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Effects of grazing and nitrogen deposition on sand dune systems.

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EFFECTS OF GRAZING AND NITROGEN DEPOSITION ON SAND DUNE SYSTEMS

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by

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To my parents

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Summary

This study investigated the sand dunes at Newborough Warren, North Wales, UK, between June 2003 and June 2005. The objective was to understand sand dune ecology under perturbation. Specific aims were to analyse the potential of management by livestock grazing to maintain and restore species-rich, open sand dune plant communities, describe the ecology of the seed bank of dune slacks and examine the potential threat of atmospheric nitrogen deposition to dune grassland vegetation.

Long-term grazing management by domestic livestock had a positive effect on vegetation communities, especially in dry dune habitats, and is recommended for sand dune conservation management. Plant species diversity increased after the introduction of grazing management, particularly for annual and biennial species, suggesting improved habitat conditions. Exclusion of rabbit and livestock grazing resulted in the increased abundance of tall, competitive graminoids, probably leading to reduced species diversity over longer time periods.

The dune grassland community responded to nitrogen fertilisation with increases in above-ground biomass. Bryophytes showed increased above-ground biomass and tissue nitrogen concentrations. This could lead to community changes in the long term. It is suggested that the critical load for nitrogen for dune grasslands is below the previously proposed 20 kg ha^{-1} $year^{-1}$, even for heavily grazed areas. The addition of nitrogen led to enhanced levels of germination from the seed bank in the majority of species. Species affected belonged to early successional communities that are threatened by several factors, including eutrophication.

The dune slacks have diverse seed banks, including species of conservation interest and early successional species with persistent seed banks. Thus, the seed bank has the potential to regenerate earlier successional stages after disturbance. Seedlings of important dune slack species were recorded, increasing the scarce information so far available on these species. Further research is needed into the effects of grazing on seed bank composition.

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CHAPTER 1

General introduction

Dactylorhiza purpurella at Newborough Warren

Coastal sand dunes are threatened ecosystems (Houston 1997). Within Europe, their area has declined by about 40 % since 1900 and by about a third since the late 1970s (O'Briain 2005). They have been damaged by a variety of human activities, including agriculture, tourism, coastal defence, housing and industry development (Ranwell & Boar 1986, van der Meulen & van der Maarel 1989, Doody *et al.* 1993, van der Maarel & Usher 1997). Climate change and rising sea levels could further threaten these low-lying habitats (Hansom 2001, Pye 2001, Brown & McLachlan 2002), and atmospheric nitrogen deposition may cause successional change (Rhind 2003). The widespread destruction and degradation of sand dunes in Europe has resulted in a loss of biodiversity and landscape value, and many sites can no longer function as natural sea defence (Doody 2005).

In the face of these threats, it is important to preserve dunes and restore damaged sites where possible. Coastal dunes include some of the last remaining near-natural habitats in Britain (Wynne *et al.* 1995) and represent a floristically rich habitat supporting rare and endangered animal and plant species (Ranwell & Ratcliffe 1977, Doody *et al.* 1993, Houston 1997, Rhind & Jones 1999). Several large British sand dune systems are of international importance for their extent and quality and because they remain relatively intact (Rhind 2003). These are protected through their designation as Special Areas of Conservation (SAC) under the EU Habitats and Species Directive 1992.

As the process of selecting and designating SACs in Europe nears completion, the questions of how to protect and manage these sites become increasingly important (O'Briain 2005). In order to be able to protect sand dune systems of high conservation value, their ecology needs to be understood so that informed decisions can be made as to how to manage these habitats. The present study is a contribution to further the understanding of the ecology of sand dunes. It addresses the threats of overstabilisation, accelerated successional development and atmospheric deposition of nitrogen, and investigates how grazing management can contribute to maintain the high conservation value of these habitats.

The study site is one of the largest remaining intact hindshore dune sites in Western Europe, Newborough Warren, Anglesey, UK. It is designated under British and European law to protect its high diversity of habitats, including shifting dunes, dune grassland and humid dune slacks, and some endangered plant species, e.g. *Petalophyllum ralfsii* and the world's rarest dock, *Rumex rupestris*. Two major threats to present day sand dune systems are addressed: the increased stability observed on many dune sites as a result of a decrease in grazing pressure by rabbits and domestic livestock; and the impact of the increased atmospheric deposition of nitrogen on the vegetation of these naturally nutrient poor habitats.

Livestock grazing is used on many sites as a management tool to counteract the acceleration of succession, loss of early successional vegetation and species diversity resulting from overstabilisation (e.g. Hewett 1985, Kooijman & de Haan 1995, de Bonte *et al.* 1999, Hootmans 2002). Some Dutch studies have indicated that it can also be used to counteract the effects of increased nitrogen deposition (Kooijman & van der Meulen 1996, Kooijman & Smit 2001). However, despite the growing importance of grazing for nature conservation management, the knowledge of conservation grazing on sand dunes is still limited and there is still a need for more long-term studies. The impacts of nitrogen deposition on British sand dunes and its interaction with grazing management are poorly understood, and the provisional range of critical loads (10-20 kg ha^{-1} $year^{-1}$) for these habitats needs further research to validate it (Bobbink *et al.* 2003, Jones *et al.* 2004b). A further aspect of sand dune conservation and remediation relates to the soil seed bank from which vegetation will regenerate. The importance of the soil seed bank as part of a plant population is increasingly recognized, and management may have an impact on potential regeneration from the seed bank (Bekker 1998). Knowledge of the seed bank of an area helps understand and predict the success or failure of conservation and especially restoration measures, and helps identify priority species and communities for nature conservation (Bekker 1998). Despite this, very little information is so far available on the seed banks of many coastal plant communities (Bossuyt *et al.* 2005).

The overall objective of this dissertation was to further understanding of sand dune ecology under perturbation. The aims of the study were to:

- Understand the impact of long-term grazing management on sand dune plant community composition.
- Describe differences in vegetation composition and structure in areas grazed by different combinations of vertebrate herbivores.
- Test the effects of increased atmospheric deposition of nitrogen on dune grassland and its interaction with grazing by rabbits and livestock, and attempt validation of the proposed critical load for dune grasslands.
- Describe the composition of the seed bank of dune slacks in two depth layers.
- Test the effects of increased nitrogen deposition on seed germination to understand how eutrophication might influence seed bank dynamics.
- Analyse differences in the composition of the seed bank in areas with different histories of grazing management in order to understand how livestock grazing might influence the seed bank and thus regeneration of species and the above-ground community.

The specific hypotheses are given below and in the introductions to each chapter.

The dissertation is written in the style of distinct scientific papers, and each experimental chapter is complete with introduction, methods, results and discussion. Because of this, some overlap in the contents of the introduction and methods sections between chapters was unavoidable, but regardless of this it was judged beneficial to present the data in this way. The thesis comprises seven further chapters as follows:

Chapter 2 reviews current knowledge of the ecology of sand dunes, their threats and management.

Chapter 3 introduces the study site, Newborough Warren, Anglesey, UK, giving information on its location and climate, importance for nature conservation, flora and fauna, geological and geomorphological features and management history.

Chapter 4 presents a study of the effects of long-term grazing management on the vegetation composition of sand dunes, analyzing data gained prior to and after a maximum of 16 years of livestock grazing. The aim was to test whether grazing management was successful in counteracting the scrub encroachment and loss of species diversity observed on site in the early 1980s, an issue which was viewed with concern by conservation managers. The hypotheses were that: 1) Livestock grazing increases species diversity. 2) Livestock grazing is especially beneficial for bryophytes and small and short-lived plant species. 3) Livestock grazing can help meet conservation management objectives by leading to the increased frequency of typical plant species. 4) Livestock grazing causes changes in the composition of plant communities. In addition, Ellenberg indicator values were used to test whether the study site might be affected by eutrophication caused by increased atmospheric deposition of nitrogen.

Chapter 5 studied the effects of increased deposition of nitrogen on vegetation composition, sward heights, above-ground biomass and soil parameters and attempted to validate the proposed range of the critical load for dune grasslands. In addition, the effects of rabbit grazing alone and in combination with livestock grazing were investigated, and the hypothesis that grazing can mitigate any potentially adverse effects of nitrogen deposition tested. The possible limitation of the vegetation by phosphorus, not nitrogen, or co-limitation of both nutrients was also addressed. The specific hypotheses were: 1) Fertilisation with nitrogen leads to changes in the composition and structure of the vegetation of fixed dune grasslands. 2) Fertilisation with nitrogen increases above-ground standing biomass. 3) Fertilisation with nitrogen alters soil chemistry and plant tissue chemistry. 4) There are differences in the impact of rabbit grazing alone and rabbit grazing in combination with livestock grazing on vegetation composition and structure. 5) Grazing by livestock and/or rabbits can mitigate any potentially adverse effects of nitrogen deposition. 6) Rabbits graze preferentially in areas with potentially increased food quality.

Chapter 6 investigated the seed bank of dune slacks, describing species composition, seed densities, seed longevity and differences between two depth layers. It is important to know if target species of conservation interest and species of early successional stages form part of the persistent seed bank, so that current site management, aimed at creating disturbance and destabilising the system, can expect to contribute to desired vegetation change through recruitment from the seed bank. In particular, historical records of the above-ground vegetation were used to test the hypothesis that the seed bank reflects earlier successional stages of the vegetation more closely than the current vegetation. It was also hypothesised that differences in diet selection and germination success of seeds after gut passage of different livestock types lead to a different composition of the seed bank in areas which have a history of cattle grazing and areas grazed by ponies.

In Chapter 7, a greenhouse experiment on the effects of increased nitrogen availability on seed germination from the soil seed bank of dune slacks is reported. The hypotheses tested were: 1) Nutrient addition increases total numbers of seedlings germinating. 2) Competitive nutrient-loving species germinate more frequently in nutrient-enriched conditions than species typical of this oligotrophic habitat. If this was found to be true, then it might lead to changes in vegetation structure and composition. 3) Are there any differences in the seed banks of two sampling areas within the same dune slack system?

Chapter 8 represents a synthesis of the experiments, discussing the threats described and the potential of grazing management to maintain and restore species-rich, open sand dune communities.

The plant nomenclature used in this dissertation follows Stace (1997) for higher plants, Smith (1990, 2004) for bryophytes and Coppins (2002) for lichens. Nomenclature of plant communities and sub-communities is based on the National Vegetation Classification (NVC) (Rodwell 2000).

CHAPTER 2

Coastal sand dunes: Ecology, threats and management

Coastal sand dunes at Newborough Warren

Introduction

Coastal sand dunes occur all over the world, in temperate as well as in arid and semi-arid climates. For the development of coastal dunes, an abundant supply of sand is necessary that dries out between the tides and is then transported inland by strong onshore winds. Where it is deposited above the high tide mark, the sediment is trapped by specialised plants that prevent further dispersal (Pethick 1984, Dargie 1993). The sand that is transported from the dry upper shore is usually replenished by wave action on the lower shore (Doody *et al.* 1993). Most transportation of sand occurs during dry weather, in Britain mainly in summer, as only dry sand can be moved (Ritsema & Dekker 1994). This is why dunes are less frequent in the tropics and sub-tropics where lush vegetation, low wind velocities and damp sand conditions preclude their development (Eisma 1997). Sand supply, strength and frequency of onshore winds and the topography of the hinterland are all important factors in determining how far dunes extend inland (Rhind 2003), which can be up to 10 km (Pethick 1984). Dune ridges can rise up to heights of 90 m, but maximum heights in Britain rarely exceed 15-30 m (Ranwell & Boar 1986), with minimum heights as low as 1-2 m (Pethick 1984).

Within Europe, dunes are widespread along the west coasts of France, Belgium, the Netherlands, Denmark and the northern coasts of Germany and Spain (King 1972). In Britain, they are widely distributed around the coastline (Doody 1989). Many important sites are situated on the west coast facing the dominant west winds, e.g. the Hebridean dunes in Scotland and Newborough Warren in Wales, and some on the east coast, including Winterton and Blakeney Point in Norfolk. They are found along an estimated 402 km or 9 % of the coastline of England and Wales (Ranwell & Boar 1986), covering areas of 50002 ha, 11897 ha and 8101 ha in Scotland, England and Wales respectively (Dargie 2000). Forty-three dune sites in the UK exceed 50 ha and are considered to be of national or international importance (DoE 1995). Welsh sand dunes amount to about 18 % of the total UK resource and consist mainly of shell-enriched calcareous sand (Rhind 2003).

Many British dunes are notified as Sites of Special Scientific Interest (SSSI). In Wales, of 34 dune sites surveyed from 1987 to 1990, 24 were designated as SSSI (UK Biodiversity Group 1999) and ten as National Nature Reserves (NNR) (Dargie 1993). Four nationally rare and thirteen nationally scarce higher plant species in Britain occur mainly, or exclusively, on dunes (Dargie 1995), and a number of sand dune species are protected under the Wildlife and Countryside Act 1981, e.g. petalwort *Petalophyllum ralfsii* and dune gentian *Gentianella uliginosa* (DoE 1995, UK Biodiversity Group 1998). Many of the rare species that are a priority for conservation are restricted to a very small number of sites, e.g. shore dock *Rumex rupestris* and belted beauty moth *Lycia zonaria* (Rhind 2003).

Table 2.1 lists the habitats and the number of sites that were designated as Special Areas of Conservation (SAC) under the EC Habitats and Species Directive 1992 in the UK.

Table 2.1. Number of British Special Areas of Conservation (SAC) designated for coastal dune habitats (March 2006, www.jncc.gov.uk). Stars indicate priority features.

EU code	Habitat	
2110	Embryonic shifting dunes	22
2120	Shifting dunes along the shoreline with *Ammophila arenaria* ('white dunes')	32
2130	* Fixed dunes with herbaceous vegetation ('grey dunes')	30
2140	* Decalcified fixed dunes with *Empetrum nigrum*	2
2150	* Atlantic decalcified fixed dunes (*Calluno-Ulicetea*)	10
2160	Dunes with *Hippophae rhamnoides*	1
2170	Dunes with *Salix repens* spp. *argentea* (*Salicion arenariae*)	14
2190	Humid dune slacks	25
21A0	Machairs	8
2250	* Coastal dunes with *Juniperus* spp.	1

Dune types

Five main types of dune system are distinguished according to topography and weather conditions (Ranwell & Boar 1986); all five types are well represented along the British coasts (Doody 1989). Offshore island dunes form under high wave energy conditions and are associated with offshore or barrier islands (Doody *et al.* 1993). Prograding dune systems, nesses and cuspate forelands prograde from an open coast where the prevailing and the dominant wind are in opposition. In Britain, both these types are mainly restricted to the eastern coast of England, e.g. Scolt Head and Winterton in Norfolk (Doody *et al.* 1993). Spit dune systems form as a sandy promontory at the mouth of estuaries, bays or lakes (Ranwell & Ratcliffe 1977), with river sediments as a major source of sand supply for dune building (Dargie 1995). Bay dunes represent the commonest dune type, forming in bays along indented rocky coasts (Goudie 1990) where sand supply is limited (Doody *et al.* 1993). The final dune type, hindshore dunes, develop on extensive sandy coasts where the prevailing wind is also the dominant, transporting the sand inland for considerable distances as a complex series of dune ridges and intervening slacks (Dargie 1993). This dune type is most common on the west coast of Britain (Doody *et al.* 1993). The Scottish machair dunes represent an extreme form of hindshore dune resulting from exceptionally strong winds (Ranwell & Boar 1986). Newborough Warren, Anglesey, is one of the largest remaining intact hindshore dune systems in Europe (Rhind 2003).

Erosion of dunes

Erosion caused by wave action at the coast may undercut dunes (Ranwell & Boar 1986). Rain erosion affects dune slopes (Jungerius & Dekker 1990) and can occasionally cut channels with unstable vertical walls up to 2 m high into low dunes (Ranwell 1955). Another factor causing erosion is wind: even winds of low velocity can readily disturb the sand surface, especially where the protective vegetation cover has been destroyed by plant diseases, overgrazing or trampling (Ranwell & Boar

1986). Jungerius & van der Meulen (1988) found that sand in the mobile dunes is easily moved by wind but less so by water, whereas sand in the semi-fixed dunes resists wind erosion but will be washed from slopes by rainfall.

In 1985, there were hardly any dune systems in Britain that actively accreted to a great extent (Doody 1985), and today many are actively eroding. Radley (1992) observed progradation exceeding retreat only on 21 out of 127 surveyed English dune sites, and Dargie (1993) concluded that there are considerably more sites eroding than advancing in Wales. Human activities such as sand extraction or modification of the nearby coastline, inappropriate grazing management or recreational pressure are all factors that can lead to erosion. There are no new extensive dune systems building up at present (Packham & Willis 1997). One reason for this might be that sediment supplies for dune building are more restricted than they were in the past due to long-term geomorphological changes (May 1985, Hansom 2001).

Dune life

Sand dunes are a rare and specialised habitat (Doody *et al.* 1993). The organisms living on them are exposed to a range of abiotic stress factors: salt spray leading to zonation of plants according to their tolerance or sensitivity to exposure to salt spray (Oostings & Billings 1942, Oostings 1945, Boyce 1954, Malloch 1997); exposure to strong winds (Maun 2004); drifting sand that can have an abrasive effect (Hesp 1991) and bury the exposed parts of plants (Maun 1998, 2004) and seeds too deep to be able to germinate (van der Valk 1974b); poor unstable soils with low nutrient contents (Hesp 1991) and a low water holding capacity at least in the first stages of dune building (García Novo *et al.* 2004) and in surface layers (de Jong 1979); high light intensities (Hesp 1991) and high temperatures on the surface of the sand in summer (Oostings & Billings 1942, Ranwell 1972, Waller 1996). Plant adaptations to these stresses are discussed in Hesp (1991). Wilson & Sykes (1999) showed that sand burial, salt spray and soil salinity may be the most important environmental factors shaping zonation, but soil moisture, soil nutrients and exposure all limit growth and influence the distribution of plants. Factors such as salt spray and burial by sand result in zonation of the vegetation in the foredunes (Oostings & Billings 1942, Maun & Perumal 1999), while water table and nutrient status of the soil are important determinants of vegetation patterns in later dune stages (Studer-Ehrensberger *et al.* 1993). Across the dune profile from foredunes to later stages of dune building, the abiotic stresses decrease (Hesp 1991) while biotic stress from competition increases (Viles & Spencer 1995). These gradients of abiotic factors and the resulting complex mosaic of different habitats according to climate, soil, aspect, ground water table and exposure are the reason for the diversity of the sand dune flora (van Dijk & de Groot 1987, Westhoff 1989, Grootjans *et al.* 1998). Abiotic stresses encountered mainly in the foredunes can also occur in blowouts which interrupt the sequence of plant succession (Hesp 1991).

Dune flora

Dunes support a rich flora (Ranwell & Ratcliffe 1977) with many specialised and often scarce plants and plant communities that are adapted to the difficult conditions for plant growth in this habitat (Doody *et al.* 1993). Some species are confined to dune habitats (van der Maarel & van der Maarel-Versluys 1996, 1997, Rodwell 2000), while others show a wider distribution (Dargie 1993, Akeroyd 1997). In the Netherlands, most Red List species have their main distribution in coastal areas, because their populations in other habitats have vanished as a result of drainage, acidification and eutrophication (Grootjans *et al.* 2002). Rare and protected plant species found on dunes include *Centaurium littorale* (seaside centaury), *Epipactis palustris* (marsh helleborine), *Gentianella uliginosa* (dune gentian), *Liparis loeselii* (fen orchid), *Parnassia palustris* (grass of Parnassus), *Petalophyllum ralfsii* (petalwort) and *Rumex rupestris* (shore dock).

Bryophytes on dunes include pioneer species like *Syntrichia ruralis* var. *ruraliformis*, *Bryum* spp. and *Brachythecium albicans*. These species colonise and stabilise bare sand and raise its organic matter content (Birse *et al.* 1960, Packham & Willis 1997) and are able to survive burial by sand and grow through it (Birse *et al.* 1960, Pluis & de Winder 1990, Martínez & Maun 1999). On more fixed dune grassland, bryophytes can also be a prominent part of the vegetation, e.g. *Rhytidiadelphus squarrosus*, *R. triquetrus*, *Pseudoscleropodium purum*, *Hylocomium splendens* (Rodwell 2000), but the most diverse assemblage is found in slacks (Wrench 2001), e.g. *Campylium stellatum* and *Calliergonella cuspidata*. Slacks are also the habitat which contains most of the rare and protected bryophyte species (Rhind & Jones 1999), some of them, e.g. *Petalophyllum ralfsii* and *Bryum warneum*, growing only in this habitat (Hill 1988). Within Wales, 22 bryophyte species occur only or mainly on sand dunes (Rhind & Jones 1999), dominating the vegetation where intensive rabbit grazing controls the growth of vascular plants (Wrench 2001) or high wind speeds keep the vegetation open (Díaz Barradas *et al.* 1992). Birse & Gimingham (1955) described how the species composition and growth habit of bryophyte communities change in the course of sand dune succession. Lichens are mainly found in semi-fixed and fixed dune grasslands, with *Cladonia* being the most abundant genus (Rhind & Jones 1999).

Dunes also represent one of the most important habitats in Britain for fungi (Rhind & Robertson 2003). Rotheroe (1995) recorded 550 species of macrofungi on sand dunes in Wales, including many species on the British and European Red Data lists, and about ten species of large fungi appear to be solely confined to sand dunes. Most species are found in semi-fixed dunes and dune slacks (Rhind & Robertson 2003). Dunes with a long history of grazing support the most diverse mycoflora (Bratton 2003); fungal diversity decreases significantly on dunes that have become rank due to a lack of grazing (Rotheroe 1995).

A more comprehensive discussion of rare and scarce plant species on Welsh dunes is provided by Rhind & Jones (1999). More detailed descriptions of the plant communities on dunes and their zonation can be found in e.g. Willis *et al.* (1959), Ranwell (1960a), Boorman & van der Maarel (1997), Boorman *et al.* (1997), van der Maarel (1997a), Rodwell (2000). In addition to sand dune communities, British dunes support a range of other vegetation types, e.g. neutral, acidic and calcicolous grasslands, mire, swamp and fen communities, and scrub, heath and woodland vegetation (Radley 1992).

Dune fauna

The dune fauna tends to show similar zonation patterns to plants, with moisture levels, sand movement, salt spray and vegetation cover being the main factors determining their distribution (McLachlan 1991). Species numbers of insects, vertebrates and interstitial fauna increase towards the landward end (McLachlan 1991). A large number of insects have been recorded on dunes (Carter 1988), with Coleoptera, Hymenoptera and Diptera being most abundant (Ranwell 1972, Viles & Spencer 1995). Surveys carried out on the Sefton coast recorded no less than 702 invertebrate species, including three Red Data Book species, 22 nationally scarce species, 23 and 16 species of butterfly and dragonfly respectively along with beetles, bees and wasps (Smith 2000). Studies carried out by Pollet & Grootaert (1996) and Wallis de Vries & Raemakers (2001) show how dune invertebrates can be used as indicators of habitat quality. The spider fauna of dunes is also extensive (Barnes 1953, Duffey 1968, Almquist 1973, Bonte *et al.* 2002), and some snails, e.g. *Cepaea nemoralis* and *Helix aspersa*, benefit from the high availability of calcium (Boaden & Seed 1985, Packham & Willis 1997). A diverse and abundant interstitial fauna can be found in dune soils (McLachlan 1991). Mammals are represented by several species of voles and mice, fox, weasel, mink, polecat, hares and rabbits. Birds such as gulls, terns and strandline waders find important breeding habitats on dunes (Doody *et al.* 1993, van der Maarel 1997a), and birds of prey, e.g. hawks and owls, use them as hunting grounds (Brooks & Agate 1979). Threatened animals living on dunes include sand lizard (*Lacerta agilis*), natterjack toad (*Bufo calamita*), belted beauty moth (*Lycia zonaria*) and dune tiger beetle (*Cicindela maritima*). A comprehensive account of dune animal communities is provided by de Bruyn (1997).

Dune succession

The marked changes that are observed in the vegetation of sand dunes provide a good example of terrestrial succession (Deshmukh 1977). Crawley (1996) describes succession as the 'process whereby one plant community changes into another' (p. 519) as both the abiotic and biotic environment alter. This change in plant and animal composition usually takes place through time, with one stage eventually replacing an earlier one. In sand dunes, however, succession does not only occur in time, but also in space. Different stages of succession can be studied at the same time because they are present within the same dune system (Hepburn 1952, Pethick 1984). This means that for any plant population at a site there are new sites for colonisation available nearby – a situation very different from the classic succession where the different stages do not exist close to each other on a small spatial scale but new colonisation of a certain stage can only be achieved through long-distance dispersal. A consequence of this is that dispersal in space and time is less important in the life cycles of sand dune plants than for most other successional species (Watkinson *et al.* 1977, Packham & Willis 1997).

The following description of the different stages of dune building and associated communities represents a complete succession from the accretion of a foredune to stable dunes with grassland or woodland. However, there are many possible deviations from this scheme, e.g. one or more stages may be absent as can be seen on the west coast of the north Frisian islands where fixed dunes and even older stages can be found right by the strandline (Ellenberg 1988). Additionally, man's influence through afforestation or other development and land use has destroyed the inland parts of many sites, especially the older and more acidic stages of succession (Doody 1985). Thus dune systems with a complete succession have become rare, and it is of major importance to protect these sites (Dargie 1993). Furthermore, this brief description can not take into account the many geographical differences in floristic composition that characterise dunes in different parts of Europe and Britain (Ranwell & Ratcliffe 1977, Westhoff & Schouten 1977, van der Maarel & van der Maarel-Versluys 1997, Provoost *et al.* 2002). For example, lyme grass (*Leymus arenarius*) is increasingly common in northern Britain, whereas wild thyme (*Thymus polytrichus*) is characteristic of southern and western dunes (DoE 1995). Plant communities and sub-communities also vary regionally (Doody *et al.* 1993, Rodwell 2000). Many nationally rare and scarce plant species that belong to the continental and Mediterranean elements of the British flora reach the northern and western limits of their distribution in the dunes of England and Wales (Dargie 1993). For more information on geographical variation within Europe, refer to Westhoff & Schouten (1977), Westhoff (1989) and van der Maarel & van der Maarel-Versluys (1996).

The strandline

The sand that is transported by the wind first comes to rest at the top of the foreshore, where it encounters tidal litter at the high water mark. The wind speed decreases to zero in the lee of the obstacle so sand is deposited (Pethick 1984). Eventually, a long streamlined ridge develops parallel to the wind direction, only growing to a height of a few cm or dm (Ellenberg 1988). These ridges could not develop into dunes if it was not for vegetation, because as soon as an obstacle left by the tides becomes buried in sand, it does not decrease wind velocities and accumulate sand any longer. The strandline plants trap sand just like tidal litter, however they are not buried by the sand but grow up as blown sand settles on them, so that the process of sand trapping can continue (Pethick 1984). Where tidal litter accumulates, it facilitates plant growth by ameliorating the lack of nutrients and soil moisture, instability of soil and high temperatures at the sand surface during the summer which are adverse to the growth of flowering plants on the strand itself (Ranwell 1972). Plants found here at the extreme high water mark are annual nitrophytes and salt resistant strandline plants such as

Cakile maritima, *Atriplex littoralis*, *Honckenya peploides* and *Puccinellia maritima*, creating what is called the strandline or driftline.

Embryo or primary dune

The plants and tidal litter of the strandline trap and accumulate sand to a level just above the high tide mark, thus creating conditions allowing dune pioneer species to establish. Among these the perennial grasses *Elytrigia juncea* and *Leymus arenarius* are most important. They bind the sand together with their fast growing vertical and lateral root and rhizome systems (Boaden & Seed 1985). If their lateral and upward growth can keep up with sand deposition, primary dunes develop. These are a series of unconnected low dunes one or two metres high on the upper slopes of the beach (Pethick 1984), a little further inland than the strandline (Ellenberg 1988). However, the ability of *Elytrigia juncea* and *Leymus arenarius* to build dunes is limited to an annual sand deposition of about 30 cm, and they are not capable of building high dunes (Ranwell 1972), probably because of moisture limitation (Boaden & Seed 1985).

Mobile dunes

The grasses of the primary dunes prepare the way for other species that build the mobile dunes, a ridge of dunes that are now connected because of lateral growth of the primary dunes. This dune ridge is parallel to the shoreline and can reach heights to 30 m high (Doody 1985). There is virtually no soil; an open plant community and a lot of bare white sand characterise this phase (Tansley 1949). Problems for plant life include the low water content and instability of the soil, absence of humus, extreme temperatures and exposure to wind which increases water loss. The dominant species is marram grass, *Ammophila arenaria*, which is the most successful dune builder on British coasts (Deshmukh 1977), and throughout the world it is either *A. arenaria* or

A. breviligulata that create the highest dunes (Ranwell 1972, Ellenberg 1988). These species can keep pace with sand deposition of up to 1 m per year by producing shoots which break through the surface and grow new tufts of leaves (Huiskes 1979). Marram grass grows in thick and tall clumps which reduce wind action considerably, even on the dune crest up to a third (Ellenberg 1988), so that mobile sand is reduced and dune stability increased. Generally, it establishes on the coasts of the North Sea when the primary dunes reach a height of more than 1 m because it can only stand little salt near its roots (Huiskes 1979), unlike *Elytrigia juncea* and *Leymus arenarius* that are tolerant of salinities up to sea water strength for a few hours at a time (Ranwell & Boar 1986). Vigorously growing marram grass is confined to areas of very active sand movement (Willis *et al.* 1959); it suffers when not covered with some fresh sand several times a year and does not grow well on older dunes some distance away from the coast (Ellenberg 1988). The reasons for this loss of vigour are not fully understood (Rodwell 2000, Maun 2004); possible explanations are discussed by e.g. Salisbury (1925), Marshall (1965), Willis (1965), Hope-Simpson & Jefferies (1966), Huiskes (1979), Wallén (1980), Eldred & Maun (1982), van der Putten *et al.* (1988, 1989), Fay & Jeffrey (1992), Little & Maun (1996) and Maun (2004).

Semi-fixed and fixed dunes

Still further inland, fixed dunes develop from mobile dunes, a process that takes much longer (10-20 years) than the development of mobile from primary dunes (Ellenberg 1988). These dunes are furthest away from the shore and thus receive almost no additional nutrients through sand blow anymore. The sand has a low water holding capacity and is easily leached by drainage water, so that in the first stage of fixed dunes soil fertility appears to be at a minimum (Ellenberg 1988). However, in the course of time humus accumulates and both water- and nutrient-holding capacities of the soil increase (Cremona 1988). *Festuca rubra*, *Hypochaeris radicata* and *Poa pratensis* are characteristic species of semi-fixed dune grasslands in those areas where accretion becomes slower and erosion more rare, while soil development has not yet progressed much (Rodwell 2000). In fixed dune grasslands further inland, sand accretion is no longer significant and soil develops. Typical species include *Galium verum*, *Cerastium fontanum*, *Viola* spp. and bryophytes such as *Homalothecium lutescens* (Rodwell 2000), whereas *Ammophila arenaria* and associated species decrease in abundance. Even in these fixed dunes with their increased stability and complete vegetation cover the sand can start moving again whenever the surface is damaged.

Fixed dunes are differentiated according to the nature of the sand into calcareous dunes with shell sand and acidic dunes without shell sand (JNCC 1989). The former are often floristically very rich and characterised by *A. arenaria* in decreasing abundance, *Carex arenaria*, *Festuca* species and numerous herbs, bryophytes, lichens and fungi, forming a varied dune grassland. The acidic dune grasslands, on the other hand, with a low pH of usually less than 5.5, are dominated by *Carex arenaria* and grasses such as *Agrostis capillaris* and *Poa pratensis* along with a small number of dicotyledonous herbs, e.g. *Galium saxatile* and *Lotus corniculatus* (Rodwell 2000).

Dune scrub and woodland

After the establishment of a herbaceous sward, scrubs such as gorse (*Ulex europaeus*) and creeping willow (*Salix repens*) can establish in the dunes. *Calluna vulgaris*, *Erica cinerea* and *Ulex* species together with mosses and lichens can form a heathland on more acidic soils (Chapman 1976). These dune heaths differ from inland heaths because they also contain characteristic sand dune plants such as *Carex arenaria* (DoE 1995). Other components of dune scrub are *Crataegus monogyna*, *Ligustrum vulgare*, *Rosa* spp., *Sambucus nigra* and, native in Britain on the east coast and introduced in other areas, *Hippophae rhamnoides* (van der Maarel 1997b). Dune scrubland eventually develops into the final stage in dune succession, which is woodland or forest, e.g. with *Pinus, Quercus, Populus* and *Abies* species (Boaden & Seed 1985, van der Maarel 1997b). In dune slack woodlands, *Alnus glutinosa* is the dominant species (van der Maarel 1997b). However, the development of scrub or woodland is only possible where grazing does not prevent the establishment of seedlings, and there are probably no extant primary woodlands on dune systems in Britain (Doody 1991, Houston 1997).

Dune slacks

Dune slacks are low-lying, flat areas or hollows that divide one dune ridge from another. The water table reaches or approaches the surface (Ranwell 1955) but can vary considerably with seasons (Grootjans *et al.* 1998). High water levels prevail during winter and spring when the water table commonly rises above the soil surface and inundation occurs (Boorman *et al.* 1997), whereas during the summer months, it can drop to 50-100 cm below the surface (Grootjans *et al.* 1998), sometimes causing drought stress (Roxburgh *et al.* 1994). Ranwell (1972) distinguished three types of slack: semi-aquatic slacks are flooded from autumn to spring with the water table never below 0.5 m from the surface; in wet slacks, the summer water table remains within 1 m of the surface, and bryophytes are particularly abundant; in dry, grass-dominated slacks, it lies between 1-2 m from the surface, and plants rely mainly on rain water. Generally, slacks tend to dry out as their vegetation communities mature and wind blown sand and organic matter accumulate (Houston 1997). Their hydrology can be complex and depends on dune geomorphology, local climate and topography (Vásquez 2004) as well as man-made disturbances such as groundwater abstraction (Grootjans *et al.* 1998).

Depending on their geomorphological history, two types of slack are distinguished: primary slacks develop from sandy beaches that have been shut off from incursions of sea water and come under the influence of a rising freshwater table. Secondary slacks result from erosion and blow-outs of older and vegetated dunes (Boorman *et al.* 1997) when the soil is removed as far as the water table or until a layer of less erodable material, e.g. shell or pebble, is uncovered (Boaden & Seed 1985).

Plant communities of dune slacks depend on the level and seasonal variations of the water table as well as the age of the slack and calcium content, acidity and nutrient status of the soil (Boorman *et al.* 1997). There is a variety of plant communities and sub-communities (Petersen 2000, Rodwell 2000) with a species diversity at least as rich as that of the drier dune habitats (Ranwell 1972). Typical plant species of calcareous wet slacks include *Salix repens*, *Calliergonella cuspidata*, *Potentilla anserina*, *Hydrocotyle vulgaris*, *Carex nigra*, *Galium palustre* and *Equisetum palustre*; drier slack communities include plants such as *Holcus lanatus*, *Festuca rubra*, *Lotus corniculatus* and *Carex flacca* (Rodwell 2000). Detailed studies of the development of slacks were carried out for example by Ranwell (1955) at Newborough Warren and Willis *et al.* (1959) at Braunton Burrows.

Dune slacks belong to the most endangered coastal habitats (Pott *et al.* 1999, Petersen 2000). They represent one of the most species-rich and diverse semi-natural habitats in Europe and are thus of high conservation value (Petersen 2000, Grootjans *et al.* 2002). In Britain, they are amongst the nationally rare habitats (Doody *et al.* 1993), containing several rare and nationally scarce plant species, such as *Epipactis leptochila*, *Equisetum variegatum*, *Liparis loeselii* and *Petalophyllum ralfsii* (Dargie 1995). They are also an important feature of the dune system because many species regenerate frequently or exclusively in slacks (Ranwell 1972).

Seed banks

The seed bank consists of ungerminated, viable seeds buried in the soil and on its surface, representing an invisible part of a plant population that can survive adverse conditions and regenerate a plant community after disturbance (Roberts 1981, Bullock *et al.* 2002, Jentsch *et al.* 2002). The importance of soil seed banks for conservation and restoration purposes is increasingly recognised (Chambers & MacMahon 1994, Bekker 1998), however information on seed longevity is still very limited for plant species of coastal communities (Owen *et al.* 2001, Bossuyt *et al.* 2005).

Studies on seed banks of coastal dunes have mainly focused on dry dune areas or individual species only (e.g. Pemadasa & Lovell 1974a, Mack 1976, Watkinson 1978a, Boorman & Fuller 1984, Westelaken & Maun 1985, Ernst & Malloch 1994, Houle 1996, Rowland & Maun 2001). More recently, work has been carried out in dune slacks (Bekker *et al.* 1999, Bossuyt & Hermy 2004, Bakker *et al.* 2005a), and some studies looked at several different communities and sub-communities along spatial gradients (Looney & Gibson 1995, Owen *et al.* 2001)

Relatively high seed densities that increased with the age of the habitat were found in dune slacks (Looney & Gibson 1995, Bossuyt & Hermy 2004), with the highest densities found in surface layers (Bekker *et al.* 1999, Bossuyt & Hermy 2004). Bossuyt & Hermy (2004) and Bossuyt *et al.* (2005) report a very low contribution of target species to the seed bank, and Bakker *et al.* (2005a) conclude that although target species were part of the seed bank, establishment from the seed bank was rare and dispersal from nearby populations more important. Other studies, however, showed that the seed bank can indeed be reactivated through management measures such as mowing and sod-cutting and contribute to the renewal of threatened plants and communities (Petersen 2004, Leten *et al.* 2005).

Soil nutrient status

Development and characteristics of dune soils are described e.g. by Jungerius (1990), Wilson (1992) and James (1993). Species composition and the vegetation succession described above are related to the changes in organic matter content and acidity of the soil as the dune ages (Bakker *et al.* 1996a).

Soil development is controlled by the interaction of geomorphological and biological processes: where geomorphological processes dominate, blowouts and shifting sands shape the landscape and allow little soil development; where vegetation has developed, plants slow down the wind and reduce erosion, organic matter production is high and soil profiles develop (Jungerius & van der Meulen 1988, van der Meulen 1990). In the foredunes, soil nutrient levels are higher than further inland because of salt spray which is a source of nutrients and organic matter (Gorham 1958, Wilson 1959, Clayton 1972, van der Valk 1974a, Bakker 1990, Rozema *et al.* 1982) and new fresh sand from the beach which is a source of available nitrogen that decreases further inland (Fay & Jeffrey 1992). Main dune soils are usually poor in organic matter and major plant nutrients because they are very soluble and easily leached out (Gorham 1958, van der Valk 1974a, Packham & Willis 1997); severe deficiencies of nitrogen, phosphorus and potassium on dunes have been documented e.g. by Willis & Yemm (1961), Willis (1963), Hassouna & Wareing (1964), Onyekwelu (1972a, b), Pemadasa & Lovell (1974a) and Olff *et al.* (1993). No deficiency of minor plant nutrients was found by Willis & Yemm (1961).

However, along with the succession from foredunes to dune woodland and associated increases in plant cover and biomass, the soil changes and the amount of major nutrients it contains increases. In the more stabilised and vegetated areas more organic matter accumulates and the ability of the soil to retain water and nutrients increases (Ranwell & Boar 1986, Packham & Willis 1997). Carbonates are gradually leached out and humus accumulates as the dune ages, which in the long term results in a growing acidity of dune soils (Willis 1985a, Ranwell & Boar 1986, Jungerius 1990, Kumler 1997a). Soil pH remains neutral to alkaline as long as carbonate concentrations are greater than about 0.3-1 %, after which it declines rapidly (Provoost *et al.* 2002). Great spatial variability in soil pH was found by Isermann (2005) in areas of open vegetation, which declined with increasing vegetation cover, and in dune slacks. Decalcification of dunes with an initial calcium carbonate content of about 3 % takes about 200 years in Britain, but this process may take much longer where the initial lime content reaches 10 % or more (Ranwell & Boar 1986). Van der Meulen & van der Maarel (1993) estimated a rate of decalcification of the dune sand of 1 % per year for a Dutch dune system.

Amounts of nitrogen increase with increasing age, vegetation cover and organic matter accumulation (Ernst *et al.* 1996, Kumler 1997a). For the Wadden island of Spiekeroog, accumulation of nitrogen was estimated at about 10 kg ha^{-1} per year. Nitrogen storage of the topsoil has been shown to increase 3-6-fold within about 50 years, after which mineralization rates drop with increasing dune age (Gerlach 1993, Gerlach *et al.* 1994). A major source for nitrogen is the decomposition of plant litter (Provoost *et al.* 2002). Cain *et al.* (1999) recorded highly variable patterns of nitrogen distribution both in space and time in early successional stages, while in older dunes, this variability decreases. Levels of nutrients contained in rainwater are higher than inland and can significantly supplement the vegetation (James & Wharfe 1984), especially lichens that are able to absorb nutrients directly from rainwater. Allen *et al.* (1968) described the importance of rainwater as nutrient supply for plants.

Possibly of great importance to the nitrogen cycle of dunes are nitrogen fixing plants such as *Hippophae rhamnoides* (sea buckthorn). Soils associated with stands of *H. rhamnoides* have a higher nitrogen content than surrounding areas (Pearson & Rogers 1962, Stewart & Pearson 1967, van Dijk & de Groot 1987), and Stewart & Pearson (1967) estimated that these plants can fix 27-179 kg N ha^{-1} $year^{-1}$ depending on their age. *H. rhamnoides* also accelerates nitrogen cycling through increased rates of mineralization and so aids plant growth (Gerlach *et al.* 1994). Fixation of atmospheric nitrogen by cyanophyta and mycorrhiza are other sources of nitrogen (Stewart 1967, Ranwell 1972, Kumler 1997b). Most dune plants have been shown to be colonised by arbuscular mycorrhizas that aid nutrient uptake, increase tolerance to drought and salt stress and protect against soil pathogens and thus are of great importance to plant growth and establishment (Koske *et al.* 2004). Kumler (1997b) offers a more detailed review of nitrogen fixation in sand dunes.

Algal and microbial mats, especially nitrogen fixing blue-green algae, play an important role by stabilising the soil, reducing erosion, influencing rainfall interception, water infiltration, moisture regime and nutrient cycling (Stewart 1965, Forster & Nicolson 1981, Lange *et al.* 1992, Vásquez 2004). By raising the nutrient content of the soil, microbial mats further colonisation by higher plants; as salinity decreases and soil nutrients and vegetation cover increase further away from the sea, the amount of microbial aggregates decreases (Forster & Nicolson 1981).

Water regimes

The main source of water for dune plants is rain (Ranwell 1972), which is no longer available to plants on dune ridges once it has percolated through the sand to the underlying water table (Boaden & Seed 1985, Boorman & van der Maarel 1997). Capillary rise is poor and restricted to only 30-50 cm above the water table (Willis *et al.* 1959). Because of the low water holding capacity of dune sands (Pye & Tsoar 1990), there is a considerable shortage of water in young dune soils in which only a limited number of plant species is able to establish (Boaden & Seed 1985). Water content of sand more than 50 cm above the water table is usually below 5 % in dry weather and can be as little as 1-2 % near the surface (Willis 1985a). Particle size and organic matter content determine the water holding capacity of the sand (Willis 1985a). Diurnal temperature changes can alleviate the problem because they lead to dew formation which aids survival of shallow rooted plants (Packham & Willis 1997). Patterns of soil moisture and dry bulk density on dunes are described by Ritsema & Dekker (1994).

Water regimes differ considerably between dune ridges, slopes and slacks (Studer-Ehrensberger *et al.* 1993), with tolerance and intolerance of plant species to flooding and anoxic conditions strongly determining boundaries between different vegetation types (Studer-Ehrensberger *et al.* 1993). The clearly defined patterns of distribution of many plant species are due to variations in moisture levels: some species are confined to dry areas (e.g. *Ammophila arenaria*, *Syntrichia ruralis* var. *ruraliformis*), other species that can tolerate waterlogging only occur in wet areas subject to flooding (e.g. *Anagallis tenella*, *Ranunculus flammula*, *Juncus articulatus*), and species such as

Carex arenaria and *Festuca rubra* grow in both dry and wet places (Willis 1985a, Pye & Tsoar 1990).

Plants survive low water availability in different ways: annuals live through dry seasons as seeds, and germinate, flower and reproduce in wet periods, i.e. autumn and winter; perennials either produce a deep rooting system allowing them to reach water at greater depths, e.g. *Ononis repens* with root systems up to 1.5 m long (Willis 1985a), or an extensive shallow rooting system that absorbs as much rain water as possible before it is lost to deeper horizons (Boaden & Seed 1985). Other adaptations for reducing water stress include leaf rolling and hairiness, succulence and cushion growth (Hesp 1991).

Soil development and water regimes in slacks

Soil development in dune slacks is controlled mainly by the fluctuating groundwater table (James 1993). Nutrients that are leached out of the dune ridges into the groundwater can enrich the slacks (Ranwell & Boar 1986, Studer-Ehrensberger *et al.* 1993). This explains why acidic heath, on higher ground, and more base-rich communities improved by nutrient rich groundwater on lower ground can be found in close proximity (Ranwell & Boar 1986). However, generally slacks are oligotrophic habitats in which nutrient availability and biomass production are low (Schat 1984, van Beckhoven 1992), and plant growth is often limited by nitrogen (Dougherty *et al.* 1990, Koerselman & Meuleman 1996, Verhoeven *et al.* 1996, Lammerts & Grootjans 1997, Sival & Strijkstra-Kalk 1999). Organic matter increases faster in slacks than on dry dunes because of lower rates of mineralization (Ranwell 1972). Eutrophication through atmospheric deposition of nitrogen is one major cause of the decline of these oligotrophic habitats and their associated species (Koerselman 1992, Ernst *et al.* 1996), especially basiphilous species of pioneer stages (Lammerts & Grootjans 1997). Ernst *et al.* (1996) described in more detail soil and vegetation development by comparing different age slacks.

The difference between vegetation on dry dune ridges and in slacks is maintained by the often anoxic conditions in slacks due to waterlogging (Studer-Ehrensberger *et al.* 1993, Grootjans *et al.* 1998), which not all species can tolerate (Jones & Etherington 1971, Schat 1984). Some typical slack species, e.g. *Schoenus nigricans*, can relieve anoxia by actively leaking oxygen from their roots, which also helps counteract potentially toxic high concentrations of sulphide under anoxic conditions. As this mechanism is not known from the common later successional species, these may be prevented from establishing so that early successional stages of the vegetation are maintained (Adema *et al.* 2002, 2003). Microbial mats also stimulate the growth of early but not later successional species (Adema *et al.* 2004). Major changes in the vegetation, both in space and time (van der Laan 1979), can result from changes in the hydrology of a slack (Grootjans *et al.* 1991).

For the maintenance of young successional stages with their associated species it is necessary that base-rich groundwater reaches the surface at least during the winter (Adema *et al.* 2002) and a high pH is maintained (Sival *et al.* 1997, Lammerts *et al.* 2001). Slacks which support basiphilous pioneer vegetation are characterised by high biodiversity, low productivity and more or less stable groundwater levels that do not fall to deep levels during the summer months (Lammerts *et al.* 2001). Increased nutrient availability favours more productive vegetation containing fewer species that are characteristic of later successional stages (Adema *et al.* 2005). In slacks with decreasing groundwater levels caused by human activities such as drainage, water catchment or the afforestation of dunes, enhanced soil aeration and increased rates of mineralization contribute to eutrophication (van Dijk 1989, Koerselman 1992). Changes in the vegetation of slacks due to eutrophication have been described by e.g. van der Meulen (1982), van Dijk (1985), van Dijk *et al.* (1985), van Dijk & de Groot (1987), Meltzer & van Dijk (1986) and Lammerts & Grootjans (1997).

Threats and management of coastal dunes

Coastal dunes are vulnerable and threatened ecosystems (Ranwell 1972, Houston 1997, van der Meulen *et al.* 2004). Although amongst the least heavily modified terrestrial habitats (Dargie 1995), many systems have been destroyed, while others can no longer function as sea defence or retain their landscape and wildlife value (Doody 2005). The threats are very diverse and thought to be largely due to human activity (Doody 1985) which has caused extensive changes in the ecology and geomorphology of dunes, e.g. agriculture and grazing (Ranwell & Boar 1986, Smith 2000), water infiltration and extraction for public water supply (van der Meulen 1982, 1997, van Dijk & de Groot 1987, van Dijk 1989, van Dijk & Grootjans 1993), public recreation and tourism (van der Maarel & Usher 1997, Neuhaus & Petersen 1999, Beunen *et al.* 2004), coastal defence (van der Meulen & van der Maarel 1989, Brown & McLachlan 2002), afforestation (Ovington 1951, Hill & Wallace 1989, Sturgess 1993, Sturgess & Atkinson 1993), invasive alien species (Doody *et al.* 1993), sand extraction (Ranwell & Boar 1986, Doody *et al.* 1993), military use (Davies 2001), housing and industry development and fragmentation (Doody *et al.* 1993, Houston 2005). Furthermore, climate change and rising sea levels could threaten these low-lying coastal habitats (van Huis 1989, van der Meulen 1990, Vestergaard 1997, Hansom 2001, Pye 2001, Brown & McLachlan 2002).

Agricultural improvement and development cause the direct loss of dune habitat, afforestation and sea defences lead to the restriction of natural geomorphological processes (Robertson 2002, Brown & McLachlan 2002, Bristow 2003). Both afforestation and water extraction can cause profound changes in the geohydrology through a lowering of the water table (Hill & Wallace 1989, van Dijk & Grootjans 1993), with major consequences mainly for the dune slack habitat. Grazing with livestock and trampling can lead to direct damage of plants, whereas alterations in climate, soil and moisture regimes damage plants indirectly (Carter 1988).

Another threat to many sand dune systems today is that they are more vegetated than they have been for centuries (Houston 1997). Until the 1980s, management mainly aimed at the stabilisation of dunes to protect settlements and agricultural areas in the hinterland. Methods employed to control erosion included building fences, planting and sowing of dune grasses and shrubs, afforestation and access restriction (Boorman 1977, Westhoff 1989, Tibbetts & Martin 1997, Houston 2005). Increased stability of dune systems accelerates succession, fossilises the dunes and prevents the creation of new bare ground, so that the vegetation develops towards scrub and woodland vegetation and younger successional habitats and associated species decline or are lost (Grootjans *et al.* 1988, Westhoff 1989, Edmondson *et al.* 1991, Houston 1997, Tibbetts & Martin 1997, Arens *et al.* 2005).

Since the 1980s, however, attitudes towards dune management have changed and the dynamic nature of sand dunes is increasingly recognised. Management today aims at allowing geomorphological processes, including natural erosion and accretion along the frontal dunes, the creation of blowouts and sand movement across the site. Management measures employed to destabilise dunes and control the growth of vegetation include turf-stripping, sod cutting, the removal of woodland and scrub, mowing and grazing (Houston 2005). Some case studies of management attempting to restore dune mobility and set back succession in order to create new habitats for pioneer vegetation are described by van Boxel *et al.* (1997), Grootjans *et al.* (2001, 2002) and Arens *et al.* (2005). Because of the need to protect developments close to the coast, it is not always possible to allow natural processes; however, current stabilisation projects increasingly acknowledge their impact on vegetation and aim at maintaining biodiversity (Houston 2005). Current issues relating to the nature conservation, restoration and management of coastal dunes in Europe were discussed at an international conference organised by the Coastal Union (EUCC) and the Flanders Marine Institute (VLIZ) in Koksijde, Belgium in 2005 and published as Herrier *et al.* (2005a, b).

The management activities mentioned above were not the only factor leading to the increased stability of many sites. The cessation of traditional forms of use such as sod-cutting and mowing, rabbit farming, marram grass cutting to make mats, nets and ropes all had an impact. Two other important causes will be described in more detail here: the increased atmospheric deposition of nutrients and eutrophication of the naturally nutrient-poor dune habitat; and a general reduction of grazing pressure on dunes.

Atmospheric deposition of nitrogen

Atmospheric deposition of nitrogen is a major problem for the British flora and is expected to remain so for the foreseeable future (NEGTAP 2001). Total nitrogen depositions in the UK have remained relatively unchanged since 1986 (NEGTAP 2001). They are dominated by reduced nitrogen as NH_3 and NH_4^+, mainly from agricultural sources (Huntley & Baxter 2005), whose emissions are difficult to quantify, rendering estimates uncertain (NEGTAP 2001, Erisman *et al.* 2003). Emissions of nitrogen oxides peaked in the 1980s and have since declined by about 40 %, while deposition has declined by about 16 % since 1990 (NEGTAP 2001, Fowler *et al.* 2005). Although wet deposition is declining moderately (NEGTAP 2001), dry deposition of nitrogen remains high (Goulding *et al.* 1998). Within Europe, efforts to reduce nitrogen deposition have not yet resulted in a significant decrease (NEGTAP 2001); indeed N_2O concentrations are steadily increasing, which is influenced by global emission trends (Erisman *et al.* 2003). Because the recovery from eutrophication can lag behind reductions in emissions and deposition rates by decades (NEGTAP 2001), its effects on natural and semi-natural habitats will be felt even after a significant reduction has been achieved. On a world-wide scale, the continued growth of the human population and conversion of natural ecosystems to agricultural land is predicted to increase the problem of eutrophication by nitrogen and phosphorus over the next 50 years (Tilman *et al.* 2001).

In most terrestrial habitats, productivity is limited by nitrogen (Vitousek & Howarth 1991, Bobbink & Lamers 2002). Strongly increased atmospheric deposition over the last half century (Bobbink & Lamers 2002) has led to the increased availability of nitrogen in many habitats, which can result in the decline of species diversity as competitive, nitrophilous species exclude species characteristic of semi-natural habitats (Bobbink *et al.* 1998, Krupa 2003, Huntley & Baxter 2005). This applies especially to oligo- and mesotrophic habitats (Bobbink *et al.* 1998, Krupa 2003), where the effects of nutrient enrichment are most pronounced because they depend on low soil fertility, e.g. species-rich calcareous grasslands (Willems *et al.* 1993). Impacts of eutrophication on British vegetation have been analysed using long-term data by Haines-Young *et al.* (2000, 2003), Smart *et al.* (2003a, b) and Preston *et al.* (2002). The results provide evidence of reduced species richness, a decline of species indicative of infertile situations, and an increase of vegetation typical of more fertile conditions. The effects of ammonia, the dominant nitrogen form in deposition, on habitats and species are reviewed in Pearson & Stewart (1993), Fangmeier *et al.* (1994) and Krupa (2003). Critical loads for eutrophication, i.e. the maximum input into a habitat that is believed not to lead to adverse effects on sensitive elements of the environment (NEGTAP 2001), are thought to be have been exceeded in almost 60 % of the total habitat area in Britain in the period 1995-1997 (Hall *et al.* 2004). This is predicted to decline by 16.3 % in 2010 (Hall *et al.* 2004). However, as emissions of ammonia are forecast to remain unchanged, other authors believe that a reduction of areas exceeding critical nitrogen loads in the short term appears unlikely (Rowe *et al.* 2005).

Sand dunes are a nutrient-poor habitat being mainly limited by nitrogen and phosphorus. Several studies, e.g. Willis & Yemm (1961), Willis (1963), Pemadasa & Lovell (1974a), Boorman & Fuller (1982) and Olff *et al.* (1993), have investigated the effects of fertilisation on sand dune vegetation in order to find out which nutrients limit plant growth. Other studies have examined the effects of increased nutrient supply on selected dune plant species in greenhouse experiments, e.g. Hassouna & Wareing (1964), Willis (1965), Onyekwelu (1972b), Pemadasa & Lovell (1974a), Ernst (1983), Kachi & Hirose (1983), Pavlik (1983) and Houle (1997). A more detailed literature review on the effects of nutrient additions on sand dunes can be found in Jones *et al.* (2002b). These fertilisation experiments are, however, of limited value when evaluating the effects of increased deposition of nitrogen, because they used high concentrations, nutrient mixtures or applied nitrogen only once or very few times per year.

Some Dutch studies have tried to establish the reasons for changes observed in the vegetation of sand dunes over the last few decades, mainly the increased dominance of tall grasses and the loss of open, species-rich grasslands (Kooijman & de Haan 1995, Kooijman & van der Meulen 1996, Veer & Kooijman 1997), and have implicated atmospheric input of nitrogen in these changes (ten Harkel & van der Meulen 1996, Veer 1997, Kooijman 2004). Esselink *et al.* (2003) reported a decline in the fauna of dunes affected by grass encroachment. Sival & Strijkstra-Kalk (1999) quantified nitrogen inputs into dune slacks on Frisian islands and illustrated that this habitat is still sensitive to enhanced atmospheric deposition. The results of these studies suggest that increased nitrogen inputs on dunes can accelerate succession, enhance graminoid growth, and lead to the dominance of tall, dense vegetation, resulting in the loss of herbs, bryophytes and species associated with early successional communities (ten Harkel & van der Meulen 1996, van der Maarel & van der Maarel-Versluys 1996, Veer & Kooijman 1997, Jones *et al.* 2002b). It can also result in increased stabilisation of dunes and reduced rates of blowout development (van Boxel *et al.* 1997). Acidification caused by nitrogen deposition can leach the upper soil layers, causing some small winter annual species that are typical of base-rich dune grasslands to decrease (Westhoff 1989).

Yet although clearly the increased deposition of nitrogen is a major problem, very little is known about its effects on the environment and more research is called for, e.g. interactions between the atmosphere and biosphere, the establishment of critical limits for different nitrogen species, consequences of nitrogen deposition on fauna and the interactions of site management and nitrogen deposition (WHO 2000, NEGTAP 2001, Erisman *et al.* 2003). Another question that needs to be researched is the difference between the continuous input of low concentrations of nitrogen and the deposition of higher doses more quickly (Hooper 2006). Many estimates of ranges of critical loads still require further confirmation (NEGTAP 2001). For dune grasslands, a critical load of 10-20 kg ha^{-1} $year^{-1}$ was suggested for by Bobbink *et al.* (2003) and Jones *et al.* (2002a, b, 2004a). However, these authors call for further work to validate this range, to understand the interactions of nitrogen input and management practices, and to identify indicators of damage caused by excess nitrogen. Moreover, research is needed using realistic nitrogen loads and sites with low background depositions (Bobbink *et al.* 2003).

Rabbit and livestock grazing on sand dunes

Another important factor contributing to the increased stabilisation of dunes is the general reduction of grazing pressure (van der Maarel & van der Maarel-Versluys 1996). The diversity of many dune areas has developed because of a long history of grazing by rabbits (*Oryctolagus cuniculus*) and domestic stock (Ranwell 1972, Boorman 1989b). The rabbit is the most widespread grazer on coastal dunes in Britain (Boorman 1989b), although it is not a native British animal (Thomas 1960). It was introduced to Britain in the 11^{th} century by the Normans and was kept in warrens for hunting as well as for meat and fur until the beginning of the 20^{th} century. The food preferences and diet quality of rabbits have been studied e.g. by Rowan (1913), Southern (1940), Gillham (1955), Watt (1957, 1960, 1981a, b), Myers & Poole (1963), Bhadresa (1977) and Wallage-Drees & Deinum (1986). They graze very selectively, prefer short swards (Oosterveld 1983, Iason *et al.* 2002), avoid rank vegetation and create bare ground by burrowing and scraping (Burggraf-van Nierop & van der Meijden 1984). This habit is important for germination of seedlings (Crofts & Jefferson 1999) and produces a valuable habitat for many invertebrates (Ausden & Treweek 1995).

In the 1950s, the rabbit disease myxomatosis killed about 99 % of the wild rabbit population of approximately 100 million animals in Britain within a couple of years (Thompson 1994, Packham & Willis 1997), and livestock grazing came to an end on many sites (Tibbetts & Martin 1997). This reduction of grazing pressure led to profound changes in the vegetation structure of dunes, with short, species rich swards containing many annuals changing to tall grass and tall herb communities which were gradually invaded by shrubs and characterised by reduced species diversity (Ranwell 1960b, White 1961). The changes in the vegetation following myxomatosis on sand dunes have been recorded by White (1961) at Blakeney Point and Ranwell (1960b) at Newborough Warren. Many dune sites became too stable for such a naturally dynamic habitat (Doody 1991).

Grazing by rabbits and/or domestic stock is regarded as necessary to maintain species-rich dune grasslands and characteristic plants and animals (Doody 1989, Doody *et al.* 1993), and overstabilisation as a result of the reduced grazing pressure on many sites is one of the most serious problems threatening the diversity of dunes (Doody 1991, Dargie 1995). Controlled livestock grazing has been introduced on many sites as a management tool to counteract the effects of grass and shrub encroachment, create a greater diversity of vegetation structure and promote species richness (e.g. Hewett 1985, Massey & Radley 1992, van Dijk 1992, Kooijman & de Haan 1995, Whatmough 1995, de Bonte *et al.* 1999, Hootmans 2002). Stock grazing can also help remove excess nutrient inputs through atmospheric deposition (Kooijman & van der Meulen 1996, ten Harkel & van der Meulen 1996, Kooijman & Smit 2001, Kooijman 2004), and encourage rabbits back to areas they could not repopulate as long as the vegetation was too tall and coarse (Oosterveld 1985, Tibbetts & Martin 1997, Boorman 2004). Although rabbit numbers returned to pre-myxomatosis levels in many parts of Britain by the end of the 1970s (Thompson 1994), livestock grazing is considered the best option for sustainable sand dune management (Houston 1997, Burton 2001), allowing for control over the degree of grazing pressure (Hewett 1985, Harris & Jones 1998). Rabbit populations fluctuate widely as a result of weather conditions, natural population variations and periodic outbreaks of diseases (Boorman 2004).

Consequently, nature conservation can not rely on rabbit grazing alone to maintain short, species rich swards (Crofts & Jefferson 1999), and on some sites, rabbits did not recover from myxomatosis (Willis 1985b, Jones & Etherington 1989, Hurford & Perry 2001).

Depending on the desired effect, different types of grazing animals such as cattle, horses, sheep or goats can be chosen, because they have different food preferences and grazing behaviour and thus produce different effects on the vegetation. However, despite insights gained through experimental research and nature conservation grazing schemes, it remains difficult to predict the impact of different livestock types on different types of grassland precisely (Oates & Bullock 1997), and knowledge of conservation grazing on sand dunes is still limited (Piek 1998).

Conclusion

Sand dunes are one of the most diverse habitats in Britain (Houston 1997). They harbour many rare and protected species and are an important habitat for nature conservation, which is reflected in the designation of many sites under national and international law. The ecology of sand dunes is complex, and the organisms living on them show many adaptations to the often harsh impacts of a variety of abiotic stress factors. They are a habitat that has attracted a lot of scientific interest since the 1950s, when Ranwell conducted pioneer studies on dune ecology (Ranwell 1955, 1958, 1959, 1960a, b). Previous research has focused mainly on plant adaptations, soil development, nutrient limitation, water regimes and vegetation succession. More recently, dune systems have become threatened by increasing stabilisation, the spread of scrub and coarse grasses and the loss of early successional vegetation. The reasons for this development and possible management interventions, e.g. grazing by domestic livestock, are addressed by more recent research. However, although livestock grazing is used as a management tool on many sites, there is still a need for scientific studies and evaluations of its success. The effects of increased atmospheric deposition of nitrogen and its interaction with grazing are not well known, and the range of the critical load for nitrogen for dune grasslands needs validation. The soil seed bank from which vegetation will regenerate is an important part of plant populations and can be important for restoration and conservation measures, but little information is so far available on the seed banks of many coastal plant communities.

Chapter 3

The study site Newborough Warren, Anglesey, UK

Sand dunes at Newborough Warren

The dune system

Newborough Warren lies on the south-west coast of the Isle of Anglesey, North Wales, UK, between the Cefni estuary and the western end of the Menai Strait (National Grid reference SH 400640) (Figure 3.1). Comprising about 1300 ha covered by sand deposits, it is one of the major calcareous dune sites on the west coast of Britain (Rhind *et al.* 2001). Despite the conversion of about 720 ha of open dunes to a conifer plantation from 1947 to 1965, mainly consisting of Corsican pine (*Pinus nigra* ssp. *laricio*) (Gibbons 1994), Newborough Warren is still the fourth largest intact dune system in Britain (Rhind & Sandison 1999). It represents one of Britain's most biologically diverse sand dune systems (Rees 1990) with the dunes showing the full succession of habitats from strandline to shingle, mobile dunes, wet and dry slacks to dune grassland and scrub.

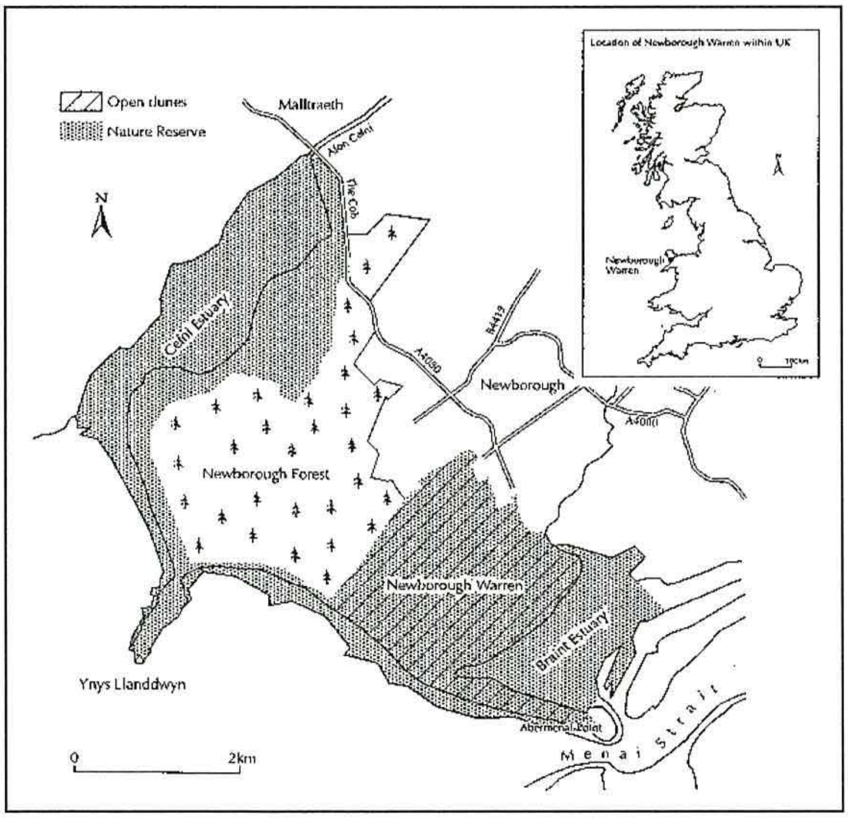


Figure 3.1. The study site Newborough Warren. Copyright: Countryside Council for Wales.

Newborough Warren is the site where pioneer work on the ecology of dunes was carried out by Ranwell (1955, 1958, 1959, 1960a, b). It has remained an important site for scientific research, e.g. studies looking at the structure of grasslands (Morton 1974a, b) and dune slack vegetation (Onyekwelu 1972a, b, c), the ecological effects of the conifer plantation (Hill & Wallace 1989) or the effects of atmospheric nitrogen deposition on dune grasslands (Mohd-Said 1999).

Designations

Because of their biological, geological and geomorphological importance, the open dunes together with associated saltmarshes, foreshore, mudflats, freshwater lake and the tidal island Ynys Llanddwyn have been declared both a Site of Special Scientific Interest (SSSI) and a National Nature Reserve (NNR) in 1955 (Figure 3.2). In 1957, the associated pine plantation, known as Newborough Forest, was also notified as SSSI for its biological and geomorphological interest. In 1995, both SSSIs were amalgamated as Newborough Warren–Ynys Llanddwyn SSSI.

The international importance of the open dunes was acknowledged in 1995 through their proposed designation as Special Area of Conservation (SAC) under the EC Habitats and Species Directive 1992 (Council Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Fauna and Flora 1992) as part of a larger site called Abermenai to Aberffraw dunes (Figure 3.2). This is because of their high diversity of habitats of European importance, including shifting dunes, dune grassland and humid dune slacks, for which Newborough Warren is considered one of the best areas in Britain. Moreover, it contains important populations of the liverwort *Petalophyllum ralfsii* and the world's rarest dock, *Rumex rupestris*, both of which are listed in Annex II of the Habitats Directive, the Red Data Book for Britain (Wigginton 1999, Church *et al.* 2001) and Schedule 8 of the Wildlife and Countryside Act 1981.

The NNR is managed by the Countryside Council for Wales (CCW). Forest Enterprise (FE) own and manage Newborough Forest.

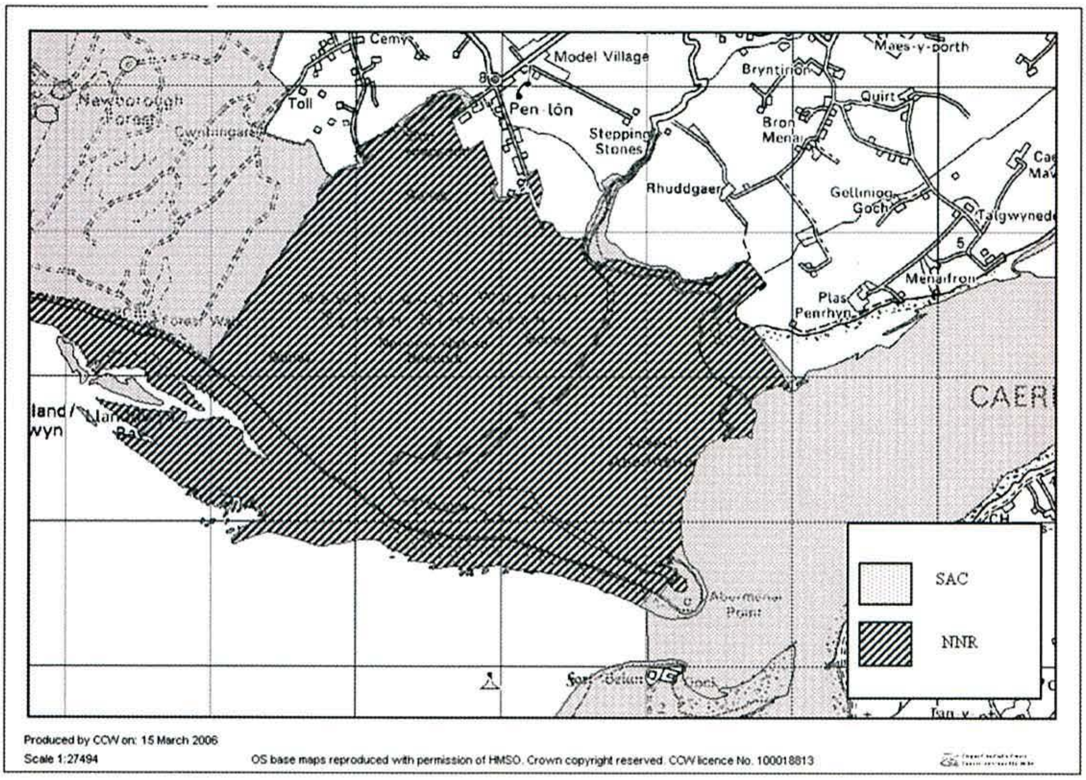


Figure 3.2. Newborough Warren National Nature Reserve (NNR) and parts of the Abermenai to Aberffraw dunes Special Area of Conservation (SAC).

Flora and fauna

Almost six hundred species of flowering plants have been recorded at Newborough Warren, along with rare bryophytes and lichens as well as a rich and outstanding invertebrate fauna (CCW 1995, Dargie 1995) (see Figure 3.3). A number of nationally scarce and rare plant and fungus species are found, e.g. variegated horsetail *Equisetum variegatum*, dune fescue *Vulpia fasciculata*, dune helleborine *Epipactis leptochila*,

Figure 3.3. Some plant species growing at Newborough Warren. Top: *Anagallis tenella* (left) and *Centaurium erythraea* (right), middle: *Centaurium littorale* (left) and *Dactylorhiza purpurella* (right), bottom: *Viola tricolor* (left) and *Potentilla anserina* (right). Pictures taken in June 2005.

seaside centaury *Centaurium littorale* and nail fungus *Poronia punctata*. The site is considered nationally important for the calcareous dune lichens it supports, e.g. *Diploschistes muscorum* (Rhind & Jones 1999). The vertebrate fauna includes water voles *Arvicola terrestris*, brown hare *Lepus europaeus*, pipistrelle bat *Pipistrellus pipistrellus*, skylark *Alauda arvensis* and great crested newts *Triturus cristatus*. Newborough Forest holds an important raven roost. Scarce and rare invertebrates include the small red damselfly *Ceriagrion tenellum*, the hairy dragonfly *Brachytron pratense*, the hoverfly *Eumerus sabulonum*, the mining bee *Colletes cunicularius* and the medicinal leech *Hirudo medicinalis*.

Geology and geomorphology

The site is also important for its geology and geomorphology. A rocky ridge running from north east to south west bisects the dune system and terminates in the large promontory of Ynys Llanddwyn. These Precambrian rocks have been brought to the surface by a major fault (Berw Fault). Most of the dune area is underlain by Precambrian metamorphic rocks of the Mona complex and spilitic lavas of the Gwna group on Ynys Llanddwyn and along the rock ridge (Bristow 2003). Carboniferous limestone and glacial till are thought to underlay the eastern part of the open dunes; however there are no exposures of these (Bristow 2003). The pillow lava exposed on Llanddwyn island is one of the best examples in Britain (Gibbons 2003).

Most of the dunes are quite stable. Only some of the foredunes are actively eroding, while Abermenai point at the eastern end of the site and the Cefni estuary show net accretion (Sandison & Hellawell 2000). The patterns of sediment transport are influenced by the two estuaries that flank Newborough Warren: the Menai Strait on the east and the Cefni estuary on the west. Offshore sandbanks restrict incoming wave energy (Rhind *et al.* 2001). The natural dynamics of the Cefni estuary were altered in the 18th century by the construction of a barrage decreasing the size of the estuary which lead to increased accretion in the estuary (Sandison & Hellawell 2000). The conifer plantation on about half of the dunes also led to a loss of natural geomorphological dynamics ('fossilisation').

The sand at Newborough Warren consists of shell fragments, a small amount of heavy minerals and a large percentage of quartz (Ranwell 1955, 1959). The sand grains mainly fall into the size range 0.1-0.3 mm with a rather uniform soil composition across the dunes corresponding to the Sandwich series as described by Rudeforth *et al.* (1984) (Turner 1999). Soil development is faster in the slacks that are closer to ground water enriched by nutrients leached from dune ridges than in surrounding drier areas (Ranwell 1955).

History of the site

According to Ranwell (1959), a sandy shoreline has almost certainly existed in the Newborough area for several thousand years, and the Newborough Warren dune system in its present form began to build in the fourteenth century. Records of sand inundations destroying agricultural land date back as far as 1409, and in the 16th century efforts were undertaken to stabilise the mobile dunes by planting marram grass (*Ammophila arenaria*) (Ranwell 1959). By the middle of the 17th century the system had become more stable. This period of relative stability, however, ended in the late 19th century, and until the early 1950s the system remained in a very mobile state, with landward movement of dunes and the creation of new dune slacks and blow-outs (Rhind *et al.* 2001).

Previous land uses on the site include activities such as rabbit farming, marram grass cutting to make mats, nets or ropes and low intensity grazing with domestic livestock, mainly cattle or sheep (Rhind & Sandison 1999). However, unlike other large dune sites, there was no system of common livestock grazing on Newborough Warren (Gibbons 1994). Rabbits were introduced by the Normans, and the area was managed as an extensive rabbit warren from the 13th century (Ashall *et al.* 1992, Sandison &

Hellawell 2000). During both World Wars the site was used for military manoeuvres (Rhind *et al.* 2001).

Since the Second World War, these activities have all but ceased, and the dunes were left rather unmanaged (Gibbons 1994, Hurford & Perry 2001). The afforestation of approximately half of the site with conifers from 1947 to 1965 coincided with the cessation of stock grazing, increased atmospheric deposition of nutrients and the decline of the marram weaving industry and rabbit farming due to an outbreak of myxomatosis (Sandison & Hellawell 2000, Rhind *et al.* 2001).

All these factors led to increased stabilisation of the dunes and succession towards more mature vegetation since the early 1950s (Dargie 1995). While mobile dunes and embryonic slacks with open vegetation amounted to about 75 % of the total dune system in the 1950s (Ranwell 1960a), there are hardly any embryonic slacks today and only about 6 % of the site could be regarded as mobile and open in 1991 (Rhind *et al.* 2001). Some marginal areas at the landward end of the dunes, supporting heath, fixed dune grassland and slack vegetation in the 1950s, were lost to agricultural improvement (Rhind *et al.* 2001). Today, the dominant vegetation types at Newborough Warren are semi-fixed and fixed dune grasslands and mature slack vegetation (Rhind *et al.* 2001). There are only few open unvegetated patches that are important for annuals and invertebrates (Hurford & Perry 2001), and successionally young communities and associated plant species are becoming rare (Sandison & Hellawell 2000). Figure 3.4 illustrates how the vegetation cover at Newborough Warren has changed between the 1950s and 1991.

Possibly the most important factor in bringing about these changes was the virtual disappearance of rabbits as a result of myxomatosis which reached Newborough Warren in 1954. The structure of sand dune communities in Europe prior to myxomatosis is thought to have been the product of intensive rabbit grazing (Ranwell 1972), and Newborough Warren was no exception to this (Ashall *et al.* 1992). The disease myxomatosis reduced the rabbit population there so severely that rabbits did not exert any significant influence on the vegetation any longer (Ranwell 1960b).

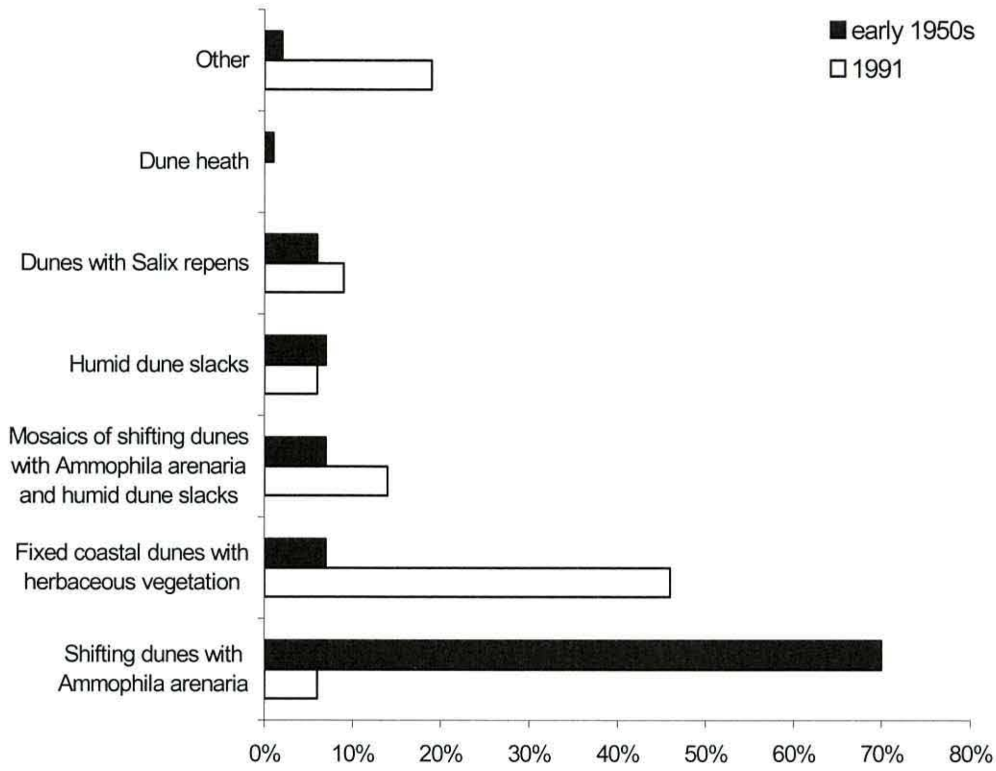


Figure 3.4. Sand dune vegetation cover at Newborough Warren in the early 1950s and 1991 illustrating the decline in shifting dunes and increase in fixed dune vegetation (adapted from CCW & FC (1999)).

The changes in the vegetation following myxomatosis were documented by Ranwell (1960b), who observed an increase in the growth and flowering of grasses and sedges and a decrease in low growing dicotyledonous herbs. Four years later, Hope-Jones (1964) noticed that the vigorous growth of grasses led to a decline of several smaller plant species and that the area of bare sand was reduced because of the spread of the vegetation. After twenty years, scrub species had colonised the dunes (Hodgkin 1984). Overall, the formerly short and species-rich dune sward with many annual plants became dominated by tall grass and herb communities with an ensuing invasion by scrub (Ashall *et al.* 1992). Like many other sites (Tibbetts & Martin 1997), the rabbit population at Newborough Warren never completely recovered from its crash following the outbreak of myxomatosis (Hurford & Perry 2001). It should also be noted that between the 1950s and 1980s, there was hardly any livestock grazing at Newborough (Hurford & Perry 2001). Had there been grazing during this time, then this may have served to counteract the negative effects of undergrazing.

National Vegetation Classification (NVC) communities

Several habitat types with their associated plant communities as defined by the National Vegetation Classification (NVC) can be recognised at Newborough Warren. The following description of communities is based on a survey carried out by Ashall *et al.* in 1992 and discusses only the shingle, strandline and sand dune communities (Rodwell 2000). In addition to these, a range of communities has been recorded at Newborough Warren, including heath, salt marsh and mire communities, woodlands and scrub, mesotrophic and calcifugous grassland communities (Ashall *et al.* 1992).

In the strandline habitat, three rather ephemeral plant communities are found at Newborough Warren. The open pioneer community SD1 (*Rumex crispus – Glaucium flavum* shingle community) is confined to Abermenai point at the eastern end of the site. SD2 (*Honckenya peploides – Cakile maritima* strandline community), the most abundant of the strandline communities, is essentially also a pioneer community; however occasionally it can initiate dune building through sand accumulation (Rodwell 2000). SD3 (*Matricaria maritima – Galium aparine* strandline community) was also recorded at places along the shoreline.

SD4 (*Elymus farctus* ssp. *boreali-atlanticus* foredune community), found at the seaward margin of the dune vegetation, is dominated by *Elymus farctus* ssp. *boreali-atlanticus*, while SD5 (*Leymus arenarius* mobile dune community) has *Leymus* *arenarius* as the only constant species. Above the tidal limit, the vegetation is characterised by the dune-building marram grass *Ammophila arenaria* (SD6 *Ammophila arenaria* mobile dune community). This community comprises the vegetation of mobile sands dominated by marram. It is now only found along the coastal fringe, while it extended up to 1 km inland in the 1950s (Rhind *et al.* 2001). This decline is thought to be a consequence of the conifer plantation changing geomorphological patterns of sand supply and restricting the extent of the mobile dune habitat (Sandison & Hellawell 2000).

Where the sand becomes less mobile, marram is still dominant in the SD7 *Ammophila arenaria – Festuca rubra* semi-fixed dune community, but a more species rich vegetation containing other grasses, perennial herbs and locally extensive bryophyte cover can develop here. In 1991, SD7 was the most abundant community at Newborough Warren (Rhind *et al.* 2001). SD8 (*Festuca rubra – Galium verum* fixed dune grassland) occurs on fixed calcareous sands further inland, has a closed sward consisting of various grasses, dicotyledons and bryophytes and is maintained by rabbit and stock grazing. All five sub-communities of SD8 are present at Newborough Warren. Where grazing pressure is low, SD9 (*Ammophila arenaria – Arrhenatherum elatius* dune grassland) is found, a rank, tall community with often abundant *Arrhenatherum elatius* which differentiates it from other communities. A rather short-lived pioneer community, SD10 (*Carex arenaria* dune community), occurs in small patches amongst fixed dune grassland on recently disturbed or deposited sand. It depends on areas of bare sand that can be created through rabbit or stock grazing and local destabilisation of the system. Another dune grassland community, SD12 (*Carex arenaria – Festuca ovina – Agrostis capillaris* dune grassland), is found on older dunes where more acidic conditions have developed through leaching.

All five NVC dune slack communities are present at Newborough Warren. The pioneer community SD13 (*Sagina nodosa – Bryum pseudotriquetrum* dune slack) is a very rare community with short and open swards, damp in winter but dry on the surface in summer. It is thought to depend both on recurrent submergence and grazing to maintain its short and open swards (Rodwell 2000). Its rarity at Newborough Warren is thought to be the result of the overstabilisation of the system and a lowering of the water table caused by the conifer plantation (Sandison & Hellawell 2000). Another rare vegetation type found in abundance at Newborough Warren is SD14 (*Salix repens – Campylium stellatum* slack community) which occupies young to medium age slacks kept damp by base-rich ground water. This community is characterised by a closed sward, abundant low growing *Salix repens*, a variety of dicotyledonous herbs and extensive bryophyte cover. SD15 (*Salix repens – Calliergon cuspidatum* dune slack community) is found in older and wetter slacks and resembles SD14 in the abundance of *Salix repens*, *Hydrocotyle vulgaris* and *Mentha aquatica*, however *Campylium stellatum* is less prominent and *Carex flacca*, *Agrostis stolonifera*, *Equisetum variegatum* and *Epipactis palustris* are more abundant. A more widespread community is SD16 (*Salix repens – Holcus lanatus* dune slack) found in older and drier slacks, where *Salix repens* forms a bushy canopy associated with various herbs but little bryophyte cover. This community is easily invaded by shrub and trees where grazing pressure is low. SD17 (*Potentilla anserina – Carex nigra* dune slack) is recorded in wet and less base-rich places and is maintained by regular inundation and grazing.

At Newborough Warren, the dry slack community SD16 is expanding at the expense of the wetter communities (Sandison & Hellawell 2000). This is due to overstabilisation and the lowering of the water table following the afforestation of parts of the site with conifers as documented by Hill & Wallace (1989). The considerable depression of the water table by up to 2 metres (Sandison & Hellawell 2000) extends into the unplanted dunes, and Rhind *et al.* (2001) state that standing water during the winter months is much less frequent nowadays than observed by Ranwell (1959) and Onyekwelu (1972a). Robertson (2002) points out that extensive winter flooding is now confined to slacks furthest from the forest. As a consequence, the area of humid dune slacks has decreased and there is no development of new humid slacks (Sandison & Hellawell 2000).

Management of the site

By the 1980s, the development towards later successional stages, the overstabilisation of the system, the spread of scrub and coarse grasses and associated loss of species diversity led to concern among site managers. From the conservation point of view, a sand dune system should preferably consist of all successional stages and communities with their associated species, particularly the early ones (Rhind & Sandison 1999). Experimental work was set up at Newborough Warren by The Institute of Terrestrial Ecology, Bangor (Hewett 1982, 1985) to investigate the effects of controlled grazing by sheep and determine appropriate stocking densities. It was shown that grazing benefited the diversity of the dune grassland, and further enclosures were established subsequently, grazed by ponies, cattle and/or sheep. Then, in the spring of 2001, the grazing regime was changed: the enclosures were opened up and since then about three quarters of the open dunes have been grazed by Welsh mountain ponies all year round at a stocking density of one pony to every 3-4 ha. This grazing regime aims at creating short sward communities with a height of 5 cm or less at the beginning of the spring growing season over at least 70 % of the grazed dune grassland while allowing flowering plants to flourish and set seed in the summer months (Sandison & Hellawell 2000, Hurford & Perry 2001). A sward height of about 5 cm in spring is considered to create and maintain optimal species diversity; *Ammophila arenaria* tussocks, scrub and inflorescences are excluded from this 5 cm limit (Hurford & Perry 2001). All year round grazing by ponies at low stocking densities coupled with rabbit grazing is thought to more closely resemble natural grazing systems comprising large and small herbivores. Unlike grazing in enclosures and in higher stocking densities, in this more natural grazing situation the animals can determine what species they eat at what time of year rather than having to forage whatever is available in the enclosure at any given time. Grazing can also reduce evapotranspiration by creating shorter swards which might benefit the wet slack communities. In order to maintain desired grazing levels it may be necessary to adjust stocking densities in response to fluctuations in the size of the rabbit population.

Invasive scrub and tree species, e.g. sea buckthorn (*Hippophae rhamnoides*) and pine seedlings from the forest, are controlled by cutting and spraying. The forest, the open dunes and beaches at Newborough, as well as Ynys Llanddwyn, are important areas for recreational activities, which is reflected in the numbers of visitors to the National Nature Reserve in the region of 250 000 per year. Visitors are encouraged to stay on marked footpaths and need permits to access any areas other than the beach.

Because of the dynamic nature of sand dunes, management aims at allowing geomorphological processes to occur without restrictions, including natural erosion and accretion along the frontal dunes and sand movement across the site. It is hoped that grazing management will create more bare sand and lead to an increase in the extent of embryonic mobile dunes. Only in the areas most affected by heavy visitor pressure, namely the main entrance onto the beach and the tidal island, may limited management be necessary to protect the frontal dunes from excessive trampling and erosion (Sandison & Hellawell 2000).

At the time of writing, plans to remove parts of Newborough Forest were under ongoing discussion amongst the organisations involved in managing the site, i.e. the Forestry Commission, the Countryside Council for Wales, and the Isle of Anglesey County Council, and other local stakeholders and the local community. The forest is seen as having a negative impact on the nature conservation interest of the dunes by preventing geomorphological processes, e.g. the natural recovery of the frontal dunes after storms and the natural exchange of sand between the dunes and the beach (Robertson 2002, Bristow 2003). The observed lowering of the water table on the open dunes is thought to be due to forest evapotranspiration and rainfall interception and threatens the wet slack communities (Cottingham 1994, Betson *et al.* 2002, Betson & Scholefield 2004). Models suggest that removal of parts of the forest would lead to increased groundwater levels (Betson *et al.* 2002). While the properly managed clearing of parts of the forest would help protect the significant conservation interest of the site, it would still retain the conservation interest and recreational value of the forest. However, local opposition to the plans has resulted in new proposals being drawn up, leading to renewed public consultation.

Climate

The climate of the Isle of Anglesey is essentially oceanic with relatively small seasonal variations in rainfall and temperature. There are no marked extremes of temperature due to its maritime nature and the warming effects of the Gulf Stream (Buchan 1990). Anglesey is warmer and drier than other parts of North Wales, receives more annual sunshine hours, has higher daily temperatures and obtains between 750 and 1000 mm annual total rainfall as opposed to more than 3000 mm in the nearby Snowdonia (The Met. Office 1997).

The information in this section is based on climatological data collected at Valley Royal Airforce station between 1961 and 1990 (Anderson 1994). Located about 15 km north-west of Newborough, this is the nearest meteorological station to Newborough Warren.

Temperature

The proximity of the sea is of major importance for the climate of Anglesey. During the summer, a breeze from the sea has a cooling effect, whereas in winter, when the sea is relatively warm compared to the land, it has a warming effect on coastal areas. Long periods of frost are rare for such a northern latitude. The average mean annual temperature is 12.9 °C. January and February are on average the coldest months with mean temperatures of about 5 °C and average daily minima of 3.2 °C and 2.5 °C respectively, while July and August are on average the warmest months with mean temperatures of about 15 °C, reaching average daily maxima of 18.4 °C and 18.5 °C. These averages are based on data collected at RAF Valley, where temperatures are measured over short grass on an open and exposed airfield site. The conditions on the open sand dunes of Newborough Warren are slightly different from those at RAF Valley, with the maximum daytime temperature probably being higher and the minimal air and ground temperatures being lower over sand than over grass.

Wind

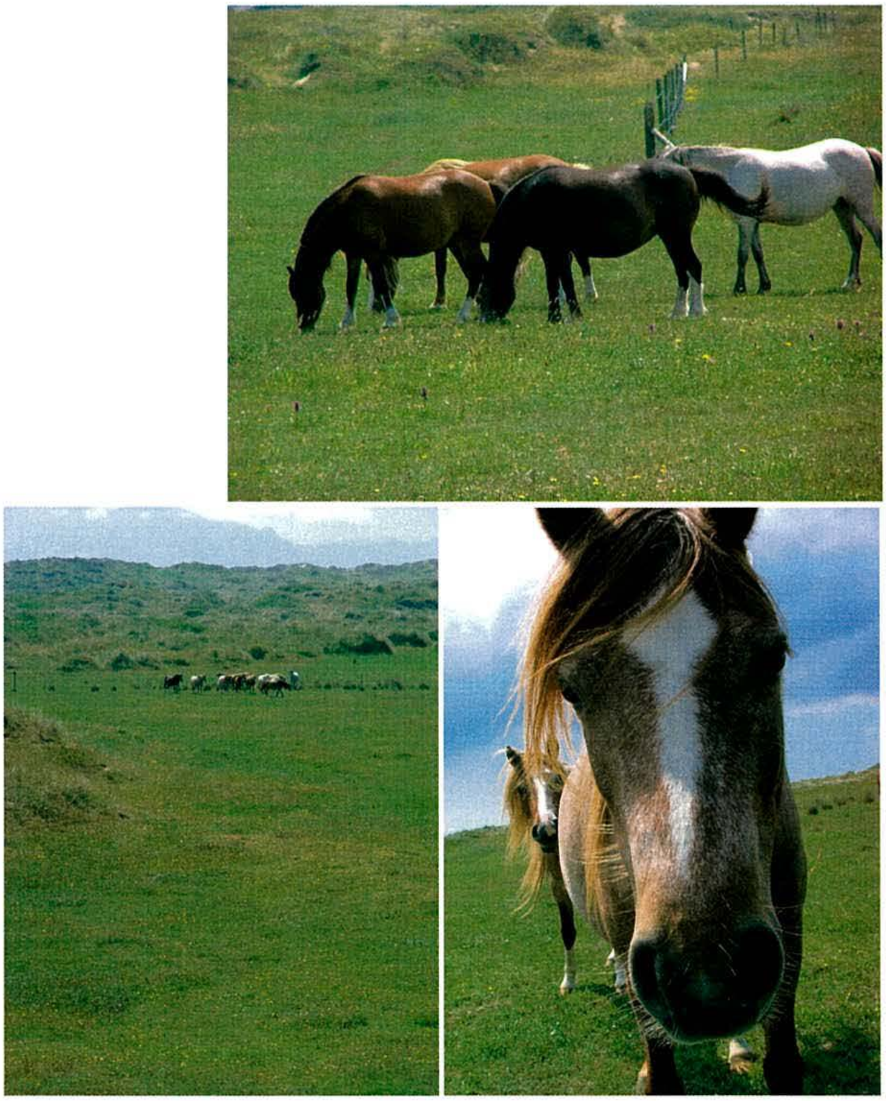
The dominant wind direction at RAF Valley is south-southwest, i.e. off the sea, and the estimated annual average wind speed for Newborough Forest is 11 knots. The coastline at Newborough Warren is very exposed to the prevailing wind and situated over most of its length at right angles to it (Ranwell 1958).

Rainfall

The average annual amount of rainfall is 843 mm, with April to June being the driest months and October to January the wettest. Snow seldom lies on the ground before December and after March, and because of the warming influence of the sea, RAF Valley has less days with snow on the ground than a nearby weather station further inland.

CHAPTER 4

Effects of long term grazing management on sand dune vegetation at Newborough Warren, Anglesey, UK



Welsh mountain ponies at Newborough Warren

Introduction

Sand dunes include examples of the last remaining near-natural habitats in Britain (Wynne *et al.* 1995). They are a floristically rich habitat and important areas for some rare and endangered animal and plant species (Ranwell & Ratcliffe 1977, Doody *et al.* 1993, Houston 1997, Rhind & Jones 1999). Several large British sand dune systems are of international importance, which is reflected in their designation as Special Areas of Conservation under the EU Habitats and Species Directive 1992, e.g. Braunton Burrows, Kenfig and Newborough Warren.

Coastal dunes are vulnerable and threatened ecosystems (Houston 1997, van der Meulen *et al.* 2004). Although amongst the least heavily modified terrestrial habitats (Dargie 1995), they have been damaged by a variety of human activities, e.g. agriculture (Ranwell & Boar 1986), water extraction and infiltration (van der Meulen 1982, van Dijk & de Groot 1987, van Dijk 1989), public recreation and tourism (van der Maarel & Usher 1997, Neuhaus & Petersen 1999), coastal defence (van der Meulen & van der Maarel 1989), afforestation (Ovington 1951, Sturgess 1993, Sturgess & Atkinson 1993), sand extraction (Ranwell & Boar 1986), and housing and industry development (Doody *et al.* 1993). Furthermore, climate change and rising sea levels could threaten these low-lying coastal habitats (Hansom 2001, Pye 2001, Brown & McLachlan 2002).

Another threat to many sand dune systems today is that they are more vegetated than they have been for centuries. They are characterised by increased stability and development towards scrub and woodland vegetation with an associated loss of species diversity (Westhoff 1989, Edmondson *et al.* 1991, Houston 1997, Tibbetts & Martin 1997). This development has been caused by several factors. Active measures have been taken to stabilise dunes, including the afforestation of parts of large dune systems and planting of marram grass (*Ammophila arenaria*) (Westhoff 1989, Jungerius & van der Meulen 1988). Increased atmospheric deposition of nutrients can lead to eutrophication, accelerated succession and the dominance of tall, dense vegetation which result in the loss of species associated with early successional communities (ten Harkel & van der Meulen 1996, van der Maarel & van der Maarel-Versluys 1996, Veer & Kooijman 1997, Jones *et al.* 2002a). It also leads to increased stabilisation of dunes and reduced rates of blowout development (van Boxel *et al.* 1997). Another important factor is the general reduction of grazing pressure on dunes (van der Maarel & van der Maarel-Versluys 1996). The diversity of many dune areas has developed because of a long history of grazing by rabbits (*Oryctolagus cuniculus*) and domestic stock (Ranwell 1972, Boorman 1989a), so that the cessation of livestock grazing on many sites in combination with the rabbit disease myxomatosis virtually wiping out about 99 % of the wild rabbit population in Britain in the 1950s (Thompson 1994, Packham & Willis 1997) led to profound changes in the vegetation structure of dunes. The short, species rich pre-myxomatosis sward containing many annuals changed to tall grass and tall herb communities which were gradually invaded by shrubs (Ranwell 1960b, White 1961). The resulting loss of species diversity concerned nature conservationists to such an extent that experiments to study possible management measures to counteract this development were undertaken. The first study directed at investigating the effects of controlled livestock grazing on sand dunes was set up at Newborough Warren in 1979 by the Institute of Terrestrial Ecology, using various combinations of intensity and timing of sheep grazing (Hewett 1982, 1985). This study has been followed by many others (e.g. Massey & Radley 1992, van Dijk 1992, Whatmough 1995).

Today it is established that grazing on sand dunes has a positive effect on the vegetation, keeping encroachment of trees and shrubs low and creating a greater diversity of vegetation structure, thus promoting species richness (Hewett 1985, Oosterveld 1985, Gibson 1988, Piek 1998). In a shorter sward, more light reaches the bryophyte and lichen layer, so that mosses and lichens develop favourably (Kooijman & de Haan 1995, Whatmough 1995, Piek 1998), and the reduction of biomass of competitive perennial species and the creation of gaps suitable for germination benefits annual species (Pemadasa *et al.* 1974, Boorman *et al.* 1997). Grazing with livestock can also encourage rabbits to come back to areas that they could not re-populate as long as the vegetation was too tall and coarse (Oosterveld 1985). Although rabbits had once more reached their pre-myxomatosis levels in many parts of Britain by the end of the 1970s (Thompson 1994), nature conservation cannot safely rely on rabbits, because their populations show great fluctuations (Crofts & Jefferson 1999) and it is extremely difficult or even impossible to manage and control rabbit grazing (Boorman 1977, Ausden & Treweek 1995). Outbreaks of rabbit haemorrhagic disease (RHD), which has become well established in wild rabbit populations in Britain (Cooke 2002), could also reduce rabbit populations significantly (Tibbetts & Martin 1997). However, it is not yet possible to allow for the effects of this disease in management plans because of a lack of data (Dolman *et al.* 1998). Grazing by domestic livestock allows for much more control over the degree of grazing pressure (Hewett 1985, Harris & Jones 1998) and is considered as the best option for sustainable sand dune management (Houston 1997, Burton 2001). However, the fluctuations in rabbit populations can make setting stocking levels difficult because over- or undergrazing can occur depending on the number of rabbits present (Crofts & Jefferson 1999, Burton 2001). Stock grazing can also be a useful tool for removing excess nutrients deposited through polluted precipitation (Kooijman & van der Meulen 1996, ten Harkel & van der Meulen 1996, Kooijman & Smit 2001) and counteracting grass encroachment (Kooijman & de Haan 1995) which cannot be offset by rabbit grazing alone (Drees & Olff 2001). Further, on large sites it is more practicable than mowing or cutting (van Dijk 1992). The presence of both large and small herbivores can increase plant species diversity because they both can have different effects on recruitment and colonisation processes (Bakker & Olff 2003).

Although much has already been learned, the knowledge of conservation grazing on dunes is still limited (Piek 1998). This case study is a contribution towards a better understanding of the long-term effects of grazing management, analysing vegetation data gained at a dune system in North Wales prior to, and after a maximum of 16 years of livestock grazing from 39 permanent vegetation monitoring quadrats. The aim was to investigate whether grazing management was successful in counteracting scrub encroachment and loss of species diversity, thereby enabling the re-establishment of more species-rich swards. It was hypothesized that: 1) Livestock grazing increases species diversity. 2) Livestock grazing is especially beneficial for bryophytes and small and short-lived plant species. 3) Livestock grazing can help meet conservation management objectives by leading to the increased frequency of typical plant species. 4) Livestock grazing causes changes in the composition of plant communities. In addition, Ellenberg indicator values were used to test whether the study site might be affected by eutrophication caused by increased atmospheric deposition of nitrogen.

Methods

Study site

This study was conducted at Newborough Warren on the south-west coast of the Isle of Anglesey, North Wales, UK (National Grid reference SH 400640). Comprising about 1300 ha of sandy deposits, it is one of the major calcareous and most biologically diverse sand dune systems on the west coast of Britain despite the afforestation of about 720 ha with conifers, mainly Corsican pine (*Pinus nigra* ssp. *laricio*) (Gibbons 1994), between the 1940s and 1960s (Rhind *et al.* 2001). The dune system consists of foredunes and ridges of compound parabolic dunes roughly parallel to the shoreline which are separated by extensive interdune slacks. It comprises the full succession of habitats from strandline to shingle, mobile dunes, wet and dry slacks to dune grassland and scrub and harbours many rare and protected species. Newborough Warren's outstanding conservation value is recognised in its designation as National Nature Reserve (NNR), Site of Scientific Interest (SSSI) and Special Area of Conservation (SAC) under the EC Habitats and Species Directive 1992. This is because of its high diversity of habitats of European importance, including shifting dunes, dune grassland and humid dune slacks, for which it is considered one of the best areas in Britain.

The climate does not show any marked extremes of temperature or rainfall (Buchan 1990) and has an average mean annual temperature of 12.9 °C (Anderson 1994). The average annual amount of rainfall is 843 mm, with April to June being the driest months and October to January the wettest (Anderson 1994).

History of the site

Activities such as marram grass cutting to make mats or ropes, low intensity grazing with domestic livestock, mainly cattle or sheep (Rhind & Sandison 1999), and the usage of the site as an extensive rabbit warren since the 13^{th} century (Ashall *et al.* 1992, Sandison & Hellawell 2000) played an important part in destabilising the system and maintaining it in a mobile state until the early 1950s, with landward movement of dunes and the creation of new dune slacks and blow-outs (Rhind *et al.* 2001). Since the Second World War, however, these activities have all but ceased, and the dunes were left rather unmanaged (Gibbons 1994, Hurford & Perry 2001). The afforestation of approximately half of the site with conifers coincided with the cessation of stock grazing, an increased deposition of atmospheric nitrogen and the decline of the marram weaving industry and of rabbit farming due to an outbreak of myxomatosis (Sandison & Hellawell 2000, Rhind *et al.* 2001).

All these factors led to increased stabilisation of the dunes and succession towards more mature vegetation (Dargie 1995). The changes in the vegetation after the virtual disappearance of rabbits as a result of myxomatosis that reached Newborough Warren in 1954 were documented by Ranwell (1960b), who observed an increase in the growth and flowering of grasses and sedges and a decrease in low growing dicotyledonous herbs. Subsequently, the vigorous growth of grasses and spread of the vegetation also led to a reduction in the area of bare sand (Hope-Jones 1964), and the dunes were colonised by scrub (Hodgkin 1984). Today, the dominant vegetation types at Newborough Warren are semi-fixed and fixed dune grasslands and mature slack vegetation (Rhind *et al.* 2001). Only about 6 % of the site could be regarded as mobile and open in 1991 (Rhind *et al.* 2001), whereas in the 1950s, mobile dunes and embryonic slacks with open vegetation amounted to about 75 % of the total dune system (Ranwell 1960a). Early successional slacks and wet slack communities are declining while mature and dry communities increase (Sandison & Hellawell 2000); the fixed dunes are rank, overgrown and dominated by tall-growing grasses (Hurford & Perry 2001).

Management of the site

By the 1980s, the spread of scrub and coarse grasses and associated loss of early successional vegetation and species diversity led to concern among site managers. From the conservation point of view, a sand dune system should preferably consist of all successional stages and communities with their associated species, particularly the early ones (Tibbetts & Martin 1997, Rhind & Sandison 1999). Thus, in 1987 winter grazing by mixed livestock was introduced at Newborough Warren in a 50 ha enclosure to counteract the loss of diversity through the over-dominance of coarse grasses and scrub and to maintain a range of successional phases. This intervention appeared to have positive effects, and another 137 ha enclosure was established in 1991 for winter grazing by cattle, and in 1996 the grazed area was expanded to include a further 84 ha grazed by Welsh mountain ponies. In early 2000, there were ten grazing enclosures which together amounted to a total grazed area of more than 300 ha and covered two thirds of the dune grassland and dune slacks of the open warren. The enclosures were grazed by either cattle, sheep or ponies only or in combination. In the spring of 2001, the grazing regime was changed and the various enclosures opened up to a herd of Welsh mountain ponies that graze most of the site all year round at a stocking density of one pony to every 3-4 ha. Although rabbits are present on site, the population at Newborough Warren has never completely recovered from the outbreak of myxomatosis (Hurford & Perry 2001).

Vegetation sampling

The original monitoring experiment was set up by McPhail (1987), who established 38 permanently marked quadrats covering the main vegetation communities at Newborough Warren, pairing grazed samples with ungrazed controls of the same community. With the exception of two 4 x 4 m quadrats, all quadrats measure 2 x 2 m. When a new enclosure was set up in the winter of 1991, it contained eight of the originally ungrazed controls. At the same time, eight new controls were established in similar vegetation outside the new enclosure to preserve the grazed/ungrazed comparison. Following the establishment of further enclosures later on, no new controls were set up so that all quadrats are grazed at present. The vegetation in all quadrats was recorded prior to the introduction of grazing, and repeat monitoring was carried out in 1988, 1991, 1992 and 1996 by the Countryside Council for Wales. Table 4.1 provides a summary of years of quadrat establishment and whether or not individual quadrats were grazed in the different years of survey.

The quadrats are located within three major habitat types: wet slacks, dry slacks and dune grassland. When the quadrats were established, they comprised the National Vegetation Classification (NVC) (Rodwell 2000) wet slack community SD14 (*Salix repens – Campylium stellatum* dune slack) and SD16 (*Salix repens – Holcus lanatus* dune slack community), which is usually found in older slacks that seldom flood. The dune grassland quadrats included SD7 (*Ammophila arenaria – Festuca rubra* semi-fixed dune community) and SD9 (*Ammophila arenaria – Arrhenatherum elatius* dune grassland), a rank and tussocky community that develops in the absence of grazing (Rodwell 2000).

In order to determine vegetational changes after up to 16 years of livestock grazing, a total of 39 permanent quadrats was resurveyed in 2003 as part of this study. Six quadrats set up in the mobile dunes and one quadrat established in dune grassland in 1987 could not be relocated in 2003 (Table 4.1). The methodology of this project followed the methods used for previous data collection on the site. For information on quadrat locations refer to Figure 4.1 and for details on quadrat design to McPhail (1987). Field recording was carried out between the beginning of June and mid-July 2003, which is consistent with the time when previous surveys were carried out (McPhail 1987). The abundance of all higher plant species, bryophytes and lichens present in the quadrats was recorded using the Domin scale. This is again consistent with earlier surveys.

Field records from previous surveys were taken into the field and compared to the new records. This allowed a deliberate search for missing species, which means that the absence of a species can be regarded as a real loss rather than a possible oversight. Nomenclature for higher plants follows Stace (1997) and for lower plants Smith (1990, 2004) and Coppins (2002). Nomenclature of plant communities and sub-communities is based on the National Vegetation Classification (NVC) (Rodwell 2000).

Table 4.1. Summary of year of establishment and grazing management in six years of survey for 46 permanent quadrats. Quadrats 19-24 and 26 could not be relocated for the present study and are not included in the analyses. Quadrats 39-46 were only established in 1992 and the only quadrats to be surveyed in that year.

Quadrat number	1987	1988	1991	1992	1996	2003
1	ungrazed	grazed	grazed		grazed	grazed
2	ungrazed	grazed	grazed		grazed	grazed
3	ungrazed	grazed	grazed		grazed	grazed
4	ungrazed	grazed	grazed		grazed	grazed
5	ungrazed	grazed	grazed		grazed	grazed
6	ungrazed	grazed	grazed		grazed	grazed
7	ungrazed	grazed	grazed		grazed	grazed
8	ungrazed	grazed	grazed		grazed	grazed
9	ungrazed	grazed	grazed		grazed	grazed
10	ungrazed	grazed	grazed		grazed	grazed
11	ungrazed	grazed	grazed		grazed	grazed
12	ungrazed	grazed	grazed		grazed	grazed
13	ungrazed	grazed	grazed		grazed	grazed
14	ungrazed	grazed	grazed		grazed	grazed
15	ungrazed	grazed	grazed		grazed	grazed
16	ungrazed	grazed	grazed		grazed	grazed
17	ungrazed	ungrazed	ungrazed		grazed	grazed
18	ungrazed	ungrazed	ungrazed		grazed	grazed
19						
20						
21						
22						
23						
24						
25	ungrazed	ungrazed	ungrazed		grazed	grazed
26						
27	ungrazed	ungrazed	ungrazed		ungrazed	grazed
28	ungrazed	ungrazed	ungrazed		ungrazed	grazed
29	ungrazed	ungrazed	ungrazed		ungrazed	grazed
30	ungrazed	ungrazed	ungrazed		ungrazed	grazed
31	ungrazed	ungrazed	ungrazed		ungrazed	grazed
32	ungrazed	ungrazed	ungrazed		ungrazed	grazed
33	ungrazed	ungrazed	ungrazed		ungrazed	grazed
34	ungrazed	ungrazed	ungrazed		ungrazed	grazed
35	ungrazed	ungrazed	ungrazed		grazed	grazed
36	ungrazed	ungrazed	ungrazed		grazed	grazed
37	ungrazed	ungrazed	ungrazed		grazed	grazed
38	ungrazed	ungrazed	ungrazed		grazed	grazed
39				ungrazed	ungrazed	grazed
40				ungrazed	ungrazed	grazed
41				ungrazed	ungrazed	grazed
42				ungrazed	ungrazed	grazed
43				ungrazed	ungrazed	grazed
44				ungrazed	ungrazed	grazed
45				ungrazed	ungrazed	grazed
46				ungrazed	ungrazed	grazed

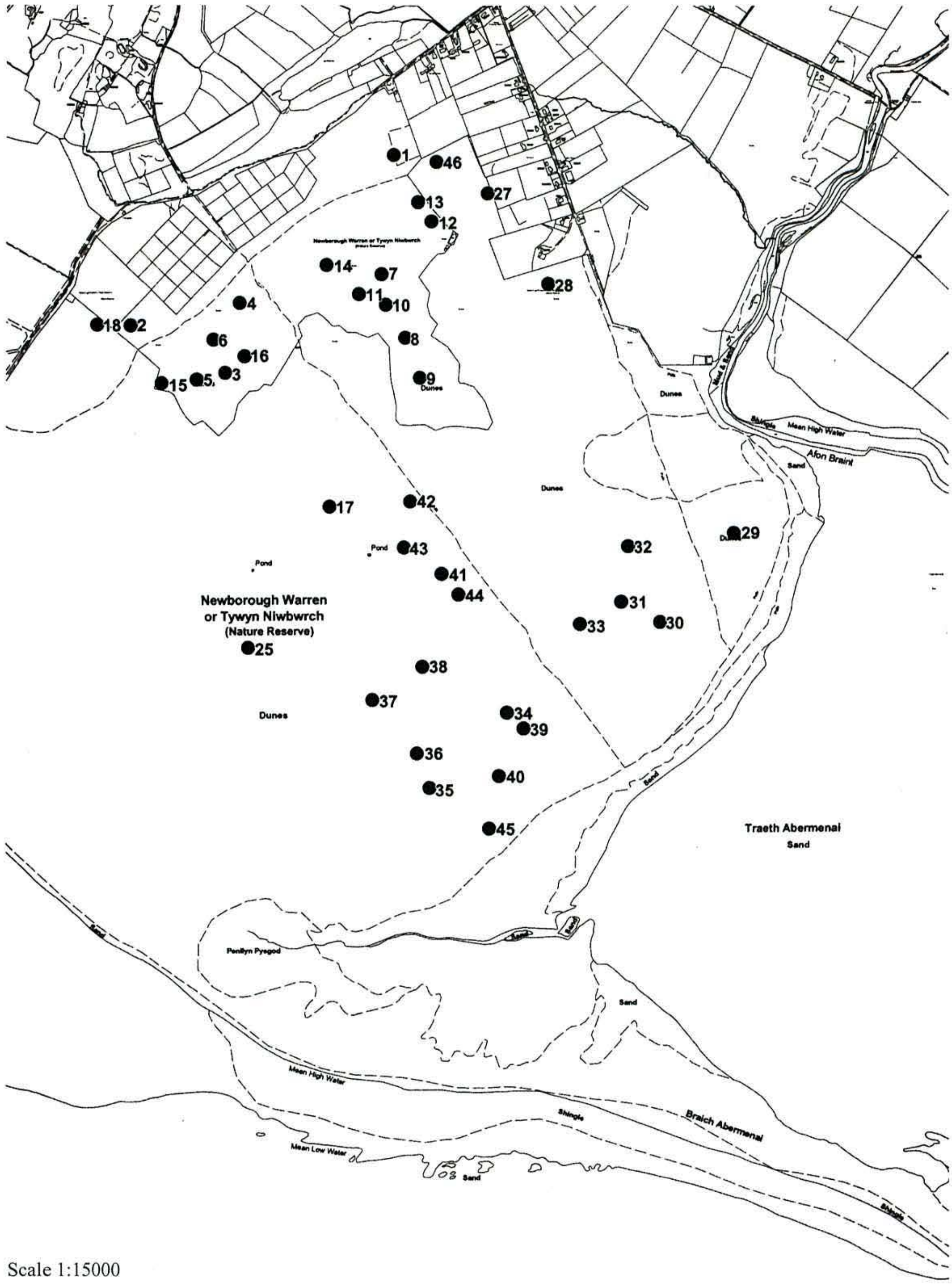


Figure 4.1. Locations of permanent quadrats at Newborough Warren. OS base maps reproduced by Countryside Council for Wales (CCW) with permission of HMSO. Crown copyright reserved.

Data analysis

A Twinspan analysis using standard settings (Hill 1979) was conducted in order to define groups of quadrats with similar floristic composition. To compare the data collected prior to and after the introduction of grazing, the entire data set as well as subsets for each of the habitat groups defined by Twinspan were analysed by Detrended Correspondence Analysis (DCA) using the program package Canoco for Windows 4.5 (ter Braak 1987). National Vegetation Classification (NVC) plant communities and sub-communities were identified using the program Match (Malloch 1992).

Weighted mean Ellenberg indicator values (Hill *et al.* 1999) for light, moisture, reaction, nitrogen and salt tolerance were calculated for each quadrat according to the following formula: Weighted average = $(y_1x_1 + y_2x_2 + \ldots + y_nx_n) / (y_1 + y_2 + \ldots + y_n)$, where $y_1, y_2, \ldots, y_n$ are the abundances of the species 1-n and $x_1, x_2, \ldots, x_n$ are the Ellenberg indicator values for species 1-n (ter Braak 1995). Weighted rather than unweighted indicator values based on presence-absence data were used because changes in species abundance were expected as a result of grazing. These indicator values were used to interpret the position of the quadrats in the ordination diagrams by Pearson correlation with axis scores because no abiotic field data were available.

The effect of grazing on mean species diversity, mean number of perennial, graminoid, annual and biennial, bryophyte and lichen species, the mean number of positive and negative indicator species and average Ellenberg indicator values for nitrogen pre and post-grazing was analysed first by General Linear Model (GLM) analysis by comparing the means of the ungrazed years of survey for each quadrat with the means of the grazed years. Because these means were based on unequal numbers of ungrazed and grazed years for different quadrats, depending on when they became grazed, the number of survey years making up the mean was included as a weighting factor in the analysis. To analyse whether changes also occurred after the introduction of grazing, and whether there was a change in species numbers associated with the number of years that the quadrats had been grazed, a GLM analysis with quadrats as a factor and the number of years since grazing started as a covariate was conducted. Differences between Ellenberg values in different years of survey were analysed by one-way Anova with Tukey's post hoc test.

Lists of positive and negative indicator plant species (Table 4.2) for the different habitats and plant communities in the study area (JNCC 2004) were used to interpret habitat condition.

Results

Habitat groups

Ordination of the whole data set indicated that abiotic factors such as soil moisture were more important determinants of floristic composition than grazing management. Because of this, classification of the ungrazed data by Twinspan analysis was used to define groups of quadrats located in dry and wet dune habitats respectively. The first dichotomy in the resulting classification table divided the samples into a group of quadrats located in dry dune habitats (18 quadrats) and a group of quadrats in slack habitats (21 quadrats) (Figures 4.2 and 4.3). These were then analysed separately, once again by Twinspan classification to determine different groups of quadrats within each habitat, and by Detrended Correspondence Analysis (DCA) to establish trends in the vegetation data in relation to grazing management.

The number of species per quadrat was not significantly different between the two habitats. Quadrats in dry dune areas supported significantly more annual and biennial species than quadrats in dune slacks, both before and after the introduction of grazing management (Mann-Whitney test, ungrazed: $p=0.004$, $U=567$, $N=85$, grazed: $p<0.001$, $U=550$, $N=94$). Although quadrats in both habitats contained about the same average number of bryophyte species, total bryophyte species richness was greater in wet slack quadrats pre- and post-grazing. For graminoids, significantly more species were recorded in slack than dry quadrats after grazing management started (Mann-Whitney test, $p=0.019$, $U=797.5$, $N=94$).

Table 4.2. Positive and negative indicator species for dune grasslands and dune slack habitats (JNCC 2004).

Calcareous dune grassland (SD7, SD8, SD9):

Positive indicator species:			Negative indicator species:
Aira praecox	*Hypochaeris radicata*	*Rhytidiadelphus squarrosus*	*Senecio jacobaea*
Carex arenaria	*Linum catharticum*	*Rhytidiadelphus triquetrus*	*Rosa* spp.
Carex flacca	*Lotus corniculatus*	*Thymus polytrichus* ssp. *britannicus*	*Cirsium arvense*
Cerastium fontanum	*Luzula campestris*	*Tortula muralis*	*Cirsium vulgare*
Cladonia spp.	*Odontites verna*	*Trifolium repens*	*Urtica dioica*
Crepis capillaris	*Ononis repens*	*Sedum acre*	*Lolium perenne*
Erodium circutarium	*Peltigera* spp.	*Veronica chamaedrys*	*Arrhenatherum elatius (not SD9)*
Euphrasia officinalis	*Pilosella officinarum*	*Viola canina*	*Pteridium aquilinum*
Festuca rubra	*Plantago lanceolata*	*Viola riviniana*	*Rubus fruticosus*
Galium verum	*Prunella vulgaris*	*Viola tricolor*	
Geranium molle	*Rhinanthus minor*		
Hypnum cupressiforme			

Dune slacks (SD13, SD14, SD15, SD16, SD17):

Positive indicator species (SD13, SD14, SD15, SD16 (part), SD17):		Negative indicator species:
Anagallis tenella	*Lotus corniculatus*	*Arrhenatherum elatius*
Calliergonella cuspidata	*Mentha aquatica*	*Cirsium arvense*
Camylium stellatum	*Ononis repens*	*Cirsium palustre*
Carex arenaria	*Potentilla anserina*	*Cirsium vulgare*
Carex flacca	*Prunella vulgaris*	*Lolium perenne*
Equisetum variegatum	*Ranunculus flammula*	*Pteridium aquilinum*
Galium palustre	*Salix repens*	*Senecio jacobaea*
Hydrocotyle vulgaris		*Urtica dioica*

Positive indicator species (SD16 with *Salix repens* dominant):	Negative indicator species:
Carex arenaria	*Arrhenatherum elatius*
Carex flacca	*Cirsium arvense*
Euphrasia officinalis	*Cirsium palustre*
Festuca rubra	*Cirsium vulgare*
Lotus corniculatus	*Lolium perenne*
Ononis repens	*Pteridium aquilinum*
Pilosella officinarum	*Senecio jacobaea*
	Urtica dioica

Figure 4.2. Two of the permanent quadrats in the dry dunes. Pictures taken in June 2005.

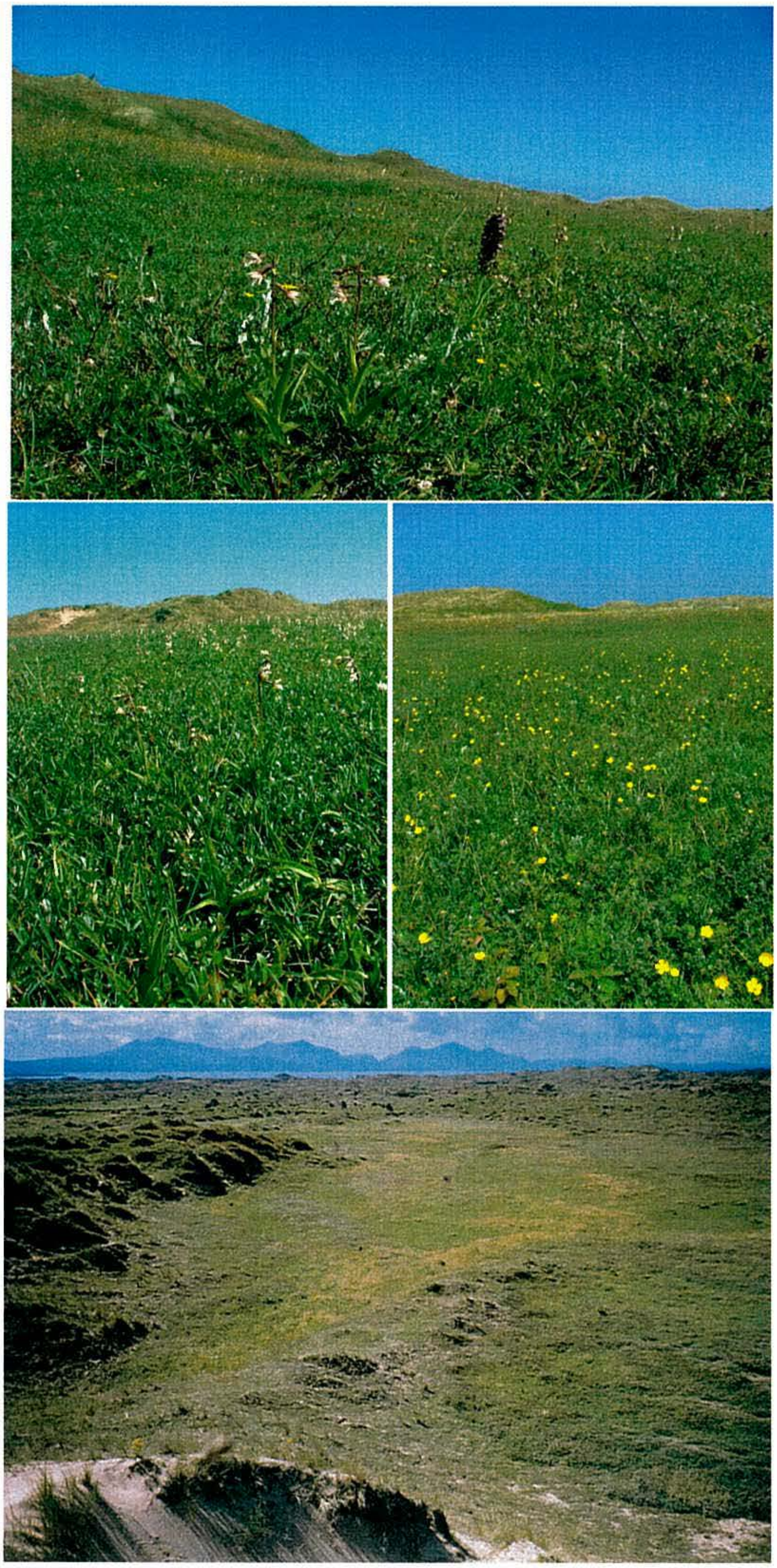


Figure 4.3. Dune slack vegetation at Newborough Warren at some of the sampling sites. Pictures taken in June 2005.

Dry dune habitats

Species richness

The total number of species recorded in dry habitats increased by 42.2 % from 83 in 1987 to 118 in 2003. Total species numbers for different groups of plants in ungrazed and grazed plots are presented in Figure 4.4a. Perennials and annual and biennial species represented the largest of these species groups both before and after the introduction of grazing management.

Average numbers of species per 4 m^2 quadrat were 62.7 % greater in grazed quadrats than the same quadrats before grazing management was introduced, with perennials increasing by 67.8 %, grasses, sedges and rushes by 33.3 %, annual and biennial species by 67.1 % and bryophyte species by 24.9 % (Figure 4.4b). This increase in grazed samples was significant for all these species groups (Table 4.3). Although the average number of lichen species per quadrat more than doubled, this was not significant because they occurred in very low numbers only (Figure 4.4b). Amongst the bryophytes, *Homalothecium lutescens*, *Hylocomium splendens*, *Rhytidiadelphus squarrosus* and *R. triquetrus* increased most in frequency, while *Centaurium erythraea*, *Crepis capillaris*, *Linum catharticum*, *Euphrasia officinalis* agg. and *Rhinanthus minor* increased most amongst the annuals and biennials. *Agrostis capillaris*, *Anthoxanthum odoratum*, *Carex arenaria*, *Festuca rubra* and *Luzula campestris* were the graminoids showing the greatest increase in frequency. Perennial dicotyledonous herbs that benefited from grazing included *Anthyllis vulneraria*, *Hypochaeris radicata*, *Lotus corniculatus* and *Thymus polytrichus*. All species that were recorded in increased frequency post-grazing are characteristic of dry dune communities. Species only recorded in ungrazed and grazed quadrats respectively are listed in Table 4.5. Most of the former only occurred in a single quadrat prior to the introduction of grazing. Similarly, most of the latter were recorded from a small number of quadrats only, however some species, especially *Anthyllis vulneraria*, *Rhinanthus minor* and *Veronica officinalis*, were found in a larger number of quadrats (up to one third of all grazed quadrats). The full data set for the quadrats in dry dune habitats is presented in Appendix 1.1 and 1.2.

Analysis of changes in total species numbers over the years after the introduction of livestock grazing indicates an increase of 1.12 ± 0.16 species per year (Table 4.4). For all species groups except lichens, this increase associated with the number of years grazed was significant (Table 4.4).

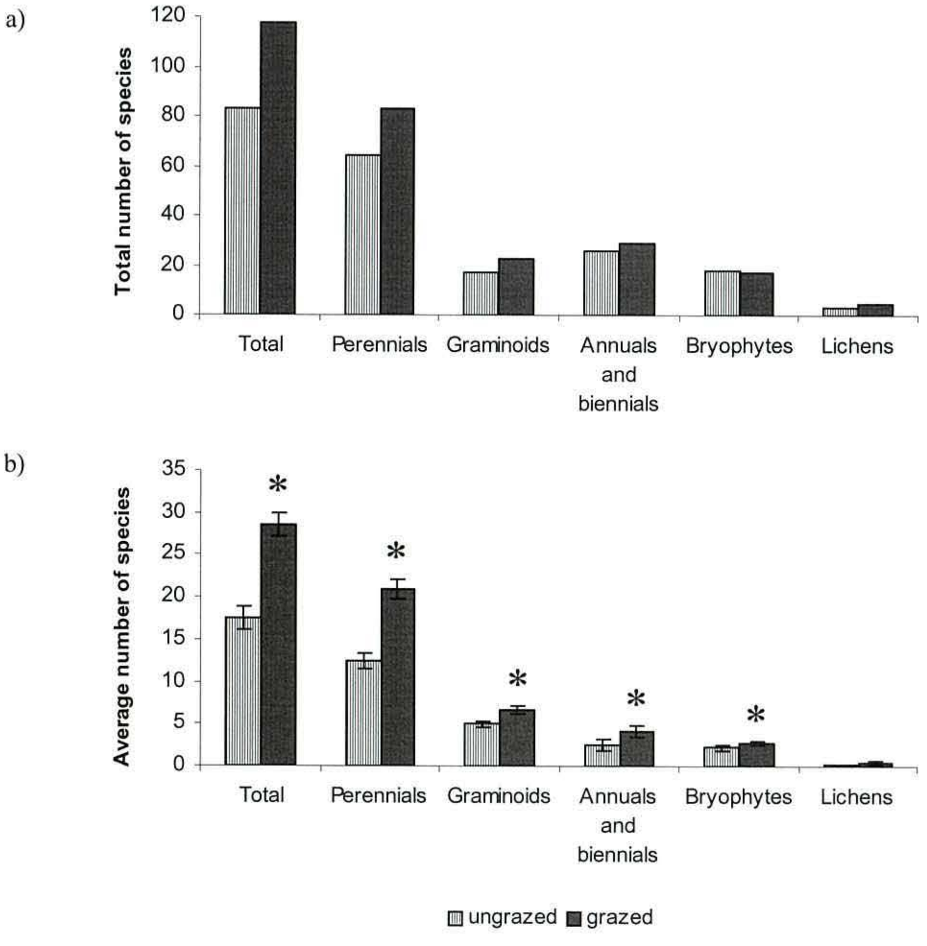


Figure 4.4. Number of total species, perennial, graminoid, annual and biennial, bryophyte and lichen species in dry dune habitats in all years without grazing (ungrazed) and with grazing (grazed). a) Total number of species. b) Average number per quadrat. Bars are standard errors. Significant differences ($p<0.05$) are indicated with a star. For results of statistical tests, see Table 4.3.

Table 4.3. Results of General Linear Modal analysis, comparing the average total number of species, average number of perennial, graminoid, annual and biennial, bryophyte and lichen species in dry dune habitats in all years without grazing and with grazing. Sample size was included in the analysis as a weighting factor because the means were based on unequal numbers of survey years for the ungrazed and grazed situation. Significant p values are in bold. Degrees of freedom (df): grazing treatment, df=1; number of permanent quadrats, df=17; error term, df=17; total error term, df=35.

	p	**F**
Total number of species	**<0.001**	101.24
Perennials	**<0.001**	088.38
Grasses, sedges, rushes	**<0.001**	016.91
Annuals and biennials	**<0.001**	023.85
Bryophytes	**<0.048**	004.53
Lichens	<0.121	002.66

Table 4.4. Results of General Linear Model analysis, testing for changes in the number of species of different species groups in dry dune habitats associated with the number of years since grazing management started. In the analysis, quadrats were included as a factor and years since grazing started as a covariate. Increase per year (± standard error) indicates the increase in the number of species per year after the introduction of grazing management. Degrees of freedom (df): number of permanent quadrats, df=17; years since grazing started, df=1; error term, df=29; total error term, df=47.

	p	**F**	**T**	**Increase per year ± standard error**
Total number of species	**<0.001**	48.27	11.52	1.1203 ± 0.1613
Perennials	**<0.001**	62.99	07.94	0.8202 ± 0.1033
Grasses, sedges, rushes	**<0.002**	11.74	03.43	0.1316 ± 0.0384
Annuals and biennials	**<0.010**	07.62	02.76	0.1495 ± 0.0541
Bryophytes	**<0.006**	08.66	02.94	0.1393 ± 0.0474
Lichens	<0.338	00.95	00.97	0.0167 ± 0.0171

Table 4.5. Graminoids, annual and biennial species, mono- and dicotyledonous herbs, bryophytes and lichens that were only recorded in ungrazed or grazed quadrats respectively for dry dune habitats.

Plant group	In ungrazed quadrats only		In grazed quadrats only	
Graminoids			*Aira caryophyllea* *Briza media* *Dactylis glomerata* *Juncus acutiflorus*	*Juncus bufonius* *Juncus tenuis* *Poa annua*
Annuals and biennials			*Aira caryophyllea* *Gentianella amarella* *Odontites vernus* *Poa annua*	*Rhinanthus minor* *Trifolium campestre* *Trifolium dubium*
Mono- and dicotyledonous herbs	*Cerastium diffusum* *Epipactis leptochila* *Erodium cicutarium*	*Senecio vulgare* *Torilis japonica* *Veronica arvensis*	*Anthyllis vulneraria* *Campanula rotundifolia* *Cardamine pratensis* *Centaurea nigra* *Dactylorhiza purpurella* *Epilobium tetragonum* *Filipendula ulmaria* *Leucanthemum vulgare*	*Parnassia palustris* *Pimpinella saxifraga* *Plantago major* *Prunella vulgaris* *Ranunculus repens* *Rumex acetosella* *Trifolium pratense* *Veronica officinalis*
Bryophytes	*Bryum* spp. *Calliergonella cuspidata* *Lophocolea* spp.	*Pseudocalliergon lycopodioides*	*Barbula* spp. *Camptothecium sericeum*	*Drepanocladus* spp. *Tortella flavovirens*
Lichens			*Cladonia rangiformis* *Hypogymnium physodes*	*Ramalina farinacea*

Species composition and plant communities

The first dichotomy in the Twinspan table within the dry dune habitats separated the communities SD9 (*Ammophila arenaria – Arrhenatherum elatius* dune grassland) and SD7 (*Ammophila arenaria – Festuca rubra* semi-fixed dune community) in the ungrazed data. The group of quadrats identified as SD9 changed into SD8 (*Festuca rubra – Galium verum* fixed dune grassland) after grazing management was introduced, whereas the other group of quadrats has remained SD7 (Figure 4.5). The shift from SD9 to SD8 occurred between 1988, when the quadrats still remained SD9, and the next survey in 1991, when they were identified as SD8 for the first time. In the sample ordination, these different plant communities were clearly separated along the first axis (Eigenvalue 0.5062), and marked changes in the vegetation composition in the quadrats after up to 16 years of livestock grazing are illustrated along the second axis (Eigenvalue 0.2036) (Figure 4.5). Weighted Ellenberg indicator values for moisture, nitrogen, light and salt were significantly correlated with the first axis in the ordination diagram. The second axis was significantly correlated with Ellenberg indicator values for moisture, nitrogen and reaction (Figures 4.5 and 4.6, Table 4.6).

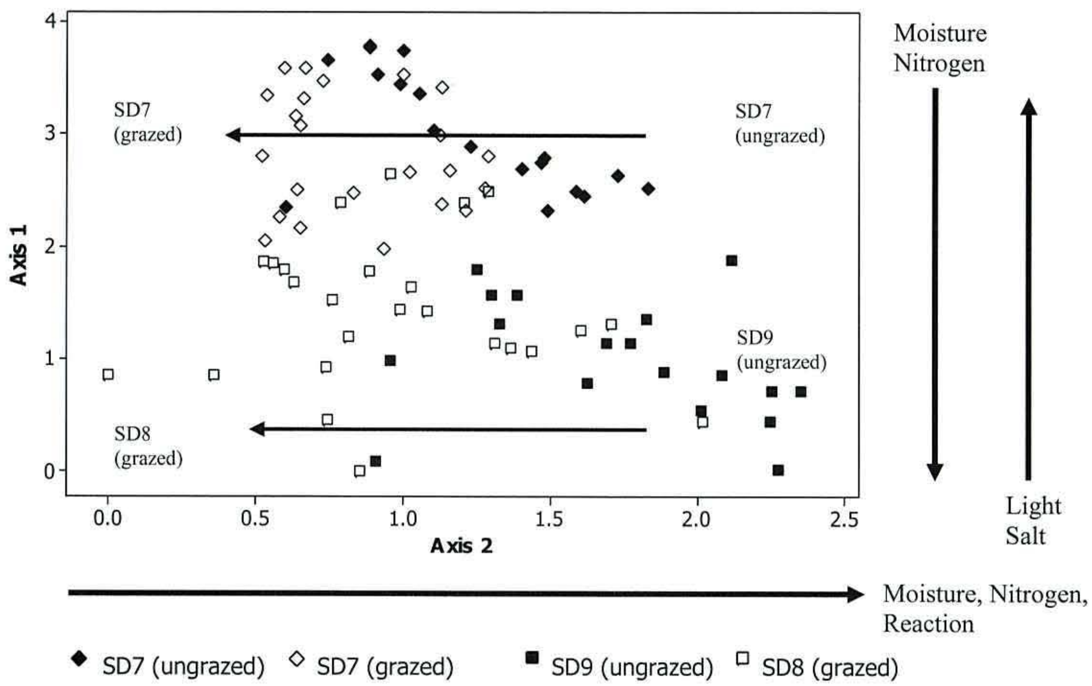


Figure 4.5. Ordination of vegetation samples in dry dune habitats by Detrended Correspondence Analysis (DCA) ungrazed (closed symbols) and grazed (open symbols), showing how samples identified as plant community SD7 prior to the introduction of livestock grazing remained SD7 after grazing management started, while samples identified as SD9 while ungrazed changed to SD8. Eigenvalues: axis 1=0.5062, axis 2=0.2020. Arrows on the right and bottom indicate increases in moisture, nitrogen, light, reaction and salt along axis 1 and axis 2 derived from Ellenberg indicator values.

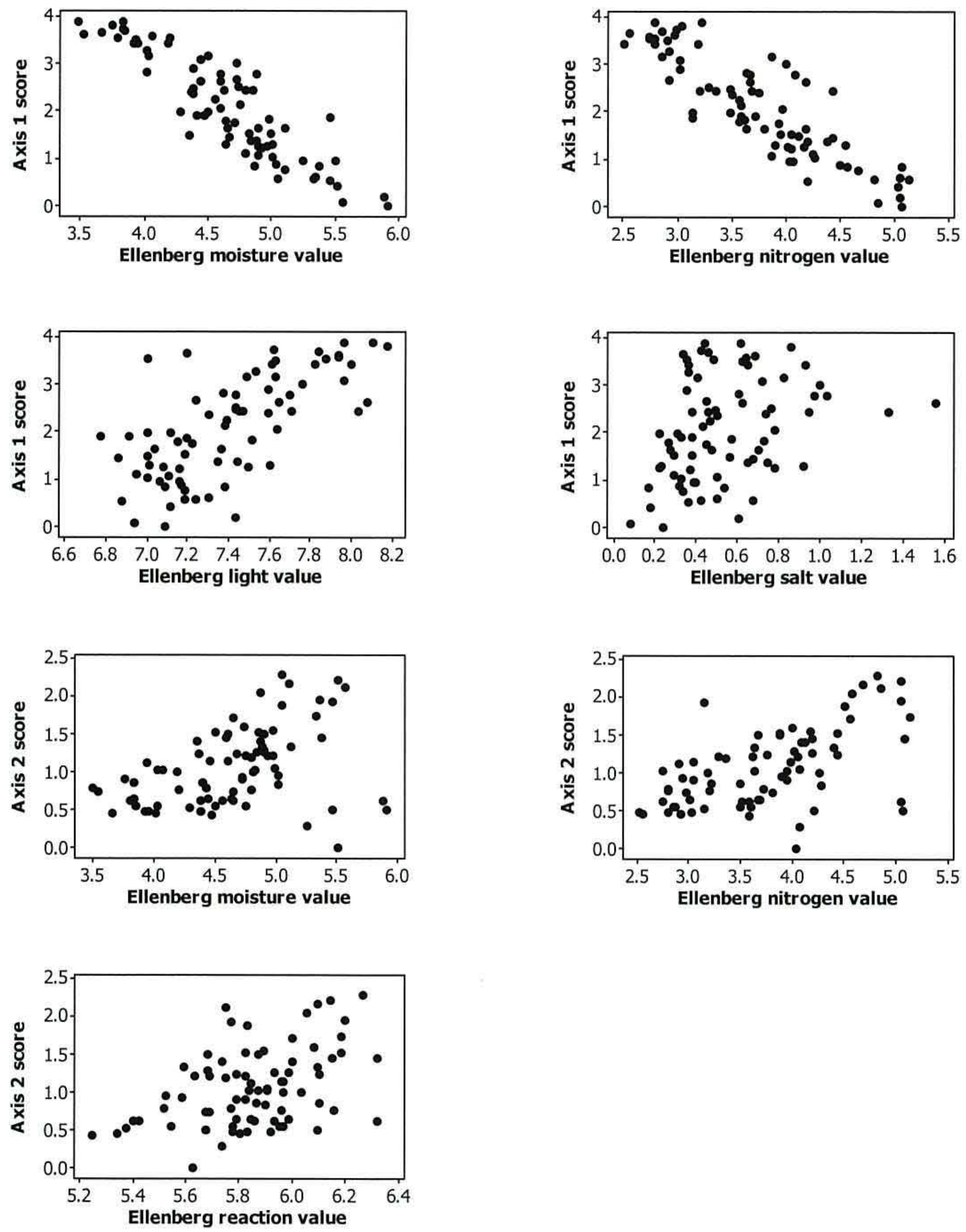


Figure 4.6. Relationship between weighted Ellenberg indicator values and sample scores on axis 1 and axis 2 of the Detrended Correspondence Analysis (DCA) for dry dune habitats.

Table 4.6. Results of Pearson correlation analysis between DCA axis scores and weighted Ellenberg values for dry dune habitats.

	Moisture	Light	Nitrogen	Reaction	Salt
Axis 1 Correlation coefficient	-0.890	0.691	-0.871	-0.166	0.330
p value	**<0.001**	**<0.001**	**<0.001**	0.153	**0.004**
Axis 2 Correlation coefficient	0.396	-0.036	0.569	0.437	0.223
p value	**<0.001**	0.756	**<0.001**	**<0.001**	0.053
Axis 3 Correlation coefficient	0.123	0.093	-0.016	0.021	0.134
p value	0.289	0.423	0.891	0.858	0.248
Axis 4 Correlation coefficient	0.201	-0.272	-0.032	-0.150	-0.107
p value	0.081	**0.017**	0.781	0.195	0.360

In Detrended Correspondence Analysis (DCA), the sample and species ordinations are plotted in the same space and any environmental gradients identified apply to both. Thus, the species ordination (Figure 4.7) suggests which species have increased as a result of grazing and which have not: species on the left of axis 2 were more frequent in grazed plots, e.g. small dicotyledonous herbs such as *Euphrasia officinalis* agg., *Linum catharticum*, *Polygala* spp. and *Thymus polytrichus*, while species on the right of axis 2 were more frequent in ungrazed samples, e.g. *Arrhenatherum elatius* and *Tragopogon pratensis*, both of which usually decrease in grazed swards (Pfitzenmeyer 1962, Boorman 1989a). Species more characteristic of SD8 are found in the lower left corner of the ordination, e.g. *Galium verum*, *Lotus corniculatus*, *Rhytidiadelphus squarrosus* and *R. triquetrus*, and species more characteristic of SD9 on the lower right, e.g. *Achillea millefolium*, *Arrhenatherum elatius* and *Cirsium arvense*. Species more abundant in SD7 are placed in the top half of the ordination, e.g. *Ammophila arenaria*, *Hypochaeris radicata* and *Ononis repens*.

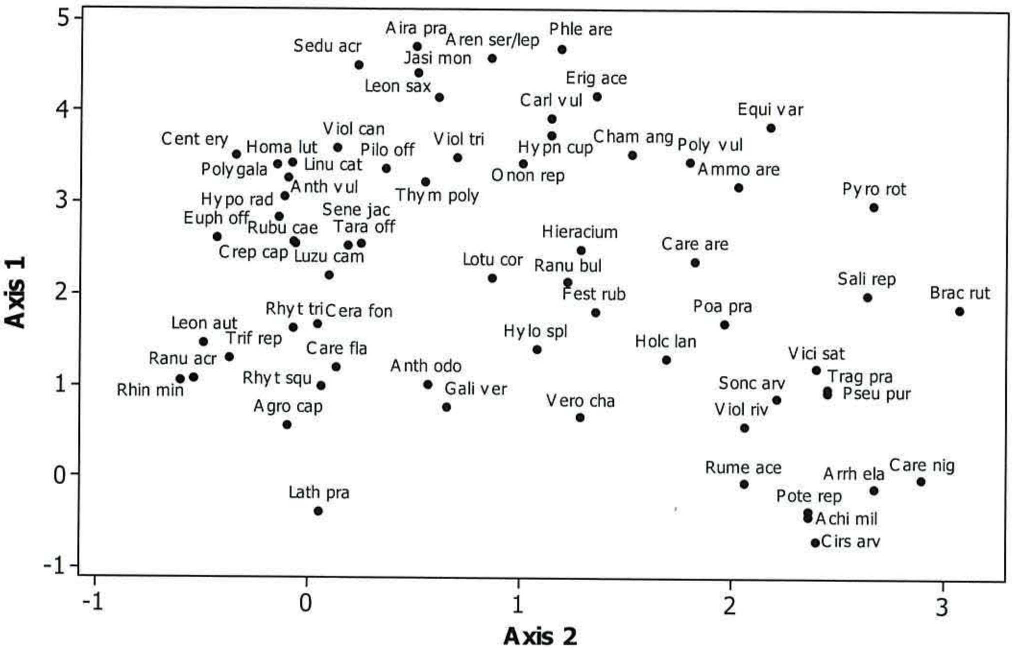


Figure 4.7. Species ordination by Detrended Correspondence Analysis (DCA) for dry dune habitats. Only species with more than ten records shown. Eigenvalues: axis 1=0.5062, axis 2=0.2020. Labels are first four and three letters of genus and species name respectively: Achi mill=*Achillea millefolium*, Agro cap=*Agrostis capillaris*, Aira pra=*Aira praecox*, Ammo are=*Ammophila arenaria*, Anth odo=*Anthoxanthum odoratum*, Anth vul=*Anthyllis vulneraria*, Aren ser=*Arenaria serpyllifolia*, Arrh ela=*Arrhenatherum elatius*, Brac rut=*Brachythecium rutabulum*, Care are=*Carex arenaria*, Care fla=*Carex flacca*, Care nig=*Carex nigra*, Carl vul=*Carlina vulgaris*, Cent ery=*Centaurium erythraea*, Cera fon=*Cerastium fontanum*, Cham ang=*Chamerion angustifolium*, Cirs arv=*Cirsium arvense*, Crep cap=*Crepis capillaris*, Equi var=*Equisetum variegatum*, Erig ace=*Erigeron acer*, Euph off=*Euphrasia officinalis* agg., Fest rub=*Festuca rubra*, Gali ver=*Galium verum*, Hieracium=*Hieracium* spp., Holc lan=*Holcus lanatus*, Homa lut=*Homalothecium lutescens*, Hylo spl=*Hylocomium splendens*, Hypn cup=*Hypnum cupressiforme*, Hypo rad=*Hypochaeris radicata*, Jasi mon=*Jasione montana*, Lath pra=*Lathyrus pratensis*, Leon aut=*Leontodon autumnalis*, Leon sax=*Leontodon saxatilis*, Linu cat=*Linum catharticum*, Lotu cor=*Lotus corniculatus*, Luzu cam=*Luzula campestris*, Onon rep=*Ononis repens*, Phle are=*Phleum arenarium*, Pilo off=*Pilosella officinarum*, Poa pra=*Poa pratensis*, Polygala=*Polygala* spp., Poly vul=*Polypodium vulgare*, Pote rep=*Potentilla reptans*, Pseu pur=*Pseudoscleropodium purum*, Pyro rot=*Pyrola rotundifolia*, Ranu acr=*Ranunculus acris*, Ranu bul=*Ranunculus bulbosus*, Rhin min=*Rhinanthus minor*, Rhyt squ=*Rhytidiadelphus squarrosus*, Rhyt tri=*Rhytidiadelphus triquetrus*, Rub cae=*Rubus caesius*, Rume ace=*Rumex acetosa*, Sali rep=*Salix repens*, Sedu acr=*Sedum acre*, Sene jac=*Senecio jacobaea*, Sonc arv=*Sonchus arvensis*, Tara off=*Taraxacum* sect. *Ruderalia (T. officinale* Wigg. group), Thym poly=*Thymus polytrichus*, Trag pra=*Tragopogon pratensis*, Trif rep=*Trifolium repens*, Vero cha=*Veronica chamaedrys*, Vici sat=*Vicia sativa*, Viol can=*Viola canina*, Viol riv=*Viola riviniana*, Viol tri=*Viola tricolor*.

Positive and negative indicator species

There was a statistically significant increase in the number of positive indicator species per sample before and after grazing management started (General Linear Model analysis, $p<0.001$, $F=100.95$; grazing treatment, df=1; number of permanent quadrats, df=17; error term, df=17; total error term, df=35) (Figure 4.8). The number of negative indicator species also increased significantly in grazed samples (General Linear Model analysis, $p<0.004$, $F=10.93$; grazing treatment, df=1; number of permanent quadrats, df=17; error term, df=17; total error term, df=35); however, only three negative indicator species were recorded in total, with only *Senecio jacobaea* present in most quadrats. After the introduction of grazing management, the number of positive indicator species increased by 0.65 ± 0.08 species per year and the number of negative indicator species by 0.02 ± 0.01 species per year (General Linear Model analysis with quadrat as a factor and years since grazing started as covariate; number of permanent quadrats, df=17; years since grazing started, df=1; error term, df=29; total error term, df=47; positive indicators: $p<0.001$, $F=63.04$, $T=7.94$, negative indicators: $p=0.082$, $F=3.26$, $T=1.80$)

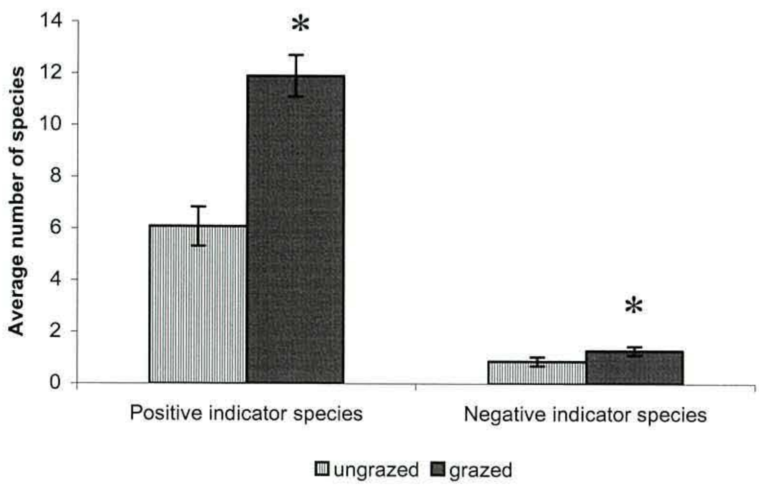


Figure 4.8. Average number of positive and negative indicator species per quadrat in dry dune habitats in all years without grazing (ungrazed) and with grazing (grazed). Bars are standard errors. Significant differences ($p<0.05$) are indicated with a star.

Wet dune habitats

Species richness

Total numbers of species increased by 21.6 % from 88 in 1987 to 107 in 2003. Perennials, bryophytes and graminoids represented the largest species groups, with bryophytes being the only group decreasing in total species numbers post-grazing (Figure 4.9a). Lichens are not shown because they were only recorded from a single quadrat in two different years of survey.

Most of the species lost from grazed quadrats (Table 4.9) were present only in a very small number of quadrats before grazing management started, and amongst the new species recorded from grazed quadrats (Table 4.9), only *Eleocharis quinqueflora* and *Rhytidiadelphus triquetrus* occurred in more than two quadrats.

Average species numbers per quadrat in grazed years were significantly greater than in ungrazed years for total species (+ 34.1 %), perennials (+ 36.1 %), graminoids (+ 41.6 %) and annuals and biennials (+ 66.1 %), but not for bryophytes (+ 6.8 %) (Figure 4.9b and Table 4.7). All graminoid, annual and biennial species that increased in frequency were dune slack assemblage species (e.g. *Agrostis stolonifera*, *Juncus articulatus, Carex flacca*, *Euphrasia officinalis* agg., *Linum catharticum*). Amongst the bryophytes, two species with increased abundance post-grazing, *Homalothecium lutescens* and *Rhytidiadelphus triquetrus*, are more characteristic of fixed dune grassland communities. Appendix 1.3 and 1.4 contain the vegetation data for all quadrats in dune slacks in all years of survey.

Analysis of changes in total species numbers over the years after the introduction of livestock grazing indicates an increase of 0.98 ± 0.17 species per year (Table 4.8). For all species groups, this increase associated with the number of years grazed was significant (Table 4.8).

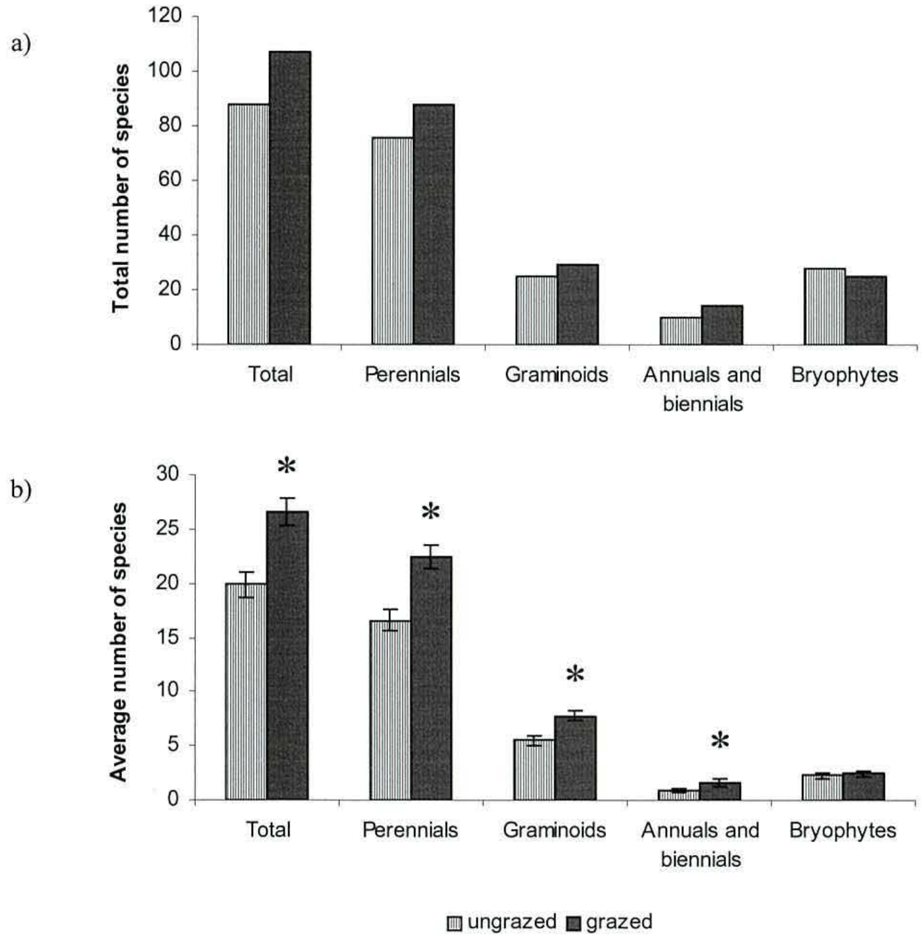


Figure 4.9. Number of perennial, graminoid, annual and biennial, bryophyte and lichen species in wet dune habitats in all years without grazing (ungrazed) and with grazing (grazed). a) Total number of species. b) Average number per quadrat. Bars are standard errors. Significant differences ($p<0.05$) are indicated with a star. For results of statistical tests, see Table 4.7.

Table 4.7. Results of General Linear Modal analysis, comparing the average total number of species, average number of perennial, graminoid, annual and biennial, bryophyte and lichen species in wet dune habitats in all years without grazing and with grazing. Sample size was included in the analysis as a weighting factor because the means were based on unequal numbers of survey years for the ungrazed and grazed situation. Significant p values in bold. Degrees of freedom (df): grazing treatment, df=1; number of permanent quadrats, df=20; error term, df=20; total error term, df=41.

	p	F
Total number of species	**<0.001**	40.77
Perennials	**<0.001**	47.78
Grasses, sedges, rushes	**<0.001**	32.62
Annuals and biennials	**<0.039**	04.87
Bryophytes	<0.669	00.19

Table 4.8. Results of General Linear Model analysis, testing for changes in the number of species for different species groups in wet dune habitats associated with the number of years since grazing management started. In the analysis, quadrats were included as a factor and years since grazing started as a covariate. Increase per year (± standard error) indicates the increase in the number of species per year after the introduction of grazing management. Degrees of freedom (df): number of permanent quadrats, df=20; years since grazing started, df=1; error term, df=24; total error term, dF=45.

	p	F	T	Increase per year ± standard error
Total number of species	**<0.001**	32.54	5.70	0.9765 ± 0.1712
Perennials	**<0.001**	33.33	5.77	0.7083 ± 0.1227
Grasses, sedges, rushes	**<0.001**	25.95	5.09	0.2712 ± 0.0533
Annuals and biennials	**<0.044**	04.53	2.13	0.0984 ± 0.0462
Bryophytes	**<0.001**	26.80	5.18	0.1733 ± 0.0335

Table 4.9. Graminoids, annual and biennial species, mono- and dicotyledonous herbs, bryophytes and lichens that were only recorded in ungrazed or grazed quadrats respectively for wet dune habitats.

Plant group	In ungrazed quadrats only		In grazed quadrats only	
Graminoids	*Agrostis vinealis* *Carex viridula oedocarpa* *Eleocharis multicaulis* *Triglochin palustre*		*Aira caryophyllea* *Aira praecox* *Arrhenatherum elatius* *Carex caryophyllea*	*Eleocharis quinqueflora* *Juncus bufonius* *Juncus maritimus* *Molinia caerulea*
Annuals and biennials	*Anagallis arvensis* *Erigeron acer* *Trifolium campestre* *Trifolium dubium*		*Aira caryophyllea* *Aira praecox* *Centaurium erythraea* *Centaurium littorale*	*Cerastium semidecandrum* *Daucus carota* *Juncus bufonius* *Trifolium micranthum*
Mono- and dicotyledonous herbs	*Samolus valerandi* *Viola riviniana*		*Campanula rotundifolia* *Cardamine pratensis* *Chamerion angustifolium* *Dactylorhiza fuchsii* *Epipactis leptochila* *Equisetum palustre*	*Primula vulgaris* *Prunus spinosa* *Sagina nodosa* *Sedum acre* *Veronica officinalis* *Viola* spp.
Bryophytes	*Amblystegium serpens* *Bryum capillare* *Campyliadelphus elodes* *Drepanocladus polygamus* *Eurynchium striatum* *Leiocolea badensis*	*Lophozia* spp. *Preissia quadrata* *Riccardia spp.* *Mnium hornum* *Tortella inclinata*	*Barbula convoluta* *Barbula* spp. *Centaurea nigra* *Drepanocladus* spp.	*Lophocolea bidentata* *Rhytidiadelphus triquetrus* *Tortella flavovirens* *Warnstorfia fluitans*

Species composition and plant communities

The results of the sample and species ordinations are shown in Figures 4.10 and 4.12. The first dichotomy in the Twinspan table within the wet dune habitats separated the communities SD14 (*Salix repens – Campylium stellatum* dune slack community) and SD16 (*Salix repens – Holcus lanatus* dune slack community) in the ungrazed data. These communities did not change after grazing management was introduced (Figure 4.10). The sample ordination suggests some changes in the vegetation composition after grazing management started along the third axis (Eigen-value 0.1484); however, this is not as obvious as in the dry dune habitats (Figure 4.5). The first ordination axis was significantly correlated with weighted Ellenberg indicator values for moisture, light, nitrogen and reaction, and the third with nitrogen only (Figures 4.10 and 4.11, Table 4.10).

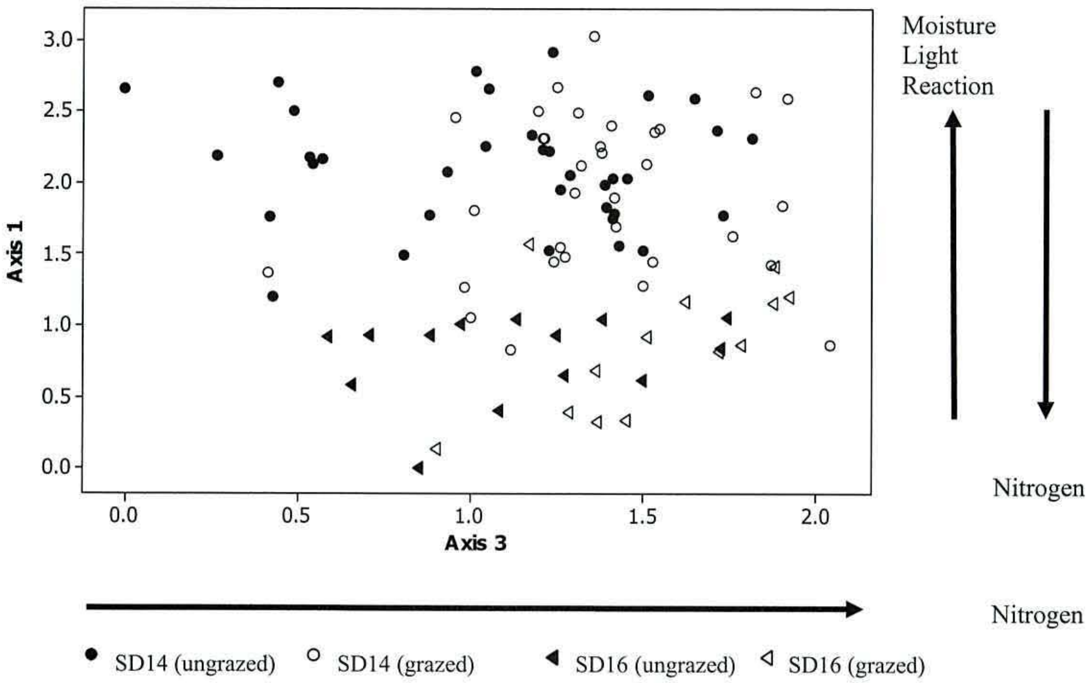


Figure 4.10. Ordination of vegetation samples in wet dune habitats by Detrended Correspondence Analysis (DCA) ungrazed (closed symbols) and grazed (open symbols). Eigenvalues: axis 1=0.3546, axis 3=0.1484. Arrows on the right and bottom indicate increases in moisture, light and reaction along axis 1 and axis 3 derived from Ellenberg indicator values.

Table 4.10. Results of Pearson correlation analysis between DCA axis scores and weighted Ellenberg values for wet dune habitats.

	Moisture	Light	Nitrogen	Reaction	Salt
Axis 1 Correlation coefficient	0.869	0.786	-0.435	0.376	0.101
p value	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.331
Axis 2 Correlation coefficient	-0.044	0.007	0.647	-0.135	0.774
p value	0.671	0.948	**<0.001**	0.192	**<0.001**
Axis 3 Correlation coefficient	-0.125	-0.173	0.232	-0.185	-0.111
p value	0.228	0.094	**0.024**	0.073	0.284
Axis 4 Correlation coefficient	0.054	0.117	-0.147	-0.018	0.017
p value	0.605	0.258	0.156	0.862	0.868

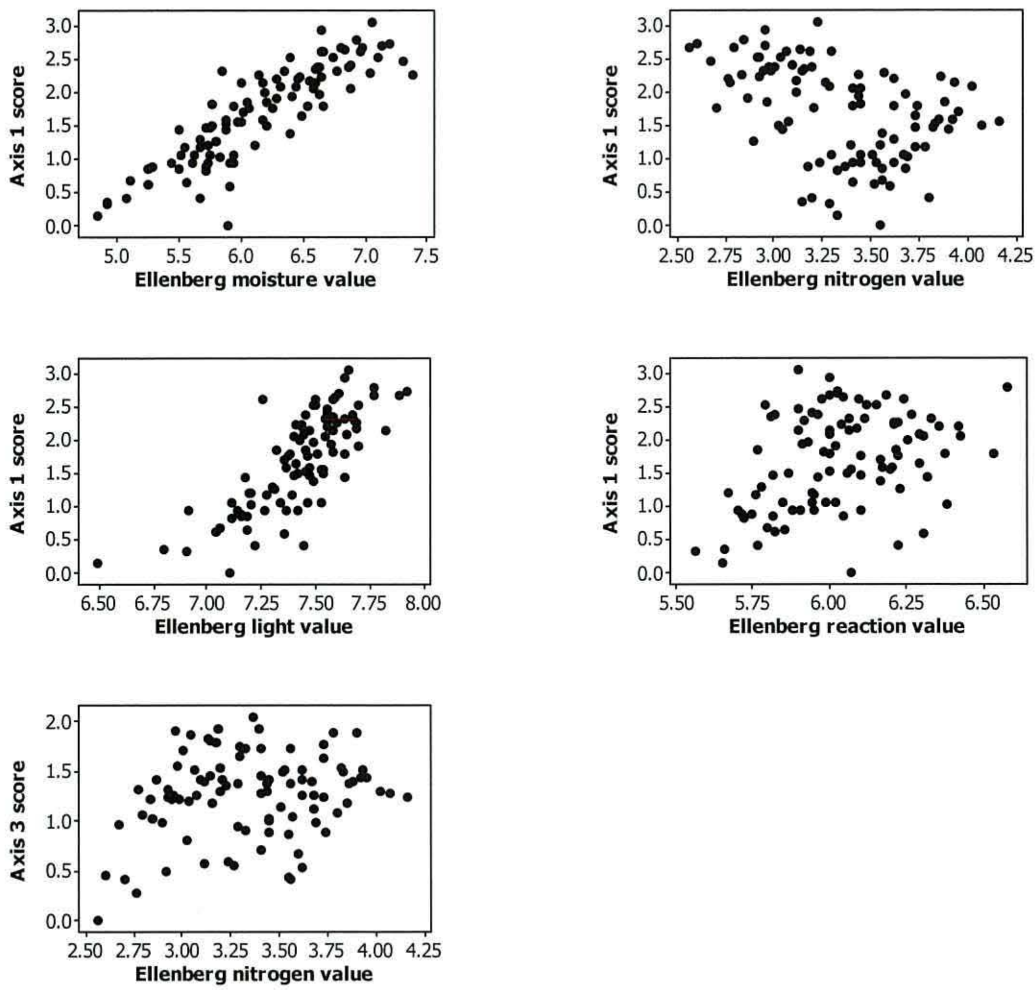


Figure 4.11. Relationship between weighted Ellenberg indicator values and sample scores on axis 1 and axis 3 of the Detrended Correspondence Analysis (DCA) for wet dune habitats.

Species that increased and decreased in frequency after the introduction of livestock grazing are not clearly separated in the species ordination (Figure 4.12). Axis 1 in the ordination diagrams represents moisture, with indicator species of wet sites, e.g. *Dactylorhiza incarnata*, *Juncus articulatus* and *Ranunculus flammula*, at the top of the ordination diagram, and species more indicative of drier ground, e.g. *Carlina vulgaris* and *Ononis repens*, at the bottom of Figure 4.12, which reflects the distribution of wet and dry slack communities in the sample ordination.

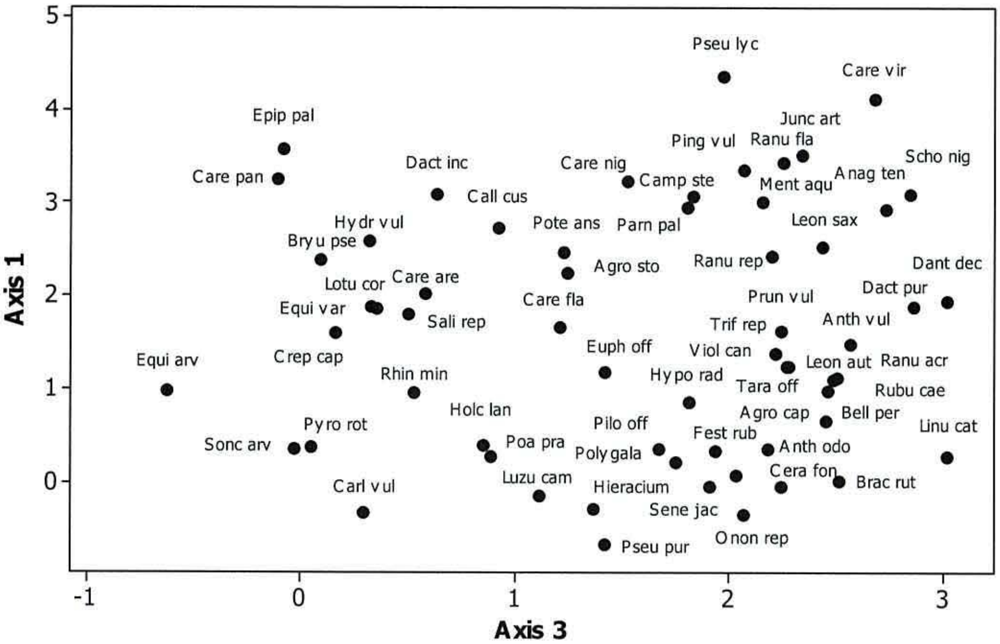


Figure 4.12. Species ordination by Detrended Correspondence Analysis (DCA) for wet dune habitats. Only species with more than ten records shown. Eigenvalues: axis 1 = 0.3546, axis 3 = 0.1484. Labels are first four and three letters of genus and species name respectively: Agro cap=*Agrostis capillaris*, Agro sto=*Agrostis stolonifera*, Anag ten=*Anagallis tenella*, Anth odo=*Anthoxanthum odoratum*, Anth vul=*Anthyllis vulneraria*, Bell per=*Bellis perennis*, Brac rut=*Brachythecium rutabulum*, Bryu pse=*Bryum pseudotriquetrum*, Call cus=*Calliergonella cuspidata*, Camp ste=*Campylium stellatum*, Care are=*Carex arenaria*, Care fla=*Carex flacca*, Care nig=*Carex nigra*, Care pan=*Carex panicea*, Care vir=*Carex viridula viridula*, Carl vul=*Carlina vulgaris*, Cera fon=*Cerastium fontanum*, Crep cap=*Crepis capillaris*, Dact inc=*Dactylorhiza incarnata*, Dact pur=*Dactylorhiza purpurella*, Dant dec=*Danthonia decumbens*, Epip pal=*Epipactis palustris*, Equi arv=*Equisetum arvense*, Equi var=*Equisetum variegatum*, Euph off=*Euphrasia officinalis* agg., Fest rub=*Festuca rubra*, Hieracium=*Hieracium* spp., Holc lan=*Holcus lanatus*, Hydr vul=*Hydrocotyle vulgaris*, Hypo rad=*Hypochaeris radicata*, Junc art=*Juncus articulatus*, Leon aut=*Leontodon autumnalis*, Leon sax=*Leontodon saxatilis*, Linu cat=*Linum catharticum*, Lotu cor=*Lotus corniculatus*, Luzu cam=*Luzula campestris*, Ment aqu=*Mentha aquatica*, Onon rep=*Ononis repens*, Parn pal=*Parnassia palustris*, Pilo off=*Pilosella officinarum*, Ping vul=*Pinguicula vulgaris*, Poa pra=*Poa pratensis*, Polygala=*Polygala* spp., Pote ans=*Potentilla anserina*, Prun vul=*Prunella vulgaris*, Pseu lyc=*Pseudocalliergon lycopoides*, Pseu pur=*Pseudoscleropodium purum*, Pyro rot=*Pyrola rotundifolia*, Ranu acr=*Ranunculus acris*, Ranu fla=*Ranunculus flammula*, Ranu rep=*Ranunculus repens*, Rhin min=*Rhinanthus minor*, Rub cae=*Rubus caesius*, Sali rep=*Salix repens*, Scho nig=*Schoenus nigricans*, Sene jac=*Senecio jacobaea*, Sonc arv=*Sonchus arvensis*, Tara off= *Taraxacum* sect. *Ruderalia (T. officinale* Wigg. group), Trif rep=*Trifolium repens*, Viol can=*Viola canina*.

Positive and negative indicator species

The average number of positive indicator species increased significantly by 17.7 % post-grazing (General Linear Model analysis, $p<0.001$, $F=18.02$; grazing treatment, df=1; number of permanent quadrats, df=20; error term, df=20; total error term, df=41) (Figure 4.13). The average number of negative indicator species per quadrat more than doubled; however, it was very low in both cases, and the increase post-grazing was not statistically significant (General Linear Model analysis, $p<0.070$, $F=3.66$; grazing treatment, df=1; number of permanent quadrats, df=20; error term, df=20; total error term, df=41) (Figure 4.13). After grazing management started, the number of positive indicator species increased by 0.13 ± 0.04 species per year and the number of negative indicator species by 0.02 ± 0.01 species per year (General Linear Model analysis with quadrat as a factor and years since grazing started as covariate; years since grazing started, df=1; number of permanent quadrats, df=20; error term, df=24; total error term, df=45; positive indicators: $p=0.006$, $F=8.99$, $T=3.00$, negative indicators: $p=0.087$, $F=3.19$, $T=1.79$)

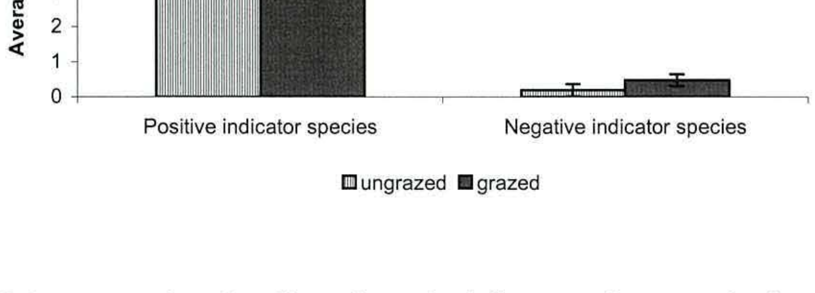


Figure 4.13. Average number of positive and negative indicator species per quadrat in wet dune habitats in all years without grazing (ungrazed) and with grazing (grazed). Bars are standard errors. Significant differences ($p<0.05$) are indicated with a star.

Ellenberg indicator value for nitrogen

Changes in the average Ellenberg indicator value for nitrogen between 1987 and 2003 were analysed by one-way Anova with Tukey's post hoc test for the whole data set, dry and wet habitats and each NVC community separately. No significant change occurred in any of the habitats or communities over the years (Table 4.11a). In all years, values were significantly higher in SD9/8 than SD7 (t-tests, $p<0.05$), whereas no significant difference existed between the two slack communities SD14 and SD16 at any time. Average Ellenberg indicator values for nitrogen were significantly lower in grazed than ungrazed quadrats in the dry habitats: the ungrazed community SD9 had a significantly higher nitrogen value than SD8, which developed from SD9 after the introduction of grazing management (Table 4.11b). After grazing management started, the Ellenberg nitrogen value decreased significantly for the whole data set, the dry habitats and SD9/8 (Table 4.11c). Both of these analyses indicate a reduction in the productivity and fertility of the habitat.

Table 4.11. a) Average weighted Ellenberg indicator values for nitrogen for the whole dataset, dry and wet habitats and NVC communities (mean ± standard deviation). Analysis of differences between years was by one-way Anova.

b) Results of General Linear Model analysis of differences between ungrazed and grazed data (mean ± standard deviation). Sample size was included in the analysis as a weighting factor because the means were based on unequal numbers of survey years for the ungrazed and grazed situation.

c) Results of General Linear Model analysis, testing for changes in the Ellenberg indicator value for nitrogen associated with the number of years since grazing management started. In the analysis, quadrats were included as a factor and years since grazing started as a covariate. Change per year (± standard error) indicates the change in the average Ellenberg nitrogen value per year after the introduction of grazing management.

Significant p values are shown in bold. Number of permanent quadrats: whole dataset, df=38; dry habitats, df=17; wet habitats, df=20; SD7, df=8; SD9/8, df=8; SD14, df=14; SD16, df=5.

a)

	1987	**1988**	**1991**	**1996**	**2003**	**p**
Whole data set	3.59 ± 0.65	3.58 ± 0.76	3.49 ± 0.53	3.52 ± 0.46	3.44 ± 0.42	0.933
Dry habitats	3.91 ± 0.74	4.00 ± 0.84	3.71 ± 0.58	3.59 ± 0.57	3.49 ± 0.50	0.226
Wet habitats	3.29 ± 0.36	3.17 ± 0.39	3.27 ± 0.39	3.48 ± 0.33	3.38 ± 0.34	0.243
SD7	3.48 ± 0.59	3.45 ± 0.64	3.29 ± 0.44	3.22 ± 0.38	3.22 ± 0.44	0.845
SD9/SD8	4.29 ± 0.66	4.48 ± 0.70	4.08 ± 0.42	3.92 ± 0.53	3.77 ± 0.40	0.055
SD14	3.23 ± 0.42	3.06 ± 0.36	3.19 ± 0.42	3.45 ± 0.38	3.36 ± 0.37	0.172
SD16	3.41 ± 0.16	3.42 ± 0.34	3.46 ± 0.26	3.55 ± 0.16	3.43 ± 0.28	0.699

b)

	Ungrazed	**Grazed**	**F**	**p**
Whole data set	3.58 ± 0.62	3.48 ± 0.51	2.32	0.136
Dry habitats	3.91 ± 0.72	3.59 ± 0.60	10.54	**0.005**
Wet habitats	3.33 ± 0.38	3.35 ± 0.36	2.10	0.163
SD7	3.38 ± 0.12	3.26 ± 0.10	1.63	0.237
SD9/SD8	4.42 ± 0.13	3.90 ± 0.11	12.38	**0.008**
SD14	3.28 ± 0.43	3.30 ± 0.39	1.81	0.200
SD16	3.47 ± 0.21	3.45 ± 0.26	0.35	0.579

c)

	p	**F**	**T**	**Change per year ± standard error**
Whole data set	**<0.003**	19.54	-3.09	-0.0184 ± 0.0060
Dry habitats	**<0.001**	15.64	-3.96	-0.0340 ± 0.0086
Wet habitats	<0.911	10.01	-0.11	-0.0007 ± 0.0064
SD7	<0.216	11.69	-1.30	-0.0121 ± 0.0093
SD9/SD8	**<0.001**	18.32	-4.28	-0.0524 ± 0.0123
SD14	<0.276	11.27	-1.12	-0.0082 ± 0.0073
SD16	<0.134	13.00	-1.73	-0.0184 ± 0.0106

Discussion

Species diversity

The increase in total plant species numbers post-grazing is in accordance with other studies that showed a positive effect of grazing on the biodiversity of sand dunes (e.g. Hewett 1985, Gibson 1988, Boorman 1989b, Massey & Radley 1992, van Dijk 1992, Kooijman & de Haan 1995, de Bonte *et al.* 1999, Hootmans 2002) and other habitats such as salt marsh (Berg *et al.* 1997, Bos *et al.* 2002a), chalk grassland (Willems 1983), lowland grassland (Treweek *et al.* 1997) and fens (Williams *et al.* 1974). An increase in plant biodiversity alone, however, is not necessarily the aim of nature conservation, but it is important that the species increasing or newly establishing are target species (Schwabe *et al.* 2004). In this study, all species that increased considerably in abundance were sand dune assemblage species, and positive indicator species were recorded more frequently after the introduction of livestock grazing. This suggests that the greater species diversity post-grazing was due to an increase of desirable species characteristic of the sand dune habitats studied, rather than to the spread of species of other habitats or undesirable species, e.g. nitrophilous species.

There are a number of ways by which grazing can enhance species richness, e.g. by changing competitive interactions between species and reducing competitive exclusion (Crawley 1983, Olff & Ritchie 1998). Small, poorly competitive species benefit from a reduction of biomass and litter accumulation, improving light availability at the soil surface (Van Wieren 1995, Bakker *et al.* 2003, Kooijman 2004). Extensive grazing can result in and sustain a more heterogeneous sward structure, which allows for increased plant and animal diversity (Andresen *et al.* 1990, Jaramillo & Detling 1992, Hearn 1995, Schley & Leytem 2004, Zehm 2004). Year-round grazing as practised at Newborough Warren since 2001 is thought to create more heterogeneity than seasonal grazing as the animals establish site-specific and individual grazing patterns (Kampf 2002) and more gradual transitions between habitat types develop (Helmer 2002). Grazing animals also play an important role for colonisation and regeneration dynamics by dispersing propagules (Fischer *et al.* 1996, Pakeman *et al.* 2002, Bakker & Olff 2003) and the creation of gaps and soil disturbances that stimulate germination (Bullock *et al.* 1995, Bakker & Olff 2003) through grazing, trampling, dust bathing and scraping. The importance of large herbivores for epi- and endozoochorous seed dispersal on sand dunes has recently been documented by Cosyns (2004), Cosyns & Hoffmann (2005), Cosyns *et al.* (2005a, b) and Couvreur *et al.* (2005), showing that they can connect spatially separate habitat patches and that less common and rare species represent an important part of the viable seed content of horse dung. Bullock *et al.* (1994) believe that disturbance and gap creation are probably the most important factors allowing dicotyledonous species to increase in grazed swards.

In both wet and dry habitats, a great average increase in species numbers per quadrat was observed for annual and biennial species. Pemadasa *et al.* (1974) showed that the distribution of dune annuals depends on the total cover of perennial vegetation, because perennial plants generally are competitively superior and exclude annual species. The latter are often small in stature and poor competitors (Boorman & Boorman 2001) and, in more mature, closed vegetation, suffer from a lack of open sites where they can germinate and establish (Ranwell 1960a, Boorman *et al.* 1997, Petersen 2000). In many annual and biennial species regeneration from seeds is only possible in gaps, and seedling establishment is hindered by dense litter and vegetation. Grazing animals can create regeneration niches for these species by trampling, poaching and opening the canopy (Bullock *et al.* 1995, Bakker & Olff 2003). The reduced grazing pressure by rabbits after myxomatosis may have been one reason why many of these species disappeared in various habitats (Grime 2001). Thus, the increased occurrence of annual species in the present study after grazing management started is probably due to the removal of biomass, opening up of the canopy and the creation of vegetation gaps where small, short-lived, competitively inferior species can establish. An increase in the number of annual and biennial species was also found in mown dunes by Anderson & Romeril (1992); while in calcareous grassland, Gibson *et al.* (1987) recorded both more annuals and seedlings in grazed areas. The same mechanisms mentioned above also apply to small perennial plants such as *Polygala* spp. or *Viola canina* which increased in abundance post-grazing.

Because of their lower moisture and nutrient supply, the dry dunes support a more open vegetation than wet slacks where the water table remains close to the surface for most of the year, allowing the development of a denser sward with much less open ground (Boorman *et al.* 1997). As a result of this, annuals are usually more abundant in dry areas than slacks (Pemadasa *et al.* 1974, Boorman *et al.* 1997), which is also reflected in the larger number of annual and biennial species in quadrats located in the dry dunes in this study. Although grazing might have been expected to have a greater impact on annuals in slacks by opening up the denser vegetation, it had a similar impact on annuals in both dry and wet habitats. This suggests that even the normally more open dry dune areas were too densely vegetated before the introduction of grazing management to allow annuals and biennials to thrive.

Average numbers of bryophyte species increased in grazed samples both in dry and wet dune habitats, with the larger increase found in the dry dunes. Herbivores generally avoid eating bryophytes because they are unpalatable, so that grazing benefits their growth (Crofts & Jefferson 1999), as shown in the present study. If there is no grazing or grazing pressure is too low, many bryophyte species can get outcompeted by taller species (Tibbetts & Martin 1997, Lake *et al.* 2001), and most species cannot thrive in the low light environment of a dense sward (Crofts & Jefferson 1999). Livestock grazing removes biomass and thus increases significantly the amount of light reaching the bryophyte layer (Kooijman 2004), which favours their growth and leads to an increase in species diversity (Kooijman & de Haan 1995). Bryophytes can also benefit from patches of open ground created by grazing animals (Lake *et al.* 2001). A greater abundance of bryophytes in grazed areas was also found in habitats such as chalk grassland (Willems 1983), upland grassland (Hulme *et al.* 1999), arctic tundra heath (Grellmann 2002) and dry pine forests (Väre *et al.* 1995), and the importance of grazing for the bryophyte flora was stressed by During & Willems (1986). In the dune slacks in this study, there was no significant increase in the average number of bryophyte species per quadrat after grazing started; however, the increase in species numbers associated with the number of years since grazing was introduced was significant.

Within a coastal dune system in Belgium, both cattle and ponies have been shown to feed mainly on grasses, sedges and rushes and preferentially graze in grassland areas as opposed to areas of scrub or woodland (Lamoot *et al.* 2005). Graminoids were also found to be the preferred food of cattle and ponies in coastal dunes studied by Cosyns (2004). The preference of ponies and horses for grasses, sedges and rushes has also been described by Gudmundsson & Dyrmundsson (1994) and Oates & Bullock (1997). Even so, grazing also had a positive effect on graminoid species numbers in this study, both in wet and dry habitats, probably by opening up the swards, reducing fast growing, competitive species and creating germination niches. Many graminoid species are tolerant of grazing because their growing meristems are located at their base, so that they can regrow after defoliation (Stewart & Eno 1998, Crofts & Jefferson 1999). The promotion of grasses by grazing is in accordance with many other studies, e.g. van Dijk (1992), Hoffmann (2002) and Stammel *et al.* (2003). In contrast, Veer & Kooijman (1997) found a reduced number of graminoid species in rank, grass dominated dune grasslands.

Plant communities

Analysis of the ordination diagrams revealed that moisture is one of the most important factors in the distribution of plant communities on sand dunes. Other important factors include soil fertility and the degree of stabilisation of the dune sands. This is in accordance with other studies showing that gradients in environmental factors correlate with the distribution of plant communities on coastal dunes, e.g. Chandapillai (1970).

In the dry dune habitats, the communities SD7, SD9 (ungrazed) and SD8 (grazed) were separated along the first axis of the ordination. These communities differ in a variety of abiotic conditions: SD7 is a semi-fixed community in areas where stabilisation of the sand has started, but no great development of the soil has occurred yet (Rodwell 2000). SD8 and SD9 are found on more fixed sands, where more humus has accumulated and more moisture and nutrients are available to the plants, which was illustrated by the increase of the Ellenberg indicator values for moisture and soil fertility along axis 1. The latter was also correlated with axis 2, with a decrease in nitrogen indicator values from SD9 to SD8, illustrating that SD9 is a ranker, more enriched community, and that grazing can counteract this nutrient enrichment. SD7 is a more open community, which was reflected in the higher Ellenberg indicator value for light at the top of axis 1. These differences in abiotic factors are the major factor shaping the distribution of the different communities. Grazing was related to the second ordination axis, which shows that it has also had a marked impact on the floristic composition of the study area.

In the dune slacks, once again moisture appeared to be the main influence on plant communities and composition, with the first ordination axis separating wet (SD14) and dry slack (SD16) communities. The separation of ungrazed and grazed quadrats was not as obvious as in the dry dune communities, and the eigenvalue of the axis related to grazing was lower (0.1484). Moreover, the increase in species numbers and positive indicator species was smaller than in the dry habitats, especially in the wet slack communities. Many plant species cannot tolerate waterlogging and the often anoxic conditions caused by it (Jones & Etherington 1971, Schat 1984), which maintains differences in the vegetation of wet and dry areas (Studer-Ehrensberger *et al.* 1993, Grootjans *et al.* 1998). For example, *Salix repens* declines in drier slacks, while grasses and smaller dicotyledonous herbs are more dominant than in wet slacks (Rodwell 2000). Because the distribution of plant species and communities is so strongly affected by the water table (Willis *et al.* 1959, Onyekwelu 1972a), changes in the hydrology or the occurrence of dry and wet periods can have an effect on the vegetation of slacks, with seasonal variation having a greater impact than short-term events such as a period of high rainfall (Grootjans *et al.* 1988, Petersen 2000). In lowland grasslands in general, short lived and low growing species may benefit from a dry year, while a wet spring can result in a grassier sward (Crofts & Jefferson 1999). This means that hydrology and moisture regime are of much greater importance for the composition of the vegetation in these areas than grazing, and the occurrence of an especially dry or wet year can mask changes occurring as a result of grazing. The smaller impact of grazing in these areas could also be due to a habitat preference of both cattle and ponies for dry rather than wet grasslands (Gudmundsson & Dyrmundsson 1994, Vulink 2002), which was observed during the whole year by Vulink & van Eerden (1998) and during the winter only by Menard *et al.* (2002). A possible explanation for this preference is that the dry grasslands offer better quality food with a higher content of digestible organic matter (Bokdam & Wallis de Vries 1992, Vulink 2002). Inundation of slacks may also prevent grazing in winter months (Bokdam & Wallis de Vries 1992).

The rank dune grassland SD9 (*Ammophila arenaria – Arrhenatherum elatius* dune grassland) disappeared as a result of grazing management. It is found on more stabilised sands that are not or only little grazed and is characterised by tussocky, tall perennial grasses, including often abundant *Arrhenatherum elatius*, whose growth in the absence of grazing leads to increased competition for water, nutrients and light and does not allow small and less competitive grasses and herbs to thrive. Similarly, there is no great variety of bryophyte species, and they are only patchy in cover (Rodwell 2000). After the introduction of livestock grazing, this rank and comparatively species-poor community changed into SD8 (*Festuca rubra – Galium verum* fixed dune grassland community), with smaller grasses such as *Agrostis capillaris* and *Anthoxanthum odoratum* and a variety of dicotyledons increasing in abundance (Rodwell 2000). This shift from a rank community to a more diverse community characterised by usually short swards and a variety of grasses, dicotyledons and bryophytes can be attributed to grazing. Several annual and biennial species characteristic of SD8 (Rodwell 2000) increased in abundance in these areas, e.g. *Aira praecox*, *Cerastium semidecandum*, *Euphrasia officinalis* agg. and *Linum catharticum*.

Most of the graminoids that increased in abundance in the dry habitats are also commonly found in the SD8 community, but some of them are very scarce or infrequent in the ranker SD9 grassland, e.g. *Agrostis capillaris*, *Anthoxanthum odoratum* and *Luzula campestris*. Contrary to SD9, bryophytes are an important feature of SD8, where they can attain high cover, with characteristic species including *Homalothecium lutescens*, *Hylocomium splendens*, *Rhytidiadelphus squarrosus* and *R. triquetrus*, all of which were recorded more frequently post-grazing. The other community of dry dunes, SD7, and both dune slack communities recorded in this study, SD14 and SD16, did not change as a result of grazing.

Ellenberg indicator values

Coastal habitats are amongst those threatened by eutrophication (van der Maarel & van der Maarel-Versluys 1996). Eutrophication through atmospheric deposition of nitrogen is one major cause of the decline of oligotrophic habitats such as dune slacks and their associated species (Koerselman 1992), especially basiphilous species of pioneer stages (Lammerts & Grootjans 1997). It can encourage tall vegetation and result in a denser sward with more litter, which leads to a decrease in annual and biennial species (Grime 2001). At Newborough Warren, atmospheric nitrogen deposition is thought to have been one reason for increased stabilisation of the dunes, enhanced growth of grasses and reduced species diversity (Rhind *et al.* 2001). Average Ellenberg indicator values for nitrogen were calculated in order to test whether this concern about eutrophication can be confirmed for the study site. This analysis did not show any significant or consistent long-term trends in any of the habitats and plant communities present, suggesting that nitrogen deposition may not be a problem at the study site. However, recent work suggests that Ellenberg indicator values for nitrogen may not be regarded as indicative of the availability of nutrients only, as it is established that they are rather a measure of productivity which also includes factors such as moisture availability, soil aeration and disturbance, all of which determine productivity (Hill & Carey 1997, Schaffers & Sýkora 2000). Thus, increased atmospheric deposition of nitrogen might not lead to a change in indicator values if productivity is limited by low soil moisture (dry dunes) or poor soil aeration (wet slacks). Livestock grazing can be used as a management tool to counteract possible negative effects of nitrogen deposition on sand dune vegetation (Kooijman & van der Meulen 1996, ten Harkel & van der Meulen 1996, Kooijman & Smit 2001), so it is also possible that no increase in nitrogen indicator values was found because the site has been grazed, at least in parts, for the last sixteen years. This is supported by the significant reduction in the indicator value when comparing ungrazed and grazed quadrats in the dry dune communities SD9 and SD8, and the decrease in the indicator value associated with the number of years since grazing started, which was significant for the whole dataset, the dry dune habitats and SD9/8. Another explanation could be that through increased nitrogen deposition, the system may have become phosphorus limited, which would then reduce further nitrogen induced growth of the vegetation (ten Harkel & van der Meulen 1996), or that changes caused by nitrogen deposition were already happening before data collection started in 1987. The possible impact of increased atmospheric nitrogen deposition on the vegetation of dune grassland with and without herbivore grazing is investigated in a controlled experiment in Chapter 5.

Limitations of the study

Since 2001, most of the study site has been grazed by domestic livestock. All the originally ungrazed control quadrats are now managed by grazing, so that no comparison of ungrazed and grazed quadrats is possible. The changes documented in the vegetation since 1987 could be due to other factors than grazing, which would become obvious by comparison with data from present-day ungrazed quadrats. These other factors could include natural successional processes, climate change and air pollution (but see above); however, it is likely that the majority of the observed changes are due to grazing.

It has been shown that the effects of grazing depend on the scale of observation, and that grazing effects can be different at different spatial scales. Tschöpe *et al.* (2002), studying the effects of grazing on three spatial scales, found that grazed areas were only more species rich than ungrazed areas at the smallest scale studied (0.25 m^2), whereas proportions of open ground were greater in the grazed treatment only at the largest scale (40 m^2). Spiegelberger *et al.* (2004) also recommend the analysis of different spatial scales in order to more fully understand the effects of habitat management.

Another factor to be taken into account is that the monitoring was carried out by different persons in different years, which may have introduced some observer error. Species detection by recorders was supposed to have increased in 1996 as compared to previous surveys, which means that some increases in species numbers might not be real. However, Perry *et al.* (1996) believed there was enough evidence for a general increase in species numbers, which is thought to apply to this study as well.

Conclusion

In spite of the growing importance of grazing as a management tool for nature conservation, more long-term data are still called for (e.g. Delescaille 2002, Kampf 2002). The results of this analysis of long-term monitoring data agree with those of other studies showing that extensive livestock grazing can result in increased plant species diversity on sand dunes. Positive effects were shown especially for annual and biennial species, while at the plant community level, a shift from a rank, species-poor community to a more species-rich community was documented. The increased frequency of positive indicator species suggests improved habitat conditions. These effects were more pronounced in dry dune habitats than wet slacks, where other environmental variables, especially soil moisture, appear to be more important determinants of species composition. These results concur with previous conclusions about the importance of grazing by large herbivores for the maintenance of species-rich, short dune slack and dune grassland vegetation (e.g. Boorman *et al.* 1997, Petersen 2000).

CHAPTER 5

Effects of grazing management and nitrogen deposition on the vegetation of fixed dune grasslands

Experimental grazing exclosures at Newborough Warren. Top: grazed by rabbits, bottom: grazed by rabbits (foreground) and ungrazed (background). Pictures taken in June 2005.

Introduction

Atmospheric deposition of nitrogen is a major problem for the British flora (NEGTAP 2001). Total nitrogen deposition in the UK is dominated by reduced nitrogen (NH_3 and NH_4^+) and has remained relatively unchanged since 1986. This is because although emissions and deposition of nitrogen oxides have declined, ammonia emissions have changed little since the late 1980s (NEGTAP 2001), and present-day efforts to reduce emissions are limited (Emmett unpubl.). Nitrogen has the potential to accumulate in ecosystems (Galloway *et al.* 2003), and even if deposition rates decline, the recovery of ecosystems from eutrophication can lag behind by decades (NEGTAP 2001, Cunha *et al.* 2002). This means that the effects of increased atmospheric deposition will remain a significant problem for semi-natural habitats well into the future in many areas (NEGTAP 2001, Emmett unpubl.), and recovery may often not be possible without active management and restoration measures (Cunha *et al.* 2002).

Productivity of most terrestrial habitats is limited by nitrogen (Vitousek & Howarth 1991, Bobbink & Lamers 2002). Oligo- and mesotrophic ecosystems are especially at risk from increased atmospheric deposition of nitrogen, because many characteristic species are adapted to nutrient poor conditions and get outcompeted by competitive species with higher nitrogen demands (Bobbink *et al.* 1998, Krupa 2003, Huntley & Baxter 2005). Impacts of increased nitrogen deposition have been investigated and modelled in many semi-natural habitats, including lowland heathland (Power *et al.* 1998a, Britton *et al.* 2001), calcareous grasslands (Wilson *et al.* 1995, Lee & Caporn 1998), acidic grassland (Lee & Caporn 1998, Stevens *et al.* 2004), heathland (Roem & Berendse 2000), meadows (Berendse *et al.* 1992) and peat moor (Mountford *et al.* 1993). Impacts of eutrophication on British vegetation have been analysed using long-term data by Haines-Young *et al.* (2000, 2003), Smart *et al.* (2003a, b), Preston *et al.* (2002) and Braithwaite *et al.* (2006). Overall, the results provide evidence of increased plant productivity, litter production and nitrogen mineralization, leading to changes in soil processes (e.g. acidification and increases in available nitrogen in the soil), reduced species richness, the competitive exclusion of species indicative of infertile situations, an increase of vegetation typical of more fertile conditions, direct toxicity and greater susceptibility of plants to stress and disturbance, e.g. pathogens, frost, drought and herbivory.

Sand dunes are nutrient poor habitats considered to be under threat from eutrophication (de Vries *et al.* 1994, Bobbink *et al.* 2003, Jones *et al.* 2004a). Several Dutch studies have tried to establish the reasons for changes observed in the vegetation of coastal dunes over the last few decades, mainly the increased dominance of tall grasses and the loss of open, species-rich grasslands (Kooijman & de Haan 1995, Kooijman & van der Meulen 1996, Veer & Kooijman 1997), and have implicated atmospheric input of nitrogen in these changes (ten Harkel & van der Meulen 1996, Veer 1997, Kooijman 2004). Sival & Strijkstra-Kalk (1999) quantified nitrogen inputs into dune slacks on Frisian Islands and illustrated that this habitat was still sensitive to enhanced atmospheric deposition. These results suggest that increased nitrogen inputs can accelerate succession, enhance graminoid growth, and lead to the dominance of tall, dense vegetation, resulting in the loss of forbs, bryophytes and species associated with early successional communities (ten Harkel & van der Meulen 1996, van der Maarel & van der Maarel-Versluys 1996, Veer & Kooijman 1997, Jones *et al.* 2002b). It can also result in increased stabilisation of dunes and reduced rates of blowout development (van Boxel *et al.* 1997), while acid rain can leach the upper soil layers, causing some small winter annual species that are typical of base-rich dune grasslands to decrease (Westhoff 1989).

Controlled livestock grazing is used on many sand dune sites as a management tool to counteract grass and shrub encroachment, create a greater diversity of vegetation structure and promote species richness (e.g. Hewett 1985, Massey & Radley 1992, van Dijk 1992, Kooijman & de Haan 1995, Whatmough 1995, de Bonte *et al.* 1999, Hootmans 2002). Stock grazing can also reduce succession and help remove excess nutrient inputs through atmospheric deposition (Kooijman & van der Meulen 1996, ten Harkel & van der Meulen 1996, Kooijman & Smit 2001). Kooijman (2004) concludes that dunes are responsive to eutrophication, but also to management by grazing which leads to reduced plant productivity, litter accumulation and mineralization. Smaller herbivores such as rabbits have been shown to graze preferentially in areas with increased food quality. This can be due to heavy grazing by larger herbivores that stimulates fresh regrowth of high quality, or to increased food quality after experimental fertilisation (Bos *et al.* 2002b, Bakker *et al.* 2005b).

Fertilisation experiments previously carried out on sand dunes to establish which nutrients restrict plant productivity are of limited value for evaluating the effects of increased deposition of nitrogen, because they used high concentrations, nutrient mixtures or applied nitrogen only once or very few times per year (e.g. Willis & Yemm 1961, Willis 1963, Pemadasa & Lovell 1974a, Boorman & Fuller 1982, Olff *et al.* 1993). Greipsson & Davy (1997) investigated a single dune species, *Leymus arenarius*, and found increased flower production and seed weights after fertilisation with nitrogen. In the only experimental studies to date investigating the effects of increased nitrogen deposition on dune grassland, species composition had not changed after four years of fertilisation, which might be due to limitation by phosphorus (ten Harkel & van der Meulen 1996, ten Harkel *et al.* 1998).

Critical loads for eutrophication, i.e. the maximum input into a habitat that is believed not to lead to adverse effects on sensitive elements of the environment, are used to develop policies and to assess current and potential future effects of pollutants (NEGTAP 2001). They are defined as ranges because the impact of nitrogen deposition for a given habitat can depend on additional factors such as management or phosphorus limitation (Cunha *et al.* 2002). For dune grasslands, a critical load of 10-20 kg ha^{-1} $year^{-1}$ was suggested by Bobbink *et al.* (2003) and Jones *et al.* (2002a, b, 2004a). However, these authors call for further work to validate this range, understand the interactions of nitrogen input and management practices, and identify indicators of damage caused by excess nitrogen. Moreover, research is needed using realistic nitrogen loads and sites with low background depositions (Bobbink *et al.* 2003). Many experiments use application rates greater than the predicted critical load, which makes defining the critical load difficult (NEGTAP 2001).

This paper presents a study investigating the effects of fertiliser application and grazing on the vegetation of fixed dune grasslands, combining three grazing treatments with four nitrogen fertilisation treatments on a dune system currently receiving relatively low levels of background deposition (Mohd-Said 1999). The aims were to study the effects of increased deposition of nitrogen on vegetation composition, structure, above-ground biomass and soil chemistry, as these effects so far are largely unknown (Jones *et al.* 2004b), and to attempt to validate the proposed range of the critical load for dune grasslands. Nitrogen applications took place throughout the year. Two realistic application rates were chosen so that total nitrogen inputs reached the upper limit of the proposed critical load range for one treatment and exceeded it for the other. In particular, it was hypothesised that fertilisation with nitrogen: 1) leads to changes in the composition and structure of the vegetation of fixed dune grasslands; 2) increases above-ground standing biomass; and 3) alters soil chemistry and plant tissue chemistry. In addition, the effects of grazing by rabbits and livestock were investigated, testing the following hypotheses: 4) There are differences in the impact of rabbit grazing alone and rabbit grazing in combination with livestock grazing on vegetation composition and structure. 5) Grazing by livestock and/or rabbits can mitigate any potentially adverse effects of nitrogen deposition. 6) Rabbits graze preferentially in areas with potentially increased food quality. The possibility of the vegetation being co-limited by phosphorus was addressed in an additional experiment applying both nitrogen and phosphorus.

Methods

Study site

This study was conducted at Newborough Warren on the south-west coast of the Isle of Anglesey, North Wales, UK (National Grid reference SH 400640). Comprising about 1300 ha of sandy deposits, it is one of the major calcareous and most biologically diverse sand dune systems on the west coast of Britain despite the afforestation of about 720 ha with conifers, mainly Corsican pine (*Pinus nigra* ssp. *laricio*) (Gibbons 1994), between the 1940s and 1960s (Rhind *et al.* 2001). The dune system consists of foredunes and ridges of compound parabolic dunes roughly parallel to the shoreline which are separated by extensive interdune slacks. It comprises the full succession of habitats from strandline to shingle, mobile dunes, wet and dry slacks to dune grassland and scrub and harbours many rare and protected species. Newborough Warren's outstanding conservation value is recognised in its designation as National Nature Reserve (NNR), Site of Scientific Interest (SSSI) and Special Area of Conservation (SAC) under the EC Habitats and Species Directive 1992. This is because of its high diversity of habitats of European importance, including shifting dunes, dune grassland and humid dune slacks, for which it is considered one of the best areas in Britain. The climate does not show any marked extremes of temperature or rainfall (Buchan 1990) and has an average mean annual temperature of 12.9 °C (Anderson 1994). The average annual amount of rainfall is 843 mm, with April to June being the driest months and October to January the wettest (Anderson 1994). The site is grazed by Welsh mountain ponies at a low stocking density of one pony to every 3-4 ha all year round. The total background deposition of nitrogen was estimated at 12 kg ha^{-1} $year^{-1}$ (Mohd-Said 1999).

Nitrogen fertilisation and grazing exclusion experiment

Experimental design and treatments

Experimental sites were chosen in three blocks of vegetation in an area of fixed dune grassland at the landward end of the dunes. Care was taken to select areas of uniform vegetation as far as possible to minimize variation within and between blocks. For practical reasons, a split-plot design was used to apply grazing and fertilisation treatments, which also enabled analysis of interactions between treatments (Figure 5.1). Each of the three blocks of vegetation contained the following three main plot grazing treatments: ungrazed, grazed by rabbits and grazed by both rabbits and ponies. Three plots excluding ponies but not rabbits were enclosed with 10 x 10 cm netted fencing. The same fencing method was employed for the three rabbit exclusion plots, which in addition were fenced with 2.7 x 3.7 cm wire mesh to a height of 1.20 m and sunk at least 20 cm into the ground and 15 cm outwards to avoid rabbits digging their way underneath. In both cases, barbed wire was placed on top of the fence. Building of the fences took place in the second half of May 2003. Plots were chosen so that remains of cut or sprayed shrubs were not included as they might influence nitrogen and nutrient contents of the soil.

Within each of these nine main plots, four different nitrogen (N) treatments were applied: unwatered control, watered control, low N treatment (7.5 kg ha^{-1} $year^{-1}$) and high N treatment (15 kg ha^{-1} $year^{-1}$), giving a total of 36 experimental subplots. These subplots were established in groups of four, as close together as possible, in suitable areas that were level, contained no shrubs or pony tracks and did not have any entrances to rabbit warrens nearby. The grazing exclusion fences were erected around these groups of subplots, with a buffer zone of at least 1.50 m between each subplot and the fence to avoid possible edge effects. The subplots measured 2.05 x 2.05 m and were separated from each other by a 75 cm or wider buffer zone. They each contained a 1 x 1 m quadrat for vegetation recording and sward height measurements as well as space allocated for soil and biomass sampling (Figure 5.2). Allocation of treatments to both main plots and subplots was randomised.

Nitrogen was applied as ammonium nitrate in 5 litres of deionised water on 13 occasions per year between June 2003 and June 2005, using a watering can with a 50 cm wide extension bar. The watered control received 5 litres of deionised water only, the unwatered control no treatment at all. As the experiment was trying to simulate increased concentrations of nitrogen deposited in rainwater, nitrogen was applied more frequently at times of higher long-term average rainfall: six times during the wettest months from October to January (every three weeks), four times in February/March and August/September (every four weeks), and three times in the driest months April to July (every six weeks).

A National Vegetation Classification (NVC) survey was carried out in the experimental area in May 2004, using eleven 2 x 2 m quadrats, and the plant community identified by the program Match (Malloch 1992).

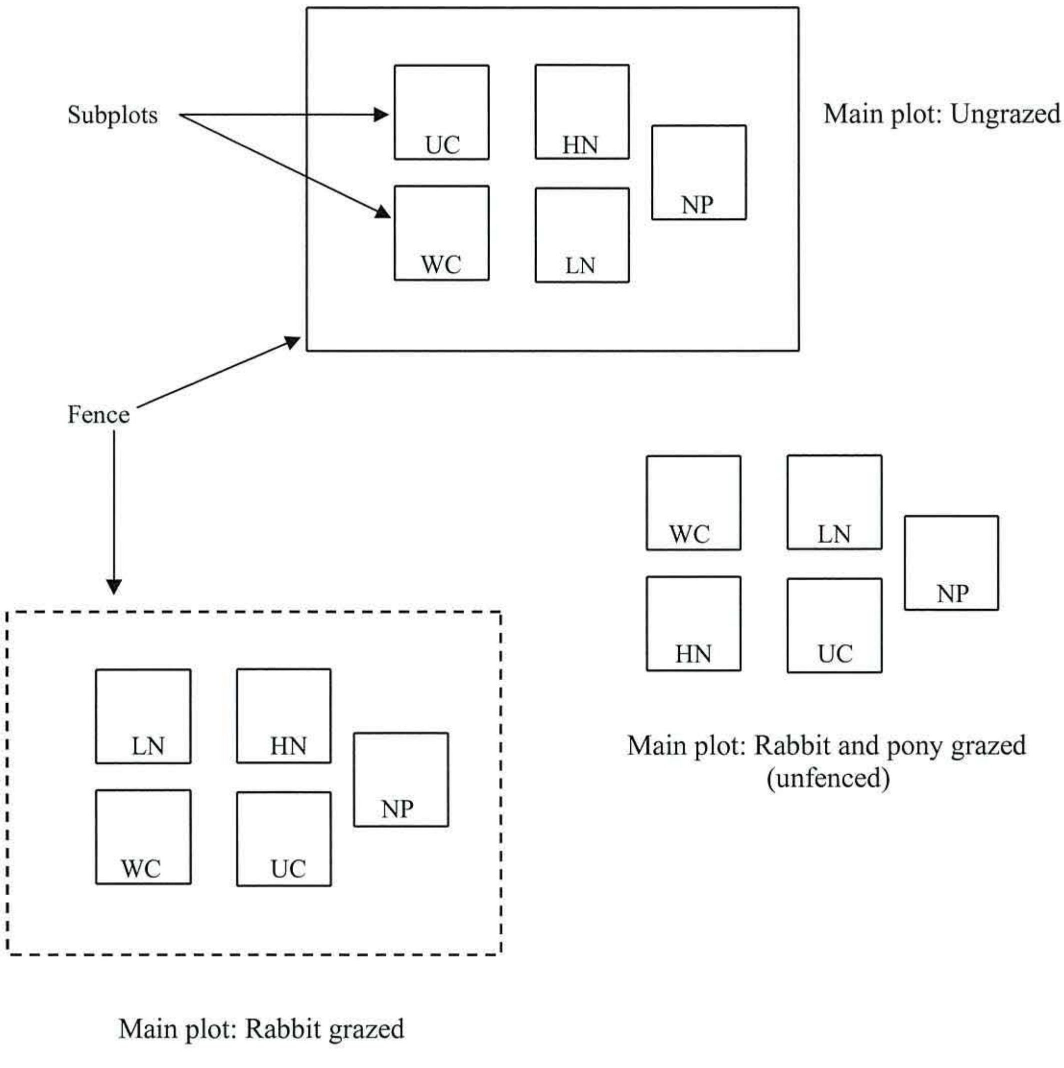


Figure 5.1. Experimental split-plot design: The main plot was grazing treatment and subplots five fertilisation treatments (UC = unwatered control, WC = watered control, LN = low nitrogen, HN = high nitrogen, NP = high nitrogen and phosphorus (see below)). There were three replicates of each main plot grazing treatment.

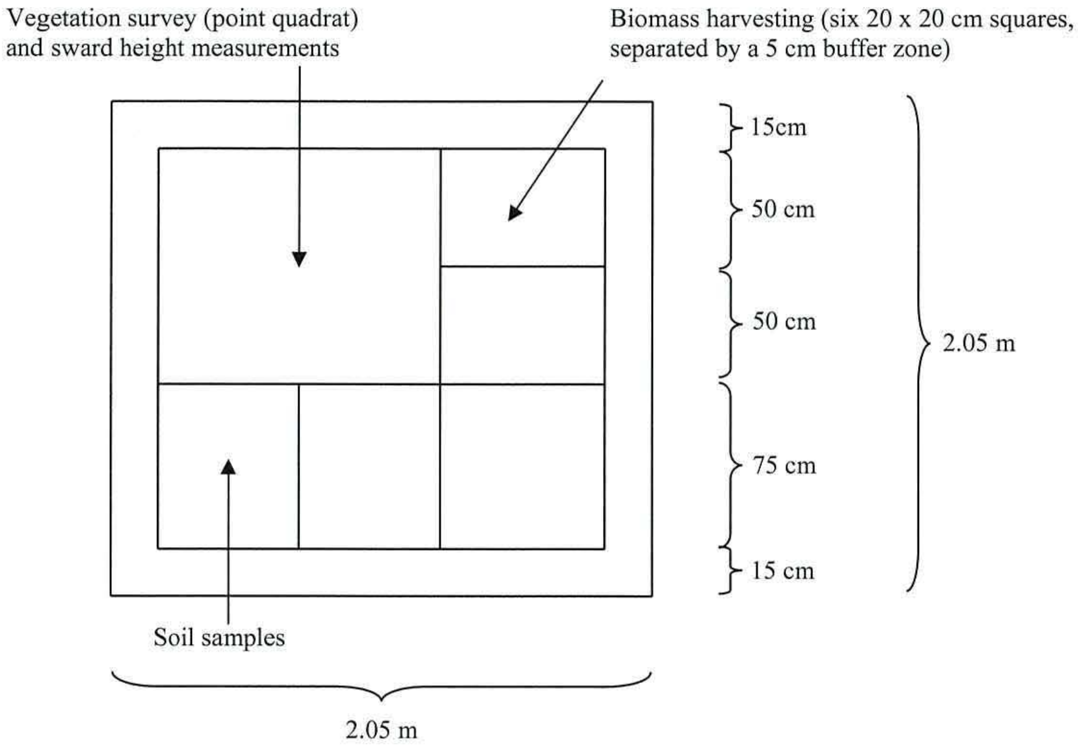


Figure 5.2. Layout of the subplots showing dimensions and where vegetation surveys and height measurements were carried out and biomass and soil samples taken. The application of nitrogen covered the whole 2.05 x 2.05 m plot. Three sections of the plot were left spare for possible future additions to the experiment.

Soil analysis

Two replicate soil samples were collected from each subplot before nitrogen applications started (May 2003) and at the end of the experiment (May 2005) to a depth of 15 cm using cores of 5 cm width. In the laboratory, the vegetation was cut to soil level, the complete core weighed and the depth of the organic top horizon measured; after that, the core was subdivided into topsoil and subsoil, which were processed separately. About a third of each horizon was used for an analysis of root biomass, while two thirds were prepared for chemical analysis, i.e. cleared of roots, stones etc. by sieving. The two replicate samples were combined and stored at 4 °C until analyses were carried out. Soil moisture was determined by weighing 7-10 g of fresh, field-moist soil after drying at 105 °C for eight hours. Soil organic matter was analysed as loss on ignition by further drying the samples at 375 °C overnight, a temperature that is high enough to burn off organic matter but not to cause decomposition of calcium carbonate (Hill & Wallace 1989). Both moisture content and organic matter content are expressed as percentage of the 105 °C dry weight. Available nitrate and ammonium were extracted in 1.0 M KCl and the filtrates analysed using colorimetric autoanalyser techniques. Total N was determined on air dried and ground soil by Kjeldahl acid digest for the baseline samples; because of the very low levels of N in the baseline soil, total N and carbon (C) were analysed in topsoil samples only using a CHN analyser for end of project samples. Soil pH was determined electrometrically using a Corning 220 pH meter both in water and 0.125 M $CaCl_2$. The ratio of soil to water was 1:2.5 by weight. Root biomass was determined by first sieving the samples and then washing off the remaining soil. The harvested material was weighed after drying at 65 °C for 48 hours. Blanks, duplicates and standard soils were included in all analyses to ensure accuracy of the methods used.

Vegetation surveys

Assessments of plant species composition were carried out in 1 x 1 m quadrats using the point quadrat method. The species of each plant hit by the needle (3 mm diameter) was recorded at 60 regularly spaced points on a 10 x 6 grid using a point quadrat frame of five pins ten cm apart. For each pin, every vascular and bryophyte species contacted was recorded, but not the number of times contacted. The first survey was carried out in early June 2003 before nitrogen applications started; repeat surveys were conducted in June, September and April of each year until June 2005 to detect possible differences in vegetation composition that may only be apparent in a particular season, e.g. in winter annuals. The points sampled at repeat surveys were scattered within a few square centimetres. From April 2004 onwards, a note was made of the highest plant species touching the pin and the height where it touched.

Nomenclature for higher plants follows Stace (1997) and for bryophytes Smith (2004). The term forbs is used to include all non-grassy, herbaceous plants (Allaby 2004).

Sward height measurements

Vegetation height was measured to the nearest mm using a 20 cm diameter (11 g) plastic disk that was lightly dropped down a vertically held ruler. Measurements were carried out randomly in the same section of the plots as the point quadrat surveys every two weeks (March to August) or three to six weeks (September-February) from June 2003 to June 2005, with five replicate measurements taken until the end of October 2003 and ten replicates taken thereafter.

Biomass sampling and analysis

Above-ground biomass, including surface litter, was harvested from 20 x 20 cm squares in April, June and September of each year between June 2003 and June 2005, coinciding with the assessment of the vegetation by the point quadrat method. The biomass was then dried at 65 °C for 48 hours and weighed. Later on, the samples (including litter) were sorted into the three plant groups graminoids, bryophytes and forbs and the sub samples weighed again. Data are presented as g dry biomass m^{-2}.

The dried material harvested at the end of the project in June 2005 was ground to a fine powder and analysed for nitrogen (N) and phosphorus (P) content for all treatments except the unwatered control. This was not done for the forbs because the amount of forb biomass was too low for analysis in most samples. Percentage N content was determined by acid digest using a Tecam DG-1 Block Digestor and a 2300 Kjeltec Analyser Unit. The samples for P analysis were prepared by dry combustion, the soluble mineral dissolved in hydrochloric acid and the concentration of P in the solution determined spectrophotometrically as the concentration of a phospho-vanadomolybdate complex (Ministry of Agriculture, Fisheries and Food 1986). Standard reference leaf material of known N and P content was included in the analyses to check accuracy of the methods used.

Data analysis

Weighted mean Ellenberg indicator values for nitrogen were calculated for each subplot according to the following formula (ter Braak 1995): Weighted average = $(y_1x_1 + y_2x_2 + \ldots + y_nx_n) / (y_1 + y_2 + \ldots + y_n)$, where $y_1, y_2, \ldots, y_n$ are the abundances of the species 1-n and $x_1, x_2, \ldots, x_n$ are the Ellenberg indicator values for species 1-n. Weighted rather than unweighted indicator values based on presence-absence data were used because changes in species abundance as a result of grazing and fertilisation were expected. Ellenberg values were based on Hill *et al.* (1999) for higher plants and Hill & Roy (unpubl.) for bryophytes.

Differences between grazing treatments, nitrogen fertilisation treatments and the interaction of grazing and nitrogen addition were analysed by split-plot Anova using Genstat 8.1. Degrees of freedom for the main plot and subplot error terms are shown in Table 5.1. Error bars in graphs represent the standard error of the differences of the means as analysed by Genstat.

Table 5.1. Outline of degrees of freedom (df) for main plot, subplot and total error terms in split-plot Anova analyses. In analyses where no covariates were included, the residual terms increased by 1.

		df
Main plot	Block	2
	Grazing	2
	Residual term	3
	Covariate	1
Subplot	Nitrogen fertilisation treatment	3
	Nitrogen fertilisation treatment*grazing	6
	Residual term	17
	Covariate	1
Total		35

Building of the fences took two weeks, and the first field measurements were taken one week after building of the fences was complete. Because of this, the first point quadrat surveys, biomass samples and sward height measurements cannot be regarded as a true baseline for the grazing treatments. However, no change in community composition was expected within two weeks, and if so, they were considered negligible compared to changes occurring over the following two years. Thus, for the analysis of species abundance and composition, the first point quadrat survey was used as a baseline in the statistical analysis. The analysis of sward heights is presented without adjusting for the baseline, because sward heights were already significantly greater in ungrazed plots at the time of the first measurement, but an analysis using the first measurement as covariate is also presented in Appendix 2.4. For biomass harvests, the baseline was only found to have an effect on subsequent bryophyte samples, but as both the analysis with and without covariate gave the same results in terms of significant differences between treatments, using the baseline was justified. Soil samples were taken before the fences were set up, so that the effects of grazing on soil parameters and root biomass were analysed using the baseline as covariate.

For the nitrogen addition treatments, the first measurements do represent a true baseline as fertilisation only started after the first point quadrat survey, sward height measurements and biomass sampling.

Vegetation composition was analysed by principal components analysis (PCA) with a log(n+1)-transformation using Canoco for Windows 4.5 (ter Braak 1987). The baseline vegetation data gathered in June 2003 before the start of nutrient applications was subtracted from all following records to adjust for initial differences in composition. A constant was then added to all samples because Canoco does not accept negative numbers. Records for *Vicia sativa* and *V. hirsuta* were pooled because they were not distinguishable at every time of year.

Nitrogen and phosphorus uptake were calculated by multiplying percentage nutrient concentrations by total stand (20 x 20 cm) biomass. Data on typical plant heights were obtained from Hill *et al.* (2004) and used to classify species as either low growing (up to 20 cm), mid-sized (20-60 cm) or tall (over 60 cm). Relative abundances were calculated for three plant groups, graminoids, bryophytes and forbs, for every subplot in each point quadrat survey by dividing the sum of all hits per plant group by the total number of hits for that quadrat; an ordination was then performed based on these relative abundances. Analysis of life forms and perennation was based on information in Hill *et al.* (2004).

Nitrogen and phosphorus addition experiment

Within the nine experimental blocks described above, another experiment was set up in April 2004 in order to assess whether vegetation growth was limited by N or P alone or co-limited by both. Experimental subplots measured 1 x 1.25 m and were separated from the main nitrogen addition subplots by a buffer zone of 1.20 m or more. The subplots were set up and a baseline survey of the vegetation using the point quadrat method as described above carried out in April 2004. Phosphorus was applied as sodium dihydrogen orthophosphate ($NaH_2PO_4 \cdot 2H_2O$) at 20 kg ha^{-1} year^{-1} in 5 litres of deionised water on two occasions at the end of April and May 2004. Nitrogen was applied in the same dosage as the high N plots of the main experiment (15 kg ha^{-1} year^{-1}) every two weeks in 2 litres of deionised water, which meant adding about the same amount of water as in the larger main nitrogen addition plots, between the end of April and August 2004 and again from April 2005 to the end of the experiment in June 2005. Repeat point quadrat surveys were conducted in June, September and April of each year until June 2005, and measurements of vegetation height and biomass sampling were carried out at the same time as for the main experiment, using the same methods.

Because fertilisation with nitrogen only proved of minor importance on most of the variables measured, the effects of additional fertilisation with phosphorus were analysed using the baseline for those plots (April 2004) as a covariate. Even for the parameters that did change after fertilisation with nitrogen alone, this was only significant after April 2004. For the interaction of grazing and fertilisation, this was not possible as April 2004 could not represent a baseline for the grazing treatments that started in May 2003. Table 5.2 shows the degrees of freedom for the subplot error terms.

Table 5.2. Outline of degrees of freedom (df) for subplot and total error terms in split-plot Anova analyses. In analyses where no covariates were included, the residual terms increased by 1.

		df
Subplot	Fertilisation treatment	4
	Fertilisation treatment*grazing	8
	Residual term	23
	Covariate	1
Total		44

Rabbit activity and counts

In order to test whether rabbits preferentially grazed in fertilised rather than control plots, pellet counts were conducted four times between June and August 2004 in 50 x 50 cm squares assuming that the number of pellets reflects time spent grazing in each plot (Jaksic & Soriguer 1981, Leigh *et al.* 1989, Bakker *et al.* 2005b). All pellets in these squares were counted and then removed.

In June and July 2004, rabbit density was estimated by dawn counts in the three areas containing one experimental block each. The size of these areas depended on local topography, with the smallest measuring 20 x 25 m and the largest 65 x 70 m. Trial counts were made at dusk from 9-10 pm and at dawn from 7-8 am. Because the trial at dawn showed greater rabbit activity which is in accordance with Romeril (1989) and Pott *et al.* (1999), three counts of rabbits feeding at dawn were made on 15-17 June

2004, and again between 24 and 28 July 2004 from 5.30-7 am, with counts made every five minutes. Disturbance of rabbits by the observers reaching the area and settling down was low, and within about 10-15 minutes the rabbits appeared to behave normally (cf. Moller & Newton (1996) who found that disturbance did not significantly disrupt rabbit counts). Some counts were much lower than previous ones, and in most cases the reason for this could be identified, e.g. the presence of foxes or ponies in the area; these counts were excluded from the analysis. Results are presented as estimated rabbit numbers per ha.

Results

National Vegetation Classification (NVC) community

An NVC survey carried out in May 2004 confirmed the plant community in the area of the experiment as SD8b, *Festuca rubra-Galium verum* fixed dune grassland, *Luzula campestris* sub-community (Rodwell 2000) (Appendix 2.1). Species richness ranged between 23 and 30 species per quadrat. The dominant graminoids were *Festuca rubra*, *Arrhenatherum elatius*, *Carex arenaria* and *Luzula campestris*. Amongst the dicotyledonous herbs, *Galium verum*, *Veronica chamaedrys*, *Lotus corniculatus*, *Senecio jacobaea*, *Cerastium fontanum*, *Ranunculus bulbosus* and *Viola tricolor* were most abundant and frequent. Bryophyte cover was high throughout the area, with *Pseudosleropodium purum*, *Hylocomium splendens*, *Rhytidiadelphus squarrosus* and *R. triquetrus* all very common.

Effects of nitrogen fertilisation and grazing treatments

Fertilisation with nitrogen had a significant effect on total above-ground biomass, bryophyte biomass and concentrations of nitrogen in bryophyte biomass. However, no changes due to the addition of nitrogen were detected for overall vegetation composition, individual plant species, sward heights, root biomass or any of the soil parameters measured. Because of this, the effects of the different grazing treatments were analysed across all nitrogen addition treatments for all variables. For total biomass, bryophyte biomass and tissue nitrogen concentrations analyses were also conducted for the unfertilised control treatments only to eliminate any possible fertilisation effect when looking at the effects of grazing.

Soil chemistry

No significant differences between treatments were observed for any of the soil parameters measured in either baseline or end of project soil samples in the topsoil. Table 5.3 and Appendix 2.2 present an overview of average values for soil parameters for the topsoil. Significant differences between grazing treatments existed in the subsoil in the baseline samples for moisture content, available NH_4-N and pH (split-plot Anova, moisture content: $p=0.008$, dry weight: $p=0.006$, NH_4-N: $p=0.038$, pH: $p=0.047$, details in Appendix 2.3). There were no initial differences between nitrogen addition treatments (Appendix 2.3).

Sward heights

Average sward heights were significantly greater in ungrazed than grazed plots on each of the 34 sampling occasions (split-plot Anova, $p<0.05$, details in Appendix 2.4), (Figure 5.3a). Using the first measurement as covariate, the difference was significant from April 2004 onwards (Appendix 2.4). Plots grazed by rabbits only and by both rabbits and ponies had very similar average vegetation heights, indicating that rabbits exerted more grazing pressure than ponies. Summer peaks of sward height were more pronounced in ungrazed than grazed plots and increased from 2003 to 2005. The greatest average height where species touched the point quadrat pins also was significantly higher in ungrazed than grazed plots (split-plot Anova, $p<0.05$, details in

Table 5.3. Average values for soil parameters in the different grazing and nitrogen addition treatments for topsoil samples taken in May 2003 (baseline) and May 2005, adjusted for the baseline as covariate, and results of Anova analyses (OM = organic matter, s.e.d. = standard error of the differences of means). C = carbon was only measured in May 2005 samples. a) By grazing treatment, b) by nitrogen fertilisation treatment. For the interaction of grazing and nitrogen treatment, see Appendix 2.2.

a)

	Year	Ungrazed	Rabbit grazed	Rabbit and pony grazed	f ratio	p value	s.e.d.
Moisture content (%)	2003	12.52	12.82	10.67	1.12	0.410	1.552
	2005	21.84	19.33	18.96	0.69	0.565	2.869
Organic matter content (%)	2003	9.18	8.59	8.22	0.49	0.647	0.980
	2005	8.68	9.04	8.76	0.04	0.961	1.371
pH (H2O)	2003	5.26	5.41	5.36	3.23	0.146	0.062
	2005	5.85	6.09	5.83	0.47	0.663	0.339
pH ($CaCl_2$)	2003	4.76	4.80	4.71	0.57	0.607	0.087
	2005	4.98	4.99	4.89	0.30	0.758	0.134
N (%)	2003	0.329	0.306	0.242	3.83	0.118	0.033
	2005	0.160	0.282	0.176	1.25	0.403	0.136
Available NO_3-N (μg/g dry soil)	2003	6.02	2.82	6.03	2.22	0.224	1.755
	2005	0.57	0.86	1.03	1.14	0.428	0.381
Available NH_4-N (μg/g dry soil)	2003	6.62	6.59	5.84	0.08	0.926	2.231
	2005	13.76	13.09	13.10	0.05	0.949	2.363
Available NO_3-N (μg/g OM)	2003	69.8	31.5	74.2	2.16	0.231	22.580
	2005	7.7	10.2	11.6	1.40	0.373	2.940
Available NH_4-N (μg/g OM)	2003	71.0	76.6	72.8	0.05	0.950	17.780
	2005	158.5	145.3	148.4	0.25	0.791	19.280
C (%)	2005	3.53	4.05	3.43	0.980	0.451	0.516
C (%) : N (%)	2005	22.60	16.60	24.40	5.650	0.068	2.430

b)

	Year	Unwatered control	Watered control	Low N	High N	f ratio	p value	s.e.d.
Moisture content (%)	2003	15.32	12.59	10.62	9.09	2.530	0.092	2.344
	2005	20.89	19.55	18.83	20.91	0.560	0.648	2.128
Organic matter content (%)	2003	10.26	8.28	7.43	8.69	2.860	0.066	0.990
	2005	8.86	8.38	8.90	9.17	0.230	0.876	1.070
pH (H2O)	2003	5.23	5.38	5.47	5.29	1.380	0.281	0.125
	2005	5.85	5.85	6.06	5.93	0.590	0.632	0.177
pH ($CaCl_2$)	2003	4.84	4.80	4.74	4.65	0.710	0.560	0.134
	2005	4.87	4.91	5.01	5.03	1.330	0.298	0.089
N (%)	2003	0.360	0.286	0.280	0.243	3.050	0.055	0.040
	2005	0.224	0.150	0.189	0.260	1.630	0.221	0.058
Available NO_3-N (μg/g dry soil)	2003	4.42	5.67	4.53	5.21	0.310	0.818	1.492
	2005	0.83	0.76	0.59	1.11	0.940	0.445	0.310
Available NH_4-N (μg/g dry soil)	2003	6.26	6.49	4.77	7.88	0.950	0.438	1.853
	2005	16.16	11.14	13.11	12.86	1.120	0.369	2.859
Available NO_3-N (μg/g OM)	2003	44.34	71.56	59.45	58.65	0.960	0.434	16.09
	2005	9.3	10.4	7.6	12.0	0.450	0.720	3.94
Available NH_4-N (μg/g OM)	2003	59.78	78.52	65.97	89.47	0.880	0.470	19.96
	2005	172.9	135.1	153.0	141.9	0.950	0.441	22.98
C (%)	2005	4.02	3.44	3.42	3.85	0.710	0.559	0.471
C (%) : N (%)	2005	18.40	25.70	20.30	20.50	2.420	0.101	2.840

Appendix 2.5) and very similar in the two grazed treatments throughout the experiment (Figure 5.3b). Figure 5.4 illustrates the differences in sward heights between the different grazing treatments.

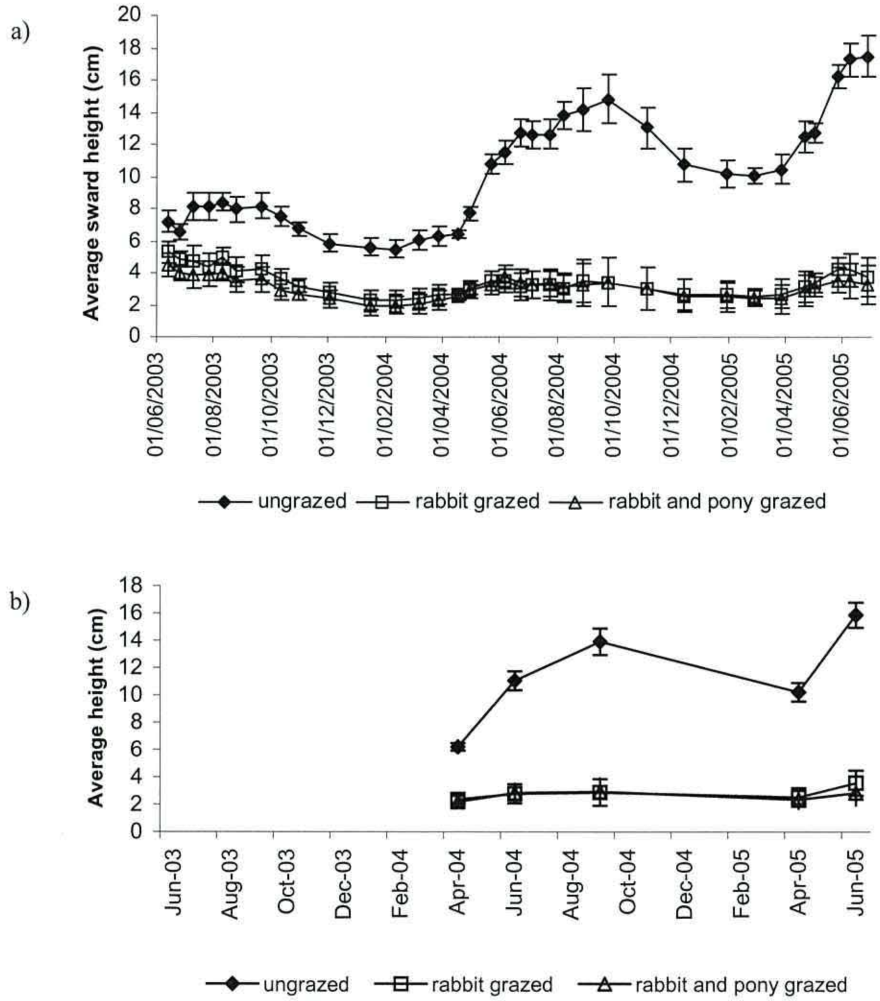


Figure 5.3. a) Average sward heights in the three different grazing treatments between June 2003 and June 2005. b) Average height of the highest hit in point quadrat surveys between April 2004 and June 2005. Differences between ungrazed and grazed treatments were significant for all sampling dates for both a) and b). Error bars represent the standard error of the differences of means.

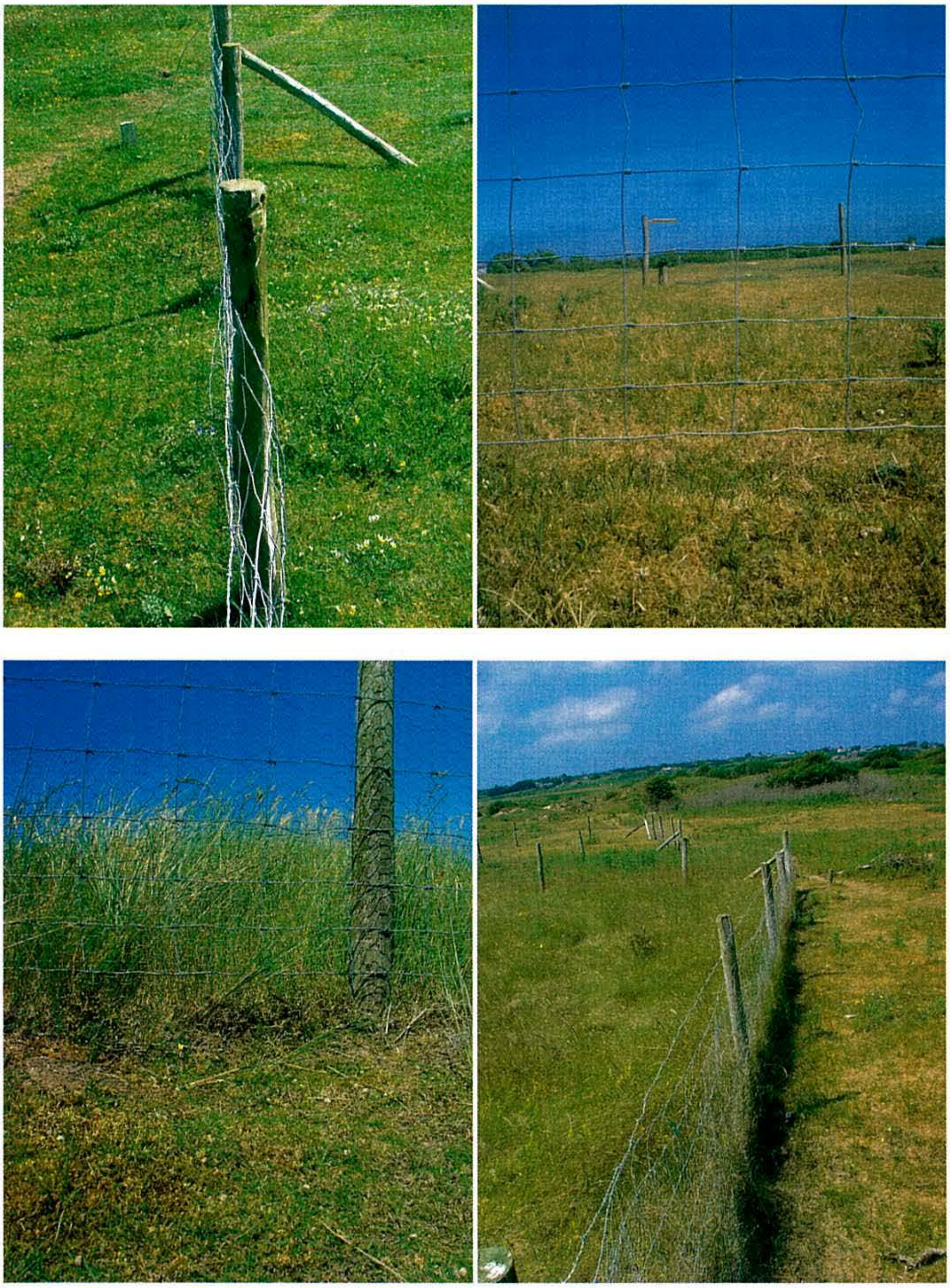


Figure 5.4. Effects of grazing treatment. Top left: Grazed by rabbits (right side of fence) and grazed by both rabbits and ponies (left side of fence). Top right: Grazed by rabbits (background) and grazed by both rabbits and ponies (foreground). Bottom left: Grazed by both rabbits and ponies (foreground) and ungrazed (background). Bottom right: Grazed by both rabbits and ponies (right side of fence) and ungrazed (left side of fence). Pictures taken in June 2005.

There was no effect of nitrogen fertilisation on sward height (Figure 5.5a) (split-plot Anova, p>0.05 on 29 out of 34 sampling occasions, see Appendix 2.4). The data were also analysed for linear effects across watered controls, low N and high N treatments and no significant effects discovered. No significant interaction of grazing and nitrogen application was found (split-plot Anova, p>0.05 on 32 out of 34 sampling dates, details in Appendix 2.4). The same was true for the height of the highest hit in the point quadrats surveys (Figure 5.5b) (split-plot Anova, p>0.05 for all point quadrat surveys, see Appendix 2.5).

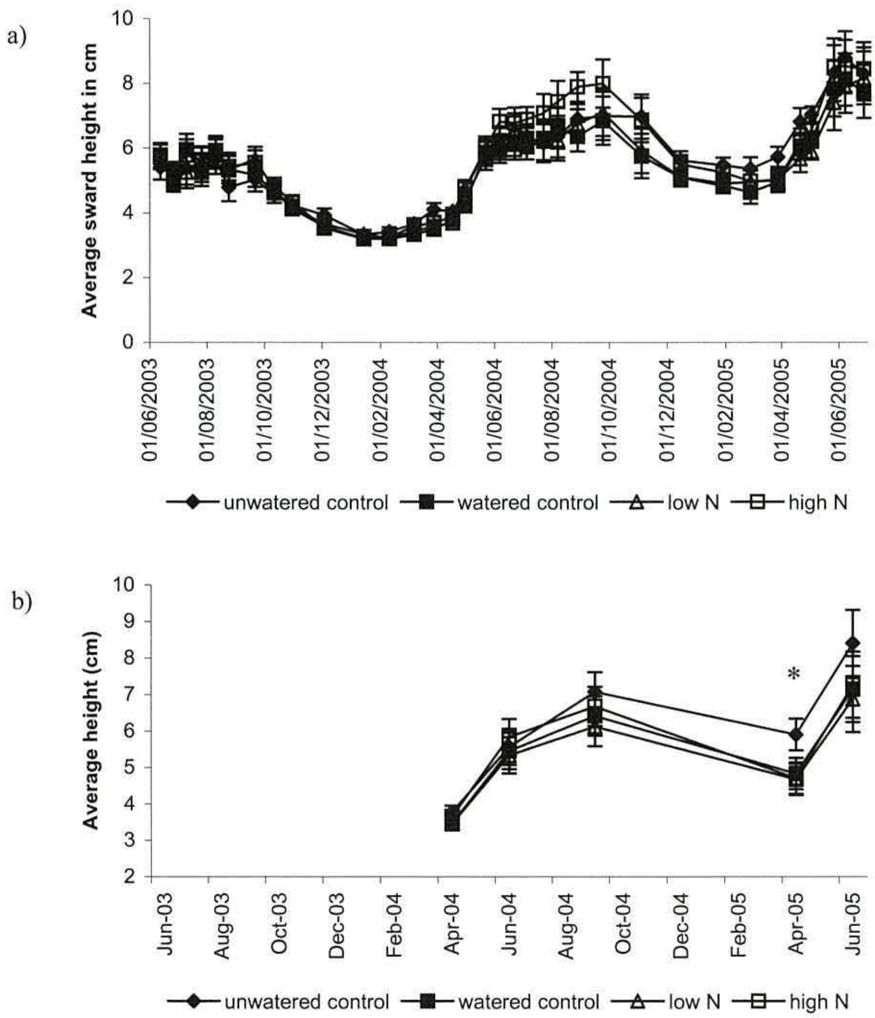


Figure 5.5. a) Average sward heights in the four nitrogen fertilisation treatments, adjusted for the baseline as covariate, between June 2003 and June 2005. b) Average height of the highest hit in point quadrat surveys between April 2004 and June 2005. Error bars represent the standard error of the differences of means. Stars indicate significant differences between treatments (p<0.05).

Above-ground biomass

Grazing exclusion significantly increased total biomass compared to the two grazed treatments by June 2005 (Figure 5.6a) (split-plot Anova, $p=0.030$, details in Appendix 2.6), which was mainly due to a significant increase in graminoids from the start of the experiment (Figure 5.6b) (split-plot Anova, $p=0.039$ in June 2003, $p=0.005$ in April 2004, $p=0.009$ in June 2005, details in Appendix 2.6). Bryophytes decreased in grazing exclusion plots and were the most important plant group in grazed plots, while graminoids dominated ungrazed subplots (Figures 5.6b, c, 5.7). No significant differences between grazing treatments were observed for the biomass of forbs (Appendix 2.6). When comparing only the unwatered control treatments to eliminate any possible fertilisation treatment effects, total biomass and bryophyte biomass were significantly greater in ungrazed than rabbit grazed plots in September 2003 (one-way Anova with Tukey's post-hoc test, total: $f=7.018$, $p=0.022$, bryophytes: $f=5.442$, $p=0.039$), while graminoid biomass was greater in ungrazed than rabbit and pony grazed plots in June 2004 and greater than both grazed treatments in June 2005 (one-way Anova with Tukey's post-hoc test, June 2004: $f=6.546$, $p=0.030$, June 2005: $f=8.148$, $p=0.026$ for ungrazed vs rabbit grazed and $p=0.035$ for ungrazed vs rabbit and pony grazed). There were no significant differences in the amount of forb biomass at any time. Although not quantified separately, dead plant material was present at the surface in ungrazed plots by the end of the experiment in greater amounts than in the two grazed treatments.

Nitrogen fertilisation resulted in increased total and increased bryophyte biomass in the low N and high N treatments compared to the watered control after two years of nutrient additions (Figure 5.8) (split-plot Anova, both total biomass and bryophytes: $p=0.024$ in June 2005, details in Appendix 2.6). No significant effects were observed for graminoids and forbs (split-plot Anova, $p<0.05$ for all samples, details in Appendix 2.6).

a)

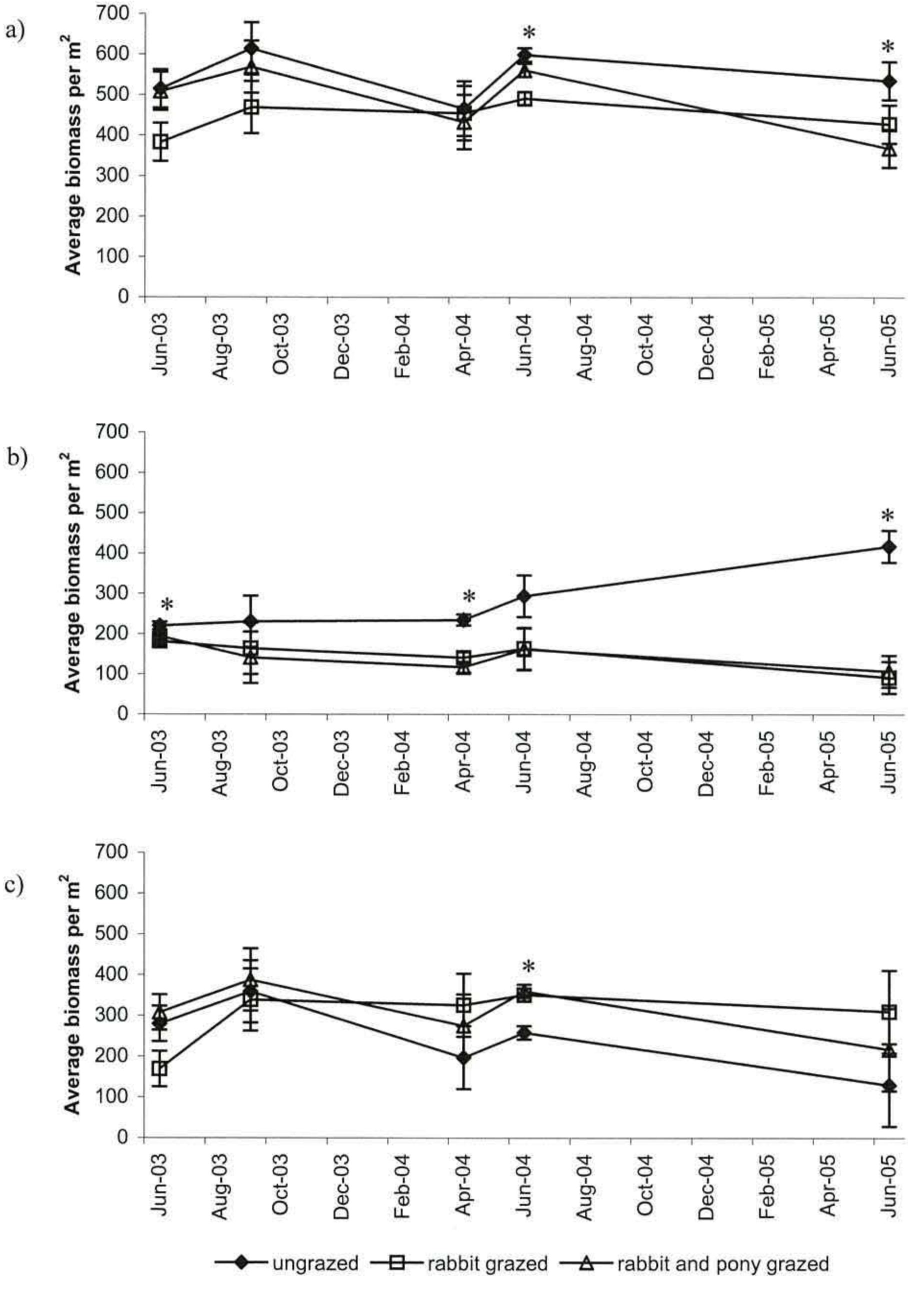


Figure 5.6. Average above-ground biomass (g dry weight m^{-2}) in three grazing treatments between June 2003 and June 2005, adjusted for the baseline as covariate. a) Total, b) graminoids, c) bryophytes. Error bars represent the standard error of the differences of means. Stars indicate significant differences between treatments ($p<0.05$).

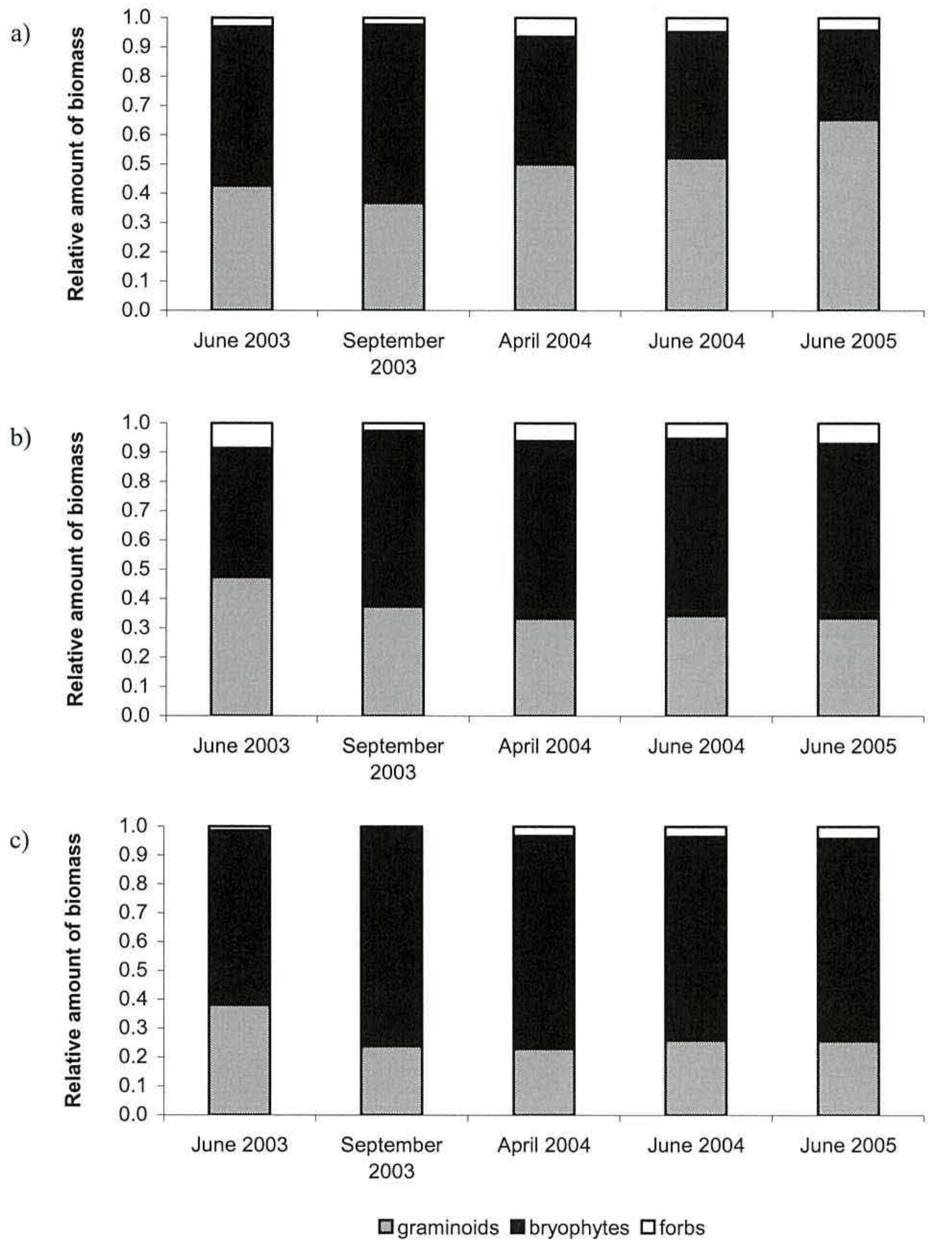


Figure 5.7. Average relative amounts of biomass of three plant groups in: a) ungrazed plots, b) rabbit only grazed plots and c) rabbit and pony grazed plots.

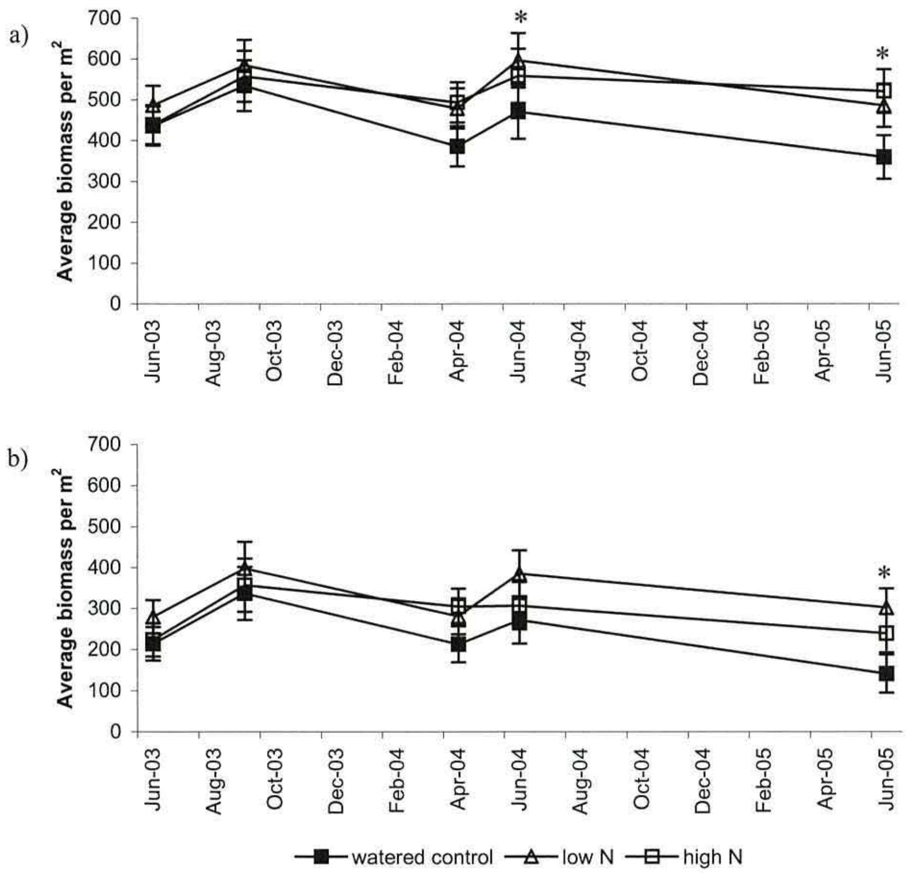


Figure 5.8. Average amount of biomass (g dry weight m^{-2}) in watered control, low N and high N treatments between June 2003 and June 2005, adjusted for the baseline as covariate. a) Total, b) bryophytes. Error bars represent the standard error of the differences of means. Stars indicate significant differences between treatments ($p<0.05$).

Root biomass

No significant differences between grazing or nitrogen treatments or their interaction were observed for the amount of root biomass measured in either baseline or end of project soil samples (Table 5.4).

Table 5.4. Average root biomass (g dry weight m^{-2}) for topsoil and subsoil samples taken in May 2003 (baseline) and May 2005, adjusted for the baseline as covariate. s.e.d. = standard error of the differences of means.

		Topsoil		Subsoil	
		2003	**2005**	**2003**	**2005**
Grazing treatment	Ungrazed	581.5	505.0	418.6	249.0
	Rabbit grazed	597.5	677.0	542.8	312.0
	Rabbit and pony grazed	710.6	470.0	373.5	267.0
	f ratio	1.18	4.91	2.00	0.36
	p value	0.396	0.113	0.25	0.722
	s.e.d.	91.8	76.0	87.6	74.2
Nitrogen treatment	Unwatered control	536.25	581.0	346.5	311.0
	Watered control	633.91	500.0	563.7	276.0
	Low N	779.40	610.0	380.5	298.0
	High N	569.82	512.0	489.1	219.0
	f ratio	0.85	0.59	2.15	1.59
	p value	0.485	0.628	0.130	0.229
	s.e.d.	165.2	96.6	96.4	54.0
Nitrogen*grazing					
Unwatered control	Ungrazed	460.1	500.0	227.7	243.0
	Rabbit grazed	478.9	642.0	443.5	379.0
	Rabbit and pony grazed	669.8	601.0	368.4	310.0
Watered control	Ungrazed	568.1	510.0	575.5	254.0
	Rabbit grazed	548.1	590.0	512.6	250.0
	Rabbit and pony grazed	785.6	401.0	603.2	325.0
Low N	Ungrazed	795.6	620.0	445.3	327.0
	Rabbit grazed	784.0	722.0	539.4	372.0
	Rabbit and pony grazed	758.6	488.0	157.0	195.0
High N	Ungrazed	502.3	391.0	425.8	172.0
	Rabbit grazed	578.9	755.0	676.0	248.0
	Rabbit and pony grazed	628.3	390.0	365.6	238.0
	f ratio	0.13	0.57	1.20	0.85
	p value	0.992	0.748	0.350	0.551
	s.e.d.	271.9	161.9	173.1	105.1

Nitrogen and phosphorus concentrations in biomass

Graminoids had significantly higher concentrations of nitrogen in grazed than ungrazed plots (Figure 5.9a) (split-plot Anova, p=0.026, see Appendix 2.7). Both nitrogen and phosphorus uptake were highest in the ungrazed treatment (Figure 5.9a) (split-plot Anova, p=0.004 and p=0.005 respectively, see Appendix 2.7), reflecting the much greater amount of graminoid biomass in ungrazed plots (Figures 5.6b, 5.7a). Concentrations of the two nutrients were not significantly different between grazing treatments for bryophytes (Figure 5.9b) (split-plot Anova, $p>0.05$, details in Appendix 2.8).

When comparing only the watered control treatments to eliminate any possible effect of fertilisation, nitrogen concentrations in graminoid tissue were significantly different between grazing treatments (one-way Anova with Tukey's post-hoc test, df=8, f=6.186, p=0.035, ungrazed vs rabbit grazed: p= 0.048, ungrazed vs rabbit and pony grazed: p=0.995, rabbit grazed vs rabbit and pony grazed: p=0.055).

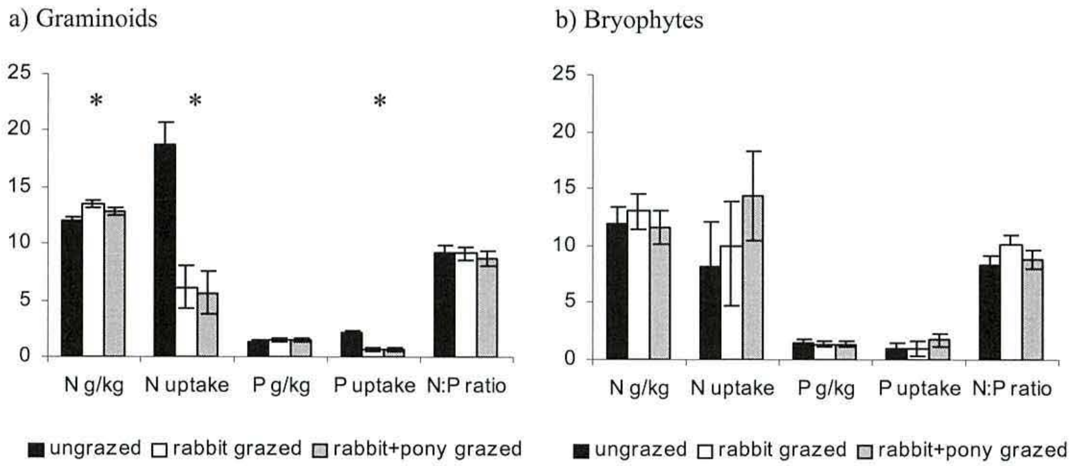


Figure 5.9. Average concentrations of nitrogen (N) and phosphorus (P) in g kg^{-1}, N and P uptake (per 20 x 20 cm sample) and N:P ratio in biomass samples from three grazing treatments. Biomass samples were taken in June 2005 after two years of treatment. a) Graminoids, b) bryophytes. Error bars represent the standard error of the differences of means. Stars indicate significant differences between treatments ($p<0.05$).

Although not significant, nitrogen uptake by graminoids was greater in the high N treatment than the low N treatment and control (Figure 5.10a, Appendix 2.7). In bryophyte samples, the high N treatment resulted in significantly higher tissue nitrogen concentrations (Figure 5.10b) (split-plot Anova, p=0.027, see Appendix 2.8), and N uptake was significantly lower in the control than in both fertilised treatments (split-plot Anova, p=0.036, see Appendix 2.8).

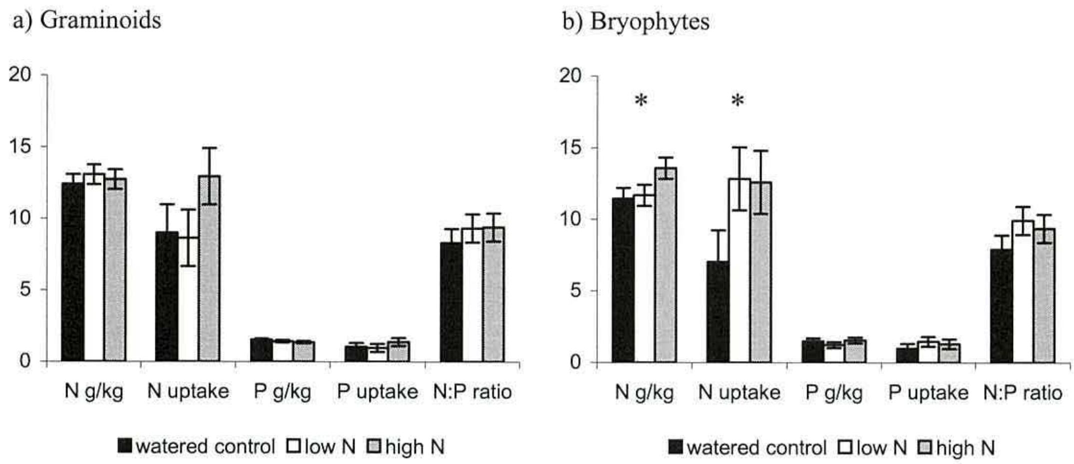


Figure 5.10. Average concentrations of nitrogen (N) and phosphorus (P) in g kg^{-1}, N and P uptake (per 20 x 20 cm sample) and N:P ratio in biomass samples taken in June 2005 after two years of nutrient applications. a) Graminoids, b) bryophytes. Error bars represent the standard error of the differences of means. Stars indicate significant differences between treatments ($p<0.05$).

N:P ratios ranged between 7 and 10 for graminoids and 7 and 11 for bryophytes and showed no significant differences between either the grazing or the nitrogen treatments (Appendix 2.7 and 2.8).

No statistically significant interactions between nutrient addition and grazing treatment were observed for either graminoids or bryophytes (split-plot Anova, $p>0.05$, details in Appendix 2.7 and 2.8).

Vegetation composition

Analysis of life forms and perennation types revealed that the vast majority of species present were perennial hemicryptophytes. Annual and biennial species, therophytes, chamaephytes and nanophanerophytes were all present, but in such low numbers and abundance that no analysis of treatment effects on these plant attributes was conducted.

From June to September 2003, the first three months of the experiment, average numbers of species increased in ungrazed and decreased slightly in grazed treatments. Thereafter, they showed similar seasonal trends for the grazed treatments, but remained more or less unchanged in ungrazed plots (Figure 5.11a). Graminoid and bryophyte species numbers did not differ significantly between grazing treatments in any of the seven point quadrat surveys (Figure 5.11b, c) (split-plot Anova, $p>0.05$ for all samples, see Appendix 2.9). Forb species numbers increased a little in ungrazed plots during the first three months, while they decreased considerably in rabbit grazed subplots (Figure 5.11d) (Appendix 2.9).

In ungrazed subplots, more species were recorded for each point quadrat pin than in grazed subplots from September 2003 onwards. These values were significantly different for four out of seven surveys (Figure 5.12a) (split-plot Anova, $p=0.024$ in September 2003, $p=0.034$ in April 2004, $p=0.048$ in June 2004 and $p=0.006$ in September 2004, details in Appendix 2.9). This was due to the dominance of graminoids in ungrazed plots (Figure 5.12b) (split-plot Anova, $p=0.047$ in June 2004, $p=0.042$ in September 2004 and $p=0.026$ in June 2005, details in Appendix 2.9) and reflects the greater amount of standing biomass and greater sward heights in these subplots. Total and graminoid abundance in ungrazed plots increased strongly within the first three months of the experiment, while over the same period of time there was a decrease in the grazed treatments (Figure 5.12a, b). No effects of grazing treatment were observed for bryophytes and forbs (Figures 5.12c, d) (split-plot Anova, $p>0.05$ for all seven point quadrat surveys except for initial significant differences for forbs, see Appendix 2.9).

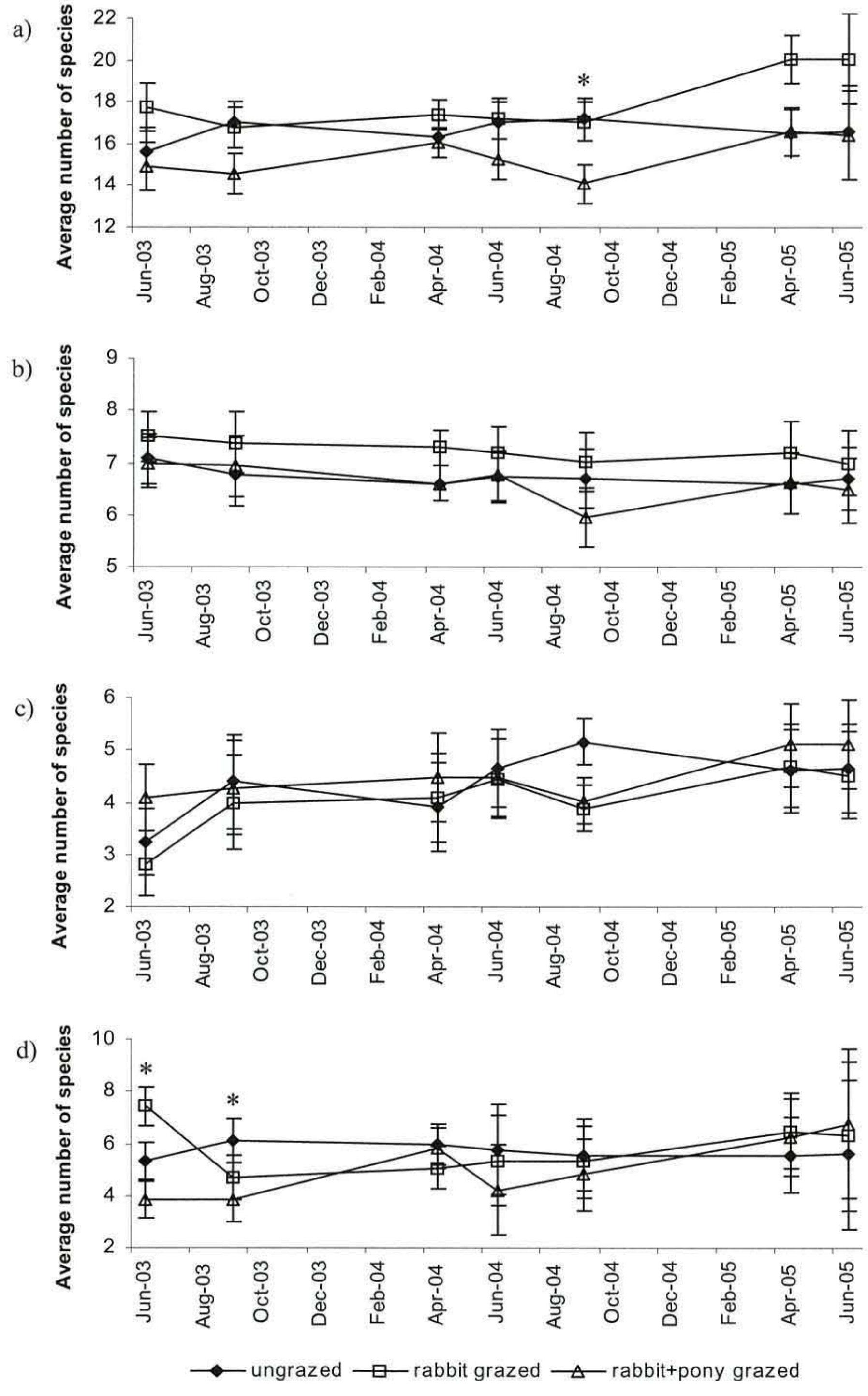


Figure 5.11. Average number of species per 1 m^2 quadrat in point quadrat surveys (60 hits each in 36 1 m^2 quadrats) in three grazing treatments between June 2003 and June 2005, adjusted for initial differences in the baseline survey. a) Total, b) graminoids, c) bryophytes, d) forbs. Error bars represent the standard error of the differences of means. Stars indicate significant differences between treatments ($p<0.05$).

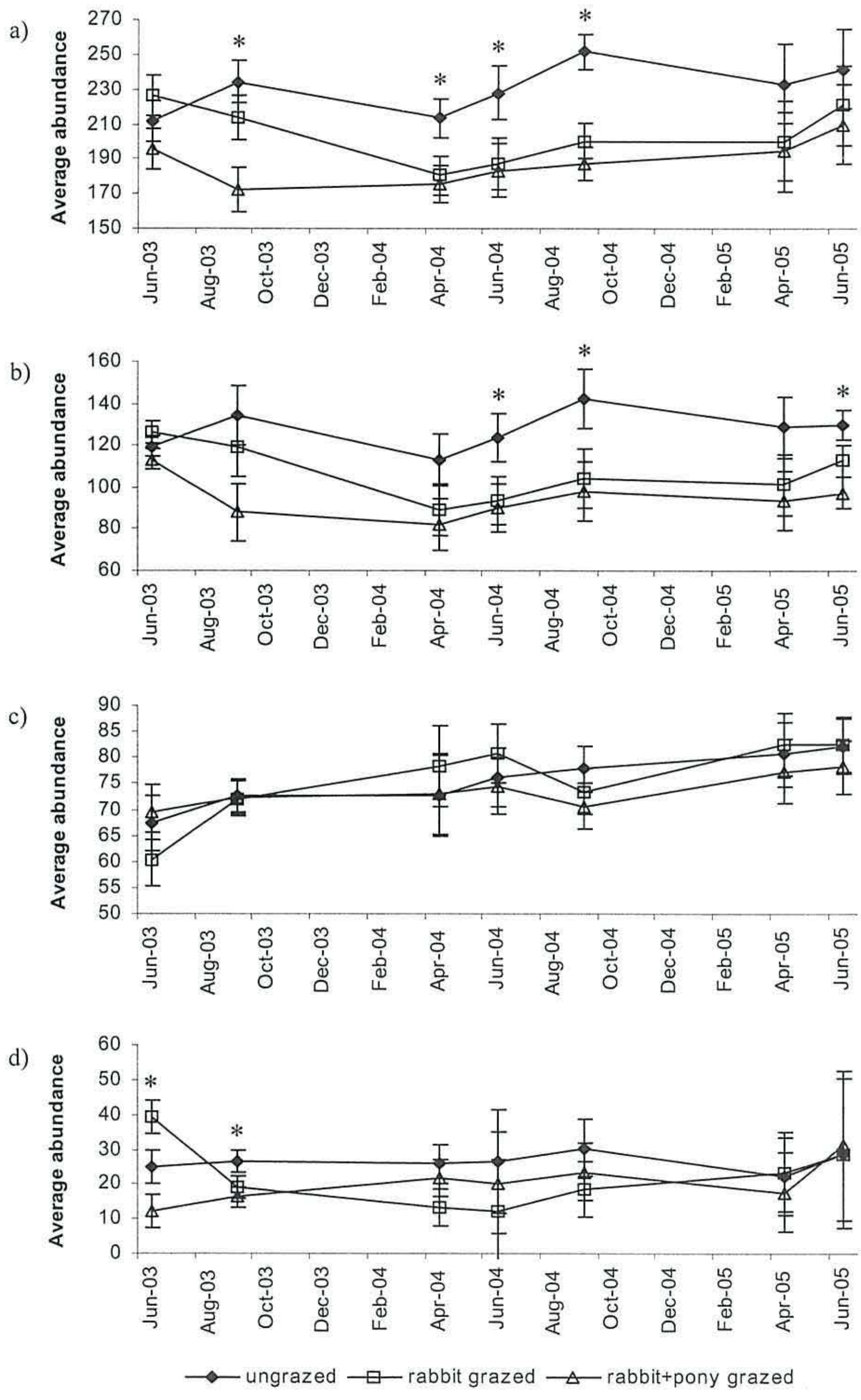


Figure 5.12. Average number of hits by point quadrat pins (60 hits each in 36 1 m^2 quadrats) in three grazing treatments between June 2003 and June 2005, adjusted for initial differences in the baseline survey. a) Total, b) graminoids, c) bryophytes, d) forbs. Error bars represent the standard error of the differences of means. Stars indicate significant differences between treatments ($p<0.05$).

Figure 5.13 shows the sample ordination, adjusted for initial differences between quadrats in the baseline survey, in relation to grazing treatment. Although the floristic composition of the quadrats remained similar after two years, the arrows indicate that there were differences between the three grazing treatments, and that these differences were as great between the two grazed treatments as between grazed and ungrazed plots.

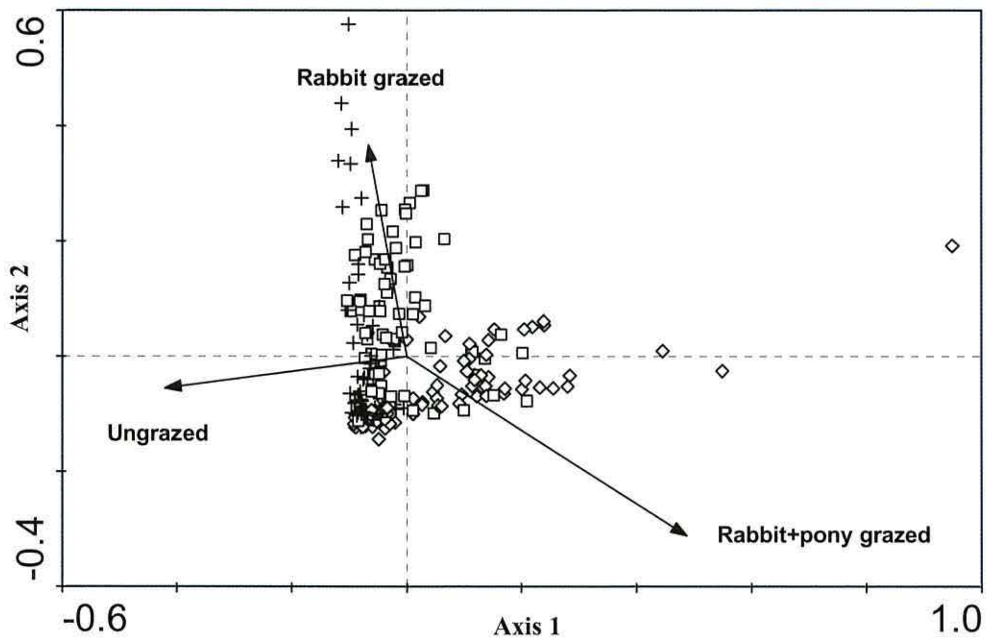


Figure 5.13. Sample ordination by Principal Components Analysis, axis 1 and axis 2, with grazing treatments as supplementary variables, adjusted for initial differences in vegetation composition. Eigenvalues: axis 1=0.5472, axis 2=0.0991. Crosses represent ungrazed plots, squares rabbit only grazed plots and diamonds rabbit and pony grazed plots.

An ordination based on the relative abundance of the three plant groups graminoids, bryophytes and forbs illustrates that graminoids were most abundant in ungrazed plots, while forbs were associated with rabbit grazing and bryophytes with the most heavily grazed plots in the pony and rabbit grazed treatment (Figure 5.14). This analysis was also conducted using data from the unwatered control quadrats only to exclude any possible effects of nitrogen fertilisation, giving the same results.

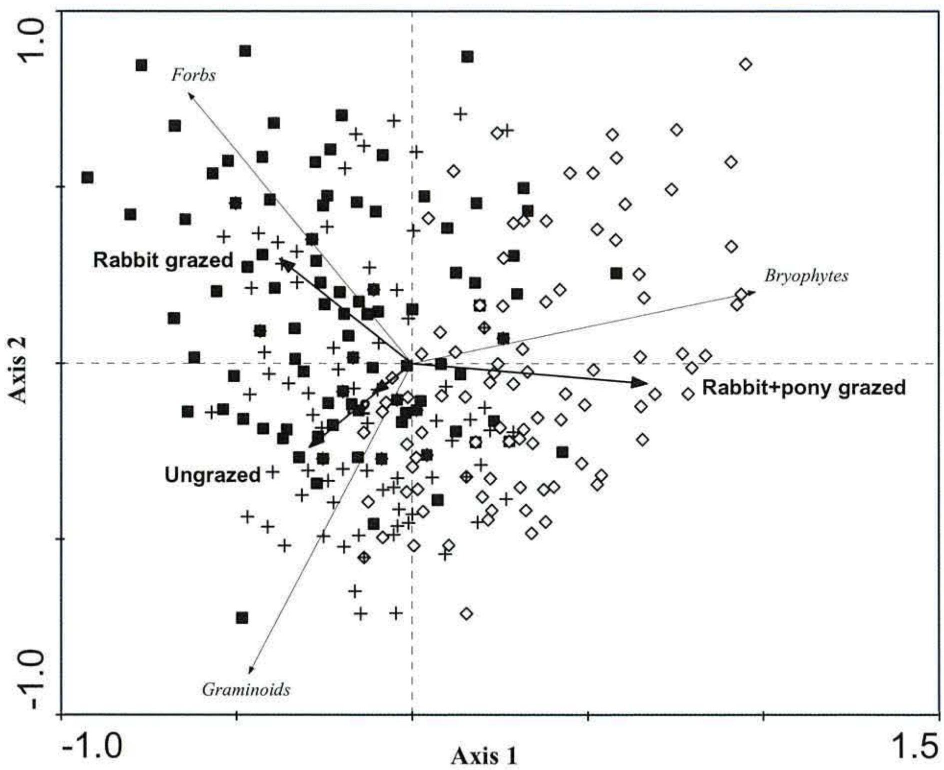


Figure 5.14 Ordination by Principal Components Analysis, axis 1 and axis 2, based on the relative abundances of three plant groups, graminoids, bryophytes and forbs, with grazing treatments as supplementary variables. Eigenvalues: axis 1=0.5500, axis 2=0.4489. Crosses represent ungrazed plots, squares rabbit only and diamonds rabbit and pony grazed plots.

Consistently significant differences in abundance in the three grazing treatments were only observed for two species (Figure 5.15): *Cerastium fontanum* (split-plot Anova, p=0.04 in April 2004, p=0.011 in June 2004, p=0.031 in April 2005) and *Vicia* spp.

(split-plot Anova, p=0.032 in June 2004, p=0.035 in September 2004, p=0.032 in April 2005, p=0.013 in June 2005) (for details see Appendix 2.10).

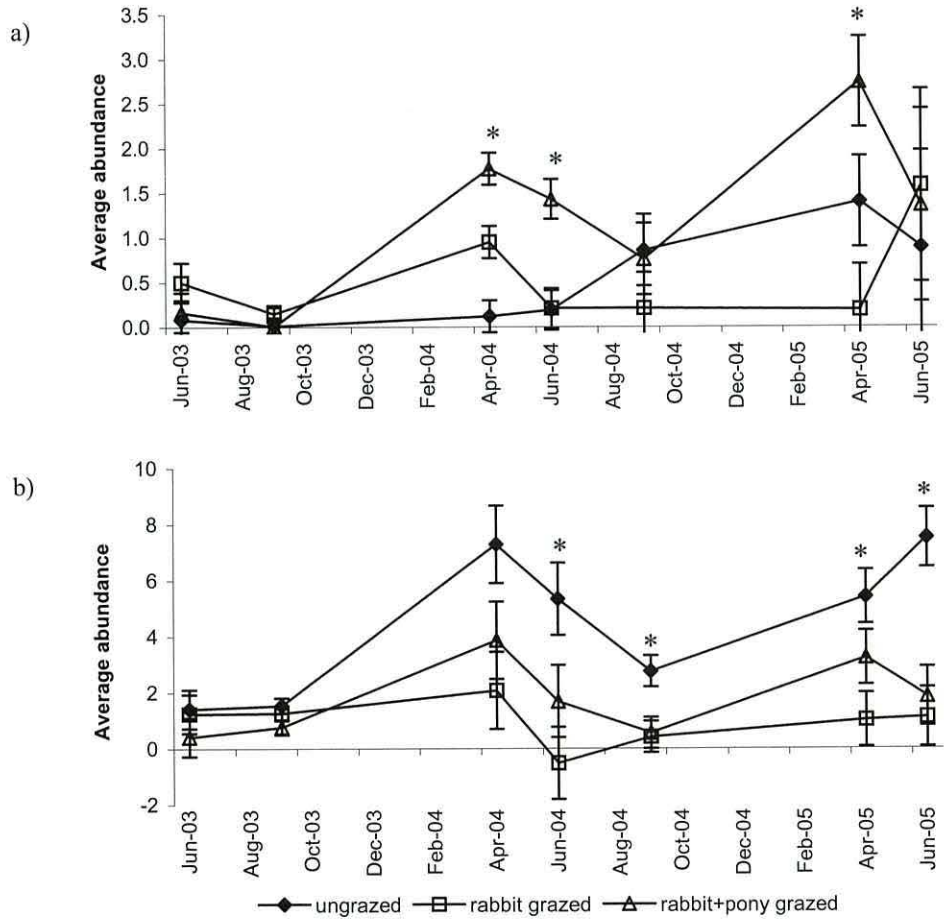


Figure 5.15. Average number of touches in point quadrat surveys (60 hits each in 36 1 m^2 quadrats) in three grazing treatments between June 2003 and June 2005, adjusted for the baseline as covariate. a) *Cerastium fontanum*, b) *Vicia* spp. Error bars represent the standard error of the differences of means. Stars indicate significant differences between treatments (p<0.05).

In the ungrazed plots, species that are characterised by tall growth (>60 cm), mainly the grasses *Festuca rubra*, *Arrhenatherum elatius*, *Agrostis capillaris* and *Holcus lanatus*, increased in abundance relative to the grazed treatments (Figure 5.16). This was significant in three point quadrat surveys (split-plot Anova, p=0.029 in June 2004, p=0.034 in September 2004, p=0.021 in June 2005, see Appendix 2.11). No significant decrease in the abundance of low growing species was detected (split-plot Anova, p>0.05 in all seven point quadrat surveys, details in Appendix 2.12).

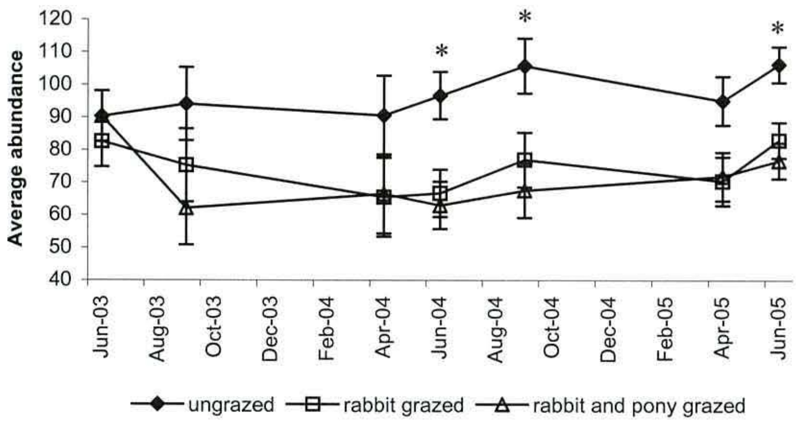


Figure 5.16. Average abundance of species typically growing taller than 60 cm in three grazing treatments between June 2003 and June 2005, adjusted for the baseline as covariate. Error bars represent the standard error of the differences of means. Stars indicate significant differences between treatments ($p<0.05$).

There was no significant impact of nitrogen fertilisation on the total number of species and hits in any point quadrat survey (split-plot Anova, p>0.05, see Appendix 2.13), and the plant groups graminoids, bryophytes and forbs did not show any consistent significant response to fertilisation (split-plot Anova, p>0.05, see Appendix 2.13). No effects could be detected for individual species. No significant interactions of fertilisation and grazing treatment were observed for any species or species group (split-plot Anova, p>0.05 for numbers of species and hits in all point quadrat surveys for total, graminoids, bryophytes and forbs, details in Appendix 2.14). This is also evident from the ordination of all point quadrat survey data which gives no indication of an effect of nitrogen fertilisation treatments on species composition (Figure 5.17).

The arrows representing the nitrogen treatments are very short and located close to the centre of the diagram, with the arrow for the high N treatment the shortest. This suggests that treatment effects on species composition were of little importance compared to the natural variation within the plots. The ordination also illustrates that grazing had a greater impact on species composition than fertilisation.

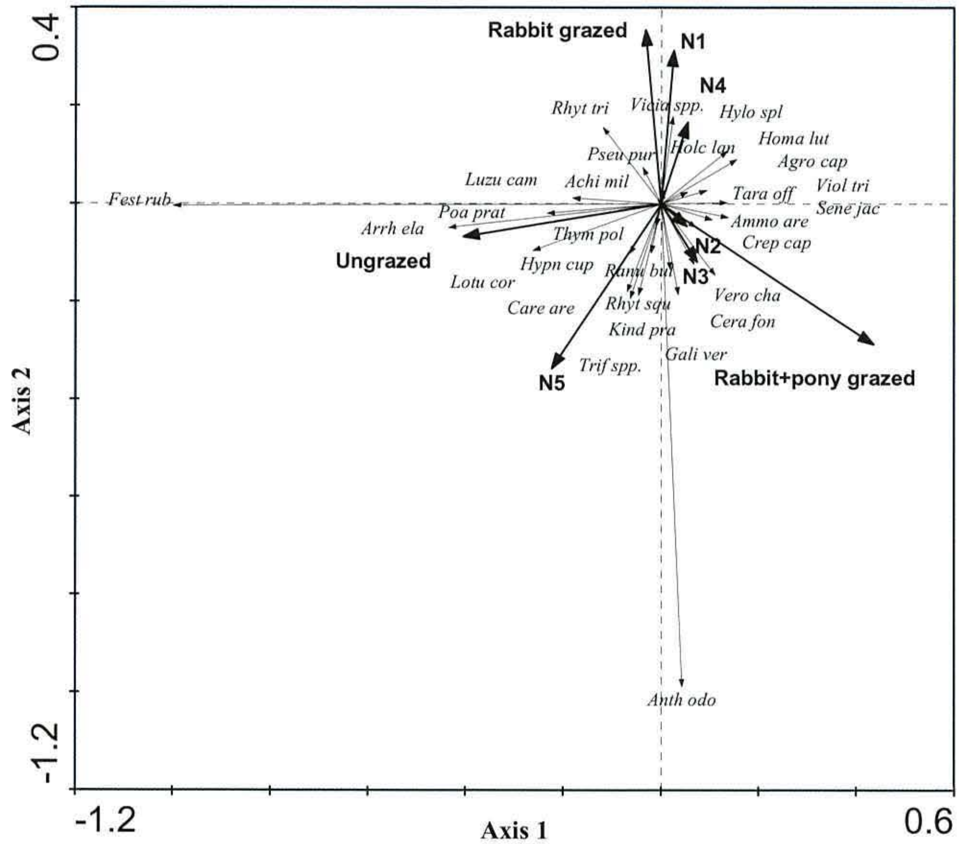
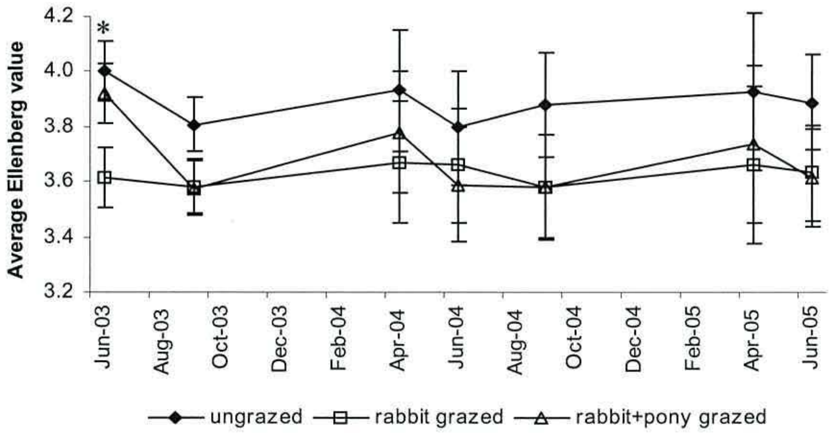


Figure 5.17. Species ordination by Principal Components Analysis, axis 1 and axis 2, adjusted for initial differences in vegetation composition. Eigenvalues: axis 1=0.152, axis 2=0.119. Supplementary variables: three grazing treatments and five nitrogen fertilisation treatments (N1=unwatered control, N2=watered control, N3=low N, N4=high N, N5=high N+P). Only species recorded in more than 10 % of all quadrats shown: Achi mil=*Achillea millefolium*, Ammo are=*Ammophila arenaria*, Anth odo=*Anthoxanthum odoratum*, Agro cap=*Agrostis capillaris*, Arrh ela=*Arrhenatherum elatius*, Care are=*Carex arenaria*, Cera fon=*Cerastium fontanum*, Crep cap=*Crepis capillaris*, Fest rub=*Festuca rubra*, Gali ver=*Galium verum*, Holc lan=*Holcus lanatus*, Homa lut=*Homalothecium lutescens*, Hylo spl=*Hylocomium splendens*, Hypn cup=*Hypnum cupressiforme*, Kind pra=*Kindbergia praelonga*, Lotu cor=*Lotus corniculatus*, Luzu cam=*Luzula campestris*, Poa pra=*Poa pratensis*, Pseu pur=*Pseudoscleropodium purum*, Ranu bul=*Ranunculus bulbosus*, Rhyt squ=*Rhytidiadelphus squarrosus*, Rhyt tri=*Rhytidiadelphus triquetrus*, Sene jac=*Senecio jacobaea*, Tara off=*Taraxacum* sect. *Ruderalia* (*T. officinale* Wigg. group), Thym pol=*Thymus polytrichus*, Trif spp.=*Trifolium* spp., Vero cha=*Veronica chamaedrys*, Vicia spp.=*Vicia sativa* and *V. hirsuta*, Viol tri=*Viola tricolor*.

Ellenberg indicator values for nitrogen

Although not statistically significant, average weighted Ellenberg values for nitrogen were greatest in ungrazed quadrats throughout the experiment (Figure 5.18) (split-plot Anova, $p>0.05$ for all but the first point quadrat survey, $p=0.049$, see Appendix 2.15). No significant effect of fertilisation or the interaction of fertilisation and grazing on average nitrogen indicator values was detected (Figure 5.18) (split-plot Anova, $p>0.05$ for all point quadrat surveys, see Appendix 2.15). Overall, values ranged between 3.5 and 4, indicating more or less infertile conditions.

a)



b)

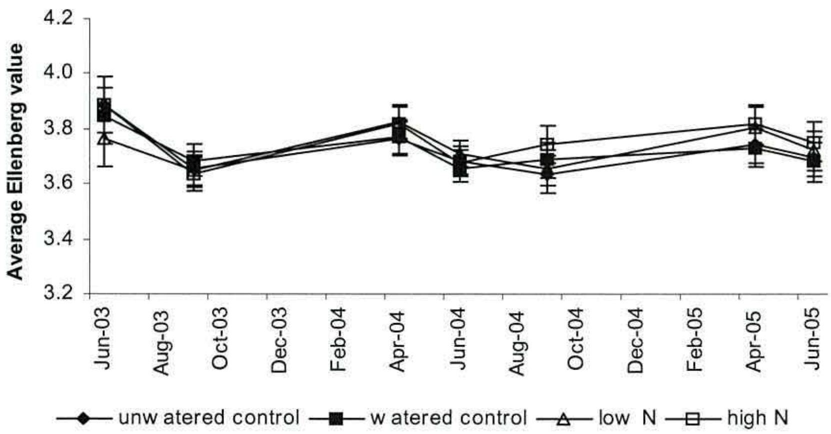


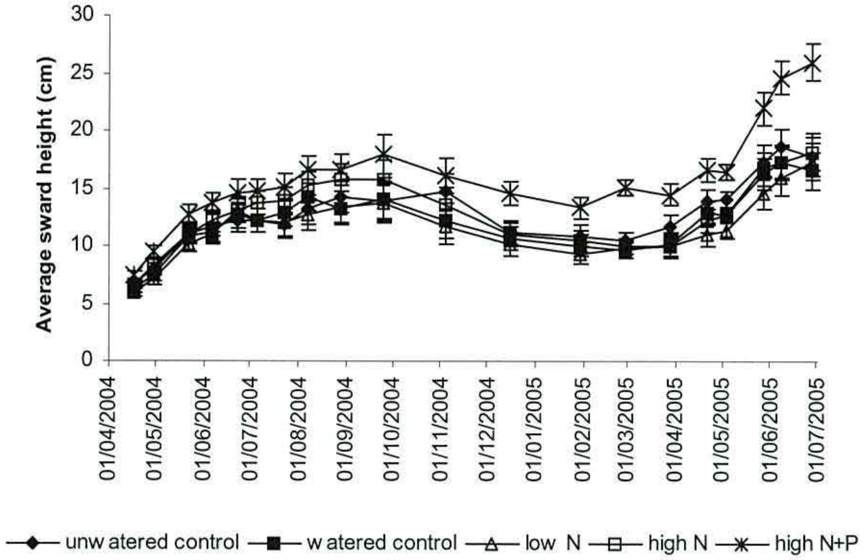
Figure 5.18. Average weighted Ellenberg indicator value for nitrogen between June 2003 and June 2005, adjusted for the baseline as covariate. a) By grazing treatment, b) by nitrogen fertilisation treatment. Error bars represent the standard error of the differences of means. Stars indicate significant differences between treatments ($p<0.05$).

Fertilisation with nitrogen and phosphorus

Addition of both nitrogen and phosphorus resulted in greater sward heights than any other treatment, which was significant on seven out of 20 sampling dates (Appendix 2.16). In ungrazed plots, the high N+P treatment resulted in statistically significantly greater sward heights than the other treatments from December 2004 onwards (Figure 5.19) (split-plot Anova, $p<0.05$ from December 2004 except for 27 May 2005, see Appendix 2.17), and in April and June 2005 for the highest touch per pin in the point quadrat surveys (Figure 5.19) (split-plot Anova, $p=0.011$ in April 2004, $p=0.003$ in June 2005, see Appendix 2.18). This difference was significant with and without adjusting for April 2004 as a baseline, before the start of nutrient additions to the high N+P plots. Although the high N+P treatment had greater sward heights than the other treatments, this difference was not statistically significant at any time in the grazed plots (Figure 5.20) (Appendix 2.17 and 2.18).

Total biomass was significantly greater in high N+P treatments than controls and low N treatments in June 2005 (Figure 5.21) (split-plot Anova, $p=0.002$ in June 2005, see Appendix 2.19). This was not statistically significant for any of the plant groups; however, for graminoids and bryophytes, fertilised treatments had increased amounts of biomass (split-plot Anova, $p>0.05$ for all samples, details in Appendix 2.19). Nutrient concentrations in the biomass of graminoids showed no significant differences (split-plot Anova, $p>0.05$, details in Appendix 2.20). In bryophytes, nitrogen concentrations were greatest in the high N treatment (Figure 5.22a), while the high N+P treatment resulted in greater nitrogen uptake than the control (Figure 5.22b) (split-plot Anova, $p=0.015$, see Appendix 2.21). There was no significant interaction of nutrient addition and grazing treatment on tissue nutrient concentrations or uptake for either graminoids or bryophytes (split-plot Anova, $p>0.05$, details in Appendix 2.20 and 2.21). N:P ratios ranged between 8 and 10 for graminoids and 7 and 11 for bryophytes and did not differ between nitrogen addition and grazing treatments (Appendix 2.20 and 2.21).

a)



b)

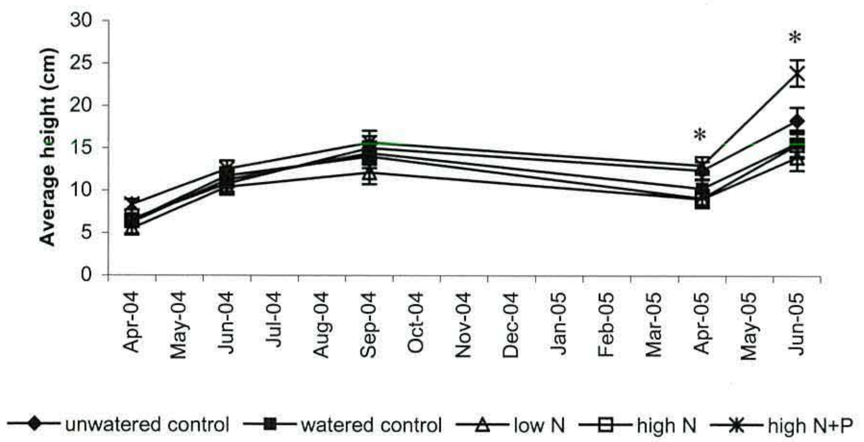


Figure 5.19. a) Average sward heights in nitrogen and phosphorus fertilisation treatments in ungrazed quadrats between April 2004 and June 2005. Differences between treatments were significant from 15 December 2004 onwards (not 27 May 2005). b) Average height of highest hit in point quadrat surveys in ungrazed quadrats between April 2004 and June 2005. Stars indicate significant differences between treatments ($p<0.05$). Error bars represent the standard error of the differences of means.

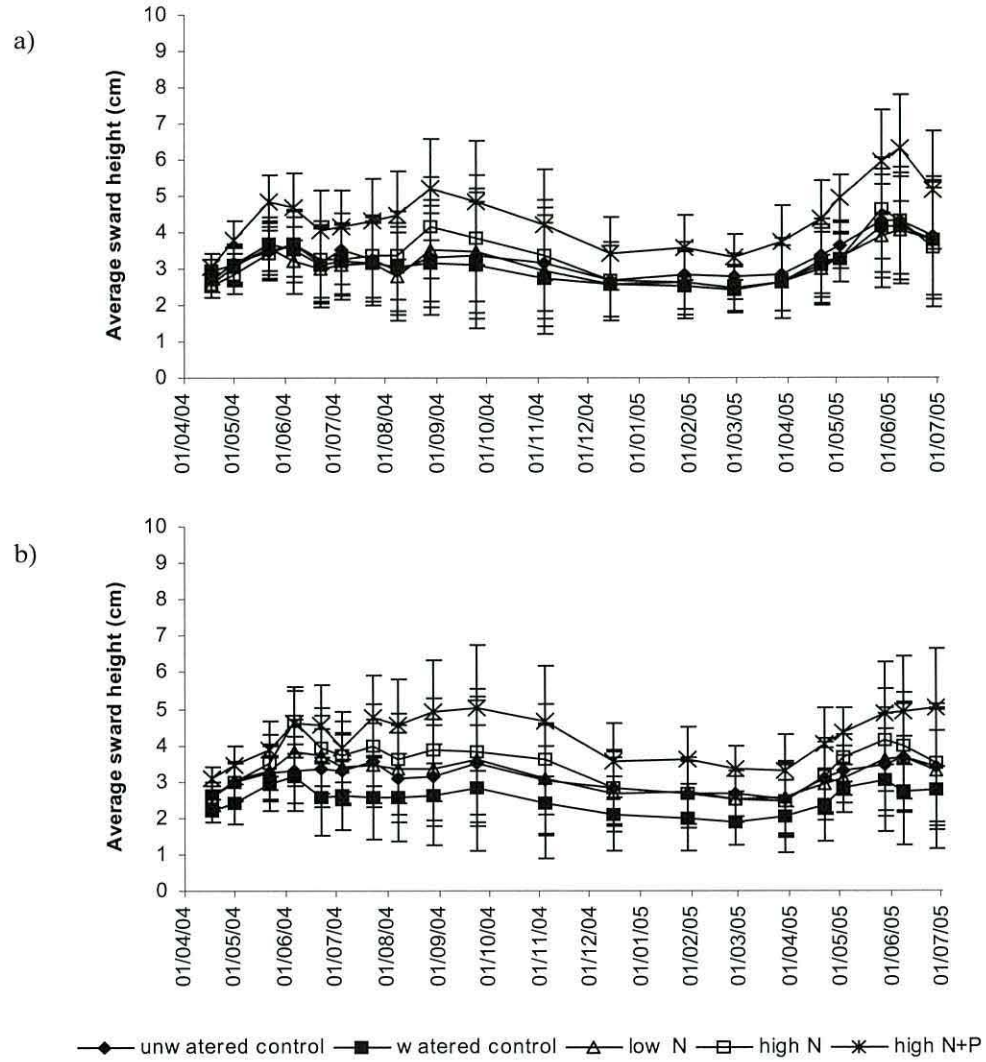


Figure 5.20. Average sward heights in nitrogen fertilisation treatments between April 2004 and June 2005. a) Rabbit only grazed plots, b) rabbit and pony grazed plots. Error bars represent the standard error of the differences of means.

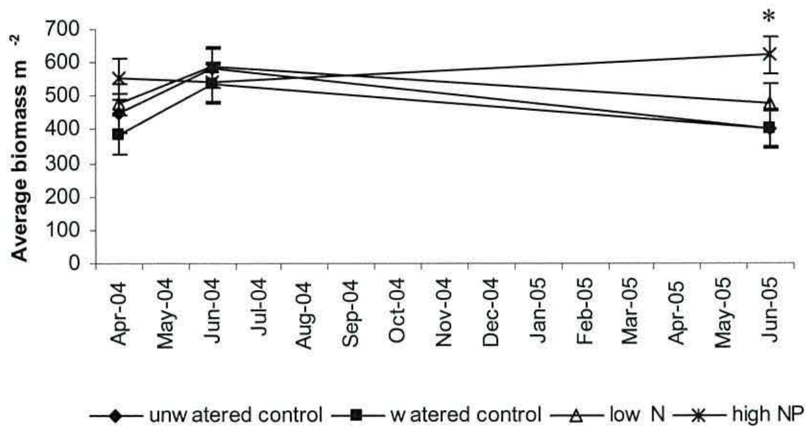


Figure 5.21. Average total above-ground biomass (g dry weight m^{-2}) in fertilisation treatments between April 2004 and June 2005, adjusted for initial differences in the baseline survey. High N treatment not shown to clearly illustrate the significant difference between the high N+P treatment and the other treatments (see Appendix 2.19). Error bars represent the standard error of the differences of means. Stars indicate significant differences between treatments ($p<0.05$).

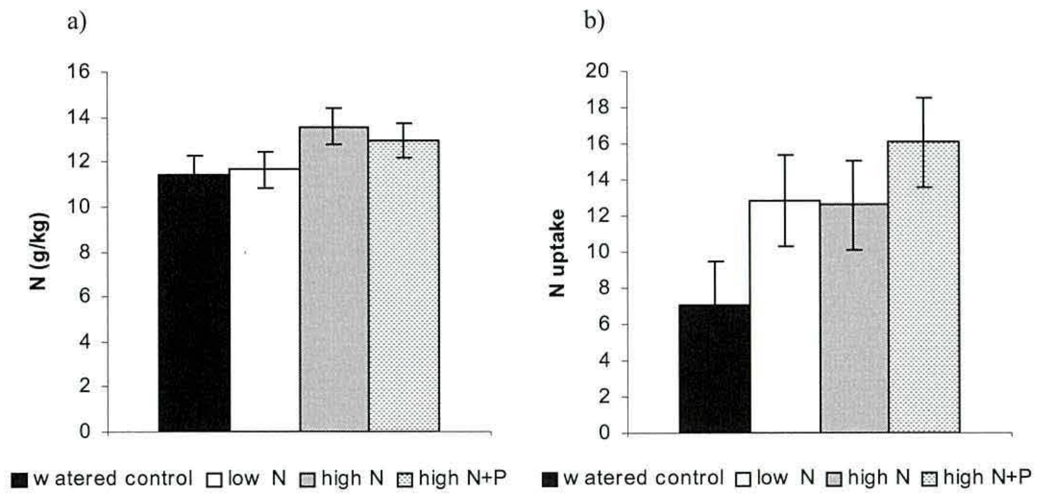


Figure 5.22. a) Average nitrogen concentration in bryophyte biomass in g kg^{-1} in June 2005. b) Average nitrogen uptake by bryophytes (per 20 x 20 cm sample) in June 2005. Error bars represent the standard error of the differences of means.

No effects of fertilisation or the interaction of fertilisation and grazing on the number of species were detected for any species or species group (split-plot Anova, p>0.05 for all five point quadrat surveys, details in Appendix 2.22 and 2.23). The average number of touches per pin was significantly greater in high N+P treatments than in the other treatments for total touches and graminoid touches in June 2004 and June 2005 (Figure 5.23) (split-plot Anova, total hits: p<0.001 in June 2004 and p=0.024 in June 2005, graminoids: p<0.001 in June 2004 and p=0.010 in June 2005, details in Appendix 2.22).

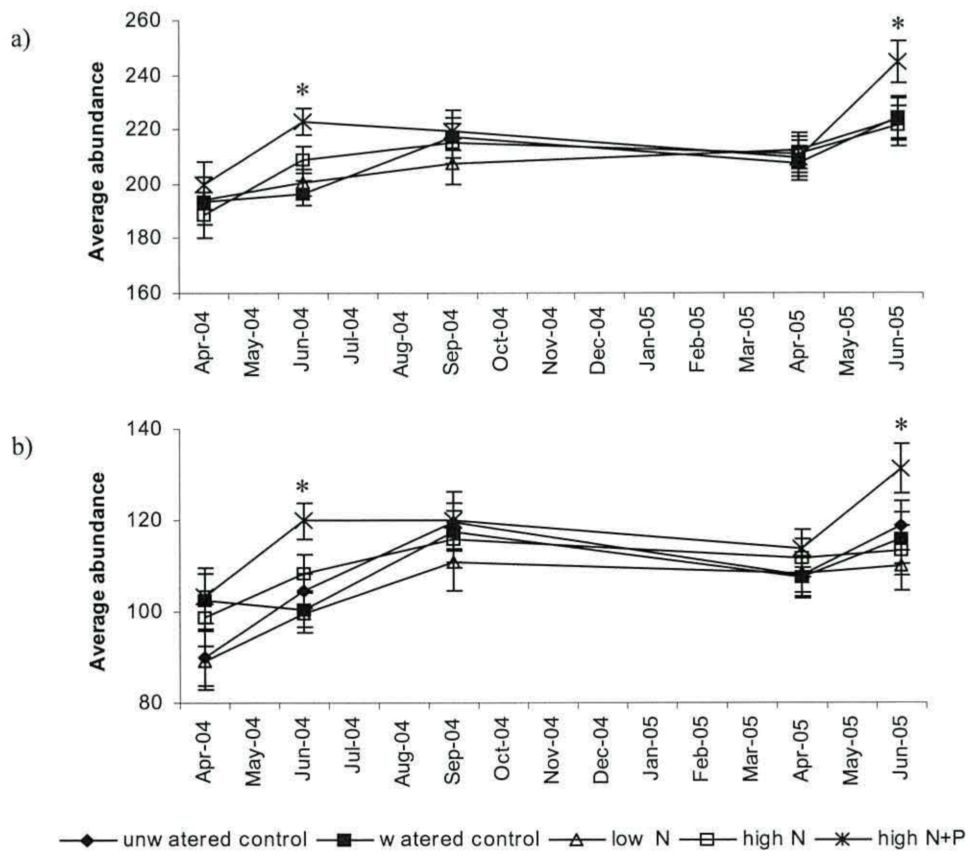


Figure 5.23. Average number of hits by point quadrat pins (60 hits each in 45 1 m^2 quadrats) in fertilisation treatments between April 2004 and June 2005, adjusted for initial differences in the baseline survey. a) Total, b) graminoids. Error bars represent the standard error of the differences of means. Stars indicate significant differences between treatments (p<0.05).

The high N+P treatment had a greater impact on vegetation composition than the low N or high N treatment (Figure 5.17). The unwatered control and the high N+P treatment are placed at opposite ends of axis 2 in the ordination diagram, suggesting that fertilisation with both nitrogen and phosphorus had an effect as compared to the untreated control (Figure 5.17). Bryophytes with a low Ellenberg indicator value for nitrogen were more closely associated with the unwatered control (*Hylocomium splendens* and *Homalothecium lutescens* with an indicator value of 2, *Rhytidiadelphus triquetrus* and *Pseudoscleropodium purum* with an indicator value of 3), whereas more nutrient-loving species were associated with the high N+P treatment (*Kindbergia praelonga* with an indicator value of 5 and *Hypnum cupressiforme* and *Rhytidiadelphus squarrosus* with an indicator value of 4).

Rabbit numbers and pellet counts

Results of rabbit dawn counts indicate that average rabbit densities may be in the region of 29 rabbits ha^{-1}, which can only be a rough estimate due to the difficulties attached to assessing population numbers (Philipps 1953, Palomares 2001, Ballinger & Morgan 2002), and a minimum estimate as it does not take into account the part of the population remaining below ground at any time. At dusk, the latter was estimated by Southern (1948) to be as much as 70-80 %. Ballinger & Morgan (2002) recorded an average of 36 % of the population above ground, but in favourable conditions, they found a maximum of 64 % of the population above ground. Because extremely low counts due to disturbance were excluded from this analysis and rabbit activity was found to be greater at dawn, it is assumed that the part of the population below ground in the present study may have been similarly low. Assuming that about 36 % of the population remained below ground, rabbit densities in the area are estimated to be about 45 rabbits ha^{-1}. Because of the topography (small hummocks), not all rabbits could always be seen, which means that total numbers could be even higher than estimated.

Rabbit pellet counts revealed no preferential use of plots that were also grazed by ponies or of fertilised rather than control subplots on any sampling occasion (Table 5.5) (split-plot Anova, p>0.05 for all samples and treatments).

Table 5.5. Average number of rabbit pellets collected on four occasions between June and August 2004 in 50 x 50 cm squares inside experimental plots and results of Anova analyses (s.e.d. = standard error of the differences of means). On each sample date, pellets were removed.

		9-Jun-04	25-Jun-04	31-Jul-04	14-Aug-04	Total
Grazing treatment	Rabbit grazed	60.6	19.6	39.5	20.8	136.6
	Rabbit and pony grazed	60.2	15.2	30.2	20.1	122.6
	f ratio	0.00	0.35	1.35	0.06	1.02
	p value	0.950	0.613	0.366	0.824	0.419
	s.e.d	5.70	7.43	8.04	2.90	13.86
Nitrogen treatment	Unwatered control	68.5	12.2	34.2	20.5	135.3
	Watered control	57.2	14.5	27.5	20.2	119.3
	Low N	58.8	16.5	37.5	20.7	133.5
	High N	61.3	26.3	34.7	17.5	139.8
	High N+P	56.2	n.a.	40.5	23.3	120.0
	f ratio	0.20	1.43	0.88	0.17	0.21
	p value	0.934	0.283	0.498	0.949	0.930
	s.e.d	15.54	7.37	7.29	7.04	28.96
Nitrogen*Grazing						
Unwatered control	Rabbit grazed	66.7	14.7	43.0	17.0	141.3
	Rabbit and pony grazed	70.3	9.7	25.3	24.0	129.3
Watered control	Rabbit grazed	57.0	22.3	30.3	18.7	128.3
	Rabbit and pony grazed	57.3	6.7	24.7	21.7	110.3
Low N	Rabbit grazed	60.0	19.3	36.7	22.0	138.0
	Rabbit and pony grazed	57.7	13.7	38.3	19.3	129.0
High N	Rabbit grazed	59.7	22.0	41.3	21.7	144.7
	Rabbit and pony grazed	63.0	30.7	28.0	13.3	135.0
High N+P	Rabbit grazed	59.7	n.a.	46.3	24.7	130.7
	Rabbit and pony grazed	52.7	n.a.	34.7	22.0	109.3
	f ratio	0.04	0.92	0.53	0.35	0.02
	p value	0.997	0.461	0.716	0.840	0.999
	s.e.d	20.47	11.93	12.24	9.37	39.16

Discussion

Effects of grazing

Before the grazing exclosures were erected, sward heights in the experimental plots were uniform. Although no strictly true baseline is available, the significantly greater sward heights in ungrazed than grazed plots after less than two weeks of grazing exclusion can almost certainly be explained by the effects of grazing exclusion. Average species numbers in ungrazed plots increased within the first three months, but subsequently showed less pronounced seasonal changes than for the grazed treatments. By the end of the experiment, there was more above-ground biomass in ungrazed plots, which was mainly due to the increased abundance of graminoids. However, graminoid species numbers did not change and in the longer term are expected to decline in ungrazed plots (Veer & Kooijman 1997), resulting in a more uniform, grassy sward. No differences in the amount of root biomass were found between grazing treatments. This is contrary to the findings of other authors (e.g. Veer 1997, Bakker *et al.* 2004) who found that grazing significantly reduces root biomass and grass encroachment increases root biomass. This difference in observations may be due to the short duration of the experiment.

Although not measured in this experiment, light penetration is likely to be much reduced in ungrazed plots (e.g. Kooijman 2004) with average vegetation heights of around 20 cm as compared to 2-6 cm in grazed plots. This might be expected to impact negatively on bryophytes as most species cannot thrive in the low light environment of a dense sward (Crofts & Jefferson 1999). Grazing removes biomass and thus significantly increases the amount of light reaching the surface layer (Kooijman 2004), which favours bryophyte growth and species diversity (Kooijman & de Haan 1995, Whatmough 1995, Piek 1998). Bryophytes can also benefit from patches of open ground created by grazing animals (Lake *et al.* 2001, Kooijman 2004), while under very low intensity grazing, many bryophytes are outcompeted by taller species (Tibbetts & Martin 1997, Lake *et al.* 2001). Van Dijk (1992), ten Harkel & van der

Meulen (1996) and Wrench (2001) all reported the benefits of grazing for mosses on dune grasslands, and Hill (1988) believed that reduced grazing pressure might be the reason for the loss of bryophyte species on Welsh dunes. A greater abundance of mosses in grazed areas was also found in habitats such as chalk grassland (Willems 1983, During & Willems 1986), upland grassland (Hulme *et al.* 1999), arctic tundra heath (Grellmann 2002) and dry pine forests (Väre *et al.* 1995).

However, although bryophyte biomass declined in ungrazed plots in the present study, this was only statistically significant for June 2004, and there was no decrease in species numbers or bryophyte abundance. This corresponds to the results of Vanderpoorten *et al.* (2004) and van der Hoeven *et al.* (1998), who did not find reduced bryophyte diversity in unmown controls compared to mown plots and observed only very small effects of reduced irradiance. Bates (1988) and van der Hoeven *et al.* (1998) believed this to be due to the better moisture conditions in denser swards. At Newborough Warren, Ranwell (1960b) recorded greatly increased sward heights three years after the rabbit population had been killed by myxomatosis, but the abundance of bryophytes had hardly changed at all. Ranwell (1960b) expected that mosses would start to decline in ungrazed swards only after 3-4 years, while Vanderpoorten *et al.* (2004) suggested that the negative impact of low irradiance leads to decreases in species numbers only after a time period of at least 20 years.

Dicotyledonous herbs were expected to initially benefit from grazing exclusion, because the release from grazing allows plants to spread and flower (e.g. Thomas 1960, Sumption & Flowerdew 1985, Drees & Olff 2001). This was not obvious in this study; however, there was a trend for slightly increased species numbers in ungrazed treatments at the beginning of the experiment, while they decreased or remained unchanged in grazed plots at the same time. *Vicia* spp. was the only species with significantly increased abundance in ungrazed quadrats from the first spring onwards. Over a longer period of time, forb numbers and abundance would probably decrease significantly following the increase of competitive, tall graminoids right from the start of the experiment. The ensuing denser and taller swards are detrimental to small, poorly competitive species that depend on the creation of vegetation gaps and soil disturbances where they can germinate. The strongly reduced light penetration at the surface layer may also lead to changes in competitive interactions and the loss of small species (Kooijman & van der Meulen 1996, Veer & Kooijman 1997). In fact, a vegetation height of 5 cm at the end of the winter (excluding *Ammophila arenaria*, inflorescences and shrubs) is considered to maintain maximum species richness (Hurford & Perry 2001); in the ungrazed quadrats in this study, swards were consistently higher than 10 cm after one year. The vigorous growth of grasses and sedges and subsequent decline of low growing dicotyledonous herbs was also observed at Newborough Warren in the 1950s and 1960s following the disappearance of rabbits after myxomatosis (Ranwell 1960b, Hope-Jones 1964).

In this study, the ungrazed treatments did not exclude the smallest and most inconspicuous herbivores such as voles and insects, and their effects on vegetation composition and structure were not examined. These animals generally do not disturb the soil to a large extent and do not create canopy gaps; however, in years of great abundance they can have significant effects on grassland vegetation (Keesing 2000). Because they prefer to forage in areas of high vegetation (Jacob & Brown 2000) as found in the plots excluding both rabbits and ponies in this study, they may have influenced the vegetation of the otherwise ungrazed treatments.

Grazing management on sand dunes

Species-rich dune grasslands have developed because of a long history of grazing by rabbits and domestic stock (Ranwell 1972, Boorman 1989a). When the rabbit disease myxomatosis killed most of Britain's wild rabbit population in the 1950s (Thompson 1994, Packham & Willis 1997), coinciding with the cessation of livestock grazing on many sites, profound changes in the vegetation of previously grazed areas were observed. At Newborough Warren, the short, species rich pre-myxomatosis sward containing many annuals changed to tall grass and tall herb communities, small species were lost, the area of bare sand reduced because of the spread of the vegetation, and shrubs gradually invaded the grasslands (Ranwell 1960b, Hope-Jones 1964, Hodgkin 1984). The exclosures in the present study only represent two years of grazing exclusion, and although species numbers had not declined, the increased sward heights, above-ground biomass and graminoid abundance are expected to lead to similar changes in the longer run. Although rabbit populations have recovered from myxomatosis in many areas, livestock grazing is used on many sand dune sites as a management tool to create a more diverse vegetation structure, promote species richness, prevent tree and shrub encroachment, encourage the bryophyte and lichen layers and create gaps suitable for the germination of small species (Hewett 1985, Oosterveld 1985, Gibson 1988, Piek 1998).

Grazing by domestic livestock is considered as the best option for sustainable sand dune management (Houston 1997, Burton 2001). Nature conservation cannot safely rely on rabbits, because their populations show great fluctuations (Crofts & Jefferson 1999) and it is extremely difficult to manage and control rabbit grazing (Boorman 1977, Ausden & Treweek 1995), whereas livestock grazing allows for more control over the degree of grazing pressure (Hewett 1985, Harris & Jones 1998). Stock grazing can also help counteract grass encroachment by tall, competitive species (Kooijman & de Haan 1995) which cannot be offset by rabbit grazing alone (Drees & Olff 2001), and the presence of both large and small herbivores can increase plant species diversity because of different effects on recruitment and colonisation processes (Bakker & Olff 2003). Livestock grazing can encourage rabbits to come back to areas that they could not re-populate as long as the vegetation was too tall and coarse, and generally improves conditions for smaller herbivores such as rabbits (Oosterveld 1985, Boorman 2004).

Rabbit and livestock grazing at Newborough Warren

At Newborough Warren, the rabbit population has never completely recovered from the outbreak of myxomatosis (Hurford & Perry 2001). Grazing management with domestic livestock was introduced on parts of the site in 1987, and the grazed area expanded gradually ever since. Today most of the site is grazed by Welsh mountain ponies at a stocking density of one pony to every 3-4 ha. The experiment presented here allowed the comparison of areas grazed by rabbits only and areas with additional grazing by ponies. After two years, there were no great differences in any of the variables measured between these two grazing treatments, both of them experiencing similar changes over time. However, analysis by ordination revealed differences in species composition and abundance, with the two grazed treatments as dissimilar from each other as from the ungrazed plots. Forbs were associated with rabbit only grazed areas and bryophytes with areas additionally grazed by ponies. This suggests that there are different effects on the floristic composition, with bryophytes benefiting most under heavier grazing, whereas forbs thrive more in plots with slightly reduced grazing pressure, at least over the short time scale of this project.

Rabbits select short swards (Iason *et al.* 2002) and might be expected to preferentially forage in the more heavily grazed areas; however, the results of the rabbit pellet counts indicated no preference of the rabbits for either grazing treatment. Sward heights were equally low under both grazing treatments, indicating that the rabbit population was large enough to maintain a short sward, and that the rabbits exerted the majority of the grazing pressure. This is in agreement with the estimates of rabbit densities of about 45 rabbits ha^{-1} in the experimental area, indicating a strong population. It is a higher figure than quoted by some authors, e.g. Thompson (1994) who reported 7-25 ha^{-1} and Kolb (1991) and Pott *et al.* (1999) who found densities of 12-16 ha^{-1} on sand dunes. However, higher values have also been documented, e.g. maximum densities of 40 ha^{-1} (Thompson 1994), 10-50 ha^{-1} (Tittensor & Lloyd 1983), 60-80 ha^{-1} (de Bruyn 1997) and up to 100 ha^{-1} (Goodman & Gillham 1954). The relatively high estimate in this study is in accordance with the observed high grazing pressure resulting in very short swards in the area, but it is below the peak densities of 65 rabbits ha^{-1} that Garson (1985) found to be too heavy for many plant species of dune slacks to flower. Pony stocking levels, on the other hand, are low, and they are not confined to the experimental area. As yet, there was no indication that rabbits could not keep the sward short, and over the time period studied, the results do not suggest that additional grazing by ponies is necessary. A similar result was obtained by Somers *et al.* (2005) comparing areas grazed by large herbivores and rabbits or rabbits only.

However, if the rabbit population was greatly reduced due to bad weather conditions or the outbreak of a disease, the swards would grow rank very quickly, as demonstrated in the ungrazed plots that had significantly higher swards after less than two weeks of grazing exclusion. Rabbits prefer short swards (Iason *et al.* 2002) because they select food with a high energy and low fibre content, that is young and actively growing plants found in swards kept constantly low (Drees & Olff 2001). Once plants grow taller than a few centimetres, food quality generally becomes too poor, and the rabbits disappear or cannot repopulate the area again when the population recovers (Oosterveld 1983, Drees & Olff 2001). By maintaining short swards, grazing livestock can help maintain the rabbit population in the area even in times of low population density.

Herbage quality and productivity

Percentage nitrogen content in graminoids was significantly lower in ungrazed than grazed swards. This is in agreement with Green & Detling (2000), Hassall *et al.* (2001), Bos *et al.* (2002b) and van der Graaf *et al.* (2005), who all found increased nitrogen content in grazed or clipped plots, because removal of biomass stimulates fresh regrowth of young shoots with high nitrogen concentrations. Especially in graminoids, nitrogen concentrations decline with increasing maturity (Whitehead 2000). Bryophytes are unpalatable and usually avoided by grazing animals (Crofts &

Jefferson 1999), which probably explains why they did not show differences in nitrogen content or uptake between grazing treatments.

Small herbivores such as rabbits and geese often prefer to forage in areas with low amounts of standing biomass because of higher food quality and nutrient intake rates (Bos *et al.* 2002b, Bakker *et al.* 2005b), although other factors such as lower foraging efficiency and greater risk of predation in dense vegetation may also contribute to this preference (Arnold 1963, van de Koppel *et al.* 1996, Iason *et al.* 2002). Nitrogen contents of graminoids in the two grazing treatments in this study were very similar, so that no preference of rabbits for either area based on food quality could be expected. This corresponds to the results of the pellet counts indicating equal usage of the two areas. Bakker *et al.* (2005b) found significantly increased use of plots with experimentally increased food quality (fertilisation and mowing); however, they added nitrogen, phosphorus and potassium in much higher concentrations than this study.

Average weighted Ellenberg indicator values for nitrogen were higher in ungrazed treatments. Recent work suggests that this indicator value is not only indicative of the availability of nutrients, but rather a measure of productivity (Hill & Carey 1997, Schaffers & Sýkora 2000). Veer (1997) and Veer & Kooijman (1997) compared grass dominated and open dune grasslands and found greater amounts of above-ground biomass, litter input and organic matter as well as a greater ability for nutrient uptake through increased root biomass in the grass dominated plots. Consequently, nitrogen mineralization, nitrogen turnover rates and nutrient availability were higher than in open dune grasslands, which in turn led to even further increased nutrient uptake and biomass production and favoured tall competitive grasses with a higher nutrient demand. These mechanisms may explain the increased Ellenberg indicator value observed in the present study. Removal of biomass by grazing animals, on the other hand, reduces nutrient availability and standing biomass. In a separate study of the long-term effects of livestock grazing at Newborough Warren, the reverse situation was investigated and the indicator value was shown to decline after grazing management was introduced (see Chapter 4).

Fertilisation with nitrogen and phosphorus

After two years, addition of nitrogen only had a small effect on the dune grassland studied. Statistically significant differences between unfertilised controls and nitrogen addition plots were observed in the amount of total biomass, bryophyte biomass, nitrogen concentrations in bryophyte biomass and nitrogen uptake by bryophytes. No changes were detected in vegetation composition, sward height, root biomass or soil parameters.

Additional fertilisation with phosphorus had a greater impact: total above-ground biomass increased; sward heights were greater in fertilised subplots, especially in ungrazed plots; in point quadrat surveys more hits were recorded per pin, especially for graminoids, indicating denser swards; and although not significant, nitrogen uptake by bryophytes was even greater than when nitrogen only was added. Bryophytes indicative of more infertile conditions were associated with control treatments and bryophytes indicative of more fertile situations with the high N+P treatment. However, because fertilisation with both nutrients started later than fertilisation with nitrogen only, the comparison of the two experiments needs to be interpreted with caution.

In the only other study to date that experimentally investigated the effects of nitrogen deposition on dune grassland (ten Harkel & van der Meulen 1996, ten Harkel *et al.* 1998), no effect of fertilisation (25 kg ha^{-1} $year^{-1}$) was found after five years in grazed or ungrazed plots. A possible explanation for this was limitation by phosphorus, which was shown to be a major limiting nutrient on sand dunes by Willis & Yemm (1961), Willis (1963) and Dougherty *et al.* (1990). Only very little or no leaching was measured and could not be the reason for the lack of vegetation response (ten Harkel *et al.* 1998). The present study was conducted at a site with a similar background deposition that was not yet affected by atmospheric deposition of either NO_2 or NH_3 (Mohd-Said 1999), used even lower concentrations of nitrogen addition and ran for only two years, but unlike ten Harkel & van der Meulen (1996), found indications of an effect of fertilisation on the vegetation of fixed dune grasslands, mainly on bryophytes. As yet, there was no change in species composition, but the observed increase in above-ground biomass in fertilised treatments may lead to changed abundances of species in the longer run. Increases in above-ground biomass lead to greater amounts of litter and soil organic matter, increasing soil development and nitrogen pools in the soil, and therefore affect soil biological processes and nitrogen cycling (NEGTAP 2001, Jones *et al.* 2002b). Increased standing crop and litter production can also result in changed competitive interactions through enhanced competition for light, especially affecting smaller understory species and the bryophyte and lichen layers.

As the combination of nitrogen and phosphorus affected the grassland more than application of nitrogen alone within a shorter period of time, co-limitation by both nutrients appears likely. The increased deposition of nitrogen would increase phosphorus demand and possibly induce limitation by this element. This implies that nitrogen alone would continue to have a limited impact on species composition even after longer experimental additions, and would likely result in increased leaching and impact on ground water quality. Contrary to the conclusion of N and P co-limitation, N:P ratios in graminoids and bryophytes were low and within the range indicating nitrogen limitation (Koerselman & Meuleman 1996, Güsewell & Koerselman 2002). A possible explanation is that the N:P ratio is not a reliable tool when factors other than N or P may be limiting, e.g. light availability or soil moisture (Güsewell & Koerselman 2002). The latter applies to the dune grassland studied, which gets very dry during the summer months.

Grazing treatment was of much greater importance for vegetation composition and structure than fertilisation, which is in agreement with other studies on calcareous grassland (Wilson *et al.* 1995) and dune grassland (ten Harkel & van der Meulen 1996). Within less than one year, fertilisation with both nitrogen and phosphorus resulted in significantly greater sward heights in ungrazed subplots, whereas no effect of fertilisation was found on grazed swards. However, it also led to denser swards, especially by encouraging graminoid growth, irrespective of grazing treatment.

Similarly, increases in total and bryophyte biomass and N tissue content of bryophytes in plots that were fertilised with nitrogen only, were statistically significantly different only between fertilisation treatments, but not in their interaction with the grazing treatment. This suggests that even in grazed areas, increased atmospheric deposition may have an impact on dune grasslands, and that grazing cannot entirely counteract it. Kooijman & Smit (2001) found reductions of standing crop, productivity and plant nutrient stocks by grazing and an overall reduction of nutrient availability of about 50 % compared to ungrazed areas, and concluded that grazing can counteract the effects of increased atmospheric deposition to a large extent.

Bryophytes appeared to be most sensitive to fertilisation. Ectohydric bryophytes obtain their nutrients from the atmosphere, which results in a positive relationship between atmospheric deposition and nitrogen content of mosses (e.g. Baddeley *et al.* 1994, NEGTAP 2001, Pearce & van der Wal 2002, Harmens *et al.* 2005). Increased concentrations of nitrogen in bryophyte biomass were also found in this study. A review of nitrogen application experiments by Cunha *et al.* (2002) concluded that bryophytes are the most sensitive component of many ecosystems and may be the first to respond. At the dosages applied in this experiment, nitrogen did not have an adverse effect on bryophytes, but stimulated overall productivity. No effects were detected on single species. This is contrary to many other studies that found decreases in moss biomass and abundance after fertilisation, e.g. Boorman & Fuller (1982), Gordon *et al.* (2001a), Grellmann (2002), Pearce & van der Wal (2002), van der Wal *et al.* (2003) and Solga *et al.* (2005), however effects are species specific and some species tolerate larger amounts than others (Virtanen *et al.* 2000, Gordon *et al.* 2001b). Changes to the chemistry of plant tissues can eventually lead to changes in decomposition and nutrient cycling, increased frost sensitivity and susceptibility to herbivory (NEGTAP 2001). Thus, the increased tissue nitrogen concentration in bryophytes found in this experiment provides an indication that ecosystem processes of the dune grassland studied are affected by increased nitrogen supply.

Although overall community composition and soil parameters were not affected after two years of nitrogen applications, the dune grassland studied showed some signs of response. Nitrogen dosages applied were 7.5 and 15 kg ha^{-1} $year^{-1}$ in addition to an estimated background deposition of 12 kg ha^{-1} $year^{-1}$, resulting in total nitrogen loads of 19.5 and 27 kg ha^{-1} $year^{-1}$. The critical load for dune grassland is estimated at 10-20 kg ha^{-1} $year^{-1}$ (Bobbink *et al.* 2003). For grazed vegetation, the higher end of the critical load for a given habitat can be applied (Wilson *et al.* 1995, Bobbink *et al.* 2003), but although the study site is intensively grazed by rabbits and ponies, increases in above-ground biomass were detected at the lower rate of nitrogen addition. This suggests that the critical load is exceeded at less than 20 kg ha^{-1} $year^{-1}$, even under heavy grazing pressure. In time, increased biomass is likely to lead to enhanced nitrogen mineralization, changed competitive interactions, denser swards, decreased light levels at the soil surface and the loss of small and competitively inferior species, eventually resulting in altered community composition and structure.

Conclusion

Over a time scale of only two years, some responses of dune grassland vegetation to fertilisation with nitrogen were detected. These may lead to community changes in the longer run through increases in above-ground biomass and litter, changed soil biological processes and nitrogen cycling, and altered competitive interactions between species. Even for heavily grazed areas with borderline limitation by phosphorus, it is suggested that the critical load for dune grasslands is below the previously proposed upper limit of 20 kg ha^{-1} $year^{-1}$. Grazing was shown to be of major importance in keeping tall, competitive grasses in check, thus maintaining species rich swards in the longer term.

CHAPTER 6

Seed banks of dune slacks

Dune slack vegetation where samples were taken

Introduction

Ungerminated but viable seeds buried in the soil and on its surface are called the seed bank (Roberts 1981). It is an invisible part of a plant population which can survive adverse conditions when no or only little recruitment is possible (Bullock *et al.* 2002). Moreover, it is able to regenerate and ensure the survival of a plant community after disturbance (Baskin & Baskin 2001, Jentsch *et al.* 2002). Much research has been carried out on the seed banks of grasslands and arable fields (see Baker 1989, Thompson *et al.* 1997, Vyvey 1989a, b, Bernhardt & Poschlod 1993), whereas the seed banks of sand dunes, and particularly dune slacks, are less well understood (Zhang & Maun 1994, Thompson *et al.* 1997, Bekker *et al.* 1999, Owen *et al.* 2001). Most work on seed banks of dunes has focused on dry dune areas or individual species only (e.g. Pemadasa & Lovell 1974b, Mack 1976, Watkinson 1978a, Boorman & Fuller 1984, Westelaken & Maun 1985, Ernst & Malloch 1994, Houle 1996, Rowland & Maun 2001). Only recently has there been an increased interest in the seed bank of dunes, and especially dune slacks (e.g. Bekker *et al.* 1999, Owen *et al.* 2001, Bossuyt & Hermy 2004), but for many typical dune slack species, seed bank data are still not available (Grootjans *et al.* 2004, Bossuyt *et al.* 2005).

Dune slacks are low-lying, flat areas or hollows that divide one dune ridge from another. In these areas, the water table reaches or approaches the surface (Ranwell 1955, Boorman 1993) but can vary considerably with season (Grootjans *et al.* 1998). High water levels prevail during winter and spring when the water table commonly rises above the soil surface and inundation occurs (Boorman *et al.* 1997), whereas during the summer months, it can drop to 50-100 cm below the surface (Grootjans *et al.* 1998). Dune slacks are of high conservation value because they represent one of the most species rich and most diverse semi-natural habitats in Europe (Petersen 2000, Grootjans *et al.* 2002). In Britain, they are amongst the nationally rare habitats (Doody *et al.* 1993), containing several rare and nationally scarce plant species, such as *Epipactis leptochila*, *Equisetum variegatum*, *Liparis loeselii* and *Petalophyllum ralfsii* (Dargie 1993).

In order to be able to protect these habitats and the rare species they contain, it is important to understand their ecology, including their seed bank and how it might be affected by management and environmental factors such as increased nitrogen deposition. A knowledge of the life cycle of the dominant species, including which species build up persistent seed banks, how long the seeds remain viable in the soil and how rich or poor the seed bank is in a particular area, can help both towards understanding vegetation changes through natural succession, and also with prediction of the success or failure of management or conservation measures (van der Valk & Verhoeven 1988, van der Valk & Pederson 1989, Thompson *et al.* 1993, Jentsch 2001).

It has been shown for many habitats that seed dispersal and seed rain can be very limited and the store of seeds in the soil very poor, e.g. flood-plain grasslands (Bischoff 2002, Donath *et al.* 2003), wet grasslands (Rosenthal 2004), machair dune communities (Owen *et al.* 2001) and dry sandy grasslands (Jentsch 2001). In a habitat such as sand dunes characterised by large and small scale disturbances, e.g. blow-outs, formation of new embryonic slacks, wind erosion, sand covering, rabbit burrowing and scraping, where most or all successional stages are present in close spatial proximity, it is suspected that many species do not have to rely on persistent seed banks because there will always be bare and disturbed patches nearby where they can establish (Harper 1977, Thompson & Grime 1979, Watkinson & Davy 1985, Packham & Willis 1997, Jentsch & Beyschlag 2003). This means that the continuous creation of gaps where plants can germinate and establish is crucial to the survival of these communities. However, a common problem associated with the conservation of slack communities is that many dune systems today are over-stabilised, so that hardly any new embryonic dune slacks are formed. Mature vegetation provides only few open unvegetated patches needed by pioneer species that require early successional stages and embryonic slacks. This means that early successional communities and associated plant species are becoming rare (James & Wharfe 1989, van Dijk 1989, Rhind & Jones 1999, Jentsch *et al.* 2002). This is why dune management today aims to restore and create characteristic early successional phases through sand blow and local destabilisation (Wanders 1989, Houston 1997, Rhind 2003). The successful conservation of wet dune slack communities has been shown not only to depend on the hydrology and flooding regime of the site, but also on the presence of a persistent seed bank of pioneer species (Grootjans *et al.* 2002). Thus, a knowledge of the composition of the seed bank is required in order to help management decisions in areas that have been stable for a long time, and to predict whether re-colonisation by species of conservation interest is possible.

Livestock grazing is used as a management tool to delay succession, and through the creation of gaps can influence recruitment from the seed bank (Olff & Ritchie 1998). Grazing herbivores impact on the structure and composition of plant communities in a variety of ways, e.g. by changing competitive interactions between species (Crawley 1983, Olff & Ritchie 1998), reducing biomass and litter accumulation (Van Wieren 1995, Bakker *et al.* 2003), changing nutrient cycles (Shankar & Singh 1996) and by selective removal of species (Sternberg *et al.* 2000). They can also play a key role for colonisation and regeneration processes, in a positive way because they disperse propagules (Chambers & MacMahon 1994, Shankar & Singh 1996, Pakeman *et al.* 2002, Bakker & Olff 2003), create gaps and soil disturbances that stimulate germination (Bullock *et al.* 1995, Bakker & Olff 2003) and in a negative way by feeding on seeds and reproductive structures (Chambers & MacMahon 1994, Cosyns 2004). However, despite much research, it is still difficult to predict precisely the impact of different livestock types on different types of grassland (Oates & Bullock 1997, Olff & Ritchie 1998). Some studies have focused on the size and composition of seed banks in grazed and ungrazed areas, e.g. on salt marshes (Jutila 1998, Ungar & Woodell 1993, 1996, Bos *et al.* 2002a), Mediterranean grassland (Sternberg *et al.* 2003), mountain pasture (Matêjková *et al.* 2003) and semi-natural grassland (Milberg 1995), but only few have tried to compare the seed bank in areas grazed by different livestock, e.g. cattle and horses in grassland (Gibson 1996) or cattle and sheep in flood meadows (McDonald *et al.* 1996). For management purposes it is important to understand how grazing impacts on the seed bank, because if it changes the seed bank then it may also influence future vegetation development, and not only current established vegetation (Smith *et al.* 2002).

The importance of soil seed banks for conservation management purposes is increasingly recognised (Chambers & MacMahon 1994) and further research is being called for, especially for habitats that have so far received little attention and/or contain rare and endangered species (Hölzel & Otte 2004), including coastal plant communities (Bossuyt *et al.* 2005). This study aims to provide a better understanding of the composition of the seed bank of dune slack species and their seed longevity. If the seed bank contains a viable store of characteristic species and of early successional species, then current site management, trying to create disturbance, destabilise the system and set back successional development, may contribute to vegetation change through encouraging germination from the seed bank. In particular, historical records of the above-ground vegetation were used to test the hypothesis that the seed bank reflects earlier successional stages of the vegetation more closely than the current vegetation. It was also hypothesised that differences in diet selection and germination success of seeds after gut passage of different livestock types lead to a different composition of the seed bank in areas which have a history of cattle grazing and areas grazed by ponies.

Methods

Study site

The seed bank and above-ground vegetation were studied at Newborough Warren on the south-west coast of the Isle of Anglesey, North Wales, UK (National Grid reference SH 400640). Comprising about 1300 ha of sandy deposits, it is one of the major calcareous and most biologically diverse sand dune systems on the west coast of Britain, despite the afforestation of about 720 ha with conifers between the 1940s and 1960s (Rhind *et al.* 2001). The dune system consists of foredunes and ridges of compound parabolic dunes roughly parallel to the shoreline which are separated by extensive interdune slacks. There are no marked extremes of temperature or rainfall (Buchan 1990) and the average mean annual temperature is 12.9 °C (Anderson 1994). The average annual amount of rainfall is 843 mm, with April to June being the driest months and October to January the wettest (Anderson 1994).

Newborough Warren comprises the full succession of habitats from strandline to shingle, mobile dunes, wet and dry slacks to dune grassland and scrub and harbours many rare and protected species. Its outstanding conservation value is recognised in its designation as National Nature Reserve (NNR), Site of Scientific Interest (SSSI) and Special Area of Conservation (SAC) under the EC Habitats and Species Directive 1992. This is because of its high diversity of habitats of European importance, including shifting dunes, dune grassland and humid dune slacks.

However, Newborough Warren is now over-stabilised and has been characterised by greater stability and succession towards more mature vegetation since the early 1950s (Dargie 1993). While mobile dunes and young slacks with open vegetation amounted to about 75 % of the total dune system in the 1950s (Ranwell 1960a), there are hardly any embryonic slacks today and only about 6 % of the site could be regarded as mobile and open in 1991 (Rhind *et al.* 2001). At present, mature slacks are amongst the dominant vegetation types at Newborough Warren (Rhind *et al.* 2001) while early successional slacks and wet slack communities are declining as mature and dry communities increase at the expense of the wetter communities (Sandison & Hellawell 2000).

Livestock grazing was introduced on site in 1987 as a management tool to counteract the loss of diversity through the over-dominance of coarse grasses and scrub, and to maintain a range of successional phases. Up to 2001, different livestock (cattle, sheep and ponies) were used on different parts of the dunes mainly during the winter. Since 2001, about three quarters of the dunes have been grazed all year by ponies at a density of one pony to every 3-4 ha. Additionally, rabbits (*Oryctolagus cuniculus*) are widespread and abundant throughout the site.

The slacks under investigation in this study are characterised by closed vegetation with a high abundance of *Salix repens*, a diverse assemblage of vascular plant species and extensive bryophyte cover. The sampling area is located in the central dune slack and shows a small-scale mosaic of different slack communities, namely SD14 (*Salix repens – Campylium stellatum* dune slack), SD15 (*Salix repens – Calliergon cuspidatum* dune slack), SD16 (*Salix repens – Holcus lanatus* dune slack) and SD17 (*Potentilla anserine – Carex nigra* dune slack) (Rodwell 2000).

Vegetation sampling

A series of permanent monitoring quadrats was established in 1987 in order to enable assessment of vegetation change at Newborough Warren (McPhail 1987). Eight of these were chosen for this study. For five of these eight quadrats, information on their botanical composition is available from 1987, 1988, 1991 and 1996, provided by the Countryside Council for Wales (CCW). The remaining three quadrats were established in 1992 and re-monitored by CCW in 1996. Livestock grazing was introduced in an enclosure containing four of these quadrats in 1991; they were grazed by cattle from 1992 to 2001 and by ponies thereafter (grazing management 1). Four quadrats have been grazed continuously by ponies since 1996 (grazing management 2). This allowed investigation of the effects different grazing regimes might have on seed bank composition.

As part of this study, all eight quadrats were assessed again in June 2003 by estimating cover-abundance for every plant species (including bryophytes and lichens) using the Domin scale, following the methods used for previous data collection (McPhail 1987, Evans 1991). Field records from previous surveys were taken into the field and compared to the new records; this allowed a deliberate search for missing species, which means that the absence of a species can be regarded as a real loss rather than a possible oversight. Most species could be identified in the field, but of those that could not, samples were taken for later identification. Nomenclature for higher plants follows Stace (1997). Nomenclature of plant communities and sub-communities is based on the National Vegetation Classification (NVC) (Rodwell 2000).

Seed bank sampling

Soil samples were collected in March 2004 before spring germination and seed set but after natural winter stratification. This was because the seeds of many species germinate in larger numbers after stratification (e.g. Raynal & Bazzaz 1973, Leck & Graveline 1979, Grime *et al.* 1981, Baskin & Baskin 1988, Gross 1990, Schütz & Rave 1999). Winter or early spring sampling is also recommended if the aim is to sample transient *and* persistent seed banks (Baskin & Baskin 2001). Twelve replicate soil cores (5 cm diameter, 10 cm depth) were taken adjacent to each of the eight permanent monitoring quadrats. The total area and volume sampled at each quadrat was 235.6 cm^2 and 2356.2 cm^3 respectively. The soil cores were placed in polythene bags to avoid contamination until further processing (Bullock 1996).

Seed bank composition and seed density were determined for two depth layers, 0-5 cm and 5-10 cm, to evaluate seed longevities (Thompson *et al.* 1997). The twelve replicate samples from each sampling location were pooled by horizon to give one sample per quadrat and over a litre of soil per horizon, which is more than recommended for studies of grassland seed banks (Hayashi & Numata 1971, Oomes & Ham 1983). Surface vegetation, large roots and stones were removed and contamination of the deeper layer with surface seeds prevented by carefully scraping off the outer layer of soil after it was pushed out of the core. The soil was then spread in a thin layer (0.5-1 cm) over a 4 cm layer of sterilized plant compost (John Innes No 1) in two and three replicate trays for the surface and deeper layer respectively. The trays were arranged randomly on a bench and covered with clear plastic hoods; control trays recorded contamination by wind-borne seeds and seeds contained in the sterilised subsoil.

Germination was carried out under glasshouse conditions with a 12 h photoperiod, regular watering and night and day temperatures of 18 °C and 20 °C respectively using the seedling emergence method (Roberts 1981). Because the soil was sampled from a wet dune slack, the trays were kept very moist because most species of this habitat are adapted to wet conditions and could be expected to germinate better from wet than dry soil (ter Heerdt *et al.* 1999). The occurrence of species such as *Ranunculus flammula* and *Radiola linoides* in this study shows that germination conditions for wet-loving species were met (ter Heerdt *et al.* 1999). All emerging seedlings were counted and removed after identification to avoid competition. Unidentified seedlings were transplanted into separate pots and grown until identification was possible. When germination appeared to have stopped, the samples were disturbed repeatedly to promote germination of seeds deeper in the sample by exposing them to more suitable light and temperature regimes (Bullock 1996, Thompson *et al.* 1997). After no new seedlings emerged, the soil was allowed to dry out for a few weeks to simulate summer conditions (Baskin & Baskin 2001), which promoted the germination of some new seedlings. Subsequently, it was stored in the cold (4 °C) for nine weeks, which allowed for seeds that needed another period of stratification to become non-dormant and germinate. No assessment of the numbers of viable seeds remaining in the soil was made at the end of the experiment in April 2005 when no more seedlings had emerged for several weeks. The terms 'seed' and 'seed bank' are used here in a broad sense including true seeds and fruits (Roberts 1981).

In the summer of 2004, the area surrounding the sampling locations was searched for additional plant species not previously recorded in the monitoring quadrats. Records of species found in the seed bank, but never recorded from the permanent monitoring quadrats, were also checked against a species inventory comprising the whole dune system obtained from the Countryside Council for Wales (CCW).

Data analysis

The spore producing species *Selaginella selaginoides*, *Equisetum arvense*, *E. palustre* and *E. variegatum* recorded in the above-ground vegetation were excluded from data analysis because the germination method does not provide reliable data on them. Species with very small seeds, e.g. orchids and *Centaurium erythraea*, were included because they did germinate in the experiment. The glaucous sedges *Carex flacca*, *C. nigra* and *C. panicea* were all present in the seed bank, but because of the difficulties attached to identifying them at the seedling stage, they were pooled into a species group named 'glaucous sedges' in both seed bank and vegetation. *Dactylorhiza incarnata* and *D. purpurella* were also pooled. All species, even those with three or less seedlings only, were included in the data analysis if they were dune slack species and therefore not resulting from contamination. Seedlings of common greenhouse weeds that grew from control trays, e.g. *Salix cinerea* and *Juncus effusus*, were excluded from the analysis.

Normality of the data was tested using the Kolmogorov-Smirnov test. Differences between the two grazing regimes were analysed for each species with more than ten seedlings using a Mann-Whitney test because of the non-normality of the data.

Ellenberg indicator values:

Weighted mean Ellenberg indicator values (Hill *et al.* 1999) for light, moisture, reaction, nitrogen and salt tolerance for seed bank and above-ground vegetation were calculated according to the following formula (ter Braak 1995): Weighted average = $(y_1x_1 + y_2x_2 + \dots + y_nx_n) / (y_1 + y_2 + \dots + y_n)$, where $y_1, y_2, \dots, y_n$ are the number of seeds in the seed bank or the cover (Domin) value of species 1-n and $x_1, x_2, \dots, x_n$ are the Ellenberg indicator values for species 1-n.

Longevity index:

One way of determining seed longevity is by looking at the ratio between seed numbers in the different depth layers (Thompson *et al.* 1997). Transient seeds are defined as present only in the surface layer, short-term persistent seeds are more abundant in the surface than deeper layers, and long-term persistent seeds are more abundant in deeper layers. However, this approach tends to underestimate longevity (Bekker *et al.* 1998, Hölzel & Otte 2004). Thus a continuous longevity index was also calculated for each species recorded in this study following the methods of Bekker *et al.* (1998) based on the database of Thompson *et al.* (1997) according to the following formula: Longevity index LI = (SP+LP)/(T+SP+LP) with T = total number of transient records in the database, SP = total number of short term persistent records in the database, LP = total number of long term persistent records in the database. This index ranges from 0 (transient) to 1 (persistent). Here it was calculated for species with four or more records in the database, so that for 21 species in the established vegetation and/or seed bank in this study no longevity index was calculated. A weighted longevity index for each seed bank and vegetation sample was calculated according to the formula: Weighted longevity index = $(y_1x_1 + y_2x_2 + \ldots + y_nx_n) / (y_1 + y_2 + \ldots + y_n)$, where $y_1, y_2, \ldots, y_n$ are the number of seeds in the seed bank or the cover (Domin) value of species 1-n and $x_1, x_2, \ldots, x_n$ is the longevity index for species 1-n.

Seed weights:

Data on mean seed weights were obtained from the Ecological Flora Database (Fitter & Peat 1994). Mean average weighted seed weights were calculated for the vegetation in each year and both depth layers of the seed bank (Weighted seed weight = $(y_1x_1 + y_2x_2 + \ldots + y_nx_n) / (y_1 + y_2 + \ldots + y_n)$, where $y_1, y_2, \ldots, y_n$ are the number of seeds in the seed bank or the cover (Domin) value of species 1-n and $x_1, x_2, \ldots, x_n$ is the seed weight for species 1-n).

Comparison of vegetation and seed bank:

The Sørensen similarity index was calculated for the comparison of above-ground vegetation and seed bank according to the formula: Similarity (%) = 2c/(a+b) x 100, where a = number of species in the seed bank, b = number of species in the established vegetation and c = number of species found in both (Greig-Smith 1964). The similarity between seed bank and vegetation was calculated for both seed bank depth layers and each year of vegetation survey and analysed for significant differences by paired t-tests. Bryophytes were excluded because they do not produce seeds. For the comparison of species numbers in vegetation and seed bank, no statistics were used because of the different sampling units (2 x 2 m for vegetation and 5 cm diameter soil cores for the seed bank). Weighted Ellenberg indicator values, longevity indices and seed weights were compared using paired t-tests, excluding above-ground vegetation data for 1992 when sample sizes were particularly small.

The floristic similarity between the two seed bank horizons and the past and present vegetation was also analysed by Detrended Correspondence Analysis (DCA) with a log(n+1)-transformation using the package Canoco for Windows 4.5 (ter Braak 1987). This was also used to detect differences in the floristic composition of seed bank and vegetation samples in relation to the two different grazing regimes.

Results

Composition of the seed bank

During the first germination period, 4807 seedlings of 56 species emerged. The second germination period after cold stratification for nine weeks resulted in 468 seedlings of 25 species, four of which had not been recorded before stratification, including the two orchids *Epipactis palustris* and *Dactylorhiza* spp. Mono- and dicotyledonous herbs represented the most species rich and abundant plant group (51.8 % of all seedlings), followed by rushes (31.5 %), sedges (8.7 %) and grasses (8.0 %). The two most abundant species, *Hydrocotyle vulgaris* and *Juncus articulatus*, together accounted for almost 50 % of all seedlings. Thirty-three species were represented by less than ten seedlings.

Total seed density was 27985 seeds m^{-2}, ranging from 10907 to 51481 seeds m^{-2} at different sampling sites and from 42 to 20796 seeds m^{-2} between species and sites (Table 6.1). The seed bank was dominated by the surface layer with 79 % of all seedlings having grown from the top 5 cm and an overall seed density of 22064 seeds m^{-2}; 24 species were found in both depths, 32 species in 0-5 cm only and four species in 5-10 cm only (Table 6.1).

Seed bank and vegetation

A total of 72 and 60 plant species were recorded from the vegetation and seed bank respectively. 26 species were only found in the vegetation, 14 species only in the seed bank, and 46 species in both (Table 6.1). Of the 14 species recorded from the seed bank only, five were observed in the study area in close proximity to the sampling locations in June 2004. Four species have not been recorded anywhere on site before: *Veronica anagallis-aquatica* and *Sagina procumbens* with more than 100 seedlings each, and *Chenopodium rubrum* and the neophyte *Epilobium brunnescens* with only one seedling each. Seeds of these species were concentrated in the lower depth layer. Seedlings of species that occur more frequently in early stages of slack development (Rodwell 2000), e.g. *Centaurium erythraea* and *Sagina nodosa*, were more abundant in the deeper soil layer (58.8 % of all seedlings in 5-10 cm depth) than the surface soil layer (42.5 % of all seedlings in 0-5 cm depth).

Table 6.1. Abundance in vegetation in 1987-2003 and numbers of seeds m^{-2} found in the seed bank in 2004 for two depth layers at eight different sampling locations. Figures are Domin values for the vegetation and seeds m^{-2} for the seed bank. 1-4: Grazing management 1, 5-8: Grazing management 2. LI=Longevity index calculated after Thompson *et al.* (1997); - = not enough data available. 42 seeds m^{-2} correspond to one seed found.

		1 Vegetation					1 Seed bank		2 Vegetation					2 Seed bank	
	LI	1987	1988	1991	1996	2003	0-5 cm	5-10 cm	1987	1988	1991	1996	2003	0-5 cm	5-10 cm
In vegetation only:															
Agrostis vinealis	0.38														
Aira praecox	1.00												1		
Ammophila arenaria	0.09														
Crepis capillaris	0.25														
Cynosurus cristatus	0.02														
Danthonia decumbens	0.29					2									
Eleocharis quinqueflora	-														
Festuca ovina	0.10														
Festuca rubra	0.14														
Galium palustre	-														
Hieracium spp.	-											1			
Leontodon saxatilis	0.40			1	1										
Listera ovata	-														
Ononis repens	0.00											1	1		
Pilosella officinarum	0.23										1	1	1		
Pinguicula vulgaris	-	1	1	1											
Plantago lanceolata	0.35														
Potentilla erecta	0.44														
Pyrola rotundifolia	-	1		2	1				5		4	5	4		
Ranunculus acris	0.24														
Rhinanthus minor	0.50				1				3		3	3	5		
Rosa canina agg.	-														
Rubus caesius	-														
Rubus fruticosus	0.54														
Schoenus nigricans	-														
Viola canina	0.69														
In seed bank only:															
Centaurium erythraea	1.00													42	
Centaurium littorale	-													212	
Chenopodium rubrum	1.00						42								
Cirsium palustre	0.26														
Daucus carota	0.68														
Epilobium brunnescens	-														
Glaux maritima	0.93														
Juncus bulbosus	0.88													170	
Persicaria maculosa	0.86							42							
Plantago major	0.79														
Reseda luteola	0.50														
Sagina procumbens	0.87														
Veronica anagallis-aquatica	-						1188	3438							
Veronica chamaedrys	0.38														

	3 Vegetation					3 Seed bank		4 Vegetation					4 Seed bank	
	1987	1988	1991	1996	2003	0-5 cm	5-10 cm	1987	1988	1991	1996	2003	0-5 cm	5-10 cm
In vegetation only:														
Agrostis vinealis										2				
Aira praecox														
Ammophila arenaria														
Crepis capillaris	2							2						
Cynosurus cristatus			3	3	3									
Danthonia decumbens														
Eleocharis quinqueflora														
Festuca ovina														
Festuca rubra			2	3	3					1	3	3		
Galium palustre					1									
Hieracium spp.	2													
Leontodon saxatilis														
Listera ovata											1			
Ononis repens	2		3	3										
Pilosella officinarum														
Pinguicula vulgaris														
Plantago lanceolata				3	2									
Potentilla erecta														
Pyrola rotundifolia	3	1	4								3			
Ranunculus acris			2	3	4				1	1	1	2		
Rhinanthus minor														
Rosa canina agg.														
Rubus caesius												1		
Rubus fruticosus														
Schoenus nigricans														
Viola canina										1	4	2		
In seed bank only:														
Centaurium erythraea														
Centaurium littorale						212	42							
Chenopodium rubrum														
Cirsium palustre														
Daucus carota														
Epilobium brunnescens														42
Glaux maritima														
Juncus bulbosus														
Persicaria maculosa														
Plantago major														
Reseda luteola														
Sagina procumbens							42							3013
Veronica anagallis-aquatica														
Veronica chamaedrys							42						42	

	5 Vegetation					5 Seed bank		6 Vegetation			6 Seed bank	
	1987	1988	1991	1996	2003	0-5 cm	5-10 cm	1992	1996	2003	0-5 cm	5-10 cm
In vegetation only:												
Agrostis vinealis												
Aira praecox												
Ammophila arenaria												
Crepis capillaris	3			1								
Cynosurus cristatus												
Danthonia decumbens					4							
Eleocharis quinqueflora										2		
Festuca ovina												
Festuca rubra												
Galium palustre												
Hieracium spp.		1										
Leontodon saxatilis	3	1										
Listera ovata												
Ononis repens												
Pilosella officinarum												
Pinguicula vulgaris	2	1	2									
Plantago lanceolata			2	1	1							
Potentilla erecta												
Pyrola rotundifolia	1		3	3	2							
Ranunculus acris										1		
Rhinanthus minor												
Rosa canina agg.	1		1	2	1							
Rubus caesius	2		1	1	2							
Rubus fruticosus		1										
Schoenus nigricans	6	8	8	8	6							
Viola canina												
In seed bank only:												
Centaurium erythraea												
Centaurium littorale						170					212	
Chenopodium rubrum												
Cirsium palustre												
Daucus carota												
Epilobium brunnescens												
Glaux maritima												
Juncus bulbosus												
Persicaria maculosa												
Plantago major											85	
Reseda luteola												
Sagina procumbens												1231
Veronica anagallis-aquatica												
Veronica chamaedrys												

	7 Vegetation			7 Seed bank		8 Vegetation			8 Seed bank	
	1992	1996	2003	0-5 cm	5-10 cm	1992	1996	2003	0-5 cm	5-10 cm
In vegetation only:										
Agrostis vinealis	1									
Aira praecox										
Ammophila arenaria	1	3								
Crepis capillaris							1	1		
Cynosurus cristatus							2	2		
Danthonia decumbens										
Eleocharis quinqueflora										
Festuca ovina							3	3		
Festuca rubra	3	3	3			3	3	4		
Galium palustre										
Hieracium spp.							1			
Leontodon saxatilis							1	1		
Listera ovata							1			
Ononis repens						2	1	2		
Pilosella officinarum										
Pinguicula vulgaris										
Plantago lanceolata							1	1		
Potentilla erecta		1								
Pyrola rotundifolia						4	3	2		
Ranunculus acris	4	2	4				1	4		
Rhinanthus minor			4					6		
Rosa canina agg.										
Rubus caesius	3	4	4							
Rubus fruticosus										
Schoenus nigricans										
Viola canina	2	1	1							
In seed bank only:										
Centaurium erythraea									42	
Centaurium littorale					42				382	
Chenopodium rubrum										
Cirsium palustre									42	
Daucus carota									42	
Epilobium brunnescens										
Glaux maritima					42					
Juncus bulbosus										
Persicaria maculosa										
Plantago major									42	
Reseda luteola				42						
Sagina procumbens										
Veronica anagallis-aquatica										
Veronica chamaedrys										

Table 6.1. Continued.

	LI	1 Vegetation 1987	1988	1991	1996	2003	1 Seed bank 0-5 cm	5-10 cm	2 Vegetation 1987	1988	1991	1996	2003	2 Seed bank 0-5 cm	5-10 cm
In seed bank and vegetation:															
Agrostis capillaris	0.66														
Agrostis stolonifera	0.38			1	1	3	3098	85				3	4	594	42
Anagallis tenella	-														
Anthoxanthum odoratum	0.29														
Anthyllis vulneraria	0.11				1	1							1		
Bellis perennis	0.56						42								
Cardamine pratensis	0.49														
Carex arenaria	-	1	2	3	3	4	1188		2	4	2	3	2	2419	
Carex viridula	-						85							127	
Cerastium fontanum	0.65												1		
Dactylorhiza incarnata/purpurella	-						42								
Epilobium montanum	0.77						85								
Epipactis palustris	-	3	3	4	4	7			4	3	5	4	5	42	
Euphrasia officinalis agg.	0.17				3		42				2	3	4		
glaucous sedge	0.33		7	5	5	8	170	42	4	8	3	6	7	127	
Holcus lanatus	0.56						42								
Hydrocotyle vulgaris	0.27	3	2	2	4	4	2037		2	1	1			170	
Hypochaeris radicata	0.32			1			42						1		
Juncus acutiflorus	0.64		2				212	42						42	
Juncus articulatus	0.88			2	2	4	1162	9167					2	2462	340
Juncus bufonius	0.87						170	170						3480	
Leontodon autumnalis	0.16						42					1	1		
Linum catharticum	0.58											2	3	85	
Lotus corniculatus	0.26	3	3	3	5	4			4	4	4	3	4	42	
Luzula campestris	0.37														
Mentha aquatica	0.39			1	3	2	1358								
Parnassia palustris	0.14			1		2	42		2	1			2	42	
Poa pratensis	0.39						255								
Polygala vulgaris	0.10					1					1			42	
Potentilla anserina	0.25														
Prunella vulgaris	0.35	1					42								
Radiola linoides	-														
Ranunculus bulbosus	0.37														
Ranunculus flammula	0.63					1	127								
Ranunculus repens	0.68														
Rumex acetosa	0.29														
Sagina nodosa	-						127						1	6239	
Salix repens	0.00	7	9	5	8	8			5	7	7	8	6	85	
Samolus valerandi	-						297	127						212	
Senecio jacobaea	0.37														
Sonchus arvensis	0.96														
Taraxacum sect. *Ruderalia*	0.30					2							2		
Trifolium pratense	0.32														
Trifolium repens	0.40				1	2	42						1		
Triglochin spp.	-			1											
Viola riviniana	0.00													85	
Total number of seedlings							22451	13114						16722	382
Total number of species		8	8	15	15	16	25	8	9	7	11	14	22	20	2

	3 Vegetation 1987	1988	1991	1996	2003	3 Seed bank 0-5 cm	5-10 cm	4 Vegetation 1987	1988	1991	1996	2003	4 Seed bank 0-5 cm	5-10 cm
In seed bank and vegetation:														
Agrostis capillaris											1			
Agrostis stolonifera					2	1146	127	3		2	3	3	3777	1019
Anagallis tenella						2589	806							
Anthoxanthum odoratum	4	7	4	4	3	42								
Anthyllis vulneraria														
Bellis perennis														
Cardamine pratensis												1	170	
Carex arenaria	2	4	2	2		2080	2037		5	4	3	2	976	255
Carex viridula						637	297						552	
Cerastium fontanum			1		3	2037	127						212	
Dactylorhiza incarnata/purpurella					1									
Epilobium montanum	1													
Epipactis palustris														
Euphrasia officinalis agg.				2										
glaucous sedge		1	2	2	3	594	552	1		3	4	5	806	42
Holcus lanatus	4	3	3	2	4	85						3	764	85
Hydrocotyle vulgaris	5	6	4	4	5	9719	1867	3	2	1	3	9	6027	1019
Hypochaeris radicata			1		2						1			
Juncus acutiflorus							42		3					
Juncus articulatus					2	806	1698					2	3098	2080
Juncus bufonius							722						509	212
Leontodon autumnalis				3	2	127					2		424	
Linum catharticum				2		85								
Lotus corniculatus	4	5	1	4	3			5	5		2	5	212	42
Luzula campestris		1	3			42								
Mentha aquatica		1		4	3	1273	340						1698	
Parnassia palustris			1											
Poa pratensis	3		4	2	3	42				3	5	3		127
Polygala vulgaris	1			2	2	42								
Potentilla anserina	1	1	1	5	2			4	7	5	5	4	382	127
Prunella vulgaris		1	2	2	2	85								
Radiola linoides														
Ranunculus bulbosus	1					42		1						
Ranunculus flammula													127	382
Ranunculus repens						127							212	85
Rumex acetosa				1	1						1	2	42	
Sagina nodosa						85	934							679
Salix repens	8	9	6	7	7			8	8	8	6	8		
Samolus valerandi						42								
Senecio jacobaea			1											
Sonchus arvensis														
Taraxacum sect. *Ruderalia*	1		2		3	85						1		
Trifolium pratense				3	5	85								
Trifolium repens			4	6	2	127								
Triglochin spp.														
Viola riviniana						85		1					1273	297
Total number of seedlings						22324	9677						21305	9507
Total number of species	16	12	22	23	26	26	15	9	7	11	17	17	19	16

	5 Vegetation 1987	1988	1991	1996	2003	5 Seed bank 0-5 cm	5-10 cm	6 Vegetation 1992	1996	2003	6 Seed bank 0-5 cm	5-10 cm
In seed bank and vegetation:												
Agrostis capillaris												
Agrostis stolonifera	1			2	3	509			3	3	4414	212
Anagallis tenella	3	3	1	1	4	8191	127					
Anthoxanthum odoratum												
Anthyllis vulneraria												
Bellis perennis	1		4	1								
Cardamine pratensis												
Carex arenaria						806	212	1	3	2	1061	
Carex viridula						85	127		2		1103	
Cerastium fontanum								1				
Dactylorhiza incarnata/purpurella	1		1	1	2							
Epilobium montanum												
Epipactis palustris										2		
Euphrasia officinalis agg.					1							
glaucous sedge	3		2	2	4	127	42	4	5	4	467	42
Holcus lanatus	4	4	5		4			4	2	1	170	
Hydrocotyle vulgaris	4	6	4	3	4	2546	85	3	3	7	19905	85
Hypochaeris radicata	1		2	1	1			4				
Juncus acutiflorus											170	42
Juncus articulatus						6494	2292	2		4	10101	5135
Juncus bufonius						127	679				127	382
Leontodon autumnalis					1				4		212	
Linum catharticum												
Lotus corniculatus	3	2	1	2	5	42		4	2	5	42	
Luzula campestris												
Mentha aquatica	3	3	3	2	4	2419	85	3	3	4	1910	42
Parnassia palustris	2		2		4			3				
Poa pratensis		3		2	2	42		3	5	2	85	
Polygala vulgaris												
Potentilla anserina	1	1	1	2	5			5	5	5	85	
Prunella vulgaris	1	1	3	2	2	212		2		3	85	
Radiola linoides						212					42	
Ranunculus bulbosus												
Ranunculus flammula			1	1	1	42		1	2	1	1825	85
Ranunculus repens								2	3	4	85	
Rumex acetosa											85	
Sagina nodosa						2037					42	42
Salix repens	3		4	2	4			7	6	8		
Samolus valerandi		1									806	255
Senecio jacobaea			1	1	1			1				
Sonchus arvensis				1								
Taraxacum sect. *Ruderalia*	3	1	2		4			2	1	4	42	
Trifolium pratense												
Trifolium repens				1	2	42		2		3	170	
Triglochin spp.											170	297
Viola riviniana											42	85
Total number of seedlings						24107	3650				43545	7937
Total number of species	22	15	22	23	26	17	8	19	15	19	27	13

	7 Vegetation 1992	1996	2003	7 Seed bank 0-5 cm	5-10 cm	8 Vegetation 1992	1996	2003	8 Seed bank 0-5 cm	5-10 cm
In seed bank and vegetation:										
Agrostis capillaris							2	2	42	
Agrostis stolonifera			5	340	42		1		170	
Anagallis tenella								3	1103	
Anthoxanthum odoratum			2			5	3	3		
Anthyllis vulneraria				42						
Bellis perennis						2		1		
Cardamine pratensis										
Carex arenaria	3	4	3	509		5	2		594	42
Carex viridula									85	
Cerastium fontanum							1			
Dactylorhiza incarnata/purpurella							1	1		
Epilobium montanum										
Epipactis palustris								1		
Euphrasia officinalis agg.			1				1	3		
glaucous sedge	3	4	5	806		2	2	4	382	
Holcus lanatus		2	4	424		2	3	1	85	
Hydrocotyle vulgaris			4	4881	637	3	2	3	1273	
Hypochaeris radicata						2	1	3	42	
Juncus acutiflorus										
Juncus articulatus				1231	764			3	2928	806
Juncus bufonius				127				2	1867	42
Leontodon autumnalis				42		2	3	2	127	
Linum catharticum							1	3	255	
Lotus corniculatus	5	2	5	85		3	3	5	85	
Luzula campestris				42		3	1	1	85	
Mentha aquatica	3	2	4	6112	509				42	
Parnassia palustris			2	127						
Poa pratensis	6	5	3			3	2	2		
Polygala vulgaris							1	2		
Potentilla anserina	6	2	4	594	85	2	1	2		
Prunella vulgaris	1		4	255		2	1	3	85	
Radiola linoides										
Ranunculus bulbosus										
Ranunculus flammula			1	170	42			1	42	
Ranunculus repens		2								
Rumex acetosa										
Sagina nodosa				85	42					
Salix repens	7	4	7			5	4	6		
Samolus valerandi										
Senecio jacobaea			1	127			1	2		
Sonchus arvensis						5	4	2	85	
Taraxacum sect. *Ruderalia*	2		2				1	2	42	
Trifolium pratense							2	4		
Trifolium repens	3		2					2		
Triglochin spp.										
Viola riviniana								1	42	
Total number of seedlings				16043	2207				10016	891
Total number of species	16	15	23	19	9	18	35	39	26	3

Figure 6.1 shows how the seed bank in 0-5 cm depth in 2004 was more species-rich than the vegetation in 1987-1992 and as diverse as the vegetation in 1996 and 2003; the 5-10 cm seed bank layer contained fewer species than the vegetation in almost all years of recording.

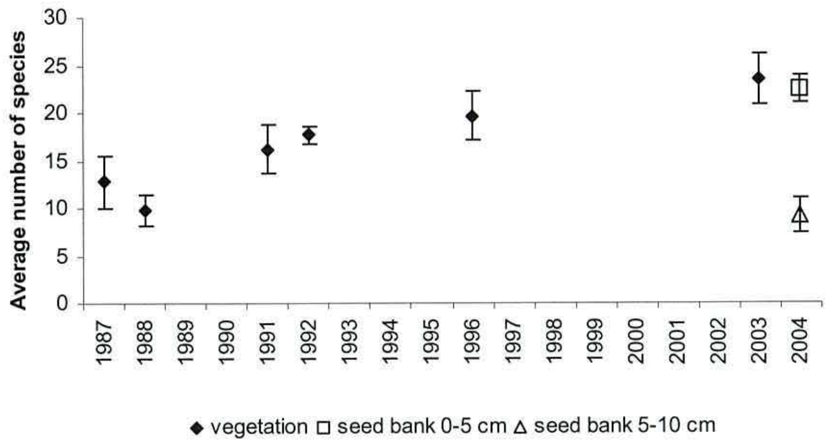


Figure 6.1. Average number of species in the vegetation between 1987 and 2003 (1987-1991: N=5, 1992: N=3, 1996 and 2003: N=8) and in the seed bank in 2004 in two depth layers, 0-5 cm and 5-10 cm (N=8). Bars represent standard errors.

Perennial species dominated both the established vegetation and seed bank. Eleven of the species in the seed bank were annuals or biennials and 49 perennials. In the above-ground vegetation, seven annual or biennial and 65 perennial species were recorded. Perennials represented 95 % of all seedlings emerging from the seed bank, with the contribution of annual and biennial seedlings being very similar in both depth layers. The number of annual and biennial species in the 0-5 cm seed bank was greater than in the vegetation for all years (Figure 6.2).

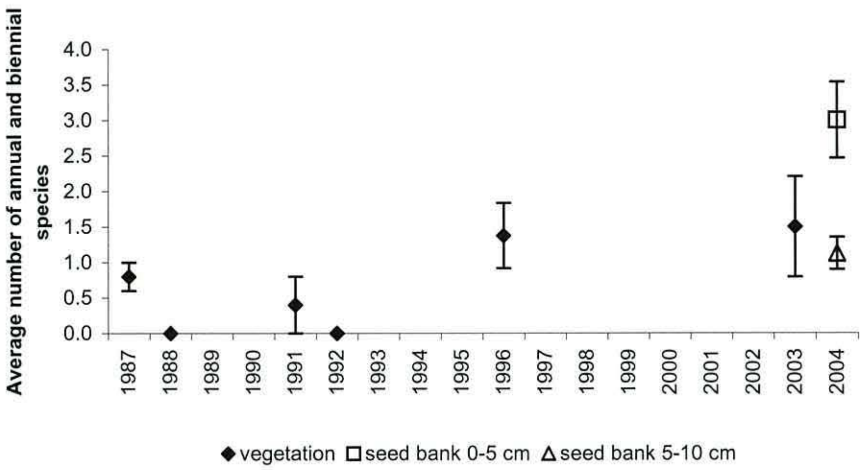


Figure 6.2. Average number of annual and biennial species in the vegetation between 1987 and 2003 (1987-1991: N=5, 1992: N=3, 1996 and 2003: N=8) and in the seed bank in 2004 in two depth layers, 0-5 cm and 5-10 cm (N=8). Bars represent standard errors.

The floristic composition of the seed bank was dissimilar to the established vegetation. In the ordination of the combined seed bank and vegetation data (Figure 6.3), there was a clear separation of the seed bank and the vegetation samples in all years of survey along the first axis. Sørensen's similarity index between the vegetation in the different years that records were available and the seed bank sampled in 2004 was greater in 2003 than in earlier years and lower for the deeper soil layer than for the 0-5 cm layer (Figure 6.4). Similarity ranged from 36.7 % to 53.2 % in 0-5 cm and 17.5 % to 28.4 % in 5-10 cm depth and was therefore rather low. The closer similarity of the surface seed bank to the vegetation is also illustrated in Figure 6.3, where the 0-5 cm layer is positioned closer to the vegetation than the 5-10 cm layer on the first DCA-axis, which separates the vegetation and the two seed bank layers.

Small seeded species were significantly more abundant in the seed bank than the above-ground vegetation in all years of survey, and the surface soil layer had significantly greater average seed weights than the deeper soil layer (paired t-test, t=4.72, p=0.002, N=8) (Figure 6.5).

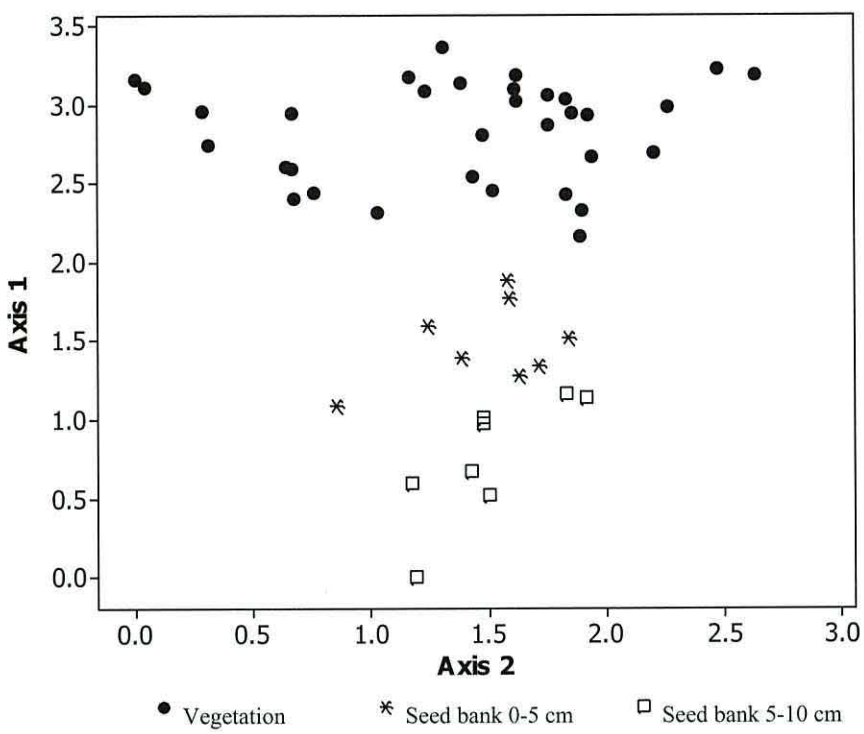


Figure 6.3. Ordination of seed bank and vegetation samples by Detrended Correspondence Analysis (DCA), axes 1 and 2 (Eigenvalues: axis 1=0.4309, axis 2=0.2508). Analysis was based on species abundance and seed numbers that have been log(+1)-transformed.

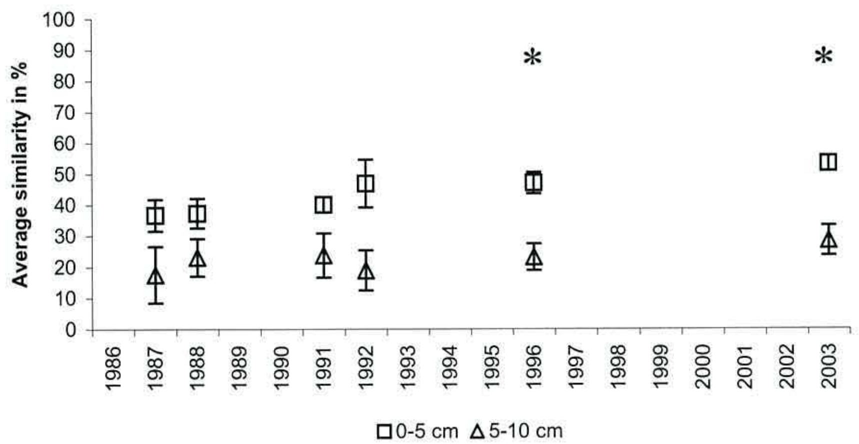


Figure 6.4. Average Sørensen similarity index between the vegetation in different years and the seed bank in 2004 in two depth layers, 0-5 cm and 5-10 cm. Bars represent standard errors. Stars indicate significant differences between seed bank layers ($p<0.05$). Results of paired t-tests comparing the two seed bank layers: 1987: $t=2.16$, $p=0.097$, $N=5$; 1988: $t=1.42$, $p=0.228$, $N=5$; 1991: $t=1.76$, $p=0.153$, $N=5$; 1996: $t=5.58$, $p=0.001$, $N=8$; 2003: $t=5.92$, $p=0.001$, $N=8$.

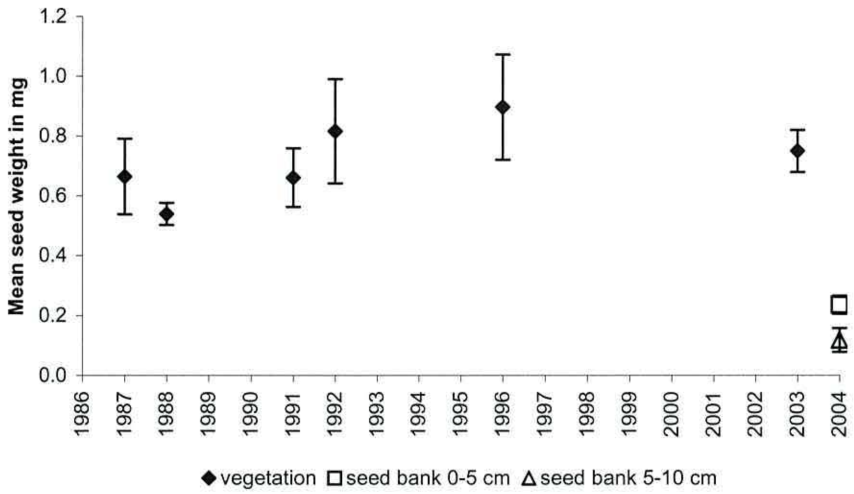


Figure 6.5. Average weighted seed weight of species in the vegetation between 1987 and 2003 and species in the seed bank in 2004 in two depth layers, 0-5 cm and 5-10 cm. Bars represent standard errors. Results of paired t-tests comparing seed bank and above-ground vegetation: a) 0-5 cm layer: 1987: $t=3.20$, $p=0.033$, $N=5$; 1988: $t=5.93$, $p=0.004$, $N=5$; 1991: $t=3.95$, $p=0.017$, $N=5$; 1996: $t=3.72$, $p=0.007$, $N=8$; 2003: $t=7.36$, $p<0.001$, $N=8$; b) 5-10 cm layer: 1987: $t=4.11$, $p=0.015$, $N=5$; 1988: $t=5.01$, $p=0.007$, $N=5$; 1991: $t=5.52$, $p=0.005$, $N=5$; 1996: $t=4.60$, $p=0.002$, $N=8$; 2003: $t=8.64$, $p<0.001$, $N=8$. Comparison of the two seed bank layers: $t=4.72$, $p=0.002$, $N=8$.

Average weighted Ellenberg indicator values for the vegetation did not show any obvious trends over the years, apart from a slight increase of the nitrogen value (Figure 6.6). Weighted seed bank Ellenberg values were significantly higher than for the vegetation for moisture and salt in both depth layers in almost all years, and for light in more recent years (Figure 6.6, Table 6.2). The 5-10 cm layer had a significantly higher value for moisture and salt than the surface layer (Figure 6.6, Table 6.2).

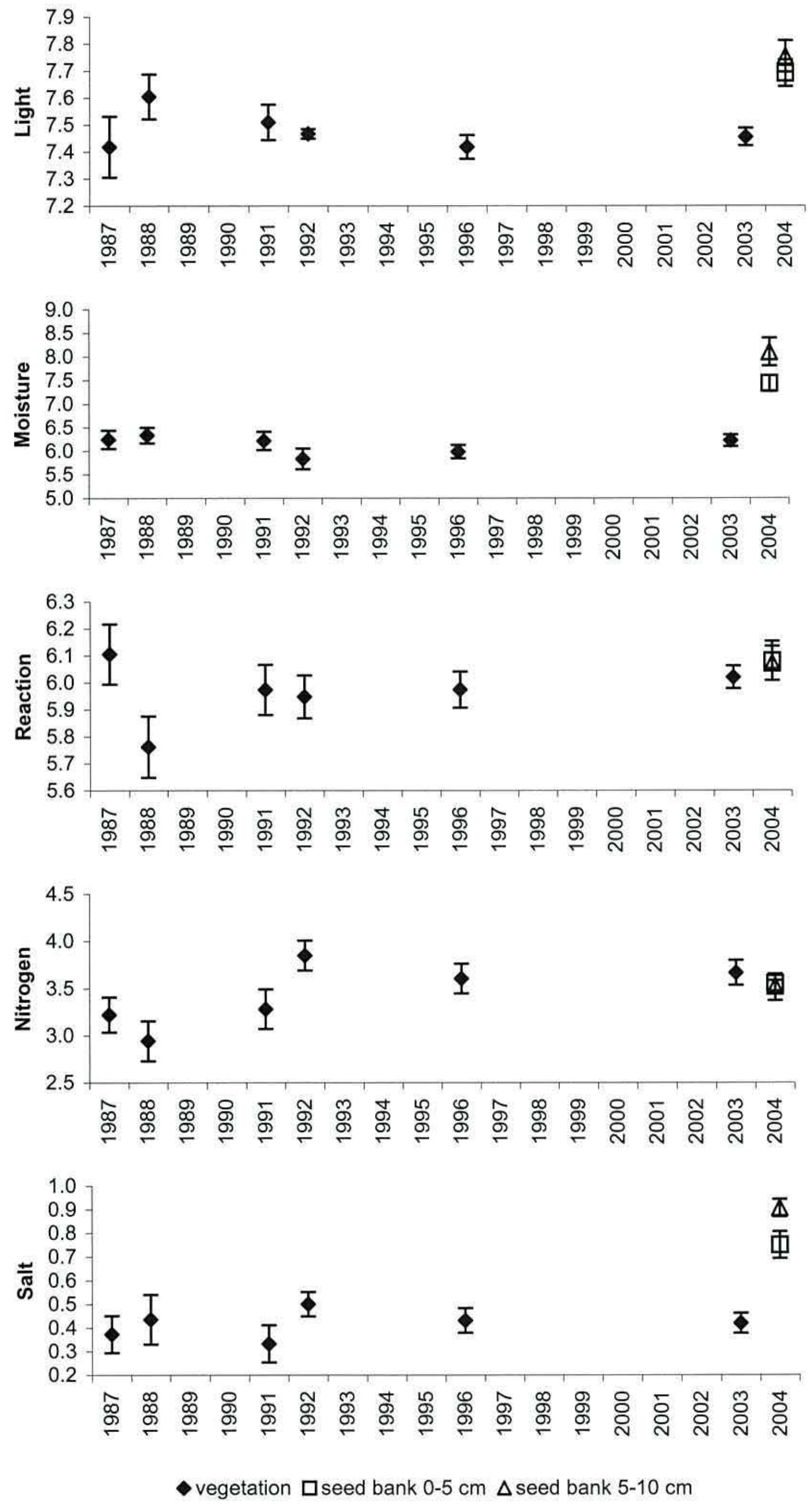


Figure 6.6. Average weighted Ellenberg indicator values for light, moisture, reaction, nitrogen and salt in the established vegetation 1987-2003 (1987-1991: N=5, 1992: N=3, 1996 and 2003: N=8) and the seed bank in 2004 in two depth layers, 0-5 cm and 5-10 cm (N=8). Bars represent standard errors.

Table 6.2. Paired t-tests between weighted Ellenberg indicator values for light, moisture, reaction, nitrogen and salt in the established vegetation between 1987 and 2003 (1987-1991: N=5, 1996 and 2003: N=8) and the seed bank in 2004 in two depth layers, 0-5 cm and 5-10 cm (N=8). Significant p values in bold.

Ellenberg	**0-5/5-10cm**		**year**	**0-5cm**		**5-10cm**	
indicator	**t value**	**p value**		**t value**	**p value**	**t value**	**p value**
Light	1.30	0.234	1987	-2.06	0.108	-1.82	0.142
			1988	-0.72	0.514	-0.76	0.487
			1991	-1.68	0.168	-1.50	0.208
			1996	-3.58	**0.009**	-3.65	**0.008**
			2003	-3.76	**0.007**	-3.71	**0.008**
Moisture	-2.51	**0.041**	1987	-5.08	**0.007**	-5.40	**0.006**
			1988	-7.72	**0.002**	-4.32	**0.012**
			1991	-7.87	**0.001**	-5.01	**0.007**
			1996	-11.55	**<0.001**	-7.30	**<0.001**
			2003	-10.43	**<0.001**	-6.23	**<0.001**
Nitrogen	0.34	0.744	1987	-1.37	0.243	-1.25	0.279
			1988	-2.21	0.092	-1.98	0.119
			1991	-0.94	0.401	-0.88	0.428
			1996	0.28	0.786	0.34	0.743
			2003	0.67	0.526	0.62	0.554
Reaction	0.26	0.804	1987	0.43	0.687	0.69	0.526
			1988	-1.62	0.180	-1.84	0.140
			1991	-0.55	0.613	-0.56	0.607
			1996	-0.90	0.400	-0.93	0.382
			2003	-0.76	0.470	-0.71	0.503
Salt	-2.81	**0.026**	1987	-3.69	**0.021**	-5.33	**0.006**
			1988	-2.39	0.075	-4.13	**0.014**
			1991	-4.40	**0.012**	-5.31	**0.006**
			1996	-3.75	**0.007**	-7.35	**<0.001**
			2003	-4.54	**0.003**	-8.67	**<0.001**

Longevity

All 26 species that were present in the established vegetation but not the seed bank can be classified as transient (Table 6.1); of the 32 species found in both seed bank layers, the following were more abundant in the deeper layer in individual samples and thus long-term persistent: *Centaurium littorale*, *Epilobium brunnescens*, *Glaux maritima*, *Juncus acutiflorus, J. articulatus*, *J. bufonius*, *Persicaria maculosa*, *Poa pratensis*, *Ranunculus flammula*, *Sagina nodosa*, *S. procumbens*, *Triglochin* spp., *Veronica anagallis-aquatica*, *V. chamaedrys* and *Viola riviniana*.

Baskin & Baskin (2001) define persistent seeds as seeds that do not germinate until at least the second germination season. Thus, the species that germinated in this experiment after the period of cold stratification can also be called persistent: *Agrostis stolonifera*, *Anthyllis vulneraria*, *Carex arenaria*, *Carex viridula*, *Cerastium fontanum*, *Dactylorhiza* spp., *Epipactis palustris*, *Euphrasia officinalis* agg., glaucous segde, *Hydrocotyle vulgaris*, *Juncus bulbosus*, *Linum catharticum*, *Lotus corniculatus*, *Parnassia palustris*, *Radiola linoides* and *Salix repens*. Some of these species were only recorded from the surface layer and would have been classed as transient according to the method of classification that looks at the ratio between numbers of seeds in the different depth layers only.

Species emerging from the seed bank that were not recorded above-ground at individual sampling locations in any year of recording nor in close proximity in 2004 include the following species: *Chenopodium rubrum*, *Cirsium palustre*, *Daucus carota*, *Epilobium montanum*, *Leontodon autumnalis*, *Luzula campestris*, *Plantago major*, *Reseda luteola*, *Rumex acetosa* and *Samolus valerandi*. These species could not be classified as long-term persistent using the above methods. Most of them are dispersed by wind (Fitter & Peat 1994). Their seeds could have come from more distant sources, so that their absence from above-ground records since 1987 does not necessarily indicate long-term persistence.

The average longevity index for species only recorded from the vegetation was 0.33, for species present in both vegetation and seed bank 0.41 and for species only found in the seed bank 0.74. The average weighted longevity index for the established vegetation increased slightly but not significantly between 1987 and 2003 (Figure 6.7). It was significantly higher in the seed bank than vegetation for all years, and highest in the deeper soil layer (paired t-test, $t=-4.35$, $p=0.003$) (Figure 6.7).

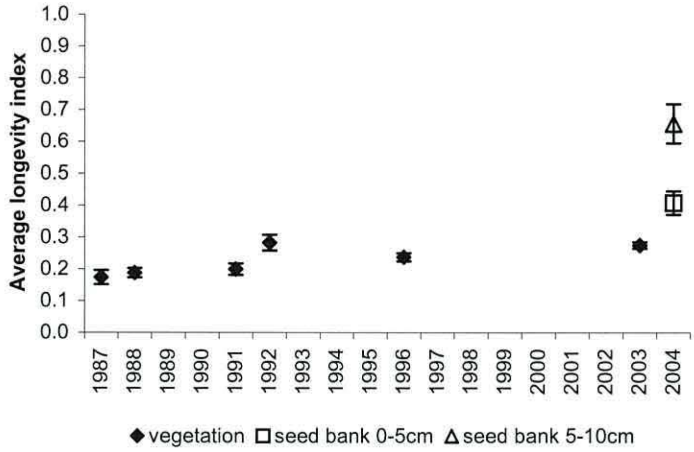


Figure 6.7. Average weighted longevity index of species in the vegetation between 1987 and 2003 and the seed bank in 2004 in two depth layers, 0-5 cm and 5-10 cm. Bars represent standard errors. Results of paired t-tests comparing seed bank and above-ground vegetation: a) 0-5 cm layer: 1987: t=-2.84, p=0.047, N=5; 1988: t=-3.19, p=0.033, N=5; 1991: t=-3.06, p=0.038, N=5; 1996: t=-4.72, p=0.002, N=8; 2003: t=-3.48, p=0.010, N=8; b) 5-10 cm layer: 1987: t=-4.81, p=0.009, N=5; 1988: t=-4.80, p=0.009, N=5; 1991: t=-4.42, p=0.012, N=5; 1996: t=-6.61, p<0.001, N=8; 2003: t=-6.10, p<0.001, N=8. Comparison of the two seed bank layers: t=-4.35, p=0.003, N=8.

Grazing management

There was a total of 49 and 42 species in samples from grazing management 1 and 2 respectively, with grazing management 1 being more species rich in both seed bank layers than grazing management 2 (Table 6.3). Eighteen species grew only from grazing management 1, 11 species only from grazing management 2, and 31 species from both (Table 6.3). Species occurring in one of the grazing treatments only generally had very low numbers of seedlings; exceptions to this were *Veronica anagallis-aquatica* and *Cerastium fontanum*. The first of these was never recorded above-ground, while the latter has been recorded in low abundance from both grazing managements (Table 6.1). In some of the more abundant species, there were large differences in seed numbers between the two grazing treatments, e.g. *Hydrocotyle vulgaris*, *Mentha aquatica*, *Anagallis tenella*, *Agrostis stolonifera*; however, these differences were not significant for any species apart from *Carex arenaria* (Mann-

Whitney test, p=0.021, U=10, N=4) and *Prunella vulgaris* (Mann-Whitney test, p=0.037, U=1, N=4) in the 0-5 cm layer. Ordination of seed bank samples, based on the composition of individual seed trays, confirmed that there was no clear difference in seed bank composition between the two grazing treatments (Figure 6.8). In the above-ground vegetation, samples from the two different grazing managements appeared to be separated along axis 1 (Figure 6.9); however, this separation also applies to ungrazed samples, indicating that the floristic composition was dissimilar even before grazing management was introduced. Most of the quadrats are positioned closer to the seed bank in 2003 than in the earliest year of recording.

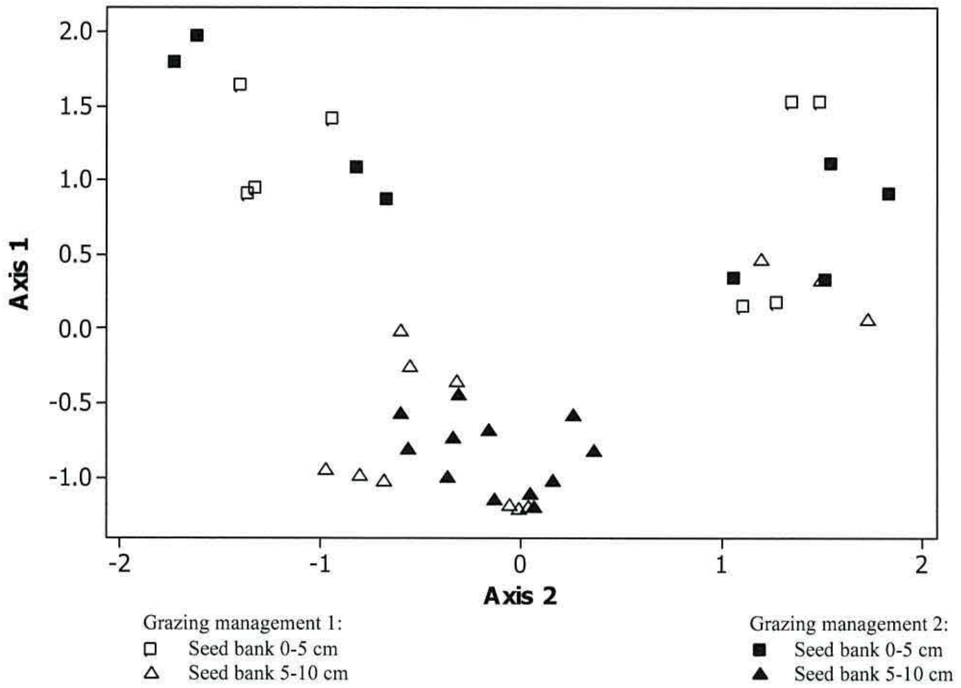


Figure 6.8. Ordination of seed bank samples by Principal Components Analysis (PCA), based on the composition of individual seed trays. Eigenvalues: axis 1=0.4048, axis 2=0.1210.

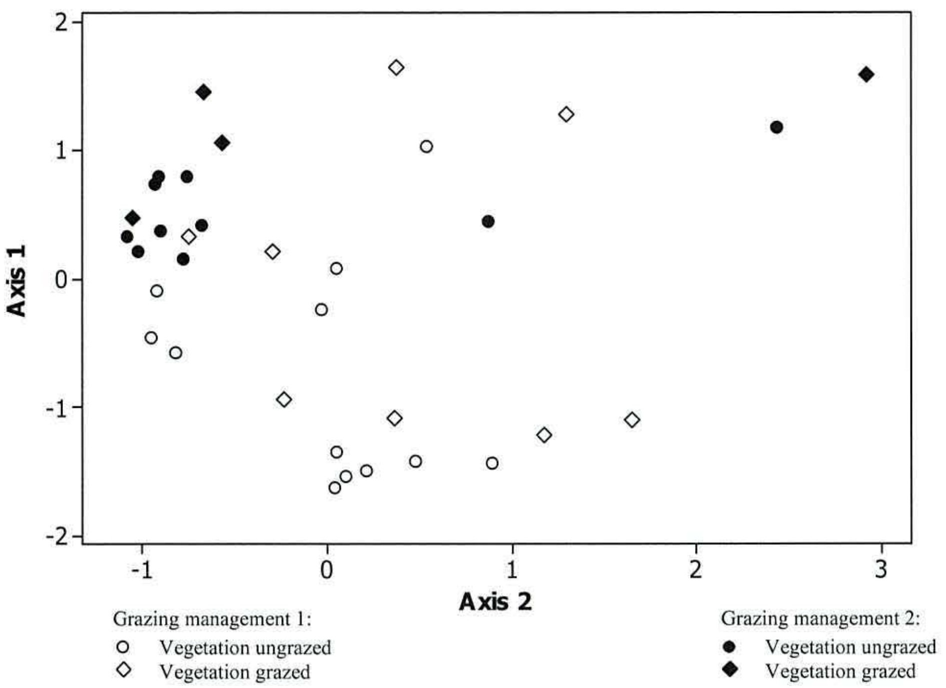


Figure 6.9. Ordination of vegetation samples by Principal Components Analysis (PCA). Eigenvalues: axis 1=0.1841, axis 2=0.1235.

More seedlings emerged from the deeper layer in grazing management 1 samples (28.3 % of all seedlings) than grazing management 2 samples (13.5 %) (Figure 6.10). The contribution of dicotyledonous seeds was greater in grazing treatment 2 (56.7 %) than 1 (46.7 %). In grazing management 1, annuals represented 14.3 % of species and 5.3 % of seedlings; these figures are 19 % and 4.5 % for grazing management 2. There was a difference between the two grazing treatments in the amount of seedlings of annual and biennial species in the two depth layers: in grazing management 1, the percentage of annual and biennial seeds was larger in the surface layer (5.9 % of seedlings in 0-5 cm and 3.6 % in 5-10 cm), whereas this situation was reversed in grazing management 2 (3.9 % in 0-5 cm and 7.8 % in 5-10 cm). Average percentages of seeds of species with long-term persistent seed banks were very similar in both depth layers and grazing treatments.

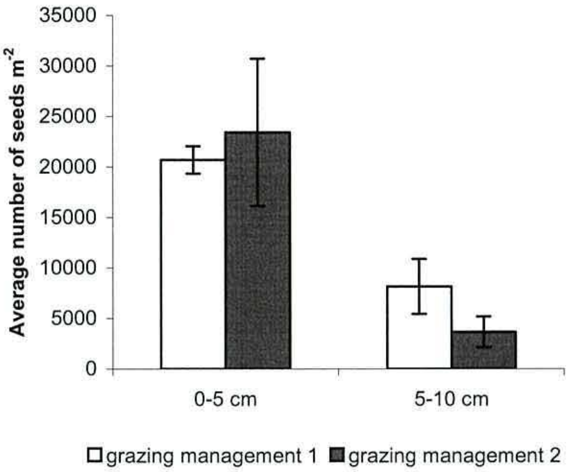


Figure 6.10. Average number of seeds m^{-2} in the seed bank in 0-5 cm and 5-10 cm depth in two grazing treatments. Bars represent standard errors.

Table 6.3. Average number of seeds m^{-2} in 0-5 cm and 5-10 cm depth for both grazing treatments. * and ** = only recorded above-ground from grazing management 1 and 2 respectively (see Table 6.1).

	Grazing management 1		**Grazing management 2**	
	0-5 cm	**5-10 cm**	**0-5 cm**	**5-10 cm**
In both grazing treatments:				
Agrostis stolonifera	2154	318	1358	127
Anagallis tenella	2589	806	4647	127
Carex arenaria	1666	1146	743	127
Carex viridula	350	297	424	127
Centaurium erythraea	42		42	
Centaurium littorale	212	42	255	42
glaucous sedge	424	212	446	42
Holcus lanatus	297	85	226	
Hydrocotyle vulgaris	4488	1443	7151	269
Hypochaeris radicata	42		42	
Juncus acutiflorus	127	42	170	42
Juncus articulatus	4499	3321	5188	2249
Juncus bufonius	1386	368	562	368
Leontodon autumnalis	198		127	
Linum catharticum	85		255	
Lotus corniculatus	127	42	64	
Luzula campestris	42		64	
Mentha aquatica	1443	340	2621	212
Parnassia palustris	42		127	
Poa pratensis	149	127	64	
Potentilla anserina	382	127	340	85
Prunella vulgaris	64		159	
Ranunculus flammula	127	382	520	64
Ranunculus repens	170	85	85	
Rumex acetosa	42		85	
Sagina nodosa	2150	806	722	42
Sagina procumbens		1528		1231
Samolus valerandi	184	127	806	255
Taraxacum sect. *Ruderalia*				
(*T. officinale* Wigg. group)	85		42	
Trifolium repens	85		106	
Viola riviniana	481	297	42	85
In grazing mangement 1 only:				
Anthoxanthum odoratum	42			
Bellis perennis	42			
Cardamine pratensis *	170			
Cerastium fontanum	1125	127		
Chenopodium rubrum	42			
Dactylorhiza incarnata	42			
Epilobium brunnescens		42		
Epilobium montanum *	85			
Epipactis palustris	42			
Euphrasia officinalis agg.	42			
Juncus bulbosus	170			
Persicaria maculosa		42		
Polygala vulgaris	42			
Ranunculus bulbosus *	42			
Salix repens	85			
Trifolium pratense	85			
Veronica anagallis-aquatica	1188	3438		
Veronica chamaedrys	42	42		
In grazing mangement 2 only:				
Agrostis capillaris			42	
Anthyllis vulneraria			42	
Cirsium palustre			42	
Daucus carota			42	
Glaux maritima				42
Plantago major			64	
Radiola linoides			127	
Reseda luteola			42	
Senecio jacobaea			127	
Sonchus arvensis **			85	
Triglochin spp.			170	297
Total number of species	46	26	40	19
Average number of seedlings	20701	8170	23428	3671

Discussion

Composition of the seed bank and relationship with the established vegetation

Species characteristic of dune slack communities represented the majority of seedlings recorded. They include one nationally rare species, *Centaurium littorale*, and several other species of conservation interest that are threatened by eutrophication, drainage of their natural habitat and the increasing rarity of early successional stages of dune slack building: *Anagallis tenella*, *Dactylorhiza incarnata*, *Epipactis palustris*, *Mentha aquatica*, *Parnassia palustris*, *Radiola linoides*, *Ranunculus flammula*, *Sagina nodosa* and *Samolus valerandi* (Preston *et al.* 2002, Grime *et al.* 1988, Grootjans *et al.* 1988). *Radiola linoides* is classified as near threatened in the UK red data list (Cheffings *et al.* 2005).

Seed densities are similar to those recorded by Looney & Gibson (1995) in wet dune slacks in Florida (22594 seeds m^{-2}) and Bakker *et al.* (2005a) who found maximum densities of 50000 seeds m^{-2} in Dutch dune slacks. Bossuyt & Hermy (2004) found a maximum of only 9160 seeds m^{-2} and an average of 2345 seeds m^{-2} in grazed dune slacks in Belgium. This may indicate a greater age of the slacks in the present study as seed density, at least in the upper soil layer, has been found by several authors to increase during the course of succession (Looney & Gibson 1995, Bossuyt & Hermy 2004), although this is in contrast to the results of other authors analysing different habitats, e.g. Donelan & Thompson (1980) and Grandin (2001). The majority of species in this study had densities of less than 500 seeds m^{-2}, which is consistent with the findings of other studies (Thompson *et al.* 1997), and many other authors have found higher seed densities in the surface layer in a variety of habitats, including dune slacks (Bekker *et al.* 1999, Bossuyt & Hermy 2004).

In a separate experiment (see Chapter 7) that ran for only six instead of 12 months, seed densities recorded in 0-5 cm depth were slightly lower (19088 seed m^{-2}) than in this study (22064 seed m^{-2}), suggesting that a longer study period is necessary to achieve more complete germination and a more accurate estimation of seed densities. The nine weeks of cold storage during the experiment proved vital for the stimulation of germination of previously ungerminated seeds and species and is thus to be recommended for future studies.

The relatively low similarity of species composition and relative abundances in the established vegetation and seed bank has been observed in many studies (Thompson 2000). This was due to species in the vegetation being absent from the seed bank (e.g. *Festuca rubra*, *Pyrola rotundifolia*), dominant species in the vegetation contributing only few seeds to the seed bank (e.g. *Salix repens*), and seeds from earlier stages persisting in the soil after those species have disappeared from the vegetation (e.g. *Samolus valerandi*, *Sagina nodosa*).

The high contribution of seeds of dicotyledonous species and *Juncus* spp. and the low contribution of grass seeds to the seed bank are in accordance with other studies in a variety of grasslands and follow the general observation that grasses tend to be underrepresented in the seed bank, whereas dicotyledonous herbs and grasslike plants are the major contributors (Rice 1989). This was also found by Bossuyt & Hermy (2004) in Belgian dune slacks. *Agrostis stolonifera* was only present in low abundance above-ground, but was the only grass that was a major contributor to the seed bank, which has also been observed in other studies (Roberts 1981). Seeds of *Veronica anagallis-aquatica* and *Chenopodium rubrum* were only found in samples from one location. The latter is known to survive gut passage of various animals (Williams 1969, Grime 2001), which explains the single occurrence of seeds of this species that is not known to grow anywhere on site.

An exceptional result of this study is the germination of two species of orchid. As Thompson *et al.* (1997) point out, the family Orchidaceae has so far not been recorded in the seed bank by any source. Thompson *et al.* (1997) wonder whether is due to a genuine failure of the family to build up seed banks or the difficulty to provide the right germination conditions in seed bank studies. The germination of two orchid seedlings in this study points to the latter, indicating that orchids form part of the seed bank.

Seed longevity

The higher average longevity index of species in the seed bank shows that the seed bank accumulates species with persistent seeds, even if they have disappeared from the established vegetation. In several species with a low longevity index (LI) according to the database in Thompson *et al.* (1997), suggesting a transient seed bank, this study found indications for a long-term persistence of the seeds, e.g. *Viola riviniana* with a longevity index of 0 (fully transient), which was found in higher abundance in the deeper soil layer, or *Anthyllis vulneraria* (LI=0.11) and *Parnassia palustris* (LI=0.14) which germinated after a second period of cold stratification, indicating that some of their seeds only germinate after two (or more) winters in the field. This shows that, as more seed bank studies are conducted and more data gathered, classifications of longevity of some species may become more accurate, especially those with long-term persistent seeds (Bekker *et al.* 1998). Species with no or few previous records in the database of Thompson *et al.* (1997) that can be classified as long-term persistent include species of conservation interest, e.g. *Centaurium littorale* and *Radiola linoides*, as well as the invasive alien species *Epilobium brunnescens*. Modelling the effects of disturbance, Schippers *et al.* (2001) concluded that dormancy is a better mechanism for plants to survive disturbance than dispersal. In a habitat such as sand dunes that is characterised by disturbance, e.g. through erosion, accretion of sand, grazing, scraping and burrowing of rabbits, this should lead to the accumulation of a large seed bank as has been shown in the present study.

Succession

During succession, dune slacks become drier (Ranwell 1955, Boorman *et al.* 1997) and there is an increase in light limitation (Olff *et al.* 1993, Berendse *et al.* 1998). Generally, early successional species have a short adult life span and produce numerous small long-term persistent seeds (Huston & Smith 1987) that require light to germinate and depend on the creation of gaps more than larger-seeded species (Grime *et al.* 1981, Gross & Werner 1982, Thompson & Grime 1983, Gross 1984, Grime 2001). Later successional species are longer lived and more tolerant of shading (Salisbury 1974, Silvertown 1981, Hodkinson *et al.* 1998, Milberg *et al.* 2000), produce fewer (Huston & Smith 1987), larger (Salisbury 1974, Leishman & Westoby 1994, Leishman *et al.* 2000) and shorter-lived seeds (Rees 1993, 1994, Grootjans *et al.* 2004). Mazer (1989) showed that perennials of wet dune habitats produced significantly larger seeds in closed swards than earlier successional stages. Annuals and biennials, which are known to build up persistent seed banks more often than perennials (Thompson *et al.* 1998), are most abundant in young successional stages and increasingly rare in older slacks because of a lack of open sites where they can establish (Ranwell 1960a, Boorman *et al.* 1997, Petersen 2000).

In this study, there were several indications that the seed bank reflects earlier successional stages rather than following above-ground succession as shown by Bossuyt & Hermy (2004) for dune slacks in Belgium: the higher number of annual and biennial species in the seed bank; the dominance of small-seeded species with a greater longevity index in the seed bank; the higher seed bank Ellenberg indicator values for light, moisture and salt; the greater number of seeds of early successional species in the deeper soil layer. All this points to the seed bank representing earlier successional stages than the present above-ground vegetation, with the short-lived, small-seeded and light demanding species that cannot compete in later successional vegetation but produce long-term persistent seeds surviving in the seed bank. The greater contribution of small seeded species to the seed bank could also be due to the higher longevity of small seeds (Bekker *et al.* 1998) and the fact that smaller seeds are more easily incorporated into the soil (Thompson *et al.* 1993) and escape predation more than larger seeds (Thompson 1987). However, during the course of succession, larger seeds increasingly become part of the seed bank (Bossuyt & Hermy 2004). The higher Ellenberg values for moisture may reflect earlier stages when the slacks were wetter. Young slacks can be more directly influenced by salt water and salt spray, so that salt indicator values are higher in pioneer stages of slack vegetation (Petersen 2000). A higher indicator value for salt in the seed bank was also found by Grandin (2001), who concluded that salt-tolerant species are preserved in the seed bank over long periods of time. The higher indicator value for light indicates that early successional, light-demanding species are more abundant in the seed bank than the vegetation. In contrast to this, Bossuyt & Hermy (2004) found a lower indicator value for light in the seed bank and concluded that later successional species were the major contributor to the seed bank in their study area. Seeds of early successional species were recorded from the seed bank, e.g. *Anagallis tenella*, *Samolus valerandi* and *Sagina nodosa*, which is in accordance with the general trend that pioneer species are often well represented in the seed bank because they ensure survival through their large production of long-term persistent seeds (Baker 1989). This corresponds to the findings of Bekker *et al.* (1999) who also documented the long-term persistence of some dune slack pioneer species. As in the study by Grandin & Rydin (1998), the lower similarity of the vegetation to the deeper than the surface seed bank layer is due to a higher proportion of early successional, long-lived and small-seeded species at greater depths. However, contrary to expectation, annual species were more concentrated in the surface soil in this study. The fact that both seed bank layers harbour large numbers of seeds characteristic of younger successional stages indicates that the pioneer vegetation has not disappeared all that long ago, and some of these species, e.g. *Juncus articulatus*, are still represented in later successional stages and can continue to contribute to the seed bank.

Management

At the study site, concerns that the vegetation became too rank and early successional stages of slack vegetation increasingly rare, led to the introduction of livestock grazing in 1987 in an attempt to counteract the loss of diversity through grass encroachment, and to maintain a range of successional phases. Disturbance and the creation of canopy gaps are necessary to facilitate germination from seed for many short-lived and competitively inferior species (e.g. Milberg 1993), and grazing animals can create the germination conditions needed by these species by trampling, poaching and opening up the sward (Bullock *et al.* 1995, Bakker & Olff 2003). As this study has shown, seeds of several target species build up persistent soil seed banks, and the seed bank might be expected to rejuvenate the sward after disturbance. On some East Friesian islands, management measures such as mowing and sod cutting have resulted in the successful restoration and conservation of threatened slack plants and plant communities through the reactivation of the seed bank (Petersen 2004), highlighting the importance of management and the potential of the seed bank for restoration of early successional communities. In contrast to this, when Bakker *et al.* (2005a) investigated the contribution of the seed bank of a dune slack to the establishment of species after the creation of gaps suitable for germination, they found that although the seed bank of their study area contained target species, establishment from the seed bank was rare and dispersal from nearby populations more important. This means that for conservation management, it is important to ensure the continued presence of target communities as seed sources and that the seed bank alone cannot always be relied upon for the restoration of earlier successional vegetation. At this study site, pioneer slacks are still present if very rare, so that seed sources are still available; however, management needs to ensure that gaps in which these species can germinate are created frequently enough to ensure long-term survival. Many species do not disperse over great distances (Verkaar *et al.* 1983), including species of sand dunes (Watkinson 1978b, Westelaken & Maun 1985, Owen *et al.* 2001), but grazing animals can help disperse seeds to potential germination sites via endo- and epizoochory. The role of grazing livestock and rabbits for seed dispersal has been analysed by e.g. Malo &

Suárez (1995, 1996), Fischer *et al.* (1996) and Pakeman *et al.* (2002). The importance of large herbivores for epi- and endozoochorous seed dispersal on sand dunes has recently been documented (Cosyns 2004, Cosyns & Hoffmann 2005, Cosyns *et al.* 2005a, b, Couvreur *et al.* 2005), showing that grazing animals can connect spatially separate habitat patches and that less common and rare species represent an important part of the viable seed content of horse dung.

No differences were found in the floristic composition of the seed bank sampled from the two grazing treatments in both depth layers. Species with persistent seed banks predominate more on grazed sites because they depend on the creation of vegetation gaps (Gibson 1996, Sternberg *et al.* 2000, Dupré & Diekmann 2001), however no difference in the number of long-term persistent seeds was found between the two grazing treatments in this experiment. Summer pony grazed swards can be more diverse than cattle grazed swards under light or moderate grazing intensities (Gibson 1996) because ponies consume less dicotyledonous herbs than cattle (Lamoot *et al.* 2005), although these differences are not always significant (Oates & Bullock 1997). The percentage of dicotyledonous herbs was higher in this study in the seed bank of pony grazed swards, which might be a reflection of their avoidance of flowering material (Gibson 1996), allowing more plants to set seed. Some authors, e.g. Bakker *et al.* (1996b), found that it takes a much longer time than in this study for grazing management to have a significant impact on seed bank composition. Differences in germination success after gut passage may lead to differences in the seed bank of areas grazed by different species of livestock over a longer period of time. Cosyns *et al.* (2005b) investigated germination success of a variety of sand dune species after gut passage of five species of herbivore and found significant differences between both plant and animal species, which they conclude might be due to complex interactions between animal behaviour, e.g. chewing, rumination and gut retention time, and seed characteristics, e.g. seed shape and mass. Effects of seed passage through herbivore guts are reviewed by Traveset (1998).

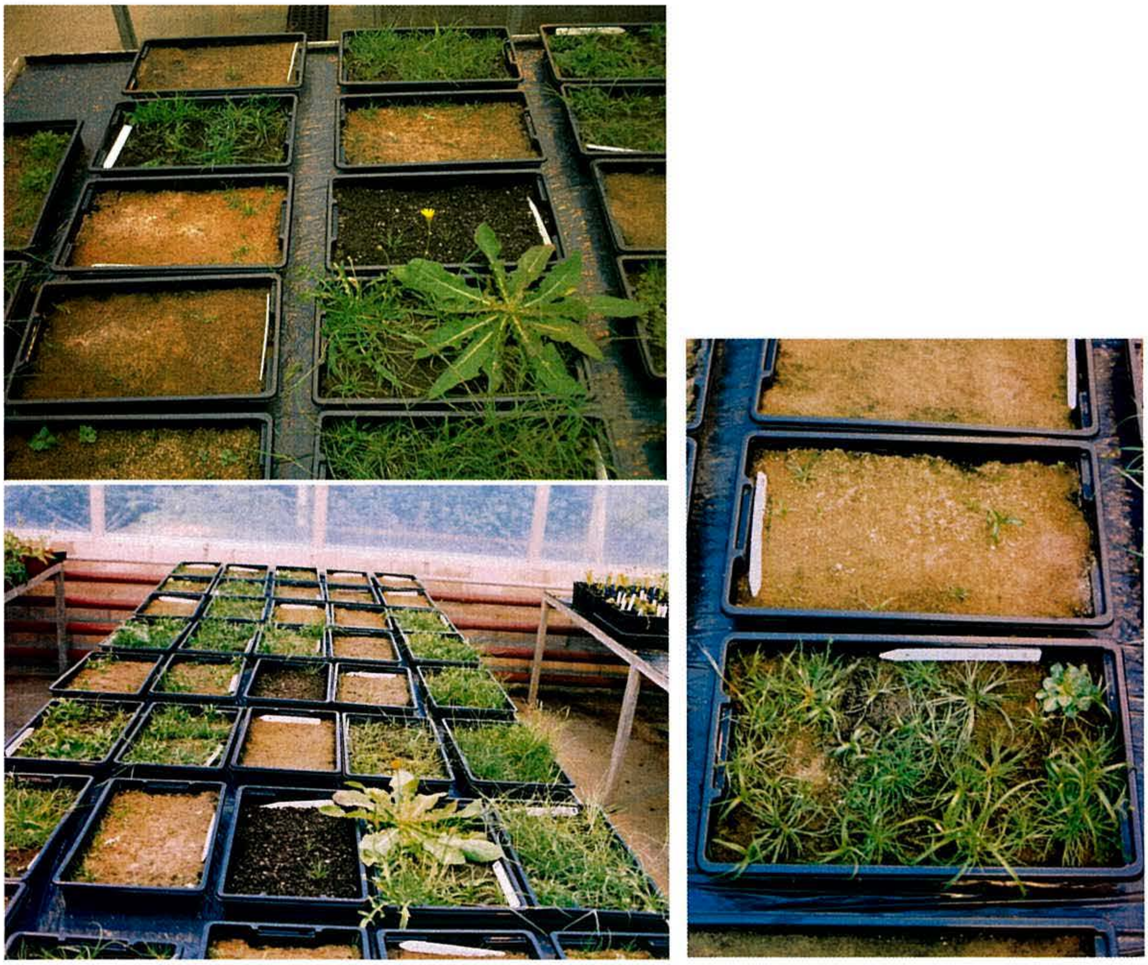
Another possible reason for the observed increase in vegetation cover and loss of early successional vegetation at Newborough Warren is nitrogen pollution (Rhind *et al.* 2001), as nutrient enrichment has been found to contribute to the establishment of later successional vegetation (Adema *et al.* 2002). The impact of increased nitrogen availability on the seed bank of dune slacks will be investigated in a separate experiment (see Chapter 7).

Conclusion

This study is a contribution towards a better understanding of seed banks of dune slacks. It has been shown that the slacks under investigation have large and diverse seed banks, including species of conservation interest, that early successional species build up persistent seed banks ensuring long-term survival, and that the seed bank has the potential to regenerate earlier successional stages after disturbance. Seedlings of important dune slack species were recorded, including one nationally rare and two orchid species, increasing the scarce information that is so far available about these species (Grootjans *et al.* 2004, Bossuyt *et al.* 2005). The composition of the seed bank did not differ between two areas with different grazing management histories. More research into the effects of different grazing animals on seed bank dynamics is needed to help future management decisions, especially considering the growing importance of grazing as a management tool for conservation and restoration (Wallis de Vries *et al.* 1998, Hoffmann 2002).

CHAPTER 7

The effects of increased nutrient supply on seed bank dynamics



Experimental set-up in the greenhouse. Dark brown samples are from 0-5 cm depth, sand coloured samples from 5-10 cm depth.

Introduction

Nutrient poor habitats can be very species-rich and of high nature conservation value; however, they are under threat from the deposition of excess nutrients through polluted precipitation and dry deposition (Wilson *et al.* 1995, Bobbink *et al.* 1998, NEGTAP 2001). In most terrestrial habitats, productivity is limited by nitrogen (Vitousek & Howarth 1991, Bobbink & Lamers 2002). Over the last half century, the atmospheric deposition of nitrogen has strongly increased in many oligotrophic and mesotrophic habitats (Bobbink & Lamers 2002), where the effects of nutrient enrichment are most pronounced because they depend on low soil fertility, e.g. species-rich calcareous grasslands (Willems *et al.* 1993). Impacts of increased nitrogen loads have been investigated and modelled in many semi-natural habitats, including lowland heathland (Power *et al.* 1998a, Britton *et al.* 2001), calcareous grassland (Wilson *et al.* 1995, Lee & Caporn 1998), acidic grassland (Lee & Caporn 1998, Stevens *et al.* 2004), heathland (Roem & Berendse 2000), meadows (Berendse *et al.* 1992), dune grassland (Boorman & Fuller 1982, ten Harkel *et al.* 1998, Jones *et al.* 2004a), and peat moor (Mountford *et al.* 1993). A variety of effects of increased atmospheric nitrogen deposition has been studied, such as on species composition and diversity (Mountford *et al.* 1993, Tilman 1987, 1993, Bobbink *et al.* 1998, Green & Galatowitsch 2002, Stevens *et al.* 2004), stress sensitivity (Power *et al.* 1998b), biomass and litter production (Tilman 1987, 1993, Power *et al.* 1998a), management and nitrogen fertilisation interactions (Jacquemyn *et al.* 2003), plant growth and development (de Graaf *et al.* 1998), soil acidification (Roem & Berendse 2000) and nitrogen mineralization processes in the soil (Lee & Caporn 1998). Overall, these experiments suggest that added nitrogen can result in changes in species composition, the competitive exclusion of species characteristic of nutrient-poor conditions by nitrogen-loving species, changes in soil processes and plant growth, direct toxicity and greater susceptibility of plants to stress and disturbance, e.g. pathogens, frost, drought and herbivory (Bobbink *et al.* 1998, Bobbink & Lamers 2002).

Coastal habitats are amongst those threatened by eutrophication (van der Maarel & van der Maarel-Versluys 1996). Dune slacks are low-lying, flat areas or hollows that divide one dune ridge from another, and represent one of the most species-rich and diverse semi-natural habitats in Europe. Therefore, they are of high conservation value, but they are also one of the most endangered coastal habitats (Pott *et al.* 1999, Petersen 2000, Grootjans *et al.* 2002). Nutrient availability is low (Schat 1984) and plant growth often limited by nitrogen (Koerselman & Meuleman 1996, Verhoeven *et al.* 1996, Lammerts & Grootjans 1997, Sival & Strijkstra-Kalk 1999, Lammerts *et al.* 1999). Eutrophication through atmospheric deposition of nitrogen is one major cause of the decline of these oligotrophic habitats and their associated species (Koerselman 1992), especially basiphilous species of pioneer stages (Lammerts & Grootjans 1997). In slacks with decreasing groundwater levels caused by human activities such as drainage, water catchment or the afforestation of dunes, enhanced soil aeration and increased rates of mineralization contribute to eutrophication (van Dijk 1989, Koerselman 1992). Changes in the vegetation of slacks due to eutrophication have been described by e.g. van der Meulen (1982), van Dijk (1985), van Dijk *et al.* (1985), van Dijk & de Groot (1987), Meltzer & van Dijk (1986) and Lammerts & Grootjans (1997).

Despite the immense interest in the changes of plant communities caused by increased atmospheric nitrogen deposition and eutrophication, little research has focused on their effects on seed bank dynamics. The seed bank is the population of viable ungerminated seeds buried in the soil, representing an invisible part of a plant population which can survive adverse conditions and times of little or no recruitment (Bullock *et al.* 2002) and is able to regenerate and secure the survival of a plant community after disturbance (Baskin & Baskin 2001, Jentsch *et al.* 2002). The germination of seeds is controlled both by internal and external factors so that it occurs at a time and place favourable to the survival of the developing seedling. Dormancy can be caused by some characteristic of the seed itself that prevents it from germinating and may be broken by metabolic changes in the seed, whereas environmental factors, such as light quality and quantity, temperature and chemical conditions, e.g. water and oxygen availability, exert external control over germination and dormancy (Baskin & Baskin 2001).

Nitrates and nitrites are the most important inorganic ions exerting a significant influence on seed dormancy and germination (Baskin & Baskin 2001). They can increase germination rates in a variety of species, e.g. Steinbauer & Grigsby (1957), Sexsmith & Pittman (1963), Williams & Harper (1965), Dotzenko *et al.* (1969), Hendricks & Taylorson (1974), Cohn *et al.* (1983), Williams (1983a, b), Pons (1989), Gul & Weber (1998), and can break dormancy either on their own or in combination with other factors, e.g. changing temperatures and light levels (Goudey *et al.* 1987, Singh & Amritphale 1992) or growth regulators such as gibberellins (Bewley & Black 1994). Peak rates of germination occur at different nitrate concentrations in different species; however, high concentrations usually inhibit germination (Goudey *et al.* 1987, Mandák & Pyšek 2001), and some species may respond to the addition of nitrates while others do not (Hendricks & Taylorson 1974, Fawcett & Slife 1978). Previous research has focused mainly on the effect of the addition of nitrogenous compounds on the dormancy and germination of individual species. A limited number of studies have looked at the effect of nutrient addition on whole seed banks, and there is a lack of information on the effects of nutrient availability on seed germination (Pietikäinen *et al.* 2005). For example, Gerritsen & Greening (1989) showed that nitrogen and phosphorus additions increased total germination from marsh seed banks, but the effect differed between species, while Catovsky & Bazzaz (2002) found no response of tree seed banks. Lepš (1999) recorded a decline in seedling recruitment in a wet meadow after fertilisation. In grasslands that are limited by nitrogen, several authors found a decrease in seed germination with increased nitrogen supply (Tilman 1997, Akinola *et al.* 1998, Foster & Gross 1998).

In order to be able to protect oligotrophic habitats such as dune slacks and the rare plant species they contain, it is important to understand their ecology, including their seed bank dynamics and how they might be affected by management and environmental factors such as increased nitrogen deposition and ensuing eutrophication. A knowledge of the life cycle of the dominant and rare species, their seed bank dynamics and the impact of changes in soil nutrient status on seed germination and seedling establishment, can help understanding of natural vegetation changes and with predictions of the success or failure of management and conservation measures (van der Valk & Verhoeven 1988, van der Valk & Pederson 1989, Thompson *et al.* 1993, Berendse 1999, Jentsch 2001). In this study, the effects of increased nutrient availability on the seed bank of a dune slack were investigated with the aim of answering the following questions: 1) Does nutrient addition increase total numbers of seedlings germinating? 2) Do competitive nutrient-loving species germinate more frequently in nutrient-enriched conditions than species typical of this oligotrophic habitat? If this second situation was found to be true, then this might lead to changes in vegetation structure and composition. 3) Are there any differences in the seed banks of two sampling areas within the same dune slack system?

Methods

Study site

This study was conducted at Newborough Warren on the south-west coast of the Isle of Anglesey, North Wales, UK, between the Cefni estuary and the western end of the Menai Strait (Grid reference SH 400640). Comprising about 1300 ha of sandy deposits, it is one of the major calcareous and most biologically diverse sand dune systems on the west coast of Britain (Rhind *et al.* 2001) despite the afforestation of about 720 ha with conifers in the 1940s and 1950s. The dune system consists of foredunes and ridges of compound parabolic dunes roughly parallel to the shoreline which are separated by extensive interdune slacks. The climate is relatively equable without marked extremes of temperature or rainfall (Buchan 1990) and has an average mean annual temperature of 12.9 °C (Anderson 1994). The average annual rainfall is 843 mm, with April to June being the driest months and October to January the wettest (Anderson 1994).

Newborough Warren comprises the full succession of habitats from strandline to shingle, mobile dunes, wet and dry slacks to dune grassland and scrub and contains many rare and protected species. Its outstanding conservation value is recognised in its designation as National Nature Reserve (NNR), Site of Scientific Interest (SSSI) and Special Area of Conservation (SAC) under the EC Habitats and Species Directive 1992. This is because of its high diversity of habitats of European importance, including shifting dunes, dune grassland and humid dune slacks, for which Newborough Warren is considered one of the best areas in Britain.

However, Newborough Warren today is overstabilised and has been characterised by greater stability and succession towards more mature vegetation since the early 1950s (Dargie 1993). While mobile dunes and young slacks with open vegetation amounted to about 75 % of the total dune system in the 1950s (Ranwell 1960a), there are hardly any embryonic slacks today and only about 6 % of the site could be regarded as mobile and open in 1991 (Rhind *et al.* 2001). At present, mature slacks are amongst the dominating vegetation types at Newborough Warren (Rhind *et al.* 2001) while early successional slacks are declining and mature and dry communities increasing at the expense of the wetter communities (Sandison & Hellawell 2000). One factor implicated in the increase of vegetation cover and development towards more mature vegetation is increased atmospheric deposition of nitrogen (Rhind *et al.* 2001).

Livestock grazing was introduced on site in 1987 as a management tool to counteract the loss of diversity through the over-dominance of coarse grasses and scrub and to maintain a range of successional phases. Up to 2001, different livestock (cattle, sheep and ponies) were used on different parts of the dunes mainly during the winter; since then, about three quarters of the dunes have been grazed all year by ponies at a density of one pony to every 3-4 ha. Additionally, rabbits (*Oryctolagus cuniculus*) are widespread and abundant throughout the site.

The slacks under investigation in this study are characterised by closed vegetation with a high abundance of *Salix repens*, a diverse assemblage of vascular plant species and extensive bryophyte cover. The sampling area is located in the central dune slack and shows a small-scale mosaic of different slack communities, namely the National Vegetation Classification (NVC) communities SD14 (*Salix repens – Campylium stellatum* dune slack), SD15 (*Salix repens – Calliergon cuspidatum* dune slack), SD16 (*Salix repens – Holcus lanatus* dune slack) and SD17 (*Potentilla anserina – Carex nigra* dune slack) (Rodwell 2000). Nomenclature for higher plants follows Stace (1991) and for lower plants Smith (1990, 2004).

Seed bank sampling

Soil samples were collected in March 2004 before spring germination and seed set but after natural winter stratification. This was because the seeds of many species germinate in larger numbers after stratification (e.g. Raynal & Bazzaz 1973, Leck & Graveline 1979, Grime *et al.* 1981, Baskin & Baskin 1988, Gross 1990, Schütz & Rave 1999). Twelve replicate soil cores (5 cm diameter, 5 cm depth) were taken at eight sampling stations. The total area and volume sampled at each point was 235.6 cm^2 and 1178.1 cm^3 respectively. Four of the sampling stations were located in an area grazed by cattle from 1991 to 2000 and by ponies thereafter (sampling area 1); the other four were situated in a part of the dunes grazed by ponies since 1996 (sampling area 2). Information on the botanical composition of permanent vegetation monitoring quadrats adjacent to the sampling locations was available from 1987, 1988, 1991 and 1996 for quadrats within sampling area 1 and these same years or 1992 and 1996 for quadrats within sampling area 2, provided by the Countryside Council for Wales (CCW). As part of this study, all eight quadrats were assessed again in June 2003 by estimating cover-abundance for every plant species using the Domin scale, following the methods used for previous data collection (McPhail 1987, Evans 1991).

The soil cores were placed in polythene bags to avoid contamination until further processing (Bullock 1996) and stored in the cold (4 °C) until the beginning of the experiment in September 2004. All four samples of each sampling area were pooled, large roots and stones removed and the soil spread in a thin layer (0.5 cm) over a 4 cm layer of sterilized plant compost (John Innes No 1). For each sampling area, there were eight unfertilized trays and eight nitrogen addition trays. The trays were arranged randomly on a bench in two blocks and covered with clear plastic hoods. Control trays recorded contamination by wind-borne seeds and seeds contained in the sterilised subsoil.

Seed bank composition, seed density and the effects of added nitrogen were determined using the seedling emergence method (Roberts 1981, Thompson *et al.* 1997). Germination was carried out under glasshouse conditions with a 12 h photoperiod, regular watering and night and day temperatures of 18 °C and 20 °C respectively. Nitrogen was applied weekly as ammonium nitrate in 150 ml water at a dose of 15 kg ha^{-1} $year^{-1}$ from September 2004 to February 2005. Unfertilised control trays received equal amounts of water as treatments. Because the soil was sampled from a wet dune slack, the trays were kept very moist because most species of this habitat are adapted to wet conditions and could be expected to germinate better from wet than dry soil (ter Heerdt *et al.* 1999). The occurrence of species such as *Ranunculus flammula* in this study shows that germination conditions for wet-loving species were met (ter Heerdt *et al.* 1999). All emerging seedlings were counted and removed after identification to avoid competition. Unidentified seedlings were transplanted into separate pots and grown until identification was possible. When germination appeared to have stopped, the samples were disturbed repeatedly to promote germination of seeds deeper in the sample by exposing them to more suitable light and temperature regimes (Bullock 1996, Thompson *et al.* 1997). No assessment was made of the numbers of viable seeds remaining in the soil at the end of the experiment in February 2005. The terms 'seed' and 'seed bank' are used here in a broad sense including true seeds and fruits (Roberts 1981).

Data analysis

The glaucous sedges *Carex flacca*, *C. nigra* and *C. panicea* were all present in the seed bank, but were pooled into a species group called 'glaucous sedge' because of the difficulties attached to identifying them at the seedling stage. Seedlings of common greenhouse weeds that grew from control trays, e.g. *Salix cinerea* and *Juncus effusus*, were excluded from the analysis.

The effects of nitrogen addition, grazing treatment and their interactions were tested using General Linear Model analysis after log(n+1)-transformation of species counts and checking for normality using the Kolmogorov-Smirnov test. Only species with ten or more seedlings were included in this analysis. Observations of large standardised residuals were checked against the data; because all of those observations represented real data points it was decided to leave them in. The regular occurrence of large standardised residuals in this experiment is probably due to the clumped distribution of seeds in the soil.

The floristic similarity between the seed bank in controls and nitrogen addition samples was analysed by Detrended Correspondence Analysis (DCA) with a log(n+1)-transformation using the package Canoco for Windows 4.5 (ter Braak 1987). This was also used to detect differences in the floristic composition of the seed bank in relation to the two different sampling areas. Differences in seed densities between unfertilised controls and nitrogen addition treatments were analysed by t-test for sampling area 1 and Mann-Whitney test for sampling area 2 because of the non-normality of the data.

Results

Composition of the seed bank

In total, 4202 seedlings of 45 species were recorded. The two most abundant species, *Hydrocotyle vulgaris* and *Juncus articulatus*, represented 29.4 % and 25 % of all seedlings respectively. In 21 species, the total number of seedlings recorded was less than ten. These species were excluded from statistical analyses as they were judged too rare to enable sensible differentiation between treatments.

Overall seed densities were 19088 seed m^{-2} in controls, and 25497 seeds m^{-2} in nitrogen addition samples. Densities of individual species reached a maximum of 6334 seeds m^{-2} in controls and 7003 seeds m^{-2} in nitrogen addition samples. Appendix 3.1 and 3.2 present information on species and seedling numbers based on individual seed trays.

Differences between the two sampling areas

There was a total of 36 and 37 species in samples from sampling area 1 and 2 respectively (Table 7.1). Eight species grew exclusively from sampling area 1 samples and nine from sampling area 2 samples. Species occurring in one of these areas only generally had very low numbers of seedlings; exceptions to this were *Cerastium fontanum*, *Centaurium erythraea* and *Plantago major*. The last two of these were never recorded from the permanent quadrats above-ground, while the first has been recorded in low abundance from both sampling areas in the past (Appendix 3.3). Figure 7.1 illustrates the different abundances of species in samples from the two areas. Total seed densities were very similar in the two sampling areas.

The seedlings of twelve species occurred in significantly different numbers in samples from area 1 and 2, six each in higher numbers in sampling area 1 and 2 samples respectively (Tables 7.1 and 7.2). In the ordination graph there is a clear split between samples taken from the two sampling areas along the first ordination axis (Figure 7.1), suggesting a distinct difference in the floristic composition of the seed bank of these areas. Ordination of the above-ground vegetation also indicates differences in the composition of samples from the two sampling areas (Figure 7.2).

Table 7.1. Number of seeds m^{-2} recorded in two different sampling areas. * and ** = only recorded above-ground from sampling area 1 and 2 respectively.

In both sampling areas	**Sampling area 1**	**Sampling area 2**	**In sampling area 1 only**	**Sampling area 1**	**Sampling area 2**
Agrostis stolonifera	2387	902	*Agrostis capillaris*	32	
Anagallis tenella	361	1273	*Anagallis arvensis*	11	
Anthoxanthum odoratum	11	21	*Cardamine pratensis* *	11	
Carex arenaria	658	446	*Cerastium fontanum*	477	
Carex viridula	615	233	*Hypochaeris radicata*	11	
Centaurium littorale	170	361	*Trifolium pratense*	11	
Epilobium montanum	85	149	*Veronica anagallis-aquatica*	21	
glaucous sedge	1199	891	*Veronica chamaedrys*	11	
Holcus lanatus	95	64			
Hydrocotyle vulgaris	6080	7035			
Juncus acutiflorus	117	74		**Sampling**	**Sampling**
Juncus articulatus	5846	5263	**In sampling area 2 only**	**area 1**	**area 2**
Juncus bufonius	1072	1411			
Leontodon autumnalis	74	53	*Bellis perennis* **		21
Lotus corniculatus	42	32	*Centaurium erythraea*		74
Luzula campestris	11	11	*Isolepis setacea*		11
Mentha aquatica	1125	2440	*Leontodon saxatilis*		11
Parnassia palustris	149	382	*Linum catharthicum*		42
Poa pratensis	32	21	*Plantago major*		64
Potentilla anserina	106	74	*Sonchus arvensis* **		32
Prunella vulgaris	53	106	*Trifolium repens*		11
Ranunculus flammula	233	552	*Triglochin* spp.		11
Ranunculus repens	138	11			
Sagina nodosa	531	74			
Samolus valerandi	106	159			
Senecio jacobaea	11	42			
Taraxacum sect. *Ruderalia*	106	42			
(*T. officinale* Wigg. group)			**Total number of seeds m^{-2}**	22176	22409
Viola riviniana	180	11	**Total number of species**	36	37

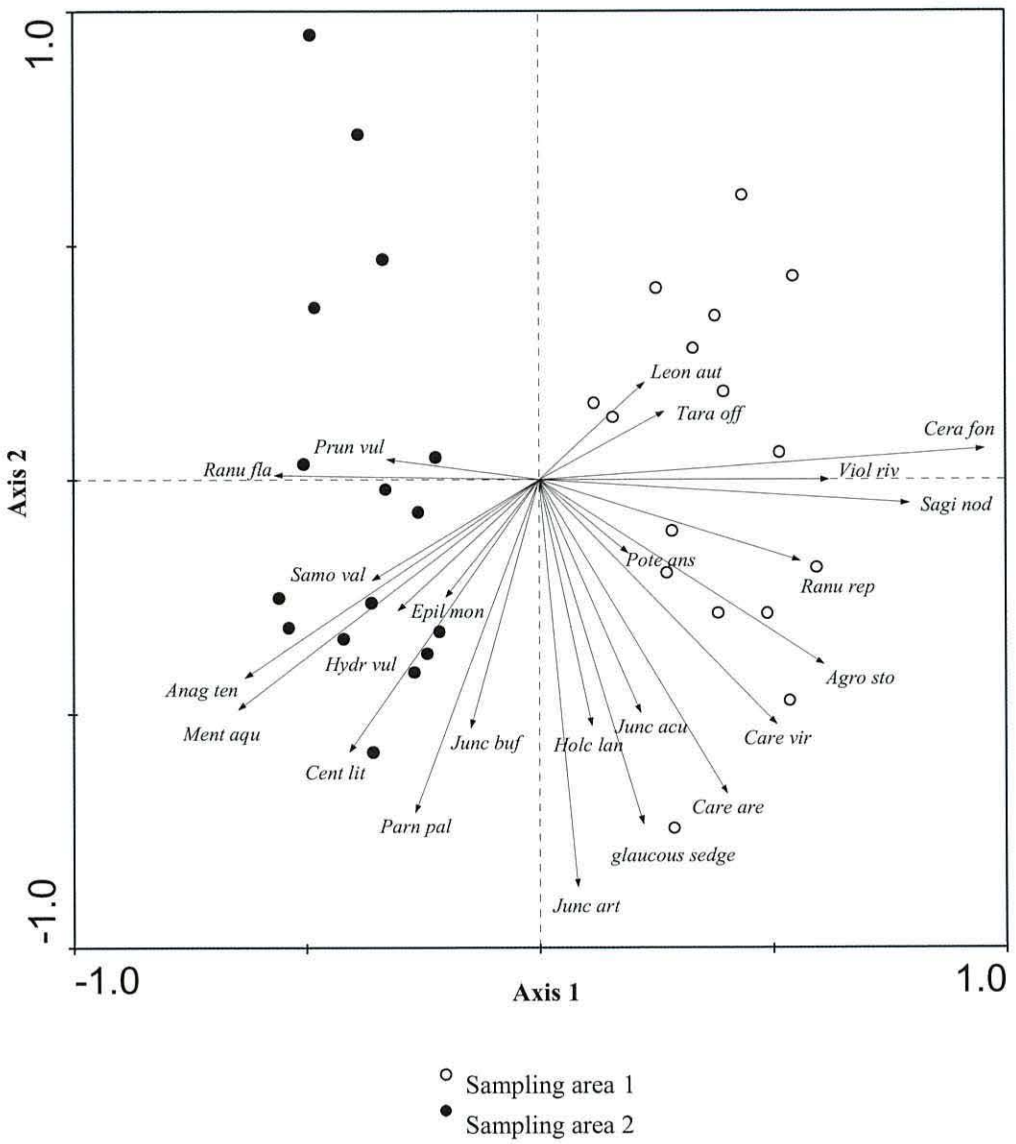


Figure 7.1. Ordination of seed bank samples and species by Principal Components Analysis (PCA). Open symbols represent samples from sampling area 1, filled symbols from sampling area 2. Eigenvalues: axis 1 = 0.2113, axis 2 = 0.1440. Data points are based on the floristic composition of individual seed trays. Only species with more than ten seedlings shown. Analysis was based on seed numbers that were log(+1)-transformed. Agro sto=*Agrostis stolonifera*, Anag ten=*Anagallis tenella*, Care are=*Carex arenaria*, Care vir=*Carex viridula*, Cent lit=*Centaurium littorale*, Cera fon=*Cerastium fontanum*, Epil mon=*Epilobium montanum*, glaucous sedge=*Carex flacca*, *C. nigra and C. panicea*, Holc lan=*Holcus lanatus*, Hydr vul=*Hydrocotyle vulgaris*, Junc acu=*Juncus acutiflorus*, Junc art=*Juncus articulatus*, Leon aut=*Leontodon autumnalis*, Ment aqu=*Mentha aquatica*, Parn pal=*Parnassia palustris*, Pote ans=*Potentilla anserina*, Prun vul=*Prunella vulgaris*, Ranu fla=*Ranunculus flammula*, Ranu rep=*Ranunculus repens*, Sagi nod=*Sagina nodosa*, Samo val=*Samolus valerandi*, Tara off=*Taraxacum* sect. *Ruderalia* (*T. officinale* Wigg. group), Viol riv=*Viola riviniana*.

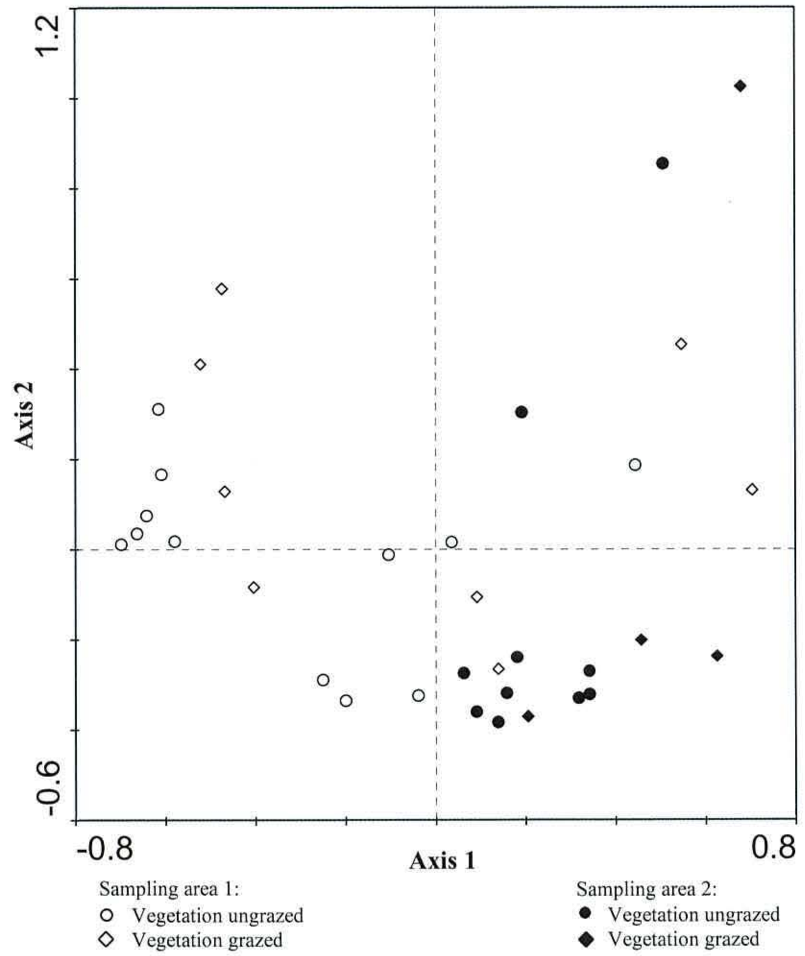


Figure 7.2. Ordination of vegetation samples by Principal Components Analysis (PCA). Eigenvalues: axis 1 = 0.1841, axis 2 = 0.1235. Open symbols = sampling area 1, closed symbols = sampling area 2. Circles denote samples before and diamonds after the introduction of grazing management.

Effects of nitrogen addition

The addition of nitrogen resulted in significantly higher numbers of seedlings as compared to the unfertilised control trays for six species, i.e. 25 % of all species with more than ten seedlings. These were: *Anagallis tenella*, *Carex viridula*, *Centaurium littorale*, *Juncus articulatus*, *Parnassia palustris* and the glaucous sedges (Table 7.2). Only in four species (*Cerastium fontanum*, *Samolus valerandi*, *Epilobium montanum* and *Viola riviniana*) were there fewer seedlings with added nitrogen than without. However, the differences in seedling numbers in nitrogen addition and control trays were not statistically significant for these four species. *Lotus corniculatus* was excluded from statistical analysis because only seven seedlings of this species emerged; however, it is worth noting that all of these seven seedlings were recorded from nitrogen addition trays. Seven species not emerging from control trays grew in the nitrogen addition treatments and vice versa (Table 7.3). No significant differences were found between the two blocks of trays on the greenhouse bench for any species.

Table 7.2. Results of General Linear Model analysis of the effects of nitrogen addition and sampling area. Figures are p values. Ellenberg indicator vales for nitrogen are also shown. Only species with more than ten seedlings in the experiment were included in the analysis. Species counts were log(n+1) transformed. Degrees of freedom (df): nitrogen addition, df=1; sampling area, df=1; block on bench (not shown in table), df=1; nitrogen addition*sampling area, df=1; error term, df=27; total error term, df=31.

	Ellenberg indicator value for N	Nitrogen addition	Sampling area	Nitrogen addition* sampling area
Nitrogen addition and/or sampling area significant				
Agrostis stolonifera	6	<0.166	**<0.001**	0.105
Anagallis tenella	3	**<0.011**	**<0.001**	0.726
Carex viridula	3	**<0.012**	**<0.001**	0.867
Centaurium littorale	3	**<0.001**	**<0.012**	0.520
Cerastium fontanum	4	<0.222	**<0.001**	0.239
glaucous sedge	2	**<0.006**	<0.167	0.519
Hydrocotyle vulgaris	3	<0.268	**<0.049**	0.890
Juncus articulatus	3	**<0.016**	<0.663	0.394
Mentha aquatica	5	<0.134	**<0.001**	0.847
Parnassia palustris	3	**<0.001**	**<0.019**	**0.009**
Potentilla anserina	6	<0.866	<0.411	**0.043**
Ranunculus flammula	3	<0.578	**<0.001**	0.067
Ranunculus repens	7	<0.333	**<0.003**	0.798
Sagina nodosa	3	<0.368	**<0.001**	0.726
Viola riviniana	4	<0.329	**<0.001**	0.796
No significant effects				
Carex arenaria	2	<0.221	<0.054	0.897
Epilobium montanum	6	<0.571	<0.267	0.218
Holcus lanatus	5	<0.180	<0.386	0.507
Juncus acutiflorus	2	<0.183	<0.356	0.532
Juncus bufonius	5	<0.336	<0.176	0.180
Leontodon autumnalis	4	<0.903	<0.363	0.771
Prunella vulgaris	4	<0.402	<0.127	0.781
Samolus valerandi	5	<0.813	<0.246	0.174
Taraxacum sect. *Ruderalia* (*T. officinale* Wigg. group)	6	<1.000	<0.144	0.351

Table 7.3. Number of seeds m^{-2} recorded in control and nitrogen addition treatments.

In control and nitrogen addition	Control	Nitrogen
Agrostis stolonifera	1581	1708
Anagallis tenella	605	1029
Anthoxanthum odoratum	21	11
Bellis perennis	11	11
Carex arenaria	488	615
Carex viridula	286	562
Centaurium erythraea	42	32
Centaurium littorale	138	393
Cerastium fontanum	286	191
Epilobium montanum	138	95
glaucous sedge	732	1358
Holcus lanatus	53	106
Hydrocotyle vulgaris	6334	6780
Juncus acutiflorus	64	127
Juncus articulatus	4106	7003
Juncus bufonius	1061	1422
Leontodon autumnalis	64	64
Linum catharthicum	32	11
Mentha aquatica	1592	1974
Parnassia palustris	85	446
Plantago major	32	32
Poa pratensis	32	21
Potentilla anserina	85	95
Prunella vulgaris	64	95
Ranunculus flammula	340	446
Ranunculus repens	53	95
Sagina nodosa	265	340
Samolus valerandi	138	127
Senecio jacobaea	32	21
Taraxacum sect. *Ruderalia* (*T. officinale* Wigg. group)	74	74
Viola riviniana	117	74

In control only	Control	Nitrogen
Agrostis capillaris	32	
Anagallis arvensis	11	
Isolepis setacea	11	
Luzula campestris	21	
Sonchus arvensis	32	
Veronica anagallis-aquatica	21	
Veronica chamaedrys	11	

In nitrogen addition only	Control	Nitrogen
Cardamine pratensis		11
Hypochaeris radicata		11
Leontodon saxatilis		11
Lotus corniculatus		74
Trifolium pratense		11
Trifolium repens		11
Triglochin spp.		11

	Control	Nitrogen
Total number of seeds m^{-2}	19088	25497
Total number of species	38	38

In the ordination graph, axis 2 appears to be related to nitrogen fertilisation, separating control samples from fertilised samples (Figure 7.3). Although the Eigenvalue for the second axis is rather low, it is still interpretable (Lepš & Šmilauer 2003). The ecological meaning of axis 3 is unclear.

The average Ellenberg indicator value for nitrogen (Hill *et al.* 1999), which is effectively a general indicator of productivity, was lower for the species with a significant response to the nitrogen treatment than for species which did not respond (t-test, $p<0.001$, $df=21.819$, $t=-4.204$). Species that did respond were indicative of infertile sites, whereas indicator values of species with no response were indicative of intermediate to richly fertile places.

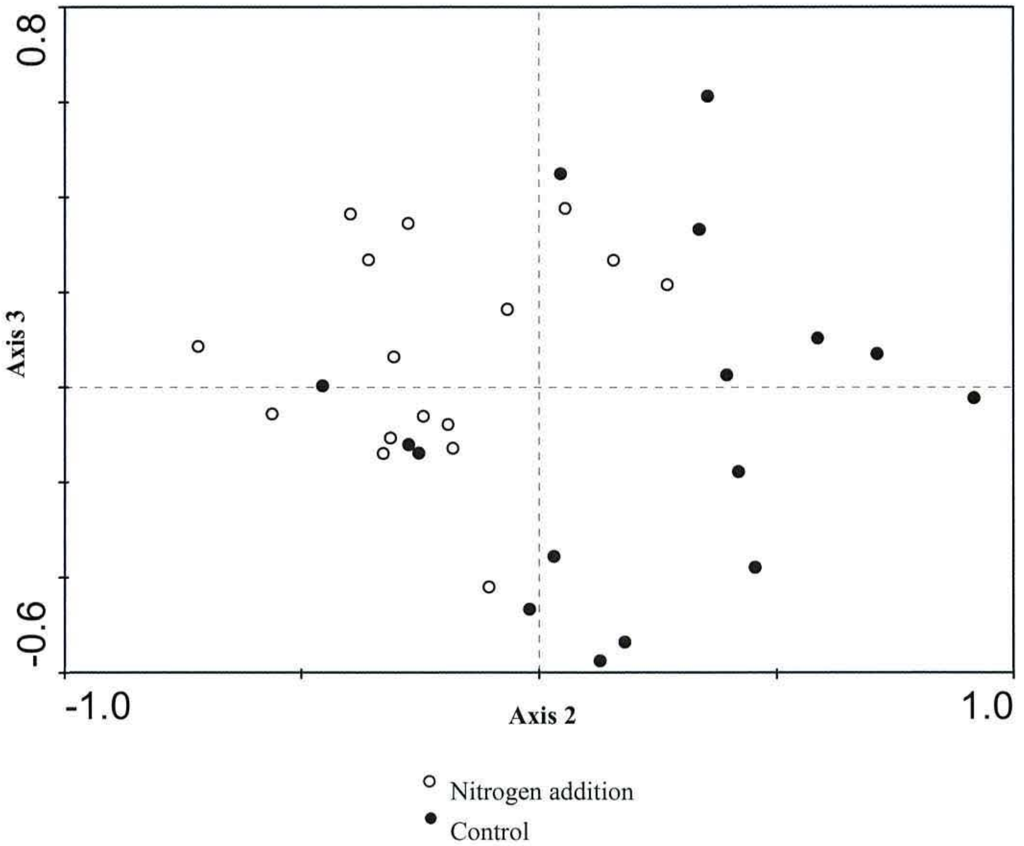


Figure 7.3. Ordination of seed bank samples by Principal Components Analysis (PCA). Open symbols represent nitrogen treatment samples, filled symbols controls. Eigenvalues: axis 2 = 0.1440, axis 3 = 0.0854. Analysis was based on seed numbers that were log(+1)-transformed. Data points are based on the floristic composition of individual seed trays.

Interaction of nitrogen and sampling area

Although total seed densities were very similar in both sampling areas, there was a difference in seed numbers in controls and nitrogen addition treatments (Figure 7.4). Sampling area 1 had higher seed densities in the nitrogen addition treatments, but this was not significant (t-test, p=0.268, df=14, t=-1.154). Sampling area 2 had significantly greater seed densities in the nitrogen addition than control treatments (Mann-Whitney test, p=0.003, U=5.000, N=16), thus showing a greater difference in seed densities between the two treatments than sampling area 1. This was significant for two species, *Parnassia palustris* and *Potentilla anserina* (Table 7.2).

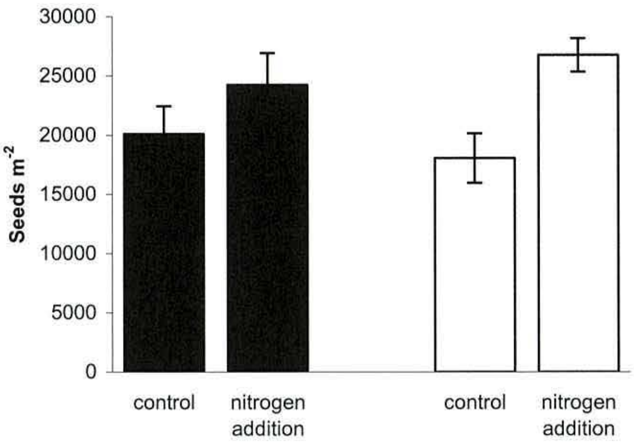


Figure 7.4. Number of seeds m^{-2} in two sampling areas in control trays and nitrogen addition treatments: Black = sampling area 1, no fill = sampling area 2. Bars are standard errors.

Discussion

Seed densities and species composition

Species characteristic of dune slacks represented the majority of seedlings recorded. They included one nationally rare species, *Centaurium littorale*, and several other species of conservation interest that are threatened by eutrophication, drainage of their natural habitat and the increasing rarity of early successional stages of dune slack building: *Anagallis tenella, Isolepis setacea*, *Mentha aquatica*, *Parnassia palustris*, *Ranunculus flammula*, *Sagina nodosa* and *Samolus valerandi* (Preston *et al.* 2002, Grime *et al.* 1988, Grootjans *et al.* 1988).

In a similar seed bank study using soil samples from the same sites and taken at the same time (see Chapter 6), seed densities recorded in untreated samples in 0-5 cm depth were slightly higher (22064 seeds m^{-2}) than in the control trays in this experiment (19088 seeds m^{-2}). This may be due to the longer time that the first study was run for, i.e. a whole year as compared to six months in the present experiment. In the samples that received added nitrogen, however, seed densities were higher (25497 seeds m^{-2}), suggesting that nitrogen addition has a positive impact on seed germination. Overall, seed densities are similar to those recorded by Looney & Gibson (1995) in wet dune slacks in Florida (22594 seeds m^{-2}). Bossuyt & Hermy (2004) found a maximum of only 9160 seeds m^{-2} and an average of 2345 seeds m^{-2} in grazed dune slacks in Belgium. This may indicate a greater age of the slacks in the present study as seed density, at least in the upper soil layer, has been found by several authors to increase during the course of succession (Looney & Gibson 1995, Bossuyt & Hermy 2004), although this is in contrast to the results of other authors analysing different habitats, e.g. Donelan & Thompson (1980) and Grandin (2001). With only 18 seeds m^{-2}, Owen *et al.* (2001) found considerably lower seed densities in machair dune slacks of the Outer Hebrides, Scotland.

Three species were recorded in this experiment that did not emerge from samples in the above mentioned experiment (Chapter 6) using soil sampled at the same place and time. These species are *Anagallis arvensis*, *Leontodon saxatilis* and *Isolepis setacea*. Species that were missing from this experiment but recorded from 0-5 cm depth in the other experiment were *Anthyllis vulneraria*, *Cirsium palustre*, *Chenopodium rubrum*, *Daucus carota*, *Euphrasia officinalis* agg., *Juncus bulbosus*, *Polygala vulgaris*, *Radiola linoides*, *Ranunculus bulbosus*, *Reseda luteola*, *Rumex acetosa* and *Salix repens*. Seedlings of all these species occurred in very low numbers. The fact that they were recorded from one experiment but not the other illustrates the patchy distribution of buried seeds (e.g. Schenkeveld & Verkaar 1984, Thompson 1986) and the difficulties attached to accurately describing the species composition of the seed bank of a given area. Indeed, as Thompson *et al.* (1997) point out, accurate sampling of the seed bank of rare species can probably not be achieved with any realistic and practicable sampling programme.

Seven species emerged only from nitrogen addition treatments but not from unfertilised controls, in too low numbers for statistical analysis. However, comparison with Chapter 6 reveals that all but one of these species (*Leontodon saxatilis*) emerged in low numbers without nitrogen fertilisation in a separate experiment. Thus, the sole occurrence of these species in the nitrogen treatments again is probably due to the patchy distribution of seeds in the soil and difficulties of recording rarer species, rather than representing any real response to nitrogen fertilisation.

Differences between sampling areas

The observation that the difference between total seed densities in control and nitrogen addition treatments was greater in sampling area 2 than 1 is difficult to explain and requires further research into the differences in abiotic and biotic factors between these areas and how they might impact seed germination. The same is true for the differences observed in the floristic composition of the seed bank between the two sampling areas. They could be due to the fact that the sampling areas have a different history of grazing treatment, which differed both by the time since grazing management was introduced (sampling area 1>2) and the livestock type used. However, the differences observed in the composition of the seed bank could also have existed even before livestock grazing started, which appears more likely because the composition of the above-ground vegetation already differed before the introduction of grazing management.

The effects of nitrogen fertilisation on the seed bank

Dune slacks are oligotrophic habitats in which nutrient availability and biomass production are low (Schat 1984, van Beckhoven 1992), and plant growth is often limited by nitrogen (Dougherty *et al.* 1990, Koerselman & Meuleman 1996, Verhoeven *et al.* 1996, Lammerts & Grootjans 1997). This means that they are sensitive to increased atmospheric deposition of nitrogen (Sival & Strijkstra-Kalk 1999), which is a major threat to these oligotrophic habitats and their associated species (Koerselman 1992), especially basiphilous species of pioneer stages (Lammerts & Grootjans 1997). Fertilisation experiments in dune slacks have described increases in biomass production and changes in the abundance of a range of species (Lammerts & Grootjans 1997). Increased availability of nutrients to the parent plant can also result in changes in seed production and quality, e.g. the production of more and larger seeds with higher germination rates (Parrish & Bazzaz 1985, Fenner 1992, Naylor 1993, Mattila & Kuitunen 2000). Some species, however, are buffered against differences in parental nutrient supply (e.g. Fenner 1986), especially wild plants as opposed to cultivated species (Roach & Wulff 1987). Plants growing from larger seeds produced at higher nutrient levels have been shown to be competitively superior to plants from smaller seeds grown at lower nutrient levels (Parrish & Bazzaz 1985, Stanton 1985). In *Phleum arenarium*, nutrient addition leads to reduced production of fruits that build up a seed bank (Ernst 1983), and Schat (1983) considered local levels of soil fertility to affect the timing of flowering and seed release which in turn impacts on germination behaviour.

In this study, the effect of increased nitrogen supply on seed bank dynamics was analysed in order to test whether seed germination might also be affected by atmospheric nutrient input. In six out of 24 species that were abundant enough for statistical analysis, nitrogen fertilisation had a significant effect by stimulating more buried seeds to germinate than in the untreated controls. This means that increased atmospheric deposition of nitrogen not only impacts on the established vegetation of dune slacks, but also has the potential to alter seed bank dynamics. Conditions in the field are of course different from the greenhouse, so that the results of this study cannot easily be transferred to field situations. In the greenhouse, all seeds had good growing conditions, i.e. they had enough light and water along with high temperatures after cold stratification, and they all were placed close to the soil surface. However, this experiment indicates which species are stimulated to germinate by increased nitrogen levels given otherwise suitable conditions.

The species with increased germination following nitrogen addition are pioneers that thrive in early successional stages of slack development, when the nutrient content of the soil is at its lowest, and build up large stores of viable buried seeds that can regenerate plant communities after disturbance. Among them are *Anagallis tenella*, *Centaurium littorale* and *Parnassia palustris*. They belong to those dune slack species that depend on nutrient-poor conditions and are most affected by eutrophication (Stewart *et al.* 1994, Sival & Grootjans 1996). The results of the present study confirm that not only are the adult plants affected by eutrophication, but also the germination of their seeds. This is in agreement with Schopp-Guth (1995) who states that species typical of infertile conditions disappear from the seed bank when fertilised. A longevity index based on the database of Thompson *et al.* (1997) and the results of the already mentioned study (Chapter 6) suggest that of the species with a positive germination response, all but *Anagallis tenella* have long-term persistent seeds. Furthermore, they all belonged to the more abundant species recorded from the seed bank. This suggests that any impact of increased nitrogen supply on seed bank dynamics will be more pronounced than if the species affected were species with small and transient seed banks.

Pioneer species with low requirements for phosphorus can initially benefit from an increase in nitrogen and may be competitively superior to species with higher phosphorus requirements (Willis 1963). However, grasses also increase when nitrogen limitation is lifted, and in the longer term, the smaller pioneer species are likely to be outcompeted (Lammerts & Grootjans 1997). This study offers another explanation for the temporary increase in pioneer species following the lifting of nitrogen limitation:

they may show increased rates of germination, stimulated by higher nitrogen levels in the soil. If seed bank dynamics are thus affected by increased nutrient supply, they can play a part in the observed vegetation change following eutrophication.

Increased germination of seeds as a result of raised nutrient levels can lead to the depletion of the seed banks of affected species. Milberg (1992) reported a smaller seed bank from fertilised than unfertilised control plots, which also points to a depletion of the seed bank when fertilised. Seeds may germinate in conditions which are not favourable to the developing seedlings, and in which they normally would not have germinated. For example, germination in the field is often prevented by the presence of plants, with many short-lived and competitively inferior species needing vegetation gaps with reduced competition to regenerate from seed (Bullock *et al.* 1995). Nitrate levels were found to be higher in gaps than under undisturbed vegetation, so that the germination response to increased nitrate can be interpreted as a gap detection mechanism which allows the seedling to establish in a low-competition environment (Pons 1989, Bullock 2000). However, when nitrate was added, seeds of *Plantago lanceolata* were not inhibited from germination by the presence of plants (Pons 1989), so that at least in some species, nitrogen addition alone can stimulate germination, even in a situation that does not favour the developing seedling. A reduced light requirement after fertilisation with nitrogen was also observed in several other species, e.g. *Chenopodium album* (Henson 1970). In accordance with this experiment, Williams (1983b) found a greater response of species with persistent seed banks to various temperature, light and nitrate addition treatments, concluding that species with persistent seed banks have more specific germination requirements than species with transient seed banks that are able to germinate under a wider range of environmental conditions. A narrow range of conditions in which germination occurs is a mechanism which increases the chance of a seed persisting and becoming part of the seed bank (Thompson & Grime 1979, Thompson 1987). If the narrow range of germination requirements is widened by increased nutrients, then fewer seeds of the species affected will become incorporated into a persistent seed bank, and only few of the developing seedlings may survive because the growing conditions are not favourable.

When germination conditions are right, *Centaurium littorale* shows rapid and complete germination of its seeds within a short period of time (Schat 1983), so that seedling mortality could be extremely high if conditions are not entirely favourable for seedling survival. This makes this species extremely vulnerable to changes of germination cues that do not reflect genuinely beneficial conditions for seedling survival. Pemadasa & Lovell (1975), Maun & Lapierre (1986) and Zhang & Maun (1990) reported the depths at which germination is most frequent and the maximum depths below which no germination is possible for several dune species. Normally, there is little germination in deeper soil layers because of the low chance of the survival of the developing seedling that may not have enough stored energy to grow all the way to the surface. However, germination at depths too great for successful emergence does occur. Emergence of germinated seedlings is often reduced with increasing depth of burial (Pemadasa & Lovell 1975), and unsuccessful emergence can be a major mortality factor (Fernandez-Quintanilla 1988) although not much is known about how many seedlings die between germination and emergence (Bullock 2000). Schat (1983) showed that the depth at which seeds are able to germinate can be influenced by environmental factors, with germination occurring at greater depths after cold-stratification. In this experiment, any possible impact of nitrogen on the depth where germination takes place was not investigated, but it could be an impact of increased nitrogen levels in the field.

Although some studies could show that nitrate and ammonia may increase germination even under low light conditions (Singh & Amritphale 1992), the germination response to nitrogen can depend on other factors being favourable to germination as well, including light and temperature or temperature fluctuations (e.g. Hilton 1984, Goudey *et al.* 1987, Hilhorst & Karssen 2000). This means that the above mentioned germination response to nitrogen in depths too great for successful emergence may not be of great importance. Considering the strong interactions of nitrogen, temperatures and light in stimulating germination, the greatest impact of increased nitrogen supply can be expected on disturbed ground and in vegetation gaps (Roberts 1972). Nitrogen deposited with rain may mainly affect autumn and winter germinating species because of higher rainfall in those seasons. However, while wet deposition is decreasing now, dry nitrogen deposition is still high and is not so influenced by the seasons (Goulding *et al.* 1998).

Conclusion

In conclusion, it can be said that the addition of nitrogen has an impact on the seed bank of dune slacks, with the majority of species showing enhanced levels of germination. Species affected are not nutrient-loving species of older slacks, but early successional species normally growing in nutrient-poor conditions, suggesting that the impact of increased nitrogen deposition on seed bank dynamics will be greatest in the early stages of slack vegetation. It is these early successional communities that are most endangered and threatened by a variety of factors, including eutrophication. The floristic composition of the seed bank was different in two sampling areas, but further research is needed to explain these differences.

CHAPTER 8

General discussion

Coastal sand dunes at Newborough Warren

Sand dunes support rare and threatened habitats and associated species and are well represented in the EU Habitats Directive, which aims to provide protection for the most threatened and important habitats and species within Europe (Hopkins & Radley 2001). Following the designations of Special Areas of Conservation (SAC) as part of the Natura 2000 network, managing these sites to protect, maintain and enhance their high conservation value is of great importance. In order to achieve this, their ecology, threats and implications for management need to be understood.

This dissertation is a study of one of the largest remaining intact hindshore dune systems in Western Europe, which is designated as a SAC because of its high diversity of habitats of European importance, including shifting dunes, dune grassland and humid dune slacks. It is one of Britain's most biologically diverse sand dune systems (Rees 1990) comprising the full succession of habitats from strandline to shingle, mobile dunes, wet and dry slacks to dune grassland and scrub. Its outstanding conservation value makes it a prime site for research, which started in the 1950s when Ranwell (1955, 1958, 1959, 1960a, b) carried out pioneer work on dune ecology. The present study is a contribution to further the knowledge of the ecology of sand dunes under perturbation. It addresses the potential threat of atmospheric nitrogen deposition to the nature conservation value of these sites, investigates the potential of management by livestock grazing to maintain and restore species-rich, open sand dune plant communities, and describes the composition of the seed bank of dune slacks.

Impacts of grazing management on sand dunes

The diversity of many dune areas has developed because of a long history of grazing by rabbits and domestic stock (Ranwell 1972, Boorman 1989a). When the combined effects of the rabbit disease myxomatosis and the cessation of traditional livestock grazing on many sites led to a great reduction in grazing pressure, major changes in the vegetation structure of dunes ensued. These resulted in the loss of early successional stages, declining species diversity and a development towards scrub and woodland vegetation. Overstabilisation due to the reduced grazing pressure on many sites is one of the most serious problems threatening the diversity of dunes (Doody 1991, Dargie 1995). Today, management by livestock grazing is widely applied in an attempt to maintain and restore open dune communities (Brouwer *et al.* 2005), and grazing by rabbits and/or domestic stock is regarded as necessary to maintain species-rich dune grasslands and characteristic plants and animals (Doody 1989, Doody *et al.* 1993). However, there is still a need for scientific studies and evaluations of its success, both for sand dunes and other habitats (Piek 1998, Delescaille 2002, Kampf 2002, Bonte & Hoffmann 2005).

The results of the long-term study on the effects of livestock grazing management (Chapter 4) indicate clearly that grazing was successful in increasing plant species diversity fro all major plant groups, especially for annual species, which was due to an increase in desirable species characteristic of sand dunes. At the plant community level, there was a change from a rank, species-poor community to a more species-rich community, and significant increases in the frequency of positive indicator species suggested improved habitat conditions. These results agree with those of other studies that documented increased species diversity following the introduction of extensive grazing on sand dunes (e.g. van Dijk 1992, de Bonte *et al.* 1999, Hoffmann *et al.* 2005). Although not studied here, seed dispersal by grazing herbivores can play an important role on sand dunes by connecting spatially separate habitat patches (e.g. Cosyns *et al.* 2005a, b, Couvreur *et al.* 2005), and grazing animals can stimulate germination of competitively inferior and target species that depend on the creation of vegetation gaps (Hoffmann *et al.* 2005). The observed increase in annual and biennial species after the introduction of grazing management suggests that this did indeed happen at the study site. The extent to which grazing actually encourages germination by activating the seed bank was not investigated in this study; however, an analysis of the composition of the seed bank of dune slacks revealed that it contains a pool of characteristic dune slack species (Chapter 6). These included species of conservation interest and early successional species that build up persistent seed banks and can be expected to contribute to regeneration after disturbance caused by grazing animals.

Studies in Dutch dune slacks found little potential for the regeneration of target species from the seed bank (Bakker *et al.* 2005a), while management measures carried out on some East Frisian Islands have resulted in the successful conservation of slack vegetation through the reactivation of target species (Petersen 2004). These contrasting findings illustrate the need for further study which should lead to more generalized conclusions. The present study contributes new data on some species that have not generally been recorded in seed bank studies before, and thereby helps modify classifications of seed longevity for several species. Although long-term persistent seeds of desirable species are a part of the seed bank, it is important to ensure their long-term survival by maintaining patches of short sward with suitable germination niches. Even where rabbit populations are strong, additional grazing by livestock will help meet this aim, since large and small herbivores have a different impact on dispersal and colonisation processes and areas grazed by both can be expected to have the greatest species diversity (Bakker 2003).

The effects of grazing were also investigated in a controlled experiment with three different grazing treatments: ungrazed, grazed by rabbits, and grazed by rabbits and ponies (Chapter 5). In ungrazed plots, sward heights increased significantly within less than two weeks, and after two years, there were greater amounts of above-ground biomass and graminoids, especially tall growing species, were more abundant than in the grazed treatments. No decreases in the abundance and diversity of dicotyledonous herbs or bryophytes were found; however, these are expected to decline over longer periods of time as the taller and denser swards will lead to a significant reduction of light reaching the soil surface. This will change competitive interactions and negatively affect small species and bryophytes. In addition, a reduction of vegetation gaps will lead to the decline of small, poorly competitive species which depend on these gaps for their germination and development. A sward height of 2-10 cm over 30-70 % of the sward is recommended for the maintenance of species-rich dune grassland (JNCC 2004); in the ungrazed quadrats in this study, swards were consistently higher than 10 cm after one year, which also indicates the possibility of reduced species diversity in the longer term.

The two grazed treatments differed in their vegetation composition, with bryophytes associated with the heavier grazing by rabbits and livestock, and forbs associated with grazing by rabbits only.

Impacts of atmospheric nitrogen deposition on sand dunes

Another threat to the diversity of sand dunes is the increased atmospheric deposition of nitrogen to this nutrient poor habitat that is considered to be negatively affected by eutrophication (de Vries *et al.* 1994, Bobbink *et al.* 2003, Jones *et al.* 2004a). Detrimental effects of eutrophication such as reduced species diversity and changes in community composition have been reported for a variety of habitats, including grasslands, bogs, fens and heathlands (Cunha *et al.* 2002), and nitrogen deposition has been implicated in the spread of tall grasses in Dutch sand dunes (ten Harkel & van der Meulen 1996, Veer 1997, Kooijman 2004). However, little information is available on the impact of increased atmospheric deposition of nitrogen on British sand dunes (Jones *et al.* 2004b).

Critical loads for eutrophication are defined as the maximum input into a habitat that is believed not to lead to adverse effects on sensitive elements of the environment (NEGTAP 2001). They are used on a European scale to develop policies, assess current and potential future effects of pollutants and represent an important scientific tool for the evaluation of efforts to reduce emissions of pollutants (NEGTAP 2001, Cunha *et al.* 2002). Field manipulation experiments are amongst the most important methods used to define critical loads and understand ecosystem responses to increased atmospheric deposition of nitrogen (Cunha *et al.* 2002). However, many experiments use application rates greater than the predicted critical load, which makes defining the critical load difficult (NEGTAP 2001), and research is needed using realistic nitrogen loads and sites with low background depositions (Bobbink *et al.* 2003).

A critical load of 10-20 kg ha^{-1} $year^{-1}$ was suggested for dune grasslands by Bobbink *et al.* (2003) and Jones *et al.* (2002a, b, 2004a), but further work is needed to validate this range and understand the interactions of nitrogen input and management practices (Bobbink *et al.* 2003). The fertilisation experiment presented here (Chapter 5) aimed to inform policy makers by assessing the risk of nitrogen deposition to a habitat whose responses are not very well known, despite the fact that it represents an important habitat for nature conservation. It was conducted at a dune system currently receiving relatively low levels of background deposition (Mohd-Said 1999) and used realistic application rates so that total nitrogen inputs reached the upper limit of the proposed critical load range for one treatment and exceeded it for the other. The specific aims of this experiment were to analyze the effects of increased nitrogen supply on the vegetation composition, structure and soil chemistry of fixed dune grasslands, validate the proposed range of critical load and determine whether grazing can counteract any potentially negative impact of fertilisation.

After two years of nitrogen additions, significant increases in above-ground standing biomass were detected, especially for bryophytes, which also had increased nitrogen tissue concentrations. A separate experiment suggested that both nitrogen and phosphorus limit sand dune vegetation. However, some effects of fertilisation with nitrogen alone were detected, which means that increased nitrogen deposition in the past has not yet induced limitation by phosphorus. Although the higher end of the range of the critical load can be applied for heavily grazed vegetation and sites with co-limitation by phosphorus such as the study site, the critical load appeared to have been exceeded at less than the proposed upper end of 20 kg ha^{-1} $year^{-1}$. This is because increases in above-ground biomass were detected even for the lower application treatment which resulted in total nitrogen inputs just below 20 kg ha^{-1} $year^{-1}$, and indicates that dune grasslands are under even greater threat from nitrogen deposition than previously thought. No changes in community composition or soil chemistry were detected after two years of nutrient applications; however, in the longer run, the observed increases in biomass production and nitrogen tissue concentrations may lead to community changes through increases in litter, changed soil biological processes and nitrogen cycling, denser swards, decreased light levels at the surface and altered competitive interactions between species.

Grazing appeared to counteract these changes to some extent, but there was little significant interaction between grazing and nitrogen fertilisation treatment. This was probably due to the short duration of the experiment. In the long-term study on the effects of grazing management (Chapter 4), it could be shown that the species-poor, rank community SD9 (*Ammophila arenaria – Arrhenatherum elatius* dune grassland) changed to the more diverse SD8 (*Festuca rubra – Galium verum* fixed dune grassland) as a result of the introduction of livestock grazing, and that this change was accompanied by a significant decrease in the average Ellenberg indicator value for nitrogen. Although it is not known if the higher Ellenberg nitrogen indicator value in the ungrazed community was a result of the greater productivity and nutrient availability in the absence of grazing or of the increased deposition of nitrogen, this is in accordance with Kooijman & van der Meulen (1996), ten Harkel & van der Meulen (1996) and Kooijman & Smit (2001) who all concluded that livestock grazing can counteract the effects of increased atmospheric deposition of nitrogen to a large extent.

The impact of increased nitrogen supply on seed bank dynamics of dune slacks was investigated in a greenhouse experiment in order to assess whether atmospheric deposition of nitrogen not only impacts on the established vegetation, but also has the potential to alter regeneration from the seed bank (Chapter 7). The majority of species showed enhanced levels of germination after nitrogen fertilisation, which was significant for 25 % of species that were abundant enough for statistical analysis. Especially affected were early successional species normally growing in nutrient poor conditions, e.g. *Anagallis tenella*, *Centaurium littorale* and *Parnassia palustris*. This indicates that the impact of nitrogen deposition may be greatest in the earlier stages of dune slack vegetation. These early successional stages are the most endangered slack communities and threatened by a variety of factors, including eutrophication (Koerselman 1992). Increased germination following raised nutrient levels can lead to the depletion of the seed banks of affected species (e.g. Milberg 1992). Fewer seeds will become incorporated into a persistent seed bank, and seeds may germinate in conditions not favourable to the survival of the developing seedling. For example, nitrate levels are higher in vegetation gaps, and the germination response to increased nitrate can be interpreted as a gap detection mechanism, allowing the seedling to establish in gaps with reduced competition (Pons 1989, Bullock 2000). However, in some species, germination is not inhibited by the presence of plants when nitrate levels are raised (Pons 1989). As this study has shown, seed bank dynamics may be affected by increased nutrient supply, which means that they may be a factor in the observed vegetation changes following eutrophication.

Sand dune management and conservation

Grazing by domestic livestock was shown to be beneficial to dune plant communities and is therefore recommended for the nature conservation management of sand dunes. In this study, the positive effects of livestock grazing documented were: increased diversity of desirable species, including annual, biennial and low growing, poorly competitive species that had become rare at the study site before grazing management started; the increased occurrence of positive indicator species; and the restoration of a more species-rich plant community from a rank, less diverse one. This study also found a rich seed bank in dune slacks, which included early successional species and species of conservation interest. Grazing is thought to allow increased germination from the seed bank by creating open ground and reducing competition from fast-growing species, which may contribute to the continued survival of these species. One aim of grazing management at the study site is to destabilise the system and create conditions suitable for the establishment of early successional communities; the existence of viable seeds of early successional species in the seed bank will contribute to the success of this management aim. Grazing also appeared to have been successful in counteracting changes in community composition caused by nutrient enrichment.

Other management techniques that aim to arrest or even set back succession, create canopy gaps and bare patches of soil suitable for the germination of annuals and small, competitively inferior species, and result in short swards which promote the bryophyte and lichens layers, will also be suitable for sand dune conservation. For the protection of this habitat from the effects of increased nitrogen deposition, it may even be more suitable to remove biomass from the system by mowing or cutting, as the amount of nutrients removed from the system by grazing animals can be small compared with nutrient inputs (Marrs 1993). However, techniques such as mowing or cutting will not be as practicable as extensive livestock grazing on larger sites and cannot be applied on difficult terrain, e.g. steep slopes (van Dijk 1992). In contrast to mowing and cutting, grazing increases species richness by creating a greater diversity of vegetation structure, and creates open ground and gaps that are important regeneration niches and habitats for invertebrates (Piek 1998, Crofts & Jefferson 1999). Ponies and horses are considered as the best choice of grazing animal because their faeces are nutrient-poor and they use latrine areas (Hurford & Perry 2001). So far, no significant enrichment effect due to dunging has been found outside of latrine areas in semi-natural vegetation, and some of the nutrients contained in dung and urine are lost from the system through leaching or to the atmosphere (Crofts & Jefferson 1999). Grazing can lower nutrient availability at larger scales (Bakker 1998) and help maintain a low nutrient status of the soil (Crofts & Jefferson 1999), but the extent to which grazing can help counteract the effects of increased deposition of nitrogen appears to depend on the seriousness of the spread of tall grasses, litter accumulation, humus development, organic matter accumulation, soil enrichment and acidification at the time when grazing management is introduced (Brouwer *et al.* 2005).

Limitations of the experiments and further research

This study was conducted at a single sand dune system and therefore the results are influenced by site specific parameters and the characteristics of the plant and herbivore species present at the site. These site specific parameters include factors such as geographical location, climate and soil, hydrological factors controlling sand supplies and water regimes in the dune slacks, geomorphological factors and the direction of the prevailing winds. Furthermore, the extent to which man has used and modified a site, e.g. by using it for livestock grazing or by stabilising the coastline, will have had an impact on species found at each site. Ranwell (1955) concluded that the development of dune slacks is primarily determined by the geographical location, the pH of the soil and the hydrology of the slack. The effects of grazing herbivores depend on habitat characteristics such as soil fertility and water availability and therefore show regional variations across gradients of environmental factors, which may explain why similar herbivores have different effects in different areas (Olff & Ritchie 1998). When interpreting the results of the present study, these issues need to be taken into account. However, while the exact effects of grazing management may not be generalised to every other sand dune site and cannot be compared with studies conducted in habitats with very different characteristics, the general principles still apply. Grazing animals can impact on the structure and composition of plant communities by influencing recruitment from the seed bank through the creation of gaps (Olff & Ritchie 1998), changing competitive interactions between species (Olff & Ritchie 1998), selective removal of species (Sternberg *et al.* 2000), reducing biomass and litter accumulation (Van Wieren 1995, Bakker *et al.* 2003), changing nutrient cycles (Shankar & Singh 1996), dispersing propagules (Chambers & MacMahon 1994, Pakeman *et al.* 2002, Bakker & Olff 2003) and feeding on seeds and reproductive structures (Chambers & MacMahon 1994, Cosyns 2004). The results of this study may also be relevant to other types of grassland such as calcareous grasslands and fens that share species with dune grasslands and slacks.

Fertilisation experiments previously carried out on sand dunes tried to establish which nutrients restrict plant productivity and are of limited value for evaluating the effects of increased deposition of nitrogen, because they used high concentrations, nutrient mixtures or applied nitrogen only once or very few times per year (e.g. Willis & Yemm 1961, Willis 1963, Pemadasa & Lovell 1974a, Boorman & Fuller 1982, Olff *et al.* 1993). The experiment on the effects of the increased atmospheric deposition of nitrogen on dune grassland reported here was the first of its kind in the UK. It suggested that this habitat is indeed affected by increased nitrogen supplies, which might have long-term implications for the species composition, soil biological processes and nutrient cycling of the ecosystem. Future research should address the question of whether other dune systems, e.g. on acidic rather than calcareous soil as in the present study, are also under threat, building up the knowledge on these effects and eventually allowing more generalised conclusions.

The effects of long-term grazing management on different dune habitats were studied using data gathered since 1987 from permanent vegetation monitoring quadrats (Chapter 4). Although this monitoring program initially included grazed areas and ungrazed controls, over the years the grazed area was gradually expanded until it included most of the dunes and the previously ungrazed controls became grazed as well. Because of this, some uncertainty remains as to how much of the observed long-term changes in the vegetation is due to grazing management and how much is due to other factors, e.g. changes in hydrological parameters, climate change or atmospheric deposition of nitrogen. For future monitoring and evaluations of the success of grazing management, some ungrazed control areas should be maintained and new vegetation monitoring quadrats set up. Further research assessing the impact of grazing on animals such as spiders, insects or birds would complement this study.

The experiment investigating the effects of increased levels of nitrogen on the vegetation of dune grasslands (Chapter 5) could only detect relatively short-term changes. Ideally, this study would be conducted over much longer time periods than possible here, because the impact of increased supply of nitrogen may only become obvious after many years of fertilisation (Cunha *et al.* 2002). The same applies to the effects of grazing exclusion and differences in grazing pressure and impact between the areas grazed by both ponies and rabbits and areas grazed by rabbits only. Additionally, more parameters should be measured, e.g. soil nitrogen mineralization rates and the amount of nitrogen leaching.

The experimental area (Chapter 5) had to be chosen with practical considerations in mind, most importantly ease of access in order to be able to bring large amounts of water to the plots on a regular basis. Other considerations included landscape issues related to the building of the grazing exclusion fences within a National Nature Reserve and the need to avoid areas with public access. The area chosen was ideal from these points of view; however, it represented a very stable area at the landward end of the dunes, where natural soil development and thus nutrient levels would be greatest within the sand dune succession. Areas of earlier successional vegetation would possibly have been of more interest and relevance because they might be more vulnerable to increased atmospheric deposition of nitrogen. The area chosen had a strong population of rabbits, and it would have been interesting to compare the effects of the exclusion of pony grazing in this area with a part of the dunes that supports a smaller rabbit population. This might have demonstrated more clearly if livestock grazing is indeed necessary for the maintenance of target communities, whereas because of the very strong rabbit population in the experimental area, no significant differences between the two grazed treatments were detected after two years. It could also be important to include a study of the effects of small herbivores such as voles that might have influenced vegetation composition and structure in the grazing exclosures.

Information on the seed banks of other dune plant communities is equally scarce as on the seed banks of dune slacks, and equally important in relation to management. Due to practical constraints, only eight sites could be sampled for this project (Chapters 6 and 7), but because of the inherent patchiness of seeds in the soil, more samples (both sample sites and number of individual soil cores at each site) would have increased the accuracy of the results. Although spring is the best time of year to take samples for detecting transient and persistent seed banks and many seeds germinate in larger numbers after natural winter stratification, sampling at different times of the year can increase the probability of finding species with different germination requirements (Devlaeminck *et al.* 2004). In this study, however, a summer drought and a second winter stratification were simulated in the greenhouse, so that the germination conditions for most species will have been met. The soil used in this experiment was not concentrated by washing it on a fine sieve as recommended by ter Heerdt *et al.* (1996) for fear of losing and damaging seeds; however, for further studies this method should be considered.

Two seed bank experiments were carried out using soil samples from the same sites, taken at the same time (Chapters 6 and 7). Some species were only recorded from one of these two experiments, mainly in very low numbers. This illustrates the patchy distribution of buried seeds (e.g. Schenkeveld & Verkaar 1984, Thompson 1986) and the difficulties attached to accurately describing the species composition of the seed bank of a given area. Thompson *et al.* (1997) point out that accurate sampling of the seed bank of rare species can probably not be achieved with any realistic and practicable sampling design. Differences in the composition of the seed bank between two areas with a different history of grazing management were detected in one but not the other experiment, so that no definite conclusions could be drawn as to how different types of livestock impact differently on the seed bank. Further research could address this question more closely in a long-term study, e.g. in the experimental plots of Chapter 5, where three grazing treatments are available in a designed experiment.

The experiment on the effects of nitrogen fertilization on seed germination from the soil seed bank gave some indications as to which species respond under the controlled conditions of the greenhouse (Chapter 7); however, the results cannot easily be transferred to the field situation. An experiment conducted in the field, e.g. a seed burial experiment, could investigate these issues under more realistic conditions. An analysis of the seed bank in the experimental plots of the nitrogen fertilization experiment could also give an indication of how changed nutrient levels affect seed bank dynamics, but once again, this would be a more long-term project than possible in the scope of this dissertation.

The impact of grazing management by different livestock on the soil seed bank was investigated in two separate studies. In one of them, the composition of the seed bank was different in two contrasted areas with a different history of grazing management, in the other it was not. Thus, no definite conclusions could be drawn as to how different types of livestock impact differently on the seed bank. Further research could address this question more closely in a long-term study, e.g. in the experimental plots of Chapter 5, where three grazing treatments are available in a designed experiment.

Conclusion

In this dissertation, some aspects of the ecology of sand dunes, threats to their diversity and nature conservation interest, and the effects of grazing management have been investigated. An important contribution was made to the knowledge of seed banks of dune slacks, their composition and seed longevity. Livestock grazing was shown to be a suitable management tool to maintain and restore typical open sand dune communities. Increased atmospheric deposition of nitrogen might be detrimental to fixed dune grasslands, and it is suggested to lower the proposed critical load for this habitat even in the presence of grazing animals and on sites with possible limitation or co-limitation by phosphorus. Although only a single site was studied, the results have wider applications, because the site was a typical calcareous sand dune system that can be used as an example for other sites.

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Appendix

APPENDIX 1: VEGETATION SURVEY DATA FOR PERMANENT QUADRATS (CHAPTER 4)

Appendix 1.1. Dry dune habitats, NVC community SD9 (ungrazed) / SD8 (grazed): Survey data 1987-2003. Figures are Domin values for percentage cover (1: <4% with few individuals, 2: <4% with several individuals, 3: <4% with many individuals, 4: 4-10%, 5: 11-25%, 6: 26-33%, 7: 34-50%, 8: 51-75%, 9: 76-90%, 10: 91-100%). Species sorted by number of occurrence across all years of survey. NVC = National Vegetation Classification (see Rodwell 2000).

	Quadrat number	1					2					4					12					13					18					27					28					46		
		ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed
	Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003
	Festuca rubra	7		4	6	6	7	6	4	5	5	3	7	4	4	4	7	7	5		6	6	8	6	4	3	5	6	3	4	4	2		2		4	8	7	7	4	5	2	4	6
	Holcus lanatus	3	4	5	3	5			7	5	4	1	5	3	2	3	3	4	4		2		3	3	2	3		7	4	4	4	5	4	3	3	6	3		2	3	6	3	1	4
	Carex arenaria				1	1	6		5	4	5	2	6	3	2	1	6	6	5	6	7	5	4	5	4	4	4		4	3	4			2	3	5	3	2	4	4	3		3	4
	Poa pratensis	3	8	3						3	2	3		2	2	2	4	4	4	3	2	4	5	4	2	1	6		4	2	3	2		3	5	3	4		4	6	5	6	4	2
	Anthoxanthum odoratum		2	5	4	5		5	5	6				1	2	3			3	5	2			3	3	3				2	4		5	4		5	6	4	3	4	5	3	4	3
	Arrhenatherum elatius	7	8	3			5	9	2	3	3										2		1			2	6	9	8	3	2	8	7	8	8	3		1	3	7	5	8	4	2
	Agrostis capillaris		7	4	8	7			2		4			1					4	5	7			3	4	4			2	4	6		5			5	2	6	2	1	4		3	5
	Luzula campestris			2	2	3			2	1	3							1	3		3			3	2	4			2		2			2		4			2	1	4	2	3	3
	Ammophila arenaria								1	2		2	4	3	4	3														2				4	4		2	4	4	3	1			
	Carex flacca					3			1	1	1								1		3									1	2							2	2	1	2			
Graminoids	*Carex nigra*					3						2					2													1	3	4	3	2		2	2							
	Agrostis stolonifera							6		3	2						2	5					5																					
	Carex caryophyllea										1																			2	2			1							2			
	Briza media																																			1					2			
	Dactylis glomerata																																		2	2								
	Carex hirta																																										1	3
	Juncus tenuis					2																									1													
	Poa annua																																											1
	Aira caryophyllea																				2																							
	Juncus acutiflorus					2																																						
	Juncus bufonius					2																																						

Appendix 1.1. Continued.

Quadrat number	1					2					4					12					13					18					27					28					46		
	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed
Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003
Annuals and biennials																																											
Crepis capillaris				1	1			1	4	2		1		2	3		2	2	1	1			2	1	1					1						1		2				2	2
Vicia sativa						1		2								1		4			3		3	1									3		2								
Euphrasia officinalis agg.					3					3			2	1					1	2					1																		
Rhinanthus minor			1		2					5					4								1						1	6													
Vicia hirsuta									1								1		1		3	4		1																	2		
Geranium dissectum			2					1																									3					1			2	3	
Centaurium erythraea				1	1					1										1																							
Daucus carota			1	2	2										2																												
Linum catharticum														1	3					3																							
Torilis japonica																															1	3	3										
Trifolium dubium																			1																3								
Stellaria media		7																													2												
Carlina vulgaris												2																															
Trifolium campestre																				1																							
Odontites vernus				1																																							
Aira caryophyllea																				2																							
Poa annua																																											1
Juncus bufonius					2																																						

Appendix 1.1. Continued.

	Quadrat number	1					2					4					12					13					18					27					28					46		
		ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed
	Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003
Perennial species	*Lotus corniculatus*			1	4	4				3	4	5	6	3	4	4	3	4	4	4	4	2	4	4	3	4	1	2		3	3					3	4	2	3	2	2		2	3
	Veronica chamaedris			2	3	2			1	2	3									1	2	3	3	4	3	5			2	3	3	3	1	3	3	4	1		3	3	4	3	4	5
	Galium verum			2	4	2				2	3				1	5				1	6				2	3	3	1	2	3	2	3			1	5	4	3	2	3	7	1	5	5
	Rumex acetosa	1	2	3	1	3		2									1	2	1	1		3					2	1	4	1	3	3	4	2	1	5					2			2
	Achillea millefolium	1	3	2	2	3		8	3	4	3																4	6	5	8	4	3	4	4	4	5						3	2	3
	Cerastium fontanum				1	3				5	3			1	1		1		1	2	2			2						1	4			2		4				2	2		1	1
	Senecio jacobaea				2	4			3	3	4		2	2	1	1				1	1			2		1					7					4					4		4	5
	Taraxacum sect. Ruderalia (T. officinale Wigg. group)					3					2	1	1	2		2			3	1	1			2	1	1					2								3	1	4	1		1
	Cirsium arvense	3	3	3	2	4											1	2									4	6	4	1		4	3	3	1							3		2
	Salix repens											9	6	8	9	8													1		2	1		1	2	4	1	2	1	3	4			
	Sonchus arvensis	1	2	3			3	3	2								3	3	2								1					2					2	3	3	2	2			
	Potentilla reptans		2	2		1		3	4	5	4																					3	3	2	3	2			1			3	5	4
	Hypochaeris radicata				3	3			1		5			3	3	4				1	2			2	4	4					4					1								2
	Trifolium repens				4	4			1		4									3	2				3	3				3	7					5		2	1		4			3
	Lathyrus pratensis	2	6	4	3	1											1	1	2	1													2		1	1			2			3		2
	Viola riviniana	1		2			1	1	3	1	3	1										1	1	1										1										
	Tragopogon pratensis								1	1							1	1	3			1	1	1															1	2		1		
	Ranunculus acris				3	3			1		3								1				1	1	2	2					1													
	Ononis repens									2			3	6	3	5																						3	2	1	4			
	Pilosella officinarum									2	1			1	1	2				1	2					2															4			
	Thymus polytrichus											1			4	4				3	6				2	7												2		2				
	Ranunculus bulbosus						1							2		1					1	1		1		2								1		1								
	Hieracium ssp.										1		1	1	1	1						1	2	2	2																			
	Leontodon autumnalis				1	1														1	1				3	2						3								1	4			
	Equisetum arvense																															2	3	2	3	2			1			3		1
	Prunus spinosa	1	2	2	2	1																																				1	3	4
	Viola tricolor												2	2		1								3	1	4										2								
	Veronica officinalis					2				1	3										3			1	3	4																		
	Potentilla erecta						1		1																		1	2	2	1	3													

Appendix 1.1. Continued.

Quadrat number	1					2					4					12					13					18					27					28					46		
	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed
Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003
Perennial species																																											
Viola canina													1	1	3			1						1	2																		
Anthyllis vulneraria									3	3			1	1									1						1														
Polygala spp.			3											2						3				1	1																		
Pyrola rotundifolia											4	2	2	3	2																												
Plantago lanceolata				1	1																									4												1	2
Centaurea nigra					3																			1	1					1					4								
Hydrocotyle vulgaris	4	5	4	1	4																																						
Potentilla anserina	2	3	2	2	2																																						
Ranunculus repens		3		1	2				2																															4			
Vicia cracca				1																												2	2	2				1					
Stellaria graminea	2		4	2	3																																						
Epipactis palustris	3	7	4									1																															
Equisetum palustre		1		4																																						1	3
Rumex acetosella								3	4	3																			1														
Polypodium vulgare												2	1	1																													
Equisetum variegatum																																				1	2				3		
Rubus caesius															2				1																								1
Heracleum sphondylium																																							1	1		1	
Crataegus monogyna																					1	1		1																			
Campanula rotundifolia									1	1																			1														
Leontodon saxatilis										1				2																													
Trifolium pratense				3																										3													
Prunella vulgaris					4																																						2
Hypericum perforatum																																	1		1								
Pimpinella saxifraga																								1	1																		
Epilobium montanum		1																																									
Parnassia palustris					1																																						
Dactylorhiza purpurella			1																																								
Epipactis leptochila											1																																
Plantago major					1																																						
Filipendula ulmaria					1																																						
Epilobium tetragonum					1																																						
Cardamine pratensis					1																																						

Appendix 1.1. Continued.

	Quadrat number	1					2					4					12					13					18					27					28					46		
		ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed
	Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003
Bryophytes	*Pseudoscleropodium purum*				3	2	4		2		2	3		3			3	2	5	5	5	3	4	6		2	2	2	4	4	4	3	4	8	4	7	2	2	4	2	4	5	3	
	Hylocomium splendens					1	5		4	5	5	5		5		5	2	2	4		4		3	4		8											4		3	2	2			
	Rhytidiadelphus squarrosus					3	7		4		7										3					2					4	2				4			2		2	4	2	4
	Rhytidiadelphus triquetrus									2	2					3	1		3	4	7			3		5					1						2		2				2	
	Brachythecium rutabulum																										4		3	1		3												
	Dicranum scoparium												8						1					2		2																		
	Hypnum cupressiforme													5	6	5																												
	Homalothecium lutescens					1										1																												
	Kindbergia praelonga																													1					2									
	Pleurozium schreberi											3		2																														
	Syntrichia ruralis var. ruraliformis																		2																									
	Campylium stellatum																														2													

Appendix 1.2. Dry dune habitats, NVC community SD7: Survey data 1987-2003. Figures are Domin values for percentage cover (1: <4% with few individuals, 2: <4% with several individuals, 3: <4% with many individuals, 4: 4-10%, 5: 11-25%, 6: 26-33%, 7: 34-50%, 8: 51-75%, 9: 76-90%, 10: 91-100%). Species sorted by number of occurrence across all years of survey. NVC = National Vegetation Classification (see Rodwell 2000).

	Quadrat number	3					11					14					16					32					36					37					40			42		
		ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed
	Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003	1992	1996	2003
Graminoids	*Ammophila arenaria*	1	1	1	1		2	4	4	3	3	4	5	5	4	5	5	7	5	7	5	7	8	7	8	7	4	6	4	3	5	4	7	6	8	7	4	3	4	5	6	3
	Carex arenaria	3	4	3	3	3	3	4	3	2	1	3	2	2					3	2	2						3	2	3	4	3	3	2	3	3	2	3	3	3		2	3
	Festuca rubra	6	5	4	4	4	1	4	2	4	5	8	7	7	7	5	8	9	5	6	6	6		8	3	4				2					4	3		2	3			
	Poa pratensis						1		2	3		2		3	2	2	4		2	3	2	3		3	3	3		1	1	2	2	2		2	3	2		1	2	2	3	
	Holcus lanatus									1	2				1	4				2	4	2	5	2	2	4					2	5	6	2	4	4		1	3	2	2	2
	Luzula campestris			1	1	2	1	1	3	2	3		1	2	2	3				1	2					2			1	3	3					1	2	3	3			
	Phleum arenarium	2	2	1	2	2	2		1	1																	3	2	3	1	1						3	2	2			
	Aira praecox				2	3		3	2	2																	2	1	3	2	2						2	1	2			
	Anthoxanthum odoratum								2	3	3	3	3	4	2	3																	2	1		2						
	Vulpia fasciculata	1																									2	1	3	3	2						4	2	2			
	Carex flacca																																			1				3	2	2
	Agrostis capillaris															1					3																					
	Agrostis stolonifera																						6																			
	Poa annua												4																													

Appendix 1.2. Continued.

	Quadrat number	3					11					14					16					32					36					37					40			42		
		ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed
	Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003	1992	1996	2003
Annuals and biennials	*Crepis capillaris*					1			3		2	1		2	2	2		1	4	3	4	1	1	1		2		1	1	3	3					1		1	3			
	Carlina vulgaris						1	1	1	2	1											1		1		1	1				2	2		2	2	1	2	1	3			2
	Erigeron acer						3	1		2	1											2		1	1				2	3	2	2		2	2	1	2	3	3			
	Arenaria serpyllifolia	1		1	1	3	3		2	3				1					1								3	2	2	3							3	3	1			
	Phleum arenarium	2	2	1	2	2	2		1	1																	3	2	3	1	1						3	2	2			
	Linum catharticum							1	2	2	3			1	3	3					3					1				2	3			1	1	1			3			
	Jasione montana					3	2	4	3	2	1												1	1				2	3	4	4				2			2	2			
	Centaurium erythraea					2	1	2	2	1	1						1				1									2	2					1		1	3			
	Aira praecox				2	3		3	2	2																	2	1	3	2	2						2	1	2			
	Euphrasia officinalis agg.								2	1	2	1	3	1	2	2															1								1			
	Cerastium semidecandrum			4		2			3					1					3										2								2	2	1			
	Vulpia fasciculata	1																									2	1	3	3	2						4	2	2			
	Daucus carota															3					4																			2	3	2
	Vicia sativa													3	1				5	2																						
	Geranium molle								1					1																						1	1					
	Valerianella locusta																		1					2										2			2					
	Rhinanthus minor														2	1					5																					
	Trifolium campestre								2					2	2																											
	Erophila verna			2					2																												2					
	Myosotis ramosissima													1					1																		2					
	Vicia hirsuta								1						1																											
	Trifolium dubium												1		1																											
	Geranium dissectum																																			2						
	Stellaria media												3																													
	Gentianella amarella												2																													
	Cerastium diffusum																																					2				
	Veronica arvensis																							1																		
	Erodium cicutarium																																					1				
	Senecio vulgaris																																				1					
	Poa annua												4																													
Lichens	*Peltigera spp.*	1					2		1	1	1																			1							2		1			
	Cladonia spp.								1	2	1																				1							1	1			
	Cladonia rangiformis					4				3	3																			1	3											
	Ramalina farinacea			1	2																									1												
	Hypogymnia physodes			1	1																																					
	Parmelia spp.																													1								1				

Appendix 1.2. Continued.

	Quadrat number	3					11					14					16					32					36					37					40			42		
		ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed
	Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003	1992	1996	2003
Perennial species	*Ononis repens*	2	3	2	1	3				1	4	5	5	5	4	5	4	4	4	4	4	4	4	4	4	7	4	5	3	5	5						5	5	8	4	1	2
	Senecio jacobaea						1			1			1	1		2		2	2	2	2	1	2	2	1	4	1			1	3	3		3	1	2	2	2	2	2	1	4
	Viola tricolor		1		1			1	2	1	3			1	1	4			2	2	3			2		4	2	1	2	2	2			1	2	1	3	2	2	1	1	
	Lotus corniculatus	3	2	4	4	4	4	6	5	4	4	4	3	3	2	4			1	4	4					2				3		4	3		3	5			2		2	
	Hypochaeris radicata					1	1		1	1	2	1		2	1	2			2	3	4	1		2		4				1	4	2		2	1	2	3	3	4			1
	Pilosella officinarum	1	1		3		2	4	5	5	5	1	2	2	2	3				2					1	2				3	5	1		2		2	2	3	4			
	Taraxacum sect. Ruderalia																																									
	(T. officinale Wigg. group)	1		1						1	2	1	1	3	1	2			1	2	2	1		1		1					2			1	1	2	2	1	1			
	Thymus polytrichus	4	5	5	5	5	4	7	3	5	6		1	1	4	2			2	4	6					2										1						
	Leontodon saxatilis	1				1	2	2	1		3										1	2			1		3	3	2	2	3		1					2	2			
	Viola canina				1	1			2	2	4				1	1								1	1	2			1	2	3					1		1	2			
	Polygala spp.			1					1	2	1				1	1			2		1					1	1				2	1		1	1			2	3			
	Sedum acre						2	4	2	2	1										2						1	1	3	4	3						2	3	3			
	Chamerion angustifolium																	1	2	5	5	1	1	1	1	1							3				2	1	1			4
	Salix repens										1				1	4																9	8	7	5	7				9	6	8
	Polypodium vulgare																					2	3	3	3	2						1				2		1	1		2	1
	Trifolium repens								3		2	1	1	2	2	3					1					2										1						
	Anthyllis vulneraria					4		1	3	3	5			1	1	2					2										2											
	Equisetum variegatum	1	3	2	2	2	3		2																												2	1	2			
	Cerastium fontanum		2							1	1				1				3					2						1	1						1					
	Ranunculus bulbosus								1	1	1		2		1	2					1			1		1																
	Rubus caesius											2	2	1	2	4										1										4			1			8
	Sonchus arvensis																5	3	2	1		3	1		1																	
	Pyrola rotundifolia																															2	3		8	4				5	7	7
	Hieracium ssp.								1						1																		1			1			1			1
	Epilobium montanum																									1						3		1		2				2	1	
	Veronica chamaedris									1	2					4					4															1						
	Leontodon autumnalis														1	1										1	1									1						
	Galium verum									1						3					3					4																
	Ranunculus acris											1		1	2	2																										
	Rumex acetosa												1		1	1																										
	Tragopogon pratensis														1					1																2						
	Veronica officinalis															1					2																					
	Plantago lanceolata																				1					1																
	Trifolium pratense														1	1																										
	Cirsium arvense																																			1						
	Viola riviniana																										1															
	Centaurea nigra										1																															
	Stellaria graminea							2																																		
	Heracleum sphondylium																			1																						
	Leucanthemum vulgare																																		1							

Appendix 1.2. Continued.

	Quadrat number	3					11					14					16					32					36					37					40			42		
		ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed
	Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003	1992	1996	2003
Bryophytes	*Hypnum cupressiforme*				2	4	4	4	3	5		5		5	2				1				9		3					4		2		2	2		2	2	3	4	2	
	Homalothecium lutescens				2	2				2	1				2	3			2		2									2				1	4	1		1			2	3
	Pseudoscleropodium purum						2						3	4	3	4			2	7	7				1	2						2									2	
	Brachythecium rutabulum																		3						1	4						2		3	1	2				2		
	Syntrichia ruralis var. ruraliformis				6	2	3	4																						2							4	3	2			
	Hylocomium splendens										2			1	2	3					2														1	4						
	Rhytidiadelphus squarrosus								2			2		3	2	4			2		1																					
	Rhytidiadelphus triquetrus								1		2	3		3	2	3																										
	Kindbergia praelonga																															3		2		3				2	3	3
	Lophocolea bidentata											4		1					1							2																2
	Dicranum scoparium									2															2															2		
	Campylium stellatum				3																	4		3																		
	Lophocolea spp.																															3		3							2	
	Pseudocalliergon lycopodioides																					9		8																		
	Tortella inclinata						4		3																																	
	Tortella flavovirens					4																																	2			
	Calliergonella cuspidata																																2									
	Bryum spp.																																					3				
	Barbula spp.																													2												
	Drepanocladus spp.																																						2			
	Homalothecium sericeum																																						1			
	Number of species	16	12	17	22	25	25	21	42	40	37	19	22	33	41	39	6	7	27	21	34	17	11	22	17	30	18	16	20	35	32	20	11	22	22	38	31	40	44	15	19	18

Appendix 1.3. Wet dune habitats, NVC community SD14: Survey data 1987-2003. Figures are Domin values for percentage cover (1: <4% with few individuals, 2: <4% with several individuals, 3: <4% with many individuals, 4: 4-10%, 5: 11-25%, 6: 26-33%, 7: 34-50%, 8: 51-75%, 9: 76-90%, 10: 91-100%). Species sorted by number of occurrence across all years of survey. NVC = National Vegetation Classification (see Rodwell 2000).

	Quadrat number	6					7					8					10					15					17					25					29					31					34					38					39			41			43			45		
		ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed
	Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003	1992	1996	2003	1992	1996	2003	1992	1996	2003
Graminoids	*Carex flacca*	2		5	2	4			3	2	3	3	1	3	2	2	8		4	2	2	4		1	2	3				5	4	4		2	6	7	4	5	2	3	4	3		2	2	4			1	3	4			3	4	5	4	5	4		3	2	3	3	5	5	3	2
	Carex arenaria	3		3	3	3		7	3	2	3							1	4	2	2	3	3	3	3	3	1	2	3	3	4	2	4	2	3	2		1	2	1							2	5	2	2	3		5	4	3	2	1	3	2	2	3	3	3	4	3	4	2	3
	Agrostis stolonifera	1		1	4	2	3			5	5	4	5		4	4	3		1	6	6	4	3		3	4			1	1	3				3	4	1		2	3	3	1			2	3			2	1	3	3		2	3	3		3	3	3	3	3			5	2	3	3
	Carex nigra	2	5	2					2			5					3	8	2	3	4										6						3		4	3	4						3		5	4	4	1				2			4			2	2	3	2	2	3	2
	Holcus lanatus						2		4	4	3	4	6	3	2	3						1			1	1																4	4	5		4				3	2					3	4	2	1		1	1		2	4		1	
	Poa pratensis						3		2	5	2	1	1		2										1																		3		2	2				2	2			3	5	3	3	5	2				6	5	3			
	Carex panicea	1											5						3		4		4	4		4		7	5		6	2	8	3		4		3	2																	5				4		5				2	3	4
	Juncus articulatus	1	4			3												5	3	2	4					3			2	2	4					2															2					2	2		4	3	1	4				2	3	3
	Festuca rubra			1			7		4	5	4	3		5	4	4			2			2		1	2	1																												1	3	3							3	3	3			
	Schoenus nigricans																					1	2	3	4	5											5	7	6	7	7	6	8	8	8	6														3	4	4						
	Danthonia decumbens					3	2	2	3	1	2					3										2					2								1	4	3					4																						
	Carex viridula viridula	1		1	2	5													2	3	3																				2																	2									2	3
	Anthoxanthum odoratum						2		2		3				3	2						3			2	3																									1														2			
	Agrostis capillaris							4	3	3	4			4	1	1																									1														1													
	Briza media											2	2	4	4	3																																																				
	Luzula campestris												2	3	2	2																																																				
	Agrostis vinealis																																																					2									1			2		
	Juncus acutiflorus												1															2																									3															
	Ammophila arenaria																																																														1	3				
	Carex hirta																																																																		1	1
	Molinia caerulea																																																																			2
	Aira praecox																																			1																																
	Carex viridula oedocarpa																																						1																													
	Carex caryophyllea																		2																																																	
	Juncus maritimus																																								2																											
	Juncus bufonius																									1																																										

Appendix 1.3. Continued.

Quadrat number	6					7					8					10					15					17					25					29					31					34					38					39			41			43			45		
	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed
Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003	1992	1996	2003	1992	1996	2003	1992	1996	2003
Perennial species																																																																			
Salix repens	6	5	7	6	5	2	5	4	8	7	4	5	5	4	7	6	6	6	4	5	6	6	5	5	7	7	9	5	8	8	5	7	7	8	6	4	7	5	6	6	3		4	2	4	8	9	8	6	5	8	8	8	6	8	7	6	8	6	5	5	7	4	7	8	5	8
Equisetum variegatum	3	5	3	3	3	1	4	1	2	3	2	8	3	3	3	4	8	2	5	4	4	5	3	3	3	6	9	6	6	4	4	8	5	4	4	3	4	3	4	3	3	3	2	2	2	3	3	2	2	2	3	3	2	2	3	3	3	3	5	3	3	5	3	3		3	2
Lotus corniculatus	6	8	8	7	5	4	6	4	3	5	6	7	5	5	3	5	4	3	5	4	3	1	3	3	4	3	3	3	5	4	4	4	4	3	4	3	1		3	4	3	2	1	2	5	5	3		2	3	5	5		2	5	4	2	5	3	3	4	5	2	5	4	7	4
Hydrocotyle vulgaris	7	9	5	4	9	7	5	3	3	8	7	7	5	1	2	5	8	5	4	7	1	1	3		1	3	2	2	4	4	2	1	1			6	9	4	4	7	4	6	4	3	4	8	8	8	7	8	3	2	1	3	9	3	3	7	2	1	3			4	4	5	7
Mentha aquatica	1	3	1	2	4							1	1	2								2	2		2			1	3	2						5	5	1	4	4	3	3	3	2	4					2						3	3	4	2	2	2	3	2	4	2	2	
Potentilla anserina	2	2	2	3		4	6	5	1	2																															1	1	1	2	5	3	7	5	3	5	4	7	5	5	4	5	5	5		1	2	6	2	4	3	2	4
Prunella vulgaris					1	1		1	2	2	1		1	2	2	2		3	1	3	2		3	1	3	1										3		3	2	2	1	1	3	2	2											2		3	2	3	3	1		4		2	
Ranunculus flammula	2	2	1	2	4												2	1	1	3		2			1					1						2	4	2		2			1	1	1		2									1	2	1		1	2			1	4		2
Taraxacum sect. Ruderalia (*T. officinale Wigg. group*)					2		2	1	2	2			1	1	2								1		1					2					2			2		1	3	1	2		4										1	2	1	4		1	2	2		2			1
Parnassia palustris	1							2	1						3				1	1	2							1		2	2	1			2	2		1	3	1	2		2		4											3			2	1	2			2	3	2	
Leontodon saxatilis	1		3	4	3									1	2	2	2	3	1	3	1		3	3	3			1	1							1	1		2	1	3	1																		2	2					2	
Epipactis palustris									1							3	4	4	6	7						3	3	4	4	7	4	3	5	4	5					1																		2	3	3	4				3	3	4
Hypochaeris radicata		2	3					1		1		1	2	1	4			3					1					1							1			3	1		1		2	1	1			1						1		4			3		2				1		
Pyrola rotundifolia											2	1	2	1				2			4	1	2		2	1		2	1		5		4	5	4						1		3	3	2									3					2	2							
Trifolium repens	1			1				2	3	2		1	2	2	3														1	2					1					1				1	2				1	7						2		3				3		2		2	
Anagallis tenella					3										2	2		3	3	4	1	1	3		4											2		2	2		3	3	1	1	4															3	4					2	
Ranunculus acris								2	3	4				2	3					1					1													1	1								1					1	1	1	2			1				4	2	4			
Leontodon autumnalis				1					2	1				2	1				3	2					1									1	1										1				2	4				2			4								4	2	
Rubus caesius				2	2														1	1																		1	4	4	2		1	1	2										1							3	4	4			
Viola canina						1		1	1	3																												1	3	3													1	4	2							2	1	1			
Pinguicula vulgaris																					2	2	2		4	1	1	1													2	1	2																3		3						
Polygala spp.										1	1		3	2	3			1		1										1			1																										2	1	1						
Dactylorhiza purpurella													2					1					1														1	1	1				1	1	2																1					1	
Senecio jacobaea										1			2	2	2									1	2																		1	1	1											1								1			
Pilosella officinarum													1	1	3						1		1	2									1	1	1																								2	2							
Dactylorhiza incarnata	1	1	1	1	1				1				1			1																									1									2																	
Ranunculus repens						1																																										1	2	4						2	3	4					2		1	1	
Sonchus arvensis						2	2	4	3		2	2	4	2																														1																							
Anthyllis vulneraria														1	1				1				1	3	3				1	1					1																																
Equisetum arvense											2	2	2	2	2																															1		1					2	1													

Appendix 1.3. Continued.

Quadrat number	6					7					8					10					15					17					25				
	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed
Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003
Perennial species																																			
Selaginella selaginoides													2		3																				
Hieracium spp.															1		1																	1	
Bellis perennis													1												1										
Eleocharis quinqueflora					2																														
Ononis repens														1	1																			1	1
Rumex acetosa																																			
Ranunculus bulbosus													1	2	2																				
Crataegus monogyna											1	1	1	1																					
Betula pubescens											1	1	1	1																					
Rosa canina agg.																																			
Cerastium fontanum															3																				1
Cirsium arvense								1																											
Plantago lanceolata																																			
Cardamine pratensis																																			
Samolus valerandi																					1														
Potentilla erecta					1																														
Listera ovata															1																				
Equisetum palustre																																			
Eleocharis multicaulis	1																																		
Triglochin palustre																												1							
Sagina nodosa																																			1
Thymus polytichus															2																				
Viola riviniana																																			
Sedum acre																		1																	
Prunus spinosa																								1											
Trifolium pratense															1																				
Campanula rotundifolia								1																											
Rubus fruticosus																																			
Veronica officinalis															2																				
Centaurea nigra															1																				
Primula vulgaris								1																											

Quadrat number	29					31					34					38					39			41			43			45		
	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed
Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003	1992	1996	2003	1992	1996	2003	1992	1996	2003
Perennial species																																
Selaginella selaginoides						4		3																		1						
Hieracium spp.							1					1																				
Bellis perennis						1		4	1																							
Eleocharis quinqueflora															3								2			4						
Ononis repens																																
Rumex acetosa															2				1	2										1		
Ranunculus bulbosus																1																
Crataegus monogyna																																
Betula pubescens																																
Rosa canina agg.						1		1	2	1																						
Cerastium fontanum																					1											
Cirsium arvense														1	2																	
Plantago lanceolata								2	1	1																						
Cardamine pratensis															1					1												1
Samolus valerandi							1																									
Potentilla erecta																												1				
Listera ovata																			1													
Equisetum palustre																				1												
Eleocharis multicaulis																																
Triglochin palustre																																
Sagina nodosa																																
Thymus polytichus																																
Viola riviniana																1																
Sedum acre																																
Prunus spinosa																																
Trifolium pratense																																
Campanula rotundifolia																																
Rubus fruticosus							1																									
Veronica officinalis																																
Centaurea nigra																																
Primula vulgaris																																

Appendix 1.3. Continued.

	Quadrat number	6					7					8					10					15					17					25					29					31					34					38					39			41			43			45		
		ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	grazed
	Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003	1992	1996	2003	1992	1996	2003	1992	1996	2003
Annuals and biennials	*Euphrasia officinalis agg.*				3					2			1	1	1	3			3	2		2		2	1	3				3				2	3	4										1					1										1	2			1			
	Rhinanthus minor									4							1		1			1		1		3				1		3		3	3	5																									1				4			
	Crepis capillaris	1		3			1										1					1															2		1			3			1		2				1	2																
	Linum catharticum														1	2				1	1				3	2									2	3																															1	
	Gentianella amarella														1	1			2																																										1							
	Carlina vulgaris														1				2					1																																												
	Anagallis arvensis																																																											2								
	Cerastium semidecandrum														1																																																					
	Trifolium micranthum															2																																																				
	Centaurium littorale																									1																																										
	Aira praecox																																			1																																
Bryophytes	*Calliergonella cuspidata*				3	3	9	8	4	8	5										2										2										4			2	8	8	9	9	9	4	6	10	9	10	6	9	7	6	8						4	2	7	7
	Campylium stellatum	4		5	2	2						3					3		2	3	7	4	4	4	4	5			8		3					4	4		3		7			2																		7			2			2
	Pseudocalliergon lycopodioides	7	7	8																							4	8	6		7						9		8	9	7																											
	Bryum pseudotriquetrum													3	2	2	4	4	3	3	1						4																																									
	Scorpidium revolvens	3															3		2		3																					3	5		2																							2
	Rhytidiadelphus triquetrus										4			2	1	3			6	2	2																																															
	Drepanocladus aduncus				2	7														2							4			6																																					3	4
	Bryum spp.															2						4			2	1										2																																
	Pseudoscleropodium purum									2	3				3	2																																																				
	Hypnum cupressiforme																																		1	2		9																												4		
	Homalothecium lutescens														3	3																				1										2																						
	Kindbergia praelonga			2	3																																				?1				2																							
	Preissia quadrata																2															2	9																																			
	Brachythecium rutabulum																																											2		3																						
	Hylocomium splendens						3		3																																																											
	Lophocolea spp.											3			1																																																					
	Plagiomnium undulatum															2																														3																						
	Lophocolea bidentata															2																																																				
	Riccardia spp.																2																																																			
	Tortella inclinata											2																																																								
	Barbula spp.																								2																																											
	Amblystegium serpens																																																																		3	
	Barbula convoluta																																		2																																	
	Bryum capillare																																	2																																		
	Campyliadelphus elodes	4																																																																		
	Warnstorfia fluitans																													4																																						
	Leiocolea badensis																										4																																									
	Lophozia spp.																3																																																			
	Drepanocladus spp.																																								2																											
	Tortella flavovirens																									3																																										
	Number of species	24	12	20	21	24	18	11	27	27	26	21	21	31	42	48	20	12	31	25	27	24	14	24	22	35	13	10	18	18	22	12	9	14	17	29	17	13	25	22	27	25	17	27	27	31	10	10	13	17	26	11	9	14	20	22	21	17	22	19	25	29	18	17	27	21	29	23

Appendix 1.4. Wet dune habitats, NVC community SD16: Survey data 1987-2003. Figures are Domin values for percentage cover (1: <4% with few individuals, 2: <4% with several individuals, 3: <4% with many individuals, 4: 4-10%, 5: 11-25%, 6: 26-33%, 7: 34-50%, 8: 51-75%, 9: 76-90%, 10: 91-100%). Species sorted by number of occurrence across all years of survey. NVC = National Vegetation Classification (see Rodwell 2000).

	Quadrat number	5					9					30					33					35					44		
		ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	grazed
	Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003
Graminoids	*Holcus lanatus*	5	7	2	3	2	2	4	3	2	3	4	6	3	3	4	6	8	5	2	5	4	3	3	2	4	2	3	1
	Poa pratensis	2		2	2	1	2	4	2	3	3	5		4	3	2	2	4	3	3		3		4	2	3	3	2	2
	Carex flacca	2	4	1		2		2	2	1	3		1	2	2	3	2	2	2	2	4		1	2	2	3	2	1	3
	Anthoxanthum odoratum			2	3	5			2	3	3			1	3	4	5		4	3	4	4	7	4	4	3	5	3	3
	Carex arenaria				2	1		2	2	2	3	2			2	2	1		2	3	3	2	4	2	2		5	2	
	Festuca rubra	5		5	7	4				2		5		8	8	5			3	7	5			2	3	3	3	3	4
	Luzula campestris	1	2	2	2	2				1	1			1	2	3		1	3		2		1	3			3	1	1
	Agrostis stolonifera	2	7	2	2	2							8				4		1	2	4				2			1	
	Agrostis capillaris			1						1									2	3	4							2	2
	Ammophila arenaria						3	4	5	5	2					3													
	Cynosurus cristatus																							3	3	3		2	2
	Danthonia decumbens		1	1		1															2								
	Arrhenatherum elatius									1	2					3													
	Carex nigra	2																			2								4
	Carex panicea																2											1	3
	Briza media				2	4																							
	Festuca ovina																											3	3
	Aira caryophyllea					3															2								
	Juncus articulatus																									2			3
	Juncus acutiflorus																1												
	Juncus bufonius																												2

Appendix 1.4. Continued.

	Quadrat number	5					9					30					33					35					44		
		ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	grazed
	Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003
Perennial species	*Equisetum variegatum*	2	4	2	3	2	1	3		2	2	3	2	3	3	2	2	4	3	2	3	3	5	4	3	3	4	4	3
	Salix repens	6	6	7	8	8	9		8	8	8	9	8	7	6	7		7	7	6	7	8	9	6	7	7	5	4	6
	Lotus corniculatus	4	2	4	5	5		2	1	2	3	4	7		2	7	5	7	1	3	5	4	5	1	4	3	3	3	5
	Pyrola rotundifolia			2			5	5	5	4	5	6	6	4	3	4	4	6	7	4	2	3	1	4			4	3	2
	Hypochaeris radicata				2	4			3	3	1			1	1	4	1	1	2	2	4			1		2	2	1	3
	Ononis repens	7		5	4		1	1		5	5		5	3	2	4					1	2		3	3		2	1	2
	Prunella vulgaris	1		1	1	3								2	2	2			1		2		1	2	2	2	2	1	3
	Polygala spp.	1		3	1	3		1	2	1	1				2	4			1			1			2	2		1	2
	Senecio jacobaea			1	2	1	2	2	3	1						1	1	1	2	1				1				1	2
	Hydrocotyle vulgaris															2	3	5	2	1	4	5	6	4	4	5	3	2	3
	Taraxacum sect. Ruderalia (T. officinale Wigg. group)					1			2	1	1			1	1	2					3	1		2		3		1	2
	Leontodon autumnalis				2	1					1				1	1				1	2				3	2	2	3	2
	Trifolium repens	1	2	2	2	4														1	3			4	6	2			2
	Cerastium fontanum			1	2	1			1					1			1		1		1			1		3		1	
	Pilosella officinarum	1		3	4	3					1					1	1		2		2								
	Ranunculus acris	1		1	3	3																		2	3	4		1	4
	Hieracium spp.					1	1	2		4	5				1			1				2						1	
	Potentilla anserina																					1	1	1	5	2	2	1	2
	Leontodon saxatilis	1	1	1	2	4			1																			1	1
	Rubus caesius						1		1	4	5	1		1	3	5													
	Sonchus arvensis														1	4				1							5	4	2
	Plantago lanceolata									1	1														3	2		1	1
	Dactylorhiza purpurella					2																			1	1		1	1
	Epilobium montanum						2	1		1	1											1							
	Bellis perennis	1		3															2								2		1
	Trifolium pratense					1																			3	5		2	4
	Listera ovata			1		1									1													1	
	Mentha aquatica																						1		4	3			
	Viola canina								1	1	2																		
	Parnassia palustris																				2			1					
	Ranunculus flammula																		1										1

Appendix 1.4. Continued.

	Quadrat number	5					9					30					33					35					44		
		ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	grazed
	Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003
Perennial species	*Anagallis tenella*					2																							3
	Selaginella selaginoides	3															2												
	Rumex acetosa																								1	1			
	Thymus polytichus	1		1																									
	Anthyllis vulneraria					1														1									
	Ranunculus repens			1	2																								
	Rubus fruticosus							1					1																
	Epipactis palustris																												1
	Dactylorhiza incarnata			1																									
	Galium palustre																									1			
	Equisetum palustre																				1								
	Dactylorhiza fuchsii					2																							
	Cirsium arvense							2																					
	Equisetum arvense		1																										
	Ranunculus bulbosus																					1							
	Chamerion angustifolium															2													
	Epipactis leptochila							1																					
	Viola spp.																												1
Annuals and biennials	*Euphrasia officinalis agg.*	2	4	3	1								1				3	2		2	3				2			1	3
	Carlina vulgaris			1		1			2	1	1	1		1		1	1	1	2										
	Linum catharticum	3		1	3	2			1	1	2				3										2			1	3
	Crepis capillaris									1				1	1		2			2		2						1	1
	Rhinanthus minor			1	4	5			2	2	1																		6
	Aira caryophyllea					3															2								
	Centaurium erythraea								2																				
	Daucus carota										4																		
	Trifolium dubium																1												
	Trifolium campestre																		2										
	Erigeron acer													1															

Appendix 1.4. Continued.

	Quadrat number	5					9					30					33					35					44		
		ungrazed	grazed	grazed	grazed	grazed	ungrazed	grazed	grazed	grazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	ungrazed	grazed	ungrazed	ungrazed	ungrazed	grazed	grazed	ungrazed	ungrazed	grazed
	Year of survey	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003
Bryophytes and lichens	*Pseudoscleropodium purum*					4	8	7	8	8	8			2	6	4	3		2	3	3								
	Brachythecium rutabulum	3		2								2	4	2	3			1		1	1				2			3	4
	Lophocolea spp.						4	1				2		2					1			3						2	
	Kindbergia praelonga													2	2				2	2		3		2					
	Homalothecium lutescens					1				2	2						1							2					
	Dicranum scoparium						2	2	2	2							1												
	Campylium stellatum	3	2													3					3								
	Plagiomnium undulatum																		2	1	1								3
	Hypnum cupressiforme						3				3			3															
	Calliergonella cuspidata																					3		4		4			
	Rhytidiadelphus squarrosus									2	2								2										
	Pleurozium schreberi								4			1		2															
	Riccardia spp.																1					3							
	Fissidens taxifolius														3													2	
	Cladonia spp.	1		1																									
	Rhytidiadelphus triquetrus					2																							
	Bryum pseudotriquetrum																											2	
	Drepanocladus polygamus																						3						
	Eurynchium striatum											2																	
	Mnium hornum																											2	
	Number of species	25	13	33	26	39	15	19	24	32	31	14	11	24	27	28	25	15	29	25	32	21	14	26	26	28	19	42	44

APPENDIX 2: RESULTS OF VEGETATION SURVEY AND STATISTICAL TESTS FOR CHAPTER 5

Appendix 2.1. National Vegetation Classification (NVC) survey data for eleven 2 x 2 m quadrats in the experimental area, May 2004. Figures are Domin values for percentage cover (1: <4% with few individuals, 2: <4% with several individuals, 3: <4% with many individuals, 4: 4-10%, 5: 11-25%, 6: 26-33%, 7: 34-50%, 8: 51-75%, 9: 76-90%, 10: 91-100%).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Achillea millefolium				2		2	2		1		
Agrostis capillaris	2	2	2	2	2	3	2		3	4	
Aira praecox	1										
Ammophila arenaria	2	1	1					1			4
Anagallis arvensis					3						
Anthoxanthum odoratum	1	2	2	3		3	3	3	5	5	3
Arenaria serpyllifolia							1				1
Arrhenatherum elatius	3	3	4	3	4	4	4	4	3	5	4
Carex arenaria	3	3	2	4	4	4	4	4	3	4	5
Cerastium fontanum	3	2	2	2	4	3	3	2	1	3	4
Crepis capillaris	1	2		2	1		2		2	2	3
Dicranum scoparium	4									2	
Festuca rubra	5	5	5	6	5	6	7	6	5	7	7
Galium verum	2	6		2	2	2	2	4	4		3
Geranium molle					1	2		1	1		
Holcus lanatus	2	4	2	5	4	3	3	2	2	2	
Homalothecium lutescens		3	4		1		2	3			7
Hylocomium splendens	7	4		4	2	4	2	2	7	7	
Hypericum perforatum								5			
Hypnum cupressiforme					3		2			4	2
Hypochaeris radicata		1	1	1	1					4	4
Kindbergia praelonga		1			4						2
Lotus corniculatus	4	2	1	4	2	2	2	4	3	4	4
Luzula campestris	4	3	4	4	3	2	4	1	4	5	5
Ononis repens					1					4	
Pilosella officinarum										1	2
Poa pratensis	2	2						1		2	
Polygala spp.									2		
Pseudoscleropodium purum	5	7	5	5	5	8	8	7	7	3	7
Ranunculus bulbosus	2	2	2	4	2	4	2			1	2
Rhytidiadelphus squarrosus	1	2	3	5	5	2	4	7	3	1	5
Rhytidiadelphus triquetrus	5	4	5	5		4	3	3	2	5	2
Rosa pimpinellifolia		1									
Rubus caesius					2				2		
Rumex acetosa		2	2						2		
Rumex acetosella										2	
Senecio jacobaea	1	2	5	4	2	2	2	4	5	1	2
Sonchus oleraceus										1	
Taraxacum sect. *Ruderalia* (*T. officinale* Wigg. group)	1	1	2	2		2	2	2	2	1	3
Thymus polytrichus	4			2						2	3
Trifolium spp.		1	2		1	1	1	2	1	2	
Veronica chamaedrys	2	3	4	3	2	2	2	4	4	4	4
Veronica officinalis				1				4			
Vicia hirsuta			1								
Vicia sativa	2	2	2	2	2	2	2	1	2		2
Viola canina								1		2	
Viola tricolor	1		1	4	2	3	2	2	4	1	
Total number of species	**26**	**28**	**24**	**25**	**27**	**23**	**26**	**26**	**26**	**30**	**25**

Appendix 2.2. Average values for soil parameters for the interaction of grazing and nitrogen treatments for topsoil samples taken in May 2003 (baseline) and May 2005, adjusted for the baseline as covariate, and results of Anova analyses (OM = organic matter, s.e.d. = standard error of the differences of means). C = carbon was only measured for May 2005 samples.

	Nitrogen	Unwatered control	Unwatered control	Unwatered control	Watered control	Watered control	Watered control	Low N	Low N	Low N	High N	High N	High N			
	Grazing	**Ungrazed**	**Rabbit grazed**	**Rabbit and pony grazed**	**Ungrazed**	**Rabbit grazed**	**Rabbit and pony grazed**	**Ungrazed**	**Rabbit grazed**	**Rabbit and pony grazed**	**Ungrazed**	**Rabbit grazed**	**Rabbit and pony grazed**	**f ratio**	**p value**	**s.e.d.**
Moisture content (%)	2003	16.55	17.62	11.80	14.23	12.30	11.23	11.54	10.30	10.31	6.87	11.07	9.343	0.50	0.797	3.843
	2005	23.14	22.07	17.44	25.19	17.50	15.97	19.34	16.87	20.28	19.67	20.90	22.160	1.46	0.254	4.116
Organic matter content (%)	2003	10.94	10.33	9.52	9.74	7.63	7.46	8.09	7.45	6.77	7.96	8.98	9.143	0.46	0.828	1.779
	2005	7.74	8.88	9.95	10.02	8.27	6.84	8.42	9.73	8.54	8.54	9.26	9.710	0.98	0.470	2.052
pH (H2O)	2003	5.29	5.24	5.17	5.22	5.49	5.41	5.37	5.60	5.45	5.15	5.32	5.41	0.43	0.848	0.197
	2005	5.84	5.98	5.74	5.93	6.09	5.53	6.02	6.11	6.05	5.61	6.19	5.98	0.75	0.618	0.390
pH ($CaCl_2$)	2003	4.89	4.92	4.70	4.81	4.80	4.77	4.60	4.89	4.73	4.73	4.59	4.64	0.40	0.871	0.219
	2005	4.95	4.90	4.76	5.05	4.87	4.81	5.00	5.02	5.00	4.92	5.17	5.00	0.86	0.544	0.186
N (%)	2003	0.393	0.353	0.337	0.290	0.287	0.280	0.313	0.273	0.257	0.317	0.320	0.097	1.43	0.259	0.068
	2005	0.151	0.372	0.149	0.169	0.179	0.102	0.164	0.251	0.152	0.154	0.326	0.299	0.81	0.578	0.137
Available NO3-N (μg/g dry soil)	2003	5.85	4.23	3.19	6.31	3.33	7.36	6.50	2.15	4.95	5.44	1.58	8.62	0.97	0.470	2.844
	2005	0.47	1.32	0.71	0.70	0.67	0.92	0.35	0.75	0.65	0.78	0.71	1.84	0.87	0.538	0.589
Available NH_4-N (μg/g dry soil)	2003	7.34	5.65	5.77	6.18	6.89	6.40	5.63	4.94	3.72	7.32	8.86	7.46	0.12	0.992	3.564
	2005	18.83	15.81	13.83	13.23	9.98	10.19	11.21	12.54	15.57	11.76	14.01	12.81	0.44	0.843	4.842
Available NO_3-N (μg/g OM)	2003	55.7	36.6	40.7	78.9	40.8	95.0	76.4	29.1	72.9	68.1	19.6	88.3	0.53	0.780	33.06
	2005	5.5	14.4	7.9	7.6	8.4	15.2	4.8	9.5	8.5	12.7	8.6	14.7	0.54	0.773	6.61
Available NH_4-N (μg/g OM)	2003	61.1	48.2	70.0	56.5	94.0	85.1	74.6	67.1	56.2	91.6	97.1	79.7	0.35	0.898	34.82
	2005	208.6	172.8	137.3	135.6	125.7	143.9	138.5	137.6	183.0	151.2	145.1	129.4	0.86	0.543	39.24
C (%)	2005	3.433	4.547	4.080	4.157	3.390	2.767	3.313	3.837	3.117	3.223	4.430	3.915	0.82	0.568	0.875
C (%) : N (%)	2005	17.300	14.400	23.500	28.800	19.600	28.700	20.700	16.800	23.300	23.500	15.600	22.300	0.30	0.928	4.900

Appendix 2.3. Average values for soil parameters in the different grazing and nitrogen addition treatments for subsoil samples taken in May 2003 (baseline) and May 2005, adjusted for the baseline as covariate, and results of Anova analyses (OM = organic matter, s.e.d. = standard error of the differences of means). Total N was not analysed in May 2005 samples. a) By grazing treatment, b) by nitrogen treatment, c) for the interaction of grazing and nitrogen treatment.

a)

		Ungrazed	Rabbit grazed	Rabbit and pony grazed	f ratio	p value	s.e.d.
Moisture content (%)	2003	1.85	4.03	1.92	19.91	**0.008**	0.394
	2005	6.97	5.44	6.41	0.59	0.606	1.513
Organic matter content (%)	2003	2.02	2.10	1.87	0.55	0.617	0.2170
	2005	1.74	1.77	1.73	0.17	0.850	0.0687
pH (H2O)	2003	5.25	5.22	5.07	0.79	0.512	0.1517
	2005	6.09	6.28	5.94	0.15	0.868	0.6235
pH ($CaCl_2$)	2003	5.08	4.96	4.83	1.39	0.347	0.1499
	2005	5.06	5.35	5.32	2.84	0.203	0.1346
N (%)	2003	0.0535	0.0587	0.0271	2.13	0.235	0.01647
Available NO_3-N (µg/g dry soil)	2003	4.64	3.82	4.29	0.40	0.696	0.928
	2005	0.56	0.43	0.39	0.43	0.685	0.1939
Available NH_4-N (µg/g dry soil)	2003	0.90	2.09	1.96	8.25	**0.038**	0.322
	2005	5.84	5.64	5.04	3.96	0.144	0.427
Available NO_3-N (µg/g OM)	2003	237	189	226	0.72	0.542	41.70
	2005	31.7	27.5	23.2	0.16	0.860	16.26
Available NH_4-N (µg/g OM)	2003	44	103	108	8.22	**0.038**	17.50
	2005	336.7	317.3	306.9	0.23	0.804	39.09

b)

		Unwatered control	Watered control	Low N	High N	f ratio	p value	s.e.d.
Moisture content (%)	2003	2.12	3.88	1.73	2.68	1.84	0.176	0.977
	2005	6.00	6.32	6.34	6.44	0.27	0.843	0.629
Organic matter content (%)	2003	1.86	2.09	1.97	2.07	0.96	0.435	0.1512
	2005	1.74	1.76	1.90	1.58	2.59	0.087	0.1132
pH (H2O)	2003	5.23	5.09	5.27	5.12	2.59	0.084	0.0749
	2005	6.05	6.12	6.12	6.12	1.02	0.408	0.0535
pH ($CaCl_2$)	2003	4.97	4.99	4.84	5.03	2.67	0.078	0.0718
	2005	5.27	5.19	5.26	5.25	1.36	0.289	0.0399
N (%)	2003	0.0378	0.0425	0.0571	0.0483	0.86	0.480	0.01261
Available NO_3-N (µg/g dry soil)	2003	5.24	4.63	3.29	3.85	2.86	0.066	0.7180
	2005	0.54	0.38	0.35	0.56	1.52	0.245	0.1268
Available NH_4-N (µg/g dry soil)	2003	1.67	1.47	1.23	2.23	0.47	0.706	0.874
	2005	5.65	5.46	5.96	4.96	2.13	0.135	0.409
Available NO_3-N (µg/g OM)	2003	284	229	171	185	2.91	0.063	42.30
	2005	31.3	21.3	19.8	37.5	2.76	0.074	7.65
Available NH_4-N (µg/g OM)	2003	88	70	65	117	0.49	0.694	47.80
	2005	345.1	308.1	322.2	305.8	0.93	0.448	26.59

Appendix 2.3. Continued.

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	Nitrogen	**Unwatered control**	**Unwatered control**	**Unwatered control**	**Watered control**	**Watered control**	**Watered control**	**Low N**	**Low N**	**Low N**	**High N**	**High N**	**High N**			
	Grazing	**Ungrazed**	**Rabbit grazed**	**Rabbit and pony grazed**	**Ungrazed**	**Rabbit grazed**	**Rabbit and pony grazed**	**Ungrazed**	**Rabbit grazed**	**Rabbit and pony grazed**	**Ungrazed**	**Rabbit grazed**	**Rabbit and pony grazed**	**f ratio**	**p value**	**s.e.d.**
Moisture content (%)	2003	1.82	2.68	1.85	1.63	8.11	1.89	0.91	1.70	2.56	3.02	3.64	1.370	2.23	0.088	1.517
	2005	7.00	5.51	5.48	6.56	6.66	5.73	6.95	4.22	7.85	7.36	5.36	6.60	1.46	0.251	1.543
Organic matter content (%)	2003	1.91	1.98	1.68	1.94	2.25	2.07	1.93	2.06	1.93	2.29	2.09	1.812	0.60	0.725	0.3139
	2005	1.58	1.67	1.97	1.79	1.83	1.66	2.02	1.91	1.76	1.56	1.66	1.52	1.24	0.334	0.1826
pH (H2O)	2003	5.20	5.31	5.18	5.15	4.97	5.15	5.46	5.39	4.96	5.17	5.20	4.99	2.70	**0.047**	0.1888
	2005	6.05	6.24	5.87	6.07	6.28	6.02	6.16	6.26	5.93	6.08	6.33	5.95	0.52	0.786	0.6180
pH ($CaCl_2$)	2003	4.90	5.14	4.86	5.15	4.91	4.91	4.96	4.77	4.78	5.30	5.03	4.75	2.84	**0.040**	0.1846
	2005	5.19	5.31	5.30	4.93	5.35	5.30	5.03	5.45	5.29	5.08	5.27	5.40	3.25	**0.026**	0.1403
N (%)	2003	0.0454	0.0529	0.0152	0.052	0.052	0.0236	0.0774	0.0701	0.0236	0.0392	0.06	0.0458	0.67	0.677	0.0251
Available NO3-N (µg/g dry soil)	2003	5.84	4.77	5.12	4.44	4.24	5.21	3.60	2.44	3.83	4.70	3.82	3.01	0.49	0.806	1.422
	2005	0.74	0.58	0.30	0.32	0.36	0.45	0.34	0.32	0.39	0.83	0.45	0.40	1.16	0.373	0.2653
Available NH_4-N (µg/g dry soil)	2003	0.57	1.35	3.08	1.46	2.14	0.81	0.87	1.69	1.13	0.69	3.17	2.82	0.68	0.665	1.350
	2005	5.78	5.71	5.47	5.44	5.5	5.44	6.92	5.91	5.07	5.22	5.45	4.21	0.87	0.538	0.7730
Available NO_3-N (µg/g OM)	2003	306	252	294	248	188	250	188	120	204	206	197	153	0.30	0.930	76.00
	2005	40.4	38.2	15.3	19.5	20.5	23.9	16.7	19.5	23.0	50.1	31.8	30.5	1.13	0.387	19.14
Available NH_4-N (µg/g OM)	2003	31	67	168	70	95	44	46	85	63	29	164	157	0.66	0.683	73.70
	2005	378.5	355.5	301.2	311.3	280.6	332.4	354	308.1	304.3	302.8	325.1	289.6	0.76	0.609	53.58

Appendix 2.4. Average sward heights in cm between 12 June 2003 and 28 June 2005 for controls, low N and high N treatments, and results of Anova analyses. Grazing effects were analysed both with and without using the first measurement as covariate, nitrogen effects and the interaction of nitrogen and grazing with covariate. s.e.d. = standard error of the differences of means.

	12-Jun-03	26-Jun-03	10-Jul-03	26-Jul-03	10-Aug-03	24-Aug-03	21-Sep-03	11-Oct-03	30-Oct-03	03-Dec-03	14-Jan-04	10-Feb-04	07-Mar-04	28-Mar-04	17-Apr-04	30-Apr-04	22-May-04
Grazing (with covariate)																	
Ungrazed	7.18	5.59	6.41	6.70	7.50	6.79	6.87	6.48	5.93	4.91	4.84	4.58	5.07	5.30	6.03	7.08	9.75
Rabbit grazed	5.30	5.06	5.17	4.70	5.21	4.41	4.60	3.88	3.40	3.01	2.49	2.57	2.64	2.86	2.77	3.21	3.79
Rabbit and pony grazed	4.51	4.66	5.19	5.00	4.75	4.46	4.60	3.74	3.34	3.12	2.49	2.68	2.82	3.01	2.78	3.34	4.03
f ratio	7.80	1.20	1.27	2.68	6.99	2.40	2.29	6.34	15.10	4.27	3.69	4.73	5.13	5.91	47.92	26.71	36.11
p value	**0.042**	0.414	0.399	0.215	0.074	0.239	0.249	0.084	**0.027**	0.133	0.156	0.118	0.108	0.091	**0.005**	**0.012**	**0.008**
s.e.d.	0.6930	0.4880	0.8050	0.9380	0.6330	1.1250	1.0940	0.7466	0.4731	0.6811	0.8937	0.6834	0.7960	0.7414	0.3439	0.5505	0.7310
Grazing (without covariate)																	
Ungrazed	7.18	6.52	8.08	8.12	8.42	7.96	8.17	7.51	6.76	5.84	5.62	5.49	6.03	6.28	6.41	7.72	10.78
Rabbit grazed	5.30	4.84	4.77	4.36	5.00	4.13	4.29	3.63	3.20	2.79	2.30	2.35	2.42	2.63	2.68	3.05	3.54
Rabbit and pony grazed	4.51	3.95	3.92	3.92	4.05	3.57	3.61	2.96	2.71	2.42	1.89	1.99	2.09	2.27	2.49	2.85	3.25
f ratio	7.80	14.03	12.90	16.50	38.14	18.77	18.40	33.07	48.86	23.62	25.25	25.48	26.99	28.82	162.83	93.01	101.54
p value	**0.042**	**0.016**	**0.018**	**0.012**	**0.002**	**0.009**	**0.010**	**0.003**	**0.002**	**0.006**	**0.005**	**0.005**	**0.005**	**0.004**	**<0.001**	**<0.001**	**<0.001**
s.e.d.	0.6930	0.4940	0.8670	0.8030	0.5260	0.7810	0.8100	0.6036	0.4468	0.5466	0.5760	0.5388	0.5943	0.5842	0.2452	0.4036	0.5990
Nitrogen																	
Unwatered control	5.41	5.16	5.37	5.37	5.66	4.79	5.04	4.57	4.24	3.94	3.33	3.43	3.66	4.11	4.05	4.70	5.91
Watered control	5.78	4.95	5.95	5.25	5.88	5.34	5.18	4.68	4.13	3.59	3.21	3.20	3.34	3.50	3.80	4.30	5.82
Low N	5.73	5.03	5.26	5.60	5.82	5.33	5.66	4.72	4.18	3.67	3.34	3.22	3.45	3.59	3.70	4.41	5.70
High N	5.73	5.28	5.78	5.64	5.92	5.43	5.55	4.83	4.35	3.54	3.20	3.26	3.59	3.70	3.89	4.74	5.99
f ratio	0.40	0.52	0.82	0.42	0.09	0.84	1.22	0.25	0.67	1.48	0.67	1.31	1.43	3.42	3.82	1.30	0.25
p value	0.753	0.677	0.501	0.743	0.964	0.491	0.333	0.858	0.584	0.256	0.581	0.303	0.268	**0.041**	**0.029**	0.306	0.860
s.e.d.	0.3790	0.2930	0.4950	0.4190	0.4550	0.4260	0.3800	0.2612	0.1680	0.2051	0.1367	0.1298	0.1762	0.1963	0.1117	0.2793	0.3710

Appendix 2.4. Continued.

	06-Jun-04	22-Jun-04	05-Jul-04	23-Jul-04	07-Aug-04	28-Aug-04	24-Sep-04	04-Nov-04	15-Dec-04	29-Jan-05	27-Feb-05	28-Mar-05	21-Apr-05	03-May-05	27-May-05	08-Jun-05	28-Jun-05
Grazing (with covariate)																	
Ungrazed	10.42	11.78	11.33	11.45	12.84	12.30	12.97	11.08	9.26	8.93	9.26	8.99	11.02	11.64	14.99	15.63	15.85
Rabbit grazed	3.80	3.37	3.60	3.51	3.27	3.98	3.90	3.52	3.01	2.96	2.72	3.04	3.52	3.64	4.56	4.61	4.15
Rabbit and pony grazed	4.59	4.15	4.22	4.30	3.91	4.65	4.85	4.54	3.73	3.48	2.98	3.51	4.02	4.03	4.53	4.78	4.50
f ratio	22.01	18.69	20.79	18.77	25.72	9.41	8.29	9.34	10.84	11.68	55.33	12.17	19.19	78.24	71.41	30.68	19.26
p value	**0.016**	**0.020**	**0.017**	**0.020**	**0.013**	**0.051**	0.108	**0.052**	**0.042**	**0.038**	**0.004**	**0.036**	**0.020**	**0.003**	**0.003**	**0.010**	**0.019**
s.e.d.	1.0670	1.4570	1.2660	1.3770	1.4010	2.0240	2.3700	1.8880	1.4364	1.3049	0.6470	1.2720	1.2720	0.6677	0.9000	1.4560	1.9580
Grazing (without covariate)																	
Ungrazed	11.55	12.77	12.60	12.64	13.83	14.15	14.83	13.05	10.75	10.19	10.01	10.44	12.51	12.73	16.25	17.30	17.49
Rabbit grazed	3.53	3.14	3.29	3.23	3.03	3.54	3.45	3.04	2.65	2.66	2.54	2.69	3.16	3.38	4.26	4.21	3.75
Rabbit and pony grazed	3.73	3.40	3.26	3.40	3.16	3.25	3.44	3.04	2.60	2.51	2.40	2.40	2.89	3.20	3.57	3.51	3.25
f ratio	75.07	80.81	77.87	74.56	109.20	43.91	39.44	38.75	44.51	50.12	167.52	48.87	68.53	164.06	188.96	107.84	84.87
p value	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.002**	**0.007**	**0.002**	**0.002**	**0.001**	**<0.001**	**0.002**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
s.e.d.	0.7460	0.8630	0.8620	0.8830	0.8390	1.3260	1.4790	1.3130	0.9940	0.8779	0.4760	0.9230	0.9360	0.6016	0.7340	1.0570	1.2400
Nitrogen																	
Unwatered control	6.28	6.23	6.36	6.16	6.36	6.91	7.00	6.98	5.62	5.47	5.36	5.73	6.82	7.03	8.32	8.80	8.29
Watered control	5.94	6.12	6.04	6.22	6.63	6.36	6.85	5.76	5.10	4.84	4.64	4.95	6.06	6.26	7.84	8.12	7.75
Low N	6.04	6.60	6.24	6.22	6.26	6.75	7.12	5.92	5.11	4.91	4.95	5.04	5.67	5.90	7.41	7.90	8.17
High N	6.82	6.78	6.89	7.09	7.44	7.90	8.00	6.87	5.50	5.25	4.98	5.00	6.19	6.55	8.53	8.54	8.45
f ratio	2.07	0.83	1.82	1.08	1.31	4.20	0.88	1.67	1.85	3.32	1.30	2.64	2.79	7.20	0.73	0.59	0.28
p value	0.143	0.497	0.182	0.384	0.303	**0.021**	0.476	0.212	0.177	**0.045**	0.305	0.083	0.072	**0.003**	0.550	0.628	0.840
s.e.d.	0.3950	0.4730	0.3880	0.5890	0.6430	0.4570	0.7460	0.6860	0.2833	0.2344	0.3590	0.3100	0.414	0.2535	0.8620	0.8100	0.8210

Appendix 2.4. Continued.

		12-Jun-03	26-Jun-03	10-Jul-03	26-Jul-03	10-Aug-03	24-Aug-03	21-Sep-03	11-Oct-03	30-Oct-03	03-Dec-03	14-Jan-04	10-Feb-04	07-Mar-04	28-Mar-04	17-Apr-04	30-Apr-04	22-May-04
Grazing*Nitrogen																		
Ungrazed	Unwatered control	6.57	5.63	6.14	6.28	7.08	5.55	6.12	6.102	5.923	5.54	4.882	5.009	5.4	6.111	6.437	7.304	9.97
	Watered control	8.03	5.22	7.10	5.90	7.41	6.84	6.21	6.55	5.69	4.73	4.85	4.57	4.87	4.85	5.83	6.74	9.81
	Low N	6.77	4.92	5.60	6.77	7.33	6.97	7.47	6.12	5.80	4.64	4.87	4.14	4.60	4.78	5.65	6.53	9.20
	High N	7.34	6.58	6.80	7.84	8.19	7.82	7.69	7.13	6.31	4.74	4.76	4.61	5.40	5.44	6.21	7.72	10.01
Rabbit grazed	Unwatered control	4.72	5.23	5.02	4.87	4.93	4.34	4.24	3.78	3.43	3.05	2.58	2.58	2.68	3.24	2.84	3.36	3.74
	Watered control	5.55	4.96	5.35	4.69	5.46	4.70	4.77	3.86	3.39	3.03	2.47	2.46	2.49	2.75	3.00	3.25	3.92
	Low N	5.58	5.05	4.85	4.68	5.33	4.48	4.96	4.12	3.39	3.01	2.50	2.78	2.82	2.85	2.63	3.19	3.82
	High N	5.35	5.01	5.47	4.55	5.14	4.13	4.44	3.75	3.39	2.97	2.40	2.46	2.59	2.62	2.61	3.02	3.66
Rabbit and pony grazed	Unwatered control	4.94	4.61	4.96	4.97	4.99	4.47	4.75	3.82	3.36	3.23	2.53	2.68	2.91	2.97	2.89	3.45	4.01
	Watered control	3.76	4.66	5.39	5.16	4.77	4.49	4.57	3.61	3.30	3.01	2.32	2.58	2.67	2.90	2.57	2.91	3.75
	Low N	4.83	5.12	5.34	5.35	4.81	4.54	4.54	3.93	3.34	3.35	2.66	2.75	2.91	3.13	2.81	3.51	4.07
	High N	4.51	4.25	5.07	4.51	4.42	4.35	4.53	3.61	3.35	2.91	2.45	2.70	2.79	3.04	2.84	3.48	4.31
	f ratio	1.82	2.38	0.33	1.44	0.47	1.24	1.26	1.12	0.56	1.01	0.20	2.45	1.40	2.11	3.07	1.07	0.36
	p value	0.152	0.074	0.914	0.258	0.819	0.33	0.328	0.394	0.757	0.453	0.974	0.068	0.272	0.105	**0.032**	0.419	0.895
	s.e.d.	0.897	0.617	1.037	0.984	0.915	1.08	1.012	0.6929	0.4419	0.5947	0.6644	0.5259	0.6331	0.6195	0.3092	0.6233	0.828

Appendix 2.4. Continued.

		06-Jun-04	22-Jun-04	05-Jul-04	23-Jul-04	07-Aug-04	28-Aug-04	24-Sep-04	04-Nov-04	15-Dec-04	29-Jan-05	27-Feb-05	28-Mar-05	21-Apr-05	03-May-05	27-May-05	08-Jun-05	28-Jun-05
Grazing*Nitrogen																		
Ungrazed	Unwatered control	10.71	11.19	10.94	10.49	12.07	12.37	12.29	12.78	9.794	9.654	9.82	10.33	12.51	13.055	15.95	16.82	15.99
	Watered control	9.97	11.73	11.03	11.86	13.38	11.46	12.91	10.10	9.00	8.69	8.82	8.67	11.19	11.54	15.21	15.95	15.21
	Low N	10.01	12.04	10.91	10.75	11.58	11.54	12.20	9.79	8.74	8.15	9.17	8.52	9.65	10.31	13.30	14.14	15.59
	High N	10.98	12.14	12.44	12.72	14.32	13.83	14.49	11.65	9.51	9.21	9.21	8.46	10.74	11.65	15.51	15.63	16.60
Rabbit grazed	Unwatered control	4.02	3.35	3.82	3.45	3.08	3.78	3.65	3.66	3.19	3.17	3.03	3.26	3.79	3.99	4.47	4.52	4.11
	Watered control	3.77	3.36	3.54	3.46	3.33	3.59	3.63	3.19	2.90	2.83	2.57	2.97	3.40	3.50	4.53	4.64	4.25
	Low N	3.46	3.27	3.44	3.49	3.06	3.96	4.03	3.39	2.89	2.91	2.62	2.97	3.33	3.53	4.27	4.54	4.24
	High N	3.96	3.50	3.59	3.65	3.61	4.58	4.29	3.84	3.05	2.93	2.65	2.96	3.56	3.53	4.97	4.74	3.99
Rabbit and pony grazed	Unwatered control	4.11	4.16	4.31	4.55	3.93	4.57	5.04	4.50	3.88	3.59	3.22	3.59	4.16	4.06	4.54	5.07	4.78
	Watered control	4.08	3.27	3.55	3.34	3.19	4.02	4.01	3.98	3.39	3.02	2.54	3.20	3.61	3.75	3.79	3.77	3.80
	Low N	4.64	4.50	4.38	4.42	4.14	4.74	5.12	4.57	3.71	3.68	3.07	3.65	4.02	3.85	4.66	5.01	4.67
	High N	5.53	4.68	4.66	4.90	4.38	5.28	5.21	5.12	3.95	3.61	3.08	3.58	4.29	4.47	5.11	5.25	4.75
	f ratio	0.66	0.39	0.83	0.68	0.66	0.61	0.34	0.75	0.40	1.67	0.13	1.62	1.65	3.86	0.42	0.56	0.16
	p value	0.684	0.873	0.561	0.665	0.682	0.720	0.906	0.617	0.871	0.188	0.990	0.203	0.195	**0.013**	0.854	0.757	0.985
	s.e.d.	1.016	1.310	1.112	1.411	1.494	1.618	2.101	1.782	1.1136	0.9941	0.776	1.037	1.145	0.6435	1.645	1.75	1.984

Appendix 2.5. Average height of the highest touch per pin in point quadrat surveys between April 2004 and June 2005 (60 hits in 36 1 m^2 quadrats) and results of Anova analyses (s.e.d. = standard error of the differences of means). Analysis was done without adjusting for the baseline as covariate because measurements only started in April 2004.

		Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
Grazing	Ungrazed	6.207	11.05	13.91	10.22	15.86
	Rabbit grazed	2.363	2.78	2.88	2.53	3.57
	Rabbit and pony grazed	2.209	2.83	2.94	2.36	2.85
	f ratio	134.92	94.68	84.9	88.94	126.7
	p value	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	s.e.d.	0.2758	0.692	0.975	0.673	0.918
Nitrogen	Unwatered control	3.783	5.57	7.08	5.91	8.41
	Watered control	3.473	5.46	6.42	4.84	7.15
	Low N	3.457	5.34	6.13	4.68	6.88
	High N	3.658	5.84	6.68	4.71	7.27
	f ratio	1.61	0.37	1.13	3.65	1.11
	p value	0.222	0.773	0.363	**0.032**	0.371
	s.e.d.	0.1743	0.495	0.537	0.433	0.906
Grazing*Nitrogen						
Ungrazed	Unwatered control	6.628	10.79	15.03	12.42	18.35
	Watered control	6.253	11.26	14.42	10.28	15.65
	Low N	5.517	10.42	12.14	9.05	13.98
	High N	6.431	11.74	14.04	9.13	15.45
Rabbit grazed	Unwatered control	2.459	2.98	3.11	2.68	3.75
	Watered control	2.263	2.71	2.59	2.42	3.55
	Low N	2.269	2.73	2.9	2.48	3.5
	High N	2.386	2.71	2.91	2.53	3.48
Rabbit and pony grazed	Unwatered control	2.339	2.94	3.1	2.62	3.12
	Watered control	1.898	2.43	2.24	1.82	2.24
	Low N	2.467	2.87	3.34	2.52	3.15
	High N	2.206	3.08	3.08	2.48	2.9
	f ratio	2.45	0.39	1.55	2.82	0.88
	p value	0.065	0.875	0.22	**0.041**	0.532
	s.e.d.	0.38	1.015	1.265	0.936	1.64

Appendix 2.6. Average above ground biomass (g dry weight m^{-2}) in three grazing treatments (ungrazed, rabbit grazed, rabbit and pony grazed) and four nitrogen fertilisation treatments (unwatered control, watered control, low N, high N) between June 2003 and June 2005, adjusted for the baseline as covariate, and results of Anova analyses (s.e.d. = standard error of the differences of means). a) Total, b) graminoids, c) bryophytes, d) forbs.

a) Total

		Jun-03	Sep-03	Apr-04	Jun-04	Jun-05
Grazing	Ungrazed	515.0	614.0	466.0	599.0	535.0
	Rabbit grazed	383.0	469.0	455.0	491.0	428.0
	Rabbit and pony grazed	509.0	569.0	433.0	561.0	368.0
	f ratio	4.990	1.990	0.280	17.300	14.030
	p value	0.082	0.281	0.777	**0.023**	**0.030**
	s.e.d.	47.30	64.50	67.30	16.50	47.00
Nitrogen	Unwatered control	514.0	526.0	447.0	575.0	408.0
	Watered control	436.0	535.0	386.0	471.0	359.0
	Low N	487.0	585.0	479.0	597.0	486.0
	High N	439.0	558.0	494.0	559.0	521.0
	f ratio	1.270	0.400	2.000	1.150	4.080
	p value	0.316	0.753	0.153	0.356	**0.024**
	s.e.d.	48.10	62.30	49.50	66.50	53.30
Grazing*Nitrogen						
Ungrazed	Unwatered control	589.0	605.0	434.0	708.0	517.0
	Watered control	476.0	605.0	400.0	553.0	532.0
	Low N	503.0	641.0	554.0	595.0	501.0
	High N	494.0	607.0	478.0	538.0	588.0
Rabbit grazed	Unwatered control	454.0	453.0	471.0	542.0	372.0
	Watered control	332.0	399.0	398.0	366.0	334.0
	Low N	390.0	483.0	412.0	513.0	452.0
	High N	354.0	543.0	539.0	543.0	552.0
Rabbit and pony grazed	Unwatered control	499.0	519.0	436.0	474.0	335.0
	Watered control	499.0	600.0	361.0	494.0	211.0
	Low N	569.0	633.0	470.0	683.0	504.0
	High N	468.0	525.0	467.0	595.0	423.0
	f ratio	0.400	0.440	0.620	0.990	1.290
	p value	0.869	0.842	0.714	0.460	0.314
	s.e.d.	86.30	112.20	94.90	108.80	93.50

Appendix 2.6. Continued.

b) Graminoids

		Jun-03	Sep-03	Apr-04	Jun-04	Jun-05
Grazing	Ungrazed	220.0	230.6	234.4	293.9	418.0
	Rabbit grazed	181.4	163.6	141.2	163.5	92.0
	Rabbit and pony grazed	194.0	141.2	117.5	161.8	107.0
	f ratio	8.160	1.390	48.400	3.690	34.410
	p value	**0.039**	0.374	**0.005**	0.155	**0.009**
	s.e.d.	9.73	63.82	13.75	51.91	39.50
Nitrogen	Unwatered control	210.1	148.6	167.1	224.5	199.0
	Watered control	193.7	199.8	145.1	180.8	190.0
	Low N	194.8	168.5	177.2	185.8	169.0
	High N	195.3	197.0	168.1	234.6	264.0
	f ratio	0.180	2.810	0.650	2.040	1.830
	p value	0.909	0.071	0.596	0.146	0.179
	s.e.d.	26.01	21.35	23.99	27.28	43.40
Grazing*Nitrogen						
Ungrazed	Unwatered control	220.7	150.9	204.9	344.8	427.0
	Watered control	204.3	286.0	221.3	267.6	427.0
	Low N	187.2	218.4	279.4	238.8	333.0
	High N	267.7	267.3	232.0	324.5	485.0
Rabbit grazed	Unwatered control	184.8	151.4	177.4	201.2	73.0
	Watered control	145.1	156.2	96.8	151.6	58.0
	Low N	208.3	154.1	109.5	126.9	66.0
	High N	187.6	192.6	180.9	174.3	169.0
Rabbit and pony grazed	Unwatered control	225.0	143.6	118.9	127.4	97.0
	Watered control	231.6	157.3	117.1	123.3	85.0
	Low N	188.7	132.9	142.6	191.6	107.0
	High N	130.7	131.1	91.4	205.0	139.0
	f ratio	1.890	1.610	1.670	1.330	0.350
	p value	0.137	0.205	0.190	0.299	0.902
	s.e.d.	40.21	58.06	43.85	60.34	82.00

Appendix 2.6. Continued.

c) Bryophytes

		Jun-03	**Sep-03**	**Apr-04**	**Jun-04**	**Jun-05**
Grazing	Ungrazed	280.0	359.0	197.0	258.0	130.0
	Rabbit grazed	169.0	339.0	326.0	351.0	310.0
	Rabbit and pony grazed	308.0	388.0	275.0	360.0	217.0
	f ratio	5.730	0.190	2.300	55.120	2.180
	p value	0.067	0.834	0.248	**0.004**	0.260
	s.e.d.	43.40	76.40	77.30	16.40	101.20
Nitrogen	Unwatered control	291.0	357.0	265.0	329.0	194.0
	Watered control	214.0	337.0	213.0	272.0	141.0
	Low N	280.0	398.0	281.0	385.0	302.0
	High N	224.0	357.0	305.0	307.0	239.0
	f ratio	1.810	0.290	1.670	0.970	4.050
	p value	0.182	0.832	0.211	0.432	**0.024**
	s.e.d.	40.70	65.00	43.80	57.60	46.50
Grazing*Nitrogen						
Ungrazed	Unwatered control	360.0	408.0	198.0	326.0	132.0
	Watered control	261.0	306.0	152.0	243.0	120.0
	Low N	305.0	392.0	234.0	313.0	202.0
	High N	193.0	332.0	203.0	149.0	64.0
Rabbit grazed	Unwatered control	244.0	311.0	326.0	360.0	290.0
	Watered control	128.0	283.0	288.0	246.0	250.0
	Low N	157.0	363.0	315.0	403.0	331.0
	High N	146.0	400.0	376.0	395.0	369.0
Rabbit and pony grazed	Unwatered control	268.0	351.0	270.0	300.0	161.0
	Watered control	252.0	423.0	198.0	326.0	52.0
	Low N	377.0	438.0	295.0	437.0	373.0
	High N	334.0	339.0	336.0	378.0	283.0
	f ratio	1.320	0.490	0.210	0.810	1.610
	p value	0.298	0.808	0.969	0.575	0.205
	s.e.d.	74.90	121.00	92.00	95.70	107.00

Appendix 2.6. Continued.

d) Forbs

		Jun-03	Sep-03	Apr-04	Jun-04	Jun-05
Grazing	Ungrazed	15.5	15.3	30.7	33.7	21.9
	Rabbit grazed	32.7	8.2	23.7	15.6	28.4
	Rabbit and pony grazed	7.3	7.6	9.8	13.1	6.4
	f ratio	4.550	2.960	3.810	1.630	2.400
	p value	0.093	0.195	0.150	0.331	0.239
	s.e.d.	8.60	5.12	10.31	18.09	9.86
Nitrogen	Unwatered control	13.3	7.2	23.4	12.6	17.2
	Watered control	27.9	9.9	17.6	23.0	17.6
	Low N	13.1	10.4	27.4	25.6	26.5
	High N	19.5	14.0	17.2	22.0	14.4
	f ratio	2.360	1.180	0.480	1.240	0.570
	p value	0.105	0.348	0.701	0.327	0.643
	s.e.d.	6.43	3.80	9.53	7.47	9.76
Grazing*Nitrogen						
Ungrazed	Unwatered control	7.7	10.0	41.7	14.4	11.5
	Watered control	10.2	11.6	23.2	40.5	32.3
	Low N	10.4	14.0	43.1	41.6	30.3
	High N	33.7	25.7	14.9	38.2	13.7
Rabbit grazed	Unwatered control	25.6	6.9	17.8	10.2	26.7
	Watered control	58.8	13.3	27.8	20.7	22.9
	Low N	25.3	11.5	26.6	14.7	44.8
	High N	20.9	1.1	22.7	17.0	19.0
Rabbit and pony grazed	Unwatered control	6.7	4.8	10.6	13.2	13.5
	Watered control	14.8	4.9	1.8	8.0	-2.5
	Low N	3.6	5.5	12.5	20.7	4.3
	High N	3.9	15.3	14.1	10.6	10.5
	f ratio	2.730	1.600	0.710	0.780	0.820
	p value	**0.046**	0.207	0.646	0.595	0.570
	s.e.d.	12.92	7.37	17.47	18.71	17.64

Appendix 2.7. Average concentrations of nitrogen (N) and phosphorus (P), N and P uptake and N:P ratio in graminoid biomass samples taken in June 2005 after two years of nutrient applications. Results of Anova analyses (s.e.d. = standard error of the differences of means) indicate significant differences.

		N g/kg	N uptake	P g/kg	P uptake	N:P ratio
Grazing	Ungrazed	11.940	18.80	1.322	2.09	9.15
	Rabbit grazed	13.43	6.12	1.511	0.67	9.13
	Rabbit and pony grazed	12.840	5.66	1.496	0.65	8.73
	f ratio	10.45	30.49	1.29	26.71	0.27
	p value	**0.026**	**0.004**	0.370	**0.005**	0.777
	s.e.d.	0.328	1.909	0.1312	0.226	0.643
Nitrogen	Watered control	12.41	9.01	1.536	1.05	8.30
	Low N	13.07	8.63	1.429	0.97	9.32
	High N	12.74	12.94	1.364	1.39	9.39
	f ratio	0.450	2.940	2.080	1.310	2.710
	p value	0.646	0.091	0.167	0.306	0.107
	s.e.d.	0.688	1.968	0.0848	0.277	0.985
Grazing/Nitrogen						
Ungrazed	Watered control	11.70	18.72	1.320	2.11	8.99
	Low N	12.43	15.10	1.416	1.75	8.85
	High N	11.70	22.58	1.228	2.43	9.62
Rabbit grazed	Watered control	13.77	3.25	1.748	0.42	8.13
	Low N	13.47	4.95	1.336	0.50	10.16
	High N	13.07	10.17	1.449	1.10	9.09
Rabbit and pony grazed	Watered control	11.77	5.06	1.539	0.63	7.77
	Low N	13.30	5.84	1.533	0.66	8.96
	High N	13.47	6.08	1.416	0.66	9.47
	f ratio	0.600	0.880	1.680	0.440	0.990
	p value	0.667	0.507	0.218	0.780	0.451
	s.e.d.	1.027	3.376	0.1778	0.453	0.985

Appendix 2.8. Average concentrations of nitrogen (N) and phosphorus (P), N and P uptake and N:P ratio in bryophyte biomass samples taken in June 2005 after two years of nutrient applications. Results of Anova analyses (s.e.d. = standard error of the differences of means) indicate significant differences.

		N g/kg	N uptake	P g/kg	P uptake	N:P ratio
Grazing	Ungrazed	11.950	204.0	1.534	24.6	8.33
	Rabbit grazed	13.090	248	1.374	26.1	10.05
	Rabbit and pony grazed	11.670	359.0	1.383	43.3	8.800
	f ratio	0.520	1.300	0.240	1.100	2.130
	p value	0.630	0.367	0.798	0.416	0.235
	s.e.d.	1.475	98.500	0.261	13.990	0.864
Nitrogen	Watered control	11.45	7.03	1.491	0.98	7.90
	Low N	11.68	12.84	1.239	1.47	9.92
	High N	13.58	12.60	1.561	1.31	9.36
	f ratio	4.980	4.460	1.330	1.120	2.220
	p value	**0.027**	**0.036**	0.300	0.358	0.151
	s.e.d.	0.740	2.202	0.207	0.338	0.990
Grazing*Nitrogen						
Ungrazed	Watered control	10.820	7.190	1.575	1.100	6.940
	Low N	11.330	10.100	1.122	0.990	10.190
	High N	13.700	7.240	1.906	0.860	7.840
Rabbit grazed	Watered control	11.730	6.670	1.481	0.980	8.320
	Low N	13.000	10.420	1.154	0.910	11.310
	High N	14.530	12.720	1.488	1.240	10.510
Rabbit and pony grazed	Watered control	11.800	7.210	1.418	0.850	8.420
	Low N	10.700	17.990	1.442	2.510	8.250
	High N	12.500	17.850	1.288	1.830	9.720
	f ratio	0.640	1.230	0.870	1.620	0.880
	p value	0.642	0.350	0.508	0.232	0.504
	s.e.d.	1.808	5.021	0.392	0.736	1.646

Appendix 2.9. Average numbers of species and hits in point quadrat surveys (60 hits in 36 1 m^2 quadrats) between June 2003 and June 2005, in three grazing treatments, for three plant groups each and total number of species and hits, adjusted for the baseline as covariate. Results of Anova analyses (s.e.d. = standard error of the differences of means) indicate significant differences.

		Jun-03	Sep-03	Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
Total: Species	Ungrazed	15.67	17.06	16.38	17.05	17.26	16.52	16.64
	Rabbit grazed	17.75	16.78	17.39	17.26	17.07	20.05	20.09
	Rabbit and pony grazed	14.92	14.57	16.06	15.27	14.08	16.59	16.44
	f ratio	3.360	5.430	1.280	2.930	10.200	4.650	1.350
	p value	0.139	0.101	0.397	0.197	**0.046**	0.121	0.382
	s.e.d.	1.132	0.972	0.721	0.970	0.909	1.163	2.146
Total: Hits	Ungrazed	211.8	234.4	213.4	228.0	251.6	233.1	241.7
	Rabbit grazed	226.1	213.6	180.6	187.1	200.2	200.3	220.9
	Rabbit and pony grazed	195.4	172.4	175.5	183.2	187.1	194.1	209.7
	f ratio	3.500	16.390	12.740	9.810	42.580	3.100	1.700
	p value	0.132	**0.024**	**0.034**	**0.048**	**0.006**	0.186	0.321
	s.e.d.	11.600	12.650	11.050	15.280	9.940	22.790	22.940
Graminoids: Species	Ungrazed	7.08	6.77	6.599	6.72	6.69	6.60	6.70
	Rabbit grazed	7.50	7.38	7.291	7.19	7.02	7.20	7.00
	Rabbit and pony grazed	7.00	6.93	6.610	6.76	5.95	6.62	6.47
	f ratio	0.630	0.540	2.510	0.500	1.830	0.600	0.340
	p value	0.577	0.631	0.229	0.648	0.303	0.605	0.735
	s.e.d.	0.476	0.585	0.3336	0.486	0.562	0.582	0.604
Graminoids: Hits	Ungrazed	119.6	134.3	113.3	123.7	142.6	128.6	130.0
	Rabbit grazed	126.4	119.1	89.4	93.6	104.1	101.2	112.8
	Rabbit and pony grazed	113.4	87.9	82.2	90.1	97.8	93.6	97.6
	f ratio	3.38	7.86	6.03	10.06	10.87	6.03	15.67
	p value	0.138	0.064	0.089	**0.047**	**0.042**	0.089	**0.026**
	s.e.d.	5.00	14.00	12.61	11.19	14.08	14.26	7.36
Bryophytes: Species	Ungrazed	3.25	4.40	3.92	4.65	5.16	4.61	4.67
	Rabbit grazed	2.83	4.00	4.09	4.45	3.89	4.70	4.53
	Rabbit and pony grazed	4.08	4.27	4.49	4.48	4.03	5.11	5.13
	f ratio	2.020	0.130	0.240	0.060	7.170	0.210	0.200
	p value	0.247	0.883	0.801	0.939	0.072	0.824	0.827
	s.e.d.	0.633	0.905	0.853	0.754	0.450	0.795	0.847
Bryophytes: Hits	Ungrazed	67.3	72.7	72.5	76.3	77.8	80.7	82.2
	Rabbit grazed	60.4	72.1	78.2	80.7	73.4	82.6	82.6
	Rabbit and pony grazed	69.6	72.4	73.1	74.6	70.7	77.4	78.2
	f ratio	1.630	0.010	0.280	0.490	1.840	0.320	0.450
	p value	0.303	0.986	0.776	0.654	0.301	0.747	0.672
	s.e.d.	5.272	3.250	7.790	5.600	4.400	6.150	5.210
Forbs: Species	Ungrazed	5.33	6.09	5.96	5.76	5.57	5.57	5.60
	Rabbit grazed	7.42	4.71	5.07	5.35	5.30	6.49	6.30
	Rabbit and pony grazed	3.83	3.86	5.81	4.23	4.80	6.27	6.76
	f ratio	12.490	13.390	1.180	1.120	0.460	0.800	0.320
	p value	**0.019**	**0.032**	0.418	0.432	0.667	0.528	0.750
	s.e.d.	0.720	0.849	0.798	1.733	1.390	1.475	2.868
Forbs: Hits	Ungrazed	25.0	26.5	25.9	26.7	30.4	22.3	28.8
	Rabbit grazed	39.2	19.1	13.2	12.3	18.6	23.5	28.9
	Rabbit and pony grazed	12.4	16.3	21.7	20.4	23.6	17.7	31.2
	f ratio	15.760	28.410	8.010	1.610	4.280	0.160	0.020
	p value	**0.013**	**0.011**	0.063	0.336	0.132	0.859	0.985
	s.e.d.	4.780	3.020	5.490	14.810	8.130	11.280	21.620

Appendix 2.10. Average abundance of *Cerastium fontanum* and *Vicia* spp. in point quadrat surveys (60 hits each in 36 1 m^2 quadrats) in three grazing treatments between June 2003 and June 2005, adjusted for the baseline as covariate. Results of Anova analyses (s.e.d. = standard error of the differences of means) indicate significant differences.

		Jun-03	Sep-03	Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
Cerastium fontanum	Ungrazed	0.083	0.012	0.12	0.19	0.86	1.40	0.89
	Rabbit grazed	0.500	0.149	0.95	0.21	0.21	0.19	1.58
	Rabbit and pony grazed	0.167	0.006	1.77	1.43	0.76	2.74	1.36
	f ratio	2.00	1.17	61.45	29.24	1.13	13.83	0.20
	p value	0.250	0.420	**0.004**	**0.011**	0.430	**0.031**	0.828
	s.e.d.	0.221	0.094	0.180	0.222	0.400	0.508	1.078
***Vicia* spp.**	Ungrazed	1.42	1.54	7.29	5.34	2.76	5.41	7.52
	Rabbit grazed	1.25	1.27	2.08	-0.52	0.42	1.02	1.12
	Rabbit and pony grazed	0.42	0.77	3.87	1.69	0.56	3.24	1.86
	f ratio	1.20	3.48	9.22	13.24	12.46	13.45	25.59
	p value	0.390	0.165	0.052	**0.032**	**0.035**	**0.032**	**0.013**
	s.e.d.	0.691	0.269	1.377	1.291	0.560	0.961	1.052

Appendix 2.11. Average abundance of tall growing species (>60 cm height) in point quadrat surveys (60 hits in 36 1 m^2 quadrats) between June 2003 and June 2005, adjusted for the baseline as covariate. Results of Anova analyses (s.e.d. = standard error of the differences of means) indicate significant differences.

		Jun-03	Sep-03	Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
Grazing	Ungrazed	90.3	94.1	90.6	96.7	105.8	95.1	106.2
	Rabbit grazed	82.6	75.3	65.5	66.7	77.0	70.4	83.0
	Rabbit and pony grazed	90.4	62.1	66.5	63.0	67.6	71.9	76.7
	f ratio	0.67	4.77	2.97	14.57	12.93	7.59	18.22
	p value	0.561	0.117	0.195	**0.029**	**0.034**	0.067	**0.021**
	s.e.d.	7.78	11.22	12.15	7.26	8.4	7.47	5.48
Nitrogen	Unwatered control	84.0	77.2	70.3	73.8	82.5	77.8	89.5
	Watered control	87.3	74.3	76.3	73.8	84.5	77.5	88.7
	Low N	89.8	79.2	73.7	76.6	79.7	79.6	86.7
	High N	90.0	78.0	76.6	77.7	87.0	81.9	89.6
	f ratio	0.54	0.69	1.23	0.15	0.57	0.38	0.14
	p value	0.662	0.569	0.328	0.926	0.644	0.772	0.932
	s.e.d.	5.38	3.43	3.55	5.49	5.86	4.30	5.46
Grazing*Nitrogen								
Ungrazed	Unwatered control	77.0	91.6	87.7	91.7	103.2	90.7	102.4
	Watered control	94.7	88.1	95.6	95.6	104.2	98.6	111.2
	Low N	102.0	102.2	91.0	106.9	106.2	93.9	103.2
	High N	87.7	94.5	88.1	92.9	109.6	98.1	107.8
Rabbit grazed	Unwatered control	85.3	78.0	66.7	66.2	78.9	74.7	91.1
	Watered control	78.7	75.2	60.4	60.7	74.5	57.8	73.5
	Low N	81.3	76.6	64.8	66.5	70.3	72.8	80.2
	High N	85.0	71.5	70.2	73.3	84.1	76.2	87.2
Rabbit and pony grazed	Unwatered control	89.7	62.0	56.4	63.5	65.2	68.1	75.0
	Watered control	88.7	59.5	72.8	65.2	74.9	76.1	81.4
	Low N	86.0	58.8	65.4	56.4	62.7	72.1	76.7
	High N	97.3	68.2	71.6	67.0	67.3	71.3	73.9
	f ratio	1.42	1.26	1.57	0.77	0.41	1.55	0.92
	p value	0.260	0.325	0.216	0.600	0.861	0.223	0.502
	s.e.d.	11.21	12.02	12.9	10.96	12.10	9.77	9.91

Appendix 2.12. Average abundance of low growing species (<20 cm height) in point quadrat surveys (60 hits in 36 1 m^2 quadrats) between June 2003 and June 2005, adjusted for the baseline as covariate. Results of Anova analyses (s.e.d. = standard error of the differences of means) indicate significant differences.

		Jun-03	Sep-03	Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
Grazing	Ungrazed	10.1	13.4	11.7	15.2	12.4	16.2	18.7
	Rabbit grazed	26.0	13.1	13.8	14.7	16.6	20.4	24.0
	Rabbit and pony grazed	6.7	10.6	12.2	13.7	12.6	16.3	22.3
	f ratio	4.24	0.77	0.18	0.24	0.37	0.56	0.44
	p value	0.103	0.536	0.841	0.801	0.717	0.619	0.68
	s.e.d.	7.090	3.108	3.253	3.036	4.708	3.860	7.110
Nitrogen	Unwatered control	10.7	11.9	12.2	14.1	12.7	15.0	21.8
	Watered control	19.0	12.2	12.8	15.6	16.0	20.4	22.0
	Low N	15.3	12.4	13.7	12.7	13.2	17.3	23.0
	High N	12.0	13.0	11.5	15.7	13.7	17.8	19.7
	f ratio	0.90	0.14	0.43	0.94	1.16	1.06	0.31
	p value	0.461	0.933	0.735	0.443	0.354	0.392	0.815
	s.e.d.	5.560	1.896	1.960	2.096	1.902	2.831	3.420
Grazing*Nitrogen								
Ungrazed	Unwatered control	6.3	11.8	11.2	12.6	10.8	11.5	16.8
	Watered control	8.3	13.2	10.7	16.1	14.6	19.9	19.3
	Low N	7.3	12.7	13.3	13.2	12.0	13.5	19.2
	High N	18.3	15.9	11.7	18.9	12.2	19.8	19.2
Rabbit grazed	Unwatered control	23.0	12.8	13.3	14.9	14.5	18.3	26.1
	Watered control	37.3	13.9	15.8	18.0	21.8	22.8	24.4
	Low N	28.7	12.1	12.1	9.6	12.3	20.1	24.3
	High N	15.0	13.4	13.9	16.3	18.0	20.5	21.1
Rabbit and pony grazed	Unwatered control	2.7	10.9	12.0	14.7	12.8	15.2	22.5
	Watered control	11.3	9.4	12.0	12.8	11.7	18.5	22.3
	Low N	10.0	12.5	15.8	15.4	15.3	18.3	25.5
	High N	2.7	9.6	9.0	12.0	10.8	13.2	18.8
	f ratio	1.07	0.46	0.78	1.39	1.69	0.58	0.21
	p value	0.415	0.829	0.597	0.276	0.184	0.743	0.968
	s.e.d.	10.95	3.92	4.07	4.15	4.79	5.50	7.84

Appendix 2.13. Average numbers of species and hits in point quadrat surveys (60 hits in 36 1 m^2 quadrats) between June 2003 and June 2005, in four nitrogen fertilisation treatments, for three plant groups each and total number of species and hits, adjusted for the baseline as covariate. Results of Anova analyses (s.e.d. = standard error of the differences of means) indicate significant differences.

		Jun-03	Sep-03	Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
Total: Species	Unwatered control	15.78	15.66	16.49	16.29	16.36	18.27	17.32
	Watered control	17.44	16.57	16.69	16.93	16.68	18.25	18.39
	Low N	15.44	15.88	16.88	16.14	15.38	17.21	18.20
	High N	15.78	16.44	16.38	16.74	16.13	17.16	16.99
	f ratio	1.04	0.40	0.07	0.22	0.40	0.56	0.54
	p value	0.399	0.756	0.977	0.880	0.756	0.648	0.659
	s.e.d.	1.252	0.966	1.244	1.097	1.281	1.187	1.349
Total: Hits	Unwatered control	206.3	203.9	187.6	194.0	214.7	207.7	231.7
	Watered control	208.8	203.8	196.2	200.1	220.3	210.1	228.3
	Low N	217.2	209.9	187.8	198.3	204.8	210.3	219.2
	High N	212.1	209.5	187.5	205.5	212.1	208.5	217.4
	f ratio	1.34	1.38	0.79	0.93	0.72	0.11	0.65
	p value	0.294	0.284	0.514	0.450	0.551	0.952	0.596
	s.e.d.	5.77	4.84	6.94	8.17	9.19	8.79	10.59
Graminoids: Species	Unwatered control	7.44	7.10	7.03	6.79	6.73	7.06	6.57
	Watered control	7.33	6.82	6.73	6.72	6.53	6.31	6.83
	Low N	7.00	6.99	6.84	6.97	6.71	7.04	7.08
	High N	7.00	7.21	6.73	7.08	6.26	6.81	6.41
	f ratio	0.430	0.620	0.580	0.560	0.580	1.970	0.980
	p value	0.735	0.613	0.636	0.650	0.636	0.156	0.428
	s.e.d.	0.495	0.292	0.272	0.307	0.406	0.359	0.429
Graminoids: Hits	Unwatered control	122.9	109.8	88.0	101.1	113.8	102.3	113.4
	Watered control	121.6	112.0	101.4	102.9	120.3	110.3	118.4
	Low N	113.7	116.2	92.7	96.7	108.7	106.4	108.5
	High N	121.1	117.1	97.8	109.2	116.4	112.3	113.6
	f ratio	1.34	0.60	5.75	3.23	0.76	1.52	0.62
	p value	0.294	0.621	**0.007**	**0.048**	0.532	0.246	0.610
	s.e.d.	5.09	6.23	3.56	3.92	7.64	5.30	6.56
Bryophytes: Species	Unwatered control	3.56	3.94	4.38	4.39	3.98	4.65	4.46
	Watered control	3.56	4.60	4.50	5.16	4.86	5.54	5.90
	Low N	3.22	3.95	3.62	3.95	3.91	4.35	4.21
	High N	3.22	4.40	4.17	4.61	4.69	4.68	4.54
	f ratio	0.380	0.970	1.350	2.030	1.190	1.760	3.940
	p value	0.772	0.428	0.292	0.148	0.344	0.193	**0.026**
	s.e.d.	0.444	0.478	0.446	0.510	0.643	0.544	0.547
Bryophytes: Hits	Unwatered control	65.2	74.1	75.5	75.6	77.2	83.8	86.3
	Watered control	59.2	72.4	79.2	82.0	77.6	82.9	85.4
	Low N	72.9	70.0	71.3	75.0	69.8	77.8	75.9
	High N	65.7	73.1	72.4	76.3	71.3	76.2	76.4
	f ratio	8.030	0.320	0.500	0.690	0.950	0.820	2.330
	p value	**0.001**	0.808	0.685	0.570	0.438	0.499	0.111
	s.e.d.	2.791	4.160	5.100	4.050	4.860	5.740	5.050

Appendix 2.13. Continued.

		Jun-03	Sep-03	Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
Forbs: Species	Unwatered control	4.78	4.45	5.25	5.11	5.66	6.58	6.45
	Watered control	6.56	5.31	5.35	4.95	5.22	6.39	5.56
	Low N	5.22	4.92	6.42	5.29	4.80	5.81	6.90
	High N	5.56	4.88	5.43	5.09	5.21	5.65	5.98
	f ratio	1.60	0.26	0.72	0.08	0.46	1.14	0.80
	p value	0.224	0.854	0.554	0.969	0.710	0.361	0.512
	s.e.d.	0.845	0.749	0.933	0.694	0.766	0.624	0.864
Forbs: Hits	Unwatered control	18.2	20.5	21.6	19.9	23.3	20.4	33.2
	Watered control	28.0	20.6	18.2	19.3	26.5	23.2	26.9
	Low N	30.7	22.4	23.4	19.2	22.3	21.0	30.3
	High N	25.3	19.2	17.8	20.8	24.7	20.1	28.1
	f ratio	2.27	0.29	0.77	0.09	0.21	0.20	0.28
	p value	0.12	0.834	0.529	0.966	0.891	0.894	0.842
	s.e.d.	5.02	3.67	4.71	3.91	6.25	5.52	6.22

Appendix 2.14. Average numbers of species and hits in point quadrat surveys (60 hits in 36 1 m^2 quadrats) between June 2003 and June 2005, for the interaction of three grazing and four nitrogen fertilisation treatments, for three plant groups each and total number of species and hits, adjusted for the baseline as covariate. Results of Anova analyses (s.e.d. = standard error of the differences of means) indicate significant differences.

			Jun-03	Sep-03	Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
	Grazing*Nitrogen								
Total: Species	Ungrazed	Unwatered control	14.7	15.7	16.4	17.0	17.2	16.4	16.2
		Watered control	16.3	18.6	16.9	17.8	19.2	18.3	18.1
		Low N	16.3	16.6	16.2	16.4	15.2	16.6	16.5
		High N	15.3	17.3	16.0	17.0	17.6	14.8	15.8
	Rabbit grazed	Unwatered control	17.0	17.3	17.6	17.6	17.0	21.3	20.2
		Watered control	20.0	17.3	16.5	17.6	18.7	20.5	20.7
		Low N	17.0	16.6	18.9	17.6	16.0	18.3	20.6
		High N	17.0	15.9	16.6	16.3	16.6	20.3	18.9
	Rabbit and pony grazed	Unwatered control	15.7	14.0	15.5	14.3	15.0	17.2	15.6
		Watered control	16.0	13.8	16.7	15.4	12.2	16.0	16.4
		Low N	13.0	14.4	15.5	14.4	15.0	16.8	17.6
		High N	15.0	16.1	16.5	17.0	14.2	16.5	16.3
		f ratio	0.48	0.93	0.38	0.55	1.07	0.70	0.20
		p value	0.811	0.501	0.880	0.760	0.417	0.656	0.972
		s.e.d.	2.193	1.720	2.057	1.906	2.159	2.101	2.746
Total: Hits	Ungrazed	Unwatered control	201.7	229.9	215.8	217.1	258.1	229.6	245.2
		Watered control	202.7	236.6	234.1	233.8	264.3	246.4	259.2
		Low N	212.3	240.7	216.0	240.4	246.5	233.4	239.6
		High N	230.7	230.2	187.5	221.0	237.5	223.0	223.0
	Rabbit grazed	Unwatered control	227.0	207.9	184.0	185.2	195.2	201.5	235.2
		Watered control	230.7	215.0	173.3	179.6	210.3	191.0	214.5
		Low N	229.3	219.2	177.0	178.5	185.2	200.7	208.9
		High N	217.3	212.2	188.1	205.2	210.1	207.8	225.2
	Rabbit and pony grazed	Unwatered control	190.3	173.9	163.0	179.7	190.9	191.9	214.6
		Watered control	193.0	159.6	181.3	186.8	186.3	192.9	211.2
		Low N	210.0	169.9	170.5	176.0	182.6	196.8	209.1
		High N	188.3	186.1	187.0	190.4	188.6	194.6	204.0
		f ratio	2.49	1.87	2.43	1.04	0.62	0.55	0.65
		p value	0.062	0.145	0.070	0.435	0.712	0.765	0.687
		s.e.d.	14.47	12.99	14.44	18.21	16.97	23.47	25.44
Graminoids: Species	Ungrazed	Unwatered control	7.0	6.8	6.7	6.8	7.0	6.7	6.4
		Watered control	7.3	6.6	6.6	6.6	6.6	6.3	6.6
		Low N	7.3	6.3	6.3	7.0	6.6	7.0	7.3
		High N	6.7	7.3	6.8	6.6	6.4	6.4	6.5
	Rabbit grazed	Unwatered control	7.7	7.6	7.9	6.8	7.2	7.6	6.9
		Watered control	7.7	7.3	6.9	7.1	7.6	6.9	7.5
		Low N	7.0	7.6	7.1	7.7	6.7	7.0	6.8
		High N	7.7	7.0	7.2	7.1	6.6	7.3	6.9
	Rabbit and pony grazed	Unwatered control	7.7	6.8	6.5	6.8	5.9	6.9	6.5
		Watered control	7.0	6.5	6.7	6.4	5.4	5.7	6.4
		Low N	6.7	7.0	7.1	6.2	6.8	7.1	7.2
		High N	6.7	7.4	6.1	7.6	5.8	6.8	5.9
		f ratio	0.38	1.19	1.63	1.63	1.01	0.51	0.56
		p value	0.883	0.357	0.200	0.200	0.449	0.795	0.757
		s.e.d.	0.882	0.711	0.5206	0.656	0.815	0.776	0.868

Appendix 2.14. Continued.

			Jun-03	Sep-03	Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
	Grazing*Nitrogen								
Graminoids: Hits	Ungrazed	Unwatered control	116.0	125.8	106.1	116.2	142.3	122.3	125.3
		Watered control	119.7	135.2	121.6	119.8	144.9	133.8	134.6
		Low N	114.7	137.5	110.6	124.7	135.9	119.2	122.6
		High N	128.0	138.7	115.0	134.1	147.1	139.3	137.6
	Rabbit grazed	Unwatered control	138.7	112.7	85.6	95.1	100.8	93.6	112.3
		Watered control	129.3	121.0	93.2	93.6	114.4	101.5	119.2
		Low N	114.7	124.9	87.3	85.4	94.5	102.0	105.1
		High N	123.0	117.7	91.6	100.1	106.7	107.5	114.7
	Rabbit and pony grazed	Unwatered control	114.0	90.9	72.4	91.8	98.3	90.9	102.5
		Watered control	115.7	79.6	89.4	95.3	101.6	95.5	101.5
		Low N	111.7	86.1	80.1	79.8	95.7	97.9	97.9
		High N	112.3	94.9	86.7	93.4	95.4	90.3	88.6
		f ratio	1.16	0.63	0.32	1.43	0.2	0.97	0.61
		p value	0.371	0.704	0.92	0.262	0.973	0.474	0.722
		s.e.d.	9.13	15.06	11.67	11.00	16.66	14.29	12.02
Bryophytes: Species	Ungrazed	Unwatered control	3.0	3.0	3.8	4.3	5.0	4.6	4.5
		Watered control	3.3	6.0	4.7	5.7	6.0	5.6	6.3
		Low N	3.7	4.3	3.9	4.3	4.4	4.4	4.4
		High N	3.0	4.3	3.2	4.3	5.3	3.9	3.5
	Rabbit grazed	Unwatered control	3.0	4.7	4.3	4.8	3.5	4.7	4.6
		Watered control	2.7	3.8	4.1	5.1	4.5	5.2	5.5
		Low N	2.7	3.8	4.1	3.8	3.5	4.2	3.8
		High N	3.0	3.7	4.0	4.1	4.2	4.7	4.3
	Rabbit and pony grazed	Unwatered control	4.7	4.1	5.0	4.1	3.5	4.7	4.3
		Watered control	4.7	4.1	4.7	4.7	4.1	5.7	6.0
		Low N	3.3	3.8	2.8	3.7	3.9	4.4	4.4
		High N	3.7	5.1	5.4	5.4	4.6	5.5	5.9
		f ratio	0.84	2.60	2.04	0.76	0.15	0.36	1.07
		p value	0.553	0.057	0.116	0.609	0.986	0.896	0.418
		s.e.d.	0.919	1.085	1.018	1.033	1.083	1.097	1.130
Bryophytes: Hits	Ungrazed	Unwatered control	67.7	76.1	71.9	70.0	83.3	83.6	84.5
		Watered control	60.7	75.6	83.0	86.0	84.0	85.1	90.4
		Low N	70.7	73.5	74.6	82.4	75.7	86.9	85.2
		High N	70.0	65.4	60.4	66.8	68.2	67.1	68.7
	Rabbit grazed	Unwatered control	62.0	73.1	83.7	83.9	76.3	87.6	95.1
		Watered control	52.7	69.7	78.0	80.5	74.4	81.8	82.8
		Low N	67.0	69.4	71.5	72.6	71.0	77.5	70.3
		High N	60.0	76.2	79.6	86.0	72.0	83.3	82.2
	Rabbit and pony grazed	Unwatered control	66.0	73.1	70.8	73.0	72.0	80.3	79.3
		Watered control	64.3	71.9	76.6	79.4	74.3	81.9	83.0
		Low N	81.0	67.0	67.6	70.0	62.8	69.0	72.0
		High N	67.0	77.6	77.3	76.2	73.8	78.3	78.4
		f ratio	0.92	1.15	1.74	3.03	0.81	1.21	2.17
		p value	0.502	0.378	0.172	**0.033**	0.579	0.35	0.098
		s.e.d.	6.73	6.49	10.11	7.65	7.86	9.79	8.49

Appendix 2.14. Continued.

			Jun-03	Sep-03	Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
	Grazing*Nitrogen								
Forbs: Species	Ungrazed	Unwatered control	4.7	6.1	6.0	6.2	5.4	5.5	5.7
		Watered control	5.7	6.3	5.7	5.6	6.7	6.7	5.6
		Low N	5.3	6.1	6.2	5.1	4.2	5.5	5.2
		High N	5.7	5.9	6.0	6.2	6.0	4.7	5.9
	Rabbit grazed	Unwatered control	6.3	4.0	4.7	5.7	5.4	7.4	6.7
		Watered control	9.7	6.1	4.2	5.1	5.9	6.7	5.2
		Low N	7.3	4.5	6.7	5.8	4.9	5.2	7.6
		High N	6.3	4.3	4.7	4.7	5.0	6.7	5.7
	Rabbit and pony grazed	Unwatered control	3.3	3.3	5.1	3.4	6.2	6.9	7.0
		Watered control	4.3	3.6	6.2	4.2	3.1	5.8	5.9
		Low N	3.0	4.2	6.3	5.0	5.3	6.8	7.9
		High N	4.7	4.4	5.6	4.3	4.6	5.6	6.3
		f ratio	0.75	0.47	0.29	0.67	1.67	1.22	0.49
		p value	0.616	0.820	0.932	0.675	0.189	0.345	0.809
		s.e.d.	1.458	1.468	1.776	1.668	1.647	1.467	2.390
Forbs: Hits	Ungrazed	Unwatered control	18.0	28.4	30.9	27.8	29.1	19.6	31.8
		Watered control	22.3	26.9	27.1	30.1	37.3	30.8	34.4
		Low N	27.0	28.5	27.8	27.2	31.5	23.0	27.8
		High N	32.7	22.0	17.7	21.5	23.6	15.6	21.2
	Rabbit grazed	Unwatered control	26.3	17.8	13.2	12.8	13.8	23.6	36.8
		Watered control	48.7	21.5	9.1	9.9	23.7	23.8	20.0
		Low N	47.7	20.9	17.2	9.3	11.2	23.8	29.6
		High N	34.3	16.3	13.2	17.3	25.7	22.7	29.3
	Rabbit and pony grazed	Unwatered control	10.3	15.2	20.8	19.0	27.0	17.9	30.9
		Watered control	13.0	13.2	18.5	18.0	18.6	14.9	26.4
		Low N	17.3	17.7	25.0	21.0	24.1	16.1	33.7
		High N	9.0	19.1	22.5	23.7	24.7	21.9	33.8
		f ratio	1.11	0.48	0.45	0.63	0.81	0.51	0.55
		p value	0.394	0.816	0.835	0.703	0.578	0.790	0.760
		s.e.d.	8.92	7.16	9.48	11.56	12.78	12.44	17.52

Appendix 2.15. Average weighted Ellenberg indicator values for nitrogen, adjusted for the baseline as covariate. Results of Anova analyses (s.e.d. = standard error of the differences of means) indicate significant differences.

		Jun-03	Sep-03	Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
Grazing	Ungrazed	4.00	3.81	3.93	3.80	3.88	3.93	3.89
	Rabbit grazed	3.61	3.58	3.67	3.66	3.58	3.66	3.63
	Rabbit and pony grazed	3.92	3.58	3.78	3.59	3.58	3.74	3.62
	f ratio	6.99	6.70	0.670	1.270	3.030	0.580	2.990
	p value	**0.049**	0.078	0.575	0.399	0.191	0.614	0.193
	s.e.d.	0.1097	0.0981	0.2230	0.2069	0.1885	0.2836	0.1745
Nitrogen	Unwatered control	3.88	3.66	3.76	3.69	3.63	3.75	3.70
	Watered control	3.85	3.69	3.77	3.66	3.69	3.73	3.68
	Low N	3.77	3.65	3.82	3.71	3.66	3.81	3.72
	High N	3.89	3.64	3.82	3.68	3.75	3.82	3.75
	f ratio	0.58	0.25	0.52	0.54	1.07	0.79	0.41
	p value	0.633	0.861	0.672	0.660	0.390	0.516	0.749
	s.e.d.	0.1022	0.0598	0.0620	0.0490	0.0673	0.0698	0.0711
Grazing*Nitrogen								
Ungrazed	Unwatered control	4.14	3.77	3.84	3.76	3.82	3.87	3.84
	Watered control	4.06	3.86	3.96	3.86	3.86	3.90	3.88
	Low N	3.91	3.85	3.95	3.84	3.92	3.96	3.86
	High N	3.89	3.76	3.98	3.74	3.93	3.97	3.98
Rabbit grazed	Unwatered control	3.58	3.62	3.64	3.63	3.52	3.61	3.59
	Watered control	3.60	3.58	3.60	3.57	3.58	3.61	3.58
	Low N	3.58	3.59	3.75	3.79	3.54	3.70	3.71
	High N	3.70	3.55	3.69	3.65	3.69	3.73	3.66
Rabbit and pony grazed	Unwatered control	3.94	3.57	3.81	3.66	3.56	3.76	3.67
	Watered control	3.88	3.62	3.75	3.54	3.63	3.68	3.58
	Low N	3.81	3.51	3.76	3.51	3.53	3.76	3.59
	High N	4.07	3.61	3.80	3.65	3.62	3.75	3.62
	f ratio	0.66	0.43	0.52	2.29	0.28	0.14	0.41
	p value	0.684	0.849	0.783	0.084	0.937	0.989	0.860
	s.e.d.	0.1885	0.1233	0.1889	0.1674	0.1753	0.2318	0.1725

Appendix 2.16. Average sward heights in cm between 17 April 2004 and 28 June 2005 for controls, low N, high N and high N+P treatments, adjusted for 17 April 2004 as covariate. s.e.d. = standard error of the differences of means.

	17-Apr-04	**30-Apr-04**	**22-May-04**	**06-Jun-04**	**22-Jun-04**	**05-Jul-04**	**23-Jul-04**	**07-Aug-04**	**28-Aug-04**	**24-Sep-04**
Nitrogen										
Unwatered control	4.03	4.67	5.87	6.21	6.22	6.33	6.16	6.36	6.88	7.06
Watered control	3.81	4.44	6.00	6.12	6.24	6.21	6.42	6.82	6.50	7.15
Low N	3.70	4.62	5.98	6.32	6.81	6.52	6.55	6.58	6.98	7.65
High N	3.89	4.82	6.09	6.93	6.84	6.99	7.19	7.54	7.98	8.22
High N+P	4.52	5.18	6.64	7.18	7.36	7.10	7.43	7.95	8.48	8.42
f ratio	11.92	0.67	0.67	2.48	2.20	1.87	1.66	1.76	4.26	1.51
p value	**<0.001**	0.390	0.373	0.072	0.101	0.150	0.193	0.171	**0.010**	0.240
s.e.d	0.1307	0.2785	0.3761	0.4230	0.5020	0.4280	0.6440	0.7290	0.5640	0.8560

	04-Nov-04	**15-Dec-04**	**29-Jan-05**	**27-Feb-05**	**28-Mar-05**	**21-Apr-05**	**03-May-05**	**27-May-05**	**08-Jun-05**	**28-Jun-05**
Nitrogen										
Unwatered control	6.91	5.56	5.44	5.31	5.67	6.76	6.98	8.31	8.85	8.33
Watered control	6.02	5.15	4.91	4.75	5.12	6.17	6.34	8.14	8.22	7.90
Low N	6.33	5.18	5.00	5.12	5.31	5.81	6.00	7.91	8.10	8.44
High N	7.01	5.54	5.29	5.04	5.09	6.25	6.59	8.69	8.59	8.53
High N+P	7.57	7.07	6.69	6.97	6.70	8.11	8.39	9.98	11.57	11.50
f ratio	0.91	3.45	3.52	4.42	3.31	2.15	5.77	0.77	1.83	2.52
p value	0.473	**0.024**	**0.022**	**0.008**	**0.028**	0.107	**0.002**	0.556	0.157	0.069
s.e.d	0.7340	0.3468	0.3125	0.3880	0.3541	0.479	0.3211	0.9020	0.8810	0.8990

Appendix 2.17. Average sward heights in cm between 17 April 2004 and 28 June 2005 for the interaction of grazing and nitrogen treatment, s.e.d. = standard error of the differences of means.

		17-Apr-04	30-Apr-04	22-May-04	06-Jun-04	22-Jun-04	05-Jul-04	23-Jul-04	07-Aug-04	28-Aug-04	24-Sep-04
Grazing*Nitrogen											
Ungrazed	Unwatered control	6.76	7.92	10.99	11.76	12.23	12.25	11.79	13.16	14.23	13.90
	Watered control	6.29	7.42	10.85	11.20	12.65	12.25	12.90	14.23	13.29	14.15
	Low N	5.99	7.15	10.23	11.09	13.06	12.20	12.01	12.64	13.39	13.78
	High N	6.61	8.37	11.04	12.13	13.12	13.69	13.88	15.28	15.68	15.81
	High N+P	7.40	9.43	12.73	13.73	14.62	14.74	15.09	16.64	16.62	17.94
Rabbit grazed	Unwatered control	2.70	3.18	3.49	3.68	3.16	3.55	3.27	2.94	3.34	3.37
	Watered control	2.93	3.11	3.67	3.53	3.11	3.23	3.14	3.05	3.15	3.11
	Low N	2.56	3.05	3.58	3.23	3.01	3.12	3.16	2.77	3.51	3.50
	High N	2.52	2.87	3.41	3.70	3.26	3.28	3.35	3.37	4.14	3.83
	High N+P	3.08	3.80	4.83	4.71	4.06	4.18	4.32	4.46	5.19	4.82
Rabbit and pony grazed	Unwatered control	2.64	2.98	3.23	3.31	3.37	3.32	3.57	3.11	3.16	3.51
	Watered control	2.21	2.39	2.95	3.12	2.58	2.63	2.57	2.56	2.63	2.82
	Low N	2.55	3.04	3.29	3.82	3.72	3.39	3.46	3.33	3.33	3.62
	High N	2.55	3.00	3.53	4.67	3.93	3.70	4.00	3.63	3.87	3.81
	High N+P	3.08	3.45	3.88	4.60	4.56	3.94	4.78	4.57	4.92	5.02
	f ratio	2.60	1.99	0.94	1.05	0.56	1.32	0.85	0.81	0.57	0.67
	p value	**0.033**	0.092	0.507	0.429	0.800	0.282	0.572	0.602	0.789	0.712
	s.e.d	0.3288	0.53	0.751	0.915	1.072	0.978	1.137	1.219	1.393	1.723

Appendix 2.17. Continued.

		04-Nov-04	15-Dec-04	29-Jan-05	27-Feb-05	28-Mar-05	21-Apr-05	03-May-05	27-May-05	08-Jun-05	28-Jun-05
Grazing*Nitrogen											
Ungrazed	Unwatered control	14.72	11.15	10.88	10.53	11.73	13.91	14.05	17.37	18.67	17.81
	Watered control	12.13	10.67	10.02	9.66	10.19	12.81	12.76	16.25	17.35	16.59
	Low N	11.74	10.14	9.39	9.89	9.93	11.08	11.33	14.66	15.93	17.35
	High N	13.63	11.03	10.49	9.98	9.92	12.25	12.76	16.73	17.24	18.19
	High N+P	16.08	14.50	13.34	15.09	14.48	16.67	16.43	21.96	24.63	25.96
Rabbit grazed	Unwatered control	3.15	2.71	2.82	2.80	2.86	3.35	3.64	4.31	4.30	3.89
	Watered control	2.73	2.60	2.54	2.41	2.65	3.08	3.28	4.17	4.17	3.78
	Low N	2.93	2.59	2.63	2.46	2.64	3.01	3.31	3.90	4.06	3.76
	High N	3.37	2.71	2.63	2.48	2.62	3.21	3.28	4.66	4.32	3.58
	High N+P	4.22	3.42	3.58	3.32	3.74	4.39	4.93	5.97	6.33	5.14
Rabbit and pony grazed	Unwatered control	3.02	2.84	2.66	2.68	2.53	3.09	3.29	3.47	3.68	3.41
	Watered control	2.43	2.10	2.00	1.90	2.03	2.36	2.80	3.02	2.73	2.78
	Low N	3.09	2.65	2.74	2.53	2.57	2.93	3.07	3.62	3.65	3.32
	High N	3.62	2.82	2.65	2.50	2.48	3.16	3.64	4.15	3.99	3.51
	High N+P	4.66	3.56	3.60	3.36	3.29	4.03	4.36	4.86	4.94	5.02
	f ratio	1.01	5.29	4.38	7.88	5.65	4.11	6.45	1.74	3.22	4.09
	p value	0.458	**<0.001**	**0.002**	**<0.001**	**<0.001**	**0.003**	**<0.001**	0.140	**0.013**	**0.003**
	s.e.d	1.523	1.019	0.9166	0.631	1.0013	1.007	0.6651	1.419	1.482	1.628

Appendix 2.18. Average height of the highest touch per pin (in cm) in point quadrat surveys between April 2004 and June 2005 (60 hits each in 45 1 m^2 quadrats) and results of Anova analyses (s.e.d. = standard error of the differences of means), adjusting for April 2004 as covariate for the effect of nitrogen addition.

		Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
Nitrogen	Unwatered control	3.78	5.58	7.12	5.93	8.42
	Watered control	3.47	5.54	6.77	5.07	7.24
	Low N	3.46	5.42	6.49	4.91	6.97
	High N	3.66	5.88	6.84	4.82	7.32
	High N+P	4.74	6.37	6.67	5.80	10.79
	f ratio	6.59	0.62	0.47	2.20	1.54
	p value	**<0.001**	0.656	0.759	0.100	0.223
	s.e.d.	0.2925	0.532	0.559	0.443	0.909
Grazing*Nitrogen						
Ungrazed	Unwatered control	6.63	10.79	15.03	12.42	18.35
	Watered control	6.25	11.26	14.43	10.28	15.65
	Low N	5.52	10.42	12.14	9.05	13.98
	High N	6.43	11.74	14.04	9.13	15.45
	High N+P	8.34	12.55	15.68	13.00	23.97
Rabbit grazed	Unwatered control	2.46	2.98	3.11	2.68	3.75
	Watered control	2.27	2.71	2.59	2.42	3.55
	Low N	2.39	2.73	2.90	2.48	3.50
	High N	2.34	2.71	2.91	2.53	3.48
	High N+P	3.03	3.50	3.55	3.14	5.19
Rabbit and pony grazed	Unwatered control	2.26	2.94	3.10	2.62	3.12
	Watered control	1.90	2.43	2.24	1.82	2.24
	Low N	2.47	2.87	3.34	2.52	3.15
	High N	2.21	3.08	3.08	2.48	2.90
	High N+P	2.85	3.64	3.51	3.02	3.94
	f ratio	1.78	0.44	1.23	3.29	4.11
	p value	0.131	0.884	0.325	**0.011**	**0.003**
	s.e.d.	0.6224	0.956	1.393	1.028	1.56

Appendix 2.19. Average above ground biomass (g dry weight m^{-2}) in nitrogen fertilisation treatments (unwatered control, watered control, low N, high N, high N+P) between April 2004 and June 2005, adjusted for the baseline as covariate for the effects of nutrient addition, and results of Anova analyses (s.e.d. = standard error of the differences of means). a) Total, b) graminoids, c) bryophytes, d) forbs.

a) Total

		Apr-04	**Jun-04**	**Jun-05**
Nitrogen	Unwatered control	449.0	585.0	405.0
	Watered control	385.0	539.0	401.0
	Low N	479.0	588.0	478.0
	High N	493.0	548.0	520.0
	High N+P	552.0	543.0	623.0
	f ratio	2.070	0.380	5.730
	p value	0.117	0.820	**0.002**
	s.e.d.	60.40	58.10	56.30
Grazing*Nitrogen				
Ungrazed	Unwatered control	478.1	727.3	553.8
	Watered control	397.8	475.4	251.4
	Low N	470.8	501.5	384.5
	High N	439.1	589.3	597.5
	High N+P	319.4	317.2	244.3
Rabbit grazed	Unwatered control	395.8	521.2	260.8
	Watered control	594.2	627.0	559.5
	Low N	336.3	455.7	347.8
	High N	507.8	699.4	536.5
	High N+P	517.8	571.3	648.0
Rabbit and pony grazed	Unwatered control	461.3	490.8	456.8
	Watered control	499.8	627.4	480.8
	Low N	455.3	625.3	877.5
	High N	523.0	468.3	462.3
	High N+P	678.8	713.3	624.2
	f ratio	0.97	0.72	0.96
	p value	0.484	0.668	0.491
	s.e.d.	118.4	113.3	125.6

Appendix 2.19. Continued.

b) Graminoids

		Apr-04	Jun-04	Jun-05
Nitrogen	Unwatered control	167.7	227.4	204.0
	Watered control	144.8	196.3	191.0
	Low N	176.9	177.5	166.0
	High N	167.9	233.3	263.0
	High N+P	178.9	229.2	273.0
	f ratio	0.850	2.340	1.720
	p value	0.509	0.085	0.180
	s.e.d.	20.81	24.13	51.20
Grazing*Nitrogen				
Ungrazed	Unwatered control	216.8	359.5	408.0
	Watered control	168.2	190.7	90.3
	Low N	118.2	133.0	113.3
	High N	232.3	277.7	401.1
	High N+P	85.3	130.0	59.8
Rabbit grazed	Unwatered control	116.8	130.8	103.8
	Watered control	289.4	244.2	300.8
	Low N	101.6	122.9	91.7
	High N	139.8	187.2	109.3
	High N+P	246.7	352.3	483.9
Rabbit and pony grazed	Unwatered control	171.8	164.6	186.9
	Watered control	85.3	184.4	118.9
	Low N	258.8	405.8	519.4
	High N	151.8	149.3	160.9
	High N+P	126.0	158.8	143.1
	f ratio	1.69	1.44	0.49
	p value	0.152	0.231	0.849
	s.e.d.	33.95	53.29	79.20

Appendix 2.19. Continued.

c) Bryophytes

		Apr-04	Jun-04	Jun-05
Nitrogen	Unwatered control	261.0	339.0	183.0
	Watered control	216.0	308.0	172.0
	Low N	279.0	385.0	291.0
	High N	307.0	292.0	244.0
	High N+P	337.0	292.0	325.0
	f ratio	1.300	0.980	2.700
	p value	0.299	0.439	0.056
	s.e.d.	57.20	58.10	56.40
Grazing*Nitrogen				
Ungrazed	Unwatered control	224.0	355.9	138.2
	Watered control	221.3	270.1	141.5
	Low N	338.8	359.9	255.8
	High N	186.3	273.3	166.6
	High N+P	192.8	156.3	149.4
Rabbit grazed	Unwatered control	268.3	385.7	152.8
	Watered control	264.3	343.3	230.8
	Low N	217.7	313.6	218.7
	High N	354.4	496.8	422.6
	High N+P	242.7	178.9	139.2
Rabbit and pony grazed	Unwatered control	279.5	305.5	260.7
	Watered control	399.2	437.5	350.9
	Low N	164.8	200.4	313.2
	High N	323.4	289.0	280.7
	High N+P	523.4	483.3	421.8
	f ratio	0.72	0.74	0.62
	p value	0.672	0.658	0.753
	s.e.d.	120.4	109.0	133.9

Appendix 2.19. Continued.

d) Forbs

		Apr-04	Jun-04	Jun-05
Nitrogen	Unwatered control	19.8	12.1	16.8
	Watered control	24.2	24.7	23.2
	Low N	23.7	24.8	23.7
	High N	17.9	22.7	18.5
	High N+P	36.2	39.1	35.1
	f ratio	1.340	1.120	1.420
	p value	0.285	0.372	0.259
	s.e.d.	8.73	11.98	9.69
Grazing*Nitrogen				
Ungrazed	Unwatered control	37.3	11.8	7.6
	Watered control	8.3	14.7	19.6
	Low N	13.8	8.6	15.5
	High N	20.5	38.3	29.8
	High N+P	41.4	30.9	35.1
Rabbit grazed	Unwatered control	10.7	4.8	4.3
	Watered control	40.5	39.5	28.0
	Low N	17.0	19.2	37.5
	High N	13.6	15.5	4.6
	High N+P	28.4	40.2	24.9
Rabbit and pony grazed	Unwatered control	10.0	20.8	9.2
	Watered control	15.4	5.5	10.9
	Low N	31.7	19.1	44.9
	High N	47.8	30.0	20.8
	High N+P	29.3	71.3	59.3
	f ratio	1.31	1.84	1.48
	p value	0.284	0.119	0.216
	s.e.d.	14.94	20.74	17.15

Appendix 2.20. Average concentrations of nitrogen (N) and phosphorus (P) in g per kg, N and P uptake and N:P ratio in graminoid biomass samples taken in June 2005. Results of Anova analyses (s.e.d. = standard error of the differences of means) indicate significant differences.

		N g/kg	N uptake	P g/kg	P uptake	N:P ratio
Nitrogen	Watered control	12.411	9.009	1.538	1.052	8.297
	Low N	13.067	8.632	1.429	0.969	9.324
	High N	12.744	12.943	1.363	1.393	9.394
	High N+P	12.467	13.063	1.396	1.469	8.953
	f ratio	0.460	2.730	1.370	1.460	1.920
	p value	0.712	0.074	0.283	0.260	0.163
	s.e.d.	0.625	2.072	0.0897	0.290	0.513
Nitrogen*Grazing						
Watered control	Ungrazed	11.700	18.716	0.132	2.106	8.985
	Rabbit grazed	13.767	3.248	0.175	0.420	8.134
	Rabbit and pony grazed	11.767	5.063	0.154	0.631	7.770
Low N	Ungrazed	12.433	15.102	0.142	1.747	8.850
	Rabbit grazed	13.467	4.953	0.134	0.499	10.160
	Rabbit and pony grazed	13.300	5.842	0.153	0.661	8.962
High N	Ungrazed	11.700	22.576	0.123	2.426	9.624
	Rabbit grazed	13.067	10.173	0.145	1.096	9.093
	Rabbit and pony grazed	13.467	6.079	0.141	0.656	9.466
High N+P	Ungrazed	11.900	23.902	0.131	2.683	9.109
	Rabbit grazed	13.100	8.190	0.140	0.878	9.359
	Rabbit and pony grazed	12.400	7.098	0.148	0.846	8.392
	f ratio	0.510	0.680	1.070	0.370	0.750
	p value	0.796	0.671	0.417	0.890	0.620
	s.e.d.	0.956	3.659	0.1584	0.499	0.899

Appendix 2.21. Average concentrations of nitrogen (N) and phosphorus (P) in g per kg, N and P uptake and N:P ratio in bryophyte biomass samples taken in June 2005. Results of Anova analyses (s.e.d. = standard error of the differences of means) indicate significant differences.

		N g/kg	N uptake	P g/kg	P uptake	N:P ratio
Nitrogen	Watered control	11.452	7.027	0.149	0.976	7.897
	Low N	11.678	12.836	0.124	1.471	9.918
	High N	13.578	12.605	0.156	1.311	9.359
	High N+P	12.950	16.064	0.163	1.976	8.367
	f ratio	3.230	4.550	1.410	2.960	1.910
	p value	**0.047**	**0.015**	0.273	0.060	0.164
	s.e.d.	0.801	2.489	0.2016	0.342	0.941
Nitrogen*Grazing						
Watered control	Ungrazed	1.082	7.195	0.157	1.100	6.942
	Rabbit grazed	1.173	6.672	0.148	0.981	8.324
	Rabbit and pony grazed	1.180	7.214	0.142	0.846	8.425
Low N	Ungrazed	1.133	10.099	0.112	0.994	10.193
	Rabbit grazed	1.300	10.416	0.116	0.908	11.312
	Rabbit and pony grazed	1.070	17.994	0.144	2.512	8.248
High N	Ungrazed	1.370	7.245	0.191	0.858	7.843
	Rabbit grazed	1.453	12.725	0.149	1.243	10.513
	Rabbit and pony grazed	1.250	17.845	0.129	1.833	9.721
High N+P	Ungrazed	1.290	14.425	0.181	1.897	7.702
	Rabbit grazed	1.392	13.531	0.161	1.599	8.740
	Rabbit and pony grazed	1.203	20.237	0.146	2.432	8.659
	f ratio	0.390	0.700	0.660	1.100	0.720
	p value	0.876	0.656	0.685	0.400	0.642
	s.e.d.	2.105	6.364	0.3922	0.815	1.507

Appendix 2.22. Average numbers of species and hits in point quadrat surveys (60 hits each in 45 1 m^2 quadrats) between April 2004 and June 2005, in five nitrogen fertilisation treatments, for three plant groups each and total number of species and hits, adjusted for April 2004 as covariate. Results of Anova analyses (s.e.d. = standard error of the differences of means) indicate significant differences.

		Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
Total: Species	Unwatered control	16.33	16.66	16.69	18.56	17.59
	Watered control	17.33	17.44	17.03	18.71	19.03
	Low N	16.56	16.15	15.43	17.20	17.11
	High N	16.22	17.19	16.54	17.52	17.33
	High N+P	18.78	17.33	18.53	18.46	18.95
	f ratio	1.270	1.410	3.750	1.190	1.180
	p value	0.308	0.262	**0.017**	0.343	0.347
	s.e.d.	1.331	0.729	0.923	0.983	1.070
Total: Hits	Unwatered control	182.8	198.0	217.6	210.6	234.4
	Watered control	193.9	196.7	217.2	207.6	224.1
	Low N	194.0	200.7	207.6	212.1	223.6
	High N	188.6	208.9	215.0	210.9	221.2
	High N+P	199.7	223.0	219.6	209.4	244.5
	f ratio	1.100	11.720	0.850	0.130	3.430
	p value	0.379	**<0.001**	0.507	0.971	**0.024**
	s.e.d.	8.610	4.720	7.430	6.560	7.670
Graminoids: Species	Unwatered control	7.11	6.75	6.65	6.98	6.56
	Watered control	6.78	6.85	6.62	6.40	6.94
	Low N	6.78	6.96	6.73	7.06	7.05
	High N	6.67	7.14	6.35	6.91	6.44
	High N+P	7.11	7.09	6.99	7.21	7.45
	f ratio	0.61	0.51	1.03	1.64	1.61
	p value	0.660	0.727	0.415	0.197	0.204
	s.e.d.	0.377	0.303	0.339	0.347	0.452
Graminoids: Hits	Unwatered control	89.9	104.6	119.7	107.8	118.6
	Watered control	102.4	100.4	117.3	107.4	116.0
	Low N	89.0	99.5	110.9	108.5	110.1
	High N	98.6	108.4	115.8	111.7	113.2
	High N+P	103.4	119.9	120.0	113.8	131.1
	f ratio	2.61	9.45	0.73	1.01	4.23
	p value	0.061	**<0.001**	0.578	0.425	**0.010**
	s.e.d.	6.000	3.910	6.400	4.300	5.460
Bryophytes: Species	Unwatered control	4.44	4.33	3.92	4.61	4.39
	Watered control	4.56	4.98	4.71	5.40	5.74
	Low N	3.56	4.55	4.43	4.81	4.68
	High N	4.11	4.59	4.68	4.67	4.55
	High N+P	4.56	4.54	4.60	5.07	4.52
	f ratio	2.10	1.21	0.82	1.03	3.59
	p value	0.112	0.332	0.523	0.413	**0.020**
	s.e.d.	0.416	0.399	0.592	0.507	0.430
Bryophytes: Hits	Unwatered control	74.90	74.06	75.55	81.90	84.68
	Watered control	72.00	75.32	71.06	75.60	78.70
	Low N	79.1	79.48	74.00	82.40	80.30
	High N	72.3	77.18	72.24	77.30	77.33
	High N+P	69.80	79.75	73.26	78.30	85.43
	f ratio	1.18	1.81	0.82	1.56	2.86
	p value	0.345	0.160	0.523	0.219	**0.046**
	s.e.d.	4.640	2.694	2.898	3.410	3.132

Appendix 2.22. Continued.

		Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
Forbs: Species	Unwatered control	4.78	5.44	5.89	6.69	6.57
	Watered control	6.00	5.49	5.62	6.85	6.28
	Low N	6.22	4.90	4.51	5.54	6.48
	High N	5.44	5.43	5.45	5.86	6.28
	High N+P	7.11	5.73	7.08	6.40	7.05
	f ratio	1.47	0.76	3.25	1.25	0.32
	p value	0.243	0.562	**0.030**	0.317	0.859
	s.e.d.	1.018	0.515	0.745	0.714	0.759
Forbs: Hits	Unwatered control	18.0	17.2	22.9	20.5	29.9
	Watered control	19.4	23.0	29.7	24.9	31.3
	Low N	25.9	19.4	20.7	19.7	30.6
	High N	17.7	23.9	28.2	22.2	31.8
	High N+P	26.4	25.2	25.8	18.5	28.8
	f ratio	1.23	1.96	1.75	0.76	0.11
	p value	0.323	0.135	0.174	0.565	0.979
	s.e.d.	5.51	3.47	4.04	4.14	5.30

Appendix 2.23. Average numbers of species and hits in point quadrat surveys (60 hits each in 45 1 m^2 quadrats) between April 2004 and June 2005, for the interaction of three grazing and five nitrogen fertilisation treatments, for three plant groups each and total number of species and hits. Results of Anova analyses (s.e.d. = standard error of the differences of means) indicate significant differences.

			Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
	Grazing*Nitrogen						
Total: Species	Ungrazed	Unwatered control	15.7	16.3	16.7	16.0	15.7
		Watered control	17.0	18.0	19.3	18.7	18.7
		Low N	16.3	16.7	15.3	17.0	17.0
		High N	15.7	16.7	17.3	14.7	15.7
		High N+P	20.3	18.3	19.3	18.7	19.7
	Rabbit grazed	Unwatered control	18.0	17.7	17.0	20.7	19.3
		Watered control	18.3	19.3	20.0	21.3	21.7
		Low N	19.3	17.7	16.0	17.7	19.7
		High N	17.0	16.3	16.7	19.7	18.0
		High N+P	20.3	18.3	20.7	20.7	21.3
	Rabbit and pony grazed	Unwatered control	15.3	14.3	15.0	17.7	16.3
		Watered control	16.7	15.7	12.3	16.7	17.3
		Low N	14.0	13.0	14.0	16.0	16.7
		High N	16.0	16.7	14.0	16.7	16.7
		High N+P	15.7	19.3	19.0	19.3	19.3
		f ratio	0.57	0.77	1.00	0.57	0.16
		p value	0.795	0.630	0.465	0.795	0.994
		s.e.d.	2.158	2.055	1.977	1.982	2.357
Total: Hits	Ungrazed	Unwatered control	205.7	210.3	251.0	224.7	235.3
		Watered control	225.0	227.7	258.0	242.0	250.3
		Low N	216.7	241.0	247.0	234.0	240.7
		High N	206.7	234.3	251.0	233.0	243.0
		High N+P	222.3	262.3	259.7	238.7	272.0
	Rabbit grazed	Unwatered control	188.0	191.7	199.3	209.0	248.7
		Watered control	181.0	188.7	217.0	200.3	231.7
		Low N	183.3	186.7	191.0	209.3	224.7
		High N	182.3	205.0	207.3	210.3	228.7
		High N+P	203.7	214.3	219.3	208.7	264.0
	Rabbit and pony grazed	Unwatered control	154.7	170.0	183.7	182.0	196.3
		Watered control	175.7	179.0	181.0	184.3	195.7
		Low N	182.0	180.0	189.3	197.0	211.0
		High N	176.7	179.3	180.0	183.7	183.7
		High N+P	173.0	211.7	196.3	195.0	217.7
		f ratio	0.68	0.57	0.35	0.35	0.57
		p value	0.702	0.788	0.938	0.937	0.788
		s.e.d.	16.22	17.69	15.70	18.76	22.38

Appendix 2.23. Continued.

			Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
	Grazing*Nitrogen						
Graminoids: Species	Ungrazed	Unwatered control	6.7	6.7	7.0	6.7	6.3
		Watered control	6.7	6.7	6.7	6.3	6.7
		Low N	6.3	7.0	6.7	7.0	7.3
		High N	6.7	6.3	6.3	6.3	6.3
		High N+P	8.0	7.7	7.7	8.0	8.3
	Rabbit grazed	Unwatered control	8.0	7.0	7.3	7.7	7.0
		Watered control	7.0	7.3	7.7	7.0	7.7
		Low N	7.0	7.7	6.7	7.0	6.7
		High N	7.3	7.3	6.7	7.3	7.0
		High N+P	7.3	7.3	7.3	7.0	7.3
	Rabbit and pony grazed	Unwatered control	6.7	7.0	6.0	7.0	6.7
		Watered control	6.7	6.3	5.3	5.7	6.3
		Low N	7.0	6.0	6.7	7.0	7.0
		High N	6.0	7.3	5.7	6.7	5.7
		High N+P	6.0	6.7	6.3	7.0	7.0
		f ratio	1.55	1.21	0.92	0.98	0.84
		p value	0.193	0.333	0.518	0.477	0.577
		s.e.d.	0.601	0.707	0.699	0.695	0.808
Graminoids: Hits	Ungrazed	Unwatered control	104.0	115.7	140.7	120.7	123.7
		Watered control	121.7	119.7	145.0	133.7	134.7
		Low N	107.7	124.0	133.7	117.0	120.3
		High N	120.0	135.0	151.0	142.7	141.3
		High N+P	125.7	154.0	167.0	155.0	170.3
	Rabbit grazed	Unwatered control	92.7	100.3	105.7	102.3	118.3
		Watered control	94.7	97.7	115.0	106.3	121.0
		Low N	80.0	87.7	88.3	100.7	100.3
		High N	89.3	103.3	104.3	109.7	113.7
		High N+P	108.3	114.0	109.7	107.0	134.0
	Rabbit and pony grazed	Unwatered control	73.0	88.3	99.3	87.7	102.3
		Watered control	91.0	92.0	103.3	93.0	102.0
		Low N	79.3	76.0	95.7	93.7	96.7
		High N	86.3	89.7	95.7	86.3	87.7
		High N+P	76.3	101.3	96.7	92.0	100.3
		f ratio	0.99	1.34	0.79	1.73	2.13
		p value	0.465	0.272	0.614	0.142	0.073
		s.e.d.	11.37	10.49	13.58	11.90	10.79
Bryophytes: Species	Ungrazed	Unwatered control	3.7	4.0	4.7	4.3	4.3
		Watered control	4.7	5.7	6.0	5.7	6.3
		Low N	4.0	4.7	4.7	4.7	4.7
		High N	3.0	4.0	5.0	3.7	3.3
		High N+P	5.7	5.0	5.7	6.0	6.0
	Rabbit grazed	Unwatered control	4.0	4.7	3.3	4.7	4.7
		Watered control	3.7	4.7	4.0	5.0	5.3
		Low N	3.7	3.3	3.0	4.0	3.7
		High N	3.7	4.0	4.0	4.7	4.3
		High N+P	3.3	3.7	3.7	4.3	3.3
	Rabbit and pony grazed	Unwatered control	5.7	5.0	4.3	5.3	4.7
		Watered control	5.3	5.7	5.0	6.3	6.3
		Low N	3.0	3.3	3.7	4.0	4.0
		High N	5.7	5.3	4.7	5.3	5.7
		High N+P	4.7	6.0	5.3	5.7	5.0
		f ratio	3.47	0.87	0.12	0.72	1.65
		p value	**0.008**	0.552	0.998	0.672	0.163
		s.e.d.	0.957	1.123	1.185	1.044	0.986

Appendix 2.23. Continued.

			Apr-04	Jun-04	Sep-04	Apr-05	Jun-05
	Grazing*Nitrogen						
Bryophytes: Hits	Ungrazed	Unwatered control	74.7	72.7	85.3	86.3	87.0
		Watered control	78.0	80.3	77.7	78.3	84.3
		Low N	80.7	88.7	81.3	93.7	91.3
		High N	65.7	72.3	73.0	73.0	74.0
		High N+P	69.7	72.7	68.7	71.3	83.3
	Rabbit grazed	Unwatered control	77.3	78.0	72.7	82.0	90.0
		Watered control	61.3	63.3	59.7	63.7	66.3
		Low N	70.7	72.7	73.3	78.7	71.3
		High N	71.0	77.7	66.0	75.0	74.7
		High N+P	61.3	66.3	65.0	66.0	72.0
	Rabbit and pony grazed	Unwatered control	72.7	74.3	71.7	81.0	80.0
		Watered control	76.7	78.7	72.0	80.3	81.7
		Low N	86.0	89.3	80.3	90.0	91.0
		High N	80.3	78.7	74.7	80.3	80.3
		High N+P	78.3	91.7	77.0	87.0	92.0
		f ratio	1.10	1.98	0.67	0.78	1.59
		p value	0.397	0.093	0.71	0.621	0.182
		s.e.d.	12.22	11.41	9.66	11.64	11.12
Forbs: Species	Ungrazed	Unwatered control	5.3	5.7	5.0	5.0	5.0
		Watered control	5.7	5.7	6.7	6.7	5.7
		Low N	6.0	5.0	4.0	5.3	5.0
		High N	6.0	6.3	6.0	4.7	6.0
		High N+P	6.7	5.7	6.0	4.7	5.3
	Rabbit grazed	Unwatered control	6.0	6.0	6.3	8.3	7.7
		Watered control	7.7	7.3	8.3	9.3	8.7
		Low N	8.7	6.7	6.3	6.7	9.3
		High N	6.0	5.0	6.0	7.7	6.7
		High N+P	9.7	7.3	9.7	9.3	10.7
	Rabbit and pony grazed	Unwatered control	3.0	2.3	4.7	5.3	5.0
		Watered control	4.7	3.7	2.0	4.7	4.7
		Low N	4.0	3.7	3.7	5.0	5.7
		High N	4.3	4.0	3.7	4.7	5.3
		High N+P	5.0	6.7	7.3	6.7	7.3
		f ratio	0.38	1.00	1.57	0.82	0.70
		p value	0.921	0.464	0.186	0.596	0.686
		s.e.d.	1.674	1.445	1.428	1.402	1.860
Forbs: Hits	Ungrazed	Unwatered control	27.0	22.0	25.0	17.7	24.7
		Watered control	25.3	27.7	35.3	30.0	31.3
		Low N	28.3	28.3	32.0	23.3	29.0
		High N	21.0	27.0	27.0	17.3	27.7
		High N+P	27.0	35.7	24.0	12.3	18.3
	Rabbit grazed	Unwatered control	18.0	13.3	21.0	24.7	40.3
		Watered control	25.0	27.7	42.3	30.3	44.3
		Low N	32.7	26.3	29.3	30.0	53.0
		High N	22.0	24.0	37.0	25.7	40.3
		High N+P	34.0	34.0	44.7	35.7	58.0
	Rabbit and pony grazed	Unwatered control	9.0	7.3	12.7	13.3	14.0
		Watered control	8.0	8.3	5.7	11.0	12.0
		Low N	16.7	14.7	13.3	13.3	23.3
		High N	10.0	11.0	9.7	17.0	15.7
		High N+P	18.3	18.7	22.7	16.0	25.3
		f ratio	0.24	0.13	0.86	0.76	0.46
		p value	0.979	0.997	0.565	0.638	0.870
		s.e.d.	9.22	10.08	11.04	8.60	14.09

APPENDIX 3: RAW DATA AND VEGETATION SURVEY DATA FOR CHAPTER 7

Appendix 3.1. Sampling area 1: Numbers of seedlings in unfertilised control trays and nitrogen addition trays. Species sorted by abundance.

	Control								Nitrogen addition							
Tray number	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Block on bench	2	1	1	2	1	2	1	2	2	2	1	1	1	1	1	2
Hydrocotyle vulgaris	28	42	50	29	35	35	38	21	37	36	41	32	30	34	39	46
Juncus articulatus	46	7	5	44	36	61	25	5	50	37	68	79	12	52	10	14
Agrostis stolonifera	18	18	9	15	15	23	10	9	10	10	21	16	9	17	11	14
glaucous sedge	5	3	4	8	3	9	2	3	17	10	14	16	3	7	6	3
Mentha aquatica	8	3	4	8	8	9	4	2	8	5	9	14	3	5	10	6
Juncus bufonius	11	3	10	9	5	8	3	1	6	6	13	9	0	10	6	1
Carex arenaria	5	5	2	2	2	7	1	2	5	5	10	3	2	5	1	5
Carex viridula	1	2	2	5	5	3	3	0	6	2	10	5	4	4	3	3
Sagina nodosa	3	4	1	0	1	4	5	4	3	4	3	3	0	5	5	5
Cerastium fontanum	2	4	2	1	4	7	2	5	2	2	2	3	2	2	2	3
Anagallis tenella	1	1	2	1	2	5	0	1	4	1	4	1	5	3	2	1
Ranunculus flammula	1	1	4	2	2	2	1	0	0	1	0	2	1	1	1	3
Viola riviniana	2	2	0	2	3	1	0	0	4	1	0	0	0	1	1	0
Centaurium littorale	1	0	0	0	0	0	1	0	2	1	3	4	1	1	0	2
Parnassia palustris	2	0	0	0	0	3	0	0	0	0	4	0	1	2	2	0
Ranunculus repens	1	0	1	0	1	2	0	0	1	0	0	1	1	2	3	0
Juncus acutiflorus	0	0	0	0	0	3	1	1	1	1	2	0	0	2	0	0
Samolus valerandi	3	0	1	1	2	0	0	0	0	3	0	0	0	0	0	0
Potentilla anserina	2	1	1	0	0	2	0	1	1	0	0	0	0	0	2	0
Taraxacum sect. *Ruderalia* (*T. officinale* Wigg. group)	1	0	2	0	0	0	1	0	0	0	0	0	1	1	2	2
Holcus lanatus	2	0	0	1	0	1	0	0	0	1	1	2	1	0	0	0
Epilobium montanum	0	0	0	0	1	2	0	0	0	2	2	1	0	0	0	0
Leontodon autumnalis	0	1	1	0	0	0	0	2	1	1	0	0	1	0	0	0
Prunella vulgaris	0	0	1	0	0	0	1	0	0	1	0	1	1	0	0	0
Lotus corniculatus	0	0	0	0	0	0	0	0	2	0	1	0	0	0	1	0
Poa pratensis	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
Agrostis capillaris	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Veronica anagallis-aquatica	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Senecio jacobaea	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Anthoxanthum odoratum	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Luzula campestris	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Hypochaeris radicata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Trifolium pratense	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Veronica chamaedrys	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Anagallis arvensis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cardamine pratensis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

Appendix 3.2. Sampling area 2: Numbers of seedlings in unfertilised control trays and nitrogen addition trays. Species sorted by abundance.

	Control								Nitrogen addition							
Tray number	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Block on bench	2	1	1	2	1	2	1	2	2	2	1	1	1	1	1	2
Hydrocotyle vulgaris	38	40	31	42	43	54	45	26	43	36	51	48	42	32	49	43
Juncus articulatus	1	42	16	13	40	30	12	4	43	53	38	59	49	38	41	17
Mentha aquatica	7	12	13	7	18	20	13	14	17	17	19	15	18	22	10	8
Juncus bufonius	2	16	2	5	6	5	9	5	17	13	7	9	10	13	9	5
Anagallis tenella	2	7	8	5	9	6	3	4	12	6	12	11	5	15	8	7
Agrostis stolonifera	2	6	6	5	5	4	4	0	7	6	11	3	4	10	6	6
glaucous sedge	1	5	4	2	9	3	4	4	8	5	5	10	11	7	3	3
Ranunculus flammula	3	1	3	2	4	2	1	3	6	1	4	7	4	3	5	3
Carex arenaria	0	6	0	1	6	3	4	0	3	2	2	7	3	1	3	1
Parnassia palustris	0	1	1	0	1	0	0	0	2	9	3	3	3	7	3	3
Centaurium littorale	0	1	2	1	1	4	2	0	2	1	6	2	3	5	3	1
Carex viridula	0	0	0	0	2	1	3	0	6	1	1	2	2	1	0	3
Samolus valerandi	0	0	0	2	1	2	1	0	0	0	1	1	2	2	2	1
Epilobium montanum	0	1	0	0	1	2	3	3	1	0	0	0	2	0	1	0
Prunella vulgaris	0	1	1	0	0	1	0	1	0	1	1	0	1	1	0	2
Sagina nodosa	0	2	0	0	0	0	0	1	1	1	1	0	0	0	0	1
Juncus acutiflorus	0	0	0	0	1	0	0	0	0	1	1	3	0	0	1	0
Potentilla anserina	0	0	0	0	0	1	0	0	0	0	0	1	2	2	0	1
Centaurium erythraea	1	0	0	1	0	1	1	0	0	2	0	0	0	0	1	0
Holcus lanatus	0	0	0	0	0	0	1	0	1	1	2	1	0	0	0	0
Plantago major	2	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0
Leontodon autumnalis	0	0	0	2	0	0	0	0	2	0	1	0	0	0	0	0
Taraxacum sect. *Ruderalia* (*T. officinale* Wigg. group)	0	2	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Senecio jacobaea	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0
Linum catharthicum	2	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Lotus corniculatus	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Sonchus arvensis	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Poa pratensis	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthoxanthum odoratum	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Bellis perennis	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Viola riviniana	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ranunculus repens	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Luzula campestris	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leontodon saxatilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Isolepis setacea	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Triglochin spp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Trifolium repens	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Appendix 3.3. Abundance in vegetation in 1987-2003 at eight different sampling locations. Figures are Domin values for percentage cover (1: <4% with few individuals, 2: <4% with several individuals, 3: <4% with many individuals, 4: 4-10%, 5: 11-25%, 6: 26-33%, 7: 34-50%, 8: 51-75%, 9: 76-90%, 10: 91-100%). 1-4: Sampling area 1, 5-8: Sampling area 2.

	1					2					3					4					5					6			7			8		
	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003	1992	1996	2003	1992	1996	2003
Agrostis capillaris																			1														2	2
Agrostis stolonifera			1	1	3				3	4					2	3		2	3	3	1			2	3		3	3			5		1	
Agrostis vinealis																		2											1					
Aira praecox										1																								
Ammophila arenaria																													1	3				
Anagallis tenella																					3	3	1	1	4									3
Anthoxanthum odoratum											4	7	4	4	3																2	5	3	3
Anthyllis vulneraria				1	1					1																								
Barbula convoluta									2																									
Bellis perennis																					1		4	1								2		1
Brachythecium rutabulum														2									2		3								3	4
Bryum spp.										2																								
Bryum capillare								2																										
Bryum pseudotriquetrum	4																																2	
Calliergonella cuspidata					2						3		4		4	10	9	10	6	9			2	8	8	7	6	8			4			
Campylium stellatum			8		3					4													2								2			
Cardamine pratensis																				1														
Carex arenaria	1	2	3	3	4	2	4	2	3	2	2	4	2	2			5	4	3	2						1	3	2	3	4	3	5	2	
Carex viridula																											2							
Cerastium fontanum										1			1		3											1							1	
Crepis capillaris											2					2					3			1									1	1
Cynosurus cristatus													3	3	3																		2	2
Dactylorhiza incarnata/purpurella															1						1		1	1	2								1	1
Danthonia decumbens					2																				4									
Drepanocladus aduncus	4			6																														
Drepanocladus polygamus												3																						
Eleocharis quinqueflora																												2						
Epilobium montanum											1																							
Epipactis palustris	3	3	4	4	7	4	3	5	4	5																		2						1
Euphrasia officinalis agg.				3				2	3	4				2											1						1		1	3
Festuca ovina																																	3	3
Festuca rubra													2	3	3			1	3	3									3	3	3	3	3	4
Fissidens taxifolius																																	2	
Galium palustre															1																			
glaucous sedge		7	5	5	8	4	8	3	6	7		1	2	2	3	1		3	4	5	3		2	2	4	4	5	4	3	4	5	2	2	4
Holcus lanatus											4	3	3	2	4					3	4	4	5		4	4	2	1		2	4	2	3	1
Homalothecium lutescens										1			2												2									
Hydrocotyle vulgaris	3	2	2	4	4	2	1	1			5	6	4	4	5	3	2	1	3	9	4	6	4	3	4	3	3	7			4	3	2	3
Hypochaeris radicata			1							1			1		2				1		1		2	1	1	4						2	1	3
Hypnum cupressiforme									1	2																								
Juncus acutiflorus		2															3																	
Juncus articulatus			2	2	4					2					2					2						2		4						3
Juncus bufonius																																		2
Kindbergia praelonga											3		2											2										
Leiocolea badensis	4																																	
Leontodon autumnalis									1	1				3	2				2						1		4					2	3	2
Leontodon saxatilis			1	1																	3	1											1	1
Linum catharticum									2	3				2																			1	3
Listera ovata																			1														1	
Lophocolea spp.											3																						2	
Lotus corniculatus	3	3	3	5	4	4	4	4	3	4	4	5	1	4	3	5	5		2	5	3	2	1	2	5	4	2	5	5	2	5	3	3	5
Luzula campestris												1	3																			3	1	1
Mentha aquatica			1	3	2							1		4	3						3	3	3	2	4	3	3	4	3	2	4			
Mnium hornum																																	2	
Ononis repens									1	1	2		3	3																		2	1	2
Parnassia palustris			1		2	2	1			2			1								2		2		4	3					2			
Pilosella officinarum								1	1	1																								
Pinguicula vulgaris	1	1	1																		2	1	2											
Plagiomnium undulatum																									3									3
Plantago lanceolata														3	2								2	1	1								1	1
Poa pratensis											3		4	2	3			3	5	3		3		2	2	3	5	2	6	5	3	3	2	2
Polygala vulgaris					1			1			1			2	2																		1	2
Potentilla anserina											1	1	1	5	2	4	7	5	5	4	1	1	1	2	5	5	5	5	6	2	4	2	1	2
Potentilla erecta																														1				
Preissia quadrata						2	9																											
Prunella vulgaris	1											1	2	2	2						1	1	3	2	2	2		3	1		4	2	1	3

Appendix 3.3. Continued.

	1					2					3					4					5					6			7			8		
	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1987	1988	1991	1996	2003	1992	1996	2003	1992	1996	2003	1992	1996	2003
Pseudocalliergon lycopodioides	4	8	6		7																													
Pyrola rotundifolia	1		2	1		5		4	5	4	3	1	4						3		1		3	3	2							4	3	2
Ranunculus acris													2	3	4		1	1	1	2								1	4	2	4		1	4
Ranunculus bulbosus											1					1																		
Ranunculus flammula					1																		1	1	1	1	2	1			1			1
Ranunculus repens																										2	3	4		2				
Rhinanthus minor				1		3		3	3	5																					4			6
Riccardia spp.											3																							
Rosa canina agg.																					1		1	2	1									
Rubus caesius																				1	2		1	1	2				3	4	4			
Rubus fruticosus																						1												
Rumex acetosa														1	1				1	2														
Sagina nodosa										1																								
Salix repens	7	9	5	8	8	5	7	7	8	6	8	9	6	7	7	8	8	8	6	8	3		4	2	4	7	6	8	7	4	7	5	4	6
Samolus valerandi																						1												
Schoenus nigricans																					6	8	8	8	6									
Scorpidium revolvens																					3	5		2										
Senecio jacobaea													1										1	1	1	1					1		1	2
Sonchus arvensis																								1								5	4	2
Taraxacum sect. *Ruderalia* (*T. officinale* Wigg. group)					2					2	1		2		3					1	3	1	2		4	2	1	4	2		2		1	2
Trifolium pratense														3	5																		2	4
Trifolium repens				1	2					1			4	6	2									1	2	2		3	3		2			2
Triglochin spp.			1																															
Viola canina																		1	4	2									2	1	1			
Viola riviniana																1																		1
Warnstorfia fluitans				4																														