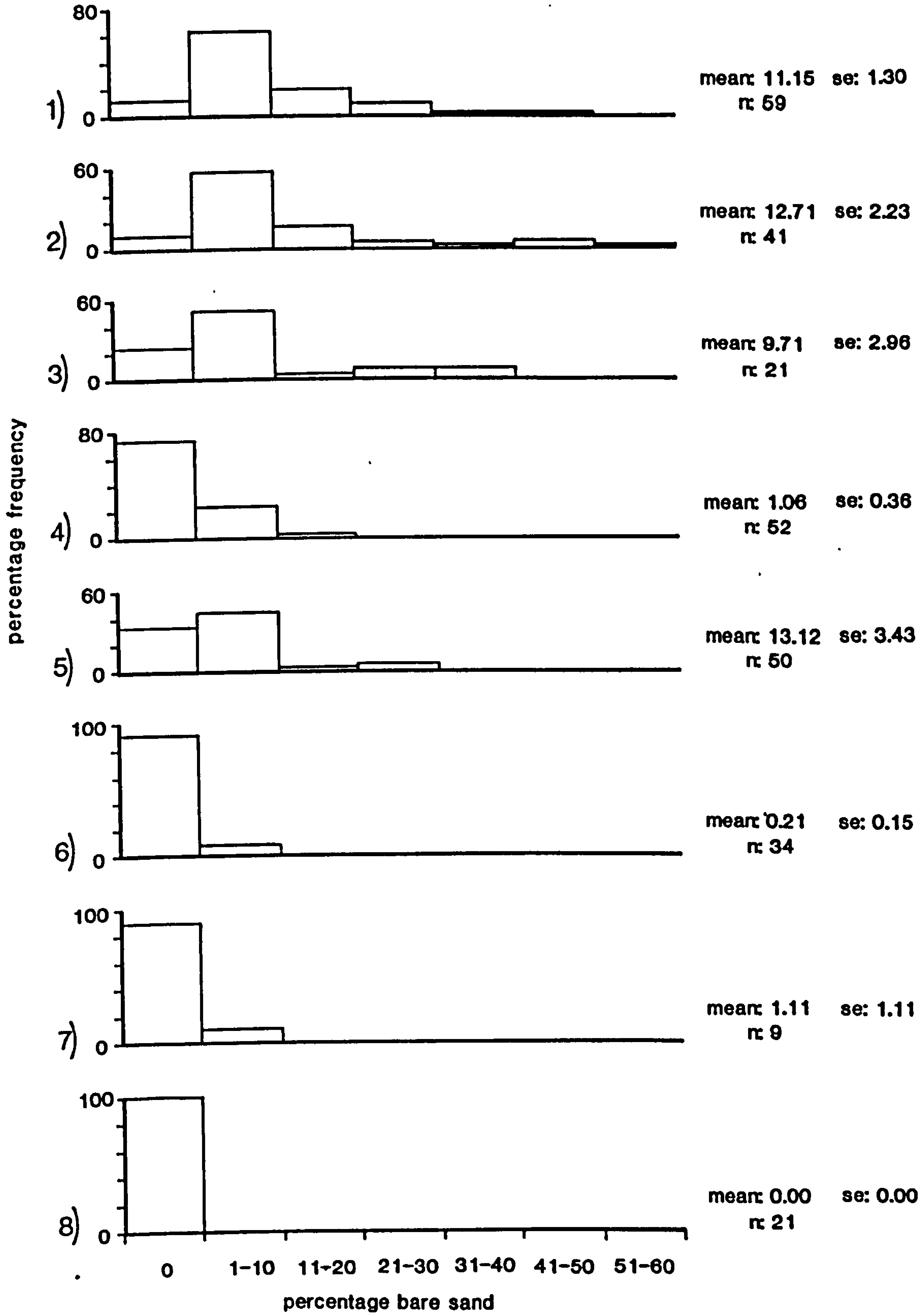



Figure 3.25 Percentage bare sand. Percentage frequencies for TWINSPAN vegetation types 1-8 at Whiteford. n= number of quadrats. se= standard error.

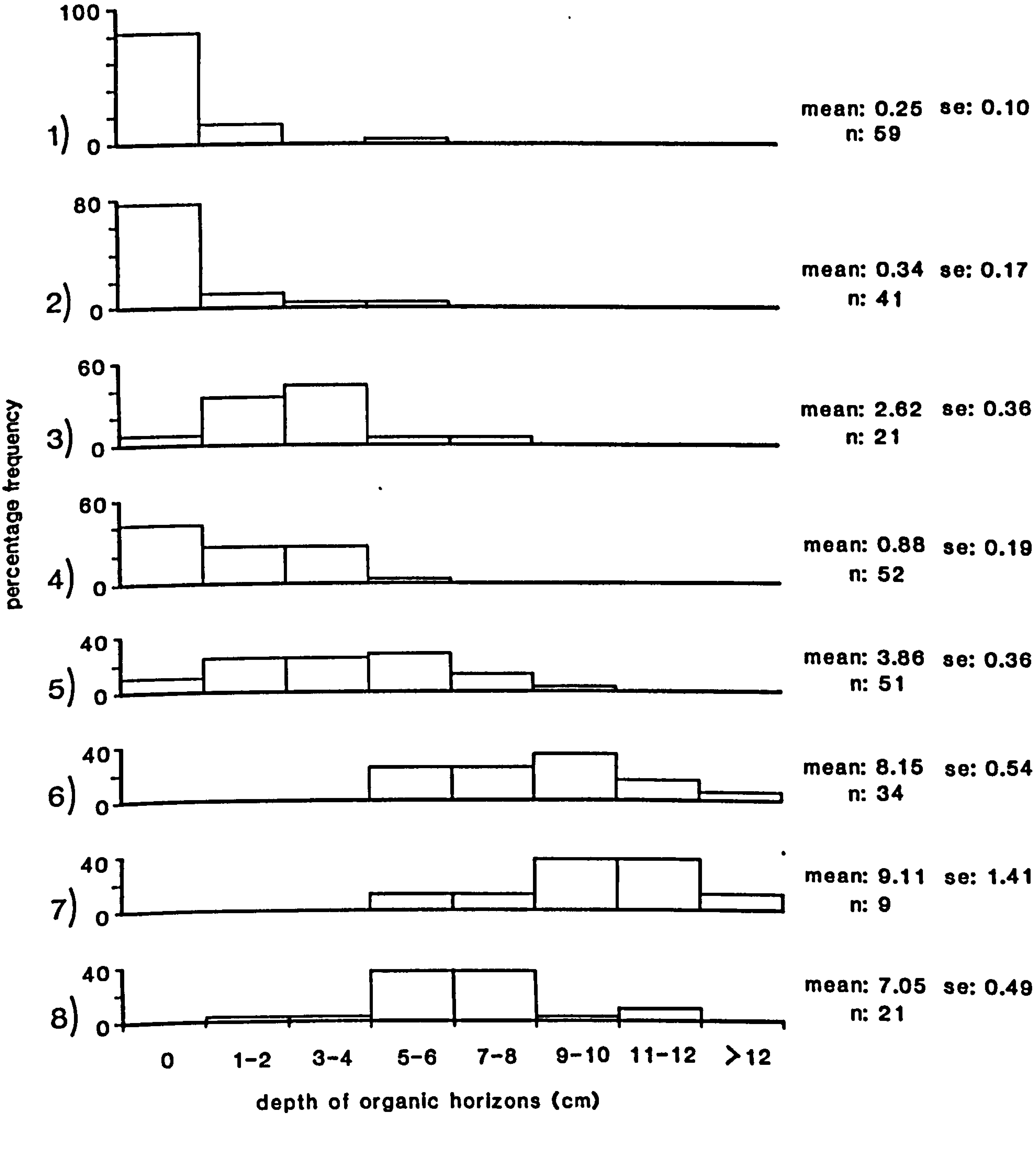



Figure 3.26 Depth of pine needle material. Percentage frequencies for TWINSPAN vegetation types 1-8 at Whiteford. n= number of quadrats. se= standard error.

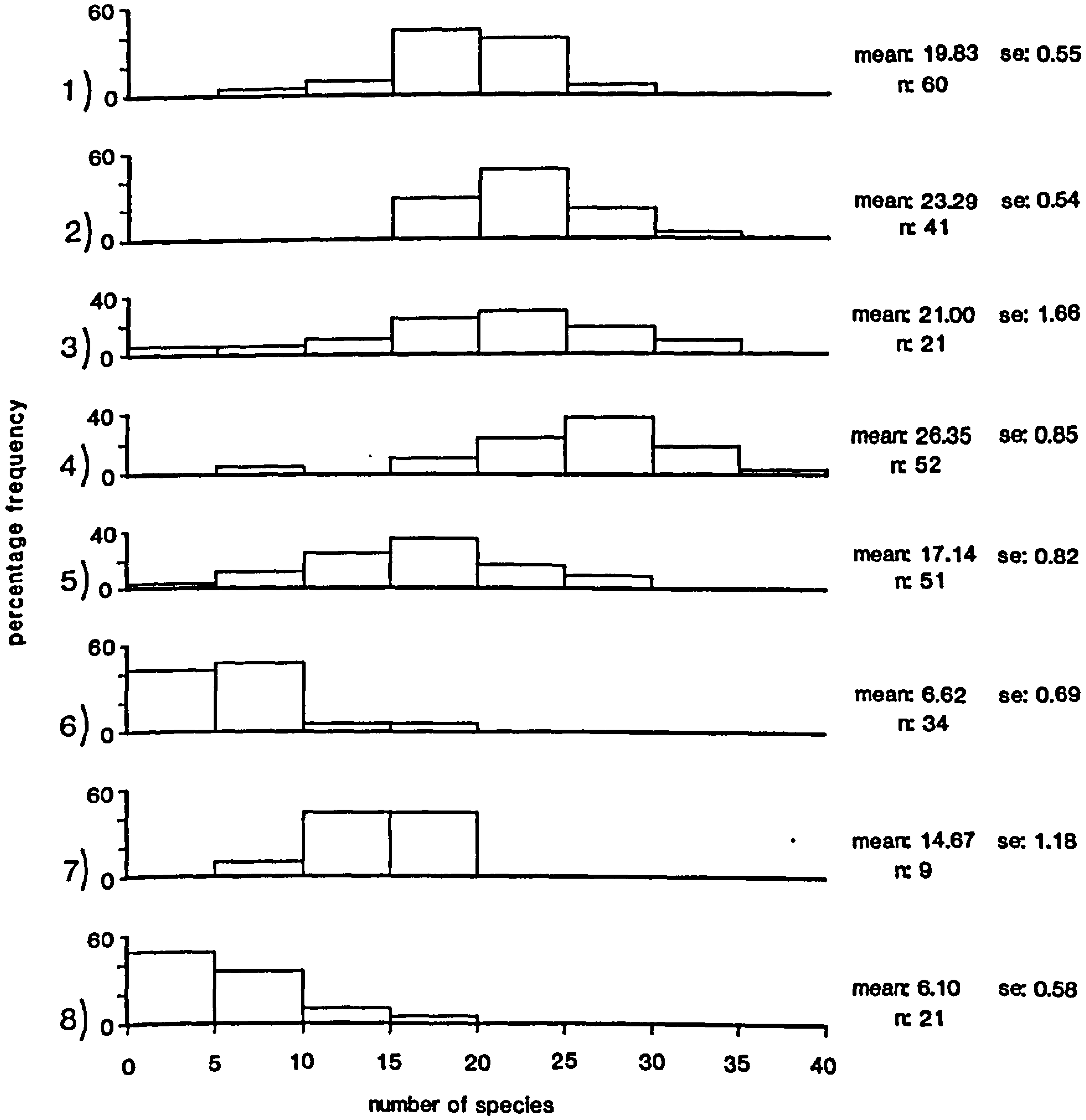



Figure 3.27 Number of species per quadrat. Percentage frequencies for TWINSPAN vegetation types 1-8 at Whiteford. n= number of quadrats. se= standard error.

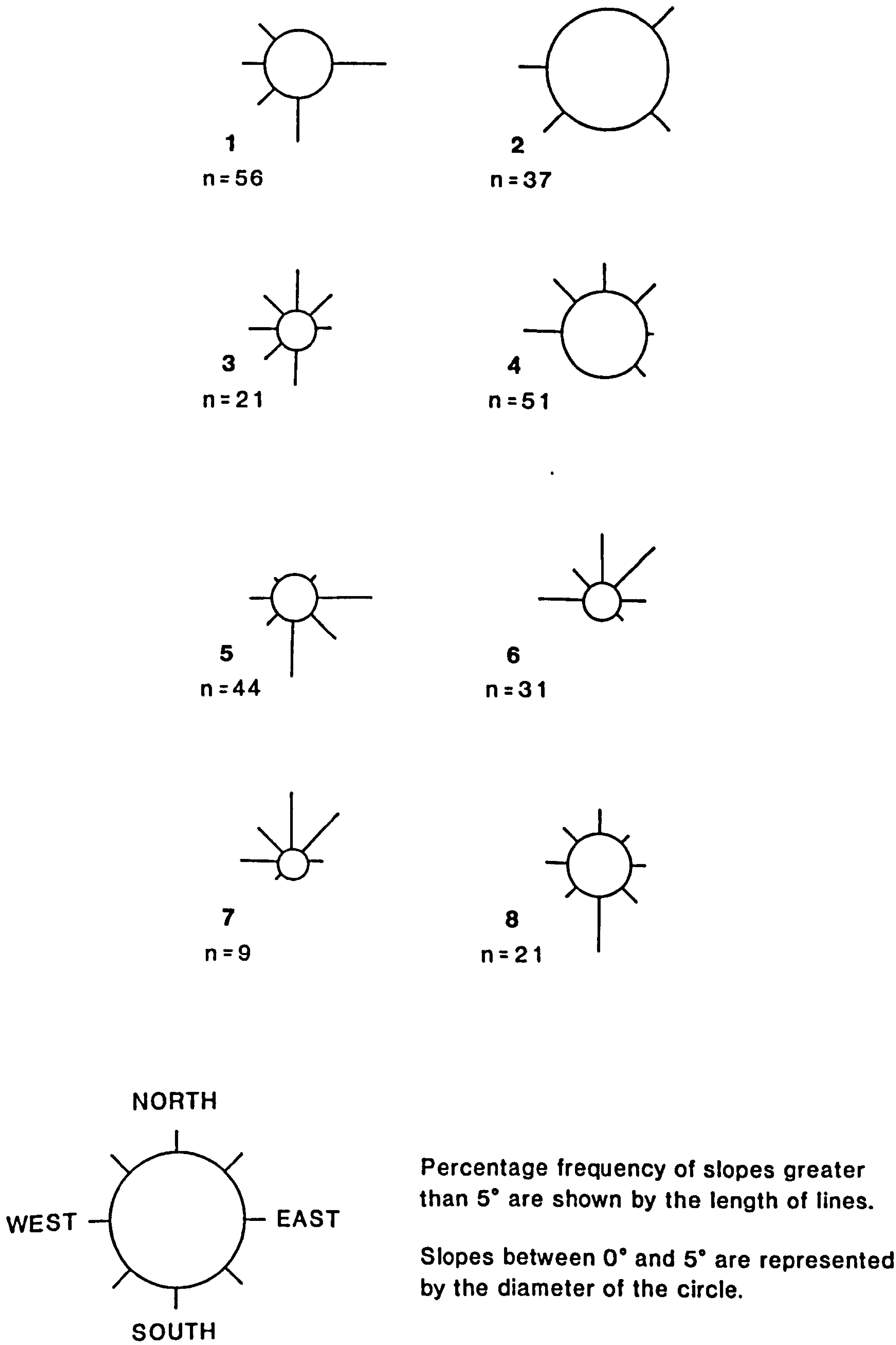



Figure 3.28 Slope and aspect. Percentage frequencies for TWINSPAN vegetation types 1-8 at Whiteford. n= number of quadrats.

Table 3.10 TWINSPAN vegetation types studied at Whiteford. For each community the species are grouped into frequency classes. Species with a constancy value of I are not shown. Species order within the frequency classes is determined by the TWINSPAN program.
DOMIN scores are summarised, giving the median value for each species, followed by the range of recorded values in brackets.

TYPE 1
Number of quadrats 60
Mean number of species per quadrat 19.83 (SE = 0.547)

| Species | Constancy | Score |
|---|---|---|
| Cerastium glomeratum | V | 3 (1-3) |
| Leontodon spp. | V | 3 (1-4) |
| Phleum arenarium | V | 3 (1-4) |
| Tortula ruraliformis | V | 6 (1-9) |
| Carex arenaria | V | 3 (1-5) |
| | | |
| Viola spp. | IV | 2 (1-4) |
| Aira praecox | IV | 2 (1-4) |
| Erophila verna | IV | 2 (1-3) |
| Saxifraga tridactylites | IV | 2 (1-3) |
| Festuca rubra | IV | 4 (1-10) |
| | | |
| Arenaria serpyllifolia | III | 3 (1-3) |
| Desmazeria rigida | III | 2 (1-3) |
| Centaurium erythraea | III | 1 (1-2) |
| Cerastium semidecandrum | III | 2 (1-3) |
| Cirsium vulgare | III | 1 (1-2) |
| Euphorbia paralias | III | 1 (1-2) |
| Ononis repens | III | 6 (1-8) |
| Vulpia fasciculata | III | 2 (1-3) |
| Brachythecium albicans | III | 2 (1-5) |
| Senecio jacobaea | III | 1 (1-3) |
| Rubus caesius | III | 1 (1-6) |
| | | |
| Ammophila arenaria | II | 2 (1-5) |
| Chamaenerion angustifolium | II | 2 (1-4) |
| Erodium cicutarium | II | 2 (1-3) |
| Myosotis arvensis | II | 1 (1-2) |
| Oenothera spp. | II | 1 (1-2) |
| Ceratodon purpureus | II | 1 (1-5) |
| Cladonia rangiformis | II | 2 (1-4) |
| Peltigera spp. | II | 2 (1-6) |
| Hypochoeris radicata | II | 1 (1-2) |
| Polygala vulgaris | II | 1 (1-3) |
| Taraxacum spp. | II | 1 (1-2) |
| Hypnum cupressiforme | II | 2 (1-8) |

TYPE 2

Number of quadrats 41

Mean number of species per quadrat 23.29 (SE = 0.544)

| Species | Constancy | Score |
|---|---|---|
| Tortula ruraliformis | V | 7 (1-9) |
| Cerastium glomeratum | V | 3 (1-3) |
| Leontodon spp. | V | 2 (1-2) |
| Phleum arenarium | V | 2 (1-3) |
| Ononis repens | V | 4 (1-8) |
| Carex arenaria | V | 3 (1-4) |
| Hypochoeris radicata | V | 2 (1-3) |
| Rubus caesius | V | 4 (1-7) |
| Erophila verna | IV | 2 (1-3) |
| Vulpia fasciculata | IV | 3 (1-6) |
| Ammophila arenaria | IV | 2 (1-6) |
| Cerastium semidecandrum | IV | 1 (1-3) |
| Oenothera spp | IV | 2 (1-6) |
| Saxifraga tridactylites | IV | 2 (1-3) |
| Viola spp. | IV | 1 (1-3) |
| Senecio jacobaea | IV | 2 (1-4) |
| Brachythecium albicans | III | 1 (1-4) |
| Aira praecox | III | 2 (1-4) |
| Arabis hirsuta | III | 1 (1-4) |
| Arenaria serpyllifolia | III | 3 (1-4) |
| Polygala vulgaris | III | 1 (1-3) |
| Hornungia petraea | II | 3 (1-3) |
| Erodium cicutarium | II | 1 (1-3) |
| Ceratodon purpureus | II | 1 (1-4) |
| Desmazeria rigida | II | 1 (1-2) |
| Festuca rubra | II | 2 (1-8) |
| Myosotis arvensis | II | 1 (1-3) |
| Sedum acre | II | 1 (1-3) |
| Peltigera spp. | II | 2 (1-4) |
| Anthyllis vulneraria | II | 2 (1-4) |
| Bromus hordeaceus | II | 2 (1-4) |
| Geranium molle | II | 1 (1-2) |
| Luzula campestris | II | 1 (1-2) |
| Holcus lanatus | II | 1 (1-2) |
| Galium verum | II | 1 (1-3) |
| Euphorbia portlandica | II | 1 (1-2) |

TYPE 3

Number of quadrats 21

Mean number of species per quadrat 21 (SE = 1.661)

| Species | Constancy | Score |
|---|---|---|
| Tortula ruraliformis | V | 2 (1-8) |
| Cerastium glomeratum | V | 3 (1-3) |
| Ceratodon purpureus | V | 2 (1-5) |
| Viola spp. | V | 1 (1-2) |
| Cladonia fimbriata | V | 3 (1-8) |
| Carex arenaria | V | 2 (1-5) |
| Rubus caesius | V | 5 (1-7) |
| Leontodon spp. | IV | 2 (1-2) |
| Saxifraga tridactylites | IV | 2 (1-3) |
| Arenaria serpyllifolia | IV | 3 (1-3) |
| Chamaenerion angustifolium | IV | 2 (1-7) |
| Senecio jacobaea | IV | 2 (1-3) |
| Peltigera spp. | IV | 2 (1-5) |
| Erophila verna | III | 1 (1-2) |
| Cerastium semidecandrum | III | 2 (1-3) |
| Brachythecium albicans | III | 1 (1-5) |
| Aira praecox | III | 3 (2-3) |
| Arabis hirsuta | III | 1 (1-2) |
| Myosotis arvensis | III | 2 (1-3) |
| Ononis repens | III | 2 (1-6) |
| Cladonia rangiformis | III | 2 (1-2) |
| Geranium molle | III | 2 (1-3) |
| Polygala vulgaris | III | 1 (1-2) |
| Euphorbia portlandica | III | 1 |
| Hypnum cupressiforme | III | 2 (1-4) |
| Erodium cicutarium | II | 1 (1-2) |
| Oenothera spp. | II | 2 (1-4) |
| Phleum arenarium | II | 1 (1-3) |
| Centaurium erythraea | II | 1 |
| Festuca rubra | II | 2 (1-4) |
| Hypochoeris radicata | II | 1 (1-2) |
| Epilobium 'montanum' | II | 1 |
| Veronica chamaedrys | II | 1 |

TYPE 4

Number of quadrats 52

Mean number of species per quadrat 26.35 (SE = 0.849)

| Species | Constancy | Score |
|---|---|---|
| Festuca rubra | V | 7 (1-9) |
| Senecio jacobaea | V | 2 (1-4) |
| Hypochoeris radicata | V | 2 (1-4) |
| Rubus caesius | V | 5 (1-7) |
| Ononis repens | IV | 5 (1-8) |
| Holcus lanatus | IV | 1 (1-4) |
| Carex arenaria | IV | 2 (1-5) |
| Polygala vulgaris | IV | 2 (1-4) |
| Poa pratensis | IV | 2 (1-3) |
| Hypnum cupressiforme | IV | 3 (1-6) |
| Viola spp. | III | 2 (1-3) |
| Aira praecox | III | 2 (1-8) |
| Anthyllis vulneraria | III | 3 (1-5) |
| Centaurium erythraea | III | 1 (1-3) |
| Cerastium glomeratum | III | 2 (1-3) |
| Chamaenerion angustifolium | III | 2 (1-7) |
| Geranium molle | III | 1 (1-3) |
| Leontodon spp. | III | 1 (1-3) |
| Lotus corniculatus | III | 2 (1-6) |
| Cladonia fimbriata | III | 3 (1-6) |
| Peltigera spp. | III | 2 (1-2) |
| Rhinanthus minor | III | 2 (1-8) |
| Luzula campestris | III | 2 (1-4) |
| Taraxacum spp. | III | 1 (1-2) |
| Ammophila arenaria | II | 2 (1-5) |
| Arabis hirsuta | II | 2 (1-3) |
| Arenaria serpyllifolia | II | 1 (1-3) |
| Bromus hordeaceus | II | 3 (1-8) |
| Carlina vulgaris | II | 1 (1-2) |
| Desmazeria rigida | II | 1 (1-3) |
| Cerastium semidecandrum | II | 1 (1-3) |
| Erodium cicutarium | II | 1 (1-2) |
| Phleum arenarium | II | 2 (1-3) |
| Saxifraga tridactylites | II | 1 (1-2) |
| Sedum acre | II | 2 (1-4) |
| Brachythecium albicans | II | 1 (1-3) |
| Homalothecium lutescens | II | 2 (1-4) |
| Ceratodon purpureus | II | 2 (1-7) |
| Tortula ruraliformis | II | 2 (1-7) |
| Cladonia rangiformis | II | 1 (1-6) |
| Carex flacca | II | 1 (1-2) |
| Hieracium pilosella | II | 2 (1-4) |
| Plantago lanceolata | II | 2 (1-3) |
| Veronica officinalis | II | 2 (1-4) |
| Dicranum scoparium | II | 2 (1-5) |
| Ranunculus spp. | II | 2 (1-4) |
| Anacamptis pyramidalis | II | 1 (1-3) |
| Epilobium 'montanum' | II | 1 (1-2) |
| Veronica chamaedrys | II | 1 (1-3) |

TYPE 5

Number of quadrats 51

Mean species per quadrat 17.14 (SE = 0.82)

| Species | Constancy | Score |
|---|---|---|
| Senecio jacobaea | V | 3 (1-6) |
| Carex arenaria | V | 2 (1-7) |
| Arenaria serpyllifolia | IV | 2 (1-5) |
| Leontodon spp. | IV | 1 (1-3) |
| Sonchus spp. | IV | 1 (1-2) |
| Poa pratensis | IV | 2 (1-3) |
| Arabis hirsuta | III | 1 (1-3) |
| Chamaenerion angustifolium | III | 1 (1-4) |
| Myosotis arvensis | III | 1 (1-3) |
| Holcus lanatus | III | 1 (1-2) |
| Hypochoeris radicata | III | 1 (1-2) |
| Epilobium 'montanum' | III | 1 (1-3) |
| Taraxacum spp. | III | 1 (1-4) |
| Rubus caesius | III | 2 (1-6) |
| Viola spp. | II | 1 (1-3) |
| Aira praecox | II | 1 (1-2) |
| Anthyllis vulneraria | II | 1 (1-2) |
| Desmazeria rigida | II | 1 (1-3) |
| Cerastium semidecandrum | II | 1 (1-3) |
| Cirsium semidecandrum | II | 1 (1-2) |
| Oenothera spp. | II | 1 (1-2) |
| Phleum arenaria | II | 1 (1-3) |
| Saxifraga tridactylites | II | 1 (1-3) |
| Festuca rubra | II | 1 (1-9) |
| Ranunculus spp. | II | 1 (1-2) |
| Polygala vulgaris | II | 1 (1-2) |
| Veronica chamaedrys | II | 1 (1-2) |
| Euphorbia portlandica | II | 1 (1-2) |
| Hypnum cupressiforme | II | 2 (1-5) |
| Epipactis helleborine | II | 1 (1-2) |

TYPE 6

Number of Quadrats 34

Mean species per quadrat 6.62 (SE = 0.696)

| Species | Constancy | Score |
|---|---|---|
| Pinus nigra (c) | V | 8 (7-10) |
| Rubus caesius | IV | 5 (1-9) |
| Hypochoeris radicata | III | 1 |
| Taraxacum spp. | III | 1 (1-2) |
| Luzula campestris | II | 1 |
| Carex arenaria | II | 2 (1-7) |
| Anacamptis pyramidalis | II | 1 |
| Poa pratensis | II | 2 (2-4) |
| Euphorbia portlandica | II | 2 (1-3) |
| Hypnum cupressiforme | II | 1 (1-5) |
| Epipactis helleborine | II | 1 (1-2) |

TYPE 7

Number of quadrats 9

Mean species per quadrat 14.67 (SE = 1.18)

| Species | Constancy | Score |
|---|---|---|
| Rubus caesius | V | 5 (2-9) |
| Geranium robertianum | V | 2 (1-3) |
| Eurynchium praelongum | V | 4 (1-6) |
| Pinus nigra (c) | V | 8 (7-9) |
| Lophocolea spp. | V | 2 (1-4) |
| Epilobium 'montanum' | IV | 1 (1-2) |
| Hypnum cupressiforme | IV | 2 (1-4) |
| Rosa pimpinellifolia | IV | 2 (2-4) |
| Holcus lanatus | III | 1 (1-2) |
| Carex arenaria | III | 2 (1-8) |
| Poa pratensis | III | 2 (1-3) |
| Veronica chamaedrys | III | 1 (1-2) |
| Taraxacum spp. | III | 1 |
| Pinus nigra (s) | III | 1 |
| Hedera helix | III | 1 (1-2) |
| Pseudoscleropodium purum | III | 2 (1-6) |
| Crataegus monogyna | III | 1 |
| Viola spp. | II | 2 (1-2) |
| Chamaenerion angustifolium | II | 2 (2-4) |
| Polygala vulgaris | II | 1 |
| Euphorbia portlandica | II | 1 (1-2) |
| Dryopteris dilatata | II | 4 (1-4) |
| Fragaria vesca | II | 3 (2-8) |
| Brachythecium rutabulum | II | 1 |

TYPE 8

Number of quadrats 21

Mean species per quadrat 6.1 (SE = 0.58)

| Species | Constancy | Score |
|---|---|---|
| Pinus nigra (c) | V | 7 (4-9) |
| Hypnum cupressiforme | IV | 8 (4-10) |
| Brachythecium rutabulum | III | 4 (1-4) |
| Eurynchium praelongum | III | 6 (1-7) |
| Lophocolea spp. | III | 2 (1-2) |
| Viola spp. | II | 1 |
| Senecio jacobaea | II | 1 |
| Carex arenaria | II | 1 (1-4) |
| Euphorbia portlandica | II | 1 (1-2) |
| Epipactis helleborine | II | 1 |
| Pseudoscleropodium purum | II | 4 (1-4) |

Figure 3.22 shows that TWINSPAN has not separated the quadrats from the unplanted dunes into a group of their own. They are distributed between groups 1, 2 and 4, together with quadrats from clear-felled sites, and do not form a majority in any of them. This shows that some of the clear-felled quadrats at Whiteford have a flora which is very similar to the unplanted dune vegetation (see plate 15). Sites felled for 17 years are found only in groups 2 and 4.

Vegetation types 1 and 2 are made up almost exclusively from quadrats from unshaded sites, the majority being from sites felled 4-8 years ago (figure 3.22). Quadrats in type 1 were mostly from plantations F and G, nearest to the sea (pers.obs.). The vegetation is low growing, and has a very high proportion of annual species including:

| | |
|---|---|
| Aira caryophyllea | Aira praecox |
| Anagallis arvensis | Arenaria serpyllifolia |
| Cerastium glomeratum | Cerastium semidecandrum |
| Desmazeria rigida | Erodium cicutarium |
| Erophila verna | Geranium molle |
| Hornungia petraea | Myosotis arvensis |
| Phleum arenarium | Poa annua |
| Saxifraga tridactylites | Vulpia fasciculata |

The annual species are favoured by a high percentage of bare sand (figure 3.25; Pemadasa & Lovell, 1974). This may be particularly high in plantations F and G because of sand blowing over the site from the mobile fore-dunes. The mean number of species per quadrat in group 1 is not as high as it is in the other groups with quadrats from unplanted dunes; this is possibly due to the mobility of the sand surface, and burial of some species by sand in this 'yellow-dune' community. A small blow-out (4 x 3 metres) formed in plantation G during the study period, demonstrating the fragility of the vegetation surface.

Vegetation type 2 has a very similar species composition to type 1 although there is often a dominance of Ononis repens, Rubus caesius and Tortula ruraliformis. Figure 2.8 shows that although vegetation type 2 has about the same percentage of bare sand as type 1, a higher proportion of its quadrats on are slopes of less than 5 degrees, which may help to explain the floristic differences between the groups.

Vegetation type 4 usually has a complete ground cover by plants (figure 3.24). The vegetation is dominated by Festuca rubra, Rubus caesius, Ononis repens, and Holcus lanatus, with a high number of species per quadrat (figure 3.27). Many quadrats from the young plantations felled 17 years ago now support this species-rich dune grassland.

Vegetation types 3 and 5 are entirely made up from quadrats from clear-felled sites (figure 3.22). Type 3 is found mostly on sites felled 4 to 8 years ago, especially in the clearings within plantations K and I, while type 5 contains most of the quadrats recorded 1 to 2 years after felling in plantation K (figure 3.1). The organic soil is deeper in the more recently felled sites than those felled 4 to 8 years ago (figure 3.26).

Vegetation type 3 has a short vegetation (figure 3.23) often dominated by crust-forming mosses and lichens incuding Tortula ruraliformis, Ceratodon purpureus, Hypnum cupressiforme, Brachythecium albicans, Cladonia fimbriata,

C. pyxidata, C. rangiformis and Peltigera species. The higher plants include perennials such as Carex arenaria, Rubus caesius and Euphorbia portlandica which have survived below the tree canopy and now continue to grow in the open conditions. Many annual species are present, often in large numbers; this again is probably a consequence of the open vegetation structure with plenty of bare sand (figure 3.25). The reason for the lack of vigorously growing higher plants may be nutrient immobilisation (see section 2.4.2), the tallest plant of these clearings is Chamaenerion angustifolium, which is known to be well adapted to coping with such conditions (Van Andel, 1975). Shade may also be important in explaining why this community is different from the other clear-felled sites; many of the quadrats were still shaded by the trees around the clearings (figure 3.22), which may favour the growth of mosses and lichens.

Vegetation type 5 includes almost all of the quadrats from the most recent felling sites. The plants of this community are often tall, but sparsely distributed, with a high percentage of the ground still covered by bare needle litter (plates 11 and 12); this means that the mean vegetation height recorded for each quadrat (figure 3.23) does not reflect that this community actually contained plants up to 80cm tall. The most frequent species in this community are Senecio jacobaea and Carex arenaria, both of which occur in the woodlands. There may be an unusually high frequency of these species, together with Rubus caesius, in this community because the sites felled in 1988 were at the edge of the plantation, where these are more common (see vegetation type 6). Following clear-felling the increased levels of light and available nutrients (chapter 2) with less competition should enable some of the already established species to grow rapidly. Some specimens of Euphorbia portlandica grew very vigorously to about 40cm tall in the first summer after felling, while those in the adjacent unplanted dunes were mostly 20 to 30cm.

Most of the plants present in vegetation type 5 had grown from seed after the trees had been felled. Plates 10 and 11 show the development of vegetation in a marked quadrat in plantation K. There was no ground flora in 1988, but in August, 1989, 8 months after the trees had been felled, Senecio jacobaea, Sonchus oleraceus, Chamaenerion angustifolium, Arabis hiruta and Myosotis arvensis are visible. These ruderal species are mostly members of the Compositae, or other plants with light, wind-blown seeds.

The only other community which includes quadrats from 1 and 2 years after felling is vegetation type 2. These quadrats, although from the same site, felled at the same time, had their needle litter removed to expose the sand beneath and allow buried seeds to germinate (compare plates 12 and 13). This experiment is described more fully in section 3.6.

Vegetation types 6, 7 and 8 include almost all of the quadrats from the plantations (figure 3.22). Unlike the woodlands at Ainsdale the younger and more heavily thinned plantations at Whiteford still have several typical dune species persisting below the trees, including:

| | |
|---|---|
| Anacamptis pyramidalis | Carex arenaria |
| Carlina vulgaris | Centaurium erythraea |

Cerastium semidecandrum
Dactylorhiza majalis
Euphorbia portlandica
Hypnum cupressiforme
Listera ovata
Viola canina
Clematis vitalba
Epipactis helleborine
Galium verum
Iris foetidissima
Polygala vulgaris
Viola riviniana

Vegetation type 6 is usually seen immediately within the plantation edges, and where more light penetrates the canopy of the 24-32 year old-woodlands (pers.obs., figure 3.22). The most frequent species are Rubus caesius which has a constancy value of IV, and Hypochoeris radicata and Taraxacum spp. with a constancy value of III. R.caesius and Carex arenaria are abundant in some quadrats.

Vegetation type 7 is a more typical woodland community, also characterised by R.caesius in the ground flora, but associated with Geranium robertianum, Rosa pimpinellifolia, and the bryophytes Eurynchium praelongum, Lophocolea cuspidata and Hypnum cupressiforme. This community was only found in the older woodlands near to Whiteford Lodge (figures 1.3 and 3.22). Several woodland plant species are found here, including:

Brachypodium sylvaticum
Clematis vitalba
Dicranella heteromalla
Dryopteris dilatata
Eurynchium praelongum
Glechoma hederacea
Ilex aquifolium
Phyllitis scolopendrium
Prunus spinosa
Rubus fruticosus
Solanum dulcamara
Urtica dioica
Brachythecium rutabulum
Crataegus monogyna
Dryopteris borreri
Dryopteris filix-mas
Geranium robertianum
Hedera helix
Ligustrum vulgare
Polytrichum formosum
Quercus petraea
Silene dioica
Tamus communis

Vegetation type 8 is probably the most widespread through the 24-32 year old plantations (plate 10). It is found where the canopy does not let through much light and there is an undisturbed layer of litter. Hypnum cupressiforme is the most abundant plant, often forming a mat over fallen pine needles. Higher plants are sparsely distributed, none have a constancy value of more than II.

The findings from the study of vegetation communities at Whiteford and the other two sites are discussed further in section 3.6.

### 3.3.4 Results: Tentsmuir

The results of the DECORANA analysis are presented in figures 3.29 to 3.32. TWINSPAN vegetation types are described in table 3.12, with percentage frequency diagrams comparing measured site variables between the groups in figures 3.33 to 3.39.

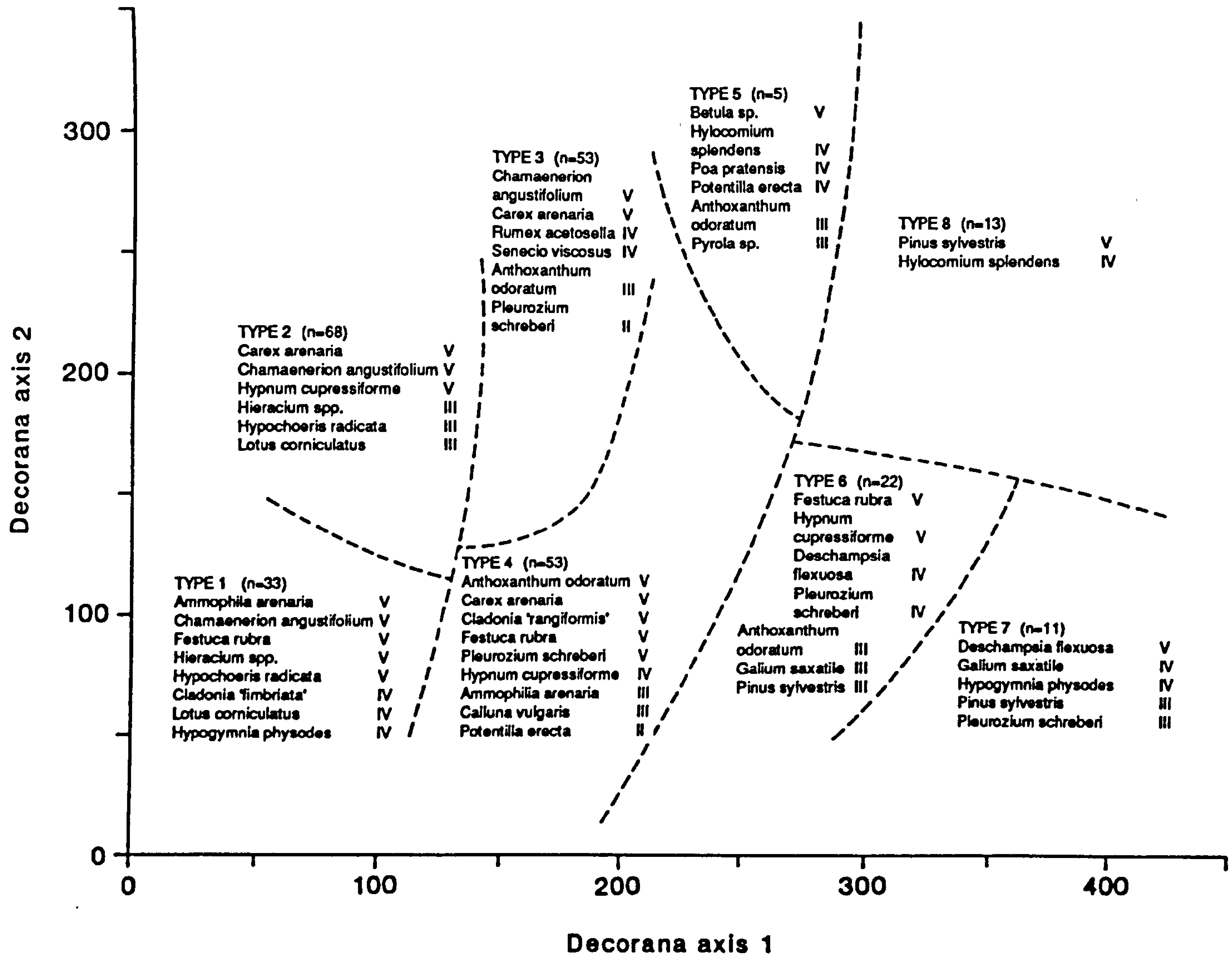
Legends for figures 3.29 to 3.32. DECORANA analysis for quadrat data from Tentsmuir.

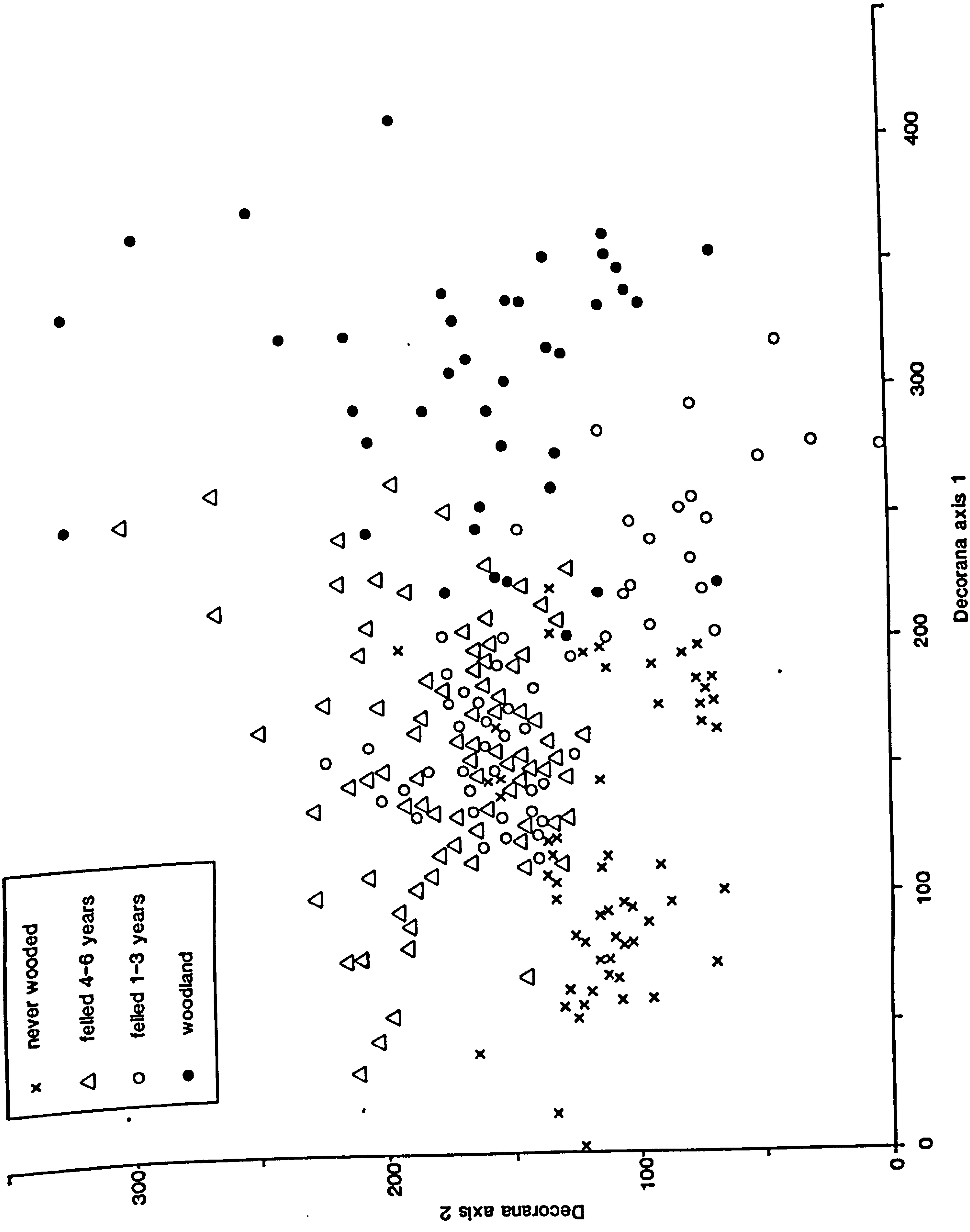
Figure 3.29. (page 148). TWINSPAN summary diagram. Positions of boundaries are approximate.

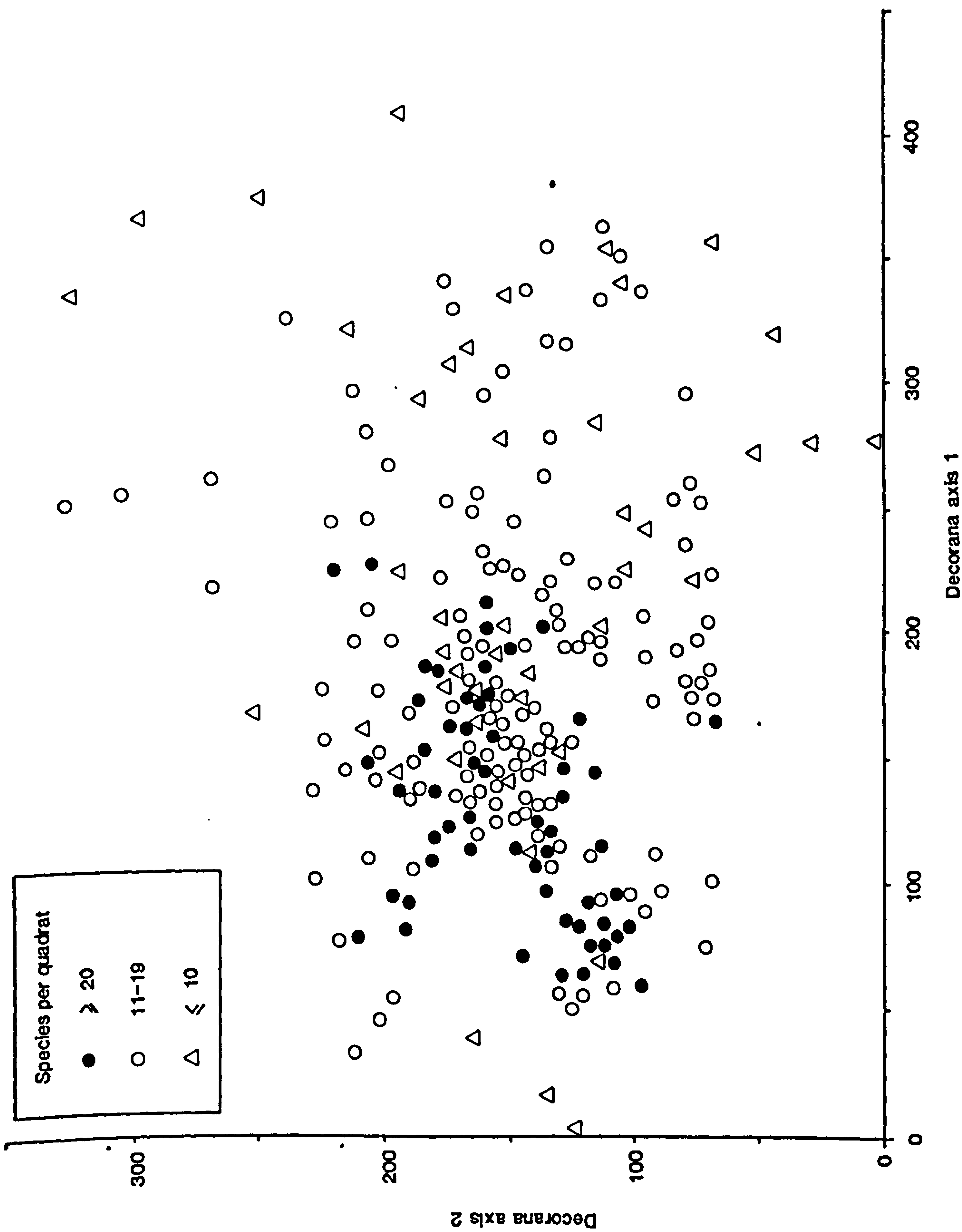
Figure 3.30. (page 149). Time after felling.

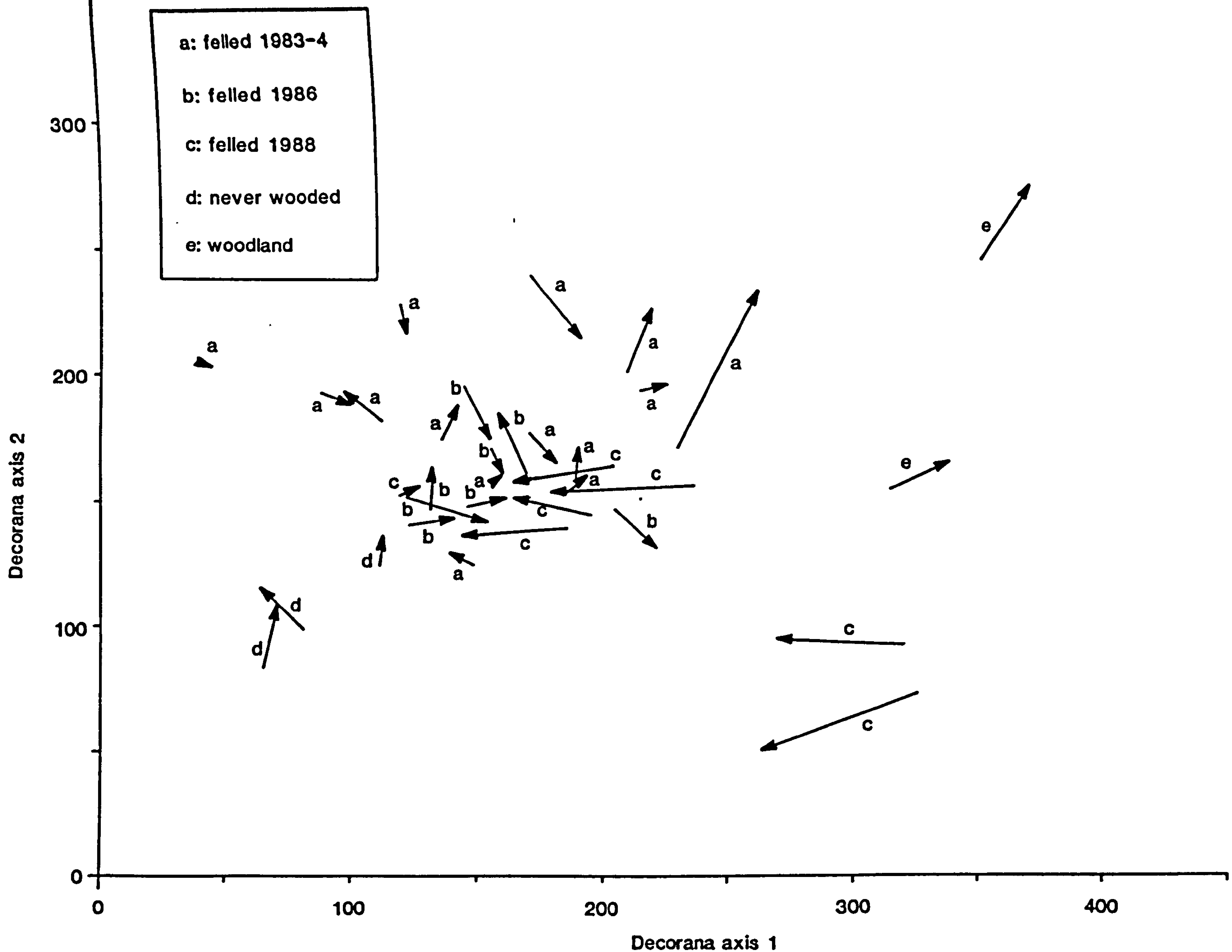
Figure 3.31. (page 150). Numbers of species per quadrat.

Figure 3.32. (page 151). Changes in the positions of permanent quadrats at Tentsmuir between 1988 and 1990. See text for explanation.


TYPE 1 (n=33)
Ammophila arenaria V
Chamaenerion angustifolium V
Festuca rubra V
Hieracium spp. V
Hypochoeris radicata V
Cladonia 'fimbriata' IV
Lotus corniculatus IV
Hypogymnia physodes IV
TYPE 2 (n=68)
Carex arenaria V
Chamaenerion angustifolium V
Hypnum cupressiforme V
Hieracium spp. III
Hypochoeris radicata III
Lotus corniculatus III
TYPE 3 (n=53)
Chamaenerion angustifolium V
Carex arenaria V
Rumex acetosella IV
Senecio viscosus IV
Anthoxanthum odoratum III
Pleurozium schreberi II
TYPE 4 (n=53)
Anthoxanthum odoratum V
Carex arenaria V
Cladonia 'rangiformis' V
Festuca rubra V
Pleurozium schreberi V
Hypnum cupressiforme IV
Ammophilia arenaria III
Calluna vulgaris III
Potentilla erecta II
TYPE 5 (n=5)
Betula sp. V
Hylocomium splendens IV
Poa pratensis IV
Potentilla erecta IV
Anthoxanthum odoratum III
Pyrola sp. III
TYPE 6 (n=22)
Festuca rubra V
Hypnum cupressiforme V
Deschampsia flexuosa IV
Pleurozium schreberi IV
Anthoxanthum odoratum III
Galium saxatile III
Pinus sylvestris III
TYPE 7 (n=11)
Deschampsia flexuosa V
Galium saxatile IV
Hypogymnia physodes IV
Pinus sylvestris III
Pleurozium schreberi III
TYPE 8 (n=13)
Pinus sylvestris V
Hylocomium splendens IV
Decorana axis 2
Decorana axis 1
0
100
200
300
400


never wooded
felled 4-6 years
felled 1-3 years
woodland
Decorana axis 1
0
100
200
300
400
Decorana axis 2
0
100
200
300


Species per quadrat
≥ 20
11–19
≤ 10
Decorana axis 1
Decorana axis 2
0
100
200
300
400
0
100
200
300



a: felled 1983-4
b: felled 1986
c: felled 1988
d: never wooded
e: woodland
Decorana axis 2
Decorana axis 1
0
100
200
300
400

The DECORANA analysis for Tentsmuir does not show such clear differences between woodland and unplanted dunes as do the other two study sites (figure 3.31; compare figures 3.6 and 3.18). This is probably because the woodland is made up of recently self-sown pine and birch, which have seeded into the unplanted dunes. This has resulted in an incomplete canopy, with patches of open vegetation, and areas only partially shaded by the trees (see plates 4 and 5).

The divisions shown on the TWINSPAN summary diagram for Tentsmuir (figure 3.29) are more diagonal in relation to axes 1 and 2 than at the other sites (compare figures 3.4 and 3.16) which were more parallel with the axes. This suggests that there is either more interaction between the factors explaining axes 1 and 2, or another factor which is influencing both. The apparent distortion of the axes may be partly explained by the relatively flat topography of the site, caused by the rapid growth of the system (compare figure 3.39 with figure 3.15 for Ainsdale and figure 3.28 for Whiteford). The relief is largely due to embryo dunes, with little distinction between slacks and dune ridges. Although sampling in sites which were obviously slacks was avoided the quadrat data from Tentsmuir was inevitably influenced by the water-table more than at the other sites.

The DECORANA axes are compared with several recorded variables in table 3.11. Although woodland age could not be measured at this site, axis 1 appears to be related to tree cover (figure 3.30). There is a significant positive correlation with organic soil depth and the number of moss

Table 3.11. Tentsmuir: Linear regression statistics for DECORANA axes 1 and 2, with recorded variables. Percentage data have been arcsine transformed.
** = p<0.005, * = p<0.05, NS = not significant.

| Variable | AXIS 1 | | | | AXIS 2 | | | |
|---|---|---|---|---|---|---|---|---|
| | t | $R^2$ | df | p | t | $R^2$ | df | p |
| Years felled | -2.8 | .032 | 238 | * | 6.8 | .162 | 238 | ** |
| organic soil depth | 11.3 | .393 | 199 | ** | 4.3 | .086 | 199 | ** |
| Percent cover | -3.3 | .045 | 234 | ** | -1.9 | .014 | 234 | NS |
| Percent sand | -5.7 | .123 | 234 | ** | 0.5 | .001 | 234 | NS |
| Height | -2.1 | .018 | 238 | * | 0.9 | .003 | 238 | ** |
| Total species | -7.5 | .190 | 238 | ** | 0.8 | .003 | 238 | NS |
| Total mosses | 6.7 | .158 | 238 | ** | 2.4 | .023 | 238 | * |
| Total lichens | -7.9 | .208 | 238 | ** | -3.7 | .054 | 238 | ** |
| Slope | -2.6 | .028 | 238 | * | -5.7 | .121 | 238 | ** |

species, while percentage cover by vegetation and by bare sand, and the mean number of species per quadrat (figure 3.31) are negatively correlated. Quadrats from clear-felled sites do not occupy an intermediate position between the open-dune and woodland communities as seen at the other sites (figure 3.30). The quadrats appear to be positioned along axis 1 according to the age of the dunes on which they were recorded. Quadrats from the youngest dunes have the lowest scores, while the natural dune heath community, although never wooded, has a higher score than many of the clear-felled sites.

DECORANA axis 2 is also positively correlated with the organic soil depth, but the greatest $R^2$ value for an environmental variable was for slope, which has a negative correlation with axis 2. This means that quadrats scoring highly on axis 2 will tend to be from flatter and possibly wetter ground. The position of the Betula woodland, which is often associated with slacks, highest on axis 2 (figure 3.29), appears to support this. Axis 2 may also be affected by tree-felling and time since disturbance, as at the other two sites; these may have interactive effects with soil moisture. The majority of quadrats from clear-felled sites have higher scores for axis 2 than dunes of the same age which have never supported trees, but they are not all from flatter or wetter sites.

Several quadrats from sites felled between 1 and 3 years ago are not very different from the woodland quadrats on DECORANA axis 1 but have very low scores on axis 2. This may be because the species present in these quadrats are remnants of the original dune flora which have survived below the trees, while the common woodland mosses such as Plagiothecium undulatum and Rhytidiadelphus triquetrus have died. A large weed flora has not developed as quickly in these sites as at Whiteford and Ainsdale; this may be because the loose needle litter was raked up and burned (see section 3.6). Quadrats from sites felled between 4 and 6 years ago are very variable, some are very similar to the unplanted dunes, others more similar to the woodland. This appears to relate to the density of the trees before felling (pers.obs.).

Permanent quadrats at Tentsmuir (shown in figure 1.4) were studied between 1988 and 1990 (as already described at Whiteford). The results of the study are shown in figure 3.32. Two main trends are apparent; almost all of the quadrats from sites felled in 1983, 1984 and 1986 have a higher score along axis 1 in 1990, while all of the quadrats from the 1988 felling site have a lower score. Unlike the study at Whiteford very few of the quadrats show a change towards the unplanted dune communities; instead, the long term change appears to be back to woodland. The change in the two woodland quadrats is also further along axes 1 and 2, suggesting that the woodland flora at those sites is still developing.

The TWINSPAN analysis for Tentsmuir identified 8 vegetation types. All but three contained over 20 quadrats; however, the smallest group, a birch scrub community, contained only 5. The first TWINSPAN division broadly separates out the quadrats from pine woodland and the most recently felled sites; the second separates the quadrats from the youngest dunes from those of the older dunes.

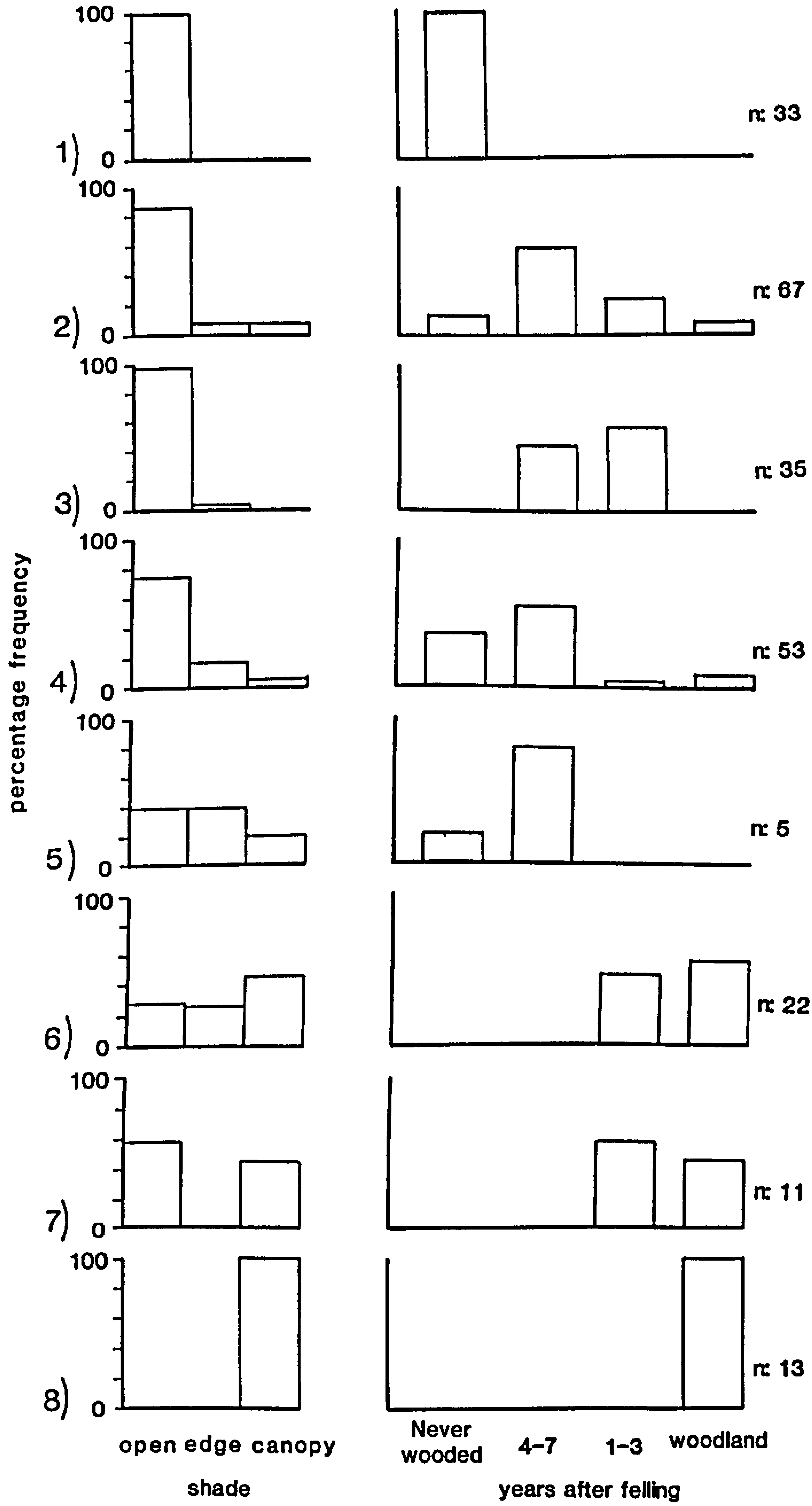



Figure 3.33 Time after felling and woodland shade. Percentage frequencies for TWINSPAN vegetation types 1-8 at Tentsmuir. n= number of quadrats.

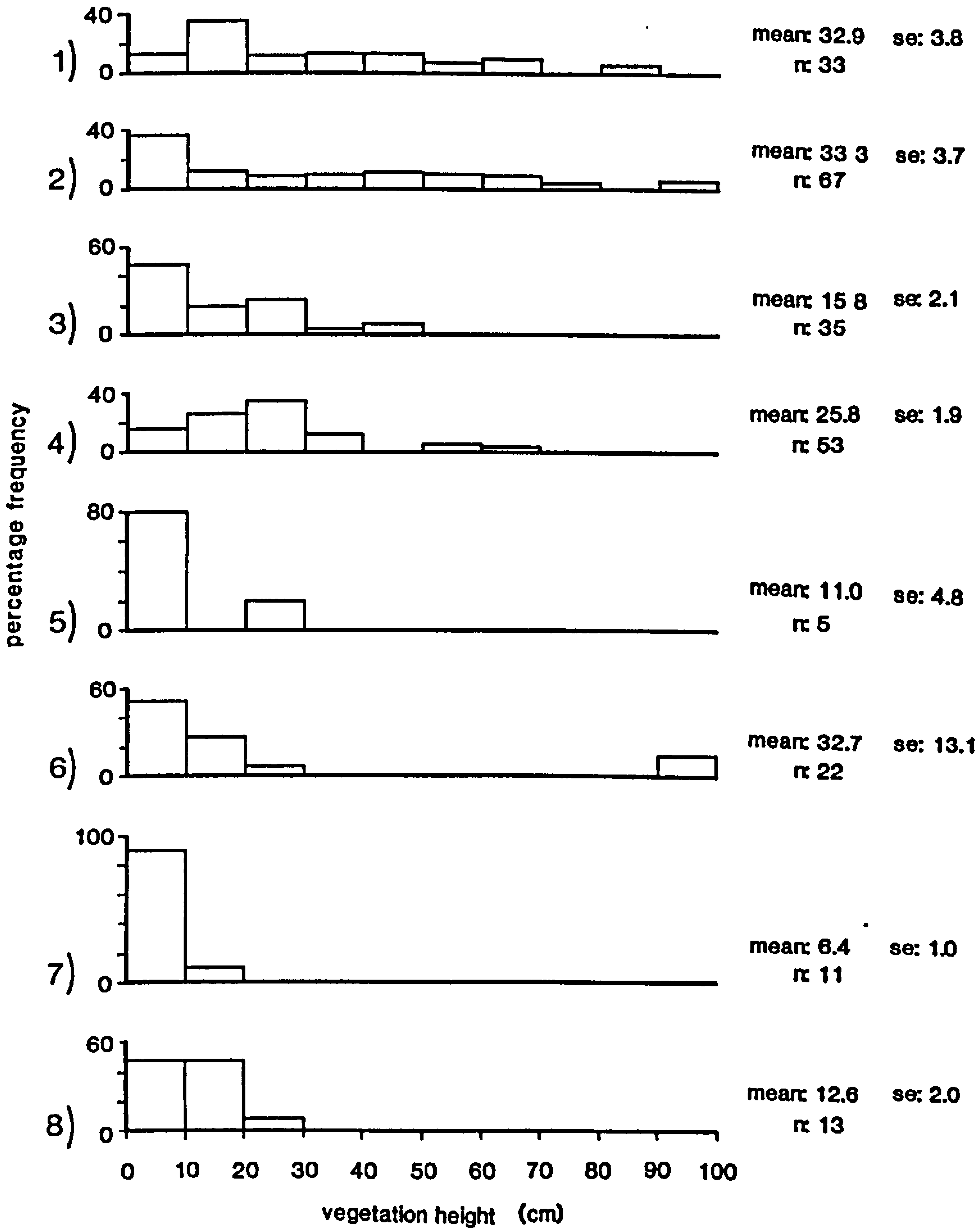



Figure 3.34 Vegetation height. Percentage frequencies for TWINSPAN vegetation types 1-8 at Tentsmuir. n= number of quadrats. se= standard error.

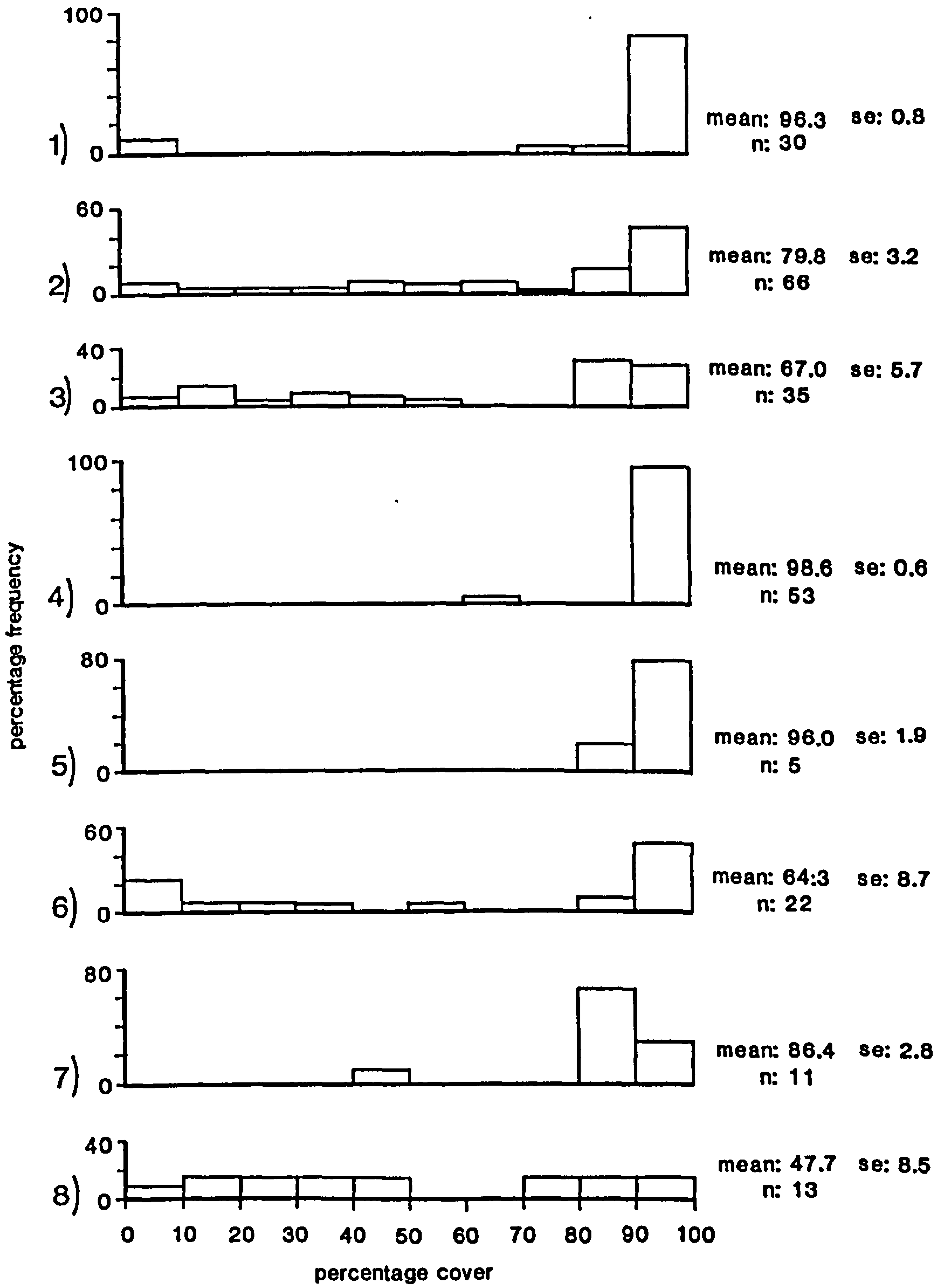



Figure 3.35 Percentage cover. Percentage frequencies for TWINSPAN vegetation types 1-8 at Tentsmuir. n= number of quadrats. se= standard error.

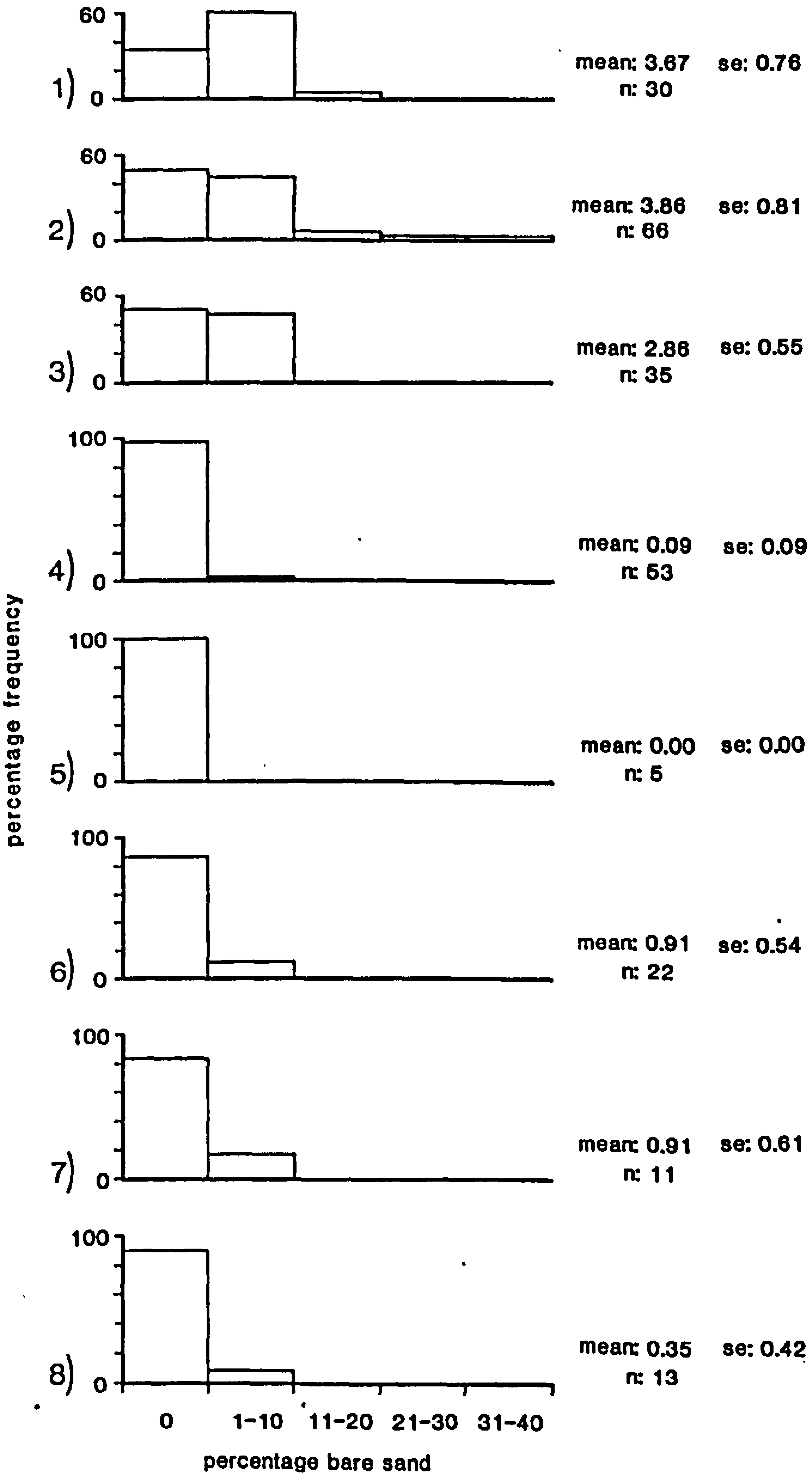



Figure 3.36 Percentage bare sand. Percentage frequencies for TWINSPAN vegetation types 1-8 at Tentsmuir. n= number of quadrats. se= standard error.

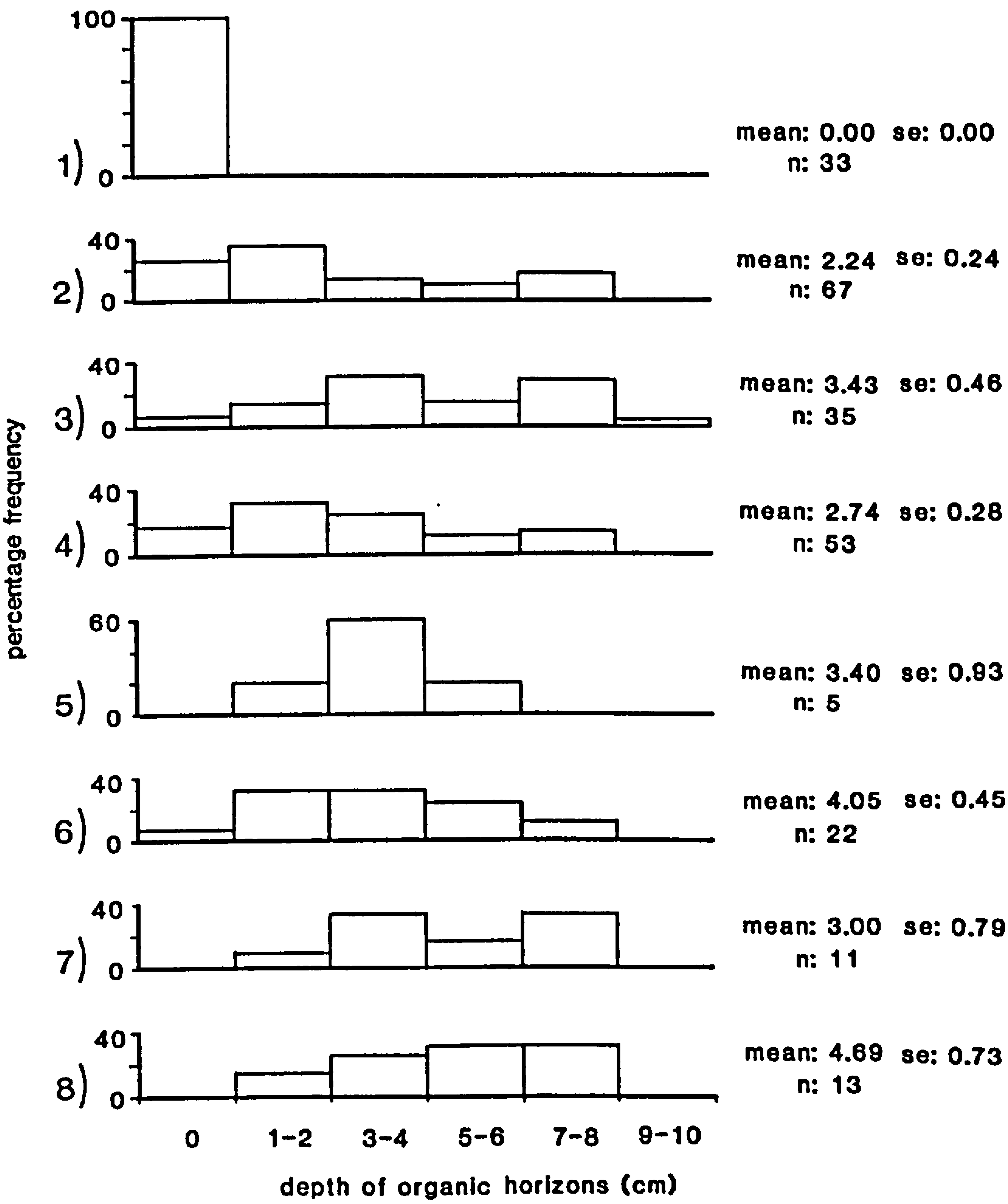



Figure 3.37 Depth of pine needle material. Percentage frequencies for TWINSPAN vegetation types 1-8 at Tentsmuir. n= number of quadrats. se= standard error.

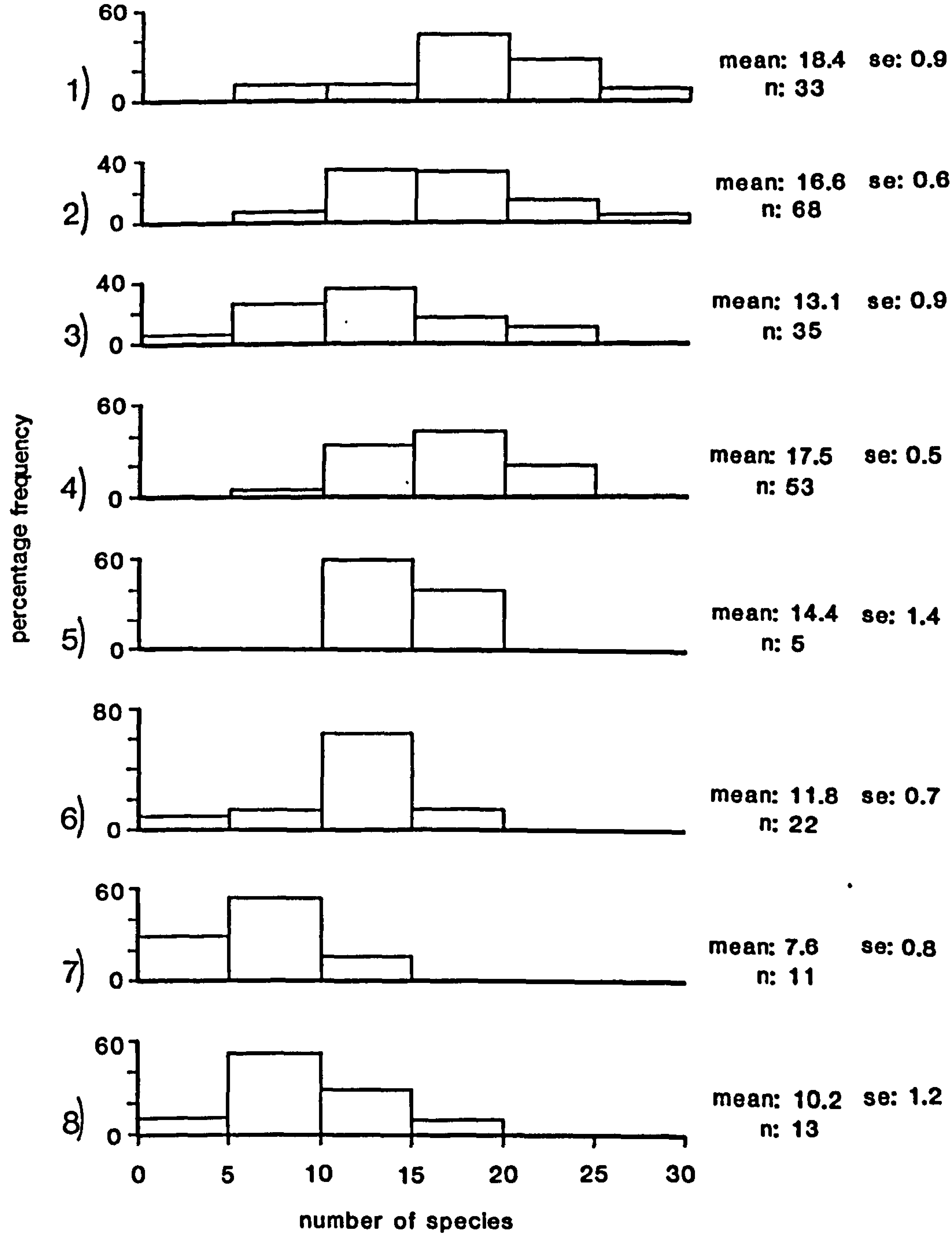



Figure 3.38 Number of species per quadrat. Percentage frequencies for TWINSPAN vegetation types 1-8 at Tentsmuir. n= number of quadrats. se= standard error.

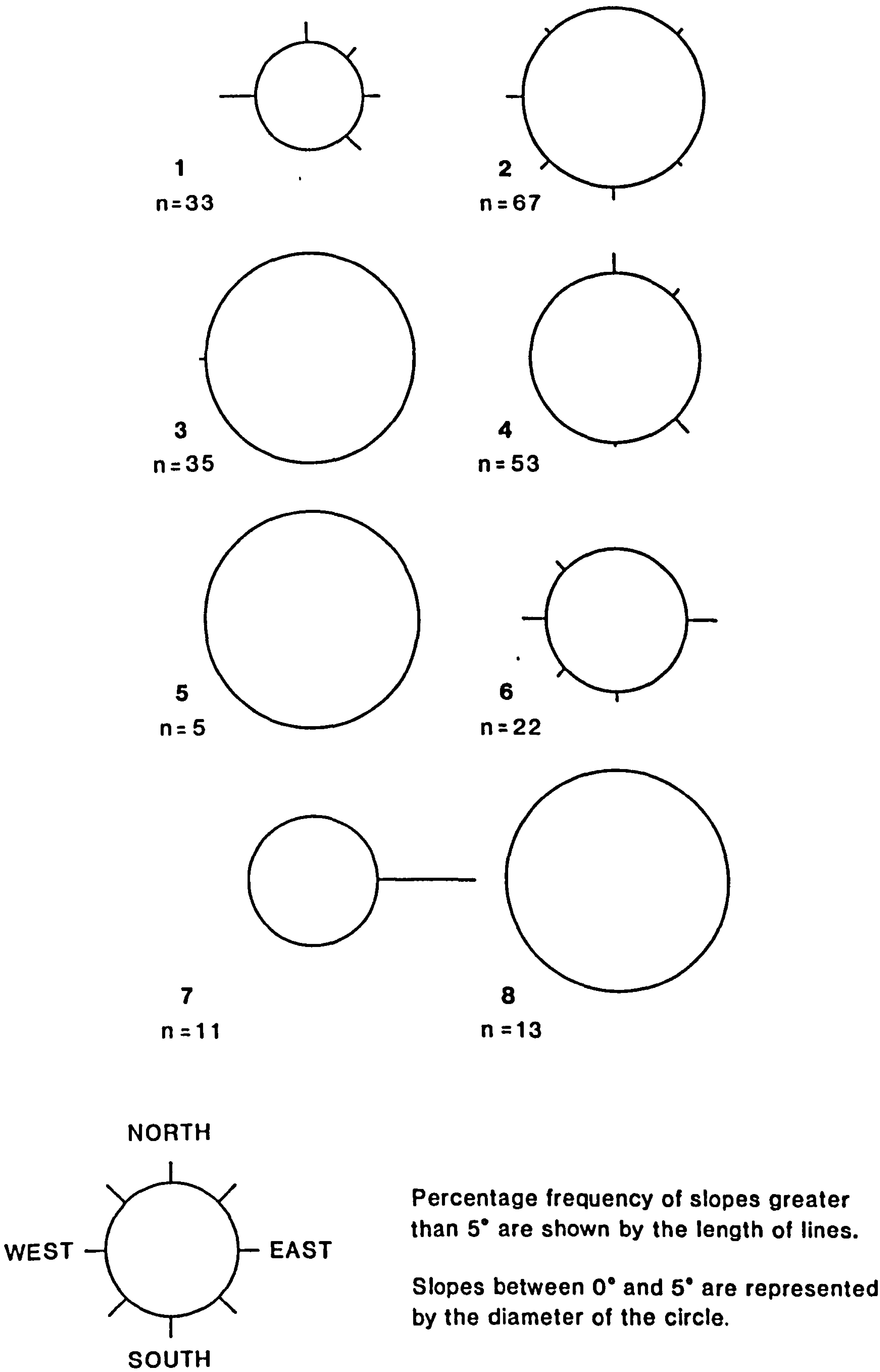



Figure 3.39 Slope and aspect. Percentage frequencies for TWINSPAN vegetation types 1-8 at Tentsmuir. n= number of quadrats.

Table 3.12 TWINSPAN vegetation types studied at Tentsmuir. Communities are as defined by TWINSPAN. For each community the species are grouped into frequency classes. Species with a constancy value of I are not shown. Species order within the frequency classes is determined by the TWINSPAN program.
DOMIN scores are summarised, giving the median value for each species, followed by the range of recorded values in brackets.

TYPE 1

Number of quadrats 33

Mean species per quadrat 18.39 (SE = 0.87)

| Species | Frequency | Score |
|---|---|---|
| Ammophila arenaria | V | 4 (1-8) |
| Chamaenerion angustifolium | V | 3 (1-6) |
| Hieracium spp. | V | 2 (1-3) |
| Hypochoeris radicata | V | 1 (1-4) |
| Hieracium pilosella | V | 2 (1-5) |
| Festuca rubra | V | 4 (1-8) |
| | | |
| Aira praecox | IV | 2 (1-3) |
| Lotus corniculatus | IV | 2 (1-4) |
| Cladonia 'fimbriata' | IV | 2 (1-3) |
| Rumex acetosella | IV | 2 (1-3) |
| Cladonia 'rangiformis' | IV | 4 (1-8) |
| Carex arenaria | IV | 3 (1-4) |
| Hypogymnia physodes | IV | 3 (1-6) |
| Luzula campestris | IV | 2 (1-2) |
| Dicranum scoparium | IV | 2 (1-6) |
| | | |
| Cerastium fontanum | III | 1 (1-3) |
| Leontodon spp. | III | 1 (1-3) |
| Poa pratensis | III | 2 (1-4) |
| Brachythecium albicans | III | 2 (1-4) |
| Ceratodon purpureus | III | 2 (1-5) |
| Taraxacum spp. | III | 1 (1-3) |
| | | |
| Cerastium glomeratum | II | 2 (1-3) |
| Senecio jacobaea | II | 1 (1-2) |
| Tortula ruraliformis | II | 2 (1-5) |
| Cornicularia aculeata | II | 3 (1-7) |
| Cladonia 'squamules' | II | 1 (1-6) |
| Filago vulgaris | II | 2 (1-3) |
| Peltigera spp. | II | 1 (1-2) |
| Vicia spp. | II | 1 (1-2) |
| Hypnum cupressiforme | II | 2 (1-5) |

TYPE 2

Number of quadrats 68

Mean species per quadrat 16.56 (SE = 0.596)

| Species | Frequency | Score |
|---|---|---|
| Chamaenerion angustifolium | V | 5 (1-8) |
| Carex arenaria | V | 3 (1-9) |
| Dicranum scoparium | V | 3 (1-9) |
| Hypnum cupressiforme | V | 3 (1-7) |
| Rumex acetosella | IV | 2 (1-8) |
| Festuca rubra | IV | 2 (1-8) |
| Luzula campestris | IV | 2 (1-3) |
| Aira praecox | III | 2 (1-3) |
| Hypochoeris radicata | III | 2 (1-3) |
| Lotus corniculatus | III | 2 (1-4) |
| Hieracium pilosella | III | 2 (1-4) |
| Senecio jacobaea | III | 1 (1-4) |
| Cladonia 'rangiformis' | III | 2 (1-9) |
| Ammophila arenaria | II | 1 (1-4) |
| Cerastium fontanum | II | 1 (1-3) |
| Poa pratensis | II | 2 (1-6) |
| Ceratodon purpureus | II | 2 (1-8) |
| Cladonia 'fimbriata' | II | 2 (1-3) |
| Taraxacum spp. | II | 1 (1-2) |
| Viola spp. | II | 1 (1-2) |
| Holcus lanatus | II | 2 (1-8) |
| Polytrichum spp. | II | 2 (1-4) |
| Senecio viscosus | II | 2 (1-3) |
| Veronica officinalis | II | 2 (1-4) |
| Hypogymnia physodes | II | 1 (1-3) |
| Vicia spp. | II | 1 (1-2) |
| Betula sp. | II | 2 (1-5) |
| Anthoxanthum odoratum | II | 2 (1-4) |

TYPE 3

Number of quadrats 35

Mean species per quadrat 13.11 (SE = 0.885)

| Species | Frequency | Score |
|---|---|---|
| Chamaenerion angustifolium | V | 2 (1-6) |
| Carex arenaria | V | 3 (1-9) |
| Dicranum scoparium | V | 3 (1-9) |
| Hypnum cupressiforme | V | 2 (1-5) |
| Rumex acetosella | IV | 3 (1-8) |
| Festuca rubra | IV | 1 (1-6) |
| Senecio viscosus | IV | 1 (1-7) |
| Cladonia 'rangiformis' | III | 1 (1-7) |
| Hypogymnia physodes | III | 2 (1-3) |
| Betula sp. | III | 2 (1-6) |
| Luzula campestris | III | 2 (1-4) |
| Anthoxanthum odoratum | III | 2 (1-8) |
| Cladonia 'fimbriata' | II | 1 (1-2) |
| Erica tetralix | II | 2 (1-6) |
| Agrostis capillaris | II | 2 (1-8) |
| Holcus lanatus | II | 1 (1-8) |
| Polytrichum spp. | II | 2 (1-3) |
| Galium saxatile | II | 2 (1-3) |
| Pleurozium schreberi | II | 2 (1-5) |

TYPE 4

Number of quadrats 53

Mean species per quadrat 17.49 (SE = 0.537)

| Species | Frequency | Score |
|---|---|---|
| Cladonia 'rangiformis' | V | 4 (1-9) |
| Carex arenaria | V | 3 (1-8) |
| Festuca rubra | V | 4 (1-9) |
| Anthoxanthum odoratum | V | 2 (1-8) |
| Pleurozium schreberi | V | 4 (1-8) |
| | | |
| Dicranum scoparium | IV | 2 (1-7) |
| Hypnum cupressiforme | IV | 2 (1-6) |
| | | |
| Ammophila arenaria | III | 2 (1-3) |
| Chamaenerion angustifolium | III | 2 (1-6) |
| Calluna vulgaris | III | 4 (1-9) |
| Erica tetralix | III | 2 (1-7) |
| Polytrichum sp. | III | 2 (1-4) |
| Veronica officinalis | III | 1 (1-5) |
| Betula sp. | III | 3 (1-8) |
| Galium saxatile | III | 2 (1-4) |
| | | |
| Hieracium pilosella | II | 2 (1-5) |
| Rumex acetosella | II | 2 (1-6) |
| Thymus praecox | II | 2 (1-3) |
| Cladonia 'fimbriata' | II | 1 (1-3) |
| Hypochoeris radicata | II | 1 |
| Viola spp. | II | 1 (1-2) |
| Agrostis stolonifera | II | 2 (1-7) |
| Potentilla erecta | II | 2 (1-4) |
| Agrostis capillaris | II | 1 (1-7) |
| Holcus lanatus | II | 1 (1-5) |
| Salix repens | II | 2 (1-6) |
| Hypogymnia physodes | II | 2 (1-4) |
| Ptilidium ciliare | II | 1 (1-2) |
| Hylocomium splendens | II | 2 (1-5) |
| Rhytidiadelphus triquetrus | II | 1 (1-2) |

TYPE 5

Number of quadrats 5

Mean species per quadrat 14.40 (SE = 1.435)

| Species | Frequency | Score |
|---|---|---|
| Betula sp. | V | 4 (3-9) |
| | | |
| Poa pratensis | IV | 2 (1-2) |
| Potentilla erecta | IV | 1 (1-2) |
| Carex arenaria | IV | 2 (2-3) |
| Hylocomium splendens | IV | 4 (3-8) |
| | | |
| Peltigera spp. | III | 3 (3-4) |
| Polytrichum spp. | III | 1 (1-2) |
| Anthoxanthum odoratum | III | 2 (1-2) |
| Pyrola sp. | III | 3 (1-6) |
| Pleurozium schreberi | III | 4 (1-5) |
| Dicranum scoparium | III | 2 (1-2) |
| Rhtyidiadelphus triquetrus | III | 7 (3-9) |
| | | |
| Agrostis stolonifera | II | 1 (1-3) |
| Calluna vulgaris | II | 1 |
| Erica tetralix | II | 1 (1-4) |
| Rhytidiadelphus squarrosus | II | 4 |
| Salix spp. | II | 1 |

TYPE 6

Number of quadrats 22

Mean species per quadrat 11.77 (SE = 0.671)

| Species | Frequency | Score |
|---|---|---|
| Festuca rubra | V | 1 (1-6) |
| Dicranum scoparium | V | 2 (1-4) |
| Hypnum cupressiforme | V | 2 (1-5) |
| | | |
| Carex arenaria | IV | 2 (1-4) |
| Pleurozium schreberi | IV | 6 (1-8) |
| Deschampsia flexuosa | IV | 2 (1-5) |
| | | |
| Luzula campestris | III | 1 (1-2) |
| Anthoxanthum odoratum | III | 1 (1-2) |
| Galium saxatile | III | 2 (1-3) |
| Pinus sylvestris (c) | III | 8 (1-10) |
| Pinus sylvestris (s) | III | 1 |
| | | |
| Cladonia 'rangiformis' | II | 4 (2-8) |
| Betula sp. | II | 1 |
| Goodyera repens | II | 1 (1-4) |
| Eurychium praelongum | II | 2 (1-2) |
| Hylocomium splendens | II | 1 (1-2) |
| Plagiothecium undulatum | II | 4 (1-6) |
| Rhytidiadelphus triquetrus | II | 1 (1-4) |

TYPE 7

Number of quadrats 11

Mean species per quadrat 7.64 (SE = 0.778)

| Species | Frequency | Score |
|---|---|---|
| Dicranum scoparium | V | 3 (1-4) |
| Deschampsia flexuosa | V | 6 (3-7) |
| Hypogymnia physodes | IV | 3 (2-3) |
| Galium saxatile | IV | 3 (1-4) |
| Carex arenaria | III | 2 (1-2) |
| Pleurozium schreberi | III | 4 (2-9) |
| Pinus sylvestris (c) | III | 9 (9-10) |
| Rhytidiadelphus triquetrus | III | 1 (1-2) |
| Festuca rubra | II | 2 (2-3) |
| Luzula campestris | II | 2 (2-3) |
| Hypnum cupressiforme | II | 2 (2-3) |
| Eurynchium praelongum | II | 3 (2-4) |
| Plagiothecium undulatum | II | 6 (1-8) |

TYPE 8

Number of quadrats 13

Mean species per quadrat 10.2 (SE = 1.195)

| Species | Frequency | Score |
|---|---|---|
| Pinus sylvestris (c) | V | 9 (4-10) |
| Carex arenaria | IV | 2 (1-6) |
| Hylocomium splendens | IV | 2 (1-4) |
| Deschampsia flexuosa | III | 2 (1-5) |
| Dicranum scoparium | III | 4 (2-4) |
| Eurynchium praelongum | III | 3 (1-6) |
| Rhytidiadelphus triquetrus | III | 5 (1-8) |
| Lophocolea spp. | III | 2 (1-2) |
| Chamaenerion angustifolium | II | 1 (1-2) |
| Betula sp. | II | 2 (1-8) |
| Goodyera repens | II | 2 (1-3) |
| Brachythecium rutabulum | II | 2 (1-4) |

Vegetation types 1 and 2 contain quadrats taken from unshaded sites (figure 3.33), most of which were from the youngest dunes. The floristic differences reflect that many quadrats from type 2 are on felled sites, while type 1 has remained free of trees. Vegetation type 1 tends to occur on the slightly steeper slopes of the youngest dune ridge (figure 3.39) and has an undeveloped soil profile with no recognisable organic horizons (figure 3.37). Type 2 occurs on cleared sites, mostly from the second dune ridge from the sea. This community has a deeper organic soil, but the disturbance from felling has resulted in more bare sand (figure 3.36) and a less complete vegetation cover (figure 3.35). Vegetation types 1 and 2 contain several species which were not found in any of the other communities, including: *Aira caryophyllea*, *Centaurium erythraea*, *Cerastium glomeratum*, *Cornicularia aculeata*, *Filago vulgaris*, *Homalothecium lutescens*, *Sagina procumbens*, *Tortula ruraliformis* and *Usnea subfloridana*.

Constant species in vegetation type 1 include *Ammophila arenaria*, *Chamaenerion angustifolium*, *Festuca rubra*, *Hieracium pilosella* and *Hypochoeris radicata*. *C.angustifolium* was not common in the unplanted dunes at Ainsdale or Whiteford, but is found throughout the dunes at Tentsmuir. Vegetation type 1 appears to be a mixture of an *Ammophila arenaria* - *Festuca rubra* semi-fixed dune community (*Senecio jacobaea* sub-community) on the steeper slopes and a *Carex arenaria* - *Cornicularia aculeata* community (Malloch, 1989) forming lichen-rich areas on flatter, dry ground. A further TWINSPAN division may have separated these.

Vegetation type 2 is dominated by Chamaenerion angustifolium and Carex arenaria, usually with the mosses Dicranum scoparium and Hypnum cupressiforme. Ammophila arenaria only reaches a constancy value of II, and there is some colonisation by Betula. However, the vegetation composition is otherwise similar to type 1.

Vegetation type 3 (plate 6) is made up entirely by quadrats from felled sites. Like type 2 the constant species are Chamaenerion angustifolium, Carex arenaria, Dicranum scoparium and Hypnum cupressiforme; however, the vegetation is shorter (figure 3.34) and more sparse (figure 3.35), with more bare litter still uncolonised. Rumex acetosella and Senecio viscosus are used by TWINSPAN as indicator species for type 3 (figure 3.29). S.viscosus is common at all the clear-felled sites at Tentsmuir but does not persist in large numbers for more than 2 or 3 years after felling (P.Kinnear, pers.comm.). Several species usually found in dune heath occur in this community, usually as seedlings or very small plants; these include: Calluna vulgaris, Cladonia fimbriata, Cladonia rangiformis, Erica tetralix, Galium saxatile, Pleurozium schreberi and Potentilla erecta. These would have been common on the site before it was colonised by the pines and may be recolonising from buried seed-bank (section 3.6) or plants persisting under the developing canopy (see vegetation type 6). The long term change for this community will probably not, however, be a reversion to a dune heath unless the Betula colonisation is controlled. Betula is present in about half of the quadrats, with a constancy value of III.

Vegetation type 4 includes all of the quadrats from the natural dune heath areas, and many from areas clear-felled 4-7 years ago. The latter would have been dune heath prior to invasion by pine. The ground vegetation appears not to have been as heavily shaded as in vegetation type 3, allowing more species to survive between the trees, even such light-demanding species as Ammophila arenaria. Cladonia lichens often form extensive carpets in sheltered gaps in the canopy.

Vegetation type 5 was found in only 5 quadrats. However, a similar type of Betula scrub is common in slacks throughout the reserve. Four of the quadrats were on sites where pine had been removed 4 to 7 years ago, one had never had pine on it. Although the ground at these sites was not noticably wetter than the others, several species usually associated with dune slacks were found in small numbers in this community, suggesting that this may be a dried slack community. These species include Agrostis stolonifera, Cirsium palustre, Erica tetralix, Juncus articulatus, Juncus conglomeratus, Lotus corniculatus, Pyrola minor and Salix repens. The ground was also very flat (figure 3.39). With the increase in Betula on some of the more recently felled sites this community could become more frequent, especially in the dune hollows.

The TWINSPAN classification for vegetation type 6 does not seem to be as clearly defined as for most of the other communities as it contains quadrats from both woodland and clear-felled sites (figure 3.33). This vegetation type appears to be intermediate between a completely closed woodland and an unforested condition. It could include quadrats from younger woodlands where a few open-dune species are persisting, and quadrats from the recently felled sites in which woodland species are still present. It has more species per quadrat than the other two woodland communities (figure 3.38). This intermediate vegetation is not seen at the sites at Ainsdale or Whiteford, where the plantations are of uniform age, and planted at a density which can quickly exclude most of the original ground flora. There are several species which are not usually present in woodlands, including: Anthoxanthum odoratum, Arrhenatherum elatius, Cladonia rangiformis, Festuca rubra, Galium saxatile and Hypochoeris radicata; and some more typical woodland species: Dryopteris dilatata, Goodyera repens, Hylocomium splendens and Plagiothecium undulatum. Other plants are apparently equally suited to either open dune or light woodland, including: Chamaenerion angustifolium, Deschampsia flexuosa, Dicranum scoparium, Hypnum cupressiforme, Pleurozium schreberi, Ptilidium ciliare, Rhytidiadelphus triquetrus and Viola sp.,

Vegetation type 7 is similar to the previous community, but represents an older woodland, with fewer plants persisting from the original dune vegetation. The canopy is darker than in type 6, and there are fewer species per quadrat (figure 3.38). However, there is a higher percentage cover of the field layer, mostly by the mosses Dicranum scoparium, Plagiothecium undulatum, Pleurozium schreberi and Rhytidiadelphus triquetrus, together with Carex arenaria and Deschampsia flexuosa. Most of these species persist after the trees are removed, and this community is still recognisable in the first year after felling (pers.obs; figure 3.33).

Vegetation type 8 (plate 4) has the densest tree cover. There were no quadrats from partially shaded areas, clear-felled sites or unplanted dunes. This woodland has the deepest litter layer of the communities identified (figure 3.37) and the ground flora has the lowest percentage cover (figure 3.35). The most common plants in the field layer were Carex arenaria and Hylocomium splendens, with Deschampsia flexuosa, Dicranum scoparium, and Rhytidiadelphus triquetrus. This community is recognisable as a Pinus sylvestris - Hylocomium splendens woodland community (Rodwell, 1991). However, it is still young and has not yet developed the full diversity of a native pine-wood or the Erica cinerea - Goodyera repens sub-community. G.repens is frequent, with a constancy value of II. Listera cordata is also present although it did not occur in any quadrats.

The significance of the findings from this site, and from Ainsdale and Whiteford, are discussed further in section 3.6.

## 3.4 Seed-bank study

Dense shade and fallen pine needles can suppress the development of a ground flora in dune plantations. Clear-felling removes these inhibitory factors, exposing the ground surface and allowing increased plant growth. Vegetation recovery may be by the expansion of the limited ground flora, from dormant seeds (or other plant propagules), or by seed-rain from outside the area. In most situations all of these processes will be operating to varying degrees, depending on local conditions.

To attempt to assess the importance of dormant seeds in this secondary succession a comparative study of soil seed-banks in unplanted and afforested dunes was undertaken, using a germination assay under greenhouse conditions to estimate numbers of viable seeds.

For the purpose of this study the word 'seed' means "a ripened ovule which develops following fertilisation in seed plants" (Little & Jones, 1980), and 'seed-bank' means the dormant reserve of viable seeds in the soil.

### 3.4.1 Methods

Six sampling sites were chosen at Ainsdale, 3 within a 62 year old plantation and 3 in an adjacent unforested grey-dune area of the reserve (see figure 1.2). The dunes were all of approximately the same age and distance from the sea.

Soil samples of approximately 500cm$^3$ were taken from each recognisable soil horizon using a trowel, and sealed in a polythene bag. The soil was kept in a cool, dark place until required for the germination assay, about 6 hours later. The study was started on 25th August, 1988.

Plastic 20 x 15cm seed trays, 5cm deep, were filled to a depth of 2cm with John Innes Seed Compost to provide a moisture retaining substrate. Each soil sample was spread onto a tray of compost to a depth of approximately 1.5cm. Each sample was replicated three times. Two trays had no soil added, but were filled with the seed compost to a depth of 3.5cm as a control measure for the investigation.

The trays were kept in a greenhouse and watered daily. The temperature was kept between 20 and 22°C by day and 15 and 18°C by night. Artificial lighting by mercury-vapour lamps gave a controlled 18 hour day.

Each tray was examined every day for the first 21 days, then every 4 to 5 days for a further 21 days. All seedlings present were counted and identified when possible. Seedlings were removed after they had been identified, or if they were dying. Some were transplanted into pots and grown on further to confirm their identity. A reference seed collection of known dune species was planted at the beginning of the investigation as an aid to identification.

### 3.4.2 Results and discussion

Total numbers of emergent seedlings from afforested and unplanted dune sites are presented in table 3.13.

Table 3.13 Total numbers of buried viable seeds. Totals are from three 500cm³ soil samples for each soil depth.

| | UNPLANTED DUNES | | WOODLAND | | | |
|---|---|---|---|---|---|---|
| Soil depth(cm)/horizon | 0-2 | 3-5 | L | F | H | 0-5 |
| Agrostis sp. | 2 | | | | | |
| Aira praecox | 106 | 225 | | | 1 | 2 |
| Ammophila arenaria | 1 | | | | | |
| Bellis perennis | 1 | | | | | |
| Carex arenaria | 1 | | | | | 2 |
| Cerastium glomeratum | 61 | | | | | |
| Cerastium holosteoides | 8 | 2 | | 1 | 1 | |
| Chamaenerion angustifolium | | 1 | 8 | 19 | | |
| Epilobium spp. | 22 | 5 | 3 | 4 | | |
| Festuca rubra | 23 | | | | | 1 |
| Lotus corniculatus | 3 | | | | | |
| Oenothera sp. | 3 | | | | | |
| Phleum arenarium | 67 | 5 | | | | |
| Pinus nigra | | | | | | 1 |
| Poa sp. | 34 | 6 | 1 | | 1 | |
| Polygala vulgaris | | 1 | | | | |
| Prunella vulgaris | 1 | | | | | |
| Rubus caesius | 20 | 2 | | | | |
| Rumex sp. | | 1 | | | | |
| Senecio jacobaea | | 1 | 1 | 1 | | |
| Solanum nigrum | 1 | | | | | |
| Sonchus sp. | 1 | | | | 1 | |
| Stellaria media | | | | 3 | | |
| Taraxacum sp. | 1 | | | | | |
| Vicia spp. | 8 | 1 | | | | |
| Viola spp. | 5 | | | | | |
| Unidentified composites | 10 | 7 | | | | |
| Total | 379 | 257 | 13 | 28 | 4 | 6 |
| Mean number of seeds | 126.3 | 86.6 | 4.3 | 9.3 | 1.3 | 2.0 |
| Mean number of species | >12.6 | >5.3 | 2.3 | 2.6 | 1.3 | 2.0 |

The unsown control trays produced only a few Erica seedlings from the peat-based compost, showing that there was little or no contamination from other seeds within the greenhouse.

The soil samples from the open dunes produced large numbers of seedlings (100-305 per site), which closely reflected the composition of the surface vegetation. The woodland samples produced relatively few seedlings (9-26 per site), and included more ruderal species than typical dune species.

The composition of the seed-bank varied with depth in the soil profile. In the unplanted dunes a greater diversity of species was seen in the seed-bank of the top two centimetres of soil (11-14 species, cf.1-7 species at 2-5cm depth). The total number of viable seeds for most species was also higher at the top of the soil profile. In the woodland samples the highest proportion of seeds was recorded in the F horizon, with very few viable seeds found in the mineral A horizon.

The germination assay technique gives a useful indication of the viable seed-banks in the study areas, although there are some disadvantages with the method. An important problem is the sample size, which must be small unless a great deal of greenhouse space is available. A small sample size is likely to underestimate the full range of species, and may fail to detect seeds with a tendency towards a clustered distribution. Rubus caesius appears to have a clustered seed distribution since all 7 seedlings occurred in just one of the replicate trays for one site. For this reason the totals of all the replicates were used to give the best representation of the seed-bank. A further complication is that some seed dormancies may be difficult to break, which may also lead to an underestimation of seed-bank size.

Needle litter accumulating over the afforested dune surface will contain only those seeds arriving at the site after the trees have been planted (Hill, 1986). Very little mixing of the organic and mineral horizons was observed at any of the woodland soil sampling sites (chapter 2). It is, therefore, possible to distinguish between the seed-bank persisting from before afforestation, and that which has arrived subsequently.

The woodland sites at Ainsdale once supported a similar vegetation to the dunes which were never afforested (Salisbury, 1925; Holder, 1953; Blanchard, 1952). If the woodland A horizon once contained a seed-bank of similar size and composition to the unplanted dunes then very few seeds have been able to survive for 62 years under woodland conditions. The paucity of seedlings germinating from A horizon samples indicates a loss of seeds from the seed-bank. It may be that the seeds germinated, but the seedlings died under the shade of the trees, or before they had emerged through the layers of pine litter (Fenner, 1987). Alternatively the seeds may have been unable to germinate and decomposed; the large microbial community of the woodland will gradually deplete the seed-bank, the longer it remains the more seeds rot (Granstrom, 1987). The exact fate of the large number of dead seeds is not within the scope of this study, although observations suggest that both germination and decay processes are operating.

The seeds of some species appear able to remain viable for longer than others. Carex arenaria and several grasses are among the few to have survived in the woodland A horizon. Hill & Wallace (1989) found that C.arenaria was the only species common in the seed-bank of afforested mobile dunes at Newborough, Anglesey.

Many dune species, notably annuals (Pemadasa et al, 1974), have a very restricted seed dispersal. When the ground flora becomes shaded out by trees, seed supply from these species is greatly reduced. Supply of wind-dispersed seeds may also be reduced, or at least concentrated at plantation edges, by interception of seeds by the canopy. However, in the sites studied, the majority of the seeds in the woodland organic horizons are wind-dispersed ruderal species such as Chamaenerion angustifolium, Epilobium spp., and various composites.

Seed supply of some species could increase following afforestation; the most obvious species being Pinus nigra. Birds roosting in the trees may bring in other species. Plants favoured by birds occurring below the pine canopy at Ainsdale include: Crataegus monogyna, Ilex aquifolium, Sambucus nigra, Mahonia aquifolium, Solanum dulcamara, Hippophae rhamnoides and Quercus robur. Seeds dispersed by birds will have a clustered spatial distribution in the seed-bank, which may explain why none were found in the samples; although seedlings of I. aquifolium and C. monogyna seedlings were observed within 2 metres of the sampling site. A wood pigeon's nest was also observed to be a seed source at the Ainsdale 1988 felling site. It was made partly from Galium aparine and contained many viable seeds which germinated a few weeks after the nest fell from the tree.

Both the germination assay and field observations show that the naturally large seed-bank of the dunes is greatly depleted, becoming replaced by seeds of ruderal species such as Chamaenerion angustifolium following 62 years of afforestation. In the event of an old dune woodland being clear-felled it is these 'weed' seeds, mostly contained within the organic litter layer, which will form the most significant immediate contribution towards the revegetation of the area.

## 3.5 Vesicular arbuscular mycorrhiza study

Several studies have shown that the majority of plants occurring in natural dune systems are infected by vesicular arbuscular (V.A.) mycorrhizal fungi (Read, 1989; Puppi & Riess, 1987; Ernst et al, 1984; Koske & Halvorson, 1981). It has also been shown that these endomycorrhizal fungi may not be present under pine woodland, which forms mostly ecto-mycorrhizal associations (Tobiessen & Werner, 1980; Kovacik et al, 1984).

Mycorrhizal associations can increase plant nutrient uptake, and therefore growth, particularly in situations where soil fertility is low (Daft & Nicholson, 1969; Baylis, 1970). The presence of V.A. mycorrhizal fungi may, therefore, be of some importance to the re-establishment of dune vegetation. This study includes an investigation of V.A. mycorrhizal infection in four species before and after afforestation and felling, to follow the transition from a community dominated by ectomycorrhizas to one in which endomycorrhizas are most prominent.

3.5.1 Methods

Chamaenerion angustifolium, Senecio jacobaea, Viola riviniana and Erodium cicutarium were chosen for examination. These species can be found on the unforested dunes, within the pinewoods, and on the recently felled areas, and are all known to support V.A. mycorrhizal infection (Harley & Harley, 1987).

On 1st September, 1989, root samples of all the species were taken from four sites at Ainsdale N.N.R.. These included an unplanted grey dune, a 60 year old plantation, a clear-felled site 6 months after felling and a fire-break, 10 years after felling (see figure 1.2).

At least 10 plants of each species were sampled from each of the sites, the only exceptions being Erodium cicutarium which was not found in the plantation, and Viola riviniana where only 2 specimens were found in the newly clear-felled site.

Entire root systems were collected, and put into plastic bags. Soil was removed from the roots by washing in tap water followed by distilled water. Samples were then transferred to jars containing formalin in acetic acid alcohol (F.A.A.).

A stock solution of F.A.A. was made up as follows:

| | |
|---|---|
| Formaldehyde | 50ml |
| Glacial Acetic Acid | 50ml |
| Ethanol | 430ml |
| Distilled Water | 430ml |

The roots must be fixed in F.A.A. for at least 12 hours as part of the preparation for staining. However, F.A.A. also acts as a preservative and the samples were left for several weeks before continuing the analysis.

Staining for V.A. mycorrhizas was carried out using the following procedure, outlined by Brundrett et al (1984).

a) The roots were taken from the F.A.A. and rinsed with distilled water.

b) Using scissors, they were carefully cut into 1cm lengths and put into staining vials. The staining vials are glass containers with an open top and a steel mesh base. They allow the roots to be transferred to different solutions avoiding the damage caused by using forceps.

c) The roots were washed by further rinses of distilled water, to remove all of the F.A.A.

d) The vials were transferred to 10% (w/v) potassium hydroxide solution at 80°C in a waterbath, and left in this for one hour to clear. Clearing removes the host cytoplasm and most of the nuclei, making it easier to see endoparasitic fungi in the cells of the cortex.

e) After cooling the samples were rinsed with several changes of tap water followed by distilled water.

f) The roots were transferred to the staining solution. This consisted of equal volumes of 85% lactic acid, glycerol and distilled water, with 0.1% (w/v) chlorazol black E. This solution was made up a few hours before use to allow undissolved stain particles to settle out. The staining process took 1-2 hours at 90°C.

g) The stained roots were left overnight in glycerol, before being mounted onto slides.

The stained root segments were put into a petri dish marked with a 1cm grid pattern, in distilled water. Roots were picked out randomly to be mounted onto slides by picking them from certain parts of the grid (for example, by picking all segments crossing a particular line), until sufficient had been taken.

The selected segments were put into a drop of 50% glycerol onto a slide and covered with a 22x50mm coverslip. The pieces were positioned closely enough to one another to be seen in each consecutive field of view, but were not overlapping.

The evaluation of infection by V.A. mycorrhizal fungi was made by scanning across the slide using bright-field optics at x400 magnification.

For each field of view in which a root crossed the vertical centre line (marked by an eye-piece graticule), the infection was scored as 'present' or 'absent'. Presence only being recorded when the fungi were present under the centre line. In this way the percentage infection per unit length of root was counted, rather than just the percentage of infected fields of view.

The fungi were coloured dark grey by the chlorazol Black E, which made them easy to see. To differentiate between V.A. mycorrhizal fungi and other fungi, the presence of at least two of their distinguishing characters had to be observed. These were: the hyphae (usually aseptate, thick and contorted), the vesicles, and the arbuscules. If none or only one of these features was seen then it was not scored as V.A. mycorrhizal infection. This very cautious approach thus avoided counting saprophytes and pathogens, but it may have meant that mycorrhizal fungi were underscored.

### 3.5.2 Results and discussion

The results are shown in figure 3.40.

All four species had a higher level of infection by V.A. mycorrhizal fungi in the grey dune site (11.2 to 30.8%) than in the woodland (1.6 to 3.4%). The level of infection in the grey dunes is similar to that observed at the North Holland Dune Reserve in the Netherlands by Ernst et al (1984).

Following afforestation the amount of infection was reduced to less than 5%. There have been several possible explanations for this phenomenon. Hayman (1974) suggested that the low levels of infection observed in onion plants grown in shaded conditions were related to the reduced transfer of photosynthate from the host-plant. Tobiessen & Werner (1980) suggested that either the absence of V.A. mycorrhizal host plants below a pine canopy resulted in a loss of endomycorrhizal inoculum, or that the V.A. mycorrhizas were suppressed by a form of chemical inhibition by pine or its ectomycorrhizas.

Six months after felling there was no evidence of infection in S.jacobaea or Viola. The small sample size may be a reason why Viola showed no infection; both plants were very young and may not have had enough time for fungal colonisation of the roots. The intensity of rabbit grazing at the site ensured that no seedlings of such 'grazable'

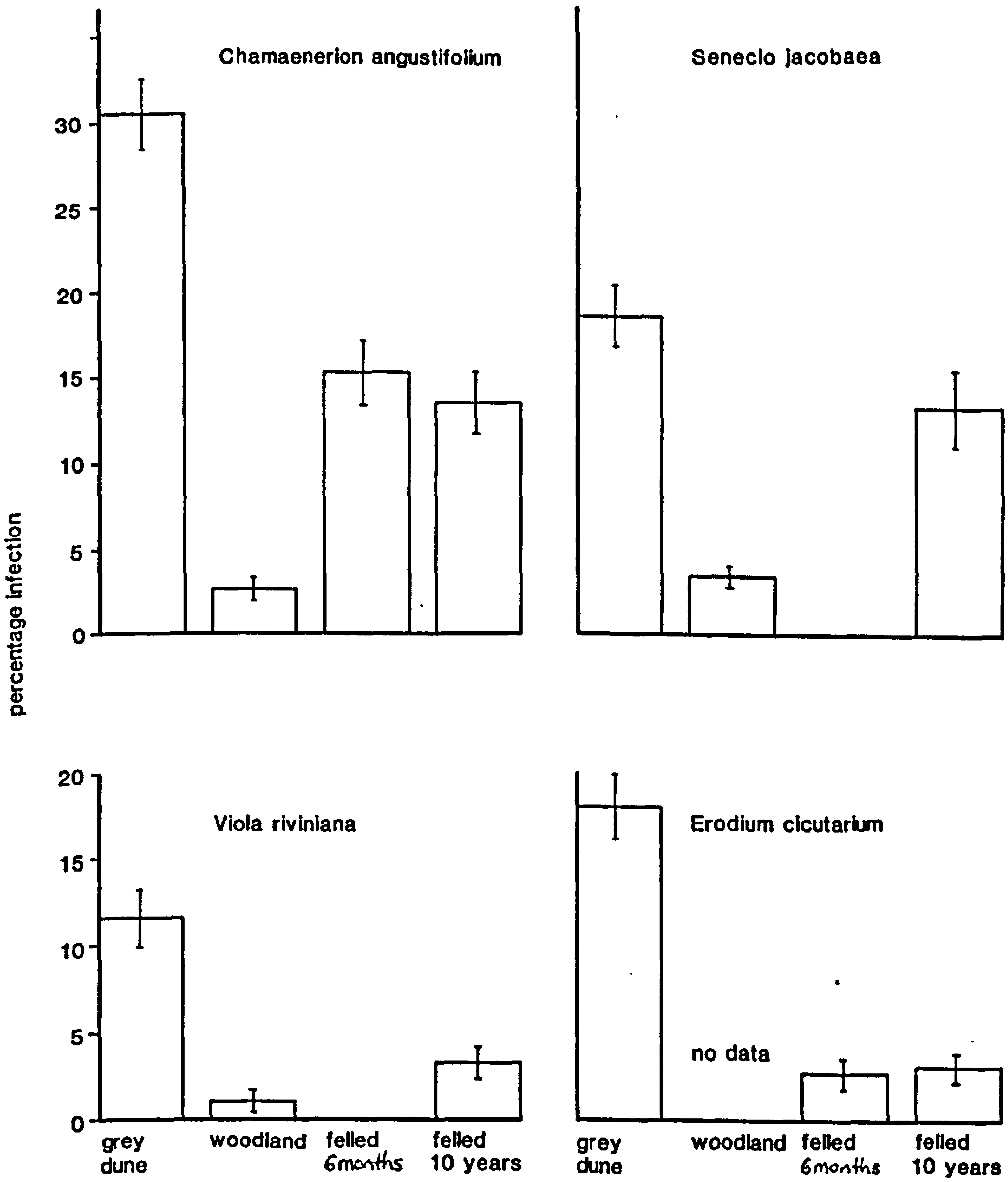



Figure 3.40 Vesicular arbuscular mycorrhizal infection in four plant species in four different sand-dune habitats. Error bars show standard error from a percentage estimate (Ebdon, 1977).

species survived for more than a few weeks (pers. obs.). S.jacobaea was growing vigorously at this site. However, its often extensive root systems showed no evidence of infection. This may be related to the unusually high abundance of available nutrients following felling. Read et al (1976) have demonstrated that there is a correlation between V.A. mycorrhizal infection and nutrient stress; thus, where there are plenty of nutrients, particularly phosphorus, a low incidence of infection may be expected. E.cicutarium was also scarcely infected. C.angustifolium had a 15.1% infection in the recently felled site, which was higher than in the woodland, but lower than in the grey dunes.

There is little evidence of host specificity in V.A. mycorrhizas (Mosse, 1975, Moser & Haselwandter, 1983), and so the fungus infecting E.cicutarium and C.angustifolium at the recently felled site could probably have infected the other two species under different circumstances. The sparse distribution of plants in the woodlands and on the recently felled site may contribute to the low incidence of infection, since V.A. mycorrhizal fungi often spreads by root to root contact (Read et al, 1976). No V.A. mycorrhizal plants were seen at the site immediately prior to the 1988 felling; this would probably result in a lower concentration of fungal inoculum. A low concentration of inoculum could result in a lower level of infection at clear-felled sites (Daft & Nicholson, 1969b).

The level of infection in the fire-break (2.5 to 13.8%) was intermediate between the woodland and grey dune in all species. The nutrient-stress theory would suggest that this site has an intermediate level of available nutrients. The acid-extractable phosphate in the soil 10 years after felling was intermediate between the grey dunes and the woodland (see section 2.3), supporting this hypothesis. However, the extremely high carbon: nitrogen ratio in woodland and felled areas (section 2.4.1) suggests that nitrogen immobilisation may also be an important nutrient stress.

Read (1989) has linked the role of V.A. mycorrhizas mainly with sandy soils with low phosphate availability, while ecto-mycorrhizas, commonly associated with Basidiomycetous fungi, are more important where organic matter is accumulating at the soil surface, concentrating the nitrogen and phosphorus and often making nitrogen the main limiting nutrient. Ten years after felling there is still an organic layer at the soil surface, which will favour the ecto-mycorrhizal species. This may be an explanation for why normally V.A. mycorrhizal species are scarce, with low levels of infection and appear to be under nutrient stress, while ecto-mycorrhizal species such as Betula and young Pinus trees are thriving.

Further investigations into the interactions between mycorrhizas of the fire-break community, possibly under the controlled conditions of a green-house, may be able to confirm the extent to which the V.A. and ecto-mycorrhizal fungi are influencing the vegetation. It would be useful to discover whether or not the ecto-mycorrhizal fungi are simply more competitive in the organic surface horizons or if they can actually supress the V.A. mycorrhizal fungi.

## 3.6 General discussion

Few species typically found in open dune vegetation were able to tolerate the shade of the densest plantations. However, some survived for longer than others. These residual species were among the most important plants of clear-felled sites. Carex arenaria was an example found at all study sites. The number of residual dune plants depends upon the age and the size of the plantation and the density its pine canopy. The number of species tends to be higher if the canopy is more open, as in the self-sown woodland at Tentsmuir. Younger plantations like those at Whiteford will have a larger population of residual plants as some perennial species, such as Rubus caesius, may take a longer time to die. Plantation size is also important as several typical dune species are found in woodland edge communities. Smaller woodlands will have a relatively larger area occupied by these edge communities.

Sand-dune plantations, especially smaller ones, may have some dune species below their canopy due to seed-rain from the unplanted dunes. They may not survive long enough to reproduce but are present mainly because of the constant input of seeds from outside. This may be why plants with wind-blown seeds, such as Hypochoeris radicata, Leontodon taraxacoides and Senecio jacobaea were often only present in plantations as seedlings.

Plants growing in the pinewoods showed a very low incidence of vesicular arbuscular mycorrhizal infection.

Some dune grassland species may be able to survive better under the trees if they are not nutritionally dependent on these mycorrhizas. The Cyperaceae are typically non-mycorrhizal (Powell, 1975), which may be a factor in the success of Carex arenaria below pines. Some ecto-mycorrhizal species are more common in the pinewoods than in the unplanted dunes. Notably, these include Pyrola species (Hill & Wallace, 1989).

Orchid species at Ainsdale and Whiteford include: Anacamptis pyramidalis, Dactylorhiza majalis, Epipactis dunensis, E.helleborine, E.phyllanthes and Listera ovata. They are all present in the unplanted dunes but survived even the densest shade of the plantations. E.dunensis was originally associated with Salix repens in dune slacks at Ainsdale before spreading into the woodland (Gray & Clitherow, 1982). The orchids do not rely solely on photosynthesis as they are mycorrhizal. Rhizoctonia is the fungal partner of the association, able to utilise many carbon sources including cellulose and other complex polysaccharides, and pass these to the host plant (Hadley, 1969). Several specimens of E.helleborine at Whiteford appeared to be completely lacking chlorophyll. Orchidaceous mycorrhizas give the roots of some species a thick, fleshy appearance. Epipactis species are not as frequent in the older woodlands at Ainsdale or Whiteford as they are in the young ones. E.dunensis appears to grow particularly well in young plantations, often forming large colonies. In the older woodlands at Formby it appears to grow well on disused paths (M.Garbett, pers.comm.). The apparent decline in abundance through time may relate to changes in the mycoflora as the woodland matures (J.Jeremy, pers.comm.).

Although large areas of the unthinned woodlands were devoid of vascular plants, the shaded and sheltered edges of the plantations often developed a particularly rich bryophyte and lichen flora, such as at Ainsdale (vegetation type 5) and Culbin Sands (Doody, 1989a). The further study that these edge communities deserve is not within the scope of this project.

The length of time under woodland conditions has important consequences for the vegetation developing after clear-felling. The most successful restoration of a typical dune flora was at Whiteford where the plantations were only about 12 years old (section 3.3.3). The short length of time under trees would probably have left more residual dune species, and caused less depletion of the seed-bank and less accumulation of pine-litter. However, being the smallest of the plantations studied there may have been an unusually high proportion of residual plants, and colonisation by seeds from the unplanted dunes would have been easier. The plantations at Ainsdale felled fifty years ago were less than 30 years old and may have retained a greater proportion of their dune seed-bank and accumulated less litter than those felled recently. They resemble the unplanted dunes but many dune species are absent (section 3.3.2) and there appears to be a higher soil fertility (sections 2.5 and 3.3.2) resulting in strong growth of competitive grassland species (eg. Holcus lanatus, Anthoxanthum odoratum, Dactylis glomerata, Festuca rubra and Carex arenaria). At Tentsmuir the areas cleared of recently self-sown pines support many of the species of the un-wooded dunes (section 3.3.4). This may be because there is still a residual population of dune plants and/or a large seed-bank.

As a plantation grows older its original seed-bank is gradually depleted, and the needle litter of the woodland floor becomes deeper. Both of these effects contribute to the differences between the post-felling flora and the flora of the unplanted dunes. The older woodlands have fewer of their original seeds (section 3.4.2), and will have accumulated a new needle litter seed-bank since afforestation. After felling it is mostly these seeds which germinate, while the litter inhibits germination of the original seed-bank. This was demonstrated in a small experimental trial at Whiteford, by removing all the organic surface material from a 6x6m square at a newly clear-felled site in plantation K (30 years old), in November, 1988. In the summer of 1989 areas which were not cleared supported a flora dominated by Senecio jacobaea, Sonchus oleraceus and other species with wind-blown seeds (vegetation type 5, plate 12), while the flora of the cleared square had a diverse flora of typical dune species growing from seed (plate 13), including:

| | |
|---|---|
| Agrostis stolonifera | Aira caryophyllea |
| Aira praecox | Ammophila arenaria |
| Anthyllis vulneraria | Arabis hirsuta |
| Arenaria serpyllifolia | Bromus hordeaceus |
| Carex arenaria | Cerastium glomeratum |
| Desmazeria rigida | Erophila verna |
| Festuca rubra | Hypochoeris radicata |
| Holcus lanatus | Leontodon taraxacoides |
| Luzula campestris | Oenothera parviflora |
| Phleum arenarium | Plantago lanceolata |

| | |
|---|---|
| Saxifraga tridactylites | Viola canina |
| Viola tricolor ssp. curtisii | Vulpia fasciculata |

It is likely that some of these seeds were blown onto the site since clear-felling since *Vulpia fasciculata* does not maintain a seed-bank (Watkinson, 1978) and must have colonised the area since the trees were removed. An exploratory examination of the seed-bank, using methods described in section 3.4.1, revealed the presence of some of the seeds of the dune species below the litter, and also showed that seeds of the ruderal plants of vegetation type 5 were mostly contained in the needle litter (section 3.4). Even if seeds had blown onto the site during winter gales the experiment still shows that seedling establishment was greater where the organic material is removed.

The low number of dune species germinating in any of the Ainsdale fire-breaks may be due to either loss of seed-bank, or, as in the experiment at Whiteford, inhibition of the seed-bank by litter. It would be useful to test this by removing the organic surface layers from some of these poorly recovered sites 10 years after felling, and studying the subsequent vegetation changes. Observations at these sites suggest that some seeds, including those of Viola spp. and Aira praecox may survive below the litter until it is either disturbed or sufficiently decayed to allow germination.

The older plantations may have more woodland species in their seed-bank. Tree and shrub species present at clear-felled sites at Ainsdale include Acer pseudoplatanus, Betula spp., Ilex aquifolium, Pinus nigra, P.sylvestris, Populus alba, Populus candicans, Prunus sp, Quercus robur, Quercus petraea, Salix spp., Sorbus sp. and Ulex europaeus. The growth of such species will once again create shade and litter, leading to a change towards woodland. The soil of the clear-felled sites appears to be well suited to tree growth; Betula and Pinus grow very well in clear-felled sites at Ainsdale. The seed-bank of a plantation will contain Pinus seeds if the crop is mature (ie. at least 25-30 years old), and Betula seeds if there is a local supply. Betula seeds do not survive for long in the soil, usually being replenished each year (Hill, 1979c).

Most pines regenerating in the fire-breaks at Ainsdale appear to be from seed which was present in the litter before the trees were felled. This can be seen by examining the age structure of the pines within a fire-break. Figure 3.41 shows a study area at Ainsdale, with 5 plots of equal area, each 10 metres wide, in a sequence of increasing distance from the adjacent plantation. The age of all the trees in each plot was estimated by counting the number of internodes up the stem. The results, shown in figure 3.42, show that the two plots nearest the woodland have the most trees. The 0-10m plot probably had fewer trees than the 10-20m plot because of the vehicle track running through it. The age distribution in these plots suggests that there is a fairly constant rate of germination and recruitment each year, with a constant supply of seeds. With increasing distance from the plantation there are fewer trees, and the frequency distribution of ages becomes more peaked, with most of the trees being about 7 years old (ie. having 7

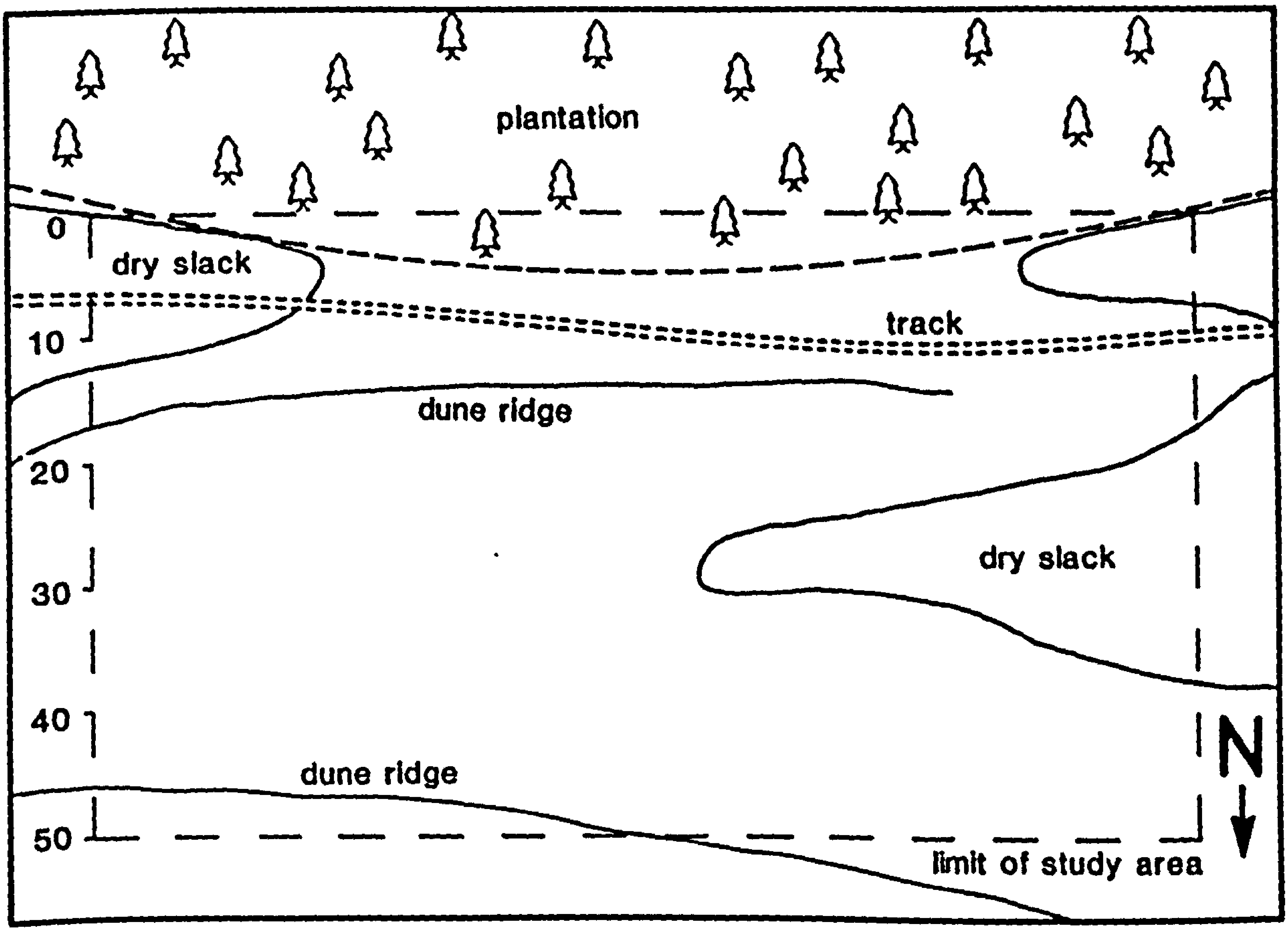



Figure 3.41 The pine regeneration study site at Ainsdale. The scale on the left indicates the distance (metres) from the woodland edge.

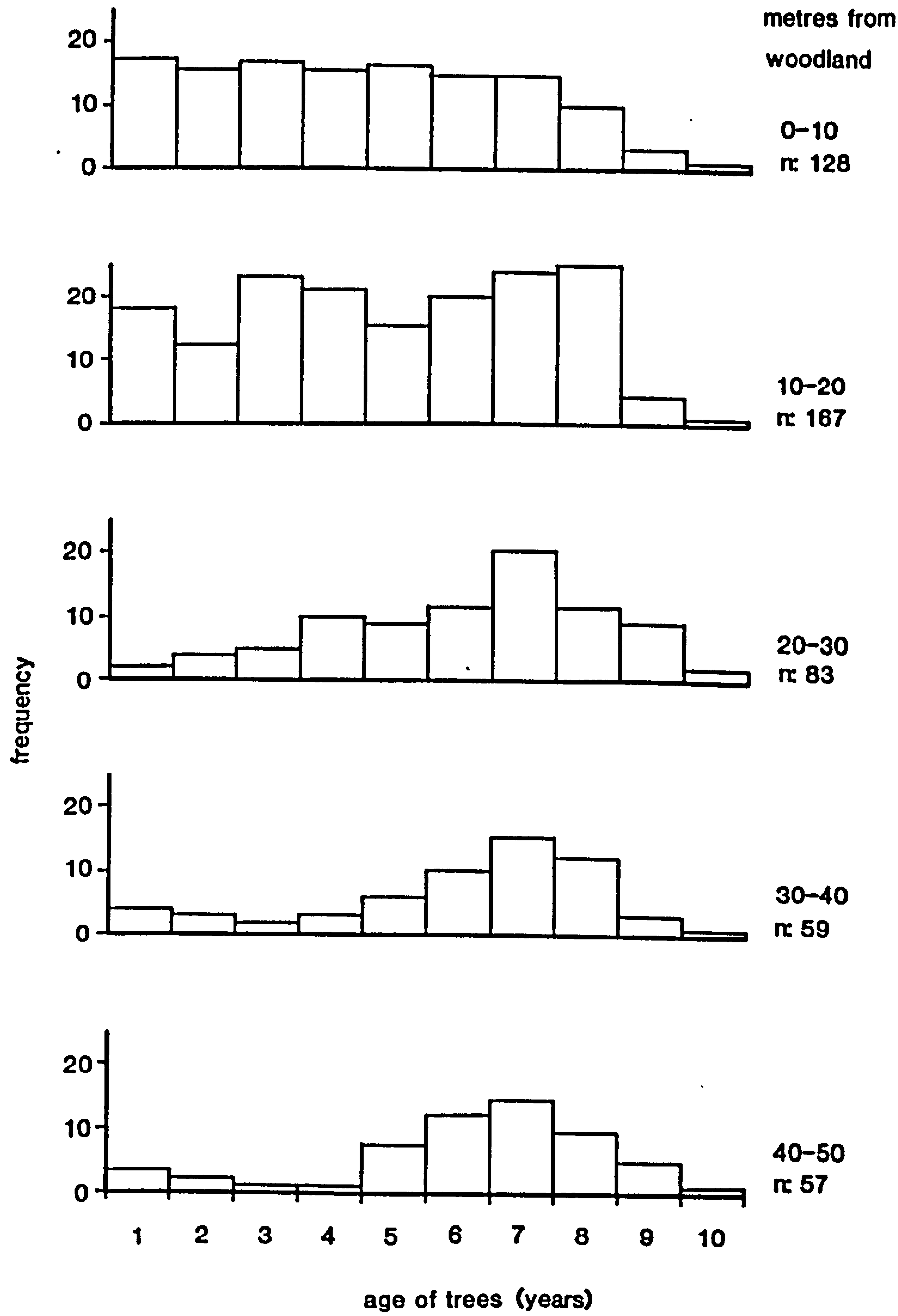



Figure 3.42 Variation in age in regenerating pines (estimated by number of internodes) in an Ainsdale fire-break.

internodes). The fire-break was felled 9 years before the survey, suggesting that most of these trees germinated within 2 years of clear-felling; the decrease in number of wind-blown seeds with increasing distance from the plantation results in most of the trees being the same age.

Betula produces its wind-blown seeds in abundance and is very successfully colonising most clear-felled sites in the older woodlands at Ainsdale and at Tentsmuir. Whiteford has remained almost free of Betula colonisation. This is probably because there are so few trees as a seed source, and because of the more intense grazing by rabbits and ponies.

Where older plantations are removed the post-felling vegetation is less similar to the unplanted dunes than after felling younger woodland. Areas at Ainsdale felled between 10 and 20 years ago are often dominated by Chamaenerion angustifolium, mosses and Betula scrub. This may be either because these sites have been afforested longer than those clear-felled 50 years ago, or because there has been less time for vegetation recovery, or, more probably, a combination of these. There are currently only a few examples of dune plantations which have been clear-felled to allow natural vegetation recovery, thus making prediction difficult. Timescales for vegetation recovery appear to vary considerably with local conditions, including grazing, climate, soil and the flora of the surrounding area.

Selective grazing by rabbits may be an important factor in determining the species found on clear-felled sites. At Whiteford, rabbit burrows now occupy one small dune on the clear-felled plantation F. The adjacent clear-felled dunes have a good variety of dune plants, but the intensively grazed area is dominated by Cirsium arvense and Senecio jacobaea with few other species. A site in the frontal woodlands at Ainsdale felled in 1989 also has a large population of rabbits, and possibly a disproportionately high grazing intensity because of the small size of the felled site. This supports a flora dominated by Cirsium arvense, Cirsium vulgare, Erodium cicutarium, Senecio jacobaea and Urtica dioica. Examination of foliage revealed that these species were not eaten by the rabbits. Other less frequent species which were not grazed included Atriplex patula, Chamaenerion angustifolium, Cynoglossum officinale, Myosotis arvensis, Rumex crispus, Rumex obtusifolius, and Sonchus asper. A much wider range of species emerged in the first year after felling. However, these were grazed by the rabbits and often did not survive the seedling stage. These species included:

| | |
|---|---|
| Agrostis stolonifera | Cardamine hirsuta |
| Carex arenaria | Carex flacca |
| Cerastium fontanum | Epilobium montanum |
| Epipactis dunensis | Hippophae rhamnoides |
| Hypochoeris radicata | Leontodon sp. |
| Lotus corniculatus | Luzula campestris |
| Montia perfoliata | Poa annua |
| Poa pratensis | Polygonum persicaria |
| Rosa canina | Rubus caesius |
| Solanum dulcamara | Solanum nigrum |
| Stellaria media | Viola riviniana |

Grazing is not the only reason for the unusual flora of this clear-felled area. The site is adjacent to an old dune slack which is dominated by Hippophae rhamnoides, with an understorey of Cirsium arvense, Cirsium vulgare, Senecio jacobaea, Solanum dulcamara and Urtica dioica; suggesting that the surrounding vegetation contributes the most important seed supply to this site, where the original seed-bank is diminished, or buried below needle litter. Similar observations can be made at all of the study sites, for example at Whiteford, where the only site to be colonised by Echium vulgare was adjacent to a patch of this species on unplanted dunes. The same phenomenon is seen after removing Ulex europaeus from dunes on Jersey, where cleared sites have tended to take on the floristic character of the nearest vegetation, rather than reverting back to the flora which was present before the Ulex (P.Anderson, pers.comm.).

The decomposition of the organic layer from an old woodland will take longer than for a younger woodland. This affects the timescale for vegetation recovery. A shallow layer taking less than, say, 10 years to decompose will break up quickly, opening up gaps through which buried seeds can germinate and grow, or into which seeds from the unplanted dunes can become established. Deep organic layers can form a compact mat which can inhibit germination from buried seed-bank and in which seeds from the unplanted dunes do not appear to grow well. Rabbits may break up deep litter layers, creating patches of disturbed sandy ground which often develop a more natural dune flora. At Ainsdale these deeper layers have developed a cover of vegetatively spreading species, particularly Carex arenaria and Chamaenerion angustifolium, and bryophytes and scrub. By the time that the organic layers have decomposed this well established flora is unlikely to return naturally to a typical dune flora, particularly if the scrub has become dominant.

Epipactis dunensis is an important national rarity, frequent in the Sefton coast woodlands but very infrequent in clear-felled sites. There were 42 flowering spikes of E.dunensis at the Ainsdale 1989 clear-fell site the summer before the trees were removed. None survived where the tree roots were removed, and although most of the others emerged after felling they were soon all eaten by rabbits. The positions of 20 flowering spikes of E.helleborine in plantation K at Whiteford were marked before the trees were felled in 1988, 10 in the felling site and 10 in an unfelled woodland. The following year all of the orchids in the woodland emerged while only 7 emerged from the felling site. None of the orchids in the woodland were grazed, but all of the ones in the felled site were at least partly eaten. An examination of the orchids' stem-buds in the autumn showed that most of the plants in the felled site had 2 or 3 buds, while those in the woodland had only 1. This is a common response to grazing (J.Jeremy, pers.comm.). The absence of rabbit grazing below the pine trees could be another factor in the success of these orchids under woodland conditions. After clear-felling there is no cover for them and they are eaten. Those still present in sites felled several years previously are usually growing in tall vegetation, which may act as a protection from grazing.

Comparing the vegetation of clear-felled sites with the unplanted dune vegetation gave a useful indication of its naturalness. However, even in cases where it was very similar to unplanted dune vegetation it was difficult to assign to any of the National Vegetation Classification sand-dune communities. This is mainly due to the loss of some of the more important indicator species, such as Ammophila arenaria, following afforestation. For example; the sand-dune survey for Whiteford classified the unplanted dunes and the clear-felled sites as a mosaic of variants of the Ammophila arenaria - Festuca rubra semi-fixed dune and Festuca rubra - Galium verum fixed dune communities, although none of the communities present matched the 'typical' dune communities accurately (Dargie, 1989). In the present study vegetation type 4 is broadly similar to a Festuca rubra - Galium verum community, although Galium verum is actually rare in this community; while types 1 and 2 are broadly similar to an Ammophila arenaria - Festuca rubra community Tortula ruraliformis sub-community, due to their being so rich in dune annuals, and their high percentage frequency of Ononis repens and Tortula ruralis. Ammophila arenaria and Festuca rubra are actually only present with a constancy value of II. It is unlikely that Ammophila arenaria will increase in abundance on clear-felled sites unless the sand is disturbed sufficiently to allow new plants to grow from seed. It is usually present in fixed dune grassland as a relict population remaining from when the dunes were forming. It rarely establishes itself on fixed dunes (Huiskes, 1979; Willis, 1989).

This chapter has described some of the trends in vegetation development which follow clear-felling. The vegetation changes are affected by several factors which can be altered by habitat management. Particularly important factors are the seed supply, the pine-needle litter, grazing, and the woodland management prior to felling. Application of these factors in management for conservation is discussed in chapter 4.

CHAPTER 4. RELEVANCE FOR CONSERVATION MANAGEMENT.

4.1 Introduction

This chapter, based on observations and discussions with staff at several sites, attempts to apply the findings described in earlier sections to problems faced by conservation managers with unwanted dune plantations. Because there are so few sites where pine-woods have been felled for conservation reasons much of this chapter is speculative, with many of the practices described still requiring testing.

Some considerations to be made before starting to fell trees have been given in section 1.5. The management of any woodland must be considered individually and in accordance with the priorities for the site. A plantation with sheltering properties, landscape value and woodland wild-life may sometimes be best left standing.

None of the desired outcomes from clear-felling a plantation can happen instantly, or easily, and time-scales for change will vary between sites. The felling operation may take several months while the subsequent recovery of the flora may take many years. Restoring a dune flora becomes more difficult as the plantation gets older. This is because of the progressive loss of ground flora, depletion of the seed-bank and accumulation of pine-litter. Soil changes below plantations will proceed more slowly where there is a high calcium carbonate content in the sand (Ball & Williams, 1974).

Difficulties may arise from the public's perception of a clear-felling project. A large-scale operation may create considerable noise and smoke in an otherwise peaceful area and the site will be visually unattractive immediately after felling. Public reaction may be unfavourable, requiring that more resources are allocated to public relations and site interpretation.

One of the major problems of clear-felling is the disposal of poor quality timber, brash, stumps and needle litter, which may be created in huge quantities. Poor quality timber may be sold for firewood if there is a local demand. Brash may be used in coastal defence work or converted to wood-chips for use on footpaths. The National Trust reserve at Formby is self-sufficient in woodchips, and able to sell all its surplus material. If any material has to be burned it is best to restrict burning to as small an area as possible, since the soil changes caused by fire will increase the amount of available nutrients and encourage weeds such as <u>Chamaenerion angustifolium</u>. Stumps, being awkwardly shaped and heavy to lift, may be difficult to burn. Bonfires are unsuitable for disposing of decomposing needle litter, especially if it has rained since felling the trees. It may be possible to utilise needle-litter for compost (R.Charles, pers.comm.). If digging machinery is available it may be easiest to bury stumps and needle litter in big holes, re-landscaping the sand surface afterwards. However, this may not be possible on sites of geomorphological interest.

Removing layers of deep organic litter is possibly the most important post-felling management requirement for restoring vegetation typical of the earlier stages of dune development. The thin layer of needles beneath plantations less than about 20 years old can probably be left *in situ* as it will decompose quickly. If deep litter is not removed the gradual release of nutrients could eventually result in increased soil fertility, leading to taller vegetation preventing the growth of low-growing and annual species.

Stumps can act as long-term nutrient stores (Newell & Heal, 1982). There may also be a case for removing stumps if they are an eye-sore. The compaction or removal of organic material after felling can expose stumps even when they are cut as close to the ground as possible. Stumps left *in situ* may remain intact for 20 years or more. However, at Whiteford, stumps of 25 year-old trees are sufficiently decomposed after about 7-8 years to be broken off and removed. Stumps left to rot may support a flora of lichens and mosses and encourage an interesting insect fauna which would not otherwise occur at the site. At Whiteford longhorn beetles, ants and goat-moth caterpillars live inside them (pers.obs.). Green woodpeckers have broken many stumps at Whiteford and Tentsmuir by searching for the insects.

Where there is no ground flora below a pine canopy the vegetation immediately after a simple felling operation will probably be dominated by ruderal species such as *Senecio* spp., *Chamaenerion angustifolium* and *Sonchus* spp., depending on local seed sources. These may grow vigorously, benefitting from the release of nutrients after felling, and may persist for several years. Weeds may be interesting in their own right, with the flowers of the compositae often attracting many insects. However, if a weed-flora is not wanted it may be reduced by removing the organic material from the sand surface as soon as possible after felling as this layer contains most of the weed seed-bank. Taking away the litter also allows germination from the remaining dune seed-bank, which would otherwise have been inhibited.

The weed seed-bank in the litter of an old plantation may not be very much larger than a young one, since the seeds of some ruderal species, such as Chamaenerion angustifolium, rarely survive for longer than one season (Hill & Stevens, 1981). But if clear-felling is taking place over several consecutive years the increase in weeds in the cleared site may also increase the size of the weed seed-bank (Atkinson & Sturgess, 1991).

## 4.2 Restoration of a semi-fixed dune community

The distinguishing feature of mobile and semi-fixed dunes is the high percentage of bare sand between the plants. They are amongst the most valuable communities, being the habitat of the natterjack toad and sand lizard at Ainsdale. Many invertebrates are also restricted to the sandy areas of young dunes (Welch, 1989; Doody, 1989a).

Mobile and semi-fixed dunes have very limited soil development. Simply removing the needle litter after felling a young, small plantation may be sufficient to restore a typical soil and vegetation, as seen at Whiteford. However, with older plantations where the woodland soil has developed further there are two ways to restore the mobile dune soil type, both based on a dynamic approach to management (van der Meulen & Jungerius, 1989; Wanders, 1989) by creating disturbance and allowing the natural processes of sand movement and soil development to re-create the habitat. The first way is to remove or stir up the woodland soil by heavy machinery, this may require the stumps to be removed. The second way involves disturbing the unplanted dunes to the windward side of the felled area, allowing fresh sand and seeds to blow over it. This is only possible if there are some available unplanted dunes in the right place.

Stump removal creates a very heterogeneous soil with some patches where organic material is still present at or near the surface and others where it is buried by sand. Wind erosion can be reduced if the site is re-profiled after removing the stumps. If erosion is allowed to happen then organic matter which is not buried deeply may become re-exposed. This would not be a problem if the organic matter could be taken away before removing the stumps; however, this is very labour-intensive and impractical for large areas. A disadvantage with stump removal is that although most of the woodland weed seed-bank is buried, so is most of the original seed-bank, which is concentrated within the top 5cm of sand. This is not so important with sites older than, say, 40 years as there may not be much of this seed-bank left (section 3.4).

Allowing sand from outside to smother a clear-felled site can very effectively re-create a mobile dune community. This situation has arisen in Plantation G at

Whiteford where sand from the beach and mobile dunes has buried the western edge of the site. This solves all problems with stump removal, nutrient enrichment and seed supply, and allows normal dune-building processes to re-establish the flora. Unless the mobile dune becomes fixed over the site it may move on, re-exposing the buried woodland (Patton & Stewart, 1917). This has happened at Ravenmeols Local Nature Reserve, Formby, where a mobile dune buried a small, 20 year old (?) woodland for about 20 years (J.Houston, pers.comm.). The dune has recently moved further inland exposing some of the stumps (plate 16). The sand which is becoming re-exposed still faintly shows a darkened layer which was the litter layer, but soil analysis shows that this is now virtually indistinguishable, in at least two important characteristics, from the sand of the mobile dune, having a pH of 7.6, and a weight-loss on ignition of less than 1% (pers.obs.).

The dominant species of mobile and semi-fixed dunes in Britain is Ammophila arenaria. At plantation F at Whiteford where most of the flora is very similar to a semi-fixed dune, Ammophila is conspicuous by its absence (plate 14). It is an important factor in the overall appearance of a semi-fixed dune but does not survive shading by a pine canopy. It has been shown that Ammophila in the seed-bank can grow if litter is removed (plate 13). However, if seeds are no longer present it may be necessary to re-introduce it. This is usually done by transplanting grass from mobile dunes where it is growing vigorously (Agate, 1986), although this has not yet been tried on clear-felled sites.

## 4.3 Restoration of a fixed-dune community

Fixed-dunes support some of the most diverse dune floras. These include species-rich grey-dunes and grassland communities. These are older dune types, and their floras may have developed over several decades, or even centuries. Restoring vegetation of the same diversity as was originally present may be impossible without considerable time and management.

If the transition to semi-fixed dunes can be accelerated by removing needle-litter, subsequent change to a fixed dune community may follow a near-natural course, being unaffected by any increase in nutrient status. Like the original vegetation development this may take several decades.

Grassland communities of the *Festuca rubra*-*Galium verum* type (Malloch, 1989) have been restored at Whiteford, where the trees were only 12 years old (section 3.3.3, and plate 15). However, 25 year-old plantations felled for 7-8 years have not recovered many of their grassland species, and instead have developed a vegetation more typical of a semi-fixed dune. In time the transition from semi-fixed to fixed dune may create a species-rich sward again, particularly as the site is surrounded by *Festuca rubra*-*Galium verum* dunes.

At Dunnet Links N.N.R., Caithness, and Bunduff Lough, County Sligo, Ireland, species-rich grasslands have been afforested for about 30 years, shading out the diverse flora. In sites clear-felled 4-5 years ago rank grasses such as Holcus lanatus and Anthoxanthum odoratum have become dominant, possibly assisted by the high rainfall at these sites, with few of the former species returning (pers.obs.). Grazing is important in maintaining the diversity of the unplanted dunes at these sites but the afforested areas are fenced to keep out livestock. Unless the grazing regime is resumed these sites are unlikely to return to their former state. Trampling by visitors is keeping some of the grass low along paths at Dunnet Links, but this does not affect a very large area, especially as stumps make walking difficult.

On drier sites fixed dunes rich in Cladonia lichens, Carex arenaria and mosses may be a relatively easy dune type to create. The Carex arenaria-Cornicularia aculeata community (Malloch, 1989) occurs naturally on dry, acid sands with a low nutrient status. It may eventually develop to dune heath. Removing organic material from plantations on acid dunes could create the right conditions for this community to colonise. Where organic material is left in place after clear-felling, nutrient immobilisation often results in similar vegetation (eg. Ainsdale, section 3.3.2, vegetation type 6), although this may be a temporary phase, later giving way to scrub or a Carex arenaria grassland community. It may be possible to increase the diversity of Carex arenaria grasslands by mowing or grazing.

Accelerating the rate of colonisation by dune species onto a site lacking its original seed-bank may be possible by spreading turf or soil from unplanted dunes as a seed source. This may be especially useful if large areas of woodlands are to be felled, or if a clear-fell site is isolated from unplanted dunes. A complete coverage would not be necessary; instead several points within the felled area could be seeded, from which species could spread. This technique could also be combined with rejuvenating unplanted parts of the dune system at sites, such as Ainsdale, where increasing stability is reducing the conservation interest of the older dunes (G.P.Radley, pers.comm.).

## 4.4 Restoration of a dune-slack community

Although slacks have not been included in the main part of this study it may be helpful from a management viewpoint to describe some examples of vegetation recovery where afforested dune-slacks have been clear-felled. Slacks retain a greater number and diversity of viable seeds than afforested dune ridges (Greenow, 1989; Hill & Wallace, 1989), and if the slack still floods in winter this may flush away excess nutrients (P.S. Jones, pers.comm.) and lose nitrogen thro denitrif

At Ainsdale one slack containing 14 year-old *Pinus contorta* felled 10 years ago shows little evidence of ever having been planted. Some species, such as *Anagallis tenella*, *Dactylorhiza incarnata*, *Epipactis palustris*, and *Parnassia palustris* may even have benefitted from the disturbance. Similar results have been seen when removing large stands of *Hippophae rhamnoides* from dune slacks in Birkdale Hills Local Nature Reserve on the Sefton Coast, Merseyside, by bulldozer. From the vegetation, there is little sign of increased nutrient status at either site (pers.obs.) as winter flooding probably removes soluble nitrogen and phosphorus. At Tentsmuir the damp cleared areas show better vegetation recovery than the drier ground, although they appear to be more susceptible to colonisation by Betula.

If there has been a lowering of the water-table since the trees were planted the slack may not recover its former species composition unless the ground surface is excavated to the new water-level. Deeper excavations into wetter ground may restore communities similar to earlier stages of succession.

## 4.5 Conversion to dune heath

Where afforestation has resulted in a post-felling environment too acid for a calcicolous flora to recolonise a site it may be worth investigating converting the area to dune heath. This occurs naturally on acid, low-nutrient sands, such as at Tentsmuir. If there is no existing local dune heath this may be inappropriate, and difficult. Heathland restoration techniques have been reviewed by Putwain (1988).

After clear-felling, the organic material may have to be removed to avoid the development of a weed-flora, and to reduce the nutrient content of the site. Heather litter scattered onto the sand and well trampled can serve as a seed source. This can be collected by hand by raking from underneath heather plants, but mechanical harvesters are available if large amounts are needed. Litter collection does not damage an existing heath and may actually increase the number of Calluna seedlings. A possible problem with using litter may be that it also contains unwanted seeds, such as Betula, depending upon the collection site.

Trials in one of the Ainsdale fire-breaks and an area felled in 1942, started by me in late March, 1990, showed that litter spread to a depth of about 2-4cm in three 2x2m plots gave a seedling density of Calluna of about 50-100 per plot by November. Very few plants survived beyond the seedling stage due to disturbance by rabbits, and these plants were subsequently grazed during the winter. The following year the seedling density was about 30-60 per plot although there was a higher survival rate with between 1 and 50 plants per plot reaching 5cm, probably because of the re-growth of Carex arenaria and Rubus caesius protecting the seedlings. This experiment is still being monitored.

At Tentsmuir, where the site supported dune heath prior to woodland there appears to have been good survival of heathland species in the seed-bank, and a convenient seed supply from intact dune heath in gaps between the trees (section 3.3.4). In such a situation the easiest way of restoring dune heath is simply to clear-fell the trees and allow the seed-bank to re-establish itself. Litter may be left in situ if the trees were younger than about 20 years. At Tentsmuir it may be necessary to control the Betula regrowth and any subsequent pine seedlings while they are young, to prevent a repetition of the succession to woodland.

## 4.6 Conversion to mixed or deciduous woodland

The older plantations at all three study sites, especially those in their second rotation at Ainsdale, have become colonised by many plants typically found in native woodlands. Older plantations have also been shown to support a bird population increasingly similar to broad-leaved woodland (Avery & Leslie, 1990). In time, and with suitable management, a dune plantation may become a valuable conservation feature. This may have particular value in Britain, where there is little natural dune woodland. However, a more natural woodland habitat may be developed from existing plantations by completely or partially removing the pines; although defining what is natural may not be easy at sites such as Tentsmuir which are close to the range of natural *Pinus sylvestris* woodlands.

Allowing an area to develop a woodland cover after clear-felling is possiby one of the easiest options for a clear-felled site. The woodland soil of an old plantation is better suited for tree growth than restoring unplanted dune vegetation and many woodland species may already be present. A young regenerating woodland can have some conservation interest in its own right, for example, by providing suitable habitat for nightjars (A. Duckells, pers.comm.). However, problems such as lowering of the water-table and increased shelter to unplanted areas will continue for as long as there is woodland on the dunes.

At the North Holland Dune Reserve, in the Netherlands, pines have been thinned and interplanted with deciduous trees to diversify the canopy structure (F. van der Meulen, pers.comm.). At Ainsdale N.N.R. a site clear-felled during the Second World War was replanted with Quercus robur, Betula pendula, and Fagus sylvatica in about 1950 (plate 17). As the trees are maturing a mull humus is developing, and several previously unrecorded species of woodland plants and animals have colonised the area.

A deciduous woodland may form by more natural processes following clear-felling. As a plantation matures its seed-bank may accumulate bird-dispersed seed from tree and shrub species (section 3.4), and if wind-dispersed seeds of trees such as Betula, Salix and Populus species are in the locality a scrub-woodland may form within a few years of felling. This will depend upon the surroundings. The developing woodland in the Ainsdale fire-breaks is dominated by Betula and pines regenerating from seed. The gradual change of woodland types by thinning and interplanting is preferable mainly because it is unlikely to meet with the same amount of public disapproval as clear-felling, it is also useful as it would not cause the major soil changes or losses of the woodland wildlife associated with clear-felling operation.

## 4.7 Epilogue

This chapter has shown that although it may not always be possible to restore a sand-dune to its original state following afforestation, it is sometimes possible to create a habitat which is very similar. It has also shown that management can develop valuable habitats which may not previously have been present on a site. This presents the dune manager with an interesting choice, and scope for some imaginative and innovative restoration work. It is hoped that this study of the few dune plantations which have been clear-felled for conservation reasons will give managers further insight into ecological changes following afforestation and felling, which will assist in the decision making.

Plate 1. Ainsdale. Much of the afforested area has no herbaceous ground flora (section 3.3.2, vegetation type 8).

Plate 2. Ainsdale. Second rotation, and older, thinned plantations may develop a field-layer dominated by Dryopteris dilatata and Rubus fruticosus (section 3.3.2, vegetation type 9).

Plate 3. Ainsdale. Sheltered plantation edges often develop a rich lichen and bryophyte communities (section 3.3.2, vegetation type 5).

Plate 4. Tentsmuir. The self-sown woodlands at Tentsmuir have a more irregular canopy structure than the plantations at the other sites (section 3.3.4, vegetation type 8).

Plate 5. Tentsmuir. Gaps in the canopy at Tentsmuir allow the survival of pockets of near-natural dune vegetation (section 1.6.3).

Plate 6. Tentsmuir. A site 5 years after clear-felling, now dominated by Rumex acetosella and bryophytes (section 3.3.4, vegetation type 3). Several dune-heath species are regenerating, and Betula is beginning to colonise the site.

Plate 7. Ainsdale. A fire-break clear-felled 10 years ago, in a 50 year old, thinned plantation. The flora is dominated by Chamaenerion angustifolium, Carex arenaria, Rubus fruticosus, Betula and Pinus regeneration and bryophytes (section 3.3.2. vegetation type 6).

Plate 8. Ainsdale; older woodland. A micropodzolised soil profile, showing the deep organic horizons, the pale, leached $E_a$ horizon and the redder developing $B_{fe}$ horizon (section 2.3.2).
Photograph by P.A. James.

Plate 9. Ainsdale. A soil profile from the site shown in plate 7. 10 years after felling the micropodzolised profile is still recognisable. The organic layers are decomposing and now form a compacted mat. There is now more incorporation of organic matter in the upper mineral horizons presumably due to increased root growth (section 2.3.3).

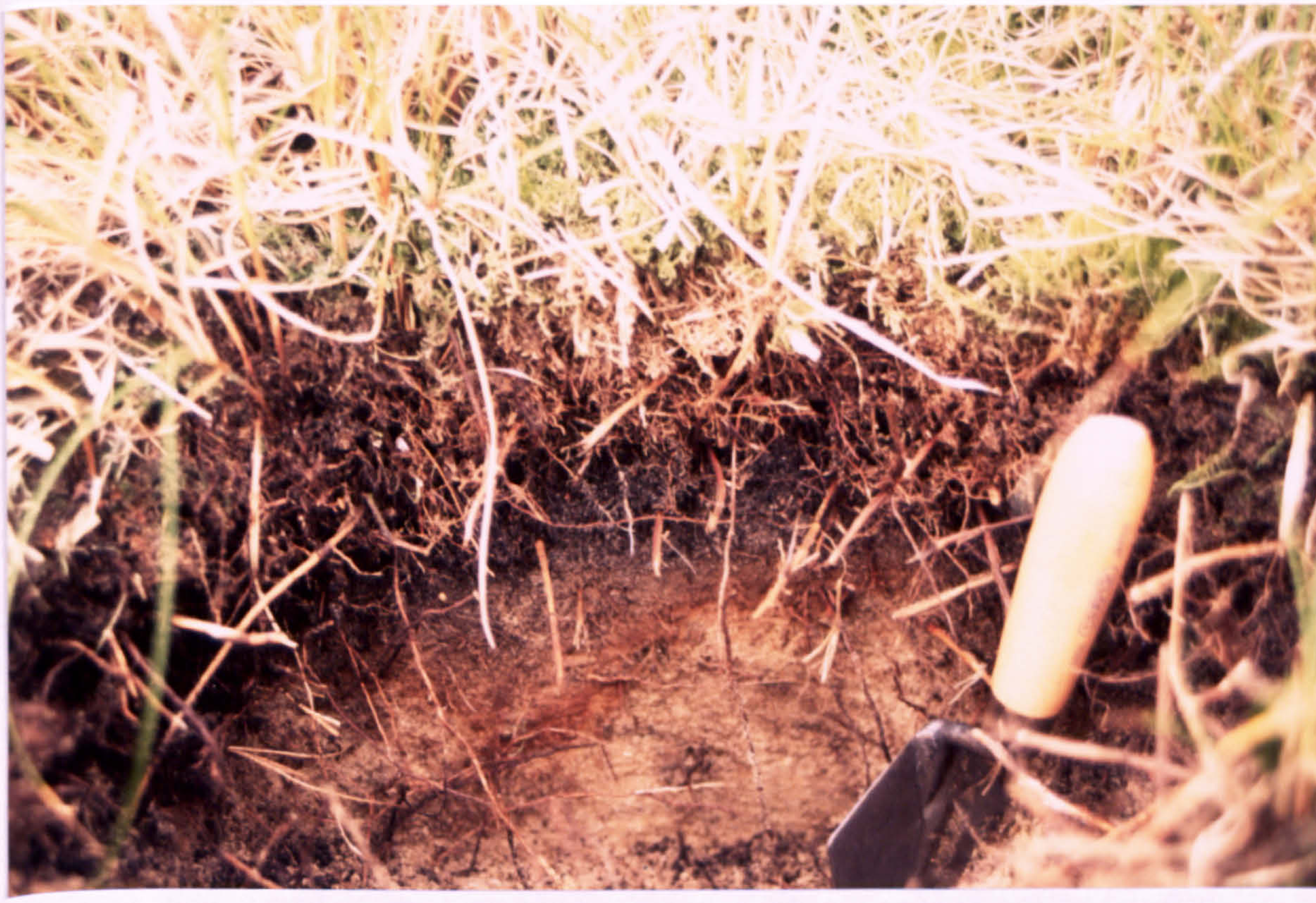


Plate 10. Whiteford. August, 1988. This 30 year-old unthinned area in plantation K has no ground-flora (section 3.2.2).

Plate 11. Whiteford. The same site in August, 1989, following clear-felling the trees during the winter. The flora now includes Senecio jacobaea, Sonchus oleraceus, Chamaenerion angustifolium and Myosotis arvensis (section 3.3.2, vegetation type 5).

Plate 12. Whiteford. An area of plantation K, August, 1989, 10 months after felling. There is vigorous growth of many ruderal species, but very few plants typical of the original dune community (section 3.3.3, vegetation type 5).

Plate 13. Whiteford. August, 1989. This adjacent site, felled at the same time as that in plate 12, had the needle litter removed immediately after felling. It now supports many species typical of the unplanted dunes, including Ammophila arenaria, Carex arenaria, Anthyllis vulneraria, Arenaria serpyllifolia and Viola riviniana (section 3.6).

Plate 14. Whiteford. Clear-felled plantation F. Six years after felling, the vegetation is similar to a typical semi-fixed dune community. However, the appearance of the dunes is still very unlike the unplanted dunes (section 4.2).

Plate 15. Whiteford. This 12 year-old plantation (L?) was felled 17 years ago, and is now virtually indistinguishable from the unplanted dunes (section 3.3.3).

Plate 16. Ravenmeols L.N.R. (Sefton Coast). This plantation was buried by a mobile dune which has since moved on, leaving only these stumps as evidence of the woodland (section 4.2).

Plate 17. Ainsdale. An area clear-felled during 1942 has been replanted with broad-leaved native species to increase the conservation value of the area (section 4.5).

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