The influence of aspect, soil compaction and management on the grassland species composition of roadside verges, in relation to improving slope stability

Ruth Starr-Keddle

April 2011

A thesis submitted for the degree of Doctor of Philosophy at

Newcastle University

School of Agriculture, Food and Rural Development

Acknowledgements

I would like to acknowledge and thank Dr Roger Smith for supervision, and especially for assistance with CANOCO. I am indebted to Robert Shiel for much needed advice with how to take soil samples and methodology, and his expert statistical knowledge. Many thanks to the BIONICS team, especially Stephanie Glendinning and Paul Hughes, for support with finance, fieldwork, transport and information on the Civil engineering aspects of the project.

I am very grateful to Close House and respective staff members for their patience over the biomass cuts and taking over all the greenhouses, and especially Alan Craig for his assistance with many tasks over the duration of the Mesocosm experiment. I tremendously appreciate the help of my friends Kelly Houston and Pauline Thomas for help with cutting and drying the biomass - tasks that couldn't be done singlehandedly. A number of good friends assisted with botanical surveys: Matthew Mudford, Tim Wallis and Joe Cantelo; a big thank-you for their help over the summers. I will be forever grateful to a number of volunteers who assisted with taking cumbersome root cores, taking Penetrometer readings and taking bulk density samples: Pauline Thomas, Tim Wallis, Brian Brown and Alan Craig: It would not have been possible to take these measurements without their help.

I would like to show appreciation to Tony Sangwine, Geoff Richards, Antonia Glyde, David Patterson and Stuart Wilson from the Highways Agency in Bristol; they gave much needed help and advice during a 6 week work placement there. I would like to thank Patrick Ilott, Eric Skiffington, Jenni Gardner and Emma Fisher, from InterRoute Area 2, for their assistance during a week long placement, and especially John Maddison, who showed me how to do geotechnical surveys. And finally the biggest thank-you goes to Jenny Haworth, who gave up her time to assist me for two weeks surveying the A303, A30 and A38; I could not have done this without her.

Summary

Roadside verge vegetation is a complex, unusual community, poorly understood and researched and a typical example of a "novel ecosystem". The land has been altered by humans, the topsoil introduced from elsewhere, a seed mixture added and a management regime implemented. Vegetation is a cost effective, sustainable method for improving slope stability on steeper roadside slopes. On newly constructed roadside verges its rapid establishment prevents soil erosion and provides an aesthetic cover. The standard grass seed mixture sown includes grass species which are quick growing, vigorous and competitive. The belowground root system increases soil strength and the aboveground canopy reduces surface erosion, although soil compaction can restrict root and shoot growth. Morphological differences between grasses and wildflowers allow the root systems to utilise different soil strata and the aboveground canopy to fully exploit aboveground niches. Therefore maybe a species-rich grassland seed mixture should be sown to improve slope stability?

The BIONICS Embankment at Nafferton Farm was used to investigate aspect and soil compaction on the establishment of a species-rich grassland. A second smaller Mesocosm experiment investigated the effects of aspect, soil compaction and cutting regimes on the aboveground composition and biomass, and the belowground rooting depths of two different seed mixtures. Also a survey of the plant communities and environmental characteristics of grass cuttings was carried out along the A303 and A38 in Wiltshire and Devon.

On the BIONICS embankment 14 generalist plant species germinated from the seed mixture and arable and injurious weeds colonised. More wildflowers, e.g. *Lotus corniculatus,* grew on the south-facing slopes while more grasses and some herbs, e.g. *Ranunculus repens,* grew on the north-facing slopes. Ellenberg Indicator Values for fertility and moisture were higher on north-facing slopes, with light values greater on south-facing slopes. *Lolium perenne*, *Medicago lupulina* and *Achillea millefolium* were associated with the less compacted subsoil.

In the Mesocosm experiment, *L. perenne, Cynosurus cristatus, Phleum bertolonii, Daucus carota, Leucanthemum vulgare, Plantago lanceolata, Rumex acetosa* and *Sanguisorba minor* were common. More wildflowers were found on the south-facing plots, such as *L. vulgare* and *P. lanceolata*, whereas the grasses *L. perenne* and *C. cristatus* preferred the north-facing plots. Frequent cutting increased species richness and diversity, favoured *C. cristatus* and *L.*

vulgare and reduced *L. perenne* and *P. lanceolata*. Grasses such as *L. perenne* and *P. bertolonii* were more reduced by compaction than the wildflowers such as *Rhinanthus minor* and *Trifolium pratense*. Plots sown with a mixture of grasses and wildflowers had greater above-ground biomass than the grasses-only plots and on the north-facing aspect had greater biomass than the flat and south-facing plots. Plots just sown with grasses had higher biomass on the flat plots. *R. minor* did not germinate well in the plots with high biomass but survived in regularly cut plots.

Plant roots in the Mesocosms grew down the whole soil profile in all treatments (40 cm). The total root mass was greater in the grasses-only plots in comparison to the grass and wildflower plots. However, the grass roots were smaller and finer, whereas the wildflower roots were bigger, yet lighter. Although the grasses-only plots had greater root mass, these plots had lower aboveground biomass, while the grass and wildflower plots had lower root mass, but greater aboveground biomass. Bulk density (BD) and Penetrometer resistance (CI) was greater in the compacted treatment, although this did not reduce root mass, or reduce aboveground biomass. However, CI was greatest in the flat and south-facing plots where root mass was less, and CI was lower in the north-facing plots where root mass was greater.

The roadside survey showed that natural colonisation could produce species-rich habitats over time with 116 species found. *Arrhenatherum elatius* was the commonest grass, *Cirsium arvense* and *Senecio jacobaea* were frequent and scrub encroachment was widespread. These roadside verges were not cut frequently enough to prevent succession into scrub and woodland. *Centaurea nigra*, *L. vulgare* and *D. carota* had higher cover on south-facing slopes, contributing to the higher diversity on this aspect. Signs of bareground and desiccation were greater on south-facing slopes. Grasses were more abundant on the north-facing slopes leading to mesotrophic communities on this aspect. Many sites had a unique and unusual combination of species that didn't fit into the National Vegetation Classification (NVC).

Roadside embankment construction does not hinder the establishment of a species-rich seed mixture, although a regular cutting regime is required of at least once a year to prevent scrub encroachment and to reduce the spread of injurious weeds. A grass and wildflower seed mixture containing a range of functional types will have greater aboveground biomass, with a denser canopy and heterogeneous root system, which will help to prevent surface erosion and runoff and increase soil strength.

Contents

2.3 Results

2.4 Discussion

1. Chapter One. General Introduction

1.1 Introduction

Whether a road is formed by cutting through existing habitats, or whether a road is built by creating embankments, the new road network and the accompanying roadside verges are an entirely human modified system. The roadside verge is classed as the land between the road edge and the hedge or fence bordering adjacent land. In 1974, the estimated amount of roadside verge vegetation in the UK was around 440,000 acres of habitat. Of this, 240,000 acres were estimated to be of open grassland (Way 1979). This estimate will be much greater now since new roads have continued to be constructed. The established roadside verge vegetation community is a diverse, complex and unusual ecosystem with over 870 native plant species associated with them (Way 1977). Recently, emphasise has been given to "Novel ecosystems" where new combinations of species occur, often from human modification and land use change (Leps *et al*. 1982; Hobbs *et al*. 2006; Hobbs *et al*. 2009; Williams *et al*. 2009). Roadside verges are a typical example of a novel ecosystem – they are not natural, the land has been completely sculpted and changed by humans, the topsoil is often introduced from elsewhere, a seed mixture is added and the management regime is altered (Hobbs *et al*. 2006; Hobbs *et al*. 2009). Roads form a direct line through many different types of habitat and the plant communities establishing is based not just on the seed mixture added, but any seeds that are in the seed bank and natural dispersal, aided by traffic movement and from adjacent land, whether this is arable, woodland, grassland or heathland (Wilson *et al*. 1996). Roadside verges can be classed as an ecotone or edge habitat, since one plant community can overlap with another and form new species assemblages (Way 1977; Tikka *at al*. 2001), and Rodwell (1992) classes roadside verges as linear habitats, grading from one community into another. Studying roadside verge communities is an ideal way to understand emerging community assembly rules (Drake 1990; Wilson *et al.* 1996; Marris 2009).

The rising significance of the roadside verge grassland habitat for conservation value was highlighted back in the 1970's by J. M. Way in a number of publications in which he emphasized the need for improved landscape management (Way 1976; 1977; 1979). However, in 1975, the Department of Transport issued instructions to cease regular grass cuttings on trunk roads and motorways, only to cut in restricted circumstances (Way 1979). This has caused a decline in species-rich grassland habitats and scrub encroachment across many roadside verges (Parr & Way 1988; Grime *et al.* 1994; Sangwine 1996; Dunnett *et al.* 1998; Muller *et al*. 1998; HA 2005a, 2005b; Thomas 2005; NBPG 2008). Generally, trunk roads and motorways are managed by The Highways Agency. In the last 15 years the management of roadside verges has improved a little, with a number of important areas of conservation interest, i.e. verges running through Sites of Special Scientific Interest (SSSI) and Areas of Outstanding Natural Beauty (AONB), being managed more appropriately by the Highways Agency, in conjunction with Wildlife Trusts and County Councils (HA 1994; Sangwine 1996). For example, Essex Wildlife Trust has Verge representatives that monitor species rich verges (EWT 2008), and several collaborative groups have formed, such as in Northamptonshire (NBPG 2008), Durham (DBP 2008) and Warwickshire (Thomas 2005), which have specific Road Verge Action Plans in place. Roadside verges are often seen as assets for conservation and havens for wildlife – for example “Life on the Verge” is the largest wildflower survey undertaken on Britain’s roadside verges. It began in summer 2009 and will continue into summer 2010 (lifeontheverge 2010).

The BIOlogical and eNgineering Impacts of Climate change on Slopes (BIONICS) project was set up in 2005 and is funded by the EPSRC as part of the Building Knowledge for Climate Change (BKCC) programme. The BIONICS project was set up to experimentally research slope instability issues on motorway slopes. Improvements in the design of newly constructed motorway embankments and cuttings have highlighted problems with the older designs. The BIONICS project involved a group of Civil engineers in the School of Civil Engineering and Geosciences at Newcastle University. A large scale embankment was built at Nafferton farm with sections divided into different treatment plots. Half of these plots were built to older construction designs and half were built to modern construction plans, detailed in the *Highways Agency Specifications for Highways Works Manuals* (HA 1991; 2007b). A number of civil engineers were investigating the belowground properties of the slope mechanics; however the above-ground vegetation is also significant and plays an important role in this system. This PhD was founded on the basis of the BIONICS project, and through this, has been able to investigate the influences of aspect, soil compaction and management on the grassland species composition of roadside verges, in relation to improving slope stability.

1.2 Seed mixtures, establishment and colonisation

A general grass seed mixture has always been sown onto newly constructed motorway embankments and cuttings since the 1950's. Although sowing a wildflower seed mixture onto newly built embankments has been suggested over the years, the grass seed mixtures are still preferred as they establish quickly and are much cheaper (Way 1976; Gray 1995; Bayfield 1995; HA 1993). Even back in 1969 in a symposium on "Road verges, their function and management", the call for a grass seed mixture was being debated. The grass species mixture usually includes *L. perenne*, *Festuca rubra*, *Festuca brevipila*, *Poa pratensis*, *Agrostis capillaris* and *Trifolium repens* as these species are cheap and quick to establish, forming a dense mat that protects the soil surface from erosion and rainfall splash (HA 1991; 1993; Gray 1995) (Table 1.1). However, maintenance engineers have complained that *L. perenne* was too aggressive, causing difficulty with cutting (Underwood 1969; Ross 1986). In the UK the management and restoration of roadside verges and motorway embankments and cuttings varies between the different Highways Agency areas, and can vary between different counties if some groups (Councils and Wildlife Trusts) take special interest in certain habitats. Generally the recommended grass seed mix is sown unless the consultant responsible for these decisions knows about suitable wildflower seed mixtures and is prepared to pay the extra cost (Streeter 1969; Underwood 1969; Ross 1986; Barker 1995; HA 1993).

Latin name	Species	kg	%
Lolium perenne	Perennial Rye Grass	12.5	25
Festuca rubra	Strong Creeping Red Fescue	10	20
Festuca brevipila	Hard Fescue	15	30
Poa pratensis	Smooth-stalked Meadow Grass	5	10
Agrostis capillaris	Highland Browntop Bent	5	10
Trifolium repens	Huia White Clover	2.5	5

Table 1.1. The standard grass seed mixture sown on roadside verges for quick, dense cover, per 50 kg. Taken from the *Highways Agency Specification for Highways Works Manual. Series 600, Earthworks, 1991.*

Prior to 1973, most wildflower seed was imported into Britain. By 1989, 90 % of seed came from Britain (Wells *et al*. 1989). Nowadays, an increasing number of people are growing native wildflowers. The popularity of wildflower seed mixtures has created a heavy demand for seed, leading to imports from abroad. There are over 50 suppliers of wildflower seeds and plants in Britain. Some of the seeds available may not represent strictly native British wildflowers. Some of these introduced species are more competitive and robust than native species and there is the possibility of crossing between native and introduced plants. In 1994, it was estimated that seed had been imported from 100 different countries. New roadside verges, cuttings and embankments use the bulk of the commercially available seed. As early as 1970, a non-native variant of *L. corniculatus* was sown on roadside verges in Britain. This variant is usually Fodder Bird's-foot-trefoil (*L. corniculatus* var. *sativus*). This species is tall and upright, with smaller yellow flowers, whereas the native plant is neater and more prostrate in habit (Akeroyd 1994). Fodder Salad Burnet (*S. minor* subsp. *muricata*), Kidney Vetch (*Anthyllis vulneraria*) and the garden hybrid of *L. vulgare* are all non-native species regularly sown on roadside verges (Wells *et al*. 1989; Akeroyd 1994). The agricultural varieties of red (*T. pratense* var. *saticum*) and Huia white clover (*T. repens*) are also frequently sown, which are enormous, with large leaflets and heads (Akeroyd 1994).

On roadside verges, vegetation cover needs to be established quickly, both to prevent soil erosion and for aesthetic reasons. The standard grass seed mixture includes grass species which are quick growing, rigorous and competitive species (Wells *et al*. 1989; HA 1994; HA 2005a). Grasses remain green throughout the year (wintergreen), whereas the majority of wildflowers die off during the winter (Wells *et al*. 1989). The Highways Agency has published a document called *The Wildflower Handbook* which gives advice about wildflower seed mixtures. It focuses on small areas which may be improved for a purely visual and amenity basis. It recommends that thought should be given to the type of vegetation the road is going through. For example, it suggests a bright green rye grass sward should not be sown on acid soils where the road is crossing a heathland. However, *The Wildflower Handbook* focuses on the high cost of wildflower seeds, the need for follow-up management and the fact that wildflowers generally take longer to establish. It recommends that only small areas are seeded and those where the visual appeal is high (HA 1993). Therefore, the standard grass seed mixture will always be the preferred option.

In the 1970's, Wells *et al.* (1989) began to create swards from the seeds of grasses and wildflowers, looking at which species from the native flora of Britain could produce large quantities of seed and which species could be established easily. The composition of the colonising seedling flora is determined by whether the conditions are suitable for their germination. Variations in requirements between species for moisture, light, temperature, competition, aspect, slope or exposure, for example, will influence which seedlings can germinate (Wells *et al*. 1989; Hillier *et al*. 1990; Gilbert & Anderson 1998). Seed mixtures, for example, can be divided into groups based on the soil conditions: clay, chalk, acid and limestone soils (Wells *et al*. 1989). It is imperative to understand the prerequisites for seedling emergence (Lindborg 2006). It is clear from numerous studies attempting to recreate grassland habitats, that the most important factor to focus on is whether the species are good colonisers, with high rates of germination (Wells *et al.* 1989; Hopkins *et al* 1998; Pywell *et al* 2003). In addition, species should be common, not competitive or invasive, locally sourced, colourful and attractive to insects. Grasses should still be the main component of the seed mixture, at least 60 %, and there should be a mixture of different plant phenologies – i.e. annuals, and longer lived perennials (Wells *et al*. 1989).

A number of studies have tried to recreate species-rich grassland using seed mixtures onto bareground, or adding seed in species-poor grassland (Wells 1990; Hopkins *et al*. 1998; Jones & Hayes 1999; Pywell *et al.* 2002; Pywell *et al.* 2003; Lindborg 2006; Leps *et al.* 2007). Wells (1990) created a replica of species-rich chalk grassland. Wells (1990) tried a combination of seven different seed mixtures and found that from a seed mixture of 40 wildflowers, 33 established. *L. vulgare* established well, and the long-lived perennials increased in cover over time: species such as C. *nigra, Centaurea scabiosa* and *S. minor*. He concluded that species-rich grassland could be established from seed and develop over a short period of time. Between 7 – 15 years was needed, with the addition of an appropriate seed mixture. Jones & Hayes (1999) sowed a range of species into a field with *L. perenne* and *T. repens*. *P. lanceolata* had the best establishment rate, followed by *C. nigra, Prunella vulgaris* and *A. millefolium*. Hopkins *et al*. (1998) used the seed mixtures from different NVC communities. From these seed mixtures, similar species established: *A. millefolium, L. vulgare, Prunella vulgaris* and *P. lanceolata*. These species colonised well and had high levels of germination. Hopkins *et al*. (1998) classed these species as “generalist” species. They concluded that it was possible to create a grassland community, but not one based on a particular NVC community. The specialist species with low levels of germination and low levels of competition could not colonise. Lindborg (2006) deliberately choose a set of six generalist species and six specialist species and looked at which seeds could be added into species-poor grassland. He concluded that the generalist species did indeed establish better than the specialist species. Therefore, should a number of generalist, easily establishing species be added into the standard seed mixture?

1.3 The influence of aspect on grassland communities

Roadside verges, especially those on dual-carriageways and motorways, are often quite steep and each slope is facing a particular direction. The orientation of each slope will change the aspect to which it is facing. Topography, slope angle and aspect influence the composition of grassland habitats (Pahlsson 1974; Hutchings 1983; Rorison *et al.* 1986a; Rorison *et al.* 1986b; Thompson & Jones 1990; Bennie *et al.* 2006; Klimek *et al.* 2007). Therefore, it would be fair to assume that topography, slope angle and aspect would also influence the establishment and composition of roadside verge grassland habitats. As southern slopes are facing the equator, they receive a higher amount of solar radiation and insulation, making them drier and warmer than the northern slopes facing away from the equator. During the morning, most of the solar energy intercepted is used for the evapotranspiration of the condensation gathered overnight. During the afternoon, the ground has already become dry on the south-facing slopes, so the energy intercepted raises the temperature of the soil. Therefore, the drier, hotter slopes are found on the south to south-east aspects and the wetter, colder slopes are found on the north and north-west-facing slopes (Pahlsson 1974; Churchhill 1982; Hutchings 1983; Rorison *et al.* 1986a; Rorison *et al.* 1986b; Thompson & Jones 1990; Kutiel & Lavee 1999; Bennie *et al.* 2006; Klimek *et al.* 2007). Rorison *et al.* (1986a; 1986b) showed that this can cause the plant species on the south-facing slopes to experience moisture stress and can lead to the more drought-tolerant species establishing. The north-facing and south-facing slopes differed by 2.5 º c in mean soil temperature and 2.9 º c in mean air temperature; the south-facing slopes being higher. Klimek *et al* (2007), showed that slope angle, solar radiation and soil quality accounted for 8 % of the variation in plant species composition (management factors were much higher). *Dactylis glomerata* preferred steeper slopes and *Heracleum sphondylium* and *A. capillaris* preferred low solar radiation.

Greater species richness and diversity is often found on south-facing slopes, usually because drought-tolerant wildflowers species can establish (Pahlsson 1974; Hutchings 1983; Kutiel 1992; Rorison *et al.* 1986a; 1986; Kutiel & Lavee 1999; Bruun 2000; Amezaga *et al.* 2004; Pykälä *et al*. 2005). This leads to a change in species composition between different slope aspects, with mesic plant communities establishing on north-facing slopes and xeric plant communities establishing on south-facing slopes (Albertson 1937; Kutiel 1992; Sebastia 2004). Sometimes woody species are more common on north-facing slopes and herbaceous species are more common on south-facing slopes (Kutiel 1992; Kutiel & Lavee 1999).

Generally, a denser mass of vegetation is found on north-facing slopes, due to the wetter conditions favouring growth (Solé-Benet *et al.* 1997; Kutiel & Lavee 1999; Bochet & Garcia-Fayos 2004); a few studies have found organic matter to be higher on north-facing slopes (Kutiel 1992; Kutiel & Lavee 1999) and north-facing slopes often have thicker soils than south-facing slopes (Albertson 1937; Pahlsson 1974; Churchhill 1982). So, with greater vegetation cover and greater soil depths, Pahlsson (1974) showed that erosion was lessened on north-facing slopes and due to the warmer and drier conditions, Churchhill (1982) showed that desiccation can sometimes be greater on south-facing slopes. However, no other studies have been able to find any significant differences in erosion between aspects, even though increases in vegetation cover, have lead to decreases in erosion (Solé-Benet *et al.* 1997; Andres & Jorba 2000; Bochet & Garcia-Fayos 2004).

Clearly, aspect differences are likely to influence species composition of roadside verges. These differences are likely to influence the establishment of seedlings too: the microclimate will effect seedling germination from the very first moment. For example, *T. repens,* the only wildflower in the standard grass seed mixture, preferred south-facing slopes in one study (Amezaga *et al.* 2004), and preferred north-facing slopes in other studies (Andres *et al.* 1996; Andres & Jorba 2000), highlighting that small scale differences in microclimate can lead to variations in germination. Studies looking at temperature and germination have shown that different species prefer different temperatures (Boeck *et al.* 2007; Dunnett & Grime 1999; Buckland *et al.* 2001). Dunnett & Grime (1999) showed that regardless of other competitors, *C. arvense* increased dramatically with higher spring temperatures, therefore may be found more often on south-facing slopes. Buckland *et al.* (2001) showed that Southern England grassland species preferred the warmer temperatures; therefore it is possible that southern species are found on the warmer south-facing slopes and northern species are found on the colder north-facing slopes.

Perring (1959; 1960) looked at sixty-two sites of chalk grassland, investigating the role of climate and topography on species composition and soil properties. He showed that the climate on southern slopes was drier, had greater organic carbon and less biomass than that of northern slopes. He believed that constant wetting and drying of the vegetation on a slope angle caused the soil to slip down the hillside. As northern slopes were constantly wetter and had more vegetation growth, the soils were less likely to be washed away. He also found that potassium content was greater on southern slopes than northern slopes, whereas phosphorus showed no pattern. He was amazed by the striking differences between species diversity among the different aspects. Of the seventy-eight species recorded in the sites in Dorset, only seven of these didn't show a relationship. In general, typical chalk grassland species, restricted to this habitat, were mainly found on the south-facing slopes, whereas the mesotrophic species, usually found in neutral grassland communities, were most commonly found on the north-facing slopes.

Bennie *et al.* (2006) looked at the same sites as Perring (1959; 1960) and found that volumetric soil moisture was typically 10-20% lower on south-facing slopes than on north-facing slopes and soil moisture on flat sites was intermediate. Bennie *et al* (2006) found that since Perring's surveys, south-facing slopes were more resistant to change than north-facing slopes, and believed water limitation and high solar radiation could account for maintaining species-rich chalk grassland. On the northern and flatter slopes there was a shift towards mesotrophic grassland communities, whereas the typical chalk grassland was restricted to the south-facing slopes.

If we relate these studies looking at how topography and climate affects grassland communities, to restoring newly built roadside embankments and cuttings where the slopes are steep and aspect varies, we can assume that the plant species establishment will vary over these areas. It may be wise to sow different plant species on different parts of the slope sides to suit the climatic conditions at the site. Or it may be better to sow a diverse seed mixture containing a number of different functional types where plant species will colonise if the conditions are right. Plant functional types can be defined as an assemblage of species responding similarly to ecological conditions and having a similar ecosystem function (Noble & Gitay 1996; Diaz & Cabido 1997). Which species are suitable for growing on south-facing slopes and which species are suitable for growing on north-facing slopes?

1.4 The management of grassland habitats and roadside verges

The conservation of grasslands in Britain has become more important in recent years as the conflict between agriculture and conservation continues. Many of the grasslands have been replaced by arable fields and in others so much artificial fertiliser has been added that the species diversity and richness has fallen with the increase in productivity (Marrs 1993;

Hodgson *et al.* 2005; Jefferson 2005). In upland hay meadows in Britain, the additional problems of ploughing, drainage, reseeding and management changes have reduced plant diversity. Upland hay meadows are mainly restricted to the lower slopes and valley bottoms of upland regions and can also be found on road verges, river banks, and in woodland glades. MG3 *Anthoxanthum odoratum – Geranium sylvaticum* meadows are regarded as a grassland with a particularly high floristic diversity and can be entitled for selection as SSSI (Jefferson 2005). In the Pennine Dales Environmentally Sensitive Area (ESA), an important conservation aim is the re-establishment of diverse mesotrophic grassland from agriculturally improved swards, intended to enhance the area of species-rich grassland (Pywell *et al.* 1997).

The Colt Park experiments in Upper Ribblesdale in North Yorkshire have been running since 1989 and have demonstrated how intricate the interactions can be involving the type and timing of cutting and grazing and the effect this has on species richness and diversity in meadow grasslands (i.e. Smith *et al.* 2008). The Colt Park Experiments looked at a number of different management regimes. These included adding artificial fertiliser to some plots and not to others, using only autumn grazing in some and spring and autumn grazing in others, looking at the differences between cutting dates and adding seed. The plots with the greatest increase in species richness were those which were cut on 21 July, grazed in both autumn and spring and with seed addition. This follows traditional hay meadow management regimes (i.e. Smith *et al.* 2008). In Smith & Rushton's paper (1994), a control treatment was added that stopped grazing altogether to see the response to the vegetation. There was an immediate reduction in species richness, with the generally competitive species becoming dominant. In France, land abandonment and cessation of grazing has lead to an increase in the highly competitive and robust species, firstly herbaceous plants, followed by woody plants (Muller *et al.* 1998).

In the Colt Park experiment, the use of mineral fertiliser reduced species richness (i.e. Smith *et al.* 2008), which has been shown in a number of other studies (Kirkham & Tallowin 1995; Janssens *et al* 1998; Hejeman *et al.* 2007), although stopping fertiliser input did not restore diversity straightaway (i.e. Smith *et al.* 2008) as high residual fertility is very persistent, particularly phosphorus, and is likely to allow the competitive grasses to dominate (Janssens *et al* 1998; Hejeman *et al.* 2007). Species diversity was improved by the addition of seed, so sowing supplementary seed should be a very practical way of restoring the diversity of species-poor swards (McDonald 1993; Smith *et al.* 2008).

The landscape management plans for grasslands on roadside verges generally include a cut once every nine years, six years or three years, and only in exceptional cases (i.e. rare, species-rich grassland) they may be cut once a year maximum (HA 1994; HA 2005a). The grassland verge habitat is extensive, but also inaccessible. It costs a large sum of money to finance cutting the verges and it is very difficult to rake and remove the cuttings, especially when the work is carried out alongside fast roads, such as dual carriageways and motorways (HA 2005a). Without regular cutting and removal of the cut vegetation, roadside verges becomes dominated by competitive weeds such as *C. arvense*, *Chamerion angustifolium* and *S. jacobaea*, and plants such as *L. perenne, P. lanceolata* and *Taraxicum officinale* spread quickly (Chancellor 1969; Way 1977; Ross 1986; Parr & Way 1988; Grime *et al.* 1994; Sangwine 1996; Dunnett *et al.* 1998; Muller *et al.* 1998; Ameloot *et al*. 2006). The next stage is scrub encroachment which is very difficult and costly to eradicate once it has become established (Parr & Way 1988; Grime *et al.* 1994; Sangwine 1996; Dunnett *et al.* 1998; Muller *et al.* 1998; Bakker *et al.* 2002; HA 2005a, 2005b; Thomas 2005; NBPG 2008). The MCHW (*Manual of Contract Documents for Highways Works*) includes guidance on the specification for Highways Works and includes a section on Weed Control. The Highways Agency must control 'injurious' weeds, as listed in the Weeds Act (1959) (HA 2000; HA 2007a, 2007b): the 'injurious' weeds being: *Cirsium vulgare, C. arvense, Rumex crispus*, *Rumex obtusifolius*, *S. jacobaea*, Himalayan Balsam, Giant Hogweed and Japanese Knotweed (HA 2007b). The topsoil used for restoration and new road projects adds to the weed problem as it is often very fertile and accelerates the establishment of un-wanted, competitive species (Parr & Way 1988; Bayfield 1995). These plants tend to be tall, fast growing species which monopolise the canopy, reducing species richness and diversity (Marrs 1993; White *et al.* 2004).

However, Hovd & Skogen (2005) showed that the roadside verges which had an annual cut had greater species richness and diversity than the unmown roadside verges. The regular mowing regime prevented succession from occurring and species characteristic of semi-natural meadows could colonise. Bobbink & Willems (1993) compared different cutting regimes, from no cut – four cuts. All of the cutting regimes increased wildflower diversity, and abandonment lead to much less diversity (0.9 H on abandoned fields vs. 1.5 H' - 1.7 H' ranging from one cut – four cuts). The changes were seen after two years. The taller, robust, weedy species were commonly found in abandoned grasslands, in arable field margins, and areas which were not cut or grazed (Bakker *et al.* 2002; Hovd & Skogen 2005). In general, the majority of papers publishing work on cutting regimes concluded that a cut of at least once, preferably twice a year, was required to prevent vegetation succession and to promote high species diversity. Greater species richness and diversity is favoured by the suppression of the taller weedy species of wildflowers and nutrient-demanding grasses, with an increase in the smaller statured wildflowers (i.e. Huston 1994; Grime 2001; Harmens *et al*. 2004; Antonsen & Olsson 2005; Pykälä *et al*.2005; Marini *et al*. 2008; Smith *et al*. 2008). It is unlikely that diverse species-rich grassland can be conserved, maintained or established on roadside verges without thought to improving the timing and frequency of cutting, finding a way to effectively remove cuttings, reducing soil fertility or without adding supplementary grassland seed mixtures (Way 1979; Parr & Way 1988; Bayfield 1995; Tikka *et al*. 2000; Tikka *et al*. 2001; HA 2005b; Ameloot *et al*. 2006).

1.5 *Rhinanthus minor* and grassland plant diversity

R. minor is found over much of Europe and is native and common in the British Isles. It grows in a range of habitats, most often in meadows, although is it also found growing alongside road verges, in ungrazed grassland, mire and occasionally in sand-dune communities. *R. minor* is in the figwort family (Scrophulariaceae) and is known as Yellow-rattle or Hay Rattle. It is a facultative hemi-parasite, which forms haustoria (xylem – xylem continuity) with the existing root system of a host plant. It is a summer annual and a therophyte meaning that it requires approximately 3 months of low temperatures to break seed dormancy (Westbury 2004). *R. minor* grows in a number of grassland habitats and is characteristically associated with hay meadow communities, especially *Anthoxanthum odoratum – Geranium sylvaticum* grassland (MG3). *R. minor* is not found in woodland as it does not like the shade, and initial germination is difficult without an open sward (Grime *et al.* 1988; Westbury 2004; Westbury & Dunnett 2007). *R. minor* is not found in very dry habitats (Westbury 2004) but is tolerant of waterlogging in the winter (Grime *et al*. 1988). *R. minor* can parasitize a number of hosts at the same time and parasitize a large range of different types of host species, although the haustoria formation is generally a random process (Gibson & Watkinson 1989; Westbury 2004). *R. minor* tends to germinate in February and March, after a period of winter stratification, and this corresponds with the growth of the available host roots.

R. minor has become more important at the present time as research has shown that *R. minor* can lessen grassland productivity and encourage wildflower colonisation by infecting the faster-growing grasses which reduces their competitive dominance and allows the wildflowers to establish (Davies *et al.* 1997; Joshi *et al.* 2000; Pywell *et al.* 2004; Bardgett *et al.* 2006; Ameloot *et al.* 2008). Pywell *et al.* (2004) demonstrated that *R. minor* increased species richness and the proportion of wildflowers, with a lessening of sward height. Pywell *et al.* (2004) suggests that *R. minor* has the capability of facilitating the establishment of introduced favourable wildflower species and promoting their colonisation. Joshi *et al.* (2000) found that the grasses were the assemblage of species most susceptible to parasite infection, and that it was legumes and non-leguminous plants which mainly counteracted the reduction in the biomass of grasses. Bardgett *et al.* (2006) found that parasitic plants can influence the composition and function of grassland communities.

As a result of these findings, *R. minor* could be used as a management tool on roadside verges for encouraging the establishment of dicotyledonous species, increasing floristic diversity and lessening competitive grasses (Austen & Treweek 1995; Davies *et al.* 1997; Pywell *et al.* 2004; Ameloot *et al.* 2006). One problem with using *R. minor* is that a number of studies have shown that *R. minor* can decrease the total above-ground biomass, and this in turn may influence the stability of roadside slopes (Davies *et al.* 1997; Joshi *et al.* 2000; Pywell *et al.* 2004; Ameloot *et al.* 2006). It is mainly the grass biomass that decreases, and the legumes and wildflowers that increase (Davies *et al.* 1997; Joshi *et al.* 2000; Pywell *et al.* 2004; Westbury *et al.* 2006; Ameloot *et al.* 2006; Ameloot *et al.* 2008). However, as *R. minor* does not germinate in all conditions and requires initial gaps in the canopy to germinate, the lack of appropriate management on roadside verges may prevent *R. minor* from establishing (Grime *et al.* 1988; Westbury 2004; Ameloot *et al.* 2006; Westbury & Dunnett 2007). Does lack of suitable management prevent *R. minor* from establishing? Should *R. minor* be used where possible to improve species diversity and allow for the possibility of a reduction of biomass?

1.6 Vegetation, slope stability and soil strength

The use of vegetation for improving slope stability on roadside embankments and cuttings is becoming more recognised as a cost effective, environmental and sustainable method. Vegetation stabilises the soil by protecting the surface from rainfall impact and water flow, root reinforcement and increasing soil strength. Shallow-seated slope failures / slips occur from 0.75 m to no more than 2 m below the ground and can be prevented by vegetation if the roots grow to this depth (Elwell & Stocking 1976; Rice *et al.* 1969; Waldron 1977; Wu *et al.* 1988; Waldron & Dakessian 1982; Nilaweera *et al.* 1999; Marden *et al.* 2005; Danjon *et al.* 2007; Tosi 2007). Most research has been done on the stabilising effects of trees and larger rooted species (Barker 1995; Brooks *et al.* 1995; Nilaweera *et al.* 1999; Marden *et al.* 2005; Norris 2005; Smethurst *et al.* 2006; Danjon *et al.* 2007; Tosi 2007); however grasses and wildflowers may also improve slope stability by intercepting rainfall, preventing surface erosion and root reinforcement - binding the soil particles together (Lutz 1936; Hudson 1957; Waldron & Dakessian 1982; Boardman 1984; 1991; Evans 1990; Fullen 1991; 1992; 1998; Bayfield *et al.* 1992; Morgan 1992; Mitchell *et al,* 2003; Norris 2005).

Plants naturally take up water from the soil and some of this water is transpired, causing an increase in pore water pressures and increasing soil suction. The differences in moisture between the seasons cause drying and wetting of the soil, leading to shrinking and swelling, especially with clay, and can cause downhill soil movement or cracking on steep slopes (Driscoll 1983; Ridley 2003; Smethurst *et al.* 2006). Tree roots have a much greater water demand than grasses and wildflowers, so the problem is aggravated by large plants such as trees and shrubs (Biddle 1983; Driscoll 1983). The soil water suction produced by grasses and wildflowers is much less (Smethurst *et al.* 2006). Anderson *et al.* (1982), showed that on motorway embankments in areas with dense grass cover, shrinkage of the clays was lessened, and cracking of the soil was prevented. In addition, trees can be blown over, causing slope stability issues (Nilaweera *et al.* 1999; Smethurst *et al.* 2006). So, there are positive and negative issues with using trees and shrubs for slope stability; whereas grasses and wildflowers may have smaller root systems, but they are not likely to be blown over or cause underlying moisture deficits (Waldron & Dakessian 1982; Smethurst *et al.* 2006).

Although the importance of vegetation and slope stability is recognised there is very little published experimental research into the role of vegetation and slope stability in roadside embankments in the United Kingdom. The Highways Agency has trialled a number of projects which mainly include investigating the role of trees and willow poles in improving slope stability (Greenwood 1996; Hillier & MacNeil 2000; MacNeil 2001; Snowdon 2004). In 1994 an International Conference on the interaction of vegetation and slopes was held in Oxford, UK. This was only the second of its kind, the first being held in 1948 (Barker 1995). It was a chance for biologists and engineers to come together and discuss the positive effects of vegetation on improving slope stability. The general literature on this topic tends to group vegetation as if it is one element and treat grasses as if it is one species. The influence of individual types of plants or the influence of a particular community of plants hasn't been looked at, or the possibility that wildflowers may influence slope stability differently to grasses due to differences in growth habit and root morphology.

A number of studies have shown that roots growing through the soil increases soil strength, i.e. improves slope stability, and this is usually measured with in situ shear tests (i.e. Waldron 1977; Waldron & Dakessian 1981; 1982; Nilaweera *et al*. 1999; van Beek *et al*. 2005; Norris 2005; Danjon *et al*. 2007; Tosi 2007). Waldron & Dakessian (1982) looked at the root reinforcement of a number of different species. Grasses were much better at stabilising the soil than oak, and pine was worse, plus thinner roots performed better than the thicker roots. Cazzuffi *et al.* (2006) showed that the roots of 4 different grasses: Vetiver, Pangrass, Eragrass and Elygrass, all increased soil strength. Direct shear tests were done on the soils with roots, and the soils without roots, and soil strength was greater in the soil with roots. Operstein & Frydman (2000) looked at a combination of factors: root tensile strength, root pull-out tests and direct shear tests on a number of different plants. They showed that soil strength is indeed improved by roots and that those roots with smaller diameters had greater tensile strength: Greater tensile strength of the root systems improved root reinforcement and soil strength. Nilaweera *et al.* (1999) have also showed that tensile strengths of roots are greater with smaller root diameters, and slope stabilisation is improved with longer root systems. When modelling vegetation and slope stability, Brooks *et al.* (1995) showed that grass systems were slightly more stable than pine covered systems and roots systems did improve slope stability. Wu *et al*. (1988) and Waldron & Dakessian (1982) showed that it wasn't just the roots themselves that improved soil strength, but the orientation of the roots too – roots that grew through potential slip failures could improve slope stability.

It has been shown in a number of studies that the amount of grassland ground cover is the most important preventative factor in surface erosion (Lutz 1936; Hudson 1957; Quinn 1980; Boardman 1984; 1991, Evans 1990; Solé-Benet *et al.* 1997; Mitchell *et al.* 2003). Morgan (1992) suggested that grassland strips should be used in agricultural and riparian habitats to reduce the impact of erosion processes (Morgan 1992). Mitchell *et al.* (2003) showed that once a dense grass cover was established, erosion decreased dramatically. Fullen (1991, 1992, and 1998) showed that erosion was three times greater on bare soil in comparison to grassland plots. Fullen looked at the differences between permanent grassland areas, newly seeded areas and bare soil in an agricultural system. He showed that surface runoff and erosion was significantly less once the cover was over 30 %, on a slope of 17 º. Average erosion rates were 0.1 – 0.3 t ha^{-1} $year^{-1}$, in comparison to the bare soil plots of 11.3 t ha^{-1} $year^{-1}$. Fullen suggested using grassland as "soakaways" in arable systems, by improving soil conservation during set-aside years. Other studies have suggested more cover is needed before erosion is prevented: Elwell & Stocking (1974; 1976) suggested that erosion begins once vegetation cover was less than 70 %, and Quinn *et al.* (1980) agrees with this figure. Rice *et al.* (1969) showed that the natural brush vegetation in California, on steep slopes, had less soil slips than the cleared areas. Areas converted to perennial grass had a ground cover of 59% and produced a soil slip erosion rate at 492 m^3/ha; an area converted to annual grass with 78% ground cover produced 321 m^3/ha; and natural brush cover with 74% ground cover had a rate of 199 m^3/ha. The natural brush cover had deeper root systems which greatly improved soil slips, yet the perennial grass also had a root depth of 160 cm. The annual grasses had a root depth of 30 cm, yet still reduced soil slips. In this case it was the percentage ground cover which was most important, in combination with a heterogeneous established habitat with a number of different plant species growing.

Grasses are quick to establish but they have a relatively shallow, fibrous root system that can form a dense mat on the surface of the soil. Grass root systems can grow anywhere between 2 - 5 feet, whereas some wildflower root systems can grow anywhere between 2 – 12 feet, usually with a large tap-root; although the exact depths are very vague as environmental factors like the below-ground water content, the available nutrient supply and soil compaction can alter the amount of growth (Elliot 1900; Weaver 1958; Jochen Schenk & Jackson 2002). The root systems of grasses and wildflowers utilise different areas of the soil strata with below-ground competition for nutrients (Albertson 1937; Weaver 1958; Berendse 1979; 1983; Wardle & Peltzer 2002). However, a grass seed mixture is often the preferred method for restoring roadside verges, embankments and cuttings (Underwood 1969; Ross 1986; HA 1993). Many of the models simulating how vegetation and increased rainfall relates to slope instability may have underestimated the depth to which wildflower plant species grow. In Smethurst *et al.* (2006) the maximum plant rooting depth for grass and wildflowers was taken at 80 cm. Some wildflowers could grow deeper than 80 cm, and could possibly assist with slope stabilisation better than grasses. Perennial grasses and wildflowers tend to have bigger root systems than annuals (Jochen Schenk & Jackson 2002; Hutchings & John 2004;

Wijesinghe *et al.* 2005). To what rooting depth does a wildflower mixture grow to? Can a grass and wildflower seed mixture aid slope stability and improve soil strength?

1.7 Above and belowground growth and soil compaction

In order to improve slope stability on embankments and cuttings of roadside verges in Britain, The Highways Agency has improved the construction methods for highways slopes and now heavily compacts the base soil, usually clay, before a 20 – 30 cm topsoil is added. The surface of the base soil is scarified (roughened with a JCB front bucket) before the topsoil is added to try and prevent an interface developing between the two surfaces (HA 1991; 2007). A grass seed mixture is usually sown, in order to establish a dense ground cover quickly (Underwood 1969; Ross 1986; HA 1992; 1993). Plant roots may grow through the topsoil easily but growth may be restricted once the roots reach the compacted base soil (Materechera *et al.* 1992). It is possible that a "root-mat" might develop, or roots deflected to the side, once the plant roots reach the base soil. This could form a boundary between the two layers (an interface) (Cockcoft *et al.* 1969; Dexter 1986a, 1986c). Chiatante *et al.* (2003) showed that plants growing on a slope changed their root anchorage in response to mechanical stress. In response to compacted soils on a slope, the same plants had a different underground structure to those same plants growing on the flat – plant roots would start to grow up and down the slope, adjusting to the slope angle (Chiatante *et al.* 2003). Bennie & Botha (1986) showed that maize and wheat preferentially extended roots into uncompacted topsoil when faced with a compacted base soil (Bennie & Botha 1986). As it is important to stabilise these slopes as much as possible, it is also key to establish a quick and effective ground cover (Underwood 1969; Ross 1986; HA 1992; 1993; Mitchell *et al.* 2003; Greenwood *et al.* 2004). If the root systems do not grow into the compacted base soil, the roots will not be able to provide any slope reinforcement, and if the plant growth is restricted, the aboveground cover may not provide the best erosion defence.

Compaction can cause reductions in above and below ground growth and could prevent species from establishing (i.e. Masle & Passioura 1987; Bamford *et al.* 1991; Andrade *et al.* 1993; Montagu *et al.* 2001). Montagu *et al.* (2001) showed that it was only when the root length was shortened that the shoot growth was also reduced. Some studies deduce that the growth of aboveground biomass is prevented due to moisture, nutrient and aeration restrictions

(Tardieu 1993; Bengough *et al.* 1997), however, other studies have controlled for this (Barley 1965; Cook *et al.* 1996; Young *et al.* 1997). These studies have shown that soil strength directly inhibits the overall growth of the plant (measured as Penetrometer resistance (MPa), or bulk density (g cm^3)) (Barley 1965; Cook *et al.* 1996; Young *et al.* 1997).

The general response to mechanical impedance is for the root cells to stop elongating and dividing (i.e. Atwell 1990; Thaler & Pages 1999; Bengough *et al.* 1997). Cook *et al.* (1997) showed that *L. perenne*, *T. repens* and *A. capillaris* all had reduced root and shoot growth in soil with penetration resistances of 1.40 MPa and 2.30 MPa. The effect was most apparent in *L. perenne*, mainly because of its faster growth rate. Bengough & Mullins (1991) showed that maize roots grew through compacted soil (resistances between 0.26 MPa – 0.47 MPa) at about 60 % of their estimated growth rate. Stolzy & Barley (1968) showed that pea radicles were reduced to 44 % of their estimated growth rate by a root penetration resistance of 0.46 MPa. Goss (1977) showed that pressures of 20 – 50 kPa (0.02 MPa – 0.05 MPa) reduced the elongation of seminal axes of barley by 50 – 80 %. Taylor & Burnett (1963) showed that bulk densities of 1.88 g cm^3 stopped growth of cotton seedlings completely and could kill the plants (this equated to 30 bars or 3 MPa). Zimmerman & Kardos (1960) tried bulk densities ranging from 1.4 g cm^{-3} – 2.0 g cm^{-3}. The effects of compaction on root growth were seen from 1.6 g cm^{-3} but were extreme from 1.8 g cm^{-3} upwards. Veihmeyer & Hendrickson (1948) showed that sunflower roots would not grow through soils with a bulk density of 1.9 g cm^{-3}. Bingham & Bengough (2003) studied the effects of soil compaction on wheat (*Triticum aestivum*) and spring barley (*Hordeum vulgare*). These species were grown in split-root chambers; half compacted to 1.1 g cm^{-3} and half compacted to 1.4 g cm^{-3}. Half of the seedlings roots were positioned in one side of the chamber, and half in the other side. The total length of roots grown in the dense soil was reduced by 46% compared with the controls. Barley and wheat growth was significantly reduced by the soil compaction.

Conversely, there is a high degree of variation in soil structure and soil strength will not be uniform all over. The soil environment is heterogeneous and interspersed with pore spaces and cracks which can be utilised by roots (Dexter 1986a, 1986b; Tardieu 1988a, 1988b; Stirzaker *et al.* 1996; Bingham 2001). Roots are restricted by pore spaces that are smaller than the diameter of the roots themselves (Taylor & Gardner 1960; Bengough & Mullins 1990). Roots will try and find a path through the soil and can grow clumped together if pre-existing pores and cracks are found (Tardieu 1988; Stirzaker *et al.* 1996; Bingham 2001). Often, it is the main roots that are restricted due to their larger size, but the smaller lateral roots can find pores large enough to grow through (Goss 1977; Dexter 1986a, 1986b; Stirzaker *et al*. 1996; Thaler & Pager 1999). The roots can exert a certain amount of turgor pressure against the soil and can displace soil particles unless the soil strength is too great (Clark *et al*. 1996; Croser *et al*. 2000; Bengough *et al.* 1997; Bengough & Mullins 1991; Stolzy & Barley 1968). Perennial plants, such as *Sanguisorba officinalis*, can sometimes grow through incredibly compacted soil over a few years by exerting much pressure over long periods of time (Elliot 1900; Russell 1997). If the compaction methods used in road construction greatly increases soil strength, this may hinder plant establishment, influence species composition and lead to less aboveground cover.

A number of studies have tried to calculate the penetration resistance of a growing tip (Stolzy & Barley 1968; Bengough & Mullins 1991). It has also been shown that root cells shorten and thicken (radial expansion and cortex thickening) to about 10 mm behind the apex when in contact with compacted soil (Wilson *et al*. 1977; Atwell 1988; Atwell 1990; Materechera 1991; 1992; Bengough & Mullins 1990; Bengough *et al.* 1997; Croser *et al.* 2000). These mechanisms allow some roots to grow into pores that were originally smaller than the root cell diameter (Bengough *et al.* 1997). Indeed, in Materechera *et al.*'s (1992) experiment, the species which had the greatest root thickening had greater penetration into the compacted layer; and in Materechera *et al*'s experiment (1991), it was the dicotyledonous species that had a significantly greater root thickening in comparison to grasses (86 % vs. 41 %) and hence greater penetration. Do grasses and wildflowers respond differently to compaction?

1.8 The relationship between biomass, functional types, canopy cover and erosion

A quick increase in aboveground biomass is required on newly constructed roadside verges in order to prevent surface erosion and rainfall splash. The standard grass seed mixture is sown because it is cheaper and because the species establish quickly (Gray 1995; HA 1991; 1993). This simple seed mixture contains one functional type – grasses, whereas a species-rich grassland seed mixture includes a number of functional types – usually grasses, legumes and wildflowers at a minimum. Plus the wildflowers themselves can be divided into annuals and perennials, or further, into Raunkiaer plant lifeforms such as Hemicryptophytes or Geophytes, with lifeforms such as basal rosette, semi-rosette and rosette (Ellenberg & Mueller-Dombois

1967). Each species themselves have certain plant traits that have been classified by Grime *et al*. (1988). So, a species-rich, diverse community contains a complex system of differentiating lifeforms, which utilises all levels of resources, and composes a structurally multifaceted leaf canopy (Naeem *et al.* 1994; Spehn *et al*. 2000; Spehn *et al.* 2005).

The BIODEPTH experiment involved a group of 8 experimental grassland sites across Europe, including two in Britain at Sheffield University and Imperial College (at Silwood Park). These experiments were designed to look at diversity, functional types, canopy use and biomass production. They found that diverse plots, with a number of functional types, used resources in a complementary way, for example, a greater amount of light was intercepted since different species utilised different areas of the canopy. The greater the species richness and diversity, the more the canopy layers were exploited – so both cover values (2-dimensional) and canopy values (3-dimensional) were greater in the higher diversity plots (Spehn *et al.* 2000, 2005; Scherer-Lorenzen *et al.* 2003). This biomass – canopy – functionality relationship has been observed in other studies (i.e. Naeem *et al.* 1994; Thompson *et al.* 1996; Tilman *et al*. 1997; Bullock *et al*. 2007; Phoenix *et al*. 2008).

It is likely that a species-rich grassland seed mixture, with a number of functional types, will produce better above-ground canopy cover than the general grass seed mixture. In fact, at the Longhorn Wood cutting on the M20, it was shown that the grass and wildflower seed mixture established better than all of the other vegetation treatments. The Willow was 1.5 – 2 m tall, with ground cover of 30 %, the gorse and broom plots only had 5 % ground cover, and the brambles after 18 months only had 10 – 15 % cover. However, the grass and wildflower seed mixture treatment established well and had 60 % cover (Greenwood 1996). Plus, although an increase in cover and canopy use will prevent surface erosion, an increase in canopy height can be detrimental. Morgan (2007) showed that it is only dense cover, close to the ground, that prevents erosion. Taller vegetation can make it worse. Rainfall hitting the high-up leaves will fall as leaf drop onto the soil. Often there are larger gaps between taller vegetation and this leaf drop will fall into the gaps between the plants. He concluded that vegetation should be no higher than 1 m, that grasses were better than shrubs and trees, that there should be over 70 % ground cover and that taller vegetation, forming clumps and channels in-between, should be avoided. In addition, Blight (2003) explained that evapotranspiration was greater in grasses in comparison to shrubs and trees since the grasses intercept the rain, whereas the rain runs off the leaves of trees and onto the ground surface. Therefore, should a diverse grass and wildflower seed mixture been sown to improve surface erosion and slope stability?

1.9 Thesis objectives and Thesis format

The following chapter goes through the results of the man-made BIONICS embankment, where a diverse seed mixture of grasses and wildflowers was sown and monitored over time. The influence of aspect and soil compaction on the establishment of the seed mixture was investigated. The third and fourth chapter goes through the results of the Mesocosm experiment; a small-scale experiment designed from the basis of the BIONICS embankment project, but with replicated treatments: aspect (north-facing, south-facing and flat plots); soil compaction (compacted and non-compacted plots); seed mixture (grasses-only seed mixture and grass and wildflower seed mixture) and a cutting regime (plots cut once during the summer, plots cut four times throughout the year and plots cut eight times throughout the year). In the third chapter the plant species composition and biomass results are discussed and in the fourth chapter the results from root cores and soil compaction measurements are discussed. The fifth chapter goes through the results of botanical surveys undertaken along the A303 and A38 in Wiltshire and Devon. Plus, data gathered from a two month placement to the Highways Agency is described and discussed. Finally, the sixth chapter draws together and discusses the results from the BIONICS embankment, Mesocosm experiment and the botanical surveys.

In each chapter, there is an element of repetition due to the main themes - aspect, soil compaction and management being looked at from a single objective, direct method, up to a landscape multifunctional scale. Where the exact details are repeated, these are referred to in the first instance and in others, the subject area may be repeated, but explained in the context of the scale it is referring to.

The main objectives are to:

1) Suggest a suitable selection of grassland plant species that can be established on roadside verges, embankments and cuttings, taking into account factors like soil compaction, aspect, management and rooting depths.

2) Suggest a suitable management regime for the establishment of a species-rich grassland seed mixture and management over time.
3) Suggest a suitable seed mixture of grassland species that can establish quickly and create a dense canopy which reduces surface erosion and improves slope stability.

2 Chapter Two. Experimental work, Part A

The BIONICS embankment

2.1 Introduction

The roadside community is very interesting and unusual with over 870 native species associated with them (Way 1977). Roadside verges can be classed as an ecotone or edge habitat, where one community overlaps with another (Way 1977; Tikka *at al*. 2001) or even classed as a “Novel ecosystem” where new combinations of species occur (Hobbs *et al*. 2006; Hobbs *et al.* 2009). The ecology of these dynamic systems have had little attention and there are only a small number of published documents in Britain, many of these being quite old (Way 1976; 1977; 1979, Grime *et al.* 1994; Dunnett *et al.* 1998; Tikka *et al*. 2001). On the other hand, there have been a few civil engineering studies looking into how vegetation can influence slope stability on steep roadside embankments and cuttings (Barker 1995; Brooks *et al.* 1995; Nilaweera *et al*. 1999; Marden *et al*. 2005; Norris 2005; Smethurst *et al.* 2006; Danjon *et al*. 2007; Tosi 2007).

The motorway and road systems across Britain cover a large expanse of land. In 1974 the estimated amount of roadside verge vegetation was around 440,000 acres of habitat. Of this, 240,000 acres were estimated to be of open grassland (Way 1979). The rising significance of this habitat for conservation value was highlighted back in the 70’s by J. M. Way in a number of papers in which he emphasized the need for improved landscape management (Way, 1976; 1977; 1979). However, in 1975, the Department of Transport issued instructions to cease regular grass cuttings on trunk roads and motorways, only to cut in restricted circumstances (Way 1979). This has caused a decline in species rich habitats and scrub encroachment across many roadside verges (HA 1994, Grime *et al.* 1994; Dunnett *et al.* 1998; HA 2005a; HA 2005b). In the last 15 years the management of roadside verges has improved a little, with a number of important areas of conservation interest, i.e. verges running through Sites of Special Scientific Interest (SSSI) and Areas of Outstanding Natural Beauty (AONB), being managed more appropriately by the Highways Agency (HA 1994).

A general grass seed mixture containing six species has always been sown onto newly constructed road systems since the 1950's (Way 1976; HA 1991; 1992) (Table 1.1). Although sowing a more diverse wildflower seed mixture onto newly built road systems has been suggested over the years, the standard grass seed mixtures are still preferred as they establish quickly and are much cheaper (Bayfield 1995; Gray 1995; HA 1992; 1993). Generally the recommended grass seed mix is sown unless the consultant responsible for these decisions is familiar with suitable wildflower seed mixtures and is prepared to pay the extra cost (Streeter 1969; Underwood 1969; Ross 1986; Barker 1995; HA 1993; Sangwine 1996). In addition to the species sown onto newly built road systems, a number of different plant species randomly colonise from surrounding local environments over time. In a number of studies looking into the vegetation on roadside verges, the initial grass seed mixture sown to restore slopes was often lost over the next few years to local seed dispersal (Ross 1986; Muller *et al.* 1998; Kiviniemi & Eriksson 1999; Tikka *et al.* 2000; Tikka *et al.* 2001; Schaffers & Sykora 2002; Ameloot *et al.* 2006). As local seed dispersal is quite important in establishing these communities, does a seed mixture need to be sown at all? If random species associations are formed, due to the various environmental conditions that prevail at each site, it may be easier to let natural dispersal colonise the slopes.

On roadside verges, especially embankments and cuttings, it is very difficult to graze as it is too steep and the animals are too close to the road. The landscape management plans for grasslands on the soft estate (the roadside habitats) generally include a cut once every three years, and only in exceptional cases (i.e. rare, species rich grassland) they may be cut once a year maximum (HA 1994; 2005a; 2005b; 2007b). Grassland plant communities have been shown to survive on roadside verges but under the current management regimes these areas are not well-suited for species-rich grassland vegetation (Tikka *et al.* 2000; Tikka *et al.* 2001; Ameloot *et al.* 2006). Without regular cutting the verges becomes dominated by competitive weeds such as *C. arvense*, *C. angustifolium* and *S. jacobaea*, and plants such as *L. perenne*, *P. lanceolata* and *T. officinale* spread quickly (Chancellor 1969; Ross 1986; Grime *et al.* 1994; Dunnett *et al.* 1998; Muller *et al.* 1998; Ameloot *et al.* 2006). The topsoil used in restoration is often very fertile and accelerates the establishment of un-wanted weeds (Bayfield 1995). It is unlikely that diverse species rich grassland of any type would be able to be sustained on roadside verges without thought to improving the timing and frequency of cutting, or reducing soil fertility (Way 1979; Bayfield 1995; Tikka *et al.* 2001).

For an introduction to the influence of aspect on grassland communities see Section 1.3

For an introduction to above and belowground growth and soil compaction, see Section 1.7

The BIOlogical and eNgineering Impacts of Climate change on Slopes (BIONICS) project was set up in 2005 and was funded by the EPSRC as part of the Building Knowledge for Climate Change (BKCC) programme. The climate change scenarios for Britain have predicted warmer and wetter winters with drier summers, plus an increase in extreme weather events and localised flooding (Hulme & Jenkins 1998). One of the many problems associated with this prediction is that soil slips on steep slopes may be increased. The Geotechnical department of the Highways Agency monitors the motorway embankments in Britain and has recorded slope failures directly associated with an increase in soil moisture content into the Highways Agency Geotechnical Data Management System (HA GDMS). In addition to the increase in rainfall and moisture content, the difference between dry summers and wet winters, and dry days and wet days, causes the soil to swell and shrink and this can accelerate slope instability (Driscoll 1983; Biddle 1983; Gray 1995). The BIONICS project was set up to experimentally research this stability problem on motorway slopes and involved a group of civil engineers in the School of Civil Engineering and Geosciences at Newcastle University. Improvements in the design of newly constructed motorway embankments and cuttings have highlighted problems with the older designs. A large scale embankment was built at Nafferton farm in 2005, with sections divided into different treatment plots. Half of these plots were built to the older construction designs (not heavily compacted) and half were built to modern construction plans (heavily compacted) detailed in the *Highways Agency Specifications for Highways Works Manuals* (HA 1991; 2007b). A manipulative climate control system was added in 2009 to research the effects of additional rainfall on the slope dynamics.

The Civil Engineers involved in the BIONICS project were interested in the slope dynamics and slope failures occurring deep beneath the soil surface. Having access to a large man-made Embankment at the beginning of the construction in 2006, allowed the opportunity to study the colonisation and establishment of a grassland seed mixture over time, on north-facing and south-facing slopes and whether the construction methods (i.e. compaction) influenced species composition. The general grass seed mixture is sown on newly constructed roadside verges in order to prevent surface erosion from occurring. These species are quick growing competitive grass species that form a dense mat on the soil surface very quickly. Any species that are sown at the beginning need to be quick colonisers to prevent surface erosion (Gray 1995, HA 1991; 1994; HA 2007b). It is clear from numerous studies attempting to recreate grassland habitats, that the most important factor to focus on is whether the species are good colonisers, with high rates of germination (Wells *et al.* 1989; Hopkins *et al* 1998; Pywell *et al* 2003). Which species from a grass and wildflower seed mixture will colonise well and produce good ground cover on the BIONICS Embankment?

Vegetation stabilises the soil by protecting the surface from rainfall impact and water flow, root reinforcement and increasing soil strength. Shallow-seated slope failures / slips occur from 0.75 m to no more than 2 m below the ground and can be prevented by vegetation if the roots grow to this depth (Elwell & Stocking 1976; Rice *et al*. 1969; Waldron 1977; Wu *et al.* 1988; Waldron & Dakessian 1982; Nilaweera *et al.* 1999; Marden *et al*. 2005; Danjon *et al.* 2007). Most research has been done on the stabilising effects of trees and larger rooted species (Barker 1995; Brooks *et al.* 1995; Nilaweera *et al*. 1999; Marden *et al*. 2005; Norris 2005; Smethurst *et al.* 2006; Danjon *et al*. 2007; Tosi 2007); however grasses and wildflowers may also improve slope stability by intercepting rainfall, preventing surface erosion and root reinforcement - binding the soil particles together (Lutz 1936; Hudson 1957; Waldron & Dakessian 1982; Boardman 1984; 1991; Evans 1990; Fullen 1991; 1992; 1998; Bayfield *et al.* 1992; Morgan 1992; Mitchell *et al,* 2003; Norris 2005). Although the seed mixture sown on roadside slopes will not influence deep-seated slope failures straight away, the species establishing will influence the slope stability in the top layers and possibly improve slope stability more in the future, once the plants are bigger.

The amount of ground cover is the most important preventative factor in surface erosion (Lutz 1936; Hudson 1957; Quinn 1980; Evans 1990; Boardman 1984; 1991; Fullen 1991; 1992; 1998; Morgan 1992; Solé-Benet *et al*. 1997; Mitchell *et al.* 2003). Surface erosion can be lessened once the cover is over 30 % in some cases, but preferably 70 % (Elwell & Stocking 1974; 1976). Mitchell *et al.* (2003) showed that once a dense grass cover was established, erosion decreased dramatically. Rice *et al*. (1969) showed that the natural brush vegetation in California, on steep slopes, had less soil slips than the cleared areas. Areas converted to perennial grass had a ground cover of 59% and produced a soil slip erosion rate at 492 m^3/ha; an area converted to annual grass with 78% ground cover produced 321 m^3/ha; and natural brush cover with 74% ground cover had a rate of 199 m^3/ha. The natural brush cover had deeper root systems which greatly reduced soil slips, yet the perennial grass also had a root depth of 160 cm, yet the annual grasses had a root depth of 30 cm, and still reduced soil slips (Rice 1969). At the Longhorn Wood cutting on the M20 in England, it was shown that the grass and wildflower seed mixture established better than all the other vegetation treatments. The Willow was 1.5 – 2 m tall, with ground cover of 30 %, the gorse and broom plots only had 5 % ground cover, and the brambles after 18 months only had 10 – 15 % cover. However, the grass and wildflower seed mixture treatment established well and had 60 % cover (Greenwood 1996).

Vegetation biomass is important to give good ground cover, but the plants shouldn't be too tall and large as this actually prevents species growing underneath, and in fact increases the amount of bare soil (Spehn *et al*. 2000; 2005; Morgan 2007). Spehn *et al*. (2000; 2005) showed that it isn't just total biomass that's important but the overall canopy structure. A diverse system utilises the available layers in a canopy, with structurally differentiated leaf layers, showing spatial complementarity. If more functional types establish, does the spatial complementarity create a dense closed canopy, with many canopy layers, lessening the amount of bare ground underneath and reducing surface rainfall erosion?

The species composition of the BIONICS Embankment was monitored over two years to study species establishment from the seed mixture, seed bank and natural dispersal. The Embankment was cut once a year, with the cuttings removed. The differences between the north-facing and south-facing aspects could be compared, along with the differences between the two construction / compaction methods, with the aim to answer these questions:

1) What was the origin of the species that established on the BIONICS embankment?: From the grass and wildflower seed mixture, the seedbank or from natural regeneration / colonisation?
2) Did the south-facing slopes have greater species richness and diversity than the north-facing slopes?
3) Did the compacted slopes have lower species richness and diversity compared to the non-compacted slopes?
4) Did aspect, soil compaction and position up the slope influence species composition and species establishment?

5) Did species preferring warm, dry conditions establish on south-facing slopes and species preferring cold, wet conditions establish on north-facing slopes?
6) Did the cutting regime of one cut in September of each year influence the species composition and species establishment from 2007 – 2008?
7) Did the north-facing slopes have greater Ellenberg Fertility and Moisture Values, and did the south-facing slopes have greater Ellenberg Light Values?
8) Did the south-facing slopes have a more xeric NVC classification and the north-facing slopes a more mesic NVC classification?

2.2 Methods

2.2.1 Site description

The BIONICS embankment was built at Nafferton Farm. Nafferton Farm is in Northumberland, just west of Newcastle on the A69 (Grid reference NZ 064 657) and is owned by Newcastle University's School of Agriculture, Food and Rural Development.

2.2.2 The BIONICS embankment

The BIONICS embankment was built by the Civil Engineering and Geosciences Department in 2005 (see Figure 2.1). It was 6 m high with side slopes of 1 in 2 and a 5 m wide crest. There were four 18 m wide test plots on each face. One side of the embankment was south-facing; the other side was north-facing. The middle test plots were constructed to the Highways Agency Specifications for newly constructed embankments (HA 1991; 2007b). The middle test plots were built up in 0.5 m lifts and each layer was compacted with an excavation plant. The outer plots have been poorly constructed and were less compact to simulate older embankment designs, being built up by raising the embankment level in 1 m lifts, then applying minimal tracking with the excavation plant to minimise compaction. The BIONICS embankment was built using Durham Lower Boulder clay. The embankment base clay surface was roughened (scarified) with the JCB front bucket before 20 cm of topsoil was added. This was to avoid a sharp interface between the topsoil and base layer. Before the BIONICS embankment was built, the topsoil in this area was taken up and stored for use on the embankment.

2.2.3 Treatments, sampling and replication

The BIONICS embankment was already designed and built before the beginning of this PhD and the embankment cost over £100,000 to build. There was only one plot for each treatment (including the climate control treatments added in 2009). However, each test plot was 18 m x 12 m which allowed random samples to be taken across each treatment. This was pseudoreplication as the samples were not independent of each other (Hurlbert 1984), but under the circumstances this was the only means of taking measurements suitable for statistical analysis. Originally the climate control treatment was to be added at the beginning of the PhD but it was not added until the end. Therefore, in the 2007 and 2008 sampling years there was replication in the sampling method. Only three treatments were investigated: aspect, compaction and position up the slope – with two replicates of each one. There were two compacted slopes on the south-facing side and two compacted slopes on the north-facing side. Each plot was divided into three so there was a bottom section, a middle section and a top section of each plot (Figure 2.2).

2.2.4 Seed mixture

A seed mixture of grasses and wildflowers (shown in Table 2.1) was sown across the embankment at the end of September 2006. This seed mixture was a general upland hay meadow mixture, similar to an NVC MG5b community, and was purchased from Emorsgate. No additional seed was added.

2.2.5 Cutting / management

The BIONICS embankment was cut with a strimmer once a year, at the end of the flowering season in September 2007 and September 2008. The cuttings were raked off each time.

2.2.6 Vegetation sampling

Each treatment plot was horizontally divided into three (approximately 3 m x 18 m). In each section three random quadrats (1 m x 1 m) were taken. Each quadrat was divided into 16 squares (25 cm x 25 cm). In each square the plant species frequency was recorded as 1. The absent plant species received a zero. If a species was present in all 16 squares, the species was given a frequency of 16. The sampling was undertaken in June – July 2007 and June – July 2008. Plant species were identified according to Stace (2010).

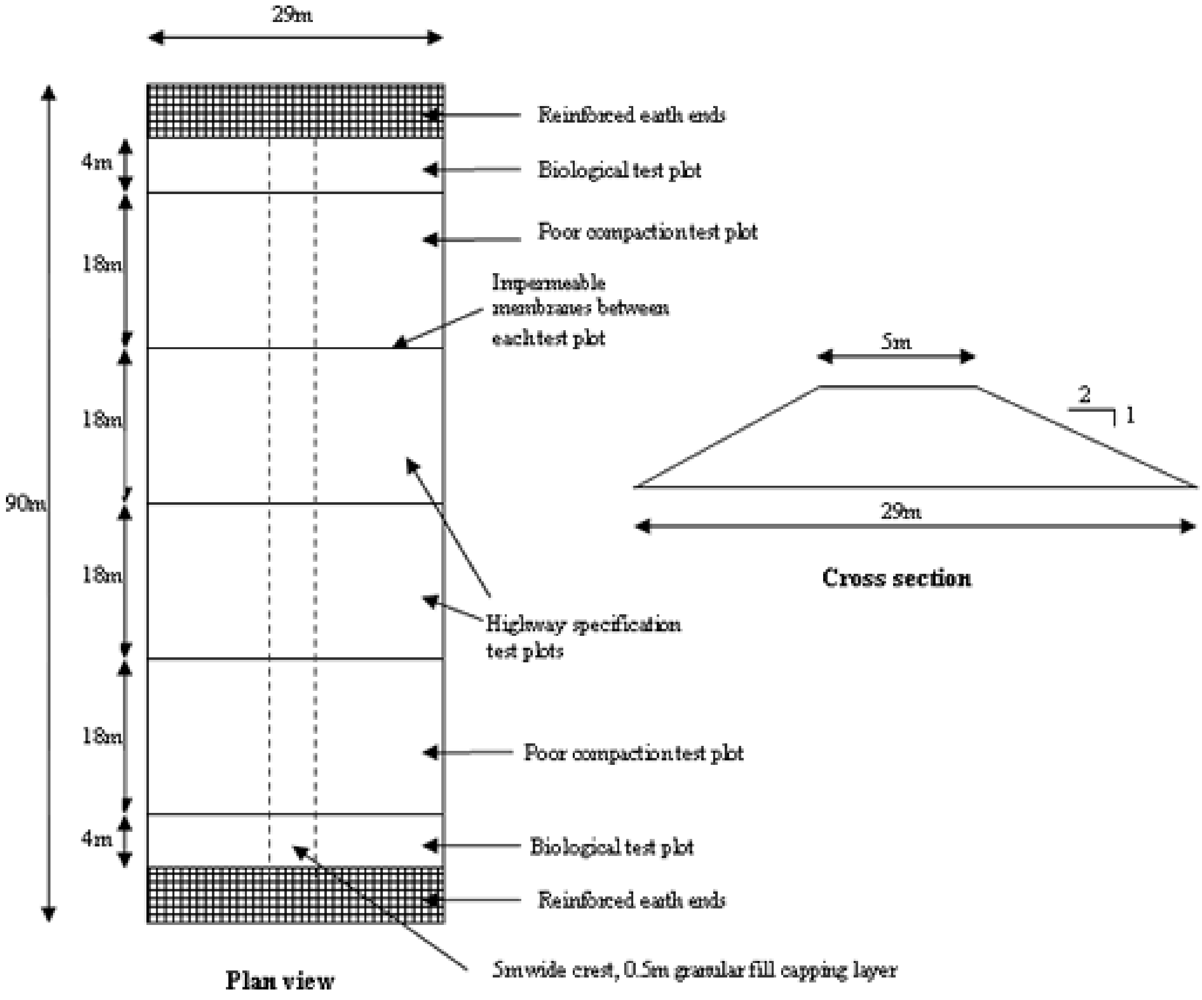

Figure 2.1. Embankment Cross Section (taken from www.ncl.bionics.co.uk).

South, Non Compacted.	South, Compacted.	South, Compacted.	South, Non Compacted.
↓	↓	↓	↓
Bottom	Bottom	Bottom	Bottom
Middle	Middle	Middle	Middle
Top	Top	Top	Top
Top	Top	Top	Top
Middle	Middle	Middle	Middle
Bottom	Bottom	Bottom	Bottom
↑	↑	↑	↑
North, Non Compacted.	North, Compacted.	North, Compacted.	North Non, Compacted.

Figure 2.2. BIONICS treatment design, with aspect, compaction and position up the slope.

Table 2.1. The grass and wildflower seed mixture sown onto the BIONICS embankment in Sept 2006: A general upland hay meadow seed mixture.

Type	Species	Common name
Wildflowers:	*Achillea millefolium*	Yarrow
	Campanula glomerata	Clustered bellflower
	Centaurea nigra	Common Knapweed
	Centaurea scabiosa	Greater Knapweed
	Clinopodium vulgare	Wild Basil
	Conopodium majus	Pignut
	Daucus carota	Wild carrot
	Filipendula ulmaria	Meadowsweet
	Galium mollugo	Hedge bedstraw
	Galium verum	Lady's bedstraw
	Geranium pratense	Meadow Crane's bill
	Knautia arvensis	Field Scabious
	Leontodon hispidus	Rough Hawkbit
	Leucanthemum vulgare	Oxeye Daisy
	Lotus corniculatus	Birdsfoot trefoil
	Lychnis flos-cuculi	Ragged Robin
	Malva moschata	Musk mallow
	Plantago lanceolata	Ribwort Plantain
	Plantago media	Hoary Plantain
	Primula veris	Cowslip
	Prunella vulgaris	Self-heal
	Ranunculus acris	Meadow buttercup
	Ranunculus bulbosus	Bulbous buttercup
	Rhinanthus minor	Yellow Rattle
	Rumex acetosa	Common Sorrel
	Sanguisorba minor ssp *minor*	Salad Burnet
	Sanguisorba officinalis	Great Burnet
	Silene dioica	Red Campion
	Silene vulgaris	Bladder Campion
	Stachys officinalis	Betony
	Trifolium pratense	Red Clover
	Vicia cracca	Tufted vetch
Grasses:	*Agrostis capillaris*	Common bent
	Alopecurus pratense	Meadow foxtail
	Anthoxanthum odoratum	Sweet vernal-grass
	Briza media	Quaking grass
	Cynosurus cristatus	Crested dogstail
	Festuca ovina	Sheep's fescue
	Festuca rubra	Slender creeping red fescue
	Lolium perenne	Perennial Ryegrass
	Phleum bertolonii	Smaller cat's tail
	Trisetum flavescens	Yellow oat-grass

2.2.7 Data analysis

2.2.7.1 Species Richness and Shannon Diversity Index (H')

The number of species recorded on each quadrat was added up and the Shannon Diversity Index (H') was calculated for each quadrat, using the total cover of all the plant species in each quadrat and the individual cover for each species in each quadrat:

$H' = - \sum p_i \ln p_i$

Where p_i = the individual cover of each species divided by the total cover for the quadrat.

The natural log of p_i was calculated and the total sum of $p_i \ln p_i$ equals the Shannon Diversity Index (H') for each quadrat (Shannon & Weaver 1949).

2.2.7.2 Ellenberg Indicator Values of 2008 data

Each plant species has been given a value for Fertility (N), Light (L) and Moisture (F) along a scale (Hill *et al.* 2000). Light (L): 1 = Plants in deep shade, to 9 = Plants in full light. Moisture (F): 1 = very dry, to 12 = submerged plants. Fertility (N): 1 = infertile, to 9 = high fertility. The Ellenberg Indicator Value for fertility, light and moisture was calculated for each quadrat: the cover for each quadrat was converted to % cover and scaled to total to 100 %. The Ellenberg Indicator Value for each species was multiplied by the percentage cover for that species and divided by 100. These values were summed to get the Ellenberg Indicator Value for each quadrat.

2.2.7.3 Analysis of variance (General Linear Model ANOVA)

In Minitab, these treatments - aspect (north-facing and south-facing); soil compaction (compacted and non-compacted plots) and position up the Embankment slopes (bottom, middle and tops of the slopes) were inputted into the "model" box in a GLM (General linear model) ANOVA (Analysis of variance) and the interaction terms were added (!) between each treatment. In turn, each of these responses listed were put into the "response" box: total number of species found (species richness); total number of grasses; total number of wildflowers; Shannon Diversity Index (H'); Ellenberg Indicator Values (Fertility, Light and Moisture) and frequency of widespread individual species. An Anderson-Darling normality test was carried out on the residuals of each test and the data was transformed if needed. A variety of transformations were used including: square root; natural log; log + 1 and to the power of 1.5. Once the data fit a linear line ($p > 0.05$) the significant values ($p < 0.05$) were deemed to be valid. A post-hoc Tukeys test was carried out on any statistically significant relationships if there were over 2 treatment levels, i.e. position (top, middle and bottom of slope), or where there were any significant interactions ($p < 0.05$).

2.2.7.4 National Vegetation Classification (NVC). TABLEFIT

All semi-natural British plant communities have been classified into common species assemblages (NVC classifications) based on field surveys throughout Britain, begun in 1975 (Rodwell 1992). In order to classify communities into NVC, 3 quadrats need to be sampled in uniform vegetation. Since 3 quadrats were taken in each position up the slope on each treatment it was possible to convert this community data into an NVC classification to see if aspect, compaction or position up the slope was making differences to the communities establishing. The mean percentage cover for each species per 3 quadrats was calculated and the data file was converted into a format read by TABLEFIT by using CanoImp, and feed into CORNTABLE and DATAENTER. TABLEFIT is a program that can classify sites to the NVC using goodness of fit. The TABLEFIT output gives 5 recommendations to the NVC, in order of goodness of fit. 0 - 49 % = very poor; 50 – 59 % = poor; 60 – 69 % = fair; 70 – 79 % = good; 80 – 100 % = very good. The NVC was predicted for each position up the slope in each treatment and the goodness of fit was compared.

2.2.7.5 Ordination – Minitab and CANOCO

Principal Compenents Analyses (PCA) were used in MINITAB to look at general treatment patterns in 2008. The plant species composition results of 2007 and 2008 were analysed using the community ecology package CANOCO (Leps and Smilauer 2003).

The quadrat data with the plant species frequency for each year was converted using CanoImp into a "species" datafile. The main environmental variables (treatments) for both years were: aspect (north-facing and south-facing slopes); soil compaction (compacted and non-compacted slopes) and position up the Embankment slope (bottom, middle and top of the slope) and these were converted using CanoImp into an "environment" file. In 2008, the Ellenberg Indicator Values and Shannon Diversity Index were included as "supplementary" data in 2008. The entire dataset of 2007 and 2008 was analysed together to look at sampling date patterns.

To begin with a Detrended Correspondence Analysis (DCA) was carried out on the plant species data to check the lengths of gradient. Just the "species" data was used for this. Detrending by segments was highlighted, using inter-species correlations and log transformed. The lengths of gradients were under 4 so a linear model was needed and so a Redundancy Analysis (RDA) was performed second. The "species" data, "environment" data and "supplementary" data were inputted into CANOCO, highlighting "inter-species correlations"; "log-transformed"; "do not use forward selection" and the Monte Carlo Permutation test box was ticked.

To test for the significant effects of each treatment the "environment" datafile was inputted as the main "environment" file and the "covariable" file. One by one, each treatment was used as a "covariable" and deleted from the environmental treatments so that the individual effects of each treatment could be partitioned out (partitioning of the variance). A Monte Carlo permutation test was performed on each test and the Trace, F-value and P-value recorded. Those treatments with $p < 0.05$ were classed as significantly effecting the species composition.

The species-environment bi-plots were interpreted visually: species close together were associated within similar plant communities and environmental variables found in particular sections of the bi-plot were associated with the species in that area. Species and environmental variables were more important the further away from the centre of the bi-plot they were. This information and the results from the ANOVA's were combined to give a general picture of the species composition.

2.3 Results

2.3.1 Species composition 2007 - 2008

30 plant species were found on the BIONICS embankment in 2008 (Table 2.2). 35 species had established in 2007. 10 species were not found in 2008 that were found in 2007 and 5 species were found in 2008 that weren't recorded the year before (Table 2.3). *Triticum vulgare* was not sampled again when this was very common in 2007. *Sonchus asper*, *Avena sativa* and *C. arvense* are arable weeds that were very common in 2007 and were only found infrequently across the embankment in 2008. Out of the 42 species in the seed mixture, only 14 species established and 5 of these species were gained in 2008 (Table 2.4).

2.3.2 Species Richness

2.3.2.1 Total Species Richness (sp. m^2) 2007 and 2008

In 2007, the south-facing slopes had greater species richness than the north-facing slopes (10.9 sp. m^2 vs. 9.1 sp. m^2) ($F_{1, 60} = 10.40$, $p = 0.002$) and the compacted slopes contained more species than the non-compacted slopes (10.7 sp. m^2 vs. 9.3 sp. m^2) ($F_{1, 60} = 7.03$, $p = 0.010$) (Table 2.6). By 2008, the species richness was not significantly different between any of the treatments (Table 2.7).

In both 2007 and 2008 aspect and soil compaction were interacting (2007: $F_{2, 60} = 7.24$, $p = 0.009$) (2008: $F_{1, 60} = 4.18$, $p = 0.045$). There were significantly more species found on the north-facing, compacted slopes, compared to the north-facing, not compacted slopes (9.9 sp. m^2 vs. 7.9 sp. m^2 in 2008), whereas there were no differences between the soil compaction treatments on the south-facing slopes (Figure 2.3).

Table 2.2. The 30 species recorded on the Embankment in June and July of 2008 and their general frequencies.

Frequency	Establishment	Species	Common Name
Very common:	Seed mixture	*Cynosurus cristatus*	Crested Dogstail
		Lolium perenne	Perennial Ryegrass
		Lotus corniculatus	Birdsfoot trefoil
	Natural regeneration	*Ranunculus repens*	Creeping Buttercup
		Trifolium repens	White Clover
		Vicia sativa	Common Vetch
Common:	Seed mixture	*Phleum bertolonii*	Smaller cat's tail
		Trifolium pratense	Red Clover
		Trisetum flavescens	Yellow Oat-grass
	Natural regeneration	*Holcus lanatus*	Yorkshire Fog
		Poa trivialis	Rough Meadow-grass
Infrequent:	Seed mixture	*Achillea millefolium*	Yarrow
		Alopecurus pratense	Meadow foxtail
		Daucus carota	Wild carrot
		Leucanthemum vulgare	Ox-eye Daisy
		Plantago lanceolata	Ribwort Plantain
		Ranunculus acris	Meadow buttercup
		Rumex acetosa	Common Sorrel
		Sanguisorba minor ssp. minor	Salad Burnet
	Natural regeneration	*Avena sativa*	Wild oat
		Cerastium fontanum	Common Mouse-ear
		Cirsium arvense	Creeping Thistle
		Epilobium montanum	Broad-leaved Willowherb
		Galium aparine	Cleavers
		Medicago lupulina	Black Medick
		Tussilargo farfara	Coltsfoot
		Rumex obtusifolius	Broad-leaved Dock
		Sonchus asper	Prickly Sowthistle
		Tarax sp.	Dandelion
		Urtica dioica	Nettle

Table 2.3. The species that have been lost and gained on the Embankment between 2007 and 2008.

Gained or Lost:	Species	Common name
Lost:	*Agrostis capillaris*	Common Bent
	Anthriscus sylvestris	Cow Parsley
	Bellis perennis	Daisy
	Conopodium majus	Pignut
	Geranium dissectum	Cut-leaved Cranesbill
	Hypochaeris radicata	Catsear
	Matricaria discoidea	Pineappleweed
	Myosotis arvensis	Field Forgetmenot
	Triticum vulgare	Wild wheat
	Veronica chamdrys	Germander Speedwell
Gained:	*Alopecurus pratense*	Meadow foxtail
	Daucus carota	Wild carrot
	Phleum bertolonii	Smaller cat's tail
	Ranunculus acris	Meadow buttercup
	Trisetum flavescens	Yellow Oat-grass

Table 2.4. The species that established on the embankment in June – July 2008 from the original seed mixture. The species highlighted with a * are the 5 species which were recorded in 2008 but not recorded in 2007.

Established from the Seed mixture	Species	Common name
Wildflowers:	*Achillea millefolium*	Yarrow
	*Daucus carota**	Wild carrot
	Leucanthemum vulgare	Ox-eye Daisy
	Lotus corniculatus	Birdsfoot trefoil
	Plantago lanceolata	Ribwort Plantain
	Rumex acetosa	Common Sorrel
	Sanguisorba minor ssp. minor	Salad Burnet
	Trifolium pratense	Red Clover
	*Ranunculus acris**	Meadow buttercup
Grasses:	*Alopecurus pratense**	Meadow foxtail
	Cynosurus cristatus	Crested Dogstail
	Lolium perenne	Perennial Ryegrass
	*Phleum bertolonii**	Smaller cat's tail
	*Trisetum flavescens**	Yellow Oat-grass

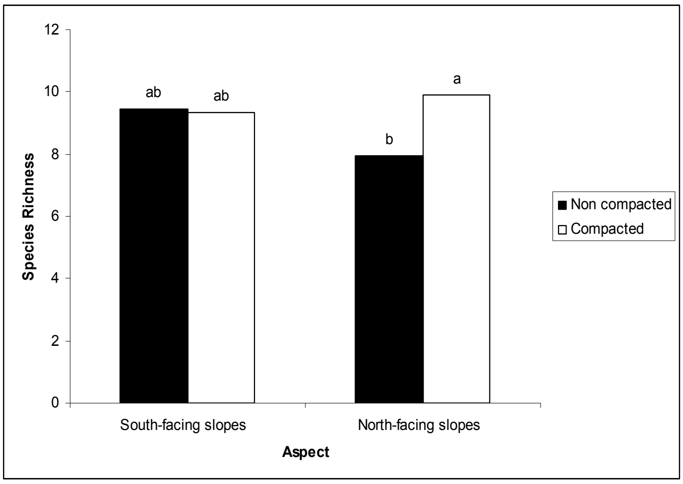

Figure 2.3. Compaction, aspect and species richness per m^2 in 2008. There were more species on the north-facing compacted slopes than the north-facing non-compacted slopes. This trend was the same in 2007.

2.3.2.2 Species Richness of the grasses in 2007 and 2008

In 2007 there were no significant differences in the species richness of the grasses (Table 2.6). In 2008, there were significantly more grasses found on the top of the Embankment than the middle and bottom of the slopes (4.8 sp. m^2, vs. 4 sp. m^2 and 4 sp. m^2) ($F_{2, 60} = 4.35$, $p = 0.017$). There were significantly less grasses growing on the south-facing slopes compared to the north-facing slopes (3.8 sp. m^2 vs. 4.7 sp. m^2) ($F_{1, 60} = 11.86$, $p = 0.001$) (Table 2.7). When aspect was looked at with soil compaction, it was just the north-facing, compacted slope that had significantly more grass species than the south-facing slopes ($F_{1, 60} = 4.11$, $p = 0.047$) (Figure 2.4).

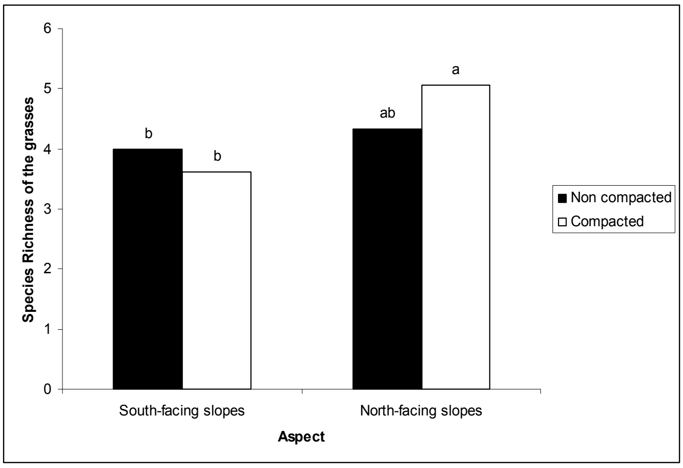

Figure 2.4. Compaction, aspect and grass species found per m^2 in 2008. The north-facing compacted slopes had more grass species than the south-facing slopes.

2.3.2.3 Species Richness of the wildflowers in 2007 and 2008

In both 2007 and 2008, there was a significantly higher number of wildflower species on the south-facing slopes in comparison to the north-facing slopes (6 sp. m^2 vs. sp. 4 m^2 in 2007 ($F_{1, 60}$ = 14.61, p = <0.001); 5.6 sp. m^2 vs. 4.2 sp. m^2 in 2008 ($F_{2, 60}$ = 11.64, p = 0.001)). In 2008, this was the opposite trend to that seen with the number of grass species: although there were no differences in total species richness in 2008, when the grasses and wildflowers were looked at separately, there were fewer grasses and more wildflowers on the south-facing slopes and more grasses and fewer wildflowers on the north-facing slopes (Table 2.6 and Table 2.7).

In 2007, when soil compaction was looked at, the compacted slopes had more wildflowers than the non-compacted slopes (6 sp. m^2 vs. 5 sp. m^2) ($F_{1, 60}$ = 8.63, p = 0.005) (Table 2.6); however, when looked at in combination with aspect, the south-facing compacted slopes had significantly fewer wildflowers than the other treatments (3.3 sp. m^2 vs. 6 sp. m^2 for the other treatments) ($F_{1, 60}$ = 12.85, p = 0.001) (Figure 2.5). This trend did not continue into 2008. In fact, in 2008, aspect, compaction and position on the slopes were interacting ($F_{2, 60}$ = 9.347, p = 0.045). It was just two combinations that were significantly different: the top of the slopes on the south-facing side, in the compacted treatment, had more wildflower species than the bottom of the slopes on the north-facing side in the non-compacted treatment (7 sp. m^2 vs. 3 sp. m^2). The other differences were not significant (Table 2.5).

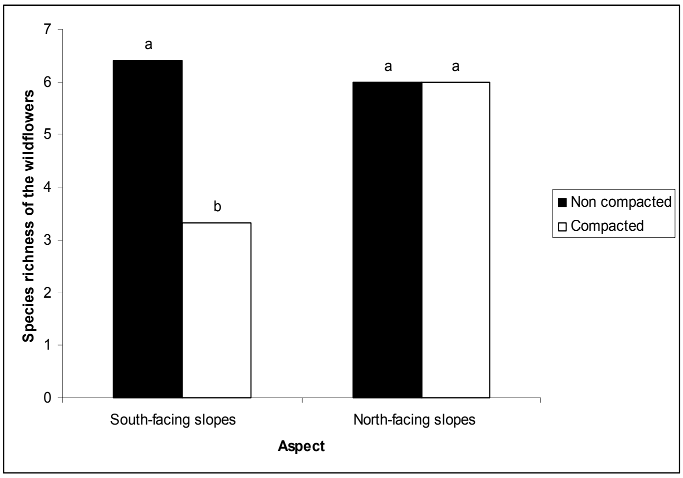

Figure 2.5. Aspect, compaction and species richness of the wildflowers. The compacted slopes had less wildflowers than all the other treatments.

Table 2.5. Species Richness of wildflowers per m^2 for all treatment combinations. The south-facing compacted slopes at the top had more wildflowers than the north-facing non-compacted slopes at the bottom.

Position on slope	Non-compacted		Compacted	
	South-facing plots	North-facing plots	South-facing plots	North-facing plots
Bottom of panels	5.3 ab	3 b	4.5 ab	5.2ab
Middle of panels	5.8 ab	4 ab	5.7 ab	5.5 ab
Top of panels	5.2ab	3.8 ab	7 a	3.8 ab

2.3.3 Shannon Diversity Index (H') 2007 - 2008

In 2007, the south-facing slopes had greater diversity than the north-facing slopes (2 H' vs. 1.7 H') ($F_{1, 60} = 20.40$, p = <0.001) and the compacted slopes had greater diversity than the non-compacted slopes (2 H' vs. 1.8 H') ($F_{1, 60} = 9.33$, p = 0.003) (Table 2.6). This trend did not continue into 2008 (Table 2.7). In 2007 and 2008, aspect and soil compaction were interacting (2007: $F_{1, 60} = 6.91$, p = 0.011) (2008: $F_{2, 60} = 7.26$, p = 0.009). In both 2007 and 2008 the north-facing, non-compacted slopes had a significantly lower Shannon Diversity Index in comparison to the north-facing, compacted slopes and south-facing, non-compacted slopes (Figure 2.6).

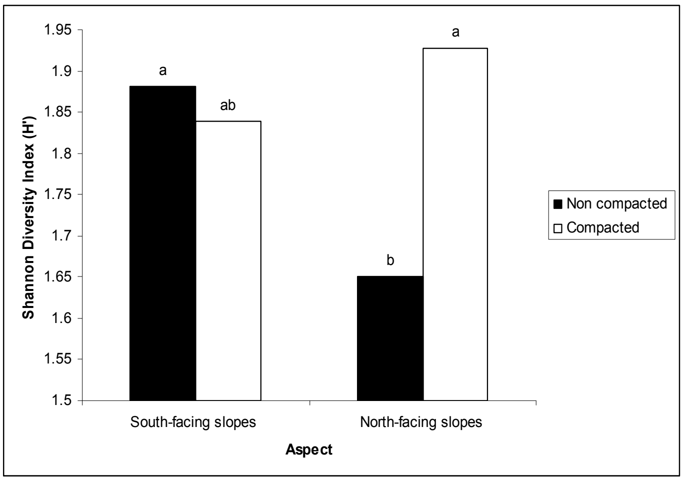

Figure 2.6. Compaction, aspect and Shannon Diversity Index (H'). The north-facing, non-compacted slopes had lower diversity than the south-facing, non-compacted slopes and the north-facing, compacted slopes.

Table 2.6. Species Richness of grasses and wildflowers and the Shannon Diversity Index across all treatments of the BIONICS embankment in 2007.

		Mean number of species and diversity 2007			
Treatment		Grasses	Wildflowers	Species Richness	Shannon Diversity Index (H')
Position up the Embankment	Bottom	4.7	5.2	9.9	1.9
	Middle	4.6	5.8	10.4	1.9
	Top	4.4	5.3	9.7	1.8
Aspect	South-facing	4.7	6.2	10.9	2.0
	North-facing	4.4	4.7	9.1	1.7
Compaction	Non-compacted	4.4	4.9	9.3	1.8
	Compacted	4.7	6.0	10.7	2.0

Table 2.7. Species Richness of grasses and wildflowers and the Shannon Diversity Index across all treatments of the BIONICS embankment in 2008.

		Mean number of species and diversity 2008			
Treatment		Grasses	Wildflowers	Species Richness	Shannon Diversity Index (H')
Position up the Embankment	Bottom	4	4.5	8.5	1.7
	Middle	4	5.2	9.2	1.8
	Top	4.8	5	9.8	1.9
Aspect	South-facing	3.8	5.6	9.4	1.9
	North-facing	4.7	4.2	8.9	1.8
Compaction	Non-compacted	4.2	4.6	8.7	1.8
	Compacted	4.3	5.3	9.6	1.9

2.3.4 Individual Species Responses 2007 - 2008

2.3.4.1 Grasses 2007 - 2008

In 2007, when the grasses were looked at independently, both *L. perenne* and *C. cristatus* did not show any significant differences between the treatments (Table 2.8). In 2008, *L. perenne* frequency was much less than in 2008, whereas *C. cristatus* frequency was much greater (Table 2.8 and Table 2.9). By 2008, *L. perenne* frequency was almost halved in the compacted treatment (11.5 per m^2 vs. 6.5 per m^2) ($F_{1,60} = 20.54$, $p = <0.001$) and *C. cristatus* still did not show any differences between the treatments (Table 2.9).

In 2007, aspect and soil compaction were interacting to influence *P. trivialis* frequency ($F_{1,60} = 12.69$, $p = 0.001$). *P. trivialis* had greater frequency on the south-facing compacted slopes, in comparison the south-facing non-compacted slopes and the north-facing compacted slopes (Figure 2.7). However, by 2008, *P. trivialis* was found in greater abundance on the north-facing slopes in comparison to the south-facing slopes (2.9 per m^2 vs. 1.6 per m^2) ($F_{1,60} = 5.27$, $p = 0.025$); although when aspect was looked at with compaction, frequency was just higher on the north-facing, non-compacted slopes, in comparison to the south-facing, non-compacted slopes (4.1 per m^2 vs. 0.7 per m^2) ($F_{1,60} = 11.54$, $p = 0.001$) (Figure 2.8).

In 2007, *Holcus lanatus* was only found in a few quadrats, but in 2008, *H. lanatus* was much more abundant. In 2008, *H. lanatus* had significantly greater frequency on the north-facing slopes in comparison to the south-facing slopes (1.8 per m^2 vs. 0.9 per m^2) ($F_{1,60} = 6.74$, $p = 0.012$) (Table 2.9).

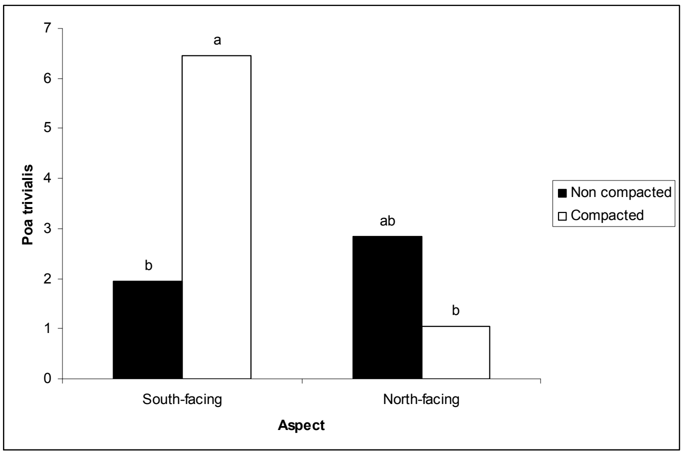

Figure 2.7. Compaction, aspect and *Poa trivialis* frequency in 2007. *Poa trivialis* had greater frequency on the south-facing compacted plots, in comparison the south-facing non-compacted plots and the north-facing compacted plots.

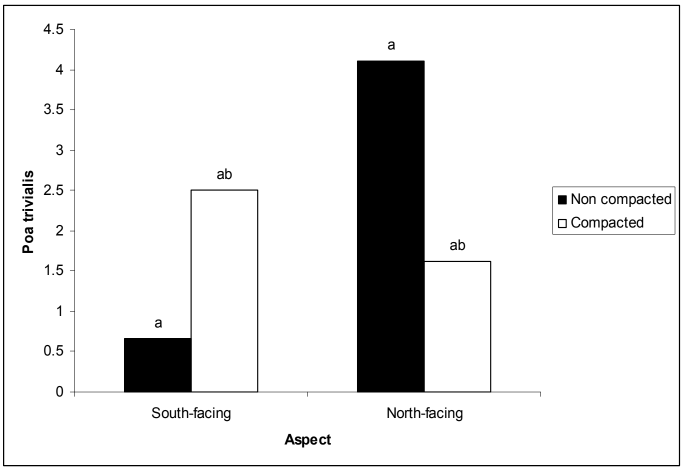

Figure 2.8. Compaction, aspect and *Poa trivialis* frequency in 2008. *Poa trivialis* had greater frequency on the south-facing compacted plots, in comparison the south-facing non-compacted plots and the north-facing compacted plots.

Table 2.8. Individual grass species frequency across all treatments of the BIONICS embankment in 2007.

Treatment		Grass frequency in 2007		
		L. perenne	*C. cristatus*	*P. trivialis*
Position up the Embankment	Bottom	12.4	3.0	3.2
	Middle	11.7	3.5	2.8
	Top	11.5	3.6	3.2
Aspect	South-facing	12.5	2.7	4.2
	North-facing	11.3	4.0	1.9
Compaction	Non-compacted	13.1	2.8	2.4
	Compacted	10.6	3.9	3.8

Table 2.9. Individual grass species frequency across all treatments of the BIONICS embankment in 2008.

		Grass frequency in 2008			
Treatment		*L. perenne*	*C. cristatus*	*P. trivialis*	*H. lanatus*
Position up the Embankment	Bottom	9.1	9.7	2.3	1
	Middle	7.8	12	1.8	1.3
	Top	9.9	11	2.6	1.8
Aspect	South-facing	10.1	10	1.6	0.9
	North-facing	7.9	11.8	2.9	1.8
Compaction	Non-compacted	11.5	10.5	2.4	1.4
	Compacted	6.5	11.3	2.1	1.4

2.3.4.2 Wildflowers 2007 - 2008

When the individual wildflower species establishment was looked at independently, there was a huge reduction in the abundance of *C. arvense* between 2007 and 2008. So much so that *C. arvense* was common in 2007 and rare in 2008. In 2007, *C. arvense* was found in greater abundance at the bottom of the slopes, in comparison to the top of the slopes (3.3. per m^2 vs. 2 per m^2) ($F_{2, 60} = 4.62$, $p = 0.014$). There was significantly more *C. arvense* on the south-facing slopes in comparison to the north-facing slopes (3.9 per m^2 vs. 1.3 per m^2) ($F_{2, 60} = 52.80$, $p = < 0.001$). The compacted slopes had significantly more thistles than the non-compacted slopes ($F_{2, 60} = 5.13$, $p = 0.027$) (Table 2.10). In 2008 the abundance of *C. arvense* was so significantly reduced that it was not possible to do any follow up analyses (Table 2.11).

The frequency of *R. repens* increased across the BIONICS Embankment between 2007 and 2008. In both 2007 and 2008 these significant differences remained the same: The bottom of the slopes had significantly less *R. repens* than the middle slopes (2 per m^2 vs. 4.5 per m^2 in 2007 ($F_{2, 60} = 6.89$, $p = 0.002$) and 3.7 per m^2 vs. 6.8 per m^2 in 2008 ($F_{2, 60} = 4.60$, $p = 0.014$)); the north-facing slopes had significantly greater frequency than the south-facing slopes (4.2 per m^2 vs. 2.1 per m^2 in 2007 ($F_{2, 60} = 14.35$, $p = < 0.001$) and 8.6 per m^2 vs. 2.8 per m^2 in 2008 ($F_{1, 60} = 43.90$, $p = <0.001$)); and the compacted slopes had significantly greater frequency than the non-compacted slopes (4.6 per m^2 vs. 1.7 per m^2 in 2007 ($F_{2, 60} = 28.34$, $p = < 0.001$) and 6.9 per m^2 vs. 4.5 per m^2 in 2008 ($F_{1, 60} = 5.05$, $p = 0.028$)) (Table 2.10 and Table 2.11).

In 2007 and 2008, position on the slope and compaction were interacting (2007: $F_{2, 60} = 3.23$, $p = 0.047$; 2008; $F_{2, 60} = 3.22$, $p = 0.047$). In 2007 it was the middle of the compacted slopes that had greater frequency of *R. repens* than the bottom of the slopes and the middle and top of the non-compacted treatment (Figure 2.8). However, in 2008, it was the top of the compacted slopes that had significantly greater frequency of *R. repens* than the bottom of all slopes and the top of the slopes in the non-compacted treatment (Figure 2.9).

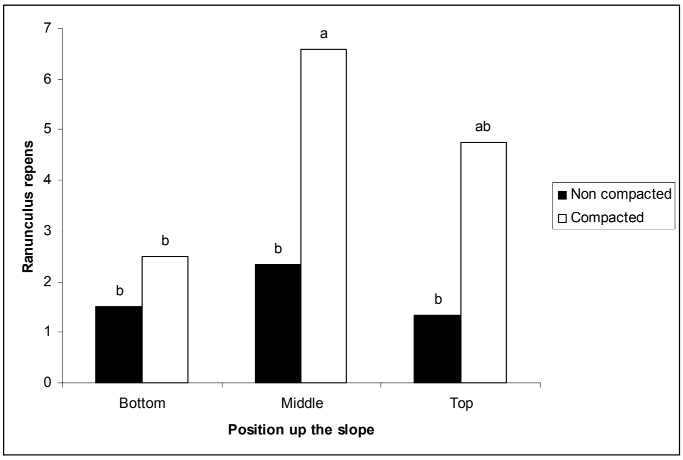

Figure 2.8. Position up the Embankment slope, compaction and *Ranunculus repens* frequency in 2007. The middle of the compacted slopes had greater frequency of *R. repens* than the middle and top of the non-compacted slopes, and the bottoms of the slopes.

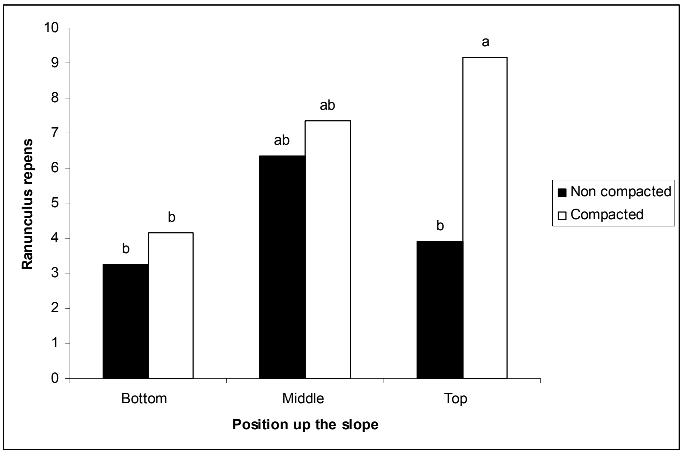

Figure 2.9. Position up the Embankment slope, compaction and *Ranunculus repens* frequency in 2008. The top of the compacted slopes had greater frequency of *R. repens* than the top of the non-compacted slopes, and the bottoms of the slopes.

Between 2007 and 2008, the frequency of the main wildflowers increased. *Vicia sativa* increased by over twice as much. In both 2007 and 2008, *L. corniculatus* and *V. sativa* frequency was significantly higher on the south-facing slopes than the north-facing slopes (1.9

per m^2 vs. 0.3 per m^2 in 2007 ($F_{1, 60} = 17.79$, $p = < 0.001$) and 3.4 per m^2 vs. 0.4 per m^2 in 2008 ($F_{1, 60} = 24.35$, $p = <0.001$); 1.9 per m^2 vs. 0.5 per m^2 in 2007 ($F_{1, 60} = 18.77$, $p = < 0.001$) and 8.4 per m^2 vs. 0.9 per m^2 in 2008 ($F_{1, 60} = 105.15$, $p = <0.001$)) (Table 2.10 and Table 2.11). In 2007, there were no significant differences in *T. repens* frequency, however, by 2008, *T. repens* was more frequent on the south-facing slopes (10.9 per m^2 vs. 6.8 per m^2) ($F_{1, 60} = 14.53$, $p = <0.001$).

In 2008, *V. sativa* had significantly lower frequency on the top of the slopes than the bottom of the slopes (3 per m^2 vs. 5.6 per m^2) ($F_{2, 60} = 3.40$, $p = 0.04$), and the compacted slopes had a higher frequency than the non-compacted slopes (5.3 per m^2 vs. 4.1 per m^2) ($F_{1, 60} = 5.08$, $p = 0.028$) (Table 2.11). When position on the slopes and aspect were looked at together all the positions on the south-facing slopes had significantly higher frequency of *V. sativa* than all of the positions on the north-facing slopes; however, the top of the slopes on the south-facing side had significantly lower frequency than the middle and bottom positions on that side (5.1 per m^2 vs. 10.6 per m^2 and 9.7 per m^2 respectively) ($F_{2, 60} = 0.83$, $p = 0.009$) (Figure 2.10).

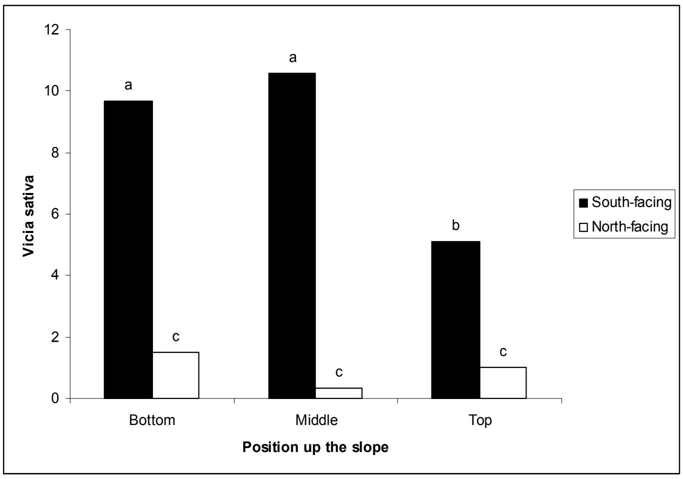

Figure 2.10. Position up the Embankment slope, aspect and *Vicia sativa* frequency in 2008. All the south-facing slopes had greater frequency of *V. sativa* than the north-facing slopes, however, the top of the south-facing slopes had lower cover than the bottom and middle of the south-facing slopes.

Table 2.10. Individual wildflower species cover across all treatments of the BIONICS embankment in 2007.

Treatment		Wildflower frequency in 2007				
		C. arvense	*R. repens*	*T. repens*	*L. corniculatus*	*V. sativa*
Position up the Embankment	Bottom	3.3	2.0	5.8	1.0	1.2
	Middle	2.3	4.5	5.9	1.3	1.5
	Top	2.0	3.0	7.3	1.2	0.9
Aspect	South-facing	2.1	2.1	6.5	1.9	1.9
	North-facing	2.9	4.2	6.2	0.3	0.5
Compaction	Non-compacted	3.8	1.7	5.4	1.2	1.1
	Compacted	1.3	4.6	7.3	1.1	1.2

Table 2.11. Individual wildflower species cover across all treatments of the BIONICS embankment in 2008.

Treatment		Wildflower frequency in 2008				
		C. arvense	*R. repens*	*T. repens*	*L. corniculatus*	*V. sativa*
Position up the Embankment	Bottom	0.3	3.7	10.3	2.1	5.6
	Middle	0.3	6.8	8.9	2.1	5.5
	Top	0.4	6.5	7.4	1.5	3
Aspect	South-facing	0.4	2.8	10.9	3.4	8.4
	North-facing	0.2	8.6	6.8	0.4	0.9
Compaction	Non-compacted	0.3	4.5	8	1.9	4.1
	Compacted	0.4	6.9	9.7	1.9	5.3

2.3.5 Ellenberg Indicator Values of 2008

2.3.5.1 Fertility (N)

The mean fertility score for the BIONICS embankment was 5.1 N. This is an indicator of sites of intermediate fertility. The fertility score was significantly greater on the north-facing slopes (i.e. more fertile) in comparison to the south-facing slopes (5.4 L vs. 4.9 L) ($F_{1, 60} = 31.44$, $p = <0.001$) (Table 2.12). When in combination with soil compaction, the significant difference was just in the non-compacted treatment on the north-facing slope ($F_{1, 60} = 4.44$, $p = 0.038$) (Figure 2.11).

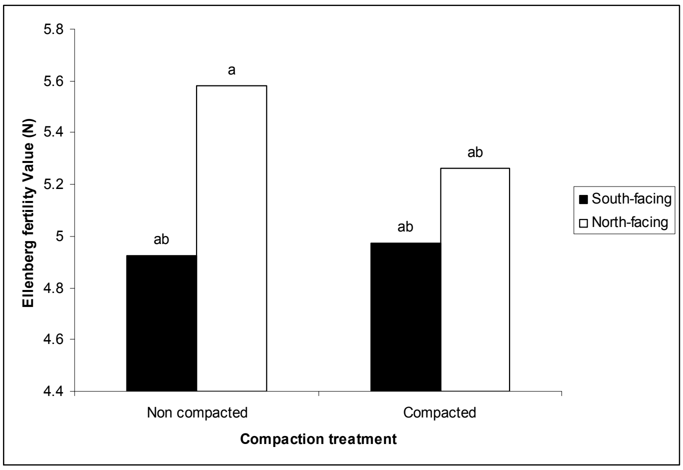

Figure 2.11. Compaction, aspect and Ellenberg Fertility Values. The north-facing, non-compacted plots had higher fertility values than the south-facing plots.

2.3.5.2 *Light (L)*

The mean light score for the BIONICS embankment was 7 L. This is an indicator of sites found in well-lit situations. The south-facing slopes had a significantly higher Ellenberg Light score (i.e. lighter) than the north-facing slopes (7.1 L vs. 6.9 L) ($F_{1,\,60} = 11.59$, p = 0.001) (Table 2.12). Position up the Embankment slope and compaction were interacting ($F_{2,\,60} = 3.93$, p = 0.025): The non-compacted top slopes had a greater Light score than the compacted top slopes and the compacted bottom slopes had a greater Light score than the compacted top slopes (Figure 2.12).

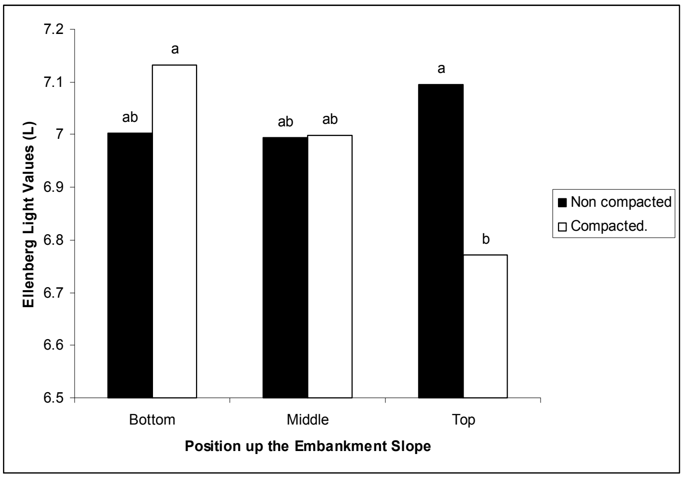

Figure 2.12. Position up the Embankment slope, compaction and Ellenberg Light Values. The non-compacted top slopes had a greater Light score than the compacted top slopes. The compacted bottom slopes had a greater Light score than the compacted top slopes.

2.3.5.3 Moisture (F)

The mean moisture score for the BIONICS embankment was 5.1 F. This is a moisture indicator of sites with average dampness. The north-facing slopes had a greater moisture score (i.e. wetter) than the south-facing slopes (5.3 F vs. 4.9 F) ($F_{1, 60} = 48.74$, $p = < 0.001$). The top of the Embankment slopes had greater moisture scores than the bottom of the slopes, with the middle slopes being intermediate (5.2 F vs. 5 F) ($F_{2, 60} = 6.87$, $p = 0.002$) (Table 2.12). However, this pattern was just restricted to the compacted treatment when the interactions were looked at: There were no differences in position up the Embankment slope on the non-compacted slopes (Figure 2.13) ($F_{2, 60} = 6.87$, $p = 0.002$).

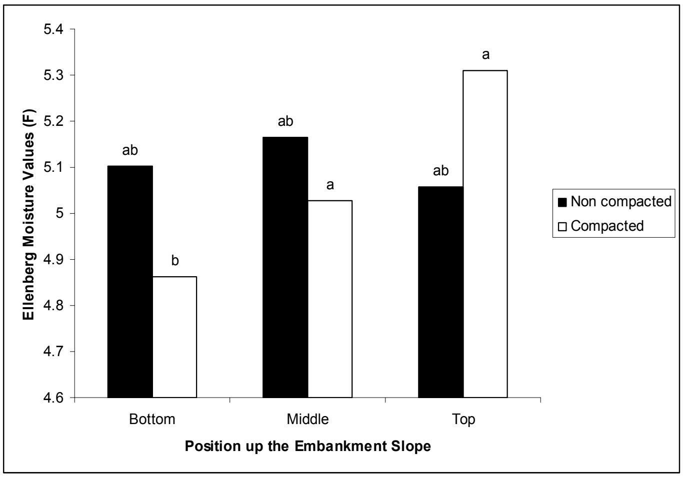

Figure 2.13. Position up the Embankment slope, Compaction and Ellenberg Moisture Values. The top compacted slopes had a higher moisture score than the bottom compacted slopes.

Table 2.12. Ellenberg Indicator Values across the BIONICS embankment.

		Ellenberg Indicator Values		
Treatment		Fertility	Light	Moisture
Position	Bottom	5.1	7.1	5
	Middle	5.1	7	5.1
	Top	5.3	6.9	5.2
Aspect	South-facing	4.9	7.1	4.9
	North-facing	5.4	6.9	5.3
Compaction	Non-compacted	5.3	7	5.1
	Compacted	5.1	7	5.1

2.3.6 National Vegetation Classification (NVC)

The NVC classification for the BIONICS embankment was MG6a. One position on the south-facing slopes was MG6c and four positions on the north-facing slopes was also MG6c (Table 2.13). MG6 is *Lolium perenne – Cynosurus cristatus* grassland. MG6a is the typical community and MG6c includes *Trisetum flavescens*. If a seed mixture had not been added onto the BIONICS embankment, the NVC classification would have been OV25a. The NVC classification of just the sown species that established is MG5a. So, the combinations of these two communities lead to a classification of MG6a.

Table 2.13. The NVC communities found on the BIONICS embankment. MG6a was found on the majority of the slopes.

South-facing cutting				North-facing cutting			
Compaction	Position	NVC classification	Goodness of fit (%)	Compaction	Position	NVC classification	Goodness of fit (%)
Non Compacted	Bottom	MG6 a	Poor (58)	Non Compacted	Bottom	MG6 a	Poor (57)
	Middle	MG6 a	Poor (55)		Middle	MG6 c	Very poor (46)
	Top	MG6 a	Fair (63)		Top	MG6 a	Poor (53)
Compacted	Bottom	MG6 a	Fair (61)	Compacted	Bottom	MG6 c	Poor (57)
	Middle	MG6 a	Poor (59)		Middle	MG6 a	Fair (65)
	Top	MG6 a	Poor (45)		Top	MG6 c	Poor (51)
Compacted	Bottom	MG6 a	Fair (65)	Compacted	Bottom	MG6 a	Fair (65)
	Middle	MG6 a	Poor (57)		Middle	MG6 a	Fair (65)
	Top	MG6 a	Fair (63)		Top	MG6 c	Fair (60)
Non Compacted	Bottom	MG6 a	Fair (67)	Non Compacted	Bottom	MG6 a	Fair (69)
	Middle	MG6 a	Fair (65)		Middle	MG6 a	Good (72)
	Top	MG6 c	Fair (68)		Top	MG6 c	Good (72)

2.3.7 Ordination – Species Composition using CANOCO

2.3.7.1 Species composition in 2007

The first axis of the PCA looking at the 2007 BIONICS results accounted for 19.7 % of the variation in the species composition and the second axis accounted for 14.3 % of the variation. When a RDA was performed, it was clear that aspect formed the first axis and soil compaction formed the second axis (Figure 2.14). Position was in the middle of the bi-plot but this was not significant when the treatments were looked at as seperately (Table 2.14). *M. lupulina* was associated with the non-compacted plots, whereas *R. repens* was associated with the compacted plots. *Conopodium majus* was more associated with the north-facing plots, and *H. lanatus*, *Lathyrus pratense* and *C. cristatus* preferred the north-facing compacted treatments. *C. arvense*, *S. minor*, *L. corniculatus* and *V. sativa* were more associated with the south-facing slopes.

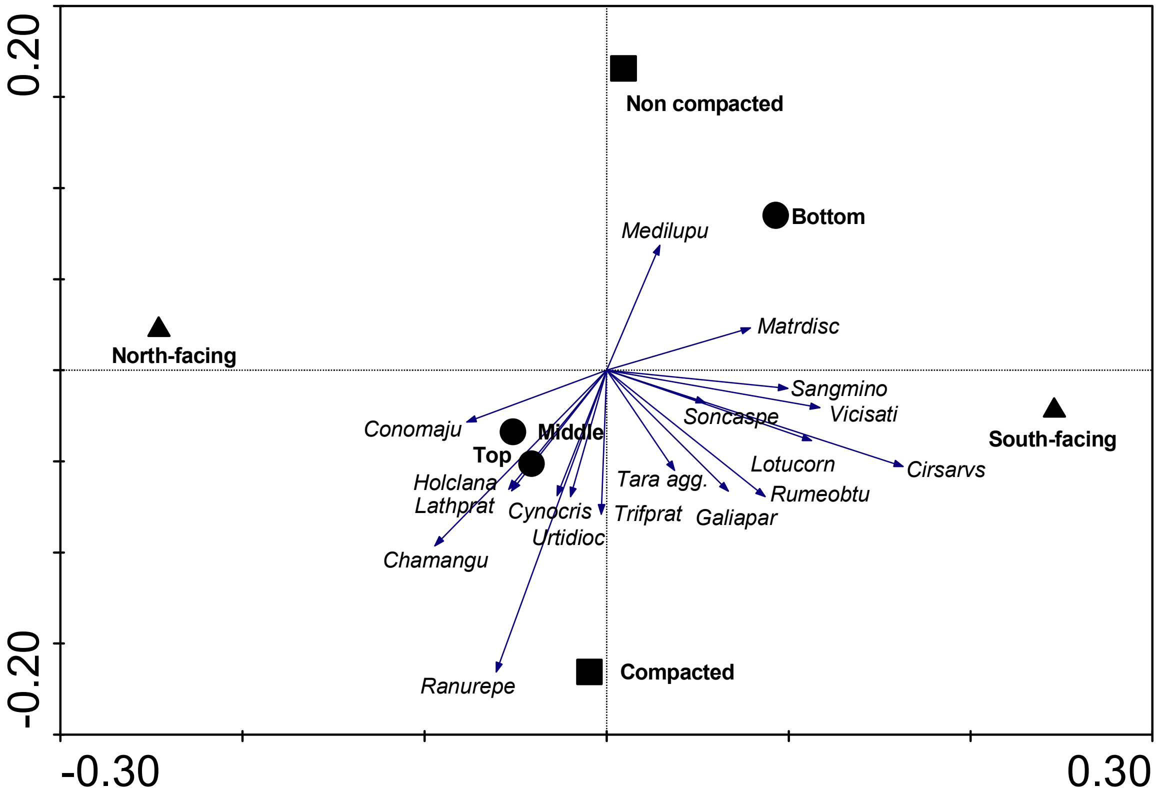

Figure 1.14. RDA showing 18 species in 2007. *Chamangu = Chamerion angustifolium, Cirsarve = Cirsium arvense, Conomaju =Conopodium majus, Cynocris = Cynosurus cristatus, Galiapar = Galium aparine, Holclana = Holcus lanatus, Lathprat = Lathyrus pratense, Lotucorn = Lotus corniculatus, Matrdisc = Matricaria discoidea, Medilupu = Medicago lupulina, Ranurepe = Ranunculus repens, Rumeobtu = Rumex obtusifolius, Sangmino = Sanguisorba minor* ssp. *minor, Soncaspe = Sonchus asper, Tara agg. = Tarax* sp.*, Trifprat = Trifolium pratense, Urtidioi = Urtica dioica, Vicisati = Vicia sativa.*

Table 1.14. Partitioning the variance of the 2007 BIONICS Embankment treatments.

Treatments	%	F-ratio	p-value
Aspect	6.2	4.659	0.002
Soil compaction	2.8	2.137	0.018
Position	2.2	0.846	0.668
Interactions	11.5	1.85	0.002
Total inertia	22.8	2.031	0.002

2.3.7.2 Species composition in 2008

The first axis of the PCA looking at the 2008 BIONICS data accounted for 26.5 % of the explained variation and the second axis explained 14.4 % of the variation. When a RDA was performed, it was clear that aspect formed the first axis and soil compaction formed the second axis (Figure 2.15). Position was in the middle of the bi-plot but this was not significant when the treatments were looked at seperately (Table 2.15). *L. perenne*, *A. millefolium* and *M. lupulina* were associated with the not compacted treatment. *V. sativa*, *L. corniculatus* and *T. repens* were associated with the south-facing aspect. *Ranunculus acris* and *D. carota* were associated with the compacted slopes. *P. bertolonii*, *P. trivialis*, *R. repens* and *Taraxacum* agg. preferred the north-facing, compacted treatments. In addition, the Ellenberg Indicator Values for fertility and moisture were associated with the north-facing slopes and light and reaction were associated with the south-facing slopes. Diversity was associated with the compacted treatments.

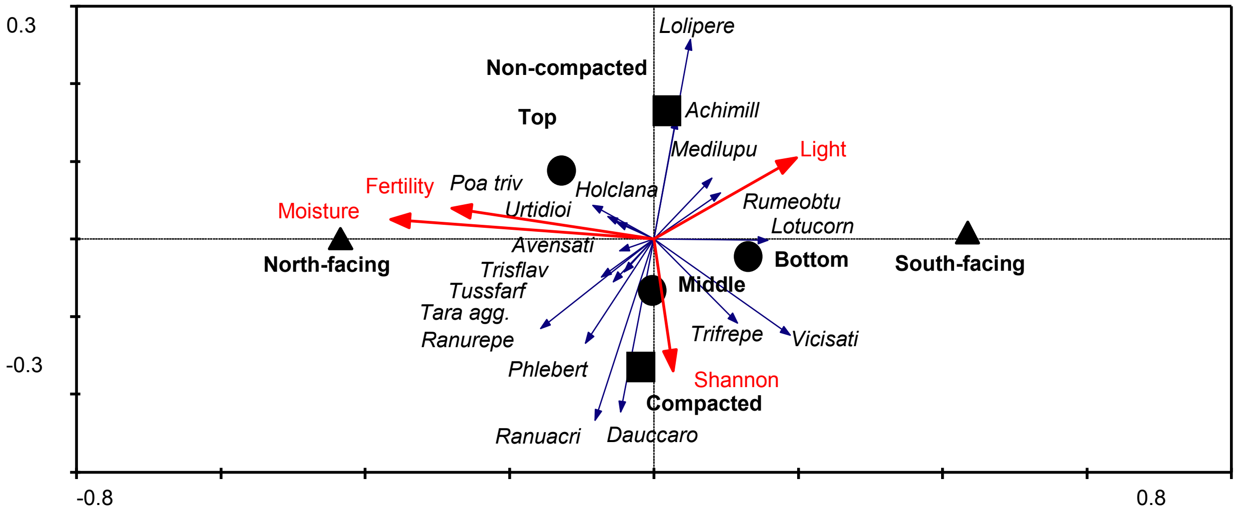

Figure 2.15. A RDA species-treatment bi-plot, showing the 18 main species found on the BIONICS embankment in June 2008. *Achimill = Achillea millefolium, Avensati = Avena sativa, Dauccaro = Daucus carota, Holclana = Holcus lanatus, Lolipere = Lolium perenne, Lotucorn = Lotus corniculatus, Medilupu = Medicago lupulina, Phlebert = Phleum bertolonii, Poa triv = Poa trivialis, Ranuacri = Ranunculus acris, Ranurepe = Ranunculus repens, Rumeobtu = Rumex obtusifolius, Tara agg. = Tarax* sp., *Trifrepe = Trifolium repens, Trisflav = Trisetum flavescens, Tussfara = Tussilargo farfara, Urtidioi = Urtica dioica, Vicisati = Vicia sativa,*

Table 2.15. Partitioning of the variance of the 2008 BIONICS treatments..

Treatments	%	F-ratio	p-value
Aspect	18.9	16.778	0.002
Soil compaction	2.8	2.524	0.008
Position	2.8	1.249	0.186
Interactions	10.3	1.962	0.002
Total inertia	34.9	3.686	0.002

2.3.7.3 Species composition between 2007 – 2008

The influence of sampling date on the species-treatment bi-plot (Figure 2.16) was very strong. 22.6 % out of 32.6 % of the variation explained by the treatments was accounted for by the date. 7.2 % of the variation is accounted for the aspect and 1.7 % by compaction (Table 2.16). As there were a number of species which were found in 2007 and not found in 2008 and vice-visa, this highly influenced the species-treatment bi-plot. *C. arvense*, *T. vulgare* and *S. asper* established from the arable seed bank, and were more associated with 2007. The frequency of these species was much less in 2008. *C. cristatus*, *T. flavescens*, *D. carota*, *L. vulgare* and *P. bertolonii* all gained in frequency from 2007 to 2008. Several species followed the same trend from 2007 to 2008. *R. repens* was associated with the north-facing compacted plots in 2007 and 2008. *V. sativa*, *L. corniculatus,* and *T. repens* were associated with the south-facing plots in 2007 and 2008 and also gained in frequency from 2007 to 2008. In general, the weeds decreased from 2007 to 2008 and the wildflowers increased from 2007 to 2008.

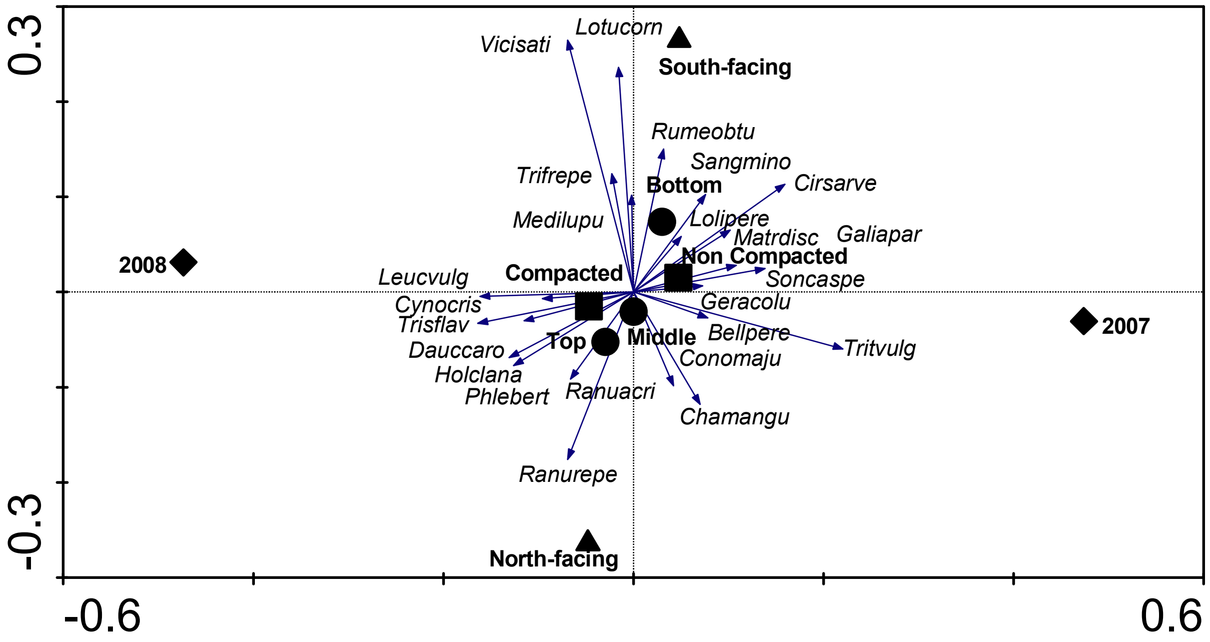

Figure 2.16. RDA of the BIONICS Embankment between 2007 and 2008 showing 24 species. *Bellpere = Bellis perennis, Chamangu = Chamerion angustifolium, Cirsarve = Cirsium arvense, Conomaju = Conopodium majus, Cynocris = Cynosurus cristatus, Dauccaro = Daucus carota, Galiapar = Galium aparine, Geradiss = Geranium dissectum, Holclana = Holcus lanatus, Leucvulg = Leucanthemum vulgare, Lolipere = Lolium perenne, Matrdisc = Matricaria discoidea, Medilupu = Medicago lupulina, Phlebert = Phleum bertolonii, Ranuacri = Ranunculus acris, Ranurepe = Ranunculus repens, Rumeobtu = Rumex obtusifolius, Sangmino = Sanguisorba minor* ssp. *minor, Soncaspe = Sonchus asper, Trifrepe = Trifolium repens, Trisflav = Trisetum flavescens, Vicisati = Vicia sativa.*

Table 2.16. Partitioning of the variance of the 2007 and 2008 BIONICS treatments.

Treatments	%	F-ratio	p-value
Aspect	7.2	14.831	0.002
Soil compaction	1.7	3.423	0.002
Position	1.1	1.175	0.22
Sampling date	22.6	46.188	0.002
Interactions	4.8	2.047	0.002
Total inertia	37.4	7.956	0.002

2.4 Discussion

2.4.1 Species Establishment

1) What was the origin of the species that established on the BIONICS embankment?: From the grass and wildflower seed mixture, the seedbank or from natural regeneration / colonisation?

35 species established in 2007 and 30 species established in 2008. Although the drop may seem negative, actually the injurious weeds and arable weeds declined and the desirable species established. Even with no additional seed addition, five of the species sown in the seed mixture of autumn 2006, established in 2008. However, only a total of 14 species germinated from a seed mixture of 42 species. A large number of species that did colonise were clearly from the seed bank. The topsoil used was taken from Nafferton Farm. Species such as *R. repens, T. repens, V. sativa, H. lanatus, P. trivialis*, *Cerastium fontanum* and *M. lupulina* were evidently from the seed bank. Arable weeds such as *A. sativa*, *R. obtusifolius* and *S. asper* would have also been in the seed bank. In addition, *C. arvense* and *E. montanum* are often wind dispersed and were growing in the vicinity of the BIONICS embankment (Hillier 1990). *C. arvense* and *R. obtusifolius* are injurious weeds. Under the Weeds Act of 1959, if these species are growing and spreading, the landowner must prevent the spread (HA 2007b).

Clearly, the BIONICS embankment was quickly colonised with a mixture of species. Since just under 50 % of the ground cover was taken up with species from the seed mixture, it could be argued that a seed mixture need not be sown at all. However, the species which established from the seed bank and natural colonisation were generally arable and injurious weeds. Not all species have a persistent seed bank, whereas a number of competitive species do, i.e. *Urtica dioica* (Hillier 1990). Without the addition of seed, the ground would have consisted of a habitat resembling a disturbed field margin, with tall, competitive, ruderal species, without a particularly dense ground cover. Matesanz *et al.* (2006) concluded that hydroseeding (a machine sends out a spray of seeds with an adhesive substance for quick sowing) was not needed on roadside verges as natural establishment was just as good at producing good ground cover. However, this was from a grass seed mixture and a desirable grassland habitat was not the objective. Natural colonisation of suitable species will only occur if these species are in close proximity to the roadside verge (Wells *et al.* 1990). The species which did establish from the seed mixture have often established in similar experiments (i.e. van Hecke *et al.* 1981; Wells *et al.* 1990; Mountford *et al.* 1993; Smith *et al.* 2000; 2008; Oglethorpe & Sanderson 1998; Hopkins *et al.* 1998; Leps *et al.* 2007). They have high germination rates and are generalist species (Lindborg 2006; Pywell *et al.* 2003). Three of the six widespread species were from the seed mixture: *C. cristatus, L. perenne,* and *L. corniculatus*. Plus three of the five common species were from the seed mixture: *P. bertolonii, T. pratense* and *T. flavescens* (Table 2.2). So, although there was a large number of species establishing from natural colonisation, these were undesirable species and the main ground cover consisted of sown species. Therefore, it is worthwhile sowing a grassland seed mixture to aid grassland regeneration with the desired outcome of producing a quick, dense ground cover.

2.4.2 Species richness and diversity

2) Did the south-facing slopes have greater species richness and diversity than the north-facing slopes?

In 2007, species richness and diversity was greater on the south-facing slopes. However, this trend did not continue into 2008. But, there were more wildflower species on the south-facing slopes in both 2007 and 2008, and in 2008, there were more grass species on the north-facing slopes than the south-facing slopes. So, although the total species richness was not higher on the south-facing slopes in 2008, there was a change in composition between the slopes. A number of studies have shown that species richness and diversity is higher on south-facing aspects (Kutiel 1992; Bruun 2000; Pykala *et al.* 2005) and a number have also explained that this is due to more wildflower species preferring south-facing aspects (Albertson 1937; Pahlsson 1974; Hutchings 1983; Amezaga *et al.* 2004). This has also been shown in this experiment.

3) Did the compacted slopes have lower species richness and diversity compared to the non-compacted slopes?

In general, when just the compaction treatment was looked at, compaction did not appear to prevent species establishing and appeared to favour the plant species. In 2007 species richness and diversity was higher in the compacted slopes and there was a greater number of wildflower species – but this pattern did not remain when the interactions were looked at. In 2007 and 2008, when aspect and compaction were looked at together, the north-facing non-compacted slopes had less species and lower diversity than the north-facing compacted slopes and the south-facing non-compacted slopes. So, here it suggests that more species are growing on the north-facing compacted slopes. However, when the grass and wildflower species were looked at separately, it was just the grasses that preferred the north-facing compacted slopes compared to all the other slopes. On the other hand, in 2007, there were less wildflower species growing on the south-facing compacted slopes in comparison to the other slopes. In general, in both 2007 and 2008, more wildflower species were found on south-facing slopes, so clearly the compaction treatment was hindering establishment more noticeably on the south-facing slopes in 2007. By 2008, this trend had not continued and in fact aspect, position and compaction were interacting – the top, south-facing compacted slopes had more species than the bottom, north-facing non-compacted slopes. So, by 2008 more wildflower species had established on the south-facing slopes and the compaction effect wasn't so noticeable.

It would seem that grasses could cope with the compaction treatment and wildflowers were affected initially on the south-facing slopes, but this influence did not remain. There was a 20 – 30 cm non-compacted topsoil in which the plant species could grow through before hitting the compacted layer. So, the compaction treatment would not influence initial seedling germination, it would only influence the growth of the plants once they have become large enough (Young *et al*. 1997; Montagu *et al*. 2001). In order for the compaction treatment to have influenced wildflower species establishment in 2007, the wildflowers must have grown big enough from the initial sowing in September 2006. It is possible that the roots hit the compacted layer by June 2007, but by the second year of establishment, the plants compensated for the compaction. Soil is heterogeneous and there are a number of cracks and pore spaces into which the plants can grow (Dexter 1986a; 1986b; 1986c; Bengough *et al*. 1997; Montagu *et al*. 2001; Bingham 2001; Bingham & Bengough 2003). The timing of the effects of compaction in relation to the stage of development of the plant will influence how much the plants growth will be restricted (Bengough *et al*. 1997; Bingham 2001; Montagu *et al*. 2001). The compaction of the soil was caused by a large JCB crossing and re-crossing over the soil. Quite possibly the compaction effects were not localised enough to prevent small roots from finding a way through. To conclude, the process of road construction and the compaction methods required for slope stability, did not influence species richness and diversity detrimentally.

2.4.3 Species composition and establishment

4) Did soil compaction and position up the slope influence species composition and species establishment?

Soil compaction did influence species composition. *L. perenne* was significantly reduced in the compaction treatment in 2008, by almost half the frequency found in the non-compacted slopes and *L. perenne* was always associated with the non-compacted slopes in the ordinations. *M. lupulina* and *A. millefolium* were associated with the non-compacted slopes. However, a number of species were found in association with the compacted slopes. *C. arvense* and *V. sativa* were found in greater frequency on the compacted slopes, plus *R. repens* and *C. cristatus* were found more often on the north-facing compacted slopes. Clearly, individual species respond in different ways to soil compaction (Bingham 2001; Clark *et al*. 2003). *L. perenne* is the key species grown in seed mixtures (Gray 1995; Bayfield 1995; Highways Agency 1991; 1992), but if this species doesn't respond well to compaction, it may be a good idea to reduce the proportion of this species in the seed mixture. *L. perenne* is often sown as it is quick to establish and forms a quick, dense ground cover (Gray 1995; Bayfield 1995; Highways Agency 1991; 1992). If the standard road construction methods do not promote the germination of this species, why spend the money on this species when other more desirable species could be sown? *L. perenne* often prevents the establishment of other species and forms a thick, dense sward which is difficult to cut (Underwood 1969: Ross 1986). The frequency of *L. perenne* reduced from 2007 – 2008, whereas other grass species spread from 2007 – 2008. *C. cristatus* is not sown in the standard HA seed mixture (HA 1991) (Table 1.1), but in the BIONICS experiment this species coped well with compaction and increased in frequency from 2007 – 2008: This species would be a good replacement.

Position along the embankment slope did influence species composition, but only very slightly. In 2007, *C. arvense* was found in greater abundance in the top position. This could be because it is wind dispersed and the top of the Embankment was very windy; the seeds could have been blown upwards (Hillier 1990). In 2008, there were more grasses found on the top position across the BIONICS embankment, *R. repens* preferred the middle of the slopes to the bottom of the slopes and *V. sativa* preferred the top of the slopes to the bottom of the slopes. However, in the ordinations, position was not significantly influencing the species composition to any great extent.

5) Did species preferring warm, dry conditions establish on south-facing slopes and species preferring cold, wet conditions establish on north-facing slopes?

The aspect effects were very apparent and were clearly influencing the species composition and establishment. A number of grass species preferred north-facing slopes: *P. trivialis, H. lanatus* and *T. flavescens*, plus the wildflower, *R. repens*; and a number of wildflower species preferred the south-facing slopes: *C. arvense, V. sativa*, *L. corniculatus* and *T. repens*. In a number of papers, grasses are more common on north-facing slopes and wildflowers are more frequent on south-facing slopes (Albertson 1937; Pahlsson 1974; Hutchings *et al*. 1983; Kutiel 1992). The exception here is *R. repens* which is a species that likes moist conditions. As north-facing slopes are generally wetter than south-facing slopes, it would seem that *R. repens* preferred the conditions on the north-facing BIONICS embankment slope. According to Grime *et al*. (1988) *P. trivialis* is found more often on north-facing slopes and prefers shaded conditions; this is confirmed by this experiment. According to Grime *et al*. (1988) *T. repens* is found more often on north-facing slopes, yet *T. repens* prefers sunny positions. In this case, *T. repens* preferred the sunny position of the south-facing slope. Amezaga *et al*. (2004) also found that *T. repens* preferred south-facing slopes. *L. corniculatus* was more commonly found on the south-facing slope, which has been noted by others, and the species doesn’t have any moisture tolerance (Grime *et al.* 1988). So, generally, over time, there are drought tolerant, sun-loving species establishing on the south-facing slopes, and species preferring wetter conditions establishing on the north-facing slopes.

6) Did the cutting regime of one cut in September of each year influence the species composition and species establishment from 2007 – 2008?

In summer 2007 there was a large amount of arable weeds and injurious weeds establishing on the BIONICS embankment. In September 2007, the BIONICS embankment was strimmed and the cuttings were raked off and removed. When the species composition was recorded in summer 2008, *C. arvense* frequency was reduced from being common to being rare. There were less species found in 2008 because some of the arable weeds were lost – like *T. vulgare*, *Matricaria discoidea* and *Anthriscus sylvestris* and a number of weeds were massively reduced – such as *C. arvense, A. sativa*, and *R. obtusifolius*. However, five more species established from the seed mixture sown and a number of species increased in frequency such as *C. cristatus, R. repens, V. sativa, L. corniculatus*. So, there was a change from arable weeds to grassland wildflower species from 2007 – 2008. If there had not been a cut in September 2007, with the cuttings raked off, the arable and injurious weeds would have continued to spread and the other species would not have established.

Clearly, a cut of at least once a year is needed to assist the establishment of the sown species and to reduce the spread of arable and injurious weeds. It is commonly recognised that cutting reduces the frequency of thistles and docks and other competitive weedy species (Warren *et al.* 1989; Wells *et al*. 1989; Bobbink & Willems 1993; Hansson & Fogelfors 1998). Cutting is also required to keep the sward dense, tight and compacted. Cutting allows for structural diversity of the canopy and smaller-statured wildflower species can establish (Wells *et al.* 1989; Grime 1990; Pywell *et al.* 2003). Without cutting, tall, vigorous, competitive species spread, with low species diversity and monopolistic dominant tendencies, i.e. *U. dioica* and *C. arvense* (Grime 1990; Bakker *et al.* 2002; Pykala 2005).

Quick germination with a good ground cover is required to prevent surface runoff and erosion. However, although an increase in cover and canopy use will improve surface erosion, an increase in canopy height can be detrimental (Spehn *et al.* 2000; Blight 2003; Morgan 2007). Morgan (2007) showed that it is only dense cover, close to the ground, that prevents erosion. Taller vegetation can make it worse. Rainfall hitting the taller leaves will fall as leaf drop onto the soil. Often there are larger gaps between taller vegetation and this leaf drop will fall into the gaps between the taller plants. In order for species richness and diversity to be maintained on roadside verges, a minimum of the annual cutting regime needs to be implemented. This will increase species richness and diversity, form dense above-ground cover and utilise full use of the canopy, plus it will prevent the plant species from growing too tall and prevent the weedy species establishing which are much taller than the other grassland species.

2.4.4 Ellenberg Indicator Values

7) Did the north-facing slopes have greater Ellenberg Fertility and Moisture Values, and did the south-facing slopes have greater Ellenberg Light Values?

The Ellenberg Fertility Values were significantly higher (more fertile) on the north-facing slopes. This is in agreement with a number of studies that have also shown that fertility is greater on north-facing slopes. Some have shown an increase in organic matter, litter accumulation and thickness of soil which can all lead to an increase in fertility (Pahlsson 1974; Churchill 1982; Kutiel 1992; Kutiel & Lavee 1999). Species such as *L. corniculatus*, which was common on the south-facing slopes, has a low fertility index (2) whereas species such as *R. repens* which was common on the north-facing slopes, has a higher fertility index (7) (Hill *et al*. 1999). The plant species changes have occurred over a relatively short period of time and are likely to continue responding to the environmental conditions if the experiment continues for longer.

The north-facing slopes did have greater Ellenberg Moisture Values than the south-facing slopes. As the north receives less sunlight, the ground takes longer to dry out and tends to be wetter. This, in turn, has influenced the species composition over time so more moisture loving species have established (Perring 1959; 1960; Pahlsson 1974; Churchhill 1982; Kutiel 1992; Kutiel & Lavee 1999; Bennie *et al*. 2006). The majority of studies looking at aspect have shown that a more mesic community establishes over time on the north-facing slopes (Perring 1959; 1960; Kutiel 1992; Sebastia 2004; Bennie *et al.* 2006). *R. repens*, for example, prefers moister sites and this was found in greater frequencies on the north-facing slopes. On the other hand, *V. sativa* and *L. corniculatus* prefer drier conditions and were found in greater frequencies on the south-facing slopes (Grime *et al.* 1988; Hill *et al.* 1999).

The south-facing slopes did have greater Ellenberg Light Values than the north-facing slopes. As the south-facing slopes received a greater amount of sunlight during the day, this in turn has lead to more sunlight-loving, drought-tolerant species establishing (Pahlsson 1974; Hutchings 1983; Pykala *et al.* 2005). The range of light values for the species found on the BIONICS Embankment was limited – however, the species with lower light ranges, such as *R. repens* (6) was common on the north-facing slopes, and *T. repens* and *V. sativa* were the commonest species on the south-facing slopes and had a indicator value of 7 (Hill *et al*. 1999).

2.4.5 NVC Classification

8) What NVC community developed over time? Are the differences in species composition under treatment combinations great enough to produce different NVC communities over three years?

The south-facing slopes all had an NVC classification of MG6a, bar one position with MG6c. The majority of the north-facing slopes had an NVC classification of MG6a, with four having the NVC classification of MG6c. So, there is an ever-so slight difference developing in the NVC classification between the slopes. MG6a is the typical *Lolium perenne – Cynosurus cristatus* community and MG6c includes *T. flavescens* (Rodwell 1992). *T. flavescens* was found in greater abundance on the north-facing slope. Other studies have shown that it is difficult to establish an exact NVC community (Hopkins *et al.* 1998; Pywell *et al.* 2003). Smith *et al.* (2008) have been trying to develop an MG3b community, but have managed to establish an MG6 community. A number of studies have sown an MG3 seed mixture and have ended up with an MG6 community (Hopkins *et al.* 1998; Pywell *et al*. 2003; Smith *et al.* 2008). Many seed mixtures include *L. perenne* and *C. cristatus* and a number of generalist, easily germinating species such as *A. millefolium*, *T. pratense*, *T. repens* and *R. repens* are common components of the MG6 community (Rodwell 1992).

Although the NVC classification came out as MG6, there was a high proportion of species which were not usual for this habitat. The BIONICS embankment had a unique mix of the sown species added by hand, the arable species found in the seed bank, and the wind dispersed species from around Nafferton Farm. Often the soil used on roadside verges is moved from one location to another location, transporting seeds from one area to another area. Although the NVC classification came out as MG6, only a few of the BIONICS slopes had a good fit to the classification (the range being from 45 % – 72 %). The established sown species had a

NVC classification of MG5a and the species that established through natural colonisation had a NVC classification of OV25a. OV25a is an open community, with *Urtica dioica - Cirsium arvense* as the main community and with a *Holcus lanatus - Poa annua* sub-community. Roadside verges can be classed as "Novel ecosystems" where an unusual mix of new species assemblages develops (Hobbs *et al*. 2006; 2009). The MG6 classification is based on the key species *L. perenne* and *C. cristatus*. *L. corniculatus*, *L. vulgare*, *V. sativa* and *A. sativa* are not usual components of MG6 habitat. The classification is based on static communities which are not new or establishing (Rodwell 1992). With such a large number of roadside verge habitats found across Britain, should a new classification be classified for the new and developing man-made habitats?

2.4.6 Future work

It wasn't possible to take a large number of root cores from the BIONICS embankment so it was not possible to measure rooting depths. Taking deep root cores would have influenced the belowground slope stability measurements being taken by the Civil Engineers. For the same reasons, aboveground biomass couldn't be measured as taking a cut in some areas and not in other areas may have influenced the belowground measurements. In the future it would be beneficial to design an experiment of a similar size, with adequate replication, where a mixture of different seed mixtures could be sown – one using the standard HA grass seed mixture – another using this mixture plus *L. corniculatus, L. vulgare*, *P. lanceolata* and *T. pratense* – and another using a large wildflower seed mixture, and where root depths and biomass could be recorded and the cutting regimes could be altered.

2.5 Conclusion

In order to allow the sown species to establish and to prevent the vegetation from becoming too tall and clumpy, with gaps throughout where water can enter, a cutting regime needs to be implemented from the first year onwards to produce a dense, thick sward, which will protect the surface of the soil from rainfall splash and run-off. *C. arvense* and *R. obtusifolius* were still present in 2008. If the cutting regime did not continue, these species would just re-colonise again. Typical grassland wildflower species like *R. minor*, *S. officinalis* and *Knautia arvensis* never established from the seed mixture and in the first year of establishment a large amount of unwanted weeds were present. *R. minor* requires low biomass and lots of sunlight in order to germinate (Westbury & Dunnett 2007). In the first year of establishment, there clearly needed to be a greater amount of cutting in order to prevent the competitive weedy species from growing, and allow the less competitive species to thrive. One cut a year may be appropriate management after a few years of establishment, but at the beginning 2 – 4 cuts should be done in the first year. A number of studies highlight the need for intensive management in the first year of establishment to allow seedling establishment (Wells *et al.* 1989; Greenwood 1996; Jones & Hayes 1999) and all studies looking at maintaining restored or created grassland habitats advocate a regular cutting regime of at least once a year, preferably twice a year, in order to promote species diversity (i.e. Wells *et al.* 1989; Bayfield *et al.* 1992; Huston 1994; Grime 2001; Bakker *et al.* 2002; Pywell *et al*. 2003; Harmens *et al*. 2004; Antonsen & Olsson 2005; Hovd & Skogen 2005).

Sowing a seed mixture onto the bareground created in the beginning of road embankment construction is needed in order to develop a good ground cover. Usually, just the standard grass seed mixture is sown on roadside verges; however, the results from the BIONICS embankment have shown that many grassland species can establish quickly forming a diverse community with dense ground cover. Should the standard seed mixture sown on newly constructed road systems be re-thought? In order for a desirable grassland community to establish, natural dispersal will take place, but with a regular management regime the grassland species will establish. On the BIONICS Embankment, a number of grasses were the main colonisers, but *L. corniculatus, R. repens* and *T. pratense* were also quick to establish. These species could be added into the standard grass seed mixture (Table 1.1) and would form a total of three functional types: grasses, legumes and wildflowers (i.e. Thompson *et al*. 1996; Diaz & Cabido 1996), allowing for structural compositional diversity (Spehn *et al.* 2000; 2005). Establishment from a species-rich seed mixture with many functional types is likely to increase ground cover, and so, improve surface erosion. *L. perenne* is the main species sown but this did not establish well in the compacted treatments. Grasses grow well on north-facing slopes, but wildflowers grow better on south-facing slopes (Albertson 1937; Pahlsson 1974; Hutchings *et al*. 1983; Kutiel 1992). For good ground cover on all aspects, the seed mixture needs to include species that can cope well with compaction and include species that can grow well on south and north-facing slopes. *L. perenne* should be replaced with *C. cristatus*, and a south-facing wildflower species such as *L. corniculatus* could be included. *L. corniculatus* is also a good choice, being a deep-rooted legume, providing soil binding potential (Grime *et al.* 1988).

3 Experimental work, Part B

The Mesocosm experiment, Aboveground section

3.1 Introduction

When a new road system is built, it creates a large amount of bareground, perfect for establishing a new habitat. Without thought, a general grass seed mixture containing six species has always been sown onto newly constructed road systems since the 1950s (Way 1976; HA 1991; 1992) (Table 1.1). However, with a little care and attention, a more thoughtful mix of species could be included. On roadside verges, vegetation cover needs to be established quickly, both to prevent soil erosion and for aesthetic reasons. However, in order for species to germinate it is crucial to understand the prerequisites for seedling emergence (Lindborg 2006). It is clear from numerous studies attempting to recreate grassland habitats, that the most important factor is whether the species are good colonisers, with high rates of germination (Wells *et al.* 1989; Hopkins *et al* 1998; Pywell *et al* 2003). The composition of the colonising seedling flora is determined by whether the conditions are suitable for their germination. Variations in requirements between species for moisture, light, temperature, competition, aspect, slope or exposure, for example, will influence which seedlings can germinate (Wells *et al.* 1989; Hillier *et al.* 1990; Gilbert & Anderson 1998). A number of studies have tried to recreate species-rich grassland using seed mixtures onto bareground, or adding seed in species-poor grassland (i.e. Wells 1990; Hopkins *et al.* 1998; Jones & Hayes 1999; Pywell *et al.* 2002; Pywell *et al.* 2003; Lindborg 2006). Hopkins *et al.* (1998) used the seed mixtures from different NVC communities. From these seed mixtures, similar species established: *A. millefolium, L. vulgare* and *P. lanceolata*. These species colonised well and had high levels of germination. Hopkins *et al.* (1998) classed these species as "generalist" species. They concluded that it was possible to create a grassland community, but not one based on a particular NVC community. The specialist species with low levels of germination and low levels of competition could not colonise.

Natural colonisation will occur over time so could be argued that seed mixtures do not need to be sown at all (Gilbert & Anderson 1998; Leps *et al.* 2007). Matesanz *et al.* (2006) concluded that hydroseeding of roadside verges was not needed, natural colonisation was just as effective and the sown species disappeared after a few years. On fertile soils, growth will happen quickly and there will be seeds in the seedbank and wind dispersed seeds to colonise (Hillier *et al*. 1990; Gilbert & Anderson 1998; Matesanz *et al*. 2006). However, the seeds in the soil are from species with a persistent seedbank only, and those species with a short-term seedbank will not be present (Dutoit & Alard 1995; Kirkham & Kent 1997). Wind dispersed species are often quick growing, tall, aggressive competitors like *C. arvense* and *C. angustifolium* which are unsuitable for grassland habitats (Hillier *et al*. 1990). It is likely that natural regeneration would be too slow and too unpredictable to suit roadside verge site conditions (Gilbert & Anderson 1998).

R. minor has become more important at the present time as research has shown that *R. minor* can lessen grassland productivity and improve biodiversity by encouraging wildflower colonisation by infecting the faster-growing grasses which reduces their competitive dominance and allows the wildflowers to establish (Davies *et al.* 1997; Joshi *et al.* 2000; Pywell *et al.* 2004; Bardgett *et al.* 2006; Smith *et al.* 2008). A number of studies have shown that aboveground biomass of the grasses is reduced, rather than other wildflowers present (Seel *et al*. 1993; Westbury & Dunnett 2007; Ameloot *et al*. 2008). Press & Phoenix (2005) suggested that this may be because the grasses and *R. minor* are shallow rooted, whereas the wildflowers are deeper rooted. *R. minor* could be used as a management tool on roadside verges for encouraging the establishment of wildflowers, increasing floristic diversity and lessening competitive grasses (Austen & Treweek 1995; Davies *et al.* 1997; Pywell *et al.* 2004; Ameloot *et al*. 2006; Ameloot *et al*. 2008; Smith *et al.* 2008). Smith *et al*. (2003) have suggested that *R. minor* should be used as a pioneer species in seed mixtures and Pywell *et al*. (2007) showed that *R. minor* establishment assisted with the germination of sown species.

A huge influence on seedling establishment in re-created grasslands, and in particular on roadside verges, is the type of soil that is used. Often the topsoil is taken from agricultural land where a huge amount of artificial fertilisers are often added. Fertiliser use has increased greatly during the last few decades and has reduced species richness and diversity in all experiments / grasslands where it has been measured (i.e. Thurston 1969; Marrs 1993; Jones & Hayes 1999; Smith *et al*. 2000; Stevens *et al*. 2004; White *et al.* 2004). An increase in fertility leads to competitive, fast growing, tall species which dominate the canopy and prevent smaller species from establishing (Wells *et al.* 1989; White *et al.* 2004). Species like *U. dioica*, *C. arvense* and *R. obtusifolius*, plus grasses such as *A. elatius* and *D. glomerata*. High fertility is often quoted as the reason why species-rich seed mixtures have failed. It is the main reason why the generalist species establish from seed mixtures and not the specialist species. Often, the generalist species are the more competitive species, which are indicative of fertile conditions (i.e. Hopkins *et al.* 1998; Jones & Hayes 1999; Pywell *et al.* 2003; White *et al.* 2004). For the successful restoration of grassland, or for the introduction of species-rich seed mixtures onto arable land / bareground, the fertility of the soil must be taken into consideration. A large number of wildflower species will not germinate on high fertility soils, including *R. minor* (i.e. Marrs 1993; Mountford *et al.* 1993; van Hecke *et al.* 1981; Hopkins *et al.* 1998; Jones & Hayes 1999; Stevens *et al.* 2004). Where the restoration of species-rich grassland habitats is needed on particularly fertile soils, the topsoil / turf is removed. In these cases, the establishment of the desirable wildflower species has been successful (Marrs 1993; Hopkins *et al.* 1998).

Once a seed mixture has established, in order to establish and maintain a species-rich grassland community, the long-term management has to be taken into consideration and applied (Wells *et al.* 1989). On roadside verges, especially embankments and cuttings, it is very difficult to graze as it is too steep and the animals are too close to the road. The long-term management of grasslands where grazing isn't possible, must include a cutting regime and this must be implemented immediately (Wells *et al.* 1989). However, the management of roadside grassland verges is lacking. Sites may only be cut once every three, six or nine years, and only in exceptional circumstances are the incredibly species-rich grasslands cut once a year (HA 1994; 2005a). In the previous examples concerning seed mixture establishment, all these studies included a grazing or cutting regime. Wells *et al.* (1989) explained that the subsequent management of re-created sites is essential. Cutting is required to prevent the competitive weeds like *C. arvense* and *R. obtusifolius* from dominating, allowing the smaller, less competitive understorey to develop. Wells *et al.* (1989) suggests that the less fertile sites need two cuts in the first year, but the fertile sites need at least five cuts in the first year, plus the cuttings should be raked off and removed to reduce fertility levels. From then onwards, one to two cuts per year are required. Wells *et al.* (1990) cut the plots in August and mid-October, removed the cuttings and successfully created a replica of chalk grassland. Jones & Hayes (1999) explained that successful establishment was needed with a minimum of two cuts a year. The worst establishment occurred where there was only one cut a year. Hopkins *et al.* (1998) implemented a mid-July hay cut and grazing throughout the year and Lindborg (2006) found that both the specialist and generalist species established better in the grazed treatments.

Close clipping forms a dense, extensive sward. For example, Grime (1990) compared species that were cut and not cut. *A. capillaris* became much denser with cutting and *F. ovina* formed a small dense tussock (Grime 1990). In an experiment looking at fertiliser levels, Mountford *et al*. (1993) found that a rigorous cutting regime reduced the taller species, lowering the canopy height. Greenwood (1996) set up an experiment on Longhorn wood cutting on the M20, a south-facing roadside verge, to look at how vegetation can improve slope stability. A number of different types of vegetation were investigated, including the standard grass seed mixture and a grass and wildflower seed mixture. All seed mixtures had good establishment. The grasses mix was cut twice a year, whereas the grass and wildflower mix was cut in September. Both options controlled *C. arvense* cover. Hovd & Skogen (2005) looked at 31 cut and uncut roadside verges in Norway. All the roadside verges which were mown annually had greater species richness than the roadside verges that were not cut. The regular mowing regime kept the habitats in an early-successional stage, with low litter accumulation and drier soil. The species which were found on the mown verges were more similar to semi-natural meadow communities. Bobbink & Willems (1993) designed an experiment with no cut, one cut, two cuts and four cuts per year. Diversity was much less in the uncut plots, whereas diversity and species richness was increased in all the cutting treatments. The biomass of the wildflowers was also increased in all the cut treatments. It was concluded that two cuts a year were enough to reduce faster growing weedy species, reduce litter accumulation and increase the smaller-statured wildflowers.

So, in general, a cutting regime equals greater species richness and diversity. It has been shown in many experiments that species richness and diversity, in particular, diversity of functional types, leads to an increase in aboveground canopy cover (i.e. Naeem *et al.* 1994; Thompson *et al.* 1996, Spehn *et al.* 2000; Scherer-Lorenzen *et al.* 2003; Spehn *et al.* 2005). An increase in dense aboveground cover, close to the ground, leads to a decrease in surface erosion and rainfall splash (i.e. Lutz 1936; Quinn 1980; Boardman 1991, Evans 1990; Fullen 1998; Mitchell *et al.* 2003; Morgan 2007). Therefore, a cutting regime will in turn lead to greater slope stability on steeper roadside embankments and cuttings, by promoting denser canopy growth and greater diversity.

For an introduction to the influence of aspect on grassland communities see Section 1.3

For an introduction to above and belowground growth and soil compaction, see Section 1.7

The monitoring of the vegetation of the BIONICS embankment gave an insight into the general establishment of a diverse seed mixture over time. However, it was not possible to alter the seed mixtures, alter the management / cutting regimes, take biomass cuttings, or take deep root cores. In order to pick out the finer influences on the species composition as regards to aspect, soil compaction, seed mixtures and cutting regimes, and to allow greater replication, a smaller-scale Mesocosm embankment experiment was designed, using the same soil from the BIONICS embankment, so that a variety of treatments could be tried and fully replicated. This was built and set up at Close house Field station, at Newcastle University in May 2006. The Mesocosm experiment aimed to answer these questions:

1) What species established from the seed mixture?
2) Did the plots that were cut more frequently have greater species richness and diversity in comparison to the plots cut once in the summer?
3) Did the south-facing plots have greater species richness than the flat and north-facing plots?
4) Did the compacted plots have lower species richness and diversity compared to the non-compacted plots?
5) Did the plots that were cut more frequently have greater abundance of *Rhinanthus minor* in comparison to the plots that were cut once?
6) Did management, aspect and soil compaction influence species composition and species establishment?
7) Did species preferring warm, dry conditions establish on south-facing slopes and species preferring cold, wet conditions establish on north-facing slopes?
8) Did the north-facing plots have greater Ellenberg Fertility and Moisture Values and did the south-facing plots have greater Ellenberg Light Values?
9) Did the treatments influence the aboveground biomass?
10) Did the plots with greater species richness, greater diversity and more functional types have greater aboveground biomass?
11) Did *Rhinanthus minor* influence the biomass of the plots? Did *Rhinanthus minor* influence the species diversity and composition of the sward?

3.2 Methods

3.2.1 *Site description*

The Mesocosm experiment was built at Newcastle University, Close House Field Station, at Heddon-on-the-Wall near Wylam, North-East England in May 2006 (Grid reference NZ 128 659).

3.2.2 *Designing and building process*

The Mesocosm experiment was designed to keep as many comparable factors as possible between the BIONICS embankment and the smaller embankment version. As the BIONICS embankment had two compaction treatments: half built to new construction methods (well compacted) and half to the older construction methods (not compacted), this formed the basis for the first treatment (Compacted vs. non-compacted plots). The angle of slope was the same as the BIONICS embankment: 2 in 1. In order to see the differences between north and south facing aspects, a flat control was needed, so this formed the second treatment (Flat, south-facing and north-facing plots). Grasses and wildflowers were separated in the third treatment (Grasses-only plots and grass and wildflowers seed mixture plots), using the same general upland hay meadow seed mixture from Emorsgate that was used on the BIONICS embankment (Table 2.1). The fourth treatment had to be modified a few times. A *R. minor* treatment and a watering treatment had to be abandoned, therefore the results from summer 2007 have three treatments (Table 3.1). A management treatment was begun in September 2007, altering the frequency of cutting throughout the year. (Table 3.2).

Due to the size of the experiment and the amount of soil that was required, the plots were as big as they could be. Each plot was 40 cm x 36 cm diameter. The flat plots were 40 cm deep and the lower edge of the sloping plots was 40 cm deep. The sloping plots contained more soil than the flat plots but this was unavoidable. 11 tonnes of soil was moved from Nafferton to Close House. Of this, half was Durham Lower Boulder clay (the base soil) and half was topsoil. A roll of strong black plastic sheeting was put into each plot around the edges and the first 20 cm of each plot was filled with the base soil. In half of the plots, the base soil was compacted using a hand-held soil compaction rammer. Each compacted plot was hit 10 times with the rammer. Half of the plots (the non-compacted treatment) were not stamped on. The topsoil was broken up and put in the top 20 cm layer of each treatment. The top 2 cm layer of topsoil was hand-sieved in order to give the seeds a better chance of germinating. In the plots with a slope, care was taken to insure a 2 in 1 slope. The topsoil was added in the same way for each treatment so it is only the base soil that has the compaction treatment added. The soil was watered afterwards (Photograph 3.1) and a few weeks were given to allow the seeds in the seed-bank to germinate. Once these plants had been weeded out and the soil broken up for one last time, the seeds were then sown (Photograph 3.2). A grass mixture was sown over half of the plots and a grass and wildflower seed mixture over the other half of the plots (Photograph 3.3).

3.2.3 Final design plan and treatments

The final experiment, running from September 2007 to August 2008 involved four main treatment options. These are: 1) Soil compaction treatment in two levels: Compacted base soil; and non-compacted base soil. 2) Seed mixture treatment in two levels: grass seed only; and grass and wildflower seed mixture. 3) Aspect treatment in three levels: north-facing slopes; south-facing slopes; and flat plots. 4) Management treatment in three levels: cut often in Autumn, Spring and once in July (totalling 8 cuts – 3 in Autumn, 4 in Spring and once at the end of July); cut less often in Autumn, Spring and once in July (totalling 4 cuts – 1 in Autumn, 2 in spring and 1 at the end of July); and cut once only in July. The four main treatments with a total of ten levels were pooled together in different combinations to make a total of 36 plots (12 plots on the south-facing side, 12 plots on the north-facing side and 12 plots on the flat). The 36 plots were replicated 3 times in a randomised block design. No treatment level was in the same position in each Block in order to avoid external influences on plot positions (Table 3.2 and Figure 3.1).

Photograph 3.1. Ruth watering the Mesocosm experiment, before the seeds were added.

Photograph 3.2. Ruth adding the seeds to the Mesocosm experiment.

Photograph 3.3. The Mesocosm experiment in full flower, before the final cut in July 2008.

Table 3.1. Summer 2007 treatments. This only included the main treatments: Soil compaction; seed mixture, and aspect, so had more replicates than expected. Each 12 treatment options were randomly repeated on south-facing slopes, north-facing slopes and flat plots. Each Block was made up of 36 plots and replicated three times.

Treatment	Compaction	Seed mixture
1	Compacted	Grasses-only
2	Compacted	Grasses-only
3	Compacted	Grasses-only
4	Compacted	Grasses and wildflowers
5	Compacted	Grasses and wildflowers
6	Compacted	Grasses and wildflowers
7	Non-compacted	Grasses-only
8	Non-compacted	Grasses-only
9	Non-compacted	Grasses-only
10	Non-compacted	Grasses and wildflowers
11	Non-compacted	Grasses and wildflowers
12	Non-compacted	Grasses and wildflowers

Table 3.2. Final treatments for Autumn 2007 until Summer 2008. A management treatment was added and *Rhinanthus minor* was added as seed to all plots. Each 12 treatment options were randomly repeated on south-facing slopes, north-facing slopes and flat plots. Each Block was made up of 36 plots and replicated three times.

Treatment	Compaction	Seed mixture	Management
1	Compacted	Grasses-only, *R. minor*	Cut eight times
2	Compacted	Grasses-only, *R. minor*	Cut four times
3	Compacted	Grasses-only, *R. minor*	Cut once in July
4	Compacted	Grasses, wildflowers, *R.minor*	Cut eight times
5	Compacted	Grasses, wildflowers, *R.minor*	Cut four times
6	Compacted	Grasses, wildflowers, *R.minor*	Cut once in July
7	Non-compacted	Grasses-only, *R. minor*	Cut eight times
8	Non-compacted	Grasses-only, *R. minor*	Cut four times
9	Non-compacted	Grasses-only, *R. minor*	Cut once in July
10	Non-compacted	Grasses, wildflowers, *R.minor*	Cut eight times
11	Non-compacted	Grasses, wildflowers, *R.minor*	Cut four times
12	Non-compacted	Grasses, wildflowers, *R.minor*	Cut once in July

3.2.4 Rhinanthus minor and seed addition

In summer 2006, *R. minor* seeds were collected from a southern ecotype (near Winchester) and a northern ecotype (near Loch Lomond) and sown into the Mesocosms in October 2006. In March – April 2007 it became clear that the ecotypes of *R. minor* had not established. This was most likely due to the aboveground biomass being so great for this year. After the July cut of 2007, additional seed was added to all of the plots, plus standard *R. minor* seed (from Emorsgate) was added to all of the plots in order to see if the establishment made a difference to the species composition.

3.2.5 Plant species recording

In July 2007 and July 2008, the plant species were recorded in each plot. A grid was made using bamboo canes, dividing the plot into nine 10 cm x 10 cm squares. If a species was present in the square it was given a frequency of 1, if it was absent, it received a 0. This gave a frequency of 9 if the species was recorded in all squares. Plant species were identified according to Stace (2010).

3.2.6 Biomass measurements (g m^{-2})

In the first year of plant growth (July 2006 – July 2007) all of the plots were cut 4 times. As each plot was cut (to 5 cm above the soil) the vegetation was bagged separately and laid out to dry. Once dry, each sample was weighed to record biomass (g m^{-2}). In the second year (2008), the plots were cut and dried, just once, at the end of July, and the vegetation was weighed to give aboveground biomass measurements for summer 2008.

3.2.7 Data analysis

3.2.7.1 Species Richness and Shannon Diversity Index (H')

For calculation for species richness and diversity see paragraph 2.2.7.1. Species richness and diversity was calculated for each plot.

3.2.7.2 Ellenberg Indicator Values

For explanation of Ellenberg Indicator Values see section 2.2.7.2. The Ellenberg Indicator Values for Fertility, Light and Moisture were calculated for each plot.

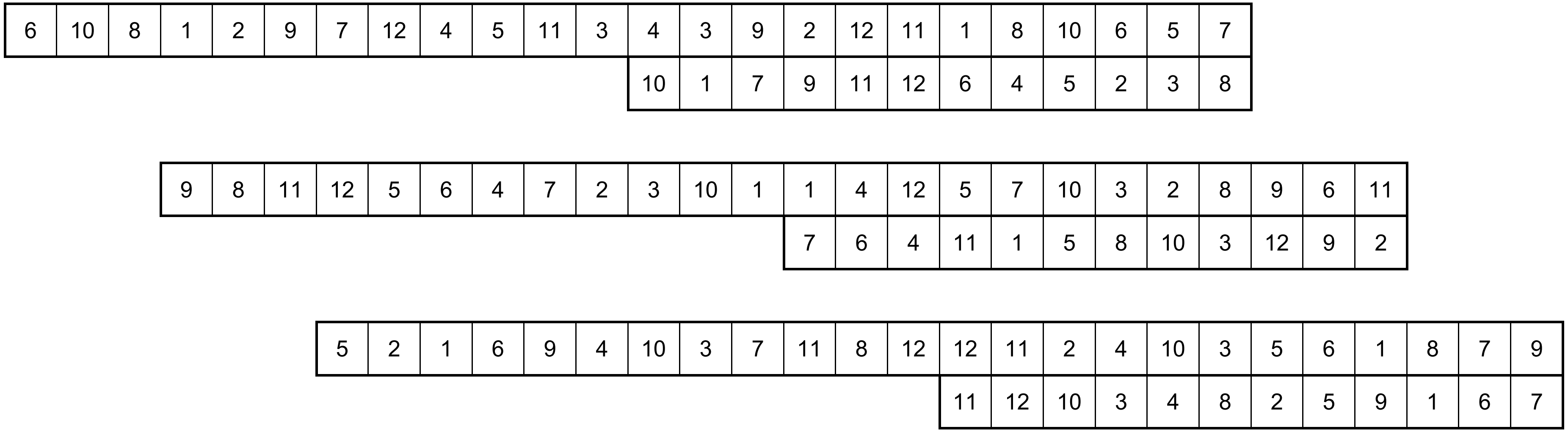

Figure 3.1. Diagram to show the positions of the different treatments. The numbers correspond to the treatment numbers in Table 1, 2, 3, 4. The positions of the treatments in each group of twelve were randomly allocated, ensuring that no treatment had the same position in the three Blocks. The actual experiment ran along 30 m with each Block adjacent to the other in a line. This was to allow for the aspect influence to be as similar as possible to each plot.

3.2.7.3 Analysis of variance: ANOVA, Kruskal Wallis and repeated measures

In Minitab, these treatments - soil compaction (compacted and non-compacted plots); aspect (north-facing, south-facing and flat plots); seed mixture (grasses-only and grass and wildflower seed mixture) and management (plots cut eight times, plots cut four times and plots cut once); were inputted into the "model" box in a GLM (General linear model) ANOVA (Analysis of variance) and the interaction terms were added (!) between each treatment. Block (first, second and third Blocks) was also added to see if this was having an effect, except that an interaction term was not included between Block and the other treatments. In turn, each of these responses listed were put into the "response" box: total number of species found (species richness); total number of grasses; total number of wildflowers; Shannon Diversity Index (H'); Ellenberg Indicator Values (Fertility, Light and Moisture); frequency of widespread individual species and aboveground biomass measurements. An Anderson-Darling normality test was carried out on the residuals of each test and the data was transformed if needed. A variety of transformations were used including: square root; natural log; log + 1 and to the power of 1.5. Once the data fit a linear line ($p > 0.05$) the significant values ($p < 0.05$) were deemed to be valid. A post-hoc Tukeys test was carried out on any statistically significant relationships if there were over 2 treatment levels, i.e. aspect where there were south-facing, north-facing and flat plots, or where there were any significant interactions ($p < 0.05$). Kruskal Wallis, a non parametric test, was used for *R. minor,* where each treatment was analysed separately. Repeated measures ANOVA was performed in SAS on the biomass data from the first year. Four biomass measurements were taken throughout the year, so the differences over the year were compared, step by step, and were significant if "Time" was $p < 0.05$.

3.2.7.4 Ordination – Minitab and CANOCO

For general methods and interpretation see section 2.2.7.5. All lengths of gradient were short so all the models were linear. Therefore PCAs (Principal Components Analysis) and RDAs (Redundancy Analysis) were performed. The main environmental variables (treatments) were: soil compaction (compacted and non-compacted plots); aspect (north-facing, south-facing and flat plots) and seed mixture (grasses-only and grass and wildflower seed mixture). The entire dataset of 2007 and 2008 was analysed to look at sampling date patterns. Management (plots cut eight times, plots cut four times and plots cut once) were included in

2008. Ellenberg Indicator Values and Shannon Diversity Index were included as supplementary variables.

In addition to the methods explained in section 2.2.7.5, this experiment had a “Block” effect. The Blocks needed to be defined by a covariable, not an environmental variable, in CANOCO, so during all tests, the blocks were classed as a covariable. On the “Permutation type” page in CANOCO, the “Blocks defined by covariables” box was ticked and the 1st, 2nd and 3rd block was moved into the covariables box.

3.3 Results

3.3.1 Species composition 2007 – 2008

30 plant species were recorded over the plots in the Mesocosm experiment during the sampling period of July 2008. 4 of these were species established from the soil seed-bank, so a total of 26 plant species established from the seed mixture (Table 3.3). 18 of these were wildflowers and 12 were grasses. 22 plant species were recorded in 2007, with a gain of 11 and a lost of 3 in 2008 (Table 3.4). A total of 42 species were in the original seed mixture; Table 3.5 shows the plant species that did not establish from the seed mixture in 2008. Only *Briza media* from the grasses did not establish from the grass seed mixture, the other species which did not establish were wildflowers. *L. perenne*, *C. cristatus* and *P. bertolonii* were the commonest grasses, found on the majority of the plots in both 2007 and 2008. *D. carota*, *L. vulgare*, *P. lanceolata*, *R. acetosa* and *S. minor* spp. *minor* were the commonest wildflowers, found in the majority of the wildflower plots in both 2007 and 2008.

Table 3.3. The 30 recorded plant species found on the Mesocosm experiment in 2008, and which ones established from the seed mixture.

Establishment	Species	Common name
Wildflowers established from seed mixture	*Achillea millefolium*	Yarrow
	Centaurea nigra	Common Knapweed
	Conopodium majus	Pignut
	Daucus carota	Wild carrot
	Galium mollugo	Hedge bedstraw
	Leucanthemum vulgare	Oxeye Daisy
	Lotus corniculatus	Birdsfoot trefoil
	Malva moschata	Musk mallow
	Plantago lanceolata	Ribwort Plantain
	Primula veris	Cowslip
	Prunella vulgaris	Self-heal
	Rhinanthus minor	Yellow Rattle
	Rumex acetosa	Common Sorrel
	Sanguisorba minor ssp *minor*	Salad Burnet
	Silene dioica	Red Campion
	Trifolium pratense	Red Clover
	Vicia cracca	Tufted vetch
Wildflower not from seed mixture	*Rumex obtusifolius*	Broad-leaved Dock
Grasses established from seed mixture	*Agrostis capillaris*	Common bent
	Alopecurus pratense	Meadow foxtail
	Anthoxanthum odoratum	Sweet vernal-grass
	Cynosurus cristatus	Crested dogstail
	Festuca ovina	Sheep's fescue
	Festuca rubra	Slender creeping red fescue
	Lolium perenne	Perennial Ryegrass
	Phleum bertolonii	Smaller cat's tail
	Trisetum flavescens	Yellow oat-grass
Grasses not from seed mixture	*Arrhenatherum elatius*	False Oat Grass
	Poa trivialis	Rough Meadow-grass
	Holcus lanatus	Yorkshire Fog

Table 3.4. Plant species gained and lost from the Mesocosm experiment in July 2008, compared to 2007; highlighting those that established from the seed mixture and those that did not establish from the seed mixture.

Gained or Lost From 2007	Seed mixture or natural dispersal?	Species	Common name
Gained	Wildflowers gained from seed mixture	*Centaurea nigra*	Common Knapweed
		Conopodium majus	Pignut
		Galium mollugo	Hedge bedstraw
		Primula veris	Cowslip
		Rhinanthus minor	Yellow Rattle
		Silene dioica	Red Campion
	Wildflower gained, not from seed mixture	*Rumex obtusifolius*	Broad-leaved Dock
	Grasses gained from seed mixture	*Festuca ovina*	Sheep's fescue
		Festuca rubra	Slender creeping red fescue
		Anthoxanthum odoratum	Sweet vernal-grass
	Grass gained, not from seed mixture	*Arrhenatherum elatius*	False Oat Grass
Lost	Wildflower lost from seed mixture	*Geranium pratense*	Meadow Cranesbill
	Wildflower lost, not from seed mixture	*Cerastium fontanum*	Common Mouse-ear
	Grass lost, not from seed mixture	*Triticum vulgare*	Wild Wheat

Table 3.5. Plant species that did not establish from the seed mixture in the Mesocosm experiment, in 2008.

Species not establishing from seed mixture	Species	Common name
Wildflowers:	*Campanula glomerata*	Clustered bellflower
	Centaurea scabiosa	Greater Knapweed
	Clinopodium vulgare	Wild Basil
	Filipendula ulmaria	Meadowsweet
	Galium mollugo	Hedge bedstraw
	Geranium pratense	Meadow Crane’s bill
	Knautia arvensis	Field Scabious
	Leontodon hispidus	Rough Hawkbit
	Lychnis flos-cuculi	Ragged Robin
	Plantago media	Hoary Plantain
	Ranunculus acris	Meadow buttercup
	Ranunculus bulbosus	Bulbous buttercup
	Sanguisorba officinalis	Great Burnet
	Silene dioica	Red Campion
	Silene vulgaris	Bladder Campion
Grass:	*Briza media*	Quaking grass

3.3.2 Species Richness 2007 - 2008

3.3.2.1 Total Species Richness 2007 - 2008

There was an increase in species richness from 2007 – 2008. In both 2007 and 2008, the grass and wildflower plots had a significantly greater number of species than the grasses-only plots (7.6 per plot vs. 4.1 in 2007 ($F_{1, 94} = 196.80$, $p < 0.001$) and 9.1 per plot vs. 6 per plot in 2008 ($F_{1, 70} = 145.21$, $p <0.001$)) (Table 3.6). In 2008, significantly less species were found in the first Block in comparison to the second (7 per plot vs. 8 per plot) ($F_{2, 70} = 5.01$, $p = 0.009$). In 2008, there were significantly more species found in the plots that had been cut 8 times throughout the year in comparison to the plots cut less frequently (8.2 per plot vs. 7.3 and 7 per plot) ($F_{2, 70} = 8.28$, $p = 0.001$) (Table 3.7).

In 2007 there were less species on the south-facing plots in comparison to the flat plots ($F_{2, 94} = 4.80$, $p = 0.010$), and there were significantly less species found in the compacted plots ($F_{2, 70} = 4.02$, $p = 0.48$) (Table 3.6). This trend did not continue into 2008 – instead, interaction effects became significant over time: The aspect and seed mixture treatments were interacting ($F_{2, 70} = 7.24$, $p = <0.001$); in general there were more species in the grass and wildflower seed mixture treatment, across all aspects, in comparison to the grasses-only seed mixture treatment, across all aspects, however, the north-facing, grass and wildflower treatment, had less species in comparison to the grass and wildflower treatment in the south-facing and flat plots (Figure 3.2). Aspect, management and soil compaction were all found to be interacting ($F_{4, 70} = 4.815$, $p = 0.039$). There was just one difference, but this was found in the two extremes, with all the intermediate treatments having no significant difference; The flat plots, which were cut 8 times throughout the year and in the compacted treatment, had a significantly greater number of plant species than the north-facing plots which were only cut once at the end of July, and in the non-compacted treatment (9.2 per plot vs. 6.2 per plot).

3.3.2.2 Species Richness of the grasses-only and the grass and wildflower treatment

In both 2007 and 2008, more grass species established in the plots with grasses-only than in the grass and wildflower seed mixture treatment (4.1 per plot vs. 3.3 per plot in 2007 ($F_{1, 94} =$

15.20, p < 0.001) (Table 3.6) and 5.4 per plot vs. 4 per plot in 2008 ($F_{1, 70}$ = 36.43, p = <0.001) (Table 3.7)). In both 2007 and 2008, there were significantly less grasses found on the south-facing plots in comparison to the flat plots (4.3 per plot vs. 5.1 per plot in 2008) ($F_{2, 94}$ = 3.72, p = 0.029) (Table 3.6 and 3.7). In 2007, there were less grass species in the compacted plots, but this trend did not continue into 2008 ($F_{1, 94}$ = 20.76, p < 0.001) (Table 3.6). However, the opposite trend occurred with the wildflowers, there was no compaction effect in 2007, but in 2008, there were more wildflower species in the compacted plots compared to the non-compacted plots (5.6 per plot vs. 4.6 per plot) ($F_{1, 34}$ = 4.97, p = 0.032) (Table 3.7). In 2007, there were significantly less wildflower species in the north-facing plots ($F_{2, 70}$ = 3.27, p = 0.047), but in 2008, this trend did not remain significant (Table 3.6 and 3.7).

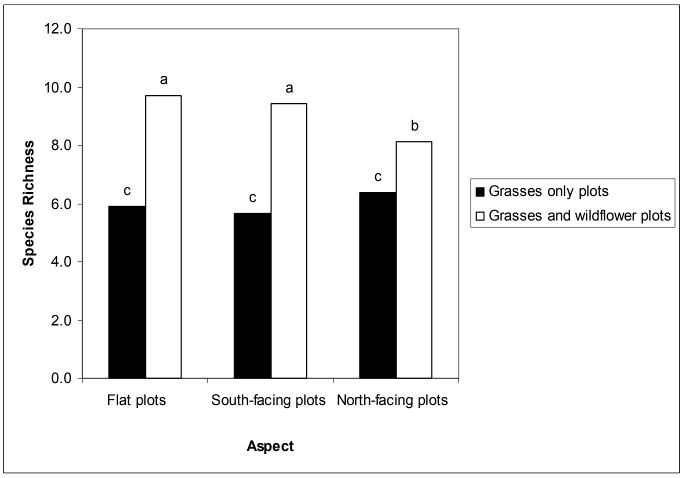

Figure 3.2. Species richness, aspect and seed mixture in 2008. The grass and wildflower plots had more species than the grasses-only plots. The north-facing grass and wildflower plots had less species than the south-facing and flat grass and wildflower plots.

3.3.3 Shannon Diversity Index

Diversity increased across all plots in all treatments between 2007 and 2008. In both 2007 and 2008, diversity was much higher in the grass and wildflower plots in comparison to the grasses-only plots (1.1 H' vs. 1.8 H' in 2007 ($F_{1, 94}$ = 350.71, p = < 0.001) and 2 H' vs. 1.5 H' in 2008 ($F_{1, 70}$ = 169.73, p = <0.001)). In 2007, there was no Block effect but in 2008 diversity was lower in the first Block in comparison to the second (1.7 H' per plot vs. 1.8 H' per plot) ($F_{2, 94}$ = 7.10, p = 0.002). In 2007, the south-facing plots had significantly lower diversity than north-facing and flat plots ($F_{2, 94}$ = 9.62, p = <0.001) and the non-compacted plots had greater diversity than the compacted plots ($F_{1, 94}$ = 8.58, p = 0.004) (Table 3.6), but this was not seen in 2008. In 2008, the plots that were cut 8 times had greater diversity than the plots cut once (1.8 H' vs. 1.6 H') ($F_{2, 70} = 9.5$, $p = <0.001$) (Table 3.7).

The only interaction in 2007 was between the seed mixture and soil compaction ($F_{2, 94} = 4.38$, $p = 0.039$): The compacted, grasses-only plots had significantly lower diversity than the all the other plots (Figure 3.3). In 2008 there were a number of significant interactions, not seen in 2007. There was a significant interaction between the aspect treatments and the seed mixture treatments ($F_{2, 70} = 7.82$, $p = 0.001$). All the grasses-only seed mixture treatments, across all aspects, had lower diversity than the grass and wildflower seed mixture treatments. The north-facing, grass and wildflower plots, had a lower diversity in comparison to the south-facing and flat grass and wildflower plots (1.8 per plot, vs. 2 and 2.1 per plot) (Figure 3.4). The aspect and management treatments were interacting ($F_{4, 70} = 4.48$, $p = 0.003$); the plots that had been cut 8 times, across all aspects, plus the south-facing plots that had been cut 4 times, were found to have significantly greater diversity in comparison to the south-facing plots that had been cut once. The flat plots which were cut 8 times had significantly greater diversity to the north-facing plots that had been cut 4 times (Figure 3.5). Although soil compaction wasn't significant on its own in 2008, in combination with aspect and management, there was an interaction ($F_{4, 70} = 3.52$, $p = 0.011$). The south-facing plots, cut once and in the compacted treatment, had lower diversity than all of the plots cut 8 times (with the exception of the north-facing, non-compacted plot which was cut 8 times); and the south-facing, cut 4 times plots plus the north-facing cut once plots in the compacted treatment (Figure 3.6).

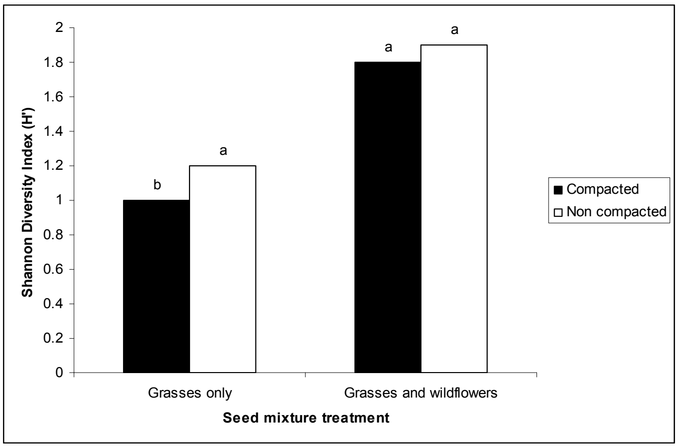

Figure 3.3. Shannon Diversity Index (H'), seed mixture and soil compaction in 2007. The grasses-only compacted plots were significantly lower than the other plots.

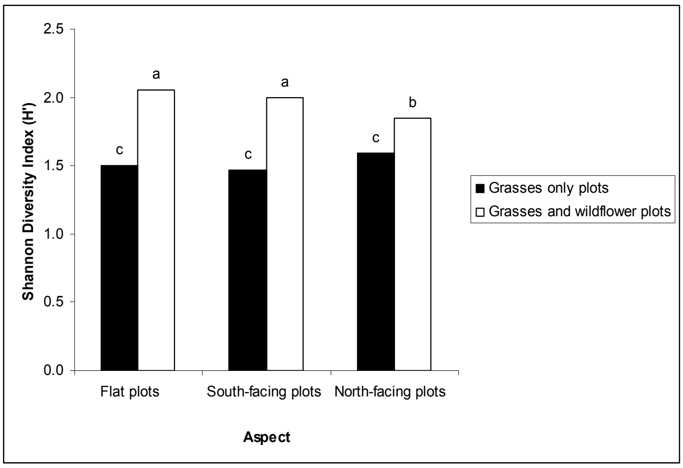

Figure 3.4. Shannon Diversity Index (H'), aspect and seed mixture in 2008. All grass and wildflower plots had greater diversity than the grasses-only plots. The north-facing grass and wildflower plots had lower diversity than the flat and south-facing plots.

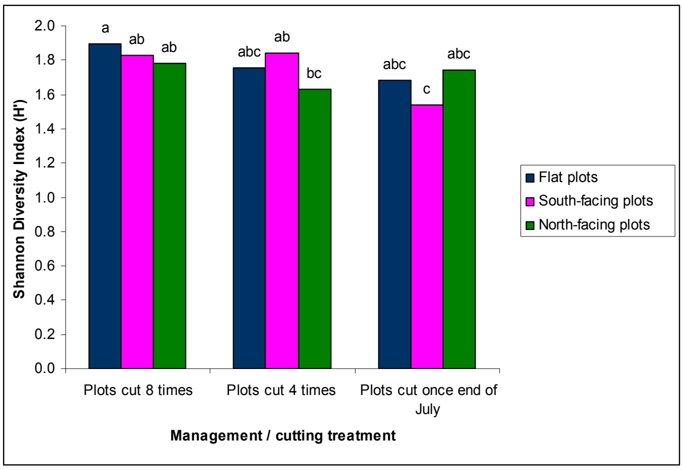

Figure 3.5. Shannon Diversity Index (H'), aspect and management in 2008. The plots that had been cut 8 times, had greater diversity than the south-facing plots that had been cut one The flat plots, cut 8 times, had higher diversity than the north-facing plots cut 4 times.

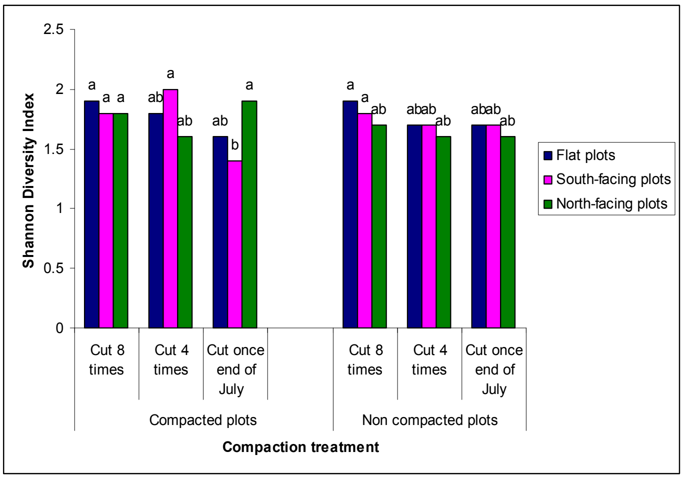

Figure 3.6. Shannon Diversity Index (H'), aspect, management and compaction in 2008. The majority of all the cut 8 times plots, plus the south-facing, compacted, cut 4 times plots and the north-facing, cut 4 times, compacted plots, had greater diversity than the south-facing, cut once plots in the compacted treatment.

Table 3.6. Species Richness and Shannon Diversity Index across all the treatments of 2007.

		Number of species and diversity 2007			
Treatment		Grasses	Wildflowers	Species Richness	Shannon Diversity Index (H')
Block	I	3.7	1.9	5.6	1.4
	II	3.9	2.4	6.3	1.5
	III	3.6	2.2	5.8	1.4
Aspect	Flat	4.2	2.2	6.4	1.5
	South-facing	3	2.4	5.4	1.3
	North-facing	3.9	1.9	5.9	1.4
Compaction	Compacted	3.3	2.3	5.6	1.4
	Non-compacted	4.1	2	6.1	1.5
Seed mixture	Grasses-only	4.1	0	4.1	1.1
	Grasses and Wildflowers	3.3	4.3	7.6	1.8

Table 3.7. Species Richness and Shannon Diversity Index across all the treatments of 2008.

		Mean number of species and diversity 2008			
Treatment		Grasses	Wildflowers	Species Richness	Shannon Diversity Index (H')
Block	I	4.7	4.4	7	1.7
	II	4.9	5.3	8	1.8
	III	4.4	5.6	7.6	1.7
Aspect	Flat	5.1	5.2	7.8	1.8
	South-facing	4.3	5.7	7.6	1.7
	North-facing	4.7	4.4	7.3	1.7
Management or Cutting	Cut 8 times	5.1	5.7	8.3	1.8
	Cut 4 times	4.5	4.9	7.4	1.7
	Cut once	4.5	4.7	7	1.7
Compaction	Compacted	4.5	5.6	7.7	1.8
	Non-compacted	4.8	4.6	7.3	1.7
Seed mixture	Grasses-only	5.4	0	6	1.5
	Grasses and Wildflowers	4	0	9.1	2

3.3.4 Individual species responses

3.3.4.1 Grasses

Between 2007 and 2008, the frequency of *L. perenne* was reduced across all plots. In both 2007 and 2008 *L. perenne* was found in greater frequency in the grasses-only plots, in comparison to the grass and wildflower plots (7.8 per plot vs. 6.2 per plot in 2007 ($F_{1, 94}$ = 17.05, p = < 0.001) and 6.4 per plot vs. 4.3 per plot in 2008 ($F_{1, 70}$ = 18.85, p = <0.001)). In 2007, *L. perenne* frequency was significantly higher on the flat plots in comparison to the south and north-facing plots (8 per plot vs. 6.4 per plot and 6.7 per plot) ($F_{1, 94}$ = 5.97, p = 0.004), whereas in 2008, a higher frequency of *L. perenne* was found on the flat plots but only in comparison to the south-facing plots (6.1 per plot vs. 4.5 per plot) ($F_{2, 70}$ = 3.80, p = 0.027). In 2007, the frequency of *L. perenne* in the third Block was much lower than the first and second Block (5.6 per plot vs. 7.5 per plot and 8 per plot) ($F_{1, 94}$ = 13.70, p = < 0.001), and in 2008, the third Block had significantly lower frequency than just the first Block (4.5 per plot vs. 6.1 per plot) ($F_{2, 70}$ = 3.70, p = 0.03) (Table 3.9 and Table 3.10).

In 2008, the plots that were cut 8 times had significantly lower frequency of *L. perenne* in comparison to the plots that were only cut once in the summer (4.4 per plot vs. 5.9 per plot) ($F_{2, 70}$ = 3.52, p = 0.035) (Table 3.10). There was an interaction between management and the seed mixture treatment ($F_{2, 70}$ = 3.81, p = 0.027). The frequency of *L. perenne* cover was not reduced by the increase in cutting frequency in the grass and wildflower seed mixture treatment, but was reduced in the grasses-only seed mixture treatment, to the same frequency as that found in the grass and wildflower seed mixture treatments (Table 3.8).

Table 3.8. Mean frequency of *Lolium perenne* per plot, in the seed mixture and management treatments in 2008.

	Seed mixture treatment	
Management / cutting	Grasses-only	Grasses and wildflowers
Cut 8 times	4.6 $_b$	4.3 $_b$
Cut 4 times	7.3 $_a$	4.3 $_b$
Cut once end of July	7.5 $_a$	4.3 $_b$

Between 2007 and 2008, the frequency of *C. cristatus* was reduced in all plots, except in the south-facing plots where there was an increase. This increase removed the aspect effect seen in 2007 where the south-facing plots had significantly lower cover of *C. cristatus* than the flat and north-facing plots (3.3 per plot vs. 6.5 per plot and 7.1 per plot) ($F_{2,94} = 33.61$, $p = < 0.001$). In both 2007 and 2008, there was significantly lower frequency of *C. cristatus* in the wildflower mixture in comparison to the grasses-only mixture (6.6 per plot vs. 4.7 per plot in 2007 ($F_{1,94} = 21.29$, $p = < 0.001$) and 5.7 per plot vs. 2.8 per plot in 2008 ($F_{1,70} = 39.90$, $p = <0.001$)) (Table 3.11 and 3.12).

In 2008, the plots that have only been cut once had significantly lower frequency of *C. cristatus* than both the plots that had been cut 4 times and the plots that had been cut 8 times (3.3 per plot vs. 4.8 and 4.8 per plot) ($F_{2,70} = 5.02$, $p = 0.009$). This is the opposite response to *L. perenne* where the plots that had been cut most often had a reduced frequency. The Block effect found with *C. cristatus* was opposite to that of *L. perenne*; there was greater frequency of *C. cristatus* in the third Block in comparison to the first (3.5 per plot vs. 5.3 per plot) ($F_{2,70} = 5.29$, $p = 0.007$) (Table 3.12).

Between 2007 and 2008 there was an increase in the frequency of *P. bertolonii* across all of the plots. There was a higher frequency of *P. bertolonii* in the grass seed mixture in comparison to the wildflower seed mixture (1.6 per plot vs. 1.1 per plot in 2007 ($F_{1,94} = 5.92$, $p = 0.017$) and 3.3 per plot vs. 1.7 per plot in 2008 ($F_{1,70} = 31.45$, $p = <0.001$)). In both 2007 and 2008, the frequency of *P. bertolonii* was lower in the plots where the soil had been compacted and higher in not compacted plots (0.7 per plot vs. 2 per plot in 2007 ($F_{1,94} = 28.49$, $p = < 0.001$) and 1.9 per plot vs. 3.1 per plot in 2008 ($F_{1,70} = 6.89$, $p = 0.011$)) (Table 3.12). In 2007 and 2008 there was a significant interaction between aspect and soil compaction ($F_{2,94} = 0.57$, $p = 0.013$, 2007 and $F_{2,70} = 4.64$, $p = 0.013$, 2008). In 2007, the compaction effect was seen in the south-facing and flat plots (Figure 3.7), and in 2008, the compaction effect was only apparent in the flat plots, where the frequency of *P bertolonii* was significantly reduced in the flat compacted plots in comparison to the flat non-compacted plots (1.6 per plot vs. 3.8 per plot) (Figure 3.8).

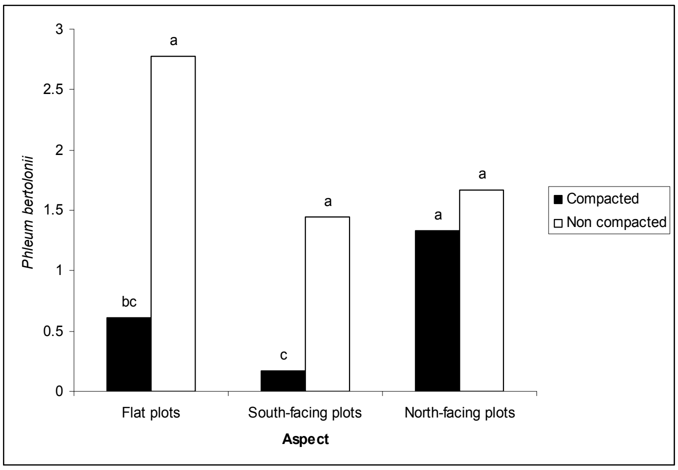

Figure 3.7. Compaction, aspect and *Phleum bertolonii* frequency in 2007. The compaction treatment has reduced growth in the flat and south-facing plots.

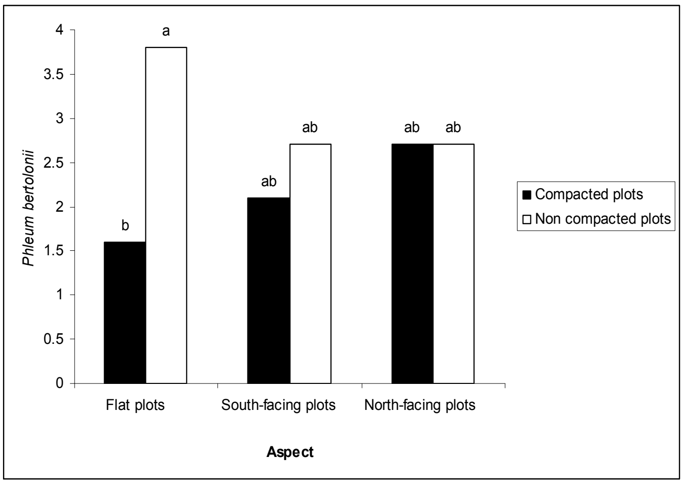

Figure 3.8. Compaction, aspect and *Phleum bertolonii* frequency in 2008. The compaction treatment has reduced growth in the flat plots.

Table 3.9. Mean frequency of the commonest grass species present in the Mesocosm experiment in 2007, across all treatments.

		Grass frequency in 2007		
Treatment		*L. perenne*	*C. cristatus*	*P. bertolonii*
Block	I	7.5	5.7	1.2
	II	8.0	5.0	1.4
	III	5.6	6.2	1.4
Aspect:	Flat	8.0	6.5	1.7
	South-facing	6.4	3.3	0.8
	North-facing	6.7	7.1	1.5
Compaction:	Compacted	7.2	5.5	0.7
	Non-compacted	6.8	5.8	2.0
Seed mixture:	Grasses-only	7.8	6.6	1.6
	Grasses and Wildflowers	6.2	4.7	1.1

Table 3.10. Mean frequency of the commonest grass species present in the Mesocosm experiment in 2008, across all treatments.

Treatment		Grass frequency in 2008		
		L. perenne	*C. cristatus*	*P. bertolonii*
Block	I	6.1	3.5	2.4
	II	5.4	4.0	2.6
	III	4.5	5.3	2.6
Aspect:	Flat	6.1	4.0	2.7
	South-facing	4.5	4.0	2.4
	North-facing	5.4	4.8	2.4
Management:	Cut 8 times	4.4	4.8	2.8
	Cut 4 times	5.7	4.8	2.5
	Cut once	5.9	3.3	2.2
Compaction:	Compacted	5.4	4.4	1.9
	Non-compacted	5.3	4.1	3.1
Seed mixture:	Grasses-only	6.4	5.7	3.3
	Grasses and Wildflowers	4.3	2.8	1.7

3.3.4.2 Wildflowers

Between 2007 and 2008 there was an increase in the frequency of *R. acetosa* across all of the plots. In 2007 and 2008, *R. acetosa* was significantly reduced in the compacted plots in comparison to the non-compacted plots (1.9 per plot vs. 3 per plot in 2007 ($F_{1,46} = 11.63$, $p = 0.001$); 3.4 per plot vs. 5 per plot in 2008 ($F_{1,34} = 7.45$, $p = 0.01$)). In 2007, the south-facing plots had lower frequency than the north-facing and flat plots ($F_{2,46} = 5.66$, $p = 0.006$), but this did not remain significant in 2008 (Table 3.11 and 3.12).

Between 2007 and 2008 there was an increase in the frequency of *L. vulgare*. In 2008, the south-facing plots had much higher frequency of *L. vulgare* than the north-facing plots (2.8 per plot vs. 0.6 per plot) ($F_{2,34} = 4.2$, $p = 0.024$). The plots cut 8 times had higher frequency of *L. vulgare* than the plots cut once (2.8 per plot vs. 1.2 per plot) ($F_{2,34} = 3.74$, $p = 0.034$) (Table 3.11 and 3.12).

Between 2007 and 2008 there was an increase in the frequency of *P. lanceolata*. In 2007, the south-facing plots had greater frequency than the north-facing and flat plots (2.7 per plot vs. 1.2 per plot and 1.8 per plot) ($F_{2,46} = 3.90$, $p = 0.027$), and by 2008, it was just the north-facing plots that had significantly lower frequency of *P. lanceolata* in comparison to the south-facing and flat plots (1.7 per plot vs. 5.1 and 5.8 per plot) ($F_{2, 34} = 11.46$, $p = <0.001$). In 2008, the plots cut 8 times had a reduced frequency of *P. lanceolata* in comparison to the plots cut once (3 per plot vs. 5.7 per plot) ($F_{2, 34} = 4.68$, $p = 0.016$) (Table 3.11 and 3.12).

Between 2007 and 2008, there was an increase in the frequency of *S. minor*. In 2008, soil compaction reduced the frequency of *S. minor* ($F_{1, 34} = 3.94$, $p = 0.055$): *S. minor* was found less often in the compacted plots in comparison to the non-compacted plots (1.2 per plot vs. 2.2 per plot) (Table 3.11 and 3.12).

In both 2007 and 2008 the frequency of *D. carota* across the plots was very similar. The only difference was in 2007 where cover was significantly lower on the north-facing plots ($F_{2, 46} = 10.89$, $p < 0.001$), but this did not continue into 2008. Otherwise, *D. carota* established well across all of the treatments, in all of the plots, showing no differences between the treatments (Table 3.11 and 3.12).

Table 3.11. A table to show the mean frequency values for the common wildflower species found in the majority of the plots, across the treatments in 2007.

Treatment		Frequency of Wildflowers in 2007				
		R. acetosa	*L. vulgare*	*D. carota*	*P. lanceolata*	*S. minor*
Block	I	2.6	0.1	1.6	2.2	0.2
	II	2.6	0.8	1.6	2.8	0.6
	III	2.2	0.1	1.3	0.7	0.6
Aspect	Flat	2.7	0.1	1.9	1.8	0.5
	South-facing	1.8	0.4	1.9	2.7	0.6
	North-facing	2.9	0.4	0.7	1.2	0.4
Compaction	Compacted	1.9	0.2	1.6	2.2	0.4
	Non-compacted	3	0.4	1.4	1.6	0.5

Table 3.12. A table to show the mean frequency values for the common wildflower species found in the majority of the plots, across the treatments in 2008.

Treatment		Frequency of Wildflowers in 2008				
		R.acetosa	*L. vulgare*	*D. carota*	*P. lanceolata*	*S. minor*
Block	I	5.1	1.7	1.7	4.5	1.1
	II	3.6	1.8	1.9	4.5	1.8
	III	4.1	1.8	1.7	3.5	2.2
Aspect	Flat	4.6	1.8	1.9	5.1	1.8
	South-facing	3.6	2.8	1.8	5.8	2.1
	North-facing	4.4	0.6	1.6	1.7	1.2
Management	Cut 8 times	4.7	2.8	1.4	3	1.5
	Cut 4 times	4.4	1.2	2.1	3.8	1.9
	Cut Once	3.6	1.2	1.8	5.7	1.7
Compaction	Compacted	3.4	1.7	1.8	4.3	1.2
	Non-compacted	5	1.9	1.7	4	2.2

3.3.4.3 Rhinanthus minor

R. minor was added into the seed mixture for all plots, grasses-only and grass and wildflower treatments. It established in some plots very well, but in others poorly. This made it difficult to analyse so a combination of ANOVA and Kruskal Wallis was used. *R. minor* establishment was significantly higher in the third Block ($H_{2, 108} = 8.40$, $p = 0.015$) (1.9 per plot vs. 1.1 per plot and 0.3 per plot). *R. minor* was found mostly in the grasses-only plots in comparison to the grass and wildflower seed mixture (2 per plot vs. 0.3 per plot). Aspect was highly significant in the ANOVA and just significant with Kruskal Wallis ($H_{2, 108} = 5.97$, $p = 0.05$). *R. minor* was found more frequently on the south-facing and north-facing plots, and less on the flat plots (1.4 per plot and 1.3 per plot vs. 0.6 per plot). *R. minor* frequency was greater on the plots cut 8 times and plots cut 4 times in comparison to the plots cut once (1.7 per plot, 1.2 per plot vs. 0.4 per plot) ($H_{2, 108} = 8$, $p= 0.018$). *R. minor* was found more frequently in the compacted plots compared to the non-compacted plots (1.5 per plot vs. 0.7 per plot) ($H_{1, 208} = 6.15$, $p = 0.013$) (Table 3.13).

Table 3.13. Mean frequency of *Rhinanthus minor*, added as seed in October 2007 to all plots.

Treatment		*R. minor*
Block	I	0.3
	II	1.1
	III	1.9
Aspect	Flat	0.6
	South-facing	1.3
	North-facing	1.4
Management	Cut 8 times	1.7
	Cut 4 times	1.2
	Cut Once	0.4
Compaction	Compacted	1.5
	Non-compacted	0.7
Seed mixture	Grasses-only	2
	Grasses and Wildflowers	0.2

3.3.5 Ellenberg Indicator Values

3.3.5.1 Fertility (N)

The mean Ellenberg Fertility Value for the Mesocosm experiment was 4.6 – this is an indicator of intermediate fertility. There were slight significant variations in the fertility scores in some of the treatments: The first Block had significantly greater values than the third Block, with the second Block intermediate (4.8 N vs. 4.5 N, and 4.6 N respectively) ($F_{2,70} = 7.68$, $p = 0.001$); Flat plots had significantly higher fertility scores than the north-facing plots, with no differences in the south-facing plots (4.8 N vs. 4.5 N and 4.6 N) ($F_{2,70} = 4.36$, $p = 0.016$); and the grasses-only plots had higher fertility scores than the grass and wildflower plots (4.8 vs. 4.4) ($F_{2,70} = 83.30$, $p < 0.001$) (Table 3.14).

3.3.5.2 Light (L)

The mean Ellenberg Light value for the Mesocosm experiment was 7.4 – which indicate plants that are mainly in the light. The only difference was between the seed mixture treatment ($F_{1,70} = 30.76$, $p < 0.001$) where the grasses-only plots had higher light scores than the grass and wildflower plots (7.5 L vs. 7.3 L) (Table 3.14). In addition there was a seed mixture and management interaction ($F_{2,70} = 4.45$, $p = 0.045$): The grasses-only, cut once plots had a higher score than all the grass and wildflower plots, plus the grasses-only, cut 8 times plots. The grasses-only, cut 4 times plots had a higher score than the grass and wildflower plots, cut 4 times (Figure 3.10).

3.3.5.3 Moisture (F)

The mean moisture value for the Mesocosm experiment was 4.8 F - which indicates normal moisture levels, not too dry or too wet, but closer to the moist side (a score of 5 would be a moisture indicator). The north-facing slopes had a score slightly higher than the south-facing plots with no differences in the flat plots (4.9 F vs. 4.8 F and 4.8 F) ($F_{2, 70} = 2.75$, $p = 0.071$). The grasses-only plots had a slightly higher value than the grass and wildflower plots (4.9 vs. 4.8) ($F_{1, 70} = 28.69$, $p < 0.001$) (Table 3.14).

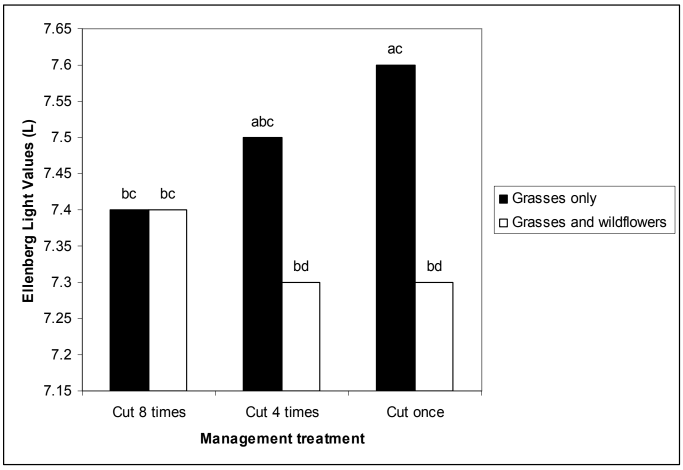

Figure 3.10. Ellenberg Light Values (L), management treatments and seed mixture treatments. The grasses-only cut once plots were much greater than all the grass and wildflower plots.

Table 3.14. Ellenberg Indicator Values across the main treatments.

		Ellenberg Indicator Values		
	Treatment	Fertility (N)	Light (L)	Moisture (F)
Block	I	4.7	7.4	4.9
	II	4.6	7.4	4.8
	III	4.5	7.4	4.8
Aspect	Flat	4.7	7.4	4.8
	South-facing	4.5	7.4	4.8
	North-facing	4.6	7.4	4.9
Management	Cut 8 times	4.6	7.4	4.8
	Cut 4 times	4.5	7.4	4.8
	Cut Once	4.7	7.4	4.8
Compaction	Compacted	4.6	7.4	4.9
	Non-compacted	4.6	7.4	4.8
Seed mixture	Grasses-only	4.8	7.5	4.9
	Grasses and wildflowers	4.4	7.3	4.8

3.3.6 Biomass

3.3.6.1 Biomass from 2007- July 2008 – repeated measures

The four cuts were taken from within the same year, and there were four biomass measurements per plot, so this could be analysed using repeated measures. Time was highly significant ($F_{3, 303} = 567.92$, $p = < 0.001$); time and Block were significant ($F_{6, 303} = 7.14$, $p = 0.0006$); time and aspect were significant ($F_{6, 303} = 17.27$, $p = < 0.001$) and time and the seed mixture treatment were significant ($F_{3, 303} = 59.67$, $p = < 0.001$). This shows that the amount of biomass produced was highly influenced by the time of year the cut was taken and this influenced the majority of the relationships shown from the treatments. At each cut, there were differences seen between these treatments.

In the first cut in January 2007: the third Block had significantly lower biomass than the other two Blocks (2 g m^{-2} vs. 2.7 and 3 g m^{-2}) ($F_{2, 94} = 11.48$, $p = <0.001$); North-facing plots had greater biomass than the flat and south-facing plots (3 g m^{-2} vs. 2.2 g m^{-2}) ($F_{2, 94} = 5.91$, $p = 0.004$) (Figure 3.11); The grass and wildflower seed mixture had much greater biomass than the grasses-only seed treatment (2.7 g m^{-2} vs. 2.2 g m^{-2}) ($F_{1, 94} = 8.10$, $p = 0.005$); but the difference between the soil compaction treatments was not quite significant ($F_{1, 94} = 3.40$, $p = 0.068$). Although there wasn't a significant effect of soil compaction on its own, there was when combined with aspect ($F_{2, 94} = 3.46$, $p = 0.036$). This was evident in the south-facing, non-compacted treatment which had significantly lower biomass than the north-facing, non-compacted treatment (2 g m^{-2} vs. 2.7 g m^{-2}) and the north-facing, compacted treatment had very high biomass (3.2 g m^{-2}) (Table 3.15).

In the second cut in April 2007, the biomass had increased from the January cut. The significant Block effect trend had continued ($F_{2, 94} = 34.25$, $p = <0.001$) with the third Block having much lower biomass to the first and second Blocks (3.7 g m^{-2} vs. 5.7 g m^{-2}). The aspect effect was opposite to the previous cut; the north-facing plots had lower biomass than the south-facing plots (4.5 g m^{-2} vs. 5.5 g m^{-2}); and the flat plots were intermediate (5 g m^{-2}) ($F_{2, 94} = 6.20$, $p = 0.003$) (Figure 3.11). The grass and wildflower seed mixture continued to have greater biomass compared to the grasses-only seed mixture (5.5 g m^{-2} vs. 4.7 g m^{-2}) ($F_{1, 94} = 13.16$, $p = < 0.001$) (Table 3.15). There was a strong interaction between aspect and seed mixture on the amount of biomass ($F_{2, 94} = 8.66$, $p = < 0.001$). The south-facing grass and wildflower plots had a much greater biomass than all the other treatments (6.5 g m^{-2}) (Table 3.16).

There was a huge amount of biomass growth across all the plots in the third summer cut of August 2007. There was still a large Block effect on the amount of biomass measured ($F_{2, 94} = 14.13$, $p = <0.001$). This time the second Block had much greater biomass than the first and third Blocks (although the third Block was still lower but not statistically different to the first Block) (42.5 g m^{-2} vs. 33 g m^{-2} and 30.2 g m^{-2}). Flat plots now had much greater biomass than south-facing plots, but the south-facing plots continued to have greater biomass than north-facing plots (44.5 g m^{-2} vs. 35.7 g m^{-2} vs. 25.5 g m^{-2}) ($F_{2, 94} = 19.54$, $p = <0.001$) (Figure 3.11). The grass and wildflower seed mixture plots had almost double the amount of biomass than the grasses-only plots (45.7 g m^{-2} vs. 24.7 g m^{-2}) ($F_{1, 94} = 77.96$, $p = <0.001$) (Table 3.15). There was a highly significant interaction of aspect and seed mixture on the amount of biomass produced ($F_{2, 72} = 6.22$, $p = 0.003$). The flat and south-facing plots with the grass and wildflower seed mixture had much greater biomass than the north-facing grass and wildflower seed mixture, with all the grass and wildflower plots greater than the grasses-only plots (58 g m^{-2} and 50.7 g m^{-2} vs. 28.7 g m^{-2}) (Table 3.16).

In the final autumn cut of October 2007, the general amount of biomass produced was much less than the summer cut. The Block effect had continued to be significant ($F_{2, 94} = 32.87$, $p = <0.001$). The trend was similar to the first cut with the third Block having a lower biomass than the first and second Blocks (6 g m^{-2} vs. 10 g m^{-2} and 10.2 g m^{-2}). The flat plots remained greater than the north and south-facing plots, with no differences between the north and south-facing plots (10 g m^{-2} vs. 8.7 g m^{-2} and 7 g m^{-2}) ($F_{2, 94} = 10.20$, $p = <0.001$) (Figure 3.11). The grass and wildflower plots produced far more biomass than the grasses-only plots (14 g m^{-2} vs. 3.2 g m^{-2}) ($F_{1, 94} = 246.57$, $p = <0.001$) (Table 3.15). A similar seed mixture and aspect pattern occurred as before, with all the grass and wildflower plots greater than the grasses-only plots, whereas compared between, the north-facing grass and wildflower plots were lower than the other grass and wildflower plots (10.5 g m^{-2} vs. 15.7 g m^{-2} and 15.2 g m^{-2}) and the flat grasses plots were higher than the other grasses-only plots (4.2 g m^{-2} vs. 2.2 g m^{-2} and 3.5 g m^{-2}) ($F_{2, 94} = 5.04$, $p = 0.008$) (Table 3.16).

To summarise - the Block effect changed between the third Block having much lower biomass, to the second Block having the highest biomass and back to the third Block being highest. The aspect treatment fluctuated: The north-facing plots started by having greater biomass but this changed to having much lower biomass by the second cut, with the south plots being much higher; followed by the south and north-facing plots remaining similar, and the flat plots with the greatest biomass, from the third cut onwards (Figure 3.11). The gap continued to widen between the grasses-only seed mixture and the grass and wildflower seed mixture treatment, and the grass and wildflower plots continually had the greatest biomass. In general, the amount of biomass produced varied throughout the year, with the summer cut having a huge amount of biomass and the spring and autumn having a lot less. The soil compaction treatment did not make a difference to the aboveground biomass.

3.3.6.2 July cut – 2008

The two summer cuts were looked at using repeated measures. Time was highly significant ($F_{1, 101} = 22.86$, $p = < 0.001$) and time and seed mixture treatment were significant ($F_{1, 101} = 18.62$, $p = < 0.001$). The gap between the grasses-only plots and the grass and wildflower plots continued to increase over time, with the biomass of the grass and wildflower plots greatly increasing more than the grasses. The other treatments were not significant between 2007 and 2008, whereas they were significant when looking at the cuts throughout 2007.

In 2008, many of the trends from 2007 remained the same, plus the management treatment had influenced the biomass measured. The amount of biomass produced across the Mesocosm experiment was much higher than the comparable cut of summer 2007. The Block effect was still strong ($F_{2, 70} = 4.53$, $p = 0.014$). It followed the same trend as summer 2007 with the second Block having greater biomass and the other Blocks the same (47 g m^{-2} vs. 39.5 g m^{-2} and 41 g m^{-2}). The aspect trend continued with the flat plots much greater and no differences between the north and south-facing plots (49.2 g m^{-2} vs. 44 g m^{-2} and 34.2 g m^{-2}) ($F_{2, 70} = 14.30$, $p = <0.001$) (Figure 3.11). The grass and wildflower seed mixture treatment, was, as always, much greater than the grasses-only mixture (21.4 g m^{-2} vs. 25.2 g m^{-2}) ($F_{1, 70} = 6.06$, $p = <0.001$) (Table 3.15). The management treatment was highly significant ($F_{2, 70} = 11.21$, $p = <0.001$), however as this was a treatment outcome, modified by hand, so this difference was to be expected. The plots only cut in the summer 2008 produced greater biomass than the plots cut throughout the year (52.2 g m^{-2} vs. 38.5 g m^{-2} and 36.7 g m^{-2}). There was no difference between the plots that were cut 4 times and the plots that were cut 8 times. Aspect and the seed mixture were interacting ($F_{2, 70} = 6.06$, $p = 0.004$) which followed a similar pattern as the summer and October 2007 cut: all the grass and wildflower plots were greater than the grasses-only plots, whereas, compared between, the north-facing grass and wildflower plots were lower than the other grass and wildflower plots (45.5 g m^{-2} per ha^{-1} vs. 67 g m^{-2} and 67.2 g m^{-2}) and the flat grasses-only plots were greater than the other grasses-only plots (31.5 g m^{-2} vs. 21.2 g m^{-2} and 23.2 g m^{-2}) (Table 3.16).

3.3.6.3 Species richness and aboveground biomass from July 2008 cut

Although there was no significant correlation between biomass (g m^{-2}) and total species richness in the ANCOVA ($F_{1, 34} = 0.06$, $p = 0.811$), doing a regression was highly significant ($p = <0.001$). The graph in Figure 3.12 showed that as species richness increased, so did aboveground biomass, however, Figure 3.13, showed that the grasses-only seed mixture plots are to the right of the graph and the grasses and wildflowers seed mixture treatment are to the left. There were less species in the grasses-only seed mixture treatments and more in the grass and wildflower treatments – this has influenced the aboveground biomass so that greater biomass was found in the grass and wildflower seed mixture treatment.

Table 3.15. Biomass (g m^{-2}) for all cuts throughout the Mesocosm experiment, with the main treatments.

Treatment		Biomass (g m^{-2})				
		Jan-07	Apr-07	Aug-07	Oct-07	Jul-08
Block	I	2.7	5.7	33.0	10.2	39.5
	II	3.0	5.7	42.5	10.0	47.2
	III	2.0	3.7	30.2	5.7	41.0
Aspect	Flat	2.2	5.0	44.5	10.0	49.2
	South-facing	2.2	5.5	35.7	8.7	44.0
	North-facing	3.0	4.5	25.5	7.0	34.2
Compaction	Compacted	2.7	5.0	36.0	8.7	44.2
	Non-compacted	2.5	5.0	34.5	8.5	40.7
Seed mixture	Grasses-only	2.2	4.7	24.7	3.2	25.2
	Grasses and wildflowers	2.7	5.5	45.7	14.0	59.7

Table 3.16. Biomass (g m^{-2}) and the interaction between seed mixture and aspect. The same trend continues across the cuts: the flat grasses-only plots on were higher than south and north-facing plots. The grass and wildflower plots were lower on the north-facing plots.

		Biomass (g m^{-2})							
		Grasses-only seed mixture				Grasses and wildflowers seed mixture			
		Apr-07	Aug-07	Oct-07	Jul-08	Apr-07	Aug-07	Oct-07	Jul-08
Aspect	Flat	4.5	30.7	4.2	31.5	5.2	58.0	15.7	67.2
	South-facing	4.5	20.7	2.2	21.2	6.5	50.7	15.2	67.0
	North-facing	4.7	22.5	3.5	23.2	4.5	28.7	10.7	45.0

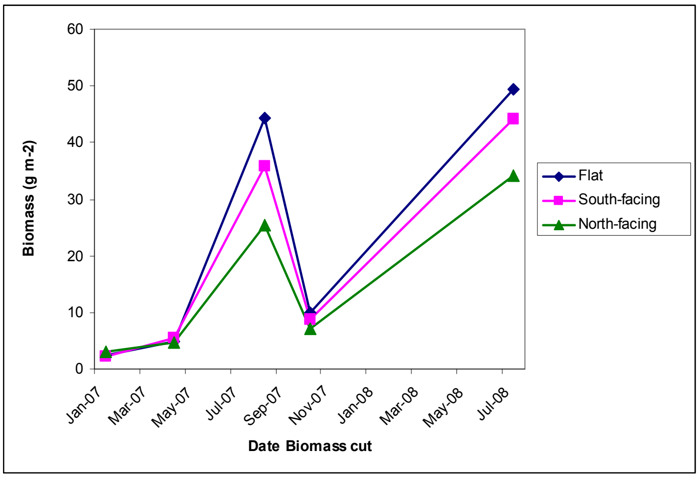

Figure 3.11. Biomass (g m-2) and aspect. Flat plots had consistently greater biomass than the south-facing plots, and the north-facing plots had consistently lower biomass from Sept 2007, although there was not a significant difference between south-facing and north-facing plots.

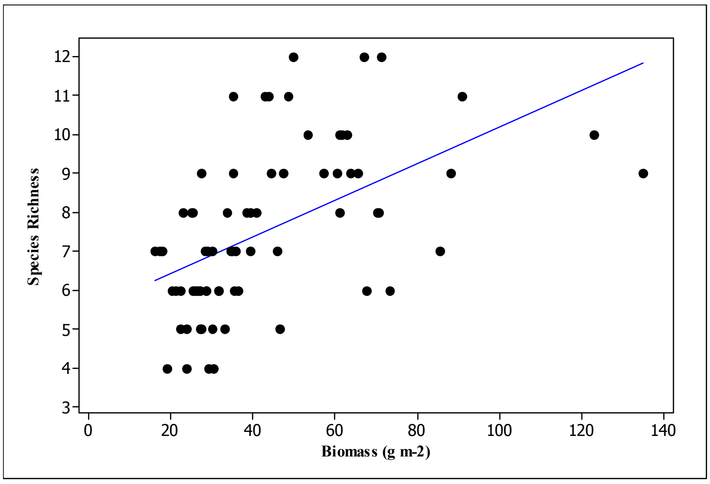

Figure 3.12. Total species richness and biomass. The regression was significant ($p < 0.001$). As species richness increased, so did biomass (g m^{-2}).

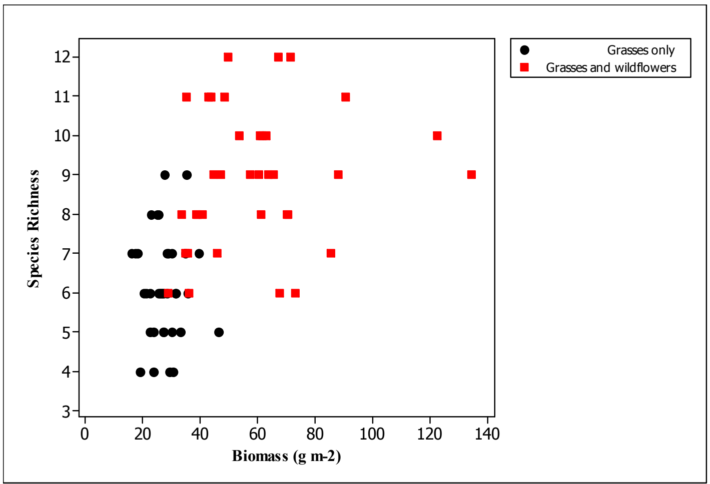

Figure 3.13. Species richness, biomass (g m^{-2}) and seed mixture. The grasses-only seed mixture treatment lies to the left of the graph and the grass and wildflower seed mixture treatment lies to the right.

3.3.6.4 Shannon Diversity Index and aboveground biomass from July 2008 cut

Although there was no significant correlation between total biomass (g m^{-2}) and Shannon Diversity Index (H') ($F_{1, 34} = 0.22$, $p = 0.644$), a regression showed there was a highly significant correlation ($p = <0.001$). The graph in Figure 3.14 showed that as biomass increased, so did the Shannon Diversity Index, although in Figure 3.15, it is clear that the grasses-only seed mixture treatment is to the right (i.e. with a low Shannon Diversity Index) and the grass and wildflower seed mixture is to the left (with high Shannon Diversity Index). This treatment effect prevents the correlation from being apparent in the ANCOVA.

3.3.7 Species composition using PCA in Minitab (2008 data only)

Figure 3.16, 3.17 and 3.18 show the 2008 grass and wildflower plots. Aspect and management treatments did not form groups in the PCA bi-plot. Figure 3.17 on the other hand, shows that soil compaction did form two obvious groups, and was influencing general species composition in the grass and wildflower plots. This is not the case for the grasses-only plots – no clustering of the treatments occurs in Figure 3.19, or when any of the treatments were looked at.

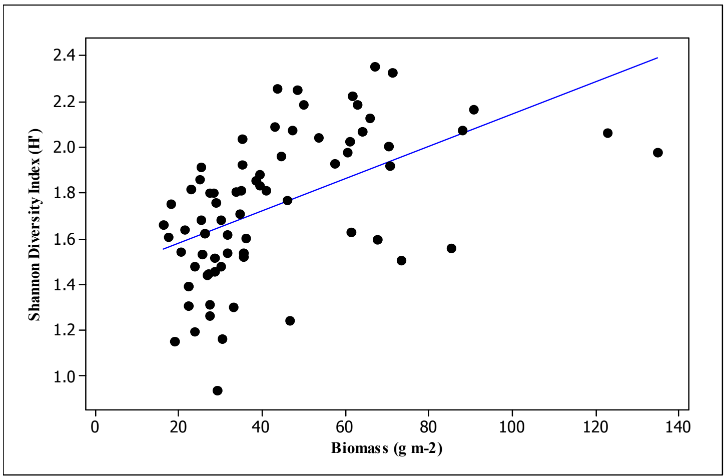

Figure 3.14. Shannon Diversity Index (H') and Biomass (g m^{-2}). The regression was significant at ($p < 0.001$). As the diversity increased, so did biomass.

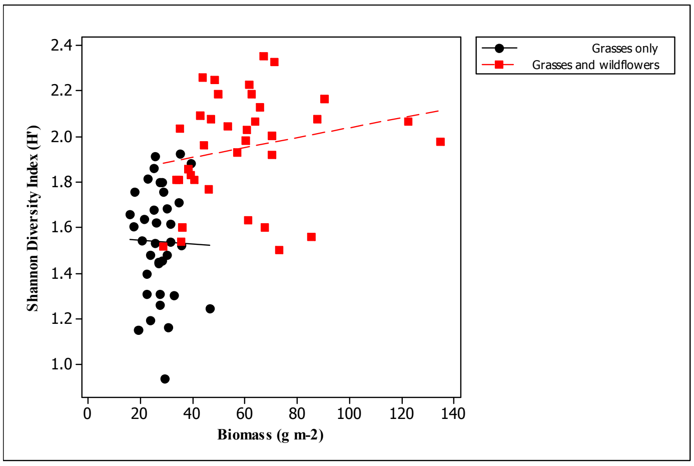

Figure 3.15. Shannon Diversity Index (H'), Biomass (g m-2) and seed mixture. When the seed mixture differences were included, the pattern seen in Figure 14 was removed.

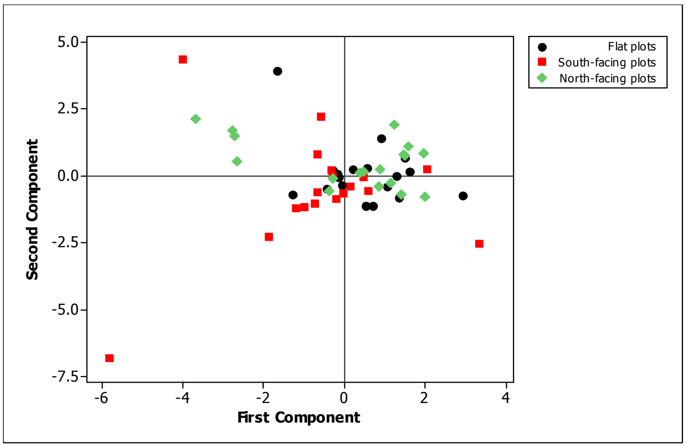

Figure 3.16. PCA – with the aspect treatment highlighted. The aspect treatment did not greatly influence the general species composition of the grass and wildflower plots in 2008.

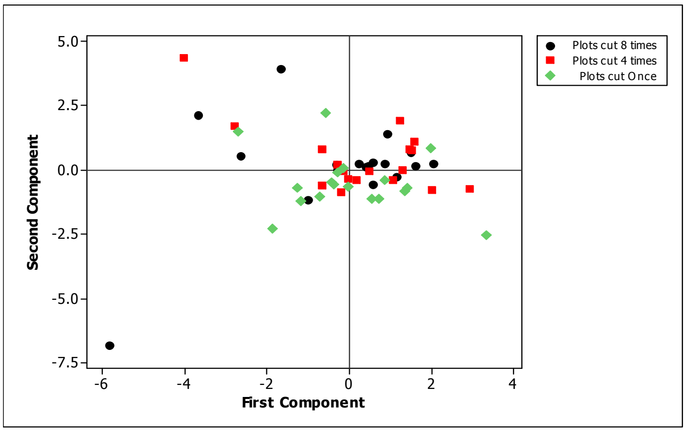

Figure 3.17. PCA – with Management. The management treatment did not influence the general species composition of the grass and wildflower plots in 2008.

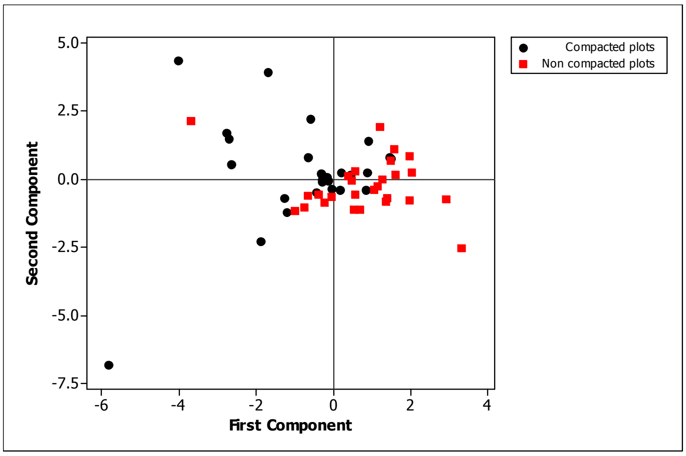

Figure 3.18. PCA – with soil compaction. The soil compaction treatment influenced the general species composition of the grass and wildflower plots in 2008.

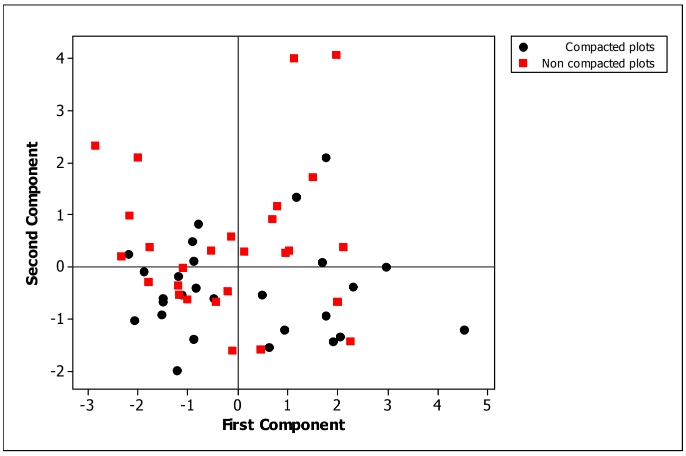

Figure 3.19. PCA – with soil compaction. The soil compaction treatment did not influence the general species composition of the grasses-only plots in 2008.

3.3.8 Ordination in CANOCO

3.3.8.1 2007 and 2008 combined, using all treatments

The analysis was firstly run with all of the 2007 and 2008 data, including all species. The first axis of the PCA explained 34.1 % of the data, and the second axis explained 9.1 % of the variation. The first axis represented the seed mixture treatment and the second axis the differences between the 2007 and 2008 data. The RDA in Figure 3.20 showed that the seed mixture treatment split the data into the two seed mixture treatments and was overshadowing the other treatment effects. 29.5 % of the variance was explained by the seed mixture treatment however all of the treatments were significant (Table 3.17). *C. cristatus*, *A. capillaris*, *L. perenne* and *Alopecurus pratensis* were more associated with north-facing and flat plots. *T. pratense*, *L. vulgare* and *S. minor* were most abundant on south-facing plots.

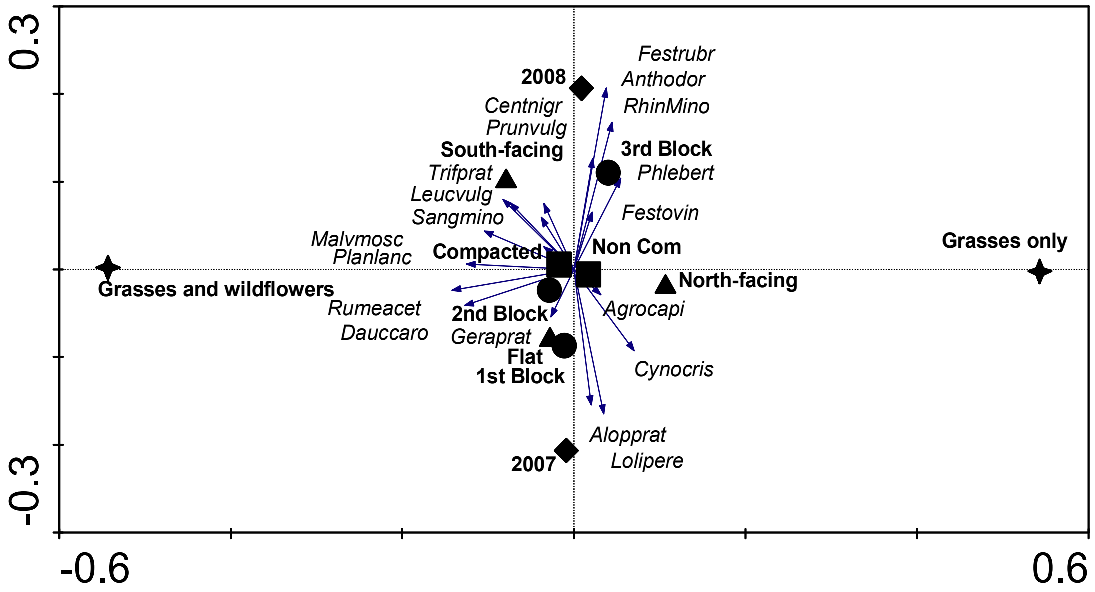

Figure 3.20. RDA of 2007 and 2008 data combined. The strength of the grass and wildflower treatment overpowers any other treatment influence so this was analysed separately. *Agrocapi = Agrostis capillaris, Alopprat = Alopecurus pratense, Anthodor = Anthoxanthum odoratum, Cynocris = Cynosurus cristatus, Dauccaro = Daucus carota, Festovin = Festuca ovina, Festrubr = Festuca rubra, Leucvulg = Leucanthemum vulgare, Lolipere = Lolium perenne, Malvmosc = Malva moscata, Phlebert = Phleum bertolonii, Planlanc = Plantago lanceolata, Prunvulg = Prunella vulgaris, Rhinmino = Rhinanthus minor, Rumeacet = Rumex acetosa, Sangmino = Sanguisorba minor ssp. minor, Trifprat = Trifolium pratense.*

Table 3.17. Partitioning of the variance of 2007 and 2008 data combined.

Treatments	%	F-ratio	p-value
Block	2	4.234	0.002
Aspect	3.3	5.841	0.002
Soil compaction	1.9	6.629	0.002
Seed mixture	29.5	105.287	0.002
Date	4.6	16.394	0.002
Interactions	11.6	8.261	0.022
Total inertia	53.2	8.261	0.002

3.3.8.2 Grasses-only plots 2007 and 2008

When the data was split into grasses-only and grasses and wildflowers, the relationships were easier to see. The first axis of the PCA looking at the grasses-only plots, explained 27.8 % of the variation and the second axis explained 13.2 % of the variation. However, the difference between the 2007 and 2008 data explained the majority of the species composition. The RDA in Figure 3.21 showed the sampling date was clearly influencing the first axis. More species were found in 2008, so the species were generally found to the left of the graph. The abundance of *L. perenne* and *C. cristatus* was greater in 2007. 14.1 % of the variation was explained by the sampling date however all treatments were significant (Table 3.18). *R. minor*, *F. rubra* and *F. ovina* were only found in 2008. *L. perenne* and *A. pratense* were found more frequently on the flat plots and in the first Block. *P. bertolonii* and *T. flavescens* were more associated with non-compacted and the second Block. *R. minor* was found most frequently on the slopes – north and south-facing plots, rather than the flat plots.

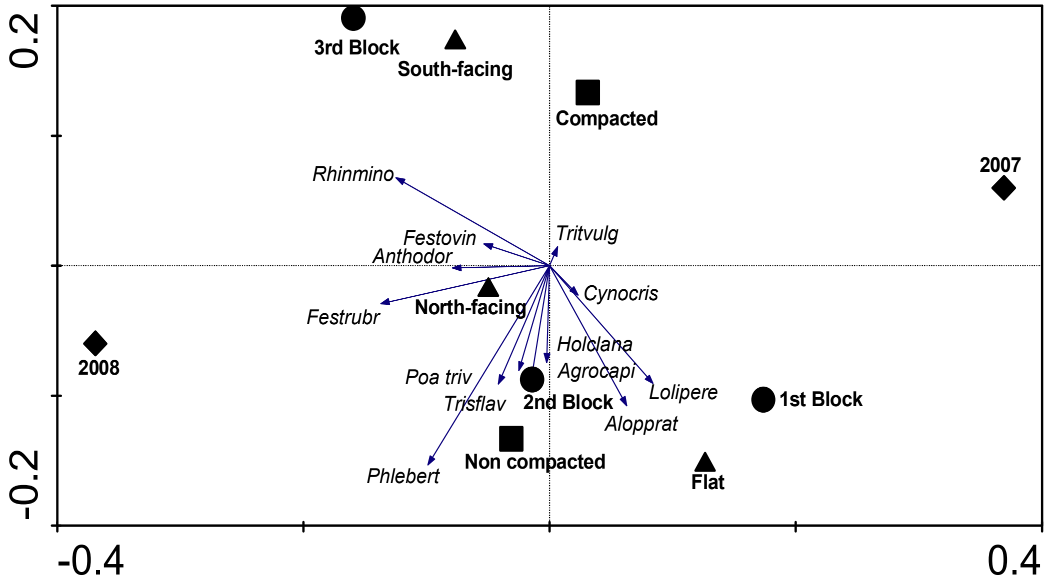

Figure 3.21. RDA of grasses-only data of 2007 and 2008 combined. The date was most significant. *Agrocapi = Agrostis capillaris, Alopprat = Alopecurus pratense, Anthodor = Anthoxanthum odoratum, Cynocris = Cynosurus cristatus, Festovin = Festuca ovina, Festrubr = Festuca rubra, Holclana = Holcus lanatus, Lolipere = Lolium perenne, Phlebert = Phleum bertolonii, Poa triv = Poa trivialis, Rhinmino = Rhinanthus minor, Trisflav = Trisetum flavescens, Tritvulg = Triticum vulgare.*

Table 3.18. Partitioning of the variance of the grasses-only data of 2007 and 2008 combined.

Treatments	%	F-ratio	p-value
Block	5.3	3.671	0.002
Aspect	4.7	3.264	0.002
Soil compaction	3.2	4.444	0.002
Date	14.1	19.633	0.002
Interactions	13.7	1.569	0.022
Total inertia	41	3.217	0.002

3.3.8.3 Grasses-only 2007

When the 2007 grasses-only plots were analysed separately the first axis of the PCA accounted for 30.1 % of the variation in the species composition and the second axis accounts for 19.8 % of the variation. Aspect accounted for 13.7 % of the variation in the species data and soil compaction and Block effects both accounted for around 7 %. The combination of treatments also contributed to a large amount of the variation in species composition and all the treatments were significant (Table 3.20). The bi-plot in Figure 3.22 has the species arrows going to the left of the graph, a pattern observed in Figure 3.21. *L. perenne, T. flavescens* and *A. pratensis* were more associated with the first and second Blocks, and the flat and south-facing plots. *P. bertolonii* was more frequently found on non-compacted plots. *C. cristatus* and *A. capillaris* were found more often on north-facing plots.

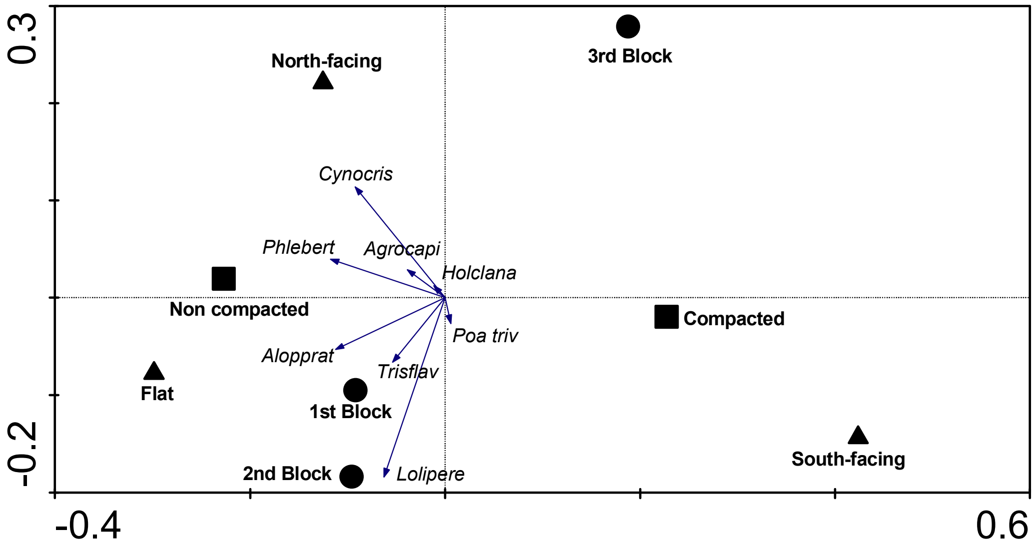

Figure 3.22. RDA of grasses-only plots in 2007. *Agrocapi = Agrostis capillaris, Alopprat = Alopecurus pratense, Cynocris = Cynosurus cristatus, Holclana = Holcus lanatus, Lolipere = Lolium perenne, Phlebert = Phleum bertolonii, Poa triv = Poa trivialis, Trisflav = Trisetum flavescens.*

Table 3.20. Partitioning the variance of the grasses-only plots in 2007.

Treatments	%	F-ratio	p-value
Block	7.3	2.427	0.002
Aspect	13.7	4.584	0.002
Soil compaction	7.1	4.765	0.002
Interactions	15.1	1.329	0.022
Total inertia	43.2	2.342	0.002

3.3.8.4 Grasses-only 2008 only

When the 2008 grasses-only plots were analysed separately the first axis of the PCA accounted for 28.6 % of the variation in the species composition and the second axis accounted for 17.4 % of the variation. All the treatments were significant on their own, but not the interactions (Table 3.20). In the bi-plot in Figure 3.23, the species were more evenly spread over the bi-plot, unlike the pattern in 2007. The bi-plot in Figure 3.22 had aspect forming a triangle, whereas in Figure 3.20, aspect was on one axis, going from south – north – flat. *L. perenne* was associated with the plots cut more often and *C. cristatus* was associated with the plots cut once – this was not substantiated by the ANOVA, where *L. perenne* frequency was higher on the plots cut once and *C. cristatus* greater in the plots cut more often. *P. bertolonii*, *P. trivialis* and *A. pratensis* were associated with non-compacted plots. *T. flavescens* was associated with flat plots and the first Block. The fertility scores were more associated with the 1st Block. *F. ovina* and *R. minor* were more associated with the third Block, compacted plots and north and south-facing plots, in the opposite direction to the increase in fertility. Shannon Diversity Index (H') increased towards the plots cut once, which was not substantiated by the ANOVA's, but was negatively associated with higher fertility scores and *L. perenne*.

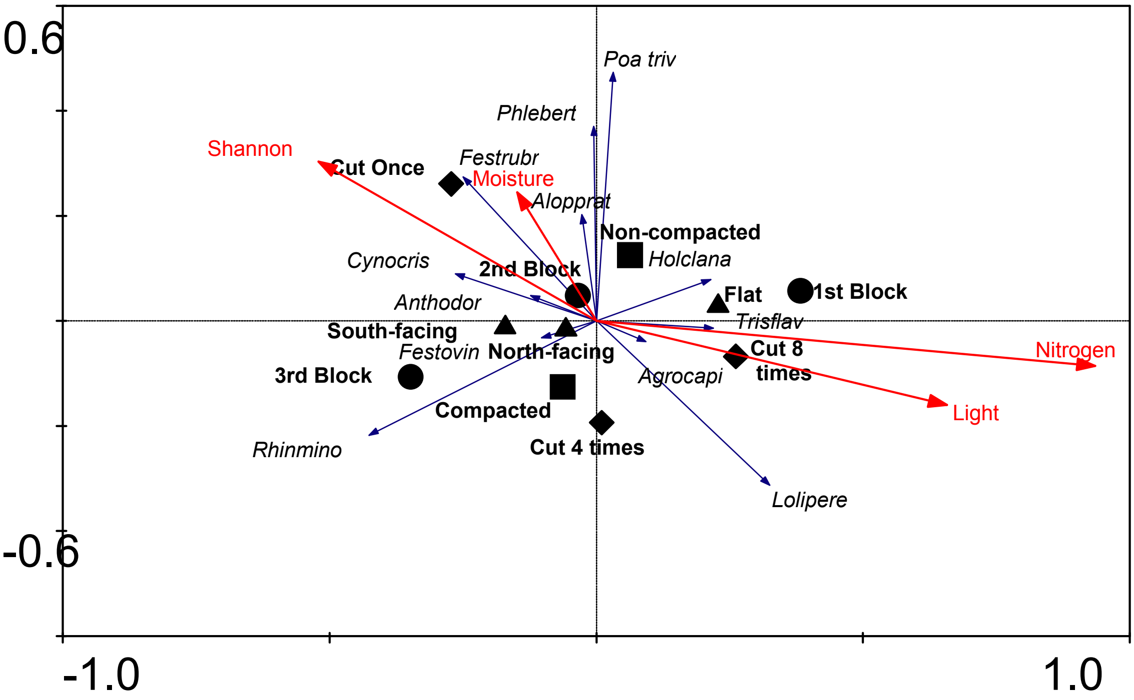

Figure 3.23. RDA of the grasses-only plots of 2008. *Agrocapi = Agrostis capillaris, Alopprat = Alopecurus pratense, Anthodor = Anthoxanthum odoratum, Cynocris = Cynosurus cristatus, Festovin = Festuca ovina, Festrubr = Festuca rubra, Holclana = Holcus lanatus, Lolipere = Lolium perenne, Phlebert = Phleum bertolonii, Poa triv = Poa trivialis, Rhinmino = Rhinanthus minor, Trisflav = Trisetum flavescens.*

Table 3.20. Partitioning of the variance of the grasses-only 2008 plots.

Treatments	%	F-ratio	p-value
Block	11.4	3.825	0.002
Aspect	5.9	1.983	0.012
Soil compaction	4.2	2.8	0.004
Management	9.8	3.268	0.002
Interactions	27.4	1.033	0.422
Total inertia	58.7	1.592	0.002

3.3.8.5 Grass and wildflower plots in 2007 and 2008

The first axis of the PCA looking at the grass and wildflower plots in both years, explained 18.8 % of the variation and the second axis explained 15.9 % of the variation. Unlike the grasses-only plots, the sampling date was not as significant a factor. The RDA in Figure 3.24 showed that all treatments were having an influence on the species composition. Date explained 5.8 % of the variation, whereas aspect explained 7.5 % and soil compaction explained 4.4 % of the variation and all the treatments were significant (Table 3.21). *R. acetosa*, *A. pratensis* and *L. perenne* had greater frequency in 2007, and *F. rubra* was only found in 2008. *C. cristatus* and *P. bertolonii* were more associated with north-facing plots. *A. odoratum* and *R. minor* were more associated with compacted plots. A large number of wildflowers were found more frequently on south-facing plots: *C. nigra*, *S. minor*, *Galium mollis*, *C. majus*, *L. vulgare*, *Malva moscata* and *P. lanceolata*.

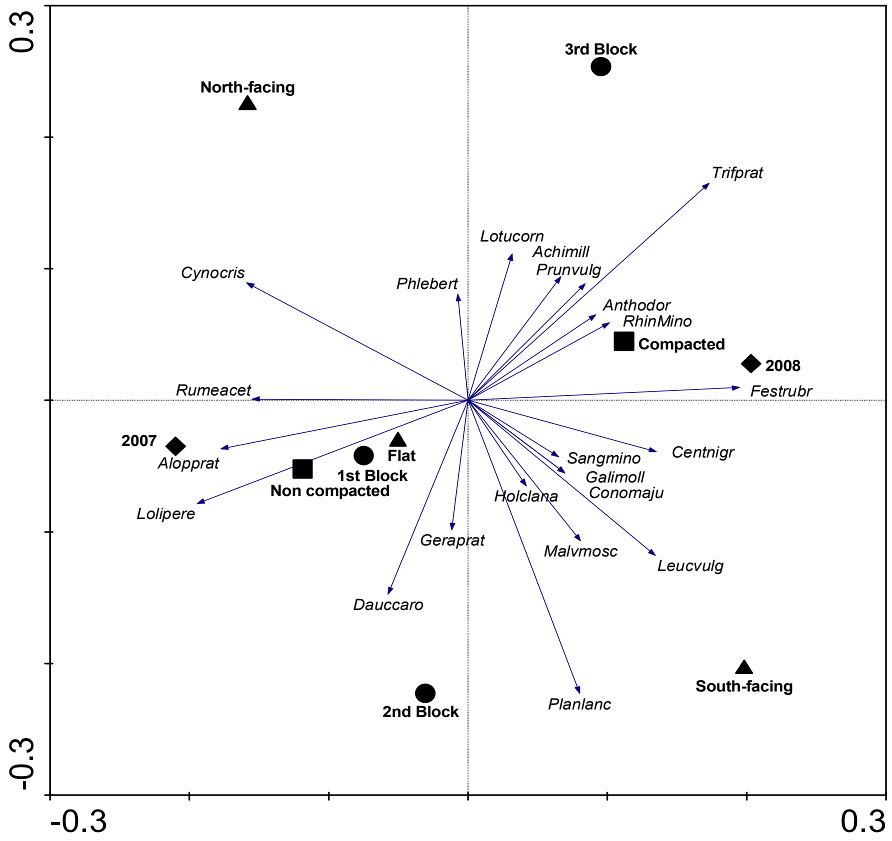

Figure 3.24. RDA showing 22 species from the combined 2007 and 2008 grass and wildflower plots. *Achimill = Achillea millefolium, Alopprat = Alopecurus pratense, Anthodor = Anthoxanthum odoratum, Centnigr = Centaurea nigra, Conomaju = Conopodium majus, Cynocris = Cynosurus cristatus, Dauccaro = Daucus carota, Festrubr = Festuca rubra, Galimoll = Galium mollugo, Geraprat = Geranium pratense Holclana = Holcus lanatus, Leucvulg = Leucanthemum vulgare, Lolipere = Lolium perenne, Lotucorn = Lotus corniculatus, Malvmosc = Malva moscata, Phlebert = Phleum bertolonii, Planlanc = Plantago lanceolata, Prunvulg = Prunella vulgaris, Rhinmino = Rhinanthus minor, Rumeacet = Rumex acetosa, Sangmino = Sanguisorba minor ssp. minor, Trifprat = Trifolium pratense.*

Table 3.21. Partitioning the variance in the grasses and wildflowers plots of the 2007 and 2008 data combined.

Treatments	%	F-ratio	p-value
Block	5.7	3.864.	0.002
Aspect	7.5	5.09	0.002
Soil compaction	4.4	6.022	0.002
Date	5.8	7.808	0.002
Interactions	14.9	2.967	0.022
Total inertia	40.3	4.915	0.002

3.3.8.6 Grass and wildflower plots 2007

When the 2007 grass and wildflower plots were analysed separately the first axis of the PCA accounted for 25.3 % of the variation in the species composition and the second axis accounted for 17.1 % of the variation. Aspect accounted for 12.8 % of the variation in the species composition, Block accounted for 12.8 % and soil compaction only accounted for 5.9 %. However, the combination of the treatments contributed to a large amount of the variation in species composition and all the treatments were significant (Table 3.22). The bi-plot in Figure 3.25 showed that *Geranium pratense*, *M. moscata* and *D. carota* were found more often on the south-facing plots. *P. lanceolata* and *L. vulgare* preferred flat and south-facing plots. *L. perenne*, *P. trivialis* and *R. acetosa* were associated with flat and non-compacted plots. *C. cristatus* and *P. bertolonii* were more associated with flat and north-facing plots. *T. pratense*, *A. millefolium* and *L. corniculatus* were associated with compacted plots.

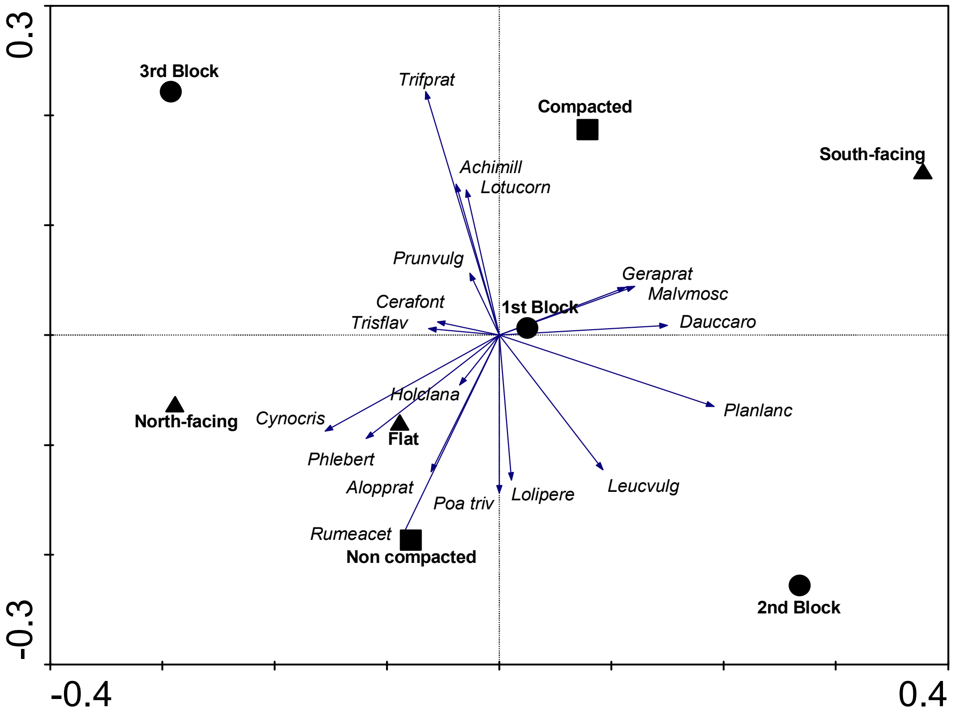

Figure 3.25. RDA of grass and wildflower plots of 2007, showing 18 species. *Achimill = Achillea millefolium, Alopprat = Alopecurus pratense, Cerafont = Cerastium fontanum, Cynocris = Cynosurus cristatus, Dauccaro = Daucus carota, Geraprat = Geranium pratense, Holclana = Holcus lanatus, Leucvulg = Leucanthemum vulgare, Lolipere = Lolium perenne, Lotucorn = Lotus corniculatus, Malvmosc = Malva moscata, Phlebert = Phleum bertolonii, Planlanc = Plantago lanceolata, Poa triv = Poa trivialis, Prunvulg = Prunella vulgaris, Rumeacet = Rumex acetosa, Trifprat = Trifolium pratense, Trisflav = Trisetum flavescens.*

Table 3.22. Partitioning the variance of the grass and wildflower plots of 2007.

Treatments	%	F-ratio	p-value
Block	11.1	3.799	0.002
Aspect	12.8	4.393	0.002
Soil compaction	5.9	4.021	0.002
Interactions	19.2	1.877	0.022
Total inertia	49	2.954	0.002

3.3.8.7 Grasses and wildflowers 2008

When the 2008 grass and wildflower plots were analysed separately the first axis accounted for 20.7 % of the variation and the second axis accounted for 12.7 % of the variation. However, only aspect was significant when the variances were partitioned, yet only explaining 6.9 % of the variation (Table 3.23). In this case, by separating the seed mixture and sampling date, the other treatments became less significant, not more. The treatments in 2007 were more significant than in 2008. The bi-plot in Figure 3.26 shows *P. lanceolata*, *L. vulgare* and

C. nigra were found most frequently on south-facing plots and *P. bertolonii*, *R. acetosa*, and *L. perenne* were found more frequently on north-facing plots. In 2007, *P. lanceolata* and *L. vulgare* were at right angles to the flat and south-facing axis. In 2008, these species were clearly associated with both flat and north-facing plots. Although Block was not significant, *S. minor* and *P. vulgaris* were more often found on the 3rd Block, with an increase in fertility being negatively associated. An increase in diversity was associated with *T. pratense* and on the plots cut 4 times. This was also negatively associated with increasing levels of fertility.

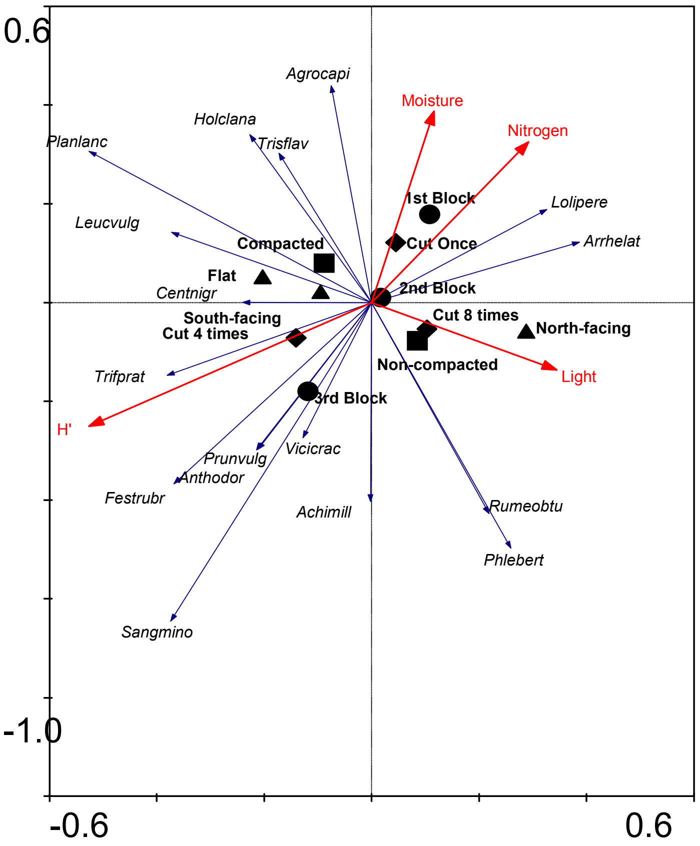

Figure 3.26. RDA of grass and wildflower plots of 2008, showing 17 species. *Achimill = Achillea millefolium, Agrocapi = Agrostis capillaris, Anthodor = Anthoxanthum odoratum, Arrhelat = Arrhenatherum elatius, Centnigr = Centaurea nigra, Festrubr = Festuca rubra, Holclana = Holcus lanatus, Leucvulg = Leucanthemum vulgare, Lolipere = Lolium perenne, Phlebert = Phleum bertolonii, Planlanc = Plantago lanceolata, Prunvulg = Prunella vulgaris, Rumeobtu = Rumex obtusifolius, Sangmino = Sanguisorba minor ssp. minor, Trifprat = Trifolium pratense, Trisflav = Trisetum flavescens, Vicicrac = Vicia cracca.*

Table 3.23. Partitioning the variance of the grass and wildflower plots of 2008.

Treatments	%	F-ratio	p-value
Block	11.4	3.825	0.002
Aspect	5.9	1.983	0.012
Soil compaction	4.2	2.8	0.004
Management	9.8	3.268	0.002
Interactions	27.4	1.033	0.422
Total inertia	58.7	1.592	0.002

3.3.8.8 Species composition of 2008

Although the treatment differences in the grass and wildflower plots of 2008 were not significant on their own, when the dataset was analysed together all of the treatments became significant (Table 3.24). Plus, the interactions that were not significant in the grasses-only plots were now significant. Obviously the seed mixture treatment dominated the first axis; however, a few patterns could be discerned and were significant. The bi-plot in Figure 3.27 shows that grasses were more associated with the north-facing aspect (i.e. *P. bertolonii* and *A. pratensis*) and a large number of wildflowers were more associated with the south-facing aspect: *A. millefolium*, *V. cracca*, *P. vulgaris*, *T. pratense*, *M. moscata*, *L. vulgare* and *S. minor*. *L. perenne*, *A. capillaris*, *H. lanatus* and *P. trivialis* were associated away from south-facing plots, between flat and north-facing plots. *R. minor* was more associated with the third Block, compacted plots and on north and south-facing plots – this was substantiated by the results of the ANOVA's and Kruskal Wallis. *R. acetosa*, *D. carota* and *P. lanceolata* were associated with south-facing and flat plots. The Shannon Diversity Index (H') was greater in the grass and wildflower plots. Compaction only accounts for 1.9 % of the variation in the data, which does not agree with the PCA analysed in Minitab where only compaction was a significant factor.

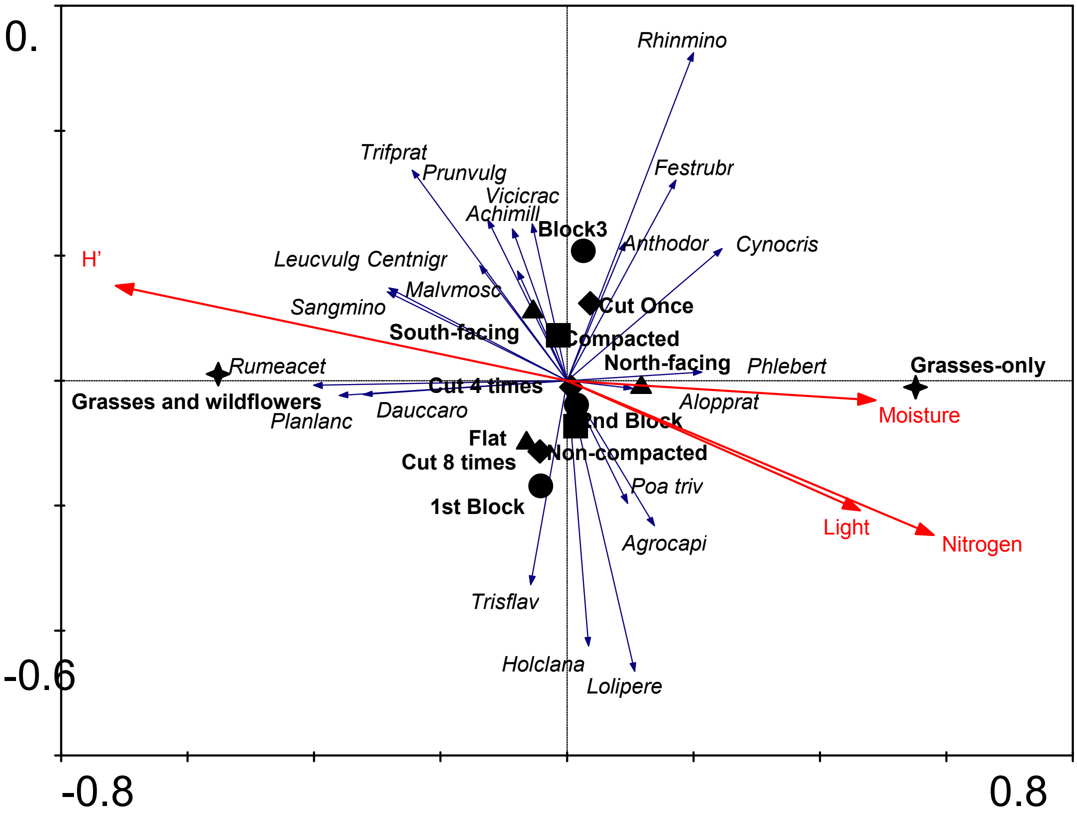

Figure 3.26. RDA of 2008, showing 22 species. *Achimill = Achillea millefolium, Agrocapi = Agrostis capillaris, Alopprat = Alopecurus pratense, Anthodor = Anthoxanthum odoratum, Centnigr = Centaurea nigra, Cynocris = Cynosurus cristatus, Dauccaro = Daucus carota, Festrubr = Festuca rubra, Holclana = Holcus lanatus, Leucvulg = Leucanthemum vulgare, Lolipere = Lolium perenne, Malvmosc = Malva moscata, Phlebert = Phleum bertolonii, Planlanc = Plantago lanceolata, Poa triv = Poa trivialis, Prunvulg = Prunella vulgaris, Rhinmino = Rhinanthus minor, Rumeacet = Rumex acetosa, Sangmino = Sanguisorba minor ssp. minor, Trifprat = Trifolium pratense, Trisflav = Trisetum flavescens, Vicicrac = Vicia cracca.*

Table 3.24. Partitioning the variance of 2008 data.

Treatments	%	F-ratio	p-value
Block	3.4	2.856	0.002
Seed mixture	30.5	51.901	0.002
Aspect	3.2	2.742	0.002
Soil compaction	1.9	3.297	0.002
Management	2.9	2.442	0.002
Interactions	19.2	1.457	0.002
Total without Interactions	41.9	8.91	0.002
Total inertia	61	3.513	0.002

3.3.9 General trends in the species composition

L. perenne, *C. cristatus*, *A. pratensis* and *A. capillaris* generally preferred north-facing and flat plots. *P. bertolonii*, *R. acetosa*, *L. perenne* and *P. trivialis* preferred the non-compacted plots. A number of species had shown some association with the compacted plots: *A. millefolium*, *R. minor*, *T. pratense*, *A. odoratum* and *H. lanatus*. The third Block had species associated with it that preferred lower fertility, shown by the fertility scores more associated with the first and second Blocks. *R. minor*, *S. minor*, *P. vulgaris* and *T. pratense* were more associated with the 3rd Block. Finally, a large number of wildflowers were associated with south-facing and flat plots: *L. vulgare*, *P. lanceolata*, *D. carota*, *C. nigra*, *S. minor* and *M. moscata*. The introduction of the cutting regime in 2008, begun to change the species composition, since there were clearly differences between the 2007 and 2008 data set. However, the trends with the management treatment were hard to pick out. *T. flavescens* and *T. pratense* were more associated with the plots cut 4 times. An increase in moisture tolerant plants was associated with the plots cut once. The ANOVA's showed that *C. cristatus* preferred the plots cut more often and *L. perenne* the plots cut once, but this trend was opposite to that seen in the RDA bi-plots. In the ANOVA's Shannon Diversity Index (H') increased in the plots cut 8 times, but this trend wasn't seen in the RDA bi-plots. There was a large difference in the general pattern seen between the grasses-only RDA bi-plots of 2007 and 2008. As well as the management treatment, the introduction of *R. minor* may have begun to alter the species composition. *Festuca ovina* was not found in 2007 but established in 2008 after the addition of more seed. It is found in association with *R. minor*.

3.4 Discussion

3.4.1 Species establishment

1) What species established from the seed mixture?

22 species established in 2007, and with a seed addition in September 2007, another 8 species established from the seed mixture in 2008. The species that did not establish were those more associated with lower fertility levels, and species that were less competitive or requiring constant grazing, i.e. *Briza media*, *Leontodon hispidus* and *Silene dioica* (Grime *et al*. 1988; Smith *et al*. 2000) (Table 3.5). Species richness increased across all plots from 2007 - 2008, and at all times the grass and wildflower plots had greater species richness than the grasses-only plots. However, this was due to more species being sown into the grass and wildflower plots: 42 species were sown in the grass and wildflower plots and only 10 in the grasses-only plots. *L. perenne, C. cristatus, P. bertolonii, D. carota, L. vulgare, P. lanceolata, R. acetosa* and *S. minor* were the commonest species and were found in the majority of the plots.

In a number of grassland experiments – either using seed mixtures from the start, establishing seed mixtures into grassland habitats or setting up experiments – a similar group of plant species have established. These species are also the same species that have established in the Mesocosm experiment. These species include *L. perenne*, *C. cristatus*, *F. rubra*, *A. odoratum*, *T. pratense*, *P. lanceolata*, *L. corniculatus* and *L. vulgare* (i.e. van Hecke *et al*. 1981; Wells *et al.* 1990; Mountford *et al.* 1993; Smith *et al.* 2000; 2008; Oglethorpe & Sanderson 1998; Hopkins *et al*. 1998; Leps *et al.* 2007). Pywell *et al.* (2003) explained that through using species-rich seed mixtures to reclaim land and recreate species-rich grassland, the same species establish from these diverse seed mixtures to create a monopoly of grassland habitats all including a similar suite of species. Hopkins *et al.* (1998) explained that it is the generalist species which develop from these seed mixtures, so that re-creating species-rich communities that conform to particular NVC communities is almost impossible. Since the aim is not to develop particular NVC communities, but rather to find a selection of species which would be useful to add into the standard seed mixture sown on roadside verges, this suite of species could be deliberately used on roadside verges as a mixture of species which will germinate well and produce a quick, dense, ground cover.

3.4.2 Species richness and diversity

2) Did the plots that were cut more frequently have greater species richness and diversity in comparison to the plots cut once in the summer?

In general, the plots that were cut 8 times throughout the year did have greater species richness and greater diversity than the plots that were cut 4 times and the plots that were cut once at the end of July. Greater species richness and diversity is found in grassland habitats where cutting regimes or grazing is regular (i.e. Bobbink & Willems 1993; Grime 2001; Bakker *et al.* 2002; Hovd & Skogen 2005; Smith *et al.* 2008). When all of the plots were looked at, it was clear that the management regime was beginning to influence the treatments to a certain extent, even after just one year.

3) Did the south-facing plots have greater species richness than the flat and north-facing plots?

It was thought that the south-facing plots would have greater species richness and diversity, however, in 2007, it was the flat plots that had the greatest diversity. However, by 2008 this trend had changed. In 2008, there were more species and greater diversity on the south-facing plots, in comparison to the flat and north-facing plots but only in the grass and wildflower treatment. Other studies have shown wildflowers were found more often on south-facing plots (Albertson 1937; Pahlsson 1974; Hutchings 1983; Amezaga *et al.* 2004). In the case of this experiment, the increase in wildflowers has lead to an increase in species richness and diversity on the south-facing plots.

4) Did the compacted plots have lower species richness and diversity compared to the non-compacted plots?

It was thought that the compacted plots may restrict plant growth – either decreasing biomass or preventing particular species from establishing, as has been shown other experiments (i.e. Masle & Passioura 1987; Bamford *et al.* 1991; Andrade *et al.* 1993; Montagu *et al.* 2001). In 2007, there was generally greater species richness in the compacted plots vs. the non-compacted plots. However, when the seed mixtures were separated, species richness and diversity was less in the compacted grasses-only plots. This trend continued into 2008, where there were more grass species in the non-compacted grasses-only plots, nevertheless, there were more wildflower species in the compacted grass and wildflower plots in comparison to the non-compacted grass and wildflower plots. This suggests that the grasses were more susceptible to compaction than the wildflowers were. Materechera *et al.* (1991) also showed that wildflowers were better at coping with compaction.

The management, aspect and soil compaction treatment acted independently of each other and also in combination. The cutting regime became more significant when looked at in combination with aspect: All the plots that were cut 8 times, plus the south-facing plots that were cut 4 times, had greater diversity that the south-facing plots that had only been cut once. The flat plots which were cut 8 times had significantly greater diversity than the north-facing plots that had been cut 4 times. And when all the treatments were combined: The majority of all the cut 8 times plots, plus the south-facing, compacted, cut 4 times plots and the north-facing, cut 4 times, compacted plots, had greater diversity than the south-facing, cut once plots in the compacted treatment. So, although south-facing plots generally had greater species richness and diversity, with the combination of lessening the cutting regime and soil compaction, the diversity was less in the compacted, cut once, south-facing plots. South-facing slopes are thought to be under greater stress – this combination can reduce the competitors and allow the stress-tolerators to increase (Pahlsson 1974; Kutiel & Lavee 1999), however, lessening the cutting regime will allow the more competitive species to dominate (Grime 1990; Rodwell 1992; Bobbink & Willems 1993; Grime 2001). Perhaps those species more adapted to compaction and those species preferring no management, will then dominate in this case. Had this experiment continued for longer, these trends were likely to have become more apparent.

5) Did the plots that were cut more frequently have greater abundance of *Rhinanthus minor* in comparison to the plots that were cut once?

R. minor was found more frequently in the plots that were cut 8 times and the plots cut 4 times, in comparison to the plots cut once. *R. minor* has a high light requirement and generally germinates in swards with lower biomass (Smith *et al.* 1996; Westbury & Dunnett 2007). *R. minor* is usually found in grasslands which have traditional management practises – including regular grazing. This keeps the biomass levels lower (Smith *et al.* 1996; Pywell *et al*. 2007; Smith *et al*. 2008). Since *R. minor* did not germinate well in the grass and wildflower plots which had greater biomass and did not germinate often in the plots only cut once, it would only be suitable to use this species in seed mixtures if the management aim included a cutting regime to reduce aboveground biomass.

3.4.3 Species composition and establishment

6) Did management, aspect and soil compaction influence species composition and species establishment?

There was a change in the species composition due to the cutting regime. In the first year the plots were cut four times, so this management treatment continued into the second year. In the second year, in a third of the plots, the management increased and in a third of the plots the management was decreased. Increasing the cutting frequency suppressed the growth of *L. perenne* and *P. lanceolata* whilst allowing *C. cristatus*, *L. vulgare* and *R. minor* to increase in abundance. *T. flavescens* and *T. pratense* were more associated with the plots cut 4 times. Mackie-Dawson (1999) and Evans (1971) showed that cutting reduced the number of tillers of *L. perenne*. Overall, it was becoming apparent that the less competitive species of grasses and wildflowers were being favoured by the cutting regimes, as supported by the literature (i.e. Mountford *et al.* 1993; Bobbink & Willems 1993; Harmens *et al.* 2004). Already, in just the space of one year, differences in composition were becoming significant. Experiments have shown that a change in management can have an influence on species composition very quickly (Pykälä *et al.* 2005; Hopkins *et al.* 1998). It would be expected that these differences would continue if the experiment had continued for longer, however, there will always be time restrictions due to the short length of PhD research. Other studies have emphasized that it takes a long time for grassland systems to adjust. The results from short-term experiments maybe misleading and the trends from this experiment will change over time (Gibson & Brown 1992; Bakker *at al.* 1996; Smith *et al.* 2008). For example, Gibson & Brown (1992) believe that grassland restoration will take 100 years before the system is natural and regulating.

The compaction treatment was influencing the species composition. A number of species were found more often in the non-compacted plots: *P. bertolonii*, *R. acetosa*, *S. minor*, *L. perenne* and *P. trivialis*. A number of species were found more often in the compacted plots:

A. millefolium, *R. minor*, *T. pratense*, *A. odoratum* and *H. lanatus*. Some species are better at coping with the effects of compaction than others (Elliot 1900; Russell 1997; Materechera *et al.* 1991; 1992).

7) Did species preferring warm, dry conditions establish on south-facing slopes and species preferring cold, wet conditions establish on north-facing slopes?

There was a difference in the plant communities establishing between the north and south-facing slopes, although most species were common and were found most of the plots. The differences were mainly due to changes in the frequency of the main species found in each plot. *L. perenne*, *C. cristatus*, *A. pratensis*, *A. capillaris* and *R. acetosa* generally preferred north-facing plots. A large number of wildflowers were more associated with south-facing plots: *L. vulgare*, *P. lanceolata*, *C. nigra*, *S. minor* and *M. moscata*. According to Grime *et al.* (1988) *R. acetosa* prefers north-facing slopes, and *L. vulgare*, *P. lanceolata*, and *C. nigra* are more commonly found on south-facing slopes. In addition, *M. moschata* and *C. nigra* likes sunlight so will prefer south-facing slopes (Hill *et al.* 1999; Grime *et al.* 1988) and *P. lanceolata* and *S. minor* do not like moist conditions and they have drought tolerance (Grime *et al.* 1988). So, slowly, over time, there are drought tolerant, sun-loving species establishing on the south-facing slopes.

3.4.4 Ellenberg Indicator Values

8) Did the north-facing plots have greater Ellenberg Fertility and Moisture Values and did the south-facing plots have greater Ellenberg Light Values?

When the Ellenberg Indicator Values were looked at, there were differences, a few obvious ones, and the others were probably down to the deliberate differences in the grasses-only and grass and wildflower seed mixtures. The grasses-only plots had greater fertility, greater light and greater moisture than the grass and wildflower plots. This was likely to be an artefact from the design of the experiment, so these differences are not meaningful.

The north-facing plots did not have greater fertility values in comparison to the south-facing plots, and actually it was the flat plots which had greater fertility values. There is a lot of runoff and leaching on slopes, meaning that the fertility levels may have remained higher in the flat plots where the rain would have slowly soaked into the soil, but lessened over time on the sloping plots (Pahlsson 1974; Kutiel 1992). However, it had already become clear that the third Block had a different set of species establishing, and the fertility values were much lower in the third Block in comparison to the first Block.

Throughout the Mesocosm experiment, there was a Block effect. There were less species and lower diversity in the first Block. Ellenberg fertility values were higher in the first Block and biomass was higher in the first Block in comparison the third Block. Fertility levels are associated with less species and lower diversity in all studies in which fertility has been measured (i.e. Thurston 1969; Marrs 1993; Mountford *et al*. 1993; White *et al*. 2004; Smith *et al*. 2000). Higher levels of fertility can lead to an increase in aboveground biomass (Mountford *et al.* 1993; Hopkins *et al.* 1998; Buckland & Grime 2000; White *et al*. 2004). A different set of species established in the third Block – *R. minor* was found in greater frequency in the third Block, along with *T. pratense* and *C. cristatus*, *S. minor* and *P. vulgaris*. *R. minor* will not establish in grasslands habitats which are too fertile (Pywell *et al*. 2007; Smith *et al*. 2008) and *C. cristatus* and *S. minor* prefer low fertility grasslands (Grime *et al.* 1988). *L. perenne* was found more often in the first and second Block, and this species often dominates in higher fertility grasslands (van Hecke *et al*. 1981; Mountford *et al.* 1993; White *et al.* 2004). This suggests that the soil in the third Block had lower fertility and so a different suite of species established.

There were no aspect differences as regarding the Ellenberg Light Values, although south-facing slopes are drier than north-facing slopes because they receive the most sunlight. The Ellenberg values for fertility and moisture were quite varied among the species and so it was easier to find significant differences. However, the light values only varied from 6 to 7 to 8 and the majority of the species had light values of 7. In this case, these species are found in habitats which are in the sunlight throughout the majority of day, regardless of whether they are found on north or south-facing cuttings (Hill *et al.* 1999). However, the north-facing plots did indeed have greater Ellenberg Moisture Values that the south-facing plots. This is in agreement with a number of studies that have seen the same response (Pahlsson 1974; Churchhill 1982; Kutiel & Lavee 1999). *L. perenne* has high moisture tolerance and was associated with north-facing slopes (Grime *et al*. 1988). *M. moschata* was only found on the south-facing plots and this had a very low moisture value of 3 (Hill *et al.* 1999). The plots that were cut once had higher moisture values. Pykälä (2005) showed that abandoned grasslands had lower species richness and this lead to the Ellenberg moisture values increasing.

3.4.5 Aboveground biomass

9) Did the treatments influence the aboveground biomass?

The amount of biomass produced varied throughout the year, and there was no difference in the amount of biomass produced between the 2007 and 2008 summer cut and the treatment effects remained the same. This shows that the amount of biomass produced was influenced by the time of year the cut was taken. The grass and wildflower treatment produced much greater amount of biomass than the grasses-only treatment, however, soil compaction made no difference to the amount of biomass produced at any point during the experiment. The influence of soil compaction on above and belowground growth is discussed in more detail in sections 4.3.4.5, 4.4.3 and 4.4.6.

The flat plots had greater biomass, and the north and south-facing slopes were relatively similar, although this fluctuated slightly throughout the experiment. However, this pattern was slightly different when the seed mixtures were looked at. The north-facing grass and wildflower plots did have greater biomass than the flat and south-facing plots. This pattern has been observed in other experiments (Pahlsson 1974; Kutiel & Lavee 1999; Bochet & Garcia-Fayos 2004). However, it was the flat plots in the grasses-only treatment that had greater biomass than the south and north-facing plots. Other experiments looking at aspect and biomass have shown that it is the wetter conditions that promote the increase in biomass (Pahlsson 1974; Kutiel & Lavee 1999; Bochet & Garcia-Fayos 2004). The flat plots, at some times of the year when the rainfall was high, became slightly waterlogged. Plus, the fertility values were greater in the flat plots, and higher fertility generally means greater biomass (Mountford *et al.* 1993; Hopkins *et al.* 1998; Buckland & Grime 2000; White *et al*. 2004).

10) Did the plots with greater species richness, greater diversity and more functional types have greater aboveground biomass?

When aboveground biomass, species richness and diversity were correlated, there was a significant relationship; however, these differences were all related to the differences in seed mixture. Species richness and diversity was greater in the grass and wildflower treatment, and aboveground biomass was also greater in the grass and wildflower treatment. The grasses-only treatment had lower species richness, lower diversity and also had lower biomass. Other studies have found a correlation between species richness, diversity and biomass (i.e. Scherer-Lorenzen *et al.* 2003; Spehn *et al.* 2000; 2005; Bullock *et al.* 2007). Many studies have shown that greater diversity means a greater use of the three-dimensional space above the ground (Naeem *et al.* 1994; Spehn *et al.* 2000; Spehn *et al.* 2005). This diversity - canopy relationship can also be related to different functional types. Tilman *et al.* (1997) explained that it is functional diversity, not species richness that relates to biomass. The grasses-only plots only contained one type of functional type – grasses – which also have a similar topological lifeform. However, the grass and wildflower plots contained a number of functional types: grasses, wildflowers and legumes – 3 different types and hence had greater biomass.

Wildflowers also come in a number of different lifeforms and there were obvious morphological differences between the main species in this experiment: For example, *P. lanceolata* is a rosette forming species, *D. carota* grew very tall and *S. minor* grew in and out of these species. Legumes are keystone species, some are drought tolerant, cold or heat tolerant (White *et al.* 2004). Thompson *et al.* (1996) used the Integrated Screening Programme (ISP) to assign species to different functional types. It was concluded that using functional types was a good way to explain vegetation structure. The grass and wildflower plots utilised a greater proportion of the aboveground canopy layer (see Photograph 3.3). In general, wildflowers form horizontal leaf surfaces while grasses have more erect leaf surfaces (Spehn *et al.* 2000). Spehn *et al.* (2000; 2005) showed that plots containing greater species richness, diversity and functional types utilised three-dimensional space and intercepted a greater amount of sunlight better than plots containing one functional type. A dense, thick cover of herbaceous vegetation is needed to prevent rainfall from hitting the ground and improving surface erosion and run-off (i.e. Elwell & Stocking 1976; Andres *et al.* 1996; Fullen *et al.* 1998; Blight 2003; Morgan 2007). So, a seed mixture containing a range of functional types will have greater biomass, with a denser canopy, and help to prevent surface erosion and runoff.

But, it must be kept in mind that an increase in fertility leads to an increase in biomass, where a number of competitive, larger species dominate (Mountford *et al.* 1993; White *et al.* 2004; Hodgson *et al.* 2005). Buckland & Grime (2000) showed that during the course of their experiment, the higher fertility plots became dominated by *U. dioica*, *R. obtusifolius* and *Elytrigia repens*. Roadside verges can be very fertile, and become dominated by these species and by *A. elatius* and *D. glomerata* – these species are also tall but can form monocultures of one life-form (Grime 1990; Rodwell 1992; Buckland & Grime 2000). Morgan (2007) showed that taller plants with little understorey did not intercept rainfall as well as an herbaceous dense canopy. These monocultures will forms clumps of vegetation with gaps underneath, where runoff can be concentrated (Blight 2003; Morgan 2007). In order to prevent the taller, competitive monocultures from establishing, an appropriate management / cutting regime is needed. Defoliation forms a dense, extensive sward with "dense-species packing" (Grime 1990; Kahmen & Poschlod 2008) and favours legumes and rosette-forming species (Bayfield *et al.* 1992). Cutting is required to encourage species richness and diversity (i.e. Huston 1994; Grime 2001; Harmens *et al.* 2004; Antonsen & Olsson 2005; Pykälä 2005; Marini *et al.* 2008; Smith *et al.* 2008), promoting structural diversity (Wells *et al.* 1989) and differentiating leaf layers (Spehn *et al.* 2000) and can therefore improve slope stability by reducing surface erosion and rainfall splash.

11) Did *Rhinanthus minor* influence the biomass of the plots? Did *Rhinanthus minor* influence the species diversity and composition of the sward?

R. minor established in the plots with the lower biomass. Studies have shown the *R. minor* germinates in swards with low aboveground cover (Smith *et al.* 1996; Westbury & Dunnett 2007). *R. minor* established in the grasses-only plots, the plots cut most frequently and the third Block - which was also where there was less biomass. The flat plots produced the greatest biomass and this was where *R. minor* had been found least. As *R. minor* did not establish in all of the plots it was not possible to statistically prove whether *R. minor* influenced the biomass or species composition, however, *F. ovina* and *R. minor* were associated in the RDA bi-plot in Figure 3.23. The pattern shown in the 2008 bi-plot (Figure 3.23) was very different to the pattern in the 2007 bi-plot (Figure 3.22) where all of the species arrows are pointing to the left of the bi-plot, whereas in the 2008 bi-plot, the species arrows are distributed around the graph. *F. ovina* and *F. rubra* only established in the second year, and other competitive species were lessened in the second year, i.e. *L. perenne* and *C. cristatus* where as *P. bertolonii* increased. This could be due to the inclusion of the management treatment, but could also be a sign that *R. minor* was reducing the biomass of *L. perenne* and *C. cristatus* (Matthies & Egli 1999; Westbury & Dunnett 2007) and allowing the other grass species to become established.

3.4.6. Future work

It would be interesting to set up an experiment looking at a range of functional types and diversity, in order to measure light interception, canopy height and gaps in the canopy to find out which mixture of species makes best use of three-dimensional space and hence have greater slope stabilising potential. Vertical canopy measurements could be taken, and a rainfall regime could be implemented, measuring the amount of runoff.

This experiment was set up at the beginning of the PhD with little knowledge of the management of roadside verges: knowledge that was gained through the Highways Agency placement (see Chapter Five). A future experiment could be set up using the standard HA seed mixture as the grasses-only treatment (which includes *T. repens*) and with a species-poor and species-rich wildflower mixture. The management treatment could specifically replicate the HA management procedures: i.e. no cut, one cut every three years, one cut a year and two cuts a year, plus a four and eight cut treatment to show how cutting regimes are required to improve seedling establishment and increase species richness and diversity.

3.5 Conclusion

In conclusion, it is better to sow a mixture of species on roadside verges – which include a number of functional types and life-forms, suited to different aspects and soil compaction. The management of roadside verges needs to improve, so that a regular cutting regime is implemented. A suitable mixture would include *L. vulgare* which has a good establishment rate; rosette forming species such as *P. lanceolata*; species with good canopy cover such as *R. acetosa*; taller herbaceous plants like *D. carota*; and legumes such as *S. minor, L. corniculatus* and *T. pratense* which can grow in amongst the plants. Grasses are needed which form a close, dense sward close to the ground, such as *F. rubra* and *F. ovina*, plus quick growing species such as *L. perenne* for the initial ground cover. In addition, *P. lanceolata* and *R. acetosa* remain wintergreen, as do the grasses (Grime *et al.* 1988), and *D. carota* and *S. minor* have a long, deep tap root. *T. pratense* grew well in the compacted treatment. *P. lanceolata* is favoured by south-facing slopes (along with a number of wildflowers) and *R. acetosa* is favoured by north-facing slopes (along with a number of grasses), so there would be good ground cover on all slopes throughout the year and hence improve slope stability. For the successful establishment of these species a cut of once a year, minimum, would be required, and preferably more if possible.

4. Chapter Four. Experimental Work. Part C

The Mesocosm experiment, Belowground section

4.1 Introduction

Vegetation can reduce slope instability problems by two main ways – by the aboveground canopy cover protecting the soil surface, and by the root systems binding the soil particles together and increasing soil strength (i.e. Elwell & Stocking 1976; Waldron 1977; Waldron & Dakessian 1981; 1982; Gray 1995; Nilaweera *et al.* 1999; Mitchell *et al.* 2003; Danjon *et al.* 2007). In order to reinforce slopes against shallow-seated failures, the roots need to grow to a depth of at least 0.75 m (Wu *et al.* 1988; Waldron & Dakessian 1981; 1982). Tree and shrub roots are thicker and generally thought to be longer than the root systems of grasses and wildflowers, however, this has been questioned in a few studies looking at the rooting depth of trees and shrubs. *C. monogyna* doesn't root deeper than 0.5 m and *Quercus* species take between 3 – 5 years of growth before they reach below 0.7 m in depth (Greenwood *et al.* 2001; Norris 2005; Cazzuffi & Crippa 2005). Often the thinner roots are better at increasing soil strength than the thicker roots, which has lead to a number of studies concluding that grasses and wildflowers were good at stabilising slopes (Waldron & Dakessian 1981; 1982; Brook *et al.* 1995; Operstein & Frydman 2000; Cazzuffi *et al.* 2006). A few studies have looked at root topology and how this relates to soil strength and slope stability (Dupuy *et al.* 2005; Ennos 1989; Stokes *et al.* 1996). Dupuy *et al.* (2005) showed that an increase in lateral branches and secondary growth can lead to greater soil strength and slope stability. Ennos (1989) explained that a large number of fibrous roots has a large surface area and hence can resist a greater force, although Stokes *et al.* (1996) pointed out that rooting depth was also very important and a tap root with vertical laterals would also resist rotational movement well.

Grass / monocotyledonous species are quick to establish and they have a relatively shallow, fibrous root system that can form a dense mat on the surface of the soil (Albertson 1937; Bayfield *et al.* 1992; Lauenroth & Gill 2003), generally not growing deeper than 0.3 m (Berendse 1981; 1983). The root systems of grasses are mainly unbranched primary roots (adventitious roots), but some grasses have roots which grow further down into the soil. Grass roots tend to be small in diameter and generally don't develop cortex thickening (Fitter 1991; Robinson *et al.* 2003; Hutchings & John 2003; Lauenroth & Gill 2003). *L. perenne*, for example, can grow roots to 0.15 m after 5 weeks of sowing and in one experiment, grew to 0.6 m after 3 months (Garwood 1967). Herbaceous / dicotyledonous species (i.e. wildflowers) tend to have a larger tap root which grows directly into the ground, with a number of smaller, lateral roots growing sideways, and from this, smaller secondary laterals can develop. The roots tend to be larger in diameter and can develop cortex thickening, but with a well branched smaller secondary root system (Fitter 1991; Robinson *et al*. 2003; Hutchings & John 2003; Lauenroth & Gill 2003). The differences in morphology allow the root systems of grasses and wildflowers to utilise different areas of the soil strata (Albertson 1937; Weaver 1958).

There is a measured differentiation of the rooting systems of plants in order to reduce root competition. Berendse (1979; 1983) showed that when grown together, *P. lanceolata* and *A. odoratum* had complete separation of the rooting systems – *P. lanceolata* growing to 0.5 m and *A. odoratum* growing in the top 0.10 m. Levang-Britz & Biondini (2002) showed that the root parameters of grasses, wildflowers and shrubs could be separated into distinct groups. Both van der Krift & Berendse (2002) and Wardle & Peltzer (2003) found that *L. perenne* had a finer and more fibrous root system than the roots of other grasses and wildflowers. Wardle & Peltzer (2002) showed that *L. vulgare* and *L. perenne* rooted at different depths due to niche separation. The root system of *L. perenne* was mainly found in the top 0.1 m, whereas the roots of *L. vulgare* were mainly found in the 0.2 – 0.3 m layer. Root and shoot biomass allocation was different in all of the 10 species studied, and competition was greatest in the top 0.1 m of soil where the majority of the roots were found.

It would be fair to assume that the greater the number of species growing together, the greater the root biomass, and therefore soil strength potential (Fornara *et al.* 2009). Although, Lamb (2008) did not find a relationship between root biomass, diversity and species richness, but concluded that this was due to the depth that root systems could grow to in order to lessen the impacts of neighbouring root competition. Lamb suggested that if fine root biomass could be measured, that this would increase with greater diversity. Casper & Jackson (1997) believe that depth and biomass of root systems are continually underestimated and it is very difficult to measure if root systems overlap. However, Caldwell *et al*. (1991) and Caldwell *et al.* (1996) used ultraviolet to distinguish root systems and showed that grass and shrub roots tended to avoid each other. Therefore, it is quite possible that increased competition in a species-rich grassland community on roadside verges could drive an increase in the depth that roots could grow to and increase the root biomass produced; this could then lead to an increase in soil strength and aid slope stability.

Due to the difficulty in sampling root systems, there hasn't been a huge amount of research on the rooting depths and structures (topology) of plants, especially in this country (Fitter & Stickland 1992). In Britain, research into the roots of agricultural crops is widespread, especially research into the effects of soil compaction of the above and below-ground yield of crops (i.e. Goss 1977; Bennie & Botha 1986; Masle & Passioura 1987; Bengough & Mullins 1990; Bamford *et al.* 1991; Materechera *et al.* 1991; Waisel *et al.* 1991; Young *et al.* 1997; Montagu *et al.* 1998; Croser *et al.* 2000; Clark *et al.* 1996; 2001). On the other hand, very little is known about the rooting depths in natural grassland habitats, or the rooting depths of individual species in Britain. McCully (1999) pointed out that much more is understood about the rooting habits of seedlings, but there was little documented research on mature plants. What we do know about rooting depths of British species comes from root experiments looking at nutrient acquisition or competition experiments set up in pots, although not necessarily from this country (but using same plants) (i.e. Boot & Mensink 1990; van der Krift & Berendse 2002; Levang-Britz 2002; Craine *et al.* 2003). Wardle & Pelzer (2003) looked at interspecific interactions between species, and grew plants in 0.3 m pots. All species (i.e. *L. perenne*, *C. arvense*, *L. vulgare*) had no trouble reaching the bottom of the pots after approximately 3 months. On the other hand, Weaver (1925; 1958a; 1958b) spent much of his life looking at the rooting habits of grassland species growing in the Prairies. He dug great trenches, excavated the soil and took away large monoliths to get rooting depths and root structures in situ. Prairie grasses had a maximum rooting depth of 6 feet and the perennial wildflowers, with extensive tap roots and spreading branches, reached far deeper than this: Alfalfa for example reached 9 m. Weaver also commented on the soil binding properties of the roots and how well the roots prevented soil erosion. Sun *et al.* (1997) used Weavers results and took another large monolith obtained from the field, to create root drawings to quantify root depth, root density and root length. Grasses had the shallowest depth and wildflowers grew deeper, however, deep-rooted wildflowers had less density per depth.

On a global scale, the maximum rooting depths of temperate grassland have been estimated at 2.6 m in comparison to tropical grassland at 15 m. *R. crispus* and *C. scabiosa* grassland in Germany reached depths of 3.3 m (Canadell *et al.* 1996). Canadell *et al.* (1996) searched through all references on global rooting depths and exclaimed "Roots commonly reach far deeper into the soil than the traditional view has held up to now", although Jackson *et al.* (1996) showed that temperate grasslands had 80 – 90 % of roots in the top 0.3 m of soil. Nepstad *et al.* (1994) showed that managed pasture in the Amazon had root depths up to 8 m, with most roots in the top 0.1 m, but the previous estimated rooting depth was 0.6 m (Nepstad *et al.* 1994). Schenk & Jackson (2002) looked at 1300 plant species from around the world and estimated that *Asteraceae* had a mean rooting depth of 1.17 m and *Poaceae* had a rooting depth of 1.02 m. It is very likely that the rooting depths of British grassland plant species have been underestimated (Canadell *et al.* 1996).

For an introduction to above and belowground growth and soil compaction, see Section 1.7

Bulk density can be related to soil compaction since an increase in bulk density occurs with dense packing of soil particles – decreasing void space. An increase in bulk density does not universally mean that the soil is compacted – but the mechanical compaction of soil, i.e. during the construction of roadside embankments, is likely to physically compress the soil particles leading to an increase in bulk density (Barley & Greacen 1967). The commonest method of estimating soil strength is to use a Penetrometer – a steel probe inserted into the ground giving a pressure resistance reading (Bengough & Mullins 1990; Atwell, 1993). Penetrometer resistance readings are often between two – eight times greater than the resistance experienced by roots since roots are smaller and can grow through pores smaller than a Penetrometer probe (Bengough & Mullins 1990; Barley & Greacen 1967), however, Atwell (1993) concluded that Penetrometer readings give a good estimate of the soil strength encountered by roots. In the majority of soil compaction experiments, bulk density and Penetrometer resistance have been measured (Taylor & Burnet 1963; Thompson *et al.* 1987; Masle & Passioura 1987; Materechera *et al.* 1992; Andrade *et al.* 1993); however, others have just measured one or the other (i.e. Veihmeyer & Hendrickson 1948; Zimmerman & Kardos 1960; Barley *et al.* 1965). It is better to measure both to get an accurate estimate of soil strength in relation to plant growth restriction and slope stability.

As the roots of plants grow through the soil and attach to soil particles it is very difficult to remove soil from the roots. This has made the study of root systems quite difficult and labour intensive. A number of methods have been employed to make this process easier, but all methods have something which makes them awkward to use. Several methods involve in-situ processes – i.e. cutting down into the soil and excavating around the root system. This process takes a long time and involves directly counting the roots. Rhizotron techniques can be used, where a see-through tube or window is installed into an experiment to watch the growth of roots over time (Andrén *et al*. 1996). This is very expensive and is mainly used for small experiments. Monoliths can be made, where a box is prepared with pins through it, keeping the roots in place (Nelson & Allmaras 1969; Schuurman & Goedewaagen 1971). However, this is bulky and time consuming. For the purposes of the Mesocosm experiment – the information that is needed is root length, diameter and root weight. To calculate root length – the roots can be put into water with a grid of the top and the number of times the root hits the grid can be counted (Newman 1965). Again, this is too time consuming so impossible for this experiment. Measuring the diameter of all of the roots would also take too long. So, we are left with root weight / mass. To do this, the standard method is to take soil cores using an auger and roots are washed, collected and dried. This is labour intensive, but relatively cheap and easiest to do for the purposes of this experiment (Schuurman & Goedewaagen 1971).

Soil cores give accurate data on the depth to which plant species grow (Schuurman & Goedewaagen 1971; McCully 1999). However, we can't obtain information on branching patterns or diameters of roots, but we can infer improved soil strength from the roots if they are found to be growing in that layer. Others methods can directly measure the soil strength given by the roots, but it was not possible to do root tensile strength methods, direct shear tests or pull-out tests as these were too costly (Wu *et al.* 1988; Waldron 1977; Waldron & Dakessian 1981; 1982; Operstein & Frydman 2000; Cazzuffi *et al.* 2006 Danjon *et al*. 2007; Tosi 2007). It would have required transporting large parts of the experiment to another laboratory and the original experiment wasn't designed with this in mind.

In this chapter, the rooting depths of plant species growing in the Mesocosm experiment were investigated, along with soil strength. Soil cores were taken and Penetrometer resistance, Bulk density and moisture contents were measured, with the aim to answer these questions:

1) What depth did the plant roots grow to? Did the aspect and seed mixture treatments influence root mass and root depth?
2) Did the compaction treatment reduce root mass and root depth? Did the roots grow through the topsoil and into the base soil, or did an interface develop?

3) Did the compacted plots have greater Penetrometer Resistance than the non-compacted plots?
4) Did aspect influence Penetrometer Resistance?
5) Did the compacted plots have greater Bulk Density than the non-compacted plots?
6) Did aspect influence Bulk density?
7) Did Penetrometer Resistance, Bulk Density and root mass correlate?
8) Did above and belowground biomass measurements correlate? Did the plots with greater species richness, greater diversity and more functional types have greater aboveground biomass and greater belowground biomass?

4.2 Methods

4.2.1 Site description

The Mesocosm experiment was built at Newcastle University, Close House Field Station, at Heddon-on-the-Wall near Wylam, North-East England in May 2006. The soil storing and washing facilities were used at Close house, provided by the Biology department.

4.2.2 Rooting depth (g m^{-2})

A rooting depth sample was taken from each plot, but only from the first and second Block due to time restraints. As the corer was 7.5 cm wide and 15 cm deep, but the depth required was 40 cm, three root cores were taken from the same place in the centre of each Mesocosm to measure rooting depth. The interface between the topsoil and base soil was at about 15 – 20 cm depth – as the corer was 15 cm deep, it was predicted that the soil may break off at this point. To prevent this from happening, the first core sample taken was 10 cm deep and the second and third samples were 15 cm deep. The interface was likely to be in the middle of the second sample. The positions were marked on the side of the corer and the root corer was hammered into the ground using a mallet until it reached the required mark. One person was needed to hold the root corer whilst the second person hammered the root corer into the ground. The root corer had a forked handle to easily pull the sample out of the soil, minimising soil damage. The root corer had a cranked piston that gently pushed the soil sample out, requiring little force and maintaining the shape and size of the soil sample. The samples from 36 plots (first Block) were taken in two days and stored in cold storage. The next 36 plots (second Block) were taken a month and a half later once the first set of samples had been recorded. Bulk density was sampled at the same time (see below for methodology).

The total 108 soil samples were stored in labelled polythene bags in cold storage until ready to be washed. Each sample was cut into 5 cm chunks (8 chunks per plot) and soaked in a tin tray with water overnight. Calgon was added to the water to aid flocculation – this breaks up the clay particles but doesn't affect the roots. The following day, once the samples had been soaked, the chunks were sieved in a 0.5 mm grid under pressurised running water. The larger stones were removed, followed by the smaller stones and other larger debris. Once the soil was completely washed away, the roots and other debris were put into a large bucket and the roots were picked out using tweezers. The washed roots were collected and put into tin trays and dried in an oven at 105 ° c for 24 hours. After 24 hours, the dry roots were weighed.

This process was repeated until all the samples had been washed and oven dried. It took approximately three months to complete.

4.2.3 Soil strength: Penetrometer Resistance (CI)

One Penetrometer sample was taken per plot, across all three Blocks, to measure soil resistance before the soil cores were taken. The Penetrometer was pushed firmly into the soil, maintaining the same pressure (approximately 2.5 cm per second) and the readings were read from the dial every 7.5 cm (every 3 seconds). Readings were taken at 7.5 cm, 15 cm, 22.5 cm, 30 cm, and 37.5 cm: five per plot. Penetration can be interrupted in order to record the dial readings – the pressure was kept steady when stopped to take an accurate reading. As this requires concentration, a second person recorded the readings onto a spreadsheet.

4.2.4 Soil strength: Bulk density (ρ) and soil moisture (%)

One Bulk density sample was taken per plot just after the soil cores had been taken, from the middle of the third soil sample. A circular bulk density tin (5 cm by 5 cm) was gently pushed into the third sample, taking care to avoid any pressure which could alter the compaction / density of the sample (The volume of soil that was removed from the third sample was taken into account and the weight of roots (g cm^{-3} was adjusted accordingly). The samples were put into tin trays and weighed instantly to give wet bulk density. The samples were then dried in an oven at 105 ° c for 24 hours and reweighed to calculate dry bulk density. Samples shouldn't include any large stones as this influences bulk density. After the final weighing, the samples were soaked in a tin tray with water overnight and Calgon was added to the water to aid flocculation. The samples were sieved, using a 0.5 cm grid and the stones were collected up, put in tin trays, dried over night and weighed the following day. The weight of the larger stones was minused from the soil samples and bulk density and moisture content were calculated. The difference between the wet and dry samples equalled the moisture content of the sample. Bulk density was calculated using the dry weight and the volume of the sample:

$$\text{Bulk density } (\rho)\ (\text{g cm}^{-3}) = \frac{\text{Oven dry weight (Ms)}}{\text{Volume (Vt)}}$$

$$\text{Moisture content } (\%) = \frac{\text{wet weight} - \text{dry weight}}{\text{Dry weight}} \times 100$$

4.2.5 Data Analysis

4.2.5.1 ANOVA's and repeated measures

In Minitab, these treatments - soil compaction (compacted and non-compacted plots); aspect (north-facing, south-facing and flat plots); seed mixture (grasses-only and grass and wildflower seed mixture) and management (plots cut eight times, plots cut four times and plots cut once) were inputted into the "model" box in a GLM (General linear model) ANOVA (Analysis of variance) and the interaction terms were added (!) between each treatment. Block (first, second and third Blocks) was also inputted into the model but without the interaction term. In addition, "Depth" was added in the model to look at the 8 measurements taken down each plot. In turn, each of these responses listed were put into the "response" box: Root mass (g m^{-2}); Penetrometer readings (CI); Bulk density (ρ) and Moisture content (%). An Anderson-Darling normality test was carried out on the residuals of each test and the data was transformed if needed. A variety of transformations were used including: square root; natural log; log + 1 and to the power of 1.5. Once the data fit a linear line ($p > 0.05$) the significant values ($p < 0.05$) were deemed to be valid. A post-hoc Tukeys test was carried out on any statistically significant relationships if there was over 2 treatment levels, i.e. aspect where there were south-facing, north-facing and flat plots, or where there were any significant interactions ($p < 0.05$). Root mass measurements (g m^{-2}), taken from eight different depths and Penetrometer readings (CI), taken at five different depths, were analysed using repeated measures ANOVA's in SAS since the samples taken were from one spot and hence related along a continuous line.

4.2.5.2 ANCOVA's

To see if soil strength and root mass were related, the Penetrometer reading (CI) and root mass (g m^{-2}) at each comparable depth were correlated using an ANCOVA in MINITAB, using one as a covariate and the other as the response and vice versa. As there were five Penetrometer readings (at 7.5 cm,; 15 cm; 22.5 cm; 30 cm and 37.5 cm) and eight root measurements, five of the rooting depths were chosen that most closely matched the Penetrometer depths (Depths 5 – 10 cm; 10 – 15 cm; 20 – 25 cm; 25 – 30 cm and 35 – 40 cm).

ANCOVA's were performed on a number of variables that could be compared: using one as a covariate and the other as the response and vice versa: Bulk density (ρ) may influence the total root mass (g m^{-2}) of each plot (Bulk density (ρ) vs. total root mass (g m^{-2})); To look at soil strength – Penetrometer resistance (CI) and Bulk density (ρ) were correlated (The final Penetrometer reading (CI) vs. Bulk density (ρ)); The aboveground biomass was likely to influence the belowground biomass, and possibly vice-versa – the biomass results from the final July cut of 2008 were used (Biomass (g m^{-2}) vs. Total root mass (g m^{-2})); The number of species found in each plot may influence the total root mass of each plot (Species Richness (2008) vs. Total root mass (g m^{-2})); The number of species found in each plot and the aboveground percentage cover (%) these species take up, may influence the total root mass of each plot (Shannon Diversity Index (H' 2008) vs. Total root mass (g m^{-2})). As each ANCOVA was carried out, the results were compared with the corresponding ANOVA to see how the treatment p-values were changed.

4.3 Results

4.3.1 Rooting depth

Roots were found in all samples, at all depths, in all of the plots. Roots were found in the last depth – 35 – 40 cm in all of the plots. As expected, repeated measures ANOVA showed that depth was highly significant ($F_{7, 357} = 341.61$, $p = <0.001$). The root mass in the first 0 – 5 cm was much greater than the other depths, it followed a negative exponential distribution for both the grasses-only seed mixture treatment and the grass and wildflower seed mixture treatment (Figure 4.1). Root mass was significantly greater in the grasses-only plots compared to the grass and wildflower plots in all depths (bar 20 – 25 cm and the last depth (35 – 40 cm)) ($F_{1,35} = 7.18$, $p = 0.011$; $F_{1,35} = 5.71$, $p = 0.022$; $F_{1,35} = 6.49$, $p = 0.015$; $F_{1,35} = 6.31$, $p = 0.017$; $F_{1,35} = 4.75$, $p = 0.036$; $F_{1,35} = 5.08$, $p = 0.031$ respectively) (Figure 4.1). This rule was slightly altered in the 5 – 10 cm depth where there was an aspect and seed mixture interaction ($F_{2,35} = 3.93$, $p = 0.029$). In this case, the significant difference between the grasses-only and the grass and wildflower seed mixture treatment was only between the flat plots; plus the north-facing grasses-only plot was significantly greater than the grass and wildflower treatment, in the flat plots (Figure 4.2).

It was expected that no compaction differences would be seen in the topsoil between 0 – 20 cm, as the compaction treatment began at 20 cm down to 40 cm. However, the only significant difference that compaction made to the root mass was in the 25 – 30 cm depth ($F_{1,35} = 6.89$, $p = 0.013$). In the 25 – 30 cm depth, the compacted treatments had a root mass of 8 g m^{-2} compared to 14 g m^{-2} in the non-compacted treatment, a reduction of 43 % (Figure 4.3).

The influence of aspect on the root mass was slightly different at some depths so the repeated measures ANOVA was significant for depth and aspect ($F_{14, 357} = 4.87$, $p = <0.001$). In the first depth, the north-facing plots had much greater root mass than the flat and south-facing plots (219 g m^{-2} vs. 107 g m^{-2} and 112 g m^{-2}) ($F_{2,35} = 6.79$, $p = 0.003$). In the third depth (10 – 15 cm) the north-facing plots had greater root mass than the south-facing plots, and flat was intermediate between the two (30 g m^{-2} vs. 22 g m^{-2} vs. 25 g m^{-2}) ($F_{2,35} = 3.28$, $p = 0.049$). At the 25 – 30 cm depth, the aspect effects changed – it was now the south-facing plots that had greater root mass than the flat plots and the north-facing plots (17 g m^{-2} vs. 9 g m^{-2} and 8 g m^{-2}) ($F_{2,35} = 6.03$, $p = 0.006$).

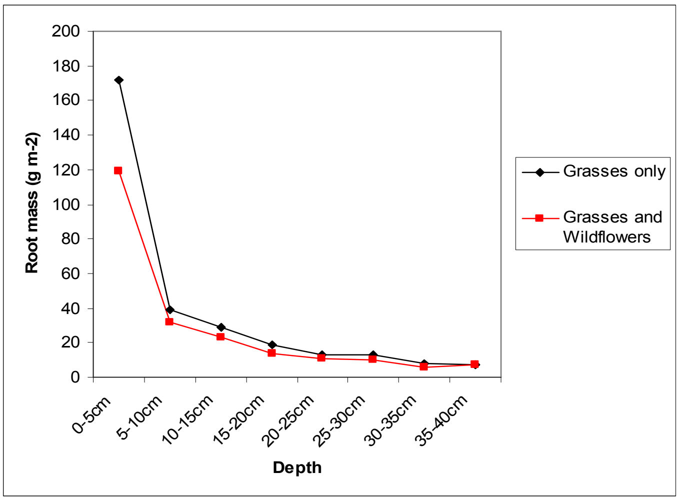

Figure 4.1. Root mass (g m^{-2}) and depth. There was a quick drop from 0 – 5 cm, after that, the root mass slowly decreased from depth to depth. The same pattern followed for the grasses-only seed mixture treatment and the grasses and wildflowers seed mixture treatment. The difference was significant (p = <0.05) at all depths bar 20 – 25 cm and 35 – 40 cm.

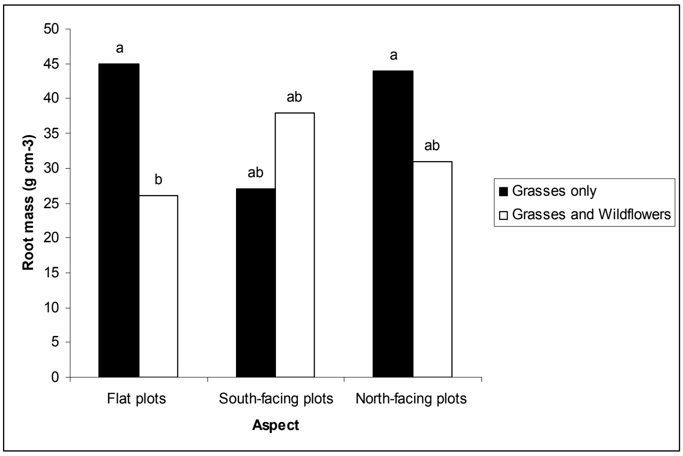

Figure 4.2. Root mass (g m^{-2}), aspect and seed mixture treatment in the 5 – 10 cm depth. The grasses-only seed mixture treatment was significantly greater than the grass and wildflower treatment in the flat plots. The north-facing grasses-only treatment was significantly greater than the flat grass and wildflower treatment, but all other plots were the same.

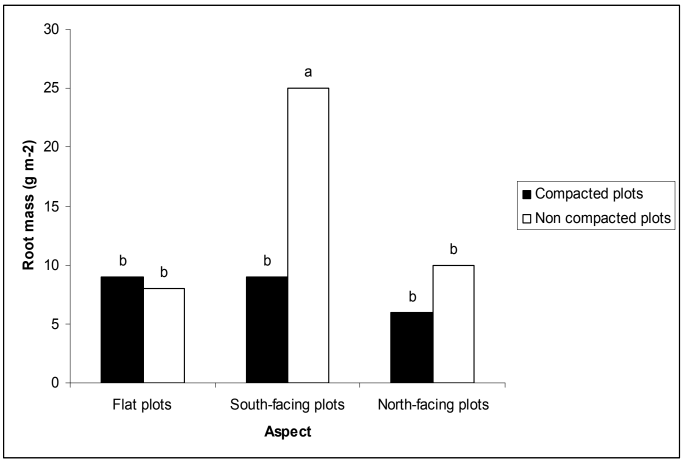

Figure 4.3. Root mass (g m^{-2}), aspect and soil compaction at depth 25 – 30 cm. The south-facing non-compacted plots had a significantly greater root mass than all of the other treatments.

4.3.2 Penetrometer resistance (CI)

The Penetrometer readings were taken from all plots, covering all three Blocks. 5 readings were taken per plot. As expected, Penetrometer resistance significantly increased with depth so repeated measures ANOVA was significant ($F_{4, 344} = 171.22$, $p = <0.001$).

There was a significant Block effect at two of the depths; at 7.5 cm and 30 cm ($F_{2,70} = 3.95$, $p = 0.024$; $F_{2,70} = 3.73$, $p = 0.029$ respectively). In both cases the first Block had a significantly greater Penetrometer resistance: At 7.5 cm the first Block was greater than the second Block, yet no different to the third (35 CI vs. 26 CI; and 28 CI for third); and at 30 cm the first Block was greater than the third Block, yet no different to the second (92 CI vs. 83 CI; and 84 CI for the second).

As expected, the compacted plots had much greater Penetrometer resistance than the non-compacted plots – this was significant at all of the depths ($F_{1,70} = 3.93$, $p = 0.051$; $F_{1,70} = 14.43$, $p = < 0.001$; $F_{1,70} = 5$, $p = 0.029$; $F_{1,70} = 5.86$, $p = 0.018$; $F_{1,70} = 15.91$, $p = <0.001$ respectively) (Figure 4.4) and since both Penetrometer Resistance and compaction increased through the depths, repeated measures ANOVA was significant ($F_{4, 344} = 171.22$, $p = 0.008$).

There was a significant aspect difference at all depths ($F_{2,70} = 8.54$, $p = <0.001$; $F_{2,70} = 6.50$, $p = 0.003$; $F_{2,70} = 5.91$, $p = 0.004$; $F_{2,70} = 11.75$, $p = <0.001$; $F_{2,70} = 19.15$, $p = <0.001$ respectively) and repeated measures ANOVA was significant ($F_{8, 344} = 4.76$, $p = <0.001$): North-facing plots had significantly lower Penetrometer resistance to the south-facing and flat plots at all depths. The flat and south-facing plots were not significantly different (Figure 4.5). However, at 30 cm and 37. 5 cm, there was an interaction between aspect and soil compaction ($F_{2,70} = 3.65$, $p = 0.031$; $F_{2,70} = 5$, $p = 0.009$). CI was greater in the flat, compacted plots in comparison to the flat, non-compacted plots, whereas there were no differences in the compaction treatment between the south and north-facing plots. In addition, the flat, compacted plots and the south-facing, compacted plots, had a greater Penetrometer resistance than all the north-facing plots (Figure 4.6 and Table 4.1).

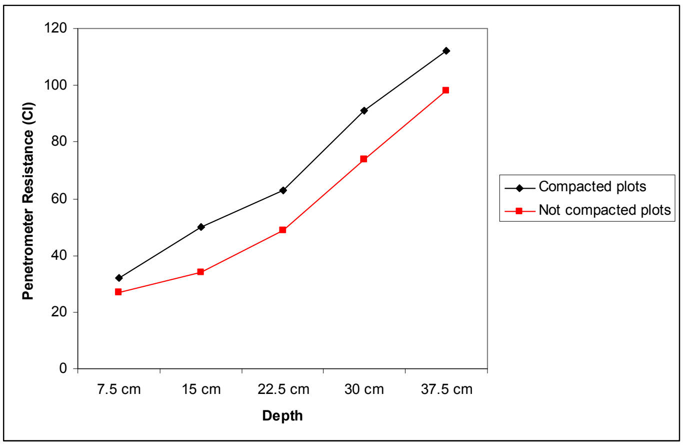

Figure 4.4. Penetrometer resistance, depth and soil compaction. Penetrometer resistance was significantly greater in the compacted plots than the non-compacted plots at all depths.

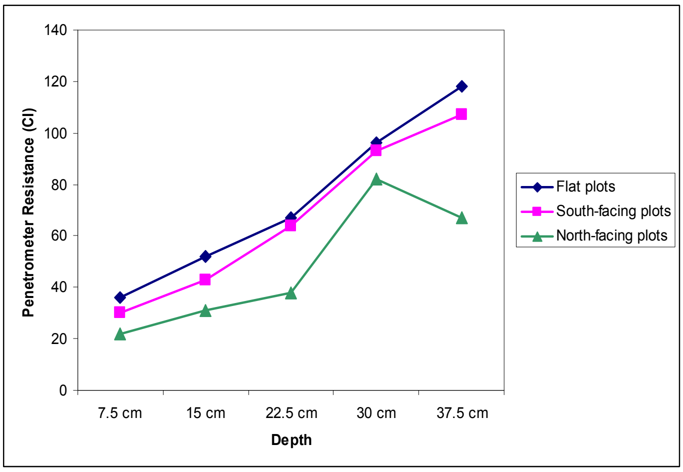

Figure 4.5. Penetrometer resistance, aspect and depth. At all depths, the aspect effect was the same – the north-facing plots were significantly lower than the south-facing and flat plots.

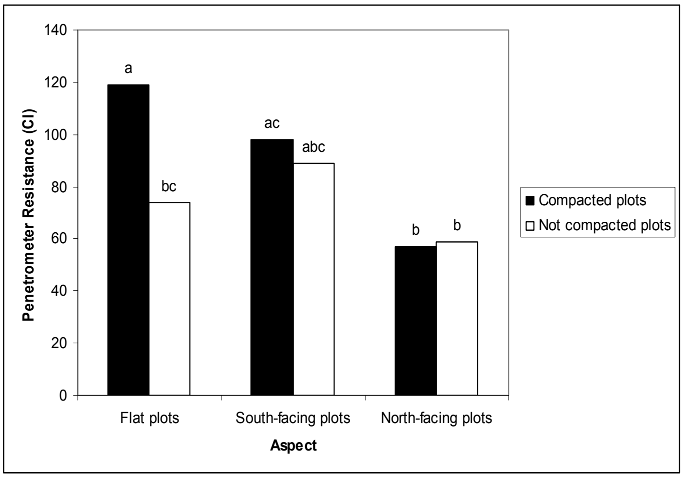

Figure 4.6. Penetrometer Resistance, aspect and soil compaction at the 30 cm depth (same pattern at 37.5 cm – but with greater CI). The soil compaction differences were only significant between the flat plots. The flat compacted plots and the south-facing compacted plots, had a greater Penetrometer resistance than all the north-facing plots.

4.3.3 Bulk density (ρ) and moisture content (%)

As expected, there was a significant difference between the compacted and non-compacted plots when bulk density was looked at ($F_{1,35} = 7.91$, $p = 0.008$): The compacted plots had a greater bulk density than the non-compacted plots (1.44 ρ vs. 1.34 ρ). There was also an aspect effect ($F_{2,35} = 9.92$, $p = <0.001$): the south-facing plots had significantly lower bulk density than the north-facing and flat plots (1.29 ρ vs. 1.4 ρ and 1.48 ρ). There were no other significant differences. The only difference with the moisture content (%) was between the aspects ($F_{2,35} = 30.80$, $p = <0.001$). The south-facing plots had significantly lower moisture content (%) than the north-facing and flat plots (20.7 % vs. 25.1 % and 21.6 %). So, when looking at aspect: where the moisture content was lower, the bulk density was lower too, and vice versa: where the bulk density was higher, the moisture content was too (Table 4.1).

4.3.4 ANCOVA's

4.3.4.1 Penetrometer resistance (CI) and rooting depths (g m^{-2})

Throughout the five depths, the Penetrometer readings and the root mass were not significantly correlated. Soil compaction was significant at all depths when just the Penetrometer readings were looked at; however, the addition of the root mass as the covariate took away the significance of the soil compaction treatment at every depth, bar the final one (i.e. The first reading: Before = $F_{1,70} = 3.93$, $p = 0.051$; After = $F_{1,71} = 0.05$, $p = 0.823$). This shows how greatly Penetrometer resistance and the soil compaction treatment were related. At the final depth, the soil compaction treatment remained significant, although the p-value was lessened (Before: $F_{1,70} = 15.91$, $p = < 0.001$; After $F_{1,71} = 5.98$, $p = 0.023$). The interaction between aspect and soil compaction in the final two depths remained significant – but again the significance was less. The pattern remained fairly similar; however it was just the flat compacted treatment that remained significantly higher than the flat non-compacted plots, but only in the final depth. Aspect remained significant, with the same pattern (As shown in Figure 4.5), but yet again, the significances were lessened.

When the Penetrometer resistance was added as the covariate to the root mass, there were no differences in the results of the ANOVA's for root mass. Aspect and seed mixture differences remained significant and the soil compaction and aspect interaction at the 25 – 30 cm depth remained the same (Table 4.1). Soil compaction did not become significant.

Table 4.1. Aspect and compaction at the 25 – 30 cm depth – looking at root mass and Penetrometer readings.

	Compacted		Not compacted	
Aspect	Penetrometer Resistance 30 cm (CI)	Root mass 25 - 30 cm ($g\ m^{-2}$)	Penetrometer Resistance 30 cm (CI)	Root mass 25 - 30 cm ($g\ m^{-2}$)
Flat plots	119	9	73	8
South-facing plots	98	9	89	25
North-facing plots	57	6	59	10

4.3.4.2 Total root mass ($g\ m^{-2}$)

Aspect remained significant ($F_{2, 35} = 6.61$, $p = 0.004$), following the same pattern as seen when the root mass was looked at per depth: North-facing plots had a significantly greater root mass than both south and flat plots (42 $g\ m^{-2}$ vs. 27 $g\ m^{-2}$ and 28 $g\ m^{-2}$). The seed mixture treatment was still highly significant ($F_{1, 35} = 9.62$, $p = 0.004$): the grasses had a greater root mass than the wildflower seed mixture (38 $g\ m^{-2}$ vs. 27 $g\ m^{-2}$). Aspect, soil compaction and the seed mixture were interacting ($F_{2, 35} = 6.61$, $p = 0.004$). Although seed mixture and aspect were significant, these differences were only seen in a few combinations once aspect, soil compaction and seed mixture were combined: The north-facing, non-compacted, grasses-only plots, had greater root mass than the south-facing, compacted, grasses-only plots (59.5 $g\ m^{-2}$ vs. 24.4 $g\ m^{-2}$) – a compaction and aspect effect here. The north-facing, non-compacted, grasses-only plots, had greater root mass than the flat and south-facing, compacted, grass and wildflower seed mixture plots (59.5 $g\ m^{-2}$ vs. 15.4 $g\ m^{-2}$ and 20.1 $g\ m^{-2}$). The north-facing, compacted, grasses-only plots had greater root mass than the flat, compacted, grass and wildflower seed mixture plots (42.9 $g\ m^{-2}$ vs. 15.4 $g\ m^{-2}$). No other differences were seen.

4.3.4.3 Bulk density (ρ) and total root mass ($g\ m^{-2}$)

There was no significant correlation between total root mass ($g\ m^{-2}$) and bulk density ($F_{1,34} = 0.03$, $p = 0.871$). The addition of bulk density (ρ) as the covariate did not make the compaction treatment significant. When total root mass was used as the covariate, the soil compaction treatment remained highly significant. When total root mass and bulk density was plotted, there was no clear pattern between total root mass, compaction and bulk density*(ρ)*, so it would seem that the compaction and bulk density (ρ) were not greatly influencing the total root mass (g m^{-2}) (Figure 4.7).

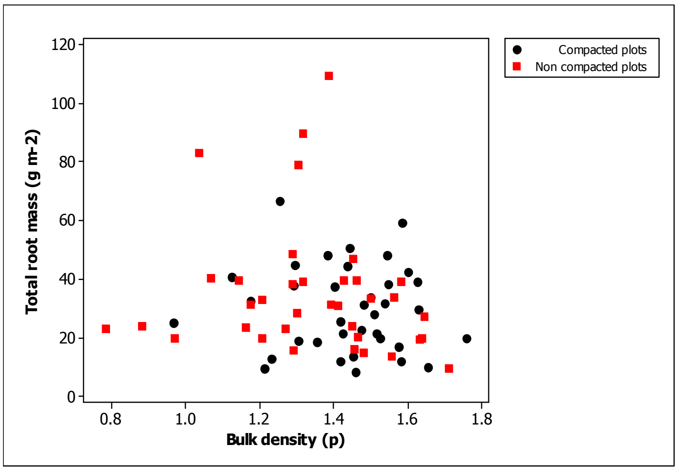

Figure 4.7. Total root mass, bulk density and compaction. The data points are spread out with no clear pattern, and the soil compacted treatments in red and black are spread out relatively evenly, showing no correlation between root mass, bulk density and compaction.

4.3.4.4 Bulk density (ρ) and Penetrometer resistance (CI)

There was no significant correlation between Penetrometer resistance (CI) and Bulk density (ρ) ($F_{1,34} = 0.25$, $p = 0.623$). With the Penetrometer reading as the covariate – all significances remained the same – i.e. soil compaction and aspect were still highly significant. With Bulk density as the covariate, all significances remained the same – aspect and soil compaction remained highly significant. It would seem that in this case, Bulk density (ρ) and Penetrometer resistance (CI) were not strongly correlated, although in Figure 4.8, there was a section of the graph, to the right, where high Penetrometer resistance, high bulk density and the compacted plots were found (Figure 4.8). In Table 4.2, the mean bulk density and Penetrometer reading for the last depth are shown. The aspect pattern is not the same for these parameters. So, although both are high in the compacted plots in comparison to the non-compacted plots, the differences between the aspect treatments were not the same – bulk density and Penetrometer resistance was high in the flat plots, but bulk density was low and Penetrometer resistance was high in the south-facing plots, and bulk density was high, but Penetrometer resistance was low in the north-facing plots.

Table 4.2. Aspect differences between bulk density, moisture content, the last Penetrometer reading and Total root mass.

Aspect	Bulk density (ρ)	Moisture (%)	Pen. Resistance 35 - 40 cm (CI)	Total Root mass (g m^{-2})
Flat plots	1.48	21.6	118	28
South-facing plots	1.29	20.7	107	27
North-facing plots	1.4	25.1	67	42

4.3.4.5 Above and Belowground comparison

There was no significant correlation between total root mass (g m^{-2}) and biomass (g m^{-2}) ($F_{1,34} = 0.25$, p = 0.623), however, a regression showed there was a correlation (p = 0.020). When this was plotted, the scatter graph (Figure 4.9) showed a slightly negative correlation. However, Figure 4.10 showed that this correlation was accounted for by the seed mixture treatment. The aboveground biomass was significantly greater in the grass and wildflower seed mixture treatment than the grasses-only treatment ($F_{1, 35} = 186.43$, p = < 0.001), but the total root mass was significantly less in the grass and wildflower seed mixture treatment in comparison to the grasses-only seed mixture treatment ($F_{1, 35} = 9.62$, p = 0.004). (To see the full results for aboveground biomass see Section 3.3.6). The ANCOVA with biomass as the covariate, removed the seed mixture treatment as significant because the differences in biomass was directly related to the differences in the seed mixture treatment (Before: $F_{1,35} = 9.62$, 0 = 0.004; After: $F_{1, 34} = 2.81$, p = 0.103). Soil compaction has made little difference to both the above and belowground biomass (Figure 4.11).

4.3.4.6 Total species richness and total root mass (g m^{-2})

There was no significant correlation between total root mass (g m^{-2}) and total species richness ($F_{1,34} = 1.70$, p = 0.201), however, total species richness removed the significant effect of the seed mixture treatment from the ANOVA (Before: $F_{1,34} = 9.62$, p = 0.004, After: $F_{1,34} = 0.50$, p = 0.483). The species richness was directly related to the seed mixture treatment (Figure 4.12). There was a significant difference in species richness between the seed mixture treatments: 6.1 sp. per plot in the grasses-only seed mixture and 9 sp. per plot in the grasses and wildflower mixture ($F_{1,34} = 73.14$, p = <0.001). It was assumed that more species would equal greater root mass, but in this case, the total root mass was greater in the grasses-only seed mixture than in the grasses and wildflower seed treatment (37.6 g m^{-2} vs. 27.3 g m^{-2}). (To see the full results of Species Richness see Section 3.3.2).

4.3.4.7 Shannon Diversity Index and total root mass (g m^{-2})

Although there was no significant correlation between total root mass (g m^{-2}) and Shannon Diversity Index ($F_{1,34} = 0.47$, $p = 0.499$), the addition of the Shannon Diversity Index, removed the significant seed mixture treatment effect from the ANOVA (Before: $F_{1,34} = 9.62$, $p = 0.004$, After: $F_{1,34} = 1.55$, $p = 0.221$). The Shannon Diversity Index was significantly higher in the grass and wildflower seed mixture treatment, yet the root mass was lower, and vice versa (For the Shannon Diversity Index results see Section 3.4.3). The Shannon Diversity Index was directly related to the seed mixture treatment, removing the significance of the seed mixture treatment from the analyses (Figure 4.12).

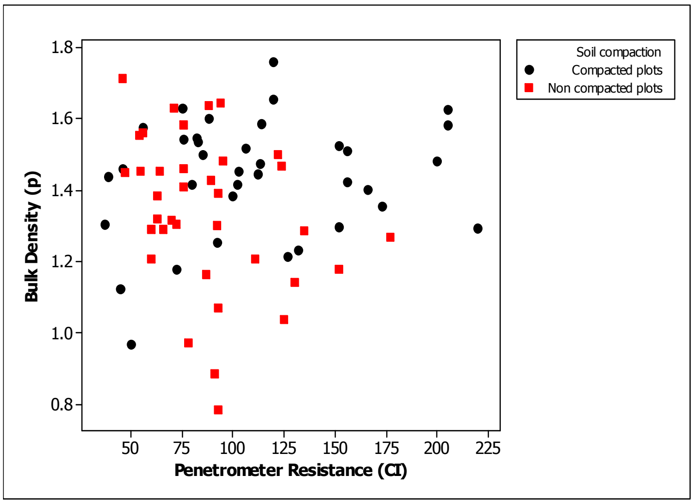

Figure 4.8. Penetrometer resistance (CI), bulk density (ρ) and compaction. The data points are relatively spread out showing no clear correlation between Penetrometer resistance, bulk density and compaction. Although there is a section to the right of the graph, where the compacted plots have high bulk density and high Penetrometer resistance – but this wasn't significant.

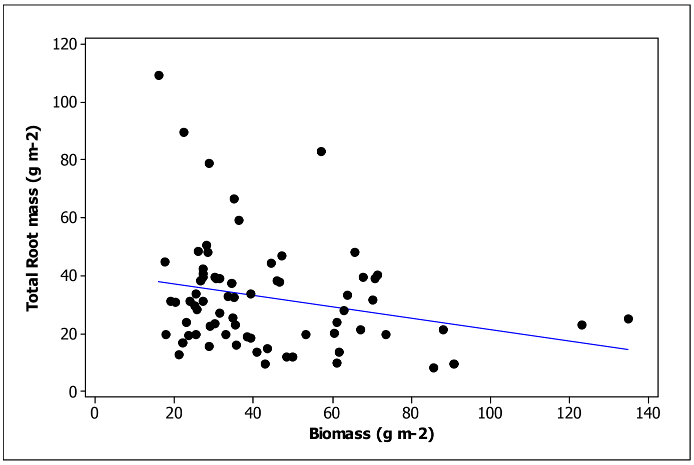

Figure 4.9. A scatterplot to show whether there was a correlation between aboveground biomass from the August cut 2008 (g m^{-2}), with the total root mass of each plot (g m^{-2}).

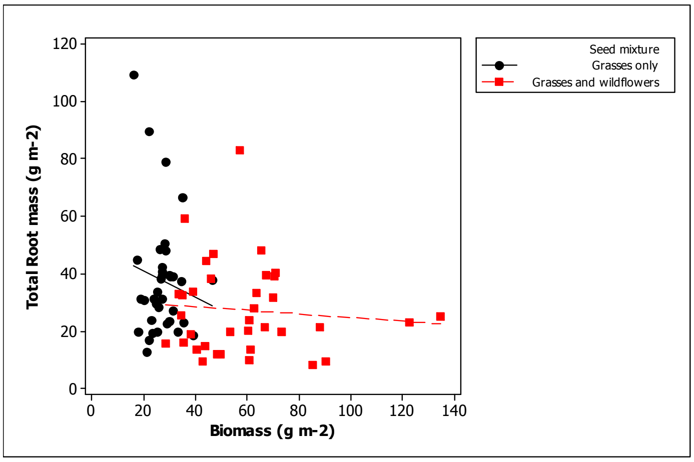

Figure 4.10. A scatterplot, plotted in MINITAB, to show whether there was a correlation between aboveground biomass from the August cut 2008 (g m^{-2}), with the total root mass of each plot (g m^{-2}). In MINITAB it is possible to show which data points are related to particular treatments and plot individual regression lines.

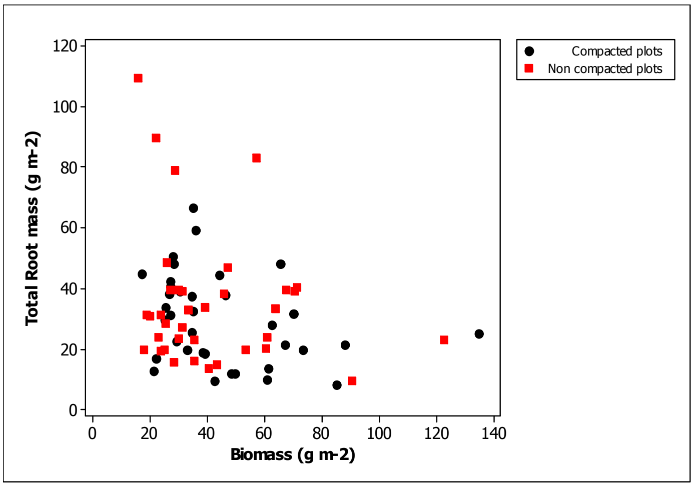

Figure 4.11. Biomass (g m^{-2}) and total root mass (g m^{-2}). The compaction treatments are spread over the graph showing little correlation with biomass and root mass.

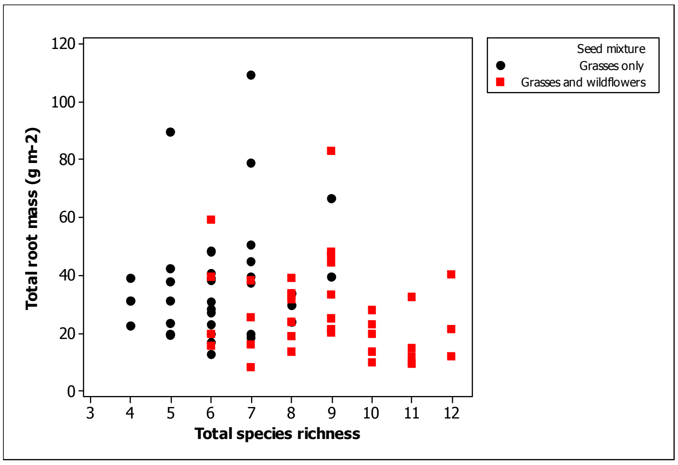

Figure 4.12. Species richness and total root mass (g m^{-2}). The seed mixture treatment neatly divides the scatter graph into two areas, showing that the seed mixture and species richness are directly related.

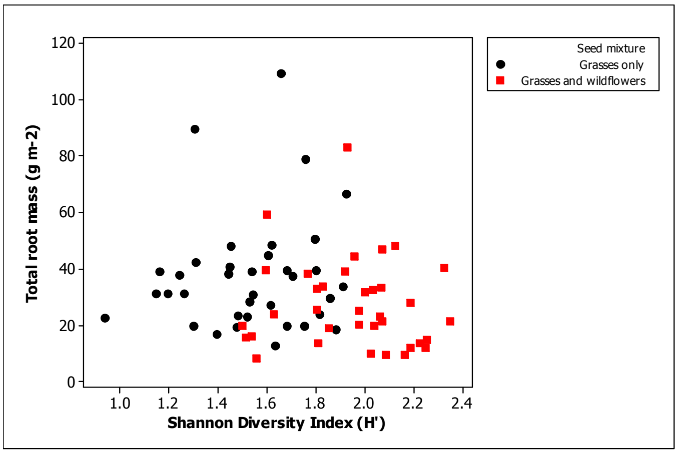

Figure 4.12. Shannon Diversity Index (H') and total root mass (g m^{-2}). The seed mixture treatment neatly divides the scatter graph into two areas, showing that the seed mixture and Shannon Diversity Index (H') are directly related.

4.4 Discussion

4.4.1 Root mass and root depth

1) What depth did the plant roots grow to? Did the aspect and seed mixture treatments influence root mass and root depth?

It was expected that the grass and wildflower seed mixture treatment would have greater root mass due to the deeper root systems of wildflowers (Fitter 1991; Schenk & Jackson 2002; Hutchings & John 2003; Lauenroth & Gill 2003). It was expected that the wildflowers would grow to 40 cm, but that the grasses would stop at 30 cm (Berendse 1981; 1983; Hutchings & John 2003). However, in this experiment, the root mass was greatest in the grasses-only treatment than the grass and wildflower seed mixture treatment, with the exception being the 5 – 10 cm depth where this difference was only in the flat plots, and in the final depth were there was no difference. In the final depth (35 – 40 cm) there was an equal amount of root mass between the two seed mixture treatments. Therefore, we could assume that grasses would be better at increasing soil strength and improving slope stability since smaller root diameters and root reinforcement equals greater soil strength (i.e. Waldron & Dakessian 1981; 1982; Nilaweera *et al.* 1999; Operstein & Frydman 2000; Tosi 2007). However, the root morphology between grasses and wildflowers are very different (i.e. Fitter & Stickland 1991; Schenk & Jackson 2002; Hutchings & John 2003; Lauenroth & Gill 2003).

In the samples which only had grass roots, the roots were much smaller and finer. The roots formed a dense mat of thin roots at the surface, which did hold together the soil very well (Waldron & Dakessian 1982; Bayfield *et al.* 1992). On the other hand, the wildflower species had larger, thicker roots, but these roots were quite light with only a small number of fine roots. This meant that the root samples from the wildflower plots often took up more space than the roots in the grasses-only plots, only they weighed less than the grasses-only plots. Schenk & Jackson (2002) noted that although the growth form of perennial grasses and wildflowers were different – grasses being fibrous rooted and wildflowers being tap rooted - this didn't significantly alter the root dimensions and root depth, and fibrous root systems were not necessarily shallower than the tap-rooted ones. A number of studies have shown that complex branching patterns of root systems can improve soil strength, and different species growing together grow to different depths (Wu *et al.* 1988; Berendse 1981; 1982; Fitter & Stickland 1992; Stokes *et al.* 1996; Dupuy *et al.* 2005). Boot & Mensink (1990) looked at the root structures of five common British grasses and found that there were significant differences between all of them. A diverse mix of species would be preferable, with different branching patterns and different rooting depths. In this experiment a dual purpose has been observed – the finer grass roots form mats which hold the soil particles together (Ennos 1989; Bayfield *et al.* 1992); on the other hand, the thicker wildflower tap roots, go directly into the ground, act as "pegs" (Waldron & Dakessian 1982; Ennos 1989; Stokes *et al.* 1996).

In addition, although the grasses-only plots had significantly greater root mass than the grass and wildflower seed mixture plots, the importance of fine root hairs could be underestimated (Boot & Mensink 1990; Bengough *et al.* 1997; McCully 1999). The small hairs often get washed away during root preparation (Schuurman & Goedewaagen 1971; McCully 1999). The method employed in this experiment can lead to roots being missed, and roots being washed away, although the easiest root method was followed for root weight (Zimmerman & Kardos 1960; Schuurman & Goedewaagen 1971). Roots also exude mucilage which binds to the soil around the root tip (Ennos 1989; McCully 1999; Bengough *et al.* 1997). Wildflowers tend to have many branches to their root systems, going from larger tap roots, to lateral roots, to secondary lateral roots and so on (Weaver 1958; Schuurman & Goedewaagen 1971; Waldron & Dakessian 1981; Fitter 1991). Some of these tiny roots may have been lost in the root washing process. This may be on a tiny scale, but this in combination with the mucilage produced, massively increases the surface area and therefore the slope stability potential of wildflower root systems, and has been ignored before (Ennos 1989; Stokes *et al.* 1996; Bengough *et al.* 1997; McCully 1999).

It is possible that the roots of the wildflowers would have continued to grow further than the 40 cm pots. Sun *et al.* (1997) noticed that although wildflowers were deep rooted, the root density was not very great at depth. Most grassland species were found at less than 0.2 m, but that maximum rooting depths were over 1 m. As explained in the introduction, Canadell *et al.* (1996) estimated temperate grassland maximum rooting depths at 2.6 m, and the *R. crispus* and *C. scabiosa* grassland in Germany reached 3.3 m (species that are commonly found on roadside verges). Berendse (1981; 1983) estimated *P. lanceolata* roots grew to at least 0. 5 m, and this species was found in all of the grass and wildflower plots. In an experiment looking at British grasses, the roots were found to 0.45 m depth (Garwood 1967). Therefore a seed mixture of both grasses and wildflowers should be sown on roadside verges to aid slope stability, because it is likely that the root systems may reach to 0.75 m depth, the depth at which shallow seated slope failures occur (i.e. Rice *et al.* 1969; Waldron 1977; Marden *et al.* 2005; Danjon *et al.* 2007).

4.4.2 Root growth and compaction

2) Did the compaction treatment reduce root mass and root depth? Did the roots grow through the topsoil and into the base soil, or did an interface develop?

These results show that the compaction treatment did not make a significant difference to the root mass and root depth. The exception was in the 25 – 30 cm depth where root mass was decreased by 43 %, except once the interactions effects were separated out, the compaction influence was lost. The compaction treatment began at about 18 – 20 cm depth and at this depth there was no obvious interface and the plant roots grew through the topsoil into the base soil with no discernable difference, unlike in a number of experiments where a "root-mat" has been observed (Dexter 1986a; 1986b; 1986c). It is likely that in this experiment the plants were big enough to penetrate compacted soil – since they had 18 - 20 cm of topsoil to grow through first. A number of compaction experiments have grown seedlings directly into compacted clay (Masle & Passioura 1987; Materechera *et al.* 1991; Cook *et al.* 1996). Masle & Passioura (1987) believed that the extreme reaction to soil compaction was due to the young, small plant roots experiencing soil compaction instantly.

Montagu *et al.* (1998) showed that it was the younger plants that were more susceptible to soil compaction. They did not find any direct effects of base soil compaction on the yield of crop since the base soil was 0.17 m below the topsoil, and they did not find a discernable "root-mat" before the compacted layer. The timing of the effects of compaction in relation to the stage of development of the plant will influence how much the plants growth will be restricted (Bengough *et al.* 1997; Bingham 2001; Montagu *et al.* 2001). Soil conditions are difficult to control with experimentally – there were likely to be pore spaces and cracks wide enough to allow for the roots to penetrate, even though the soil was compacted well (i.e. Bengough *et al.* 1997; Montagu *et al.* 2001; Bingham 2001; Bingham & Bengough 2003). Young *et al.* (1997) have suggested that as the plant matures and grows bigger, the root systems are more likely to find pore spaces and cracks that the roots can penetrate. Stirzaker *et al.* (1996) and Thaler &

Pages (1999) showed that the main roots were often compacted, but the laterals could compensate for the restriction and grow through the smaller pores, although Materechera *et al.* (1992) concluded that the tap-roots were more robust and were less prone to buckling.

4.4.3 Penetrometer Resistance (CI)

3) Did the compacted plots have greater Penetrometer Resistance than the non-compacted plots?

This experiment has confirmed that Penetrometer resistance (CI) was greater in the compacted plots and CI increased with depth, as has been shown in a number of previous studies (i.e. Masle & Passioura 1987; Materechera *et al.* 1991; Cook *et al.* 1996; Bengough *et al.* 1997; Montagu *et al.* 1998; Clark *et al.* 2003). The ANCOVA demonstrated that Penetrometer Resistance was directly linked to the soil compaction treatment. This was to be expected due to the base soil being manually compacted at 18 - 20 cm. However, Penetrometer Resistance was also greater in all of the depths of the compacted treatment in comparison to the non-compacted treatment.

4) Did aspect influence Penetrometer Resistance?

The compaction treatment was applied evenly throughout the experiment, yet differences in aspect were seen. The north-facing plots had lower CI than the south and flat plots, and at 30 – 35 cm and 35 – 40 cm, the compaction differences were only seen in the flat plots. Over time, the weight of the aboveground vegetation and water inputs were likely to influence the compaction of the soil. Rain may run off the sloped plots (Boardman 1984; Fullen 1991; 1992; 1998; Mitchell *et al.* 2003), but the flat plots were likely to soak up much of the water. This may explain why the compaction effects were seen more clearly in the flat plots and why the CI was greater. In fact, although the compaction treatment didn't significantly influence the total root mass per plot and root mass at each depth, the total root mass per plot was greater in the north-facing plots, where the Penetrometer Resistance was less and the total root mass per plot was less in the flat plots where the Penetrometer Resistance was greater. So, soil strength has lessened the total root biomass over time, but only where the compaction was very great - in the flat plots, as demonstrated by a wealth of soil compaction experiments (for reviews see Atwell 1990; Bengough & Mullins 1990).

4.4.4 Bulk density (ρ) and moisture

5) Did the compacted plots have greater Bulk Density than the non-compacted plots?

This experiment has established that Bulk density (ρ) was greatest in the compacted plots, which has been demonstrated in many studies (i.e. Zimmerman & Kardos 1960; Bamford *et al.* 1991; Stirzaker *et al.* 1996; da Silva *et al.* 1997; Lampurlanés & Cantero-Martinez 2003). Although, the ANCOVA showed that Bulk density was not directly related to the compaction treatment.

6) Did aspect influence Bulk density?

South-facing plots had lower bulk density than north-facing and flat plots. Moisture content followed the same pattern to bulk density – south-facing plots had lower moisture than the north-facing and flat plots, although there were no differences in the compaction treatment. As has been suggested above, it is possible that the flat plots have been compacted over time - the flat and north plots were wetter than the south facing plots. Since south-facing slopes receive greater sunlight than north-facing slopes, this aspect is warmer and drier than north-facing slopes (i.e. Perring 1959, 1960; Pahlsson 1974; Bennie *et al.* 2006). By the south-facing slopes drying out, this in turn is reducing Bulk density (Zimmerman & Kardos 1960; Thompson *et al.* 1987; Russell 1973; da Silva *et al.* 1997).

4.4.5 Soil strength – Penetrometer Resistance (CI), Bulk density (ρ) and root mass

7) Did Penetrometer Resistance, Bulk Density and root mass correlate?

The ANCOVA with Penetrometer and bulk density showed they were not correlated, although both were greater in the compacted plots in comparison to the non-compacted plots. However, they were different with respect to aspect. Penetrometer resistance was much greater on flat and south-facing plots, whereas Bulk density was higher on the flat and north-facing plots. Penetrometer resistance, bulk density and moisture contents were all higher on the flat plots. The north-facing plots had high bulk density and high moisture content, but not high Penetrometer resistance. The south-facing plots had low bulk density and low moisture content, but still high Penetrometer resistance. So, the drying of the soil on the south-facing plots was reducing bulk density and moisture, but increasing the Penetrometer resistance (Russell 1973; Andrade *et al*. 1993; Young *et al*. 1997).

Total root mass per plot was lowest in the flat plots – this was likely to be due to a combination of both Penetrometer resistance and bulk density. However, the north-facing plots had greater total root mass, where bulk density and moisture content were high but the Penetrometer resistance was low. The south-facing plots on the other hand, had low bulk density, low moisture content, but had high Penetrometer Resistance, and this lead to lower total root mass in comparison to the north-facing plots (see Table 4.2). Therefore, Penetrometer resistance is more related to root mass in this experiment. However, Table 4.1, shows a confusing pattern. At the 25 – 30 cm depth, the root mass was low in all of the plots, except root mass was much greater in the south-facing, non-compacted treatment (25 g m^{-2}), with a CI of 89. The north-facing, compacted plots, only had a CI of 57, yet the root mass was only 6 g m^{-2}, although at other depths the root mass has been greater. A number of studies have shown that increasing the temperature of the soil, increases root production (Kaspar & Bland 1992; de Boeck *et al.* 2007) – south-facing slopes are much warmer, therefore, root production may have increased and overcome the pressure of soil compaction at this depth – the south-facing, compacted plots had a CI of 98 CI, with root mass of 9 g m^{-2} – this may be the limiting soil strength in this case.

It should also be noted that soil is heterogeneous and Penetrometer resistance and bulk density may not have been uniform across each layer (i.e. Veihmeyer & Hendrickson 1948; Zimmerman & Kardos 1960; Masle & Passioura 1987). In Masle & Passioura's (1987) experiment, they were able to control the soil strength experienced by the roots but expressed that this was not the conditions usually experienced by plants in the field. Zimmerman & Kardos (1960) also developed a method to create field cores with uniform bulk densities, but this was not possible due to the large size of this experiment. This experiment was designed to replicate as closely as possible the soil conditions experienced by plant species growing on roadside verges.

In this experiment, it was generally Penetrometer resistance, not bulk density, which was influencing the total root mass per plot, although clearly, high Penetrometer resistance did not impede root growth in the 25 – 30 cm layer. Atwell (1993) concluded that Penetrometer Resistance was a good way of measuring the soil strength detected by roots and high bulk density was not always a sign of a compacted soil. Although Thompson *et al.* (1987), concluded that bulk density, not Penetrometer Resistance, impeded root growth. Dexter (2004) defined a soil physical quality parameter, modelling a number of different soil properties and showed that this parameter was a much better indicator of how easily roots could grow into the soil in comparison to bulk density alone.

The bulk density of the compacted plots was 1.44 ρ and the non-compacted plots was 1.34 ρ: Lampurlanés & Cantero-Martinez (2003) showed that roots were only prevented at very high bulk densities of between 1.46 ρ and 1.9 ρ. In their experiment, bulk densities were not high enough to prevent root growth. The bulk densities in this experiment were not particularly high in comparison to other experiments looking at bulk density and compaction (i.e. Zimmerman & Kardos 1960; Taylor & Burnett 1963; Atwell & Newsome 1990; Bamford *et al.* 1991; Andrade *et al.* 1993; Stirzaker *et al.* 1996;), although Bingham & Bengough (2003), used 1.1 ρ for the non-compacted treatment and 1.4 ρ for the compacted treatment and found differences, but, they used seedlings grown straight onto compacted soil which would have been affected by the compaction instantly. Also, the difference between the two compaction treatments were much greater than in this experiment – it is possible that bulk densities of 1.34 ρ in the non-compacted treatment were also affecting root growth – as shown in Masle & Passioura's (1987) experiment where they looked at bulk densities between 1.17 ρ and 1.45 ρ and noticed soil compaction effects at all soil strengths.

4.4.6 Above and belowground biomass

8) Did above and belowground biomass measurements correlate? Did the plots with greater species richness, greater diversity and more functional types have greater aboveground biomass and greater belowground biomass?

A number of studies have shown a link with aboveground biomass and belowground biomass – generally the greater the aboveground biomass, the greater the belowground biomass, but this wasn't seen in this case – the grass and wildflower plots had much greater aboveground biomass than the belowground root biomass (i.e. Casper & Jackson 1997; Cahill 2002; Lamb & Cahill 2008; Schenk & Jackson 2002). It could be that the whole of the root system wasn't sampled, especially since there were still roots found in the 35 – 40 cm depth. Lamb (2008) showed that root systems cover a greater area than aboveground canopies. Only one root core was taken per plot and the measurement was adjusted to relate to the same area as the aboveground biomass. Although there wasn't a link between species richness, diversity and root mass, it was clear that different plant species utilised different areas of the soil profile. The finer roots of grasses could be seen clearly and the deep red tap roots of *D. carota.* A number of studies have shown that niche partitioning and root separation occur belowground in order to reduce belowground competition (i.e. Berendse 1979; 1983; Caldwell *et al.* 1996; Levang-Britz & Biondini 2002; Wardle & Peltzer 2003). Campbell *et al*. (1991) explained that dominant plants tend to monopolise aboveground light and develop underground root systems which they term *high scale foraging*, whereas the smaller, less competitive species have more plastic morphologies that can make small scale adjustments to their leaf canopy and finer root distribution – termed *high precision foraging*. Campbell *et al*. explained that grasses are not plastic, whereas wildflowers can forage belowground and aboveground with more precision.

The greater the aboveground cover, the more surface erosion is prevented, especially on slopes (i.e. Waldron & Dakessian 1982; Anderson *et al.* 1982; Evans 1990; Boardman 1991; Fullen 1991; 1992; 1998; Bayfield *et al.* 1992; Solé-Benet *et al*. 1997). Hudson (1957) and Elwell & Stocking (1976) compared erosion between soil with a dense vegetation cover, to soil with a protective man-made cover over the top. There was no difference. So, they both concluded that the role of aboveground vegetation in preventing erosion by intercepting rainfall splash, is more important than the reinforcing effect of the belowground root mass underneath. So although the grasses-only plots had greater root mass, these plots had much less aboveground biomass. On the other hand, the more diverse and species-rich grass and wildflower plots had lower root mass, but greater aboveground biomass. Greenwood *et al*. (2004) commented that on highways slopes the grass seed mixture is sown only for landscaping aesthetics, and the prevention of erosion is only of secondary benefit. The results of this experiment lead onto the question - why shouldn't grassland species be used on highways slopes to aid structural stability? In Malaysia, grass species are often used to prevent surface erosion, and it is known that the roots can penetrate up to 1 m (Bayfield *et al.* 1992).

Therefore, for both the aboveground prevention of surface run-off and the belowground binding effects of rooting systems, a species-rich, diverse community of many functional types would be recommended for improving slope stability and at the same time, creating an aesthetically pleasing, biodiverse habitat. I would recommend a 60 % grass and 40 %

wildflower seed mixture to provide both aboveground and belowground stability on roadside verges, and especially on the steeper embankments and cuttings.

4.5 Conclusion and future work

Most experiments focus on a combination to two factors, i.e. Roots and compaction (i.e. Stolzy & Barley 1968; Goss 1977; Masle & Passioura 1987; Materechera *et al*. 1991; Montagu *et al*. 1998); Roots in relation to improving soil strength and stability (i.e. Waldron & Dakessian 1982; Wu *et al*. 1988; Cazzuffi *et al*. 2006; Danjon *et al*. 2007; Tosi 2007); Roots and competition (i.e. Boot & Mensink 1990; Berendse 1981; 1983; de Boeck *et al*. 2007), but what about combining these together? The belowground results of this experiment have shown how these are interlinking factors, and that a grass and wildflower seed mixture has the potential to improve slope stability on compacted Highways slopes. To validate the results of this experiment, it would be essential to combine all these factors into a future experiment: with different compaction treatments (not compacted – through to very compacted); with different numbers of species and functional types; with much deeper Mesocosms; and measuring root depth AND doing direct shear strength tests (on soil with roots and on soil without roots) (i.e. Waldron & Dakessian 1982; Wu *et al*. 1988; Cazzuffi *et al*. 2006) and root tensile strength tests (i.e. Nilaweera *et al*. 1999; Operstein & Frydman 2000; Cazzuffi *et al*. 2006; Tosi 2007). This experiment would be able to see which combination of species improves soil strength, which species and functional types grow deeply into compacted soil and which species have better tensile strength. It would also be able to see what happens to the soil strength of compacted clay with the growth of roots, comparing the shear strength of compacted soils with no roots to the shear strength of soil with roots – does root growth in compacted soil, improve or lessen soil strength?

5 Chapter Five

Botanical Survey along the A303 and A38

5.1 Introduction

The transport systems across the UK cover a large expanse of land. In 1974, the estimated amount of roadside verge vegetation was around 440,000 acres of habitat. Of this, 240,000 acres were estimated to be of open grassland, with an interesting and unusual vegetation community of over 870 native plant species (Way 1977). The Highways Agency manages roughly 10,400 km of motorways, dual-carriageways and Trunk roads across England, with volumes of traffic between 5,000 vehicles per day to 200,000 vehicles per day. The area owned by the Highways Agency, between the highway fences, but not taken up by the road carriageway, is known as the soft estate. The soft estate covers approximately 30,000 hectares of land, sustaining a wide variety of habitats (HA 2000). This is the most recent estimate; it is not known what proportion of grassland habitat there is on the soft estate, or how many plant species are found.

Roadside verges can be classed as an ecotone or edge habitat, where one community overlaps with another (Way 1977; Tikka *et al.* 2001) or even classed as a "Novel ecosystem" where new combinations of species occur (Hobbs *et al.* 2006; Hobbs *et al.* 2009; Williams *et al.* 2009). Roadside verges can act as habitat corridors, allowing for the dispersal of seeds (Kiviniemi & Eriksson 1999; Tikka *et al.* 2001), movement of insects (Munguira & Thompson 1992), mammals, birds (Way 1977; Laursen 1981) and even earthworms (Cameron & Bayne 2009) between habitats. The ecology of these dynamic systems has not been thoroughly studied in Britain, especially on the soft estate, mainly due to the difficulty of access to embankments and cuttings, safety constraints due to working next to fast roads, and financial limitations (Parr & Way 1988; Sangwine 1996; HA 2000; 2005a).

The rising significance of the roadside grassland habitat for conservation value was highlighted back in the 1970s by Way in a number of publications in which he emphasized the need for improved landscape management (Way, 1976; 1977; 1979). However, in 1975, the Department of Transport issued instructions to cease regular grass cuttings on trunk roads and motorways, only to cut in restricted circumstances (Way 1977; 1979). In 1977 and 1979, Way had predicted that this would mean an increase in competitive plant species such as *A. elatius* and *C. arvense* and that *Crataegus monogyna* and *Prunus spinosa* scrub were likely to be the commonest colonisers. By 1988, this was indeed happening (Parr & Way 1988) and there has been a decline in species-rich grassland habitats and scrub encroachment across many roadside verges ever since (Parr & Way 1988; Grime *et al.* 1994; Sangwine 1996; Dunnett *et al.* 1998; Muller *et al*. 1998; HA 2003; 2005a; 2005b; Thomas 2005; NBPG 2008).

In the last 15 years the management of roadside verges has improved a little, with a number of important areas of conservation interest, i.e. verges running through Sites of Special Scientific Interest (SSSI) and Areas of Outstanding Natural Beauty (AONB), being managed more appropriately by the Highways Agency, in conjunction with Wildlife Trusts and County Councils (Sangwine 1996; HA 1994; 2000). For example, Essex Wildlife Trust has Verge representatives that monitor species rich verges (EWT 2008), and several collaborative groups have formed, such as in Northamptonshire (NBPG 2008), Durham (DBP 2008) and Warwickshire (Thomas 2005), which have specific Road Verges Action Plans in place.

A general grass seed mixture containing six species has always been sown onto newly constructed road systems since the 1950s (Way 1976; HA 1991; 1992) (Table 1.1). Although sowing a more diverse wildflower seed mixture onto newly built road systems has been suggested over the years, the standard grass seed mixtures are still preferred as they establish quickly and are much cheaper (Bayfield 1995; Gray 1995; HA 1992; 1993; 2000). In the UK the management and restoration of roadside verges and motorway embankments and cuttings varies between the different Highways Agency areas, and varies between different counties if some groups (i.e. County Councils and Wildlife Trusts) take special interest in certain habitats. Generally the recommended grass seed mix is sown unless the consultant responsible for these decisions is familiar with suitable wildflower seed mixtures and is prepared to pay the extra cost (Streeter 1969; Underwood 1969; Ross 1986; Barker 1995; HA 1993; Sangwine 1996).

At the UN Conference on Environment and Development at Rio de Janeiro in June 1992, over 150 heads of state or government (together with the UK) established the Convention on Biological Diversity, pledging each country to take action to conserve and enhance biodiversity. The UK Government set up a Biodiversity Steering Group to investigate the country's endemic species and habitats, particularly those species and habitats which were threatened. In early 1994, "*Biodiversity: the UK Action Plan*" was published, including species and habitats which should be protected, and how best to protect and conserve them. In 2000, in response to the Government's 10 Year Plan for Transport, the Highways Agency declared a target to "manage the core HA road network in line with Biodiversity Action Plans" by 2006. The Highways Agency established a Biodiversity Partnership of significant groups, including (at the time), English Nature and The Environment Agency, DTLR (Department for Transport), the Wildlife Trusts and the RSPB. The Partnership developed the Highways Agency Biodiversity Action Plan (HABAP); part of a long-term strategy for the conservation of habitats and species on the soft estate of motorways and trunk roads in England (HA 2000).

Six different types of action plans for grassland are found in the UKBAP: lowland calcareous grassland; upland calcareous grassland; lowland hay meadows; upland hay meadows; purple moor grass and rush pasture; and lowland dry acid grassland. Any of these habitats could occur on, or neighbouring, the soft estate, however the Highways Agency only holds records for calcareous and dry acid grassland. Calcareous grasslands are found on alkaline soils (pH above 7.0) that have not had fertiliser added, and most often where the underlying base rock is limestone or chalk (HA 2000). Calcareous grassland has declined drastically over the last 50 years, due to under or overgrazing and agricultural intensification, and the majority of the remaining habitat occurs in Dorset, Wiltshire and the South Downs (HA 2007b). It is the commonest UKBAP habitat recorded on the soft estate (81 sites), often occurring on large chalk embankments. Dry acid grassland is found on acidic soils (pH less than 5.5), and occurs as a fundamental element of lowland heath landscapes. Dry acid grassland may be relatively species-poor, but a significant number of plant and invertebrate species favour this habitat and are not found in other types of grassland (HA 2000).

The Highways Agency has published a number of documents that detail the procedural guidelines for the management of the road estate. The TRMM (*Trunk Road Maintenance Manual*) states that grassland roadside verges with high nature conservation value or botanical importance should be managed to protect and enhance this value. The TRMM states that "where designated sites lie within or adjacent to the highway boundary, the soft estate should be maintained on the advice of Natural England or local wildlife trusts" (HA 1996; 2000). The DMRB (*Design Manual for Roads and Bridges*) gives recommendations for the management, creation or translocation of valuable grassland habitat on roadside verges (HA 1992; 1993; 1994). Some sites on the soft estate (For example, the A303 in Wiltshire) have management plans for calcareous grassland, including specific action plans for plant and invertebrate species associated with this habitat (HA 2004; 2005a; 2007b). The MCHW (*Manual of Contract Documents for Highways Works*) includes guidance on the specification for Highways Works and includes a section on Weed Control. The Highways Agency must control 'injurious' weeds, as listed in the Weeds Act (1959) (HA 2000; 2007b): the 'injurious' weeds being: *C. vulgare*, *C. arvense*, *R. crispus*, *R. obtusifolius*, *S. jacobaea*, Himalayan Balsam, Giant Hogweed and Japanese knotweed (HA 2007b).

The Highways Agency has pledged:

- To ensure that "existing calcareous and dry acid grassland sites are managed appropriately to maintain and enhance their nature conservation value."
- "As part of new infrastructure or ongoing maintenance, to create/enhance calcareous grassland habitat (40 sites) and dry acid grassland habitat (15 sites)."
- To "create specific Adonis blue habitat (5 sites)."
- "Whenever possible to use a wildflower and grass seed mix in preference to an amenity grass seed mix."
- To "Take care to ensure that all seed used is native and appropriate to the geographical region and soil type."
- "Wherever possible, avoid using imported agricultural topsoil". (HA 2000).

The conservation of semi-natural grasslands in Britain has become more important in recent years as the conflict between agriculture and conservation continues. Many of the grasslands have been replaced by arable fields and in others so much artificial fertiliser has been added that the species diversity and richness has fallen with the increase in productivity (Hodgson *et al.* 2005; Jefferson 2005). Semi-natural grassland habitats have evolved from traditional management practices including grazing by livestock at certain times of the year and a hay-cut at the end of the growing season. Changes in spring and autumn grazing, and differences in the hay-cut date have been shown to influence the composition of the grasslands over time (Kirkham & Tallowin 1995; Smith & Rushton 1994; Smith *et al.* 1996; 2000; 2008). Smith & Rushton (1994) have shown that when grazing is stopped, there is a very quick loss of species richness and diversity. This species loss cannot be reversed without implementing traditional management practices and without the addition of extra seed (Smith & Rushton 1994; Muller *et al.* 1998; Smith *et al.* 2000). In order to maintain grassland habitats where grazing is not possible, manual cutting, including raking and removing the cuttings, can be used in order to maintain species richness and diversity (Duffey *et al.* 1994; Austen & Treweek 1995; Wells *et al.* 1989; Schaffers *et al.* 1998).

On roadside verges, especially embankments and cuttings, it is very difficult to graze as it is too steep and the animals are too close to the road. Although the Highways Agency has BAPs and guidelines in place for the management of species-rich BAP habitat grasslands (calcareous and lowland dry acid), the landscape management plans for general grasslands on the roadside verges only include a cut once every three, six or nine years, and only in exceptional cases (i.e. rare, species-rich grassland), they may be cut once a year maximum (HA 1994; 2005a). The grassland verge habitat is extensive, but also inaccessible. It costs a large sum of money to finance cutting the verges and it is very difficult to rake and remove the cuttings, especially when the work is carried out alongside fast roads, such as dual carriageways and motorways (HA 2005a). Grassland plant communities are maintained on roadside verges but under the current management regimes species-rich grassland communities will be lost (Parr & Way 1988; Tikka *et al.* 2000; Tikka *et al.* 2001; Ameloot *et al.* 2006).

Without regular cutting (i.e. more than once a year), the roadside verges becomes dominated by injurious weeds and plants such as *C. angustifolium*, *A. elatius, L. perenne*, *P. lanceolata* and *T. officinale* spread quickly (Chancellor 1969; Way 1977; Ross 1986; Parr & Way 1988; Grime *et al.* 1994; Sangwine 1996; Dunnett *et al.* 1998; Muller *et al.* 1998; Ameloot *et al.* 2006). The topsoil used for restoration and new road projects adds to this problem as it is often very fertile and accelerates the establishment of un-wanted, competitive weeds (Parr & Way 1988; Bayfield 1995). It is unlikely that diverse species-rich grassland can be conserved, maintained or established on roadside verges without thought to improving the timing and frequency of cutting, finding a way to effectively remove cuttings, reducing soil fertility or without adding supplementary grassland seed mixtures into areas where species loss has already occurred (Way 1978; Parr & Way 1988; Bayfield 1995; Tikka *et al.* 2000; Tikka *et al.* 2001; HA 2005b).

For an introduction to the influence of aspect on grassland communities see Section 1.3

It is clear from the previous explanation of the Highways Agency's biodiversity plans that a little thought goes towards grasslands and biodiversity on roadside verges. However, this is nothing compared to the importance of safety on roads. There is an entire Geotechnical department devoted to surveying the roadsides for any problems, and records the surveys in a database called the Highways Agency Geotechnical Data Management System (HAGDMS). This department is particularly looking for risks of slope failures and the surveys look for signs of shallow-seated slope failures such as slips, slope bulges, ravelling and subsistence. Signs of surface erosion are recorded, along with desiccation, terracing and bareground patches. General vegetation is noted, especially since the vegetation growing on the sides of roadside verges also has a recognised role in slope stability (Rice *et al.* 1969; Waldron & Dakessian 1982; Barker 1995; HA 1992; 1996).

It is well known that deep growing tree roots can prevent shallow slipping and other landslides (i.e. Greenwood *et al.* 1996; MacNeil 2001; Snowdon 2004). However, although tree roots can improve slope stability – they can also cause more problems. Trees have a high water demand which leads to the soil swelling and shrinking in response (Biddle 1983; Driscoll 1983; Smethurst *et al.* 2006). This response is much reduced in grasses and wildflowers (Anderson *et al.* 1982; Smethurst *et al.* 2006). Anderson *et al.* (1982) showed that cracks developed more often near to tree roots and were uncommon in grassland areas. John Maddison from the Highways Agency said “You don’t find slips on grassland slopes”. Many in agriculture use grassland areas to prevent surface erosion and runoff on steeper slopes (i.e. Fullen 1991; 1992; 1998; Morgan 1992; Mitchell *et al*. 2003). Do slips and failures occur in grassland areas or do they mainly occur in wooded areas?

Perring (1959; 1960) looked at sixty-two sites of chalk grassland, investigating the role of climate and topography on species composition and soil properties. He showed that the climate on southern slopes was drier, had greater organic carbon and less biomass than that of northern slopes. He believed that constant wetting and drying of the vegetation on the south-facing steeper slopes caused the soil to slip down the hillside. As north-facing slopes were constantly wetter and had more vegetation growth, the soils were less likely to be washed away (Perring 1959; 1960). Are there more slips and failures on south-facing slopes?

With the issues of lack of management and slope stability in mind; and the possibility that aspect, changes in soil type and slope angle may influence grassland composition and surface erosion on different sides of roadside verges; a surveying experiment was designed to look at south-facing and north-facing cuttings, on slopes above 25 ° on a dual-carriageway in the south of Britain (A303 and A38). In addition, a database from the Highways Agency

Geotechnical Data Management System (HAGDMS) was collated to examine the link between slope stability and vegetation type, with the aim to answer these questions:

1) Did species sown from the standard grass seed mixture dominate? Or did injurious weeds dominate? Or did weedy, competitive species such as *A. elatius* dominate the roadside cuttings?
2) Did south-facing cuttings have greater species richness and diversity than the north-facing cuttings?
3) Did species preferring warm, dry conditions establish on south-facing cuttings and species preferring cold, wet conditions establish on north-facing cuttings?
4) Did south-facing cuttings have more signs of surface erosion than north-facing cuttings? Did the steeper slopes have more signs of surface erosion and slips?
5) Did the chalk soils along the A303 mean that a calcareous community developed?
6) Did the north-facing cuttings have greater Ellenberg Fertility and Moisture Values, and did the south-facing cuttings have greater Ellenberg Light Values?
7) Did the north-facing cuttings have more competitive species establishing than the south-facing cuttings?
8) Did the NVC classification differ between north-facing and south-facing cuttings?
9) Did the roadside verge habitats fit into the NVC classifications?
10) Did woodland sites have more records of slips and failures than the grassland sites in the HA GDMS?

5.2 Methods

5.2.1 Site description

The surveying began at grid reference SU 014 386 near Wylye on the A303, a main dual carriageway in Southern England, and finished at grid reference SX 676 572 on the A38 near Plymouth. The survey covered approximately 150 miles of road and encompassed 3 counties: Wiltshire, Somerset and Devon. The A30 wasn't sampled as there were no suitable cuttings. Each site was found on Ordinance Survey maps and the grid reference was recorded. The A303 was built in 1988 and most of the roadside verges received a standard grass seed mixture. There was 22 years of vegetation establishment on the A303.

5.2.2 Sampling method

The A303, A30 and A38 were firstly examined and a number of suitable sites were identified. Suitable sites were those of grassland cuttings of around 20 m high, with a slope angle of above 25 º (in order to compare with the BIONICS and Mesocosm slope angles) and where grassland was found on either side of the road. As many sites as possible were found with comparable north-facing and south-facing cuttings. The embankments were inaccessible so only the cuttings were surveyed. Parking was only possible in lay-bys and the sites were walked to along the road. This was dangerous and a maximum of quarter of a mile was walked, wearing full high visibility gear and a hard hat. The road was never crossed, so the sites were clearly marked on the map and the corresponding site was driven to. In some cases the corresponding site was too difficult to get to, i.e. no parking within a quarter of a mile, so the closest corresponding site was recorded. 13 pairs were directly opposite each other and the remaining 6 pairs were not directly opposite. This equalled a total of 38 sites altogether and 19 pairs.

5.2.3 Botanical recording

Three 1 m x 1 m quadrats were randomly placed in uniform vegetation at around 10 m away from the road, and the plant species were identified. All vascular plant species were identified, nomenclature according to Stace (2010). Each quadrat was divided into 16 squares, to aid the calculation of percentage cover (%) to each species, and the percentage cover (%) of each species was recorded.

5.2.4 Soil texture / soil type

At each site, soil texture / soil type was estimated by hand and sight, and put into 8 different categories, based on the soil texture triangle and percentages of sand, silt and clay: Sandy loam; Loam; Silty loam, Silty clay; Clay; Sandy clay; Chalk and Slate (Wild 1993).

5.2.5 Slope angle and slope orientation

At each site the slope angle was estimated using a spirit level and protractor. Sites were not sampled that were over 40 ° due to risk of slips and falls. Sites were not sampled that were under 25 °. A compass bearing was taken at each site to record aspect. As the road ran from East to West, the majority of sites were directly facing north or south. The slopes were categorised into shallow < 30 ° slopes; medium 31 – 34 ° slopes and steep 35 - 40 ° slopes.

5.2.6 Geotechnical survey

John Maddison from the Highways Agency went through the geotechnical survey methodology on site, and the same method was followed. At each site, a general geotechnical survey was undertaken, recording signs of slips, failures, desiccation and terracing. As only a few signs of terracing and desiccation were found, this was grouped into presence and absence of surface erosion. The percentage of bareground was recorded and this was grouped to presence and absence of bareground.

5.2.7 Highways Agency Geotechnical Data Management Systems (HA GDMS)

The HA GDMS is a database where all geotechnical surveys are inputted as “Observations”. Each observation sheet contains tick boxes for: Slips; Surface Erosion; Slope Bulge; Desiccation; Terracing; Cracks; Ravelling; Planar Failure; Toe debris; Subsidence; Dislodged Structure; Dislodged Trees; Repair; High MC; Bareground and Rabbit burrows. Vegetation was recorded using tick boxes for grass, brambles, scrub, shrub or trees. One – all of these boxes would be ticked. The soil formation for the area was recorded, as was slope angle and aspect. These observations were converted into an excel data sheet.

Each observation was attached to a map of road systems. Observations were inputted into the excel data sheet in a blocked area from the map. Some areas had more completed information than others so these areas were used: A303, Junctions 20 – 15 of the M4 and Junctions 7 – 12 of the M25. These areas had a higher proportion of slope slips and failures. This gave a bias to slopes with a greater risk of failure, however, there were still half of the observations where no faults were recorded, so a comparison could be made. 423 observations were recorded.

The vegetation recording system was converted to habitat types. Grass only = Grassland; Grass and brambles, or grass and scrub = Scrub encroachment; Brambles = Brambles, Scrub = Scrub; Scrub, Shrubs and Trees = Trees and Scrub; When nearly all boxes were ticked, including grasses and trees, this = Woodland.

5.2.8 Data analysis

5.2.8.1 Species richness and Shannon Diversity Index (H’)

For calculation for species richness and diversity see paragraph 2.2.7.1. Species richness and diversity was calculated for each quadrat.

5.2.8.2 Ellenberg Indicator Values

For explanation of Ellenberg Indicator Values see section 2.2.7.2. The Ellenberg Indicator Values for Fertility, Light and Moisture was calculated for each quadrat.

5.2.8.3 General Linear Model, Analysis of variance (GLM ANOVA)

In Minitab, these treatments - aspect (north-facing and south-facing cuttings), soil texture / type (sandy loam; loam; silty loam, silty clay; clay; sandy clay; chalk and slate); slope (shallow < 30 º; medium 31 – 34 º and steep 35 - 40 º) surface erosion (presence and absence) and bareground (presence and absence) were, inturn, inputted into the "model" box in a GLM (General linear model) ANOVA (Analysis of variance). In turn, each of these responses listed were put into the "response" box: total number of species found (species richness); total number of grasses; total number of wildflowers; Shannon Diversity Index (H'); Ellenberg Indicator Values (Fertility, Light and Moisture); cover (%) of widespread individual species and aboveground biomass measurements. An Anderson-Darling normality test was carried out on the residuals of each test and the data was transformed if needed. A variety of transformations were used including: square root; natural log; log + 1 and to the power of 1.5. Once the data fit a linear line ($p > 0.05$) the significant values ($p < 0.05$) were deemed to be valid. A post-hoc Tukeys test was carried out on any statistically significant relationships if there was over 2 treatment levels, i.e. soil type.

5.2.8.4 Ordination using CANOCO

A Detrended Correspondence Analysis (DCA) and a Canonical Correspondence Analysis (CCA), using the ordination program CANOCO (Leps & Smilauer 2003), was carried out on the species data following the main method explained in section 2.2.7.5. A DCA and CCA was possible since the lengths of gradient was 4.111, indicating that the model was unimodal. The "environmental" variables were: Aspect (north-facing and south-facing cuttings) and soil texture / type (Sandy loam; Loam; Silty loam, Silty clay; Clay; Sandy clay; Chalk and Slate). Surface erosion (presence and absence) and bareground (presence and absence) were included as "supplementary" variables, as was the Ellenberg Indicator Values and Shannon Diversity Index.

The HA GDMS excel data sheet was converted by CanoImp into a format readable in CANOCO. A PCA (Principal Components Analysis) and a RDA (Redundancy Analysis) was carried out since the lengths of gradient were short and the model was linear. The soil formations, aspect and slope angle were the “environmental” data; the habitat classifications were the “species” data and the slips and failure data were used as “supplementary” data.

The species-environment bi-plots were interpreted visually: species close together were associated within similar plant communities and environmental variables found in particular sections of the bi-plot were associated with the species in that area. Species and environmental variables were more important the further away from the centre of the bi-plot they were.

5.3.8.5 Grime’s CSR Plant Strategies

The majority of European plant species have been allocated a plant functional trait strategy, founded on Grime’s CSR theory. At the heart of CSR theory is the balance between stress and disturbance. Stress = the restriction of growth caused by shortages of factors such as light, water and nutrients; Disturbance = the whole or partial destruction of plant biomass caused by activities such as trampling, cutting, drought and soil erosion. *Competitors* (C) dominate where stress and disturbance are low, a *stress-tolerator* (S) dominates where stress is high but disturbance is low and a *ruderal* (R) dominates where disturbance is high but stress is low. Where stress and disturbance is high, no plants will survive. An intermediate between these is CSR – the *competitive-stress-ruderal*, and all other intermediates are possible (Grime *et al.* 1988; Grime *et al.* 2001). The CCA plot produced in CANOCO was used to look at CSR strategies. Each species label was changed to the respective CSR trait and the patterns were observed.

5.2.8.6 National Vegetation Classification (NVC). TABLEFIT

For explanation of NVC and TABLEFIT see section 2.2.7.4. The NVC was classified for each site. The CCA plot produced in CANOCO was used to look at NVC classifications. Each site label was changed to the respective NVC classification and the patterns were observed.

5.2.8.7 Paired t-samples.

Sites 1, 2, 3, 4, 5, 6, 9, 12, 13, 14, 16, 21, and 24 were pairs with the south-facing and north facing cuttings directly opposite each other (13 pairs). The goodness of fit of the NVC classification was looked at for pairs of sites where the predicted NVC classification was the same in one of the five predictions of the TABLEFIT output. The differences in aspect were tested using a paired sample t-test in MINITAB.

5.4 Results

5.4.1 Species composition

There were 116 species found in total; 8 were widespread (found in over 35 % of the quadrats), 17 were common (found in over 14 % of the quadrats), 16 were infrequent (found in over 9 % of the quadrats). The most widespread of all was *A. elatius*, found in over 73% of the quadrats. The other widespread grasses were: *D. glomerata* (47 %), *F. ovina* (42 %) and *H. lanatus* (37 %). The widespread wildflowers were; *P. lanceolata* (51 %), *L. vulgare* (41 %), *A. millefolium* (40 %) and *C. nigra* (35 %) (Table 5.1). All five of the injurious weeds were found; *C. arvense* (33 %), *C. vulgare* (4 %), *R. crispus* (8 %), *R. obtusifolius* (2 %) and *S. jacobaea* (17 %). The tree saplings of Elder (5 %), Sycamore (3 %), Hazel (1 %) and Oak (2 %) were found along with many types of scrub / shrubs; Brambles (32 %), Blackthorn (9 %), Gorse (7 %), Hawthorn (4 %), Bracken (3 %) and Dog Rose (2 %).

5.4.2 General observations from the Geotechnical surveys

North-facing slopes had lush and tall vegetation in comparison to the south-facing slopes (Photos 5.1 – 5.2). There were signs of scrub encroachment along all the roadside verges; small scrub / brambles, tree saplings and tall ruderal plant species were found in the majority of quadrats (Photos 5.7 – 5.10). There were no signs of slips or failures on any grassland site sampled, or any grassland habitats observed along the A303, A30 and A38. There were signs of terracing and desiccation in a few of the south-facing sites (Photos 5.3 – 5.6) and a few signs of slips and failures were observed on a number of wooded habitats, especially along the A38, whilst driving past.

Table 5.1. The widespread and common species found across all sites surveyed.

Frequency	Plant Species found
Widespread: Found in over 35 % of the quadrats	*Achillea millefolium* *Arrhenatherum elatius* *Dactylis glomerata* *Festuca ovina* *Holcus lanatus* *Leucanthemum vulgare* *Plantago lanceolata* *Centaurea nigra*
Common: Found in over 14 % of the quadrats	*Agrostis capillaris* *Cirsium arvense* *Cynosurus cristatus* *Daucus carota* *Festuca rubra* *Galium mollugo* *Glechoma hederacea* *Lathyrus pratense* *Lotus corniculatus* *Medicago lupulina* *Potentilla reptans* *Prunella vulgaris* *Ranunculus repens* *Rubus fruticosus* *Rumex acetosa* *Trifolium repens* *Vicia sepium*

Photo 5.1. A303. Differences in Aspect; North-facing on the left, south-facing on the right.

Photo 5.2. A303. Differences in Aspect; North-facing in the foreground, south-facing in the background.

Photo 5.3. A38. South-facing bareground, signs of surface erosion.

Photo 5.4. A38. South-facing bareground, signs of surface erosion on slate.

Photo 5.5. A303. South-facing bareground, signs of surface erosion.

Photo 5.6. A303. South-facing bareground, signs of surface erosion.

Photo 5.7. A303. Signs of scrub encroachment. South-facing. Bramble growing in foreground.

Photo 5.8. A38. Signs of scrub encroachment. South-facing. Grassland close to the road, scrub behind.

Photo 5.9. A38. Signs of scrub encroachment. South-facing. Grassland patch next to the road with gorse behind.

Photo 5.10. A38. Signs of scrub encroachment. South-facing. The grassland patch in the middle will soon be covered with brambles.

5.4.3 Species Richness and Shannon Diversity Index

The clay and sandy clay soils had significantly more species than the slate areas (13 sp. per m^2 and 12.6 sp. per m^2 vs. 9 sp. per m^2) (F $_{7,\ 99}$ = 2.82, p = 0.01) (Table 5.4). The Shannon Diversity Index was greater on the south-facing slopes in comparison to the north-facing slopes (2 H' vs. 1.7 H') (F $_{1,\ 99}$ = 6.33, p = 0.013) (Table 5.2). The steeper slopes had higher diversity in comparison to the shallowest slopes (1.9 H' vs. 1.7 H') (F $_{2,\ 99}$ = 3.07, p = 0.051) (Table 5.3). Chalk sites had significantly lower diversity in comparison to sandy loam, loam, silty clay and clay soils, and slate had a significantly lower diversity index in comparison to clay soils (F $_{7,\ 99}$ = 5.70, p = <0.001) (Table 5.4).

5.4.4 Species richness of grasses, wildflowers, scrub and injurious weeds

There were significantly less grass species on the steeper slopes in comparison to the other slopes (2.5 sp. per m^2 vs. 2.9 sp. per m^2 and 3.1 sp. per m^2) (F $_{2,\ 99}$ = 5.95, p = 0.004) (Table 5.3). More wildflower species were found on south-facing cuttings in comparison to north-facing cuttings (8.7 sp. per m^2 vs. 6.5 sp. per m^2) (F $_{1,\ 99}$ = 3.88, p = 0.052) (Table 5.2). More scrub species were found on the steepest slopes in comparison to the shallow and medium slopes (1 sp. per m^2 vs. 0.4 sp. per m^2 and 0.5 sp. per m^2) (F $_{2,\ 99}$ = 4.68, p = 0.011) (Table 5.3). Sandy loam soils had a much greater number of weedy species than the other soils (2 sp. per m^2 vs. 0.1 – 1.1 sp. per m^2) (F $_{7,\ 99}$ = 5.68, p = <0.001) (Table 5.4).

Table 5.2. The significant differences (p= < 0.05) between the south-facing and north-facing cuttings of the Shannon Diversity Index, number of wildflowers, Ellenberg Moisture Values and Ellenberg Fertility Values.

Aspect	Shannon Diversity Index (H')	Number of wildflower species	Ellenberg Moisture Value	Ellenberg Fertility Value
South-facing cuttings	2	8.7	4.9	4.5
North-facing cuttings	1.7	6.5	5.2	5.3

Table 5.3. The significant differences ($p = < 0.05$) between the shallow, medium and steep slopes of the Shannon Diversity Index, number of grass and wildflower species and Ellenberg Light Values.

Slope Angle	Shannon Diversity Index (H')	Number of Grasses	Number of wildflowers	Ellenberg Light Value
Shallow < 30 °	1.7 b	2.9 a	0.4 b	6.9 ab
Medium 31 – 34 °	1.9 ab	3.1 a	0.5 b	6.9 a
Steep 35 – 40 °	1.9 a	2.5 b	1.0 a	6.7 b

Table 5.4. The significant differences ($p= < 0.05$) between the different soil textures / types of species richness, Shannon Diversity Index, the number of weeds and Ellenberg Moisture Values.

Soil texture/type	Species Richness	Shannon Diversity Index (H')	Number of Weeds	Ellenberg Moisture Value
Sandy loam	9.2 ab	1.7 a	2.0 a	4.9 ab
Loam	10.2 ab	2.0 a	0.4 b	5.3 ab
Silty Loam	9 ab	1.8 ab	1.1 b	5.1 ab
Silty Clay	9 ab	1.9 a	0.7 b	5.5 ab
Clay	12.3 a	1.9 ac	0.7 b	5.2 a
Sandy Clay	13 a	2.1 ab	0.4 b	5 ab
Chalk	9 ab	1.4 b	0.1 b	4.9 ab
Slate	9 b	1.6 abd	0.2 b	4.6 b

5.4.5 Cover of common grass species (%) and aspect

A number of grass species had greater cover (%) on north-facing cuttings in comparison to south-facing cuttings: *A. elatius* (55 % vs. 22.2 %) ($F_{1, 99} = 9.05$, $p = 0.003$); *D. glomerata* (11.7 % vs. 6.9 %) ($F_{1, 99} = 6.24$, $p = 0.014$); *F. rubra* (8.4 % vs. 0.6 %) ($F_{1, 99} = 17.47$, $p = <0.001$) and *H. lanatus* (9.5 % vs. 2.2 %) ($F_{1, 99} = 9.53$, $p = 0.003$). Only *F. ovina* had greater cover on south-facing cuttings in comparison to north-facing cuttings (21.7 % vs. 8.4 %) ($F_{1, 99} = 4.05$, $p = 0.047$)

5.4.6 Cover (%) of common wildflower species and aspect

Two wildflower species had significantly greater cover (%) on south-facing cuttings in comparison to north-facing cuttings: *L. vulgare* (14.1 % vs. 1.6 %) ($F_{1, 99} = 29.39$, $p = <0.001$) and *C. nigra* (12.4 % vs. 6 %) ($F_{1, 99} = 4.58$, $p = 0.035$).

5.4.7 Species composition using ordination

The first axis on the DCA accounted for 47.8 % of the variation in the species data, and the second axis accounted for 37.5 % of the variation. In the species-environment bi-plot shown in Figure 5.1, the species were spread out over the bi-plot and the environmental variables were clumped in the centre. Even so, slight patterns could be seen: Aspect was going from left to right – South - North; Slate and Sandy clay was on the left, with Silty loam on the right; Chalk was to the bottom left, with Loam towards the upper right; Sandy loam was towards the bottom right corner; Silty clay towards the upper right corner; and Clay was in the centre. The more competitive species were associated on the left of the figure (north-facing): *A. elatius, D. glomerata, C. arvense*, *U. dioica*, *A. sylvestris* and *V. cracca,* whereas wildflowers such as *L. vulgare*, *Hypochaeris radicata*, *A. millefolium* and *C. nigra* were on the far left of the bi-plot (south-facing). *D. carota*, *A. capillaris* and *M. lupulina* were more associated with Chalk. Species associated with steeper slopes were clustered in the top left corner: Species such as *Ulex europaeus*, *Viola riviniana*, and *Rubus fruticosus*.

The first axis on the CCA accounted for 30.5 % of the variation in the species data, and the second axis accounted for 25.7 % of the variation. In the species-environment bi-plot, shown in Figure 5.2, the plant species were forming more defined groups, although the environmental variables were still towards the middle, with the species around the edge. The competitive weedy species, typical of roadside verges were to the right hand side (north-facing): *A. elatius, D. glomerata, A. sylvestris*, *C. arvense* and *U. dioica* – associated with Sandy loams and Silty clays; a group of species were associated with the chalky soils on the top left of the plot: *L. hispidus*, *Pastinaca sativa, C. majus* and *Erigeron acer*. A group of species were associated with Slate: *Pilosella officinarum, Hypericum maculatum* and *Centaurium erythraea.* Aspect forms a slight west to east gradient with south on the west and north on the right. Signs of bareground point to the left, in close association with *Bryophytes* and the south-facing slopes; signs of surface erosion point towards the Slate sites and the steeper slopes. No signs of bareground and no signs of surface erosion point to the right, in close association with the north-facing aspects and Silty clays and Silty loams. Clay was in the centre, with no particular species associated with it. The bi-plot in Figure 5.2 also showed the Ellenberg Indicator Values as supplementary data. Light (L) had a very short line, however, fertility (N) and moisture (M) were pointing towards the west side, i.e. towards the northern slopes, with Silty loam, Silty clay and Sandy loam; and moisture and signs of no bareground were closely associated. The Shannon Diversity Index (H') was pointing towards the lower right of the plot, where there were more wildflower species. The only grass: *C. cristatus* was found to the right, all the other grass species were found to the left, associated with north-facing slopes.

When the environmental variables were looked at independently, the soil type / texture accounted for 15 % of the variation in the plant composition, the slope angle accounted for 6 % and aspect only accounted for 2 %, although all were highly significant. However, in combination, more of the variance was explained (24 %), and when all the interactions were included, this accounted for 45 % of the variation. So, the plant composition was better explained by a combination of factors (Table 5.5).

Table 5.5. A table to show the partitioning of the variance of the environmental variables, with a CCA. The interactions account for 45 % of the variation

Environmental variable	Trace	%	p-value
Soil texture / type	1.201	15%	0.002
Slope angle	0.486	6%	0.002
Aspect	0.142	2%	0.002
Soil, Slope, Aspect	1.967	24%	0.002
Plus Interactions	3.637	45%	0.002
Total inertia	8.115		

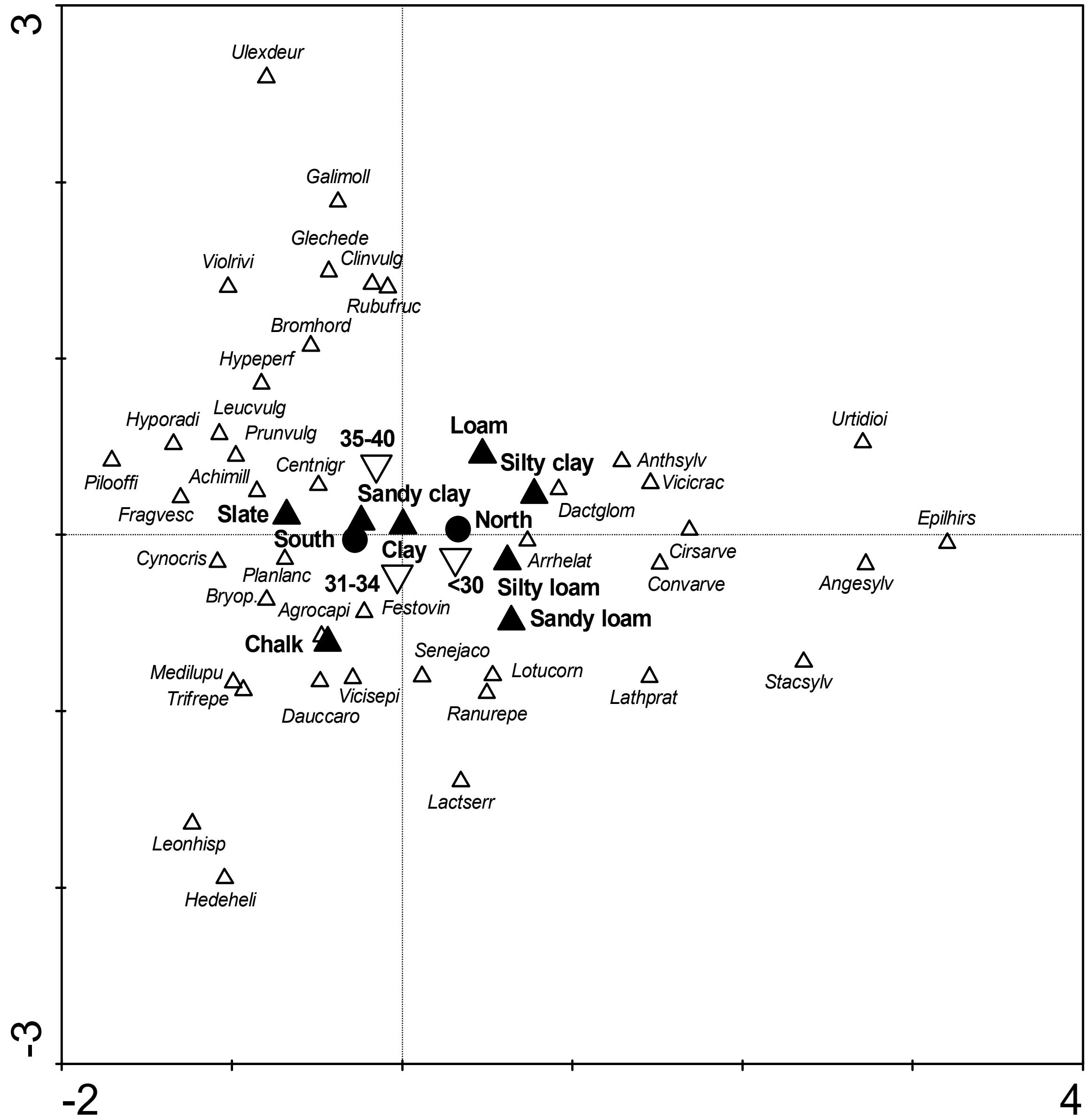

Figure 5.1. A bi-plot from a Detrended Correspondence Analysis (DCA), showing the main 41 species and not constrained by the environmental variables. *Achimill =Achillea millefolium, Agrocapi = Agrostis capillaris, Angesylv = Angelica sylvestris, Anthsylv = Anthriscus sylvestris, Arrhelat = Arrhenatherum elatius, Bryop. = Bryophytes, Bromhord = Bromus hordeaceus, Centnigr = Centaurea nigra, Cirsarve = Cirsium arvense, Clinvulg = Clinopodium vulgare, Convarve = Convolvulus arvensis, Cynocris = Cynosurus cristatus, Dactglom= Dactylis glomerata, Dauccaro = Daucus carota, Epilhirs = Epilobium hirsutum, Festovin = Festuca ovina, Fragvesc = Fragaria vesca, Galimoll = Galium mollugo, Glechede = Glechoma hederacea, Hedeheli = Hedera helix, Hypeperf = Hypericum perforatum, Hyporadi = Hypochaeris radicata, Lactserr = Lactuca serriola, Lathprat = Lathyrus pratensis, Leonhisp = Leontodon hispidus, Leucvulg = Leucanthemum vulgare, Lotucorn = Lotus corniculatus, Medilupu = Medicago lupulina, Pilooffi = Pilosella officinarum, Planlanc = Plantago lanceolata, Prunvulg = Prunella vulgaris, Ranurepe =Ranunculus repens, Rubufrut = Rubus fruticosus, Senejaco = Senecio jacobaea, Stacsylv = Stachys sylvatica, Trifrepe = Trifolium repens, Ulexeuro = Ulex europaeus, Urtidioi = Urtica dioica, Vicicrac = Vicia cracca, Vicisepi = Vicia sepium, Violrivi = Viola riviniana.*

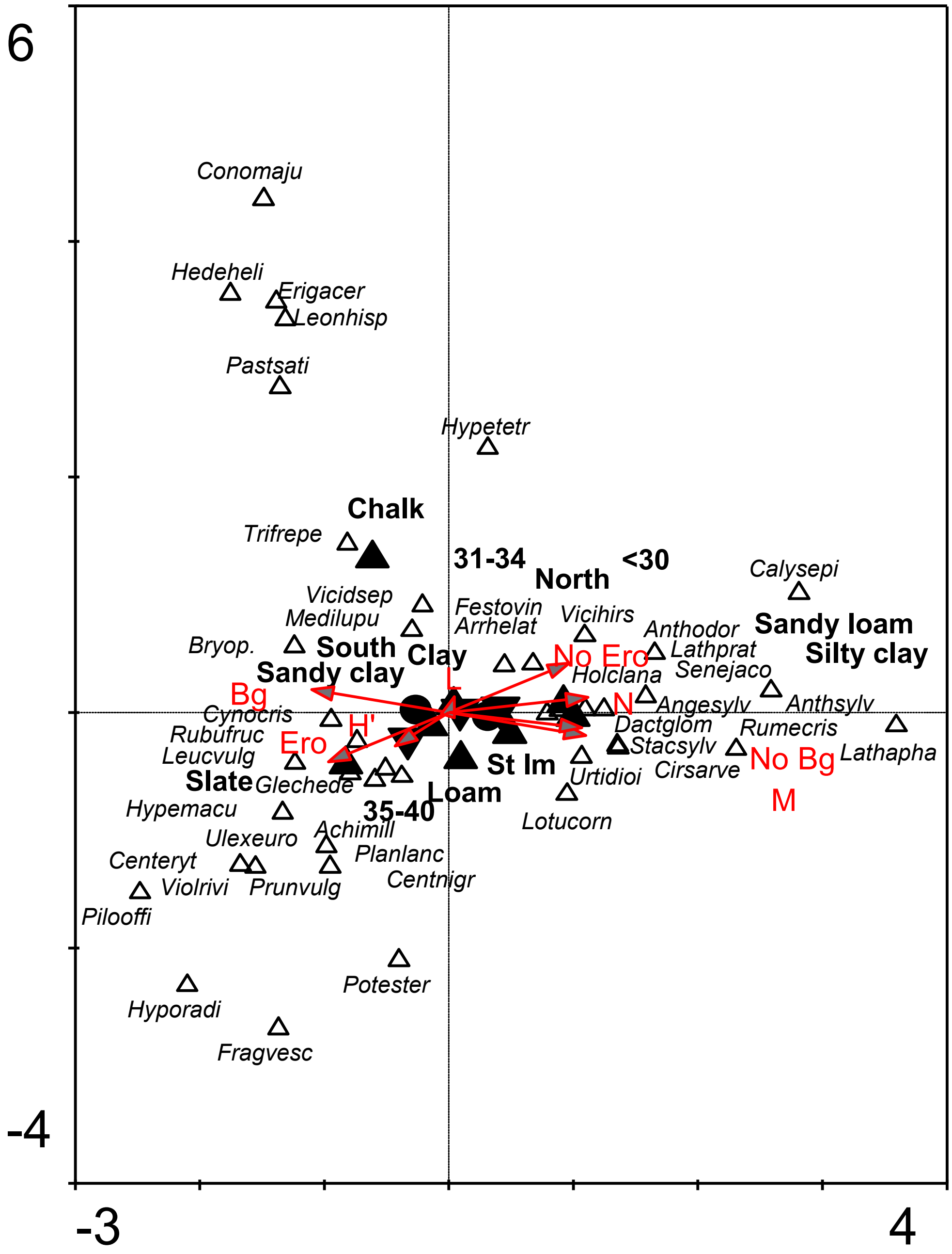

Figure 5.2. A bi-plot from a Canonical Correspondence Analysis (CCA), showing the main 43 species and constrained by the environmental variables. Environmental variables: South = south-facing cuttings, North = North-facing cuttings; <30 = shallow slopes, 31-34 = medium slopes, 35-40 = steep slopes; St lm = Silty loam. Supplementary variables - not influencing the model: No bg = no signs of bareground; Bg = signs of bareground; No Ero = no signs of surface erosion; Ero = signs of surface erosion. The Ellenberg Indicator Values and Shannon Diversity Index (H') are shown as supplementary variables: R = Ph, L = Light, F = Moisture and N = Fertility. *Achimill = Achillea millefolium, Angesylv = Angelica sylvestris, Anthodor = Anthoxanthum odoratum, Anthsylv = Anthriscus sylvestris, Arrhelat = Arrhenatherum elatius, Bryop. = Bryophytes, Calysepi = Calystegia sepium, Centeryt = Centaurium erythraea, Centnigr = Centaurea nigra, Cirsarve = Cirsium arvense, Conomaju = Conopodium majus, Cynocris = Cynosurus cristatus, Dactglom= Dactylis glomerata, Erigacer = Erigeron acer, Festovin = Festuca ovina, Fragvesc = Fragaria vesca, Glechede = Glechoma hederacea, Hedeheli = Hedera helix, Holclana = Holcus lanatus, Hypemacu = Hypericum maculatum, Hypetetr = Hypericum tetrapterum, Hyporadi = Hypochaeris radicata, Lathapha = Lathyrus aphaca, Lathprat = Lathyrus pratensis, Leonhisp = Leontodon hispidus, Leucvulg = Leucanthemum vulgare, Lotucorn = Lotus corniculatus, Medilupu = Medicago lupulina, Pastsati = Pastinaca sativa, Pilooffi = Pilosella officinarum, Planlanc = Plantago lanceolata, Potester = Potentilla sterilis, Prunvulg = Prunella vulgaris, Rubufruc = Rubus fruticosus, Rumecris = Rumex crispus, Senejaco = Senecio jacobaea, Stacsylv = Stachys sylvatica, Trifrepe = Trifolium repens, Ulexeuro = Ulex europaeus, Urtidioi = Urtica dioica, Vicihirs = Vicia hirsuta, Vicisepi = Vicia sepium, Violrivi = Viola riviniana.*

5.4.8 Ellenberg Indicator Values

5.4.8.1 Light (L)

There was a significant difference between the slope angles when looking at the Ellenberg Indicator Values for Light (L) ($F_{2, 99} = 3.62$, $p = 0.03$). The steepest slopes had a significantly lower light values than the middle slopes (6.7 L vs. 6.9 L) but there were no other significant differences. This still remains in the same Light category, but the steeper slopes tended to have slightly more shade tolerant species (Table 5.3).

5.4.8.2 Moisture (F)

The Ellenberg Indicator Values for Moisture (F) were significantly lower on the south-facing slopes (4.9 F) in comparison to the north-facing slopes (5.2 F) ($F_{1, 99} = 10.21$, $p = 0.002$). These fit into different categories. Category 4 = species mainly found on dry ground but tolerant of moisture, and category 5 = species that are mainly found in moister conditions (Table 5.2). There was a significant difference with the soil type ($F_{7, 99} = 2.64$, $p = 0.015$), between the slate and clay soils. Slate had a much lower value, indicating less moisture at 4.6 F, whereas clay had a higher value, indicating moister conditions at 5.2 F (Table 5.4).

5.4.8.3 Fertility (N)

The Ellenberg Indicator Value for Fertility (N) was significantly higher on the north-facing cuttings than on the south-facing cuttings (5.3 N vs. 4.5 N) ($F_{1, 99} = 5.09$, $p = 0.026$). Category 4 = low fertility, category 5 = intermediate fertility, so the north-facing slopes had higher fertility than the south-facing slopes (Table 5.2).

5.4.9 Grime's CSR plant strategies

Figure 5.3 showed a bi-plot of the CCA in CANOCO, but with the species allocated to their CSR plant strategies. It was clear that the majority of the species grouped to the right of the bi-plot were competitive – competitive ruderal (C – CR) species. These were the species which were associated with north-facing slopes, on silty loam, silty clay and sandy loam soils, i.e. *competitor* (C) species such as *C. arvense*, *U. dioica, Pteridium aquilinum* and *Epilobium* *hirsutum*; competitive-ruderal (CR) species such as *A. sylvestris* and *Artemisia absinthium;* and competitive – competitive-ruderal (C – CR) species like *Angelica sylvestris, Stachys sylvatica* and *Calystegia sepium.* Plus a few competitive-stress – competitive-stress-ruderal (CS – CSR) species such as *A. elatius* and *D. glomerata* were found. On the other hand, to the bottom left of the bi-plot, the majority of species found were stress - competitive-stress-ruderal (S - CSR) species, found on the more south-facing, steeper, slate slopes, with more signs of bareground and erosion: i.e. CSR species such as *H. radicata, Fragaria vesca, P. vulgaris, P. lanceolata* and *C. nigra,* or stress (S) species such as *Potentilla sterilis* and *U. europaeus.* The species associated with Chalk were more stress – stress-ruderal species, such as *L. hispidus* (S) *C. majus* (SR) and *E. acer* (SR).

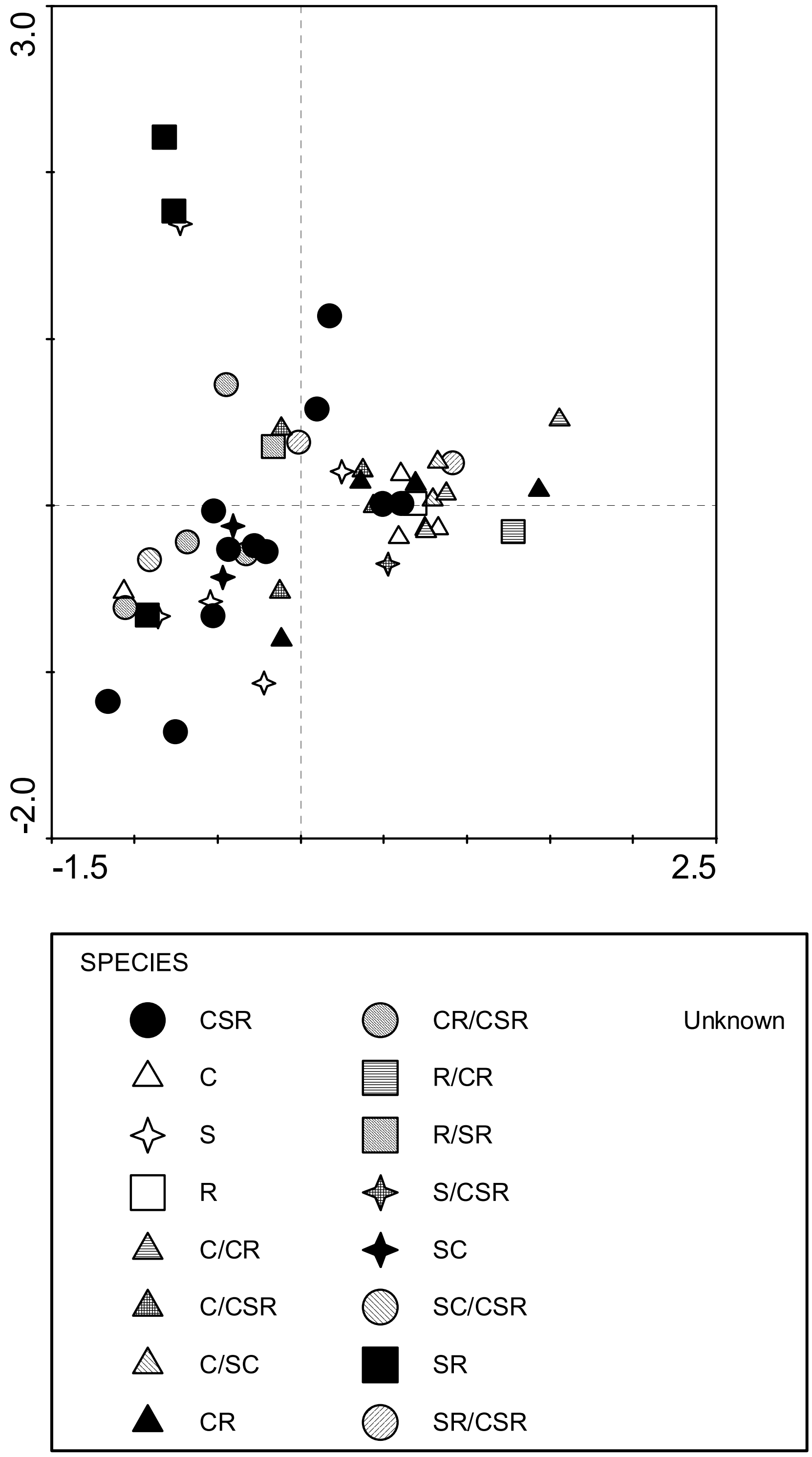

Figure 5.3. A bi-plot from a Canonical Correspondence Analysis (CCA), showing just the main 64 species, classified to their CSR strategy.

5.4.10 National Vegetation Classification

MG1 – *Arrhenatherum elatius* grassland - was the habitat most frequently found on south-facing and north-facing cuttings. 12 MG1 sites were on north-facing cuttings and 7 were on south-facing cuttings. 11 different types of NVC were found on south-facing cuttings and 6 types of NVC were found on north-facing cuttings (Table 5.6). Several types of calcareous and acid grassland were found including species-rich MG5 *Cynosurus cristatus-Centaurea nigra* grassland. MG5 is mainly found in meadows, but not often in the south of Britain. There were a few woodland NVC types predicted, even though the sites sampled were grassland habitats and were not in wooded areas (Table 5.7).

When the goodness of fit was compared between aspects, it became clear that there were distinctly different patterns emerging between south-facing and north-facing cuttings. Table 5.8 showed that the goodness of fit was much better on the north-facing cuttings than on the south-facing cuttings. Only two fair – very good fits were found on the south-facing cuttings, whereas thirteen fair – very good fits were found on the north-facing cuttings, and most of these were MG1. The south-facing cuttings had a number of different NVC suggestions, but all were poor fits.

9 pairs of sites (directly opposite each other) had a NVC classification of MG1 on both south-facing and north-facing cuttings, using one of the five recommendations from TABLEFIT. Table 5.9 showed the goodness of fit (%) for each one. Only at one site: site 3, did the goodness of fit for MG1 fit better on the south-facing cutting than the north-facing cutting. A paired t-test showed that the goodness of fit was significantly better on the north-facing cuttings than the south-facing cuttings ($p = 0.025$) and this was also confirmed by a Mann-Whitney test ($p = 0.0217$).

Figure 5.4 showed the NVC classification in CANOCO. The samples / sites have been classified into the corresponding NVC classification. The red filled circles are MG1 and this formed a group on the right side of the bi-plot, with north-facing, flatter slopes, Silty loam, Silty clay and Sandy loam. Most of the MG5, calcicolous classifications and woodland sites were in the bottom left hand corner of the bi-plot, associated with steeper slopes and Slate. MG1 d and MG1 e were more associated with the Chalk soils.

Table 5.6. The number of each NVC class of the best fit between North and South-facing sites.

NVC classification	South-facing cutting	North-facing cutting
CG2 c	1	0
CG10 b	1	0
MG1	7	12
MG1 a	0	3
MG1 d	1	1
MG1 e	3	0
MG5	1	1
MG5 a	1	0
OV23 d	1	0
U1 d	0	1
U1 f	1	1
W23 b	1	0
W24a	1	0

Table 5.7. The community and sub-community types for each NVC code found on roadside verges of the best fit.

NVC code	NVC habitat	NVC community/sub community name
CG2 c	Calcicolous grassland	*Festuca ovina - Avenula pratensis* grassland
CG10 b	Calcicolous grassland	*Festuca ovina - Agrostis capillaris - Thymus praecox grassland, Carex pulicaris - Carex panicea* sub-community
MG1	Mesotrophic grassland	*Arrhenatherum elatius* grassland
MG1 a	Mesotrophic grassland	*Arrhenatherum elatius* grassland, *Festuca rubra* sub-community
MG1 d	Mesotrophic grassland	*Arrhenatherum elatius* grassland, *Pastinaca sativa* sub-community
MG1 e	Mesotrophic grassland	*Arrhenatherum elatius* grassland, *Centaurea nigra* sub-community
MG5	Mesotrophic grassland	*Cynosurus cristatus-Centaurea nigra* grassland
MG5 a	Mesotrophic grassland	*Cynosurus cristatus-Centaurea nigra* grassland, *Lathyrus pratensis* sub-community
OV23 d	Open habitat	*Lolium perenne - Dactylis glomerata* community, *Arrhenatherum elatius - Medicago lupulina* sub-community
U1 d	Calcifugous grassland	*Festuca ovina - Agrostis capillaris - Rumex acetosella* grassland*, A. odoratum - Lotus corniculatus* sub-community
U1 f	Calcifugous grassland	*Festuca ovina - Agrostis capillaris - Rumex acetosella* grassland, *Hypochaeris radicata* sub-community
W23 b	Woodland	*Ulex europaeus - Rubus fruticosus* scrub, *Rumex acetosella* sub-community.
W24 a	Woodland	*Rubus fruticosus - Holcus lanatus* underscrub, *Cirsium arvense - Cirsium vulgare* sub-community

Table 5.8. The NVC classification of the best fit, showing the goodness of fit between the North-facing and South-facing sites.

	South-facing cutting			North-facing cutting		
	Site	NVC classification	Goodness of fit (%)	Site	NVC classification	Goodness of fit (%)
Paired Sites	Site 1 S	MG1	Very Poor (32)	Site 1 N	MG1 a	Poor (58)
	Site 2 S	MG1 d	Poor (47)	Site 2 N	MG1 a	Good (70)
	Site 3 S	MG1	Very good (84)	Site 3 N	MG1	Poor (53)
	Site 4 S	MG1	Good (76)	Site 4 N	U1d	Poor (59)
	Site 5 S	MG1	Fair (61)	Site 5 N	MG1	Very good (85)
	Site 6 S	MG1 e	Poor (51)	Site 6 N	MG1	Very good (81)
	Site 9 S	CG2 c	Very poor (45)	Site 9 N	MG1	Good (76)
	Site 12 S	U1f	Very poor (42)	Site 12 N	MG1 a	Very good (80)
	Site 13 S	W23 b	Very poor (32)	Site 13 N	MG1	Good (72)
	Site 14 S	MG5	Very poor (49)	Site 14 N	MG1	Fair (60)
	Site 16 S	MG1	Very poor (33)	Site 16 N	MG1	Good (71)
	Site 21 S	W24 a	Poor (52)	Site 21 N	MG1	Very good (84)
	Site 24 S	OV23 d	Very poor (43)	Site 24 N	MG1	Fair (67)
Non Paired Sites	Site 10 S	MG1	Poor (49)	Site 7 N	MG1	Poor (50)
	Site 11 S	MG1 e	Very poor (34)	Site 8 N	MG1	Fair (65)
	Site 15 S	MG1	Poor (49)	Site 17 N	MG1 d	Very poor (30)
	Site 22 S	MG5 a	Very poor (28)	Site 18 N	MG1	Fair (60)
	Site 23 S	MG1 e	Very poor (38)	Site 19 N	MG5	Very poor (46)
	Site 25 S	CG10 b	Very poor (40)	Site 20 N	U1f	Very good (80)

Table 5.9. The goodness of fit (%) of the south-facing and north-facing pairs of sites that had MG1 in one of the five recommendations from TABLEFIT.

Site	South-facing cutting	North-facing cutting
1	32	48
2	33	54
3	84	53
5	61	85
6	40	81
14	49	60
16	33	71
21	52	76
24	33	67

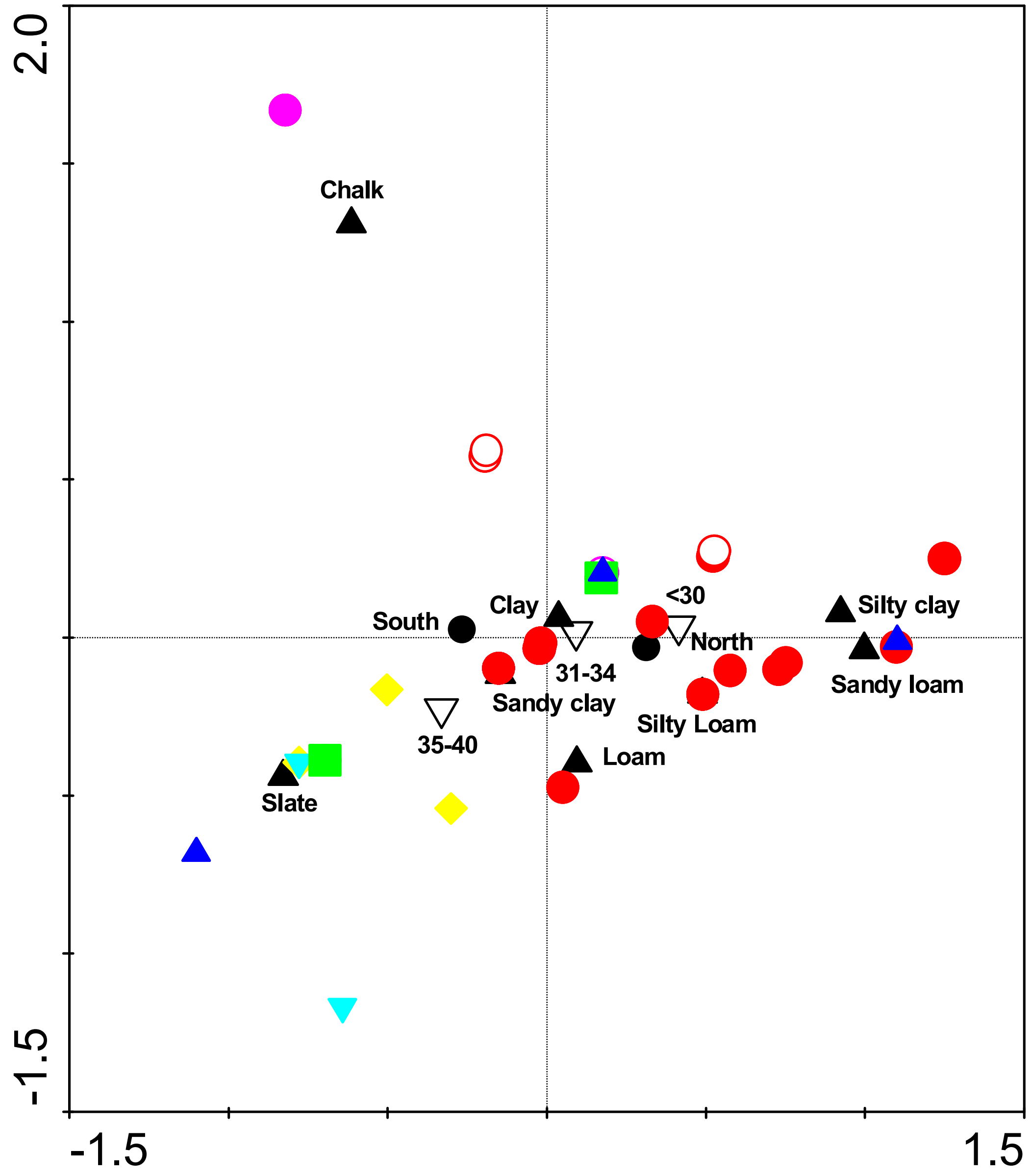

Figure 5.4. The samples were classed into NVC classifications. Red filled circles = MG1, Red open circles = MG1 a, Pink filled circles = MG1 d, Pink open circles = MG1 e, Blue upwards triangles = U1 d and U1 f, Light blue downwards triangles = MG5, Green squares = CG2 and CG10 b, Yellow diamonds = W23 b, W24 a and OV23 d.

5.4.11 HAGDMS ordination

The first axis on the PCA accounted for 26.2 % of the variation and the second axis accounted for 19.4 % of the variation. The bi-plot in Figure 5.5 showed that slips, ravelling, and slope bulges were associated with sites with trees and scrub, scrub and brambles. Slopes that were at risk, along with terracing and cracks, were associated with trees, scrub and scrub encroachment on the steeper slopes. Slips were associated with Limestone and Oxford Clay soil formations. Grassland was associated with surface erosion and rabbit burrows, found more often on Upper Greenaway. Woodland was associated with dislodged trees, dislodged structures and bareground. Woodland was more often found on Gault clay, Mudstone and Kellaway formation soils.

The first axis of the RDA accounted for 26.3 % and the second axis accounted for 19.1 %. The bi-plot in Figure 5.6 showed that Woodland was associated with dislodged trees, bareground, dislodged structures and desiccation on Gault Clay and Mudstone. Slopes with scrub encroachment and scrub are the slopes at risk – with slips, ravelling, slope bulges, terracing and cracks, but there wasn't a particular soil formation associated with these slope stability problems. Grassland was associated with surface erosion and rabbit burrows on Upper Greenaway Sands. When the environmental variables were looked at separately, aspect and angle were unimportant, soil formation accounted for 6.4 % of the variability, and the total was 8.3 %. However, when all the interactions were included, this accounted for 18.6 % of the variation. The environmental variables were not as important on their own as when in combination with each other (Table 5.10).

Table 5.10. Partitioning of the variance of the HAGDMS data in RDA.

Environmental variable:	Trace	F-ratio	p-value
Slope angle	0.20%	0.996	0.442
Aspect	0.60%	1.1	0.304
Soil formation	6.40%	2.549	0.002
Interactions	18.60%	1.57	0.002
Total	8.30%	2.277	0.002
Not accounted for:	74%		

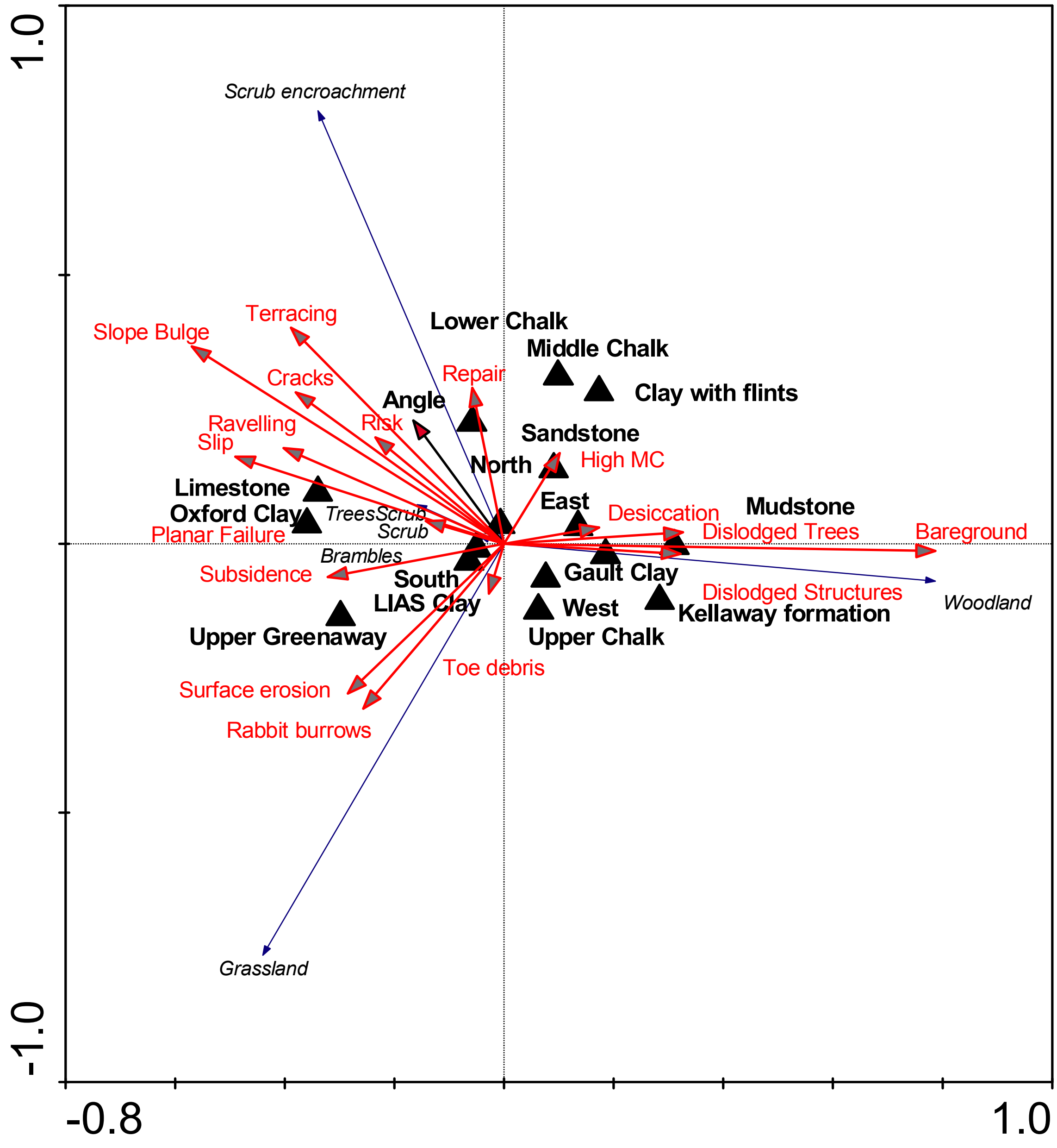

Figure 5.5. PCA ordination, not constrained by the environmental variables. Aspect, angle and soil formations are environmental variables, with geotechnical observations as supplementary data.

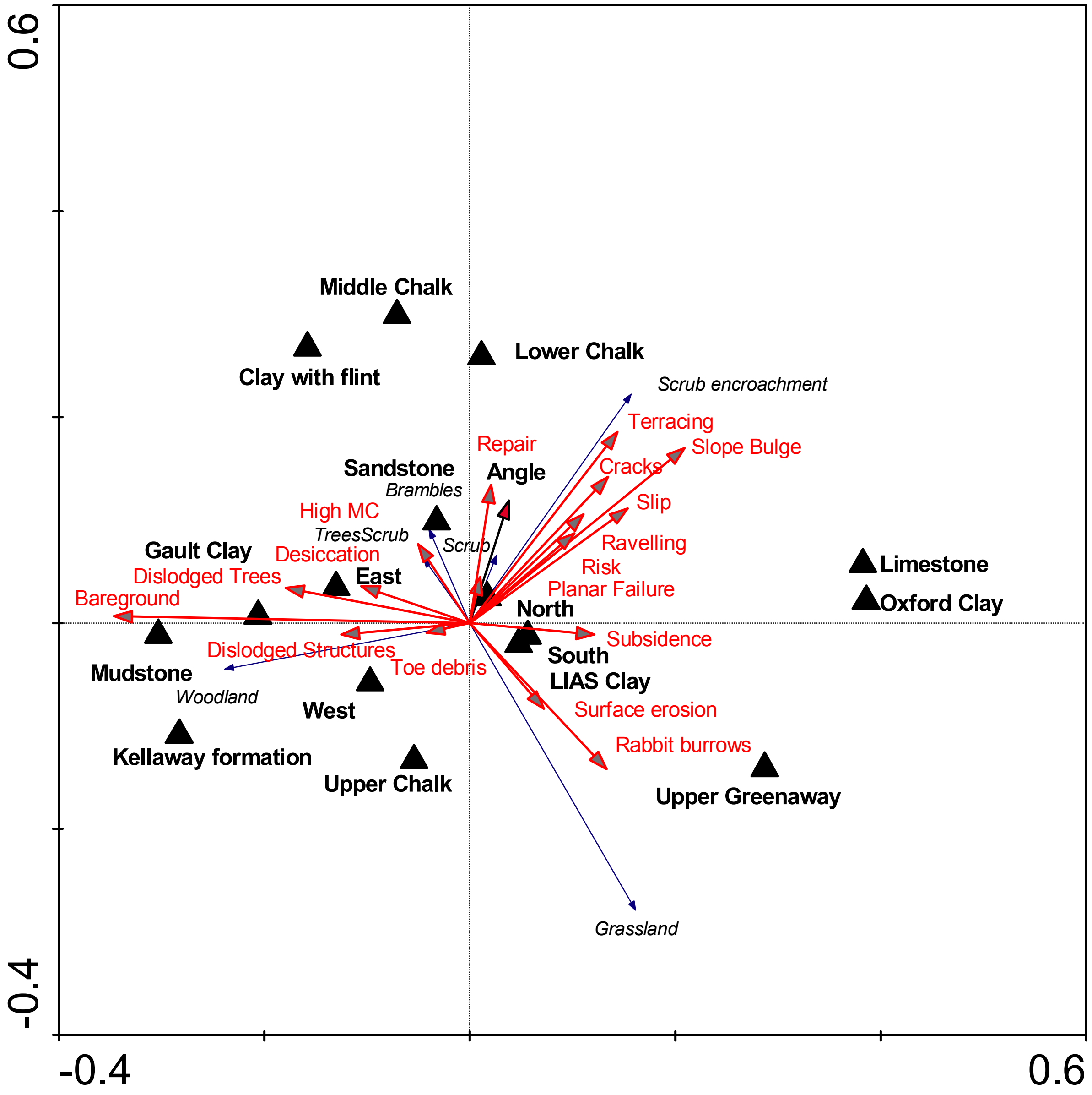

Figure 5.6. RDA ordination, constrained by the environmental variables. Aspect, angle and soil formations as environmental variables, with geotechnical observations as supplementary data.

5.5 Discussion

5.5.1 Species establishment

1) Did species sown from the standard grass seed mixture dominate? Or did injurious weeds dominate? Or did weedy, competitive species such as *A. elatius* dominate the roadside cuttings?

The A303 was built in 1988: the standard grass seed mixture (Table 1.1) was sown on the majority of the roadside verges. These results show that natural re-colonisation can produce species-rich habitats over time: a total of 116 species were found. Some of the species sown in the original standard seed mixtures were not that common now. For example, *L. perenne* was only found in 1 % of the quadrats and *F. brevipila* and *P. pratensis* were not found at all. *F. rubra*, *A. capillaris* and *T. repens* were common (in over 14 % of the quadrats).

Photos 5.7 – 5.10 show many sites had obvious scrub encroachment. A number of sites were particularly species-rich. Site 14 was the most species-rich; the south-facing site had 28 species and the north-facing site had 35 species. This site had a good mixture of wildflowers such as *Primula vulgaris*, *Pulicaria dysenterica* and *Orchis mascula* on the north and *C. erythraea*, *H. radicata* and *Viola riviniana* on the south, and there were brambles and tree saplings, plus *A. elatius* and *D. glomerata*. This was a pattern found on many of the sites: Brambles, shrubs and tree saplings were found alongside weedy species, which were found alongside wildflower species more typical of species-rich grassland habitats. This lead to some of the sites receiving a woodland or open habitat NVC classification, even though they were on species-rich grassland sites. The cover of scrub was also higher on the steepest slopes, suggesting that these slopes were cut less frequently due to the difficulty of cutting on steep slopes.

All five of the injurious weeds were found: *C. arvense* and *S. jacobaea* were the commonest. *A. elatius* was found in the majority of quadrats and was the commonest grass. *A. elatius* is susceptible to cutting / grazing; it is a sign of lack of management in habitats (Mahmoud *et al.* 1975). The large cover of *A. elatius* and injurious weeds, plus the amount of scrub encroachment found, shows that these roadside verges are not cut frequently enough. Over time, the cover of *A. elatius* and injurious weeds will continue to dominate and the small saplings and brambles will grow into bigger trees and bushes, out-competing the smaller grassland species.

The management regime for these areas is one cut every three, six or nine years (HA 2005a). Even after one year the saplings will have become bigger. If these sites were only cut once every nine years – they would no longer be grassland habitats and the wildflowers more typical of species-rich grassland habitats would be lost. The sites allocated to species-rich grassland habitats / priority BAP habitats by the Highways Agency are cut once a year (HA 2005a). Even this isn't enough. The cover of *A. elatius* will only be reduced with regular cutting, a minimum of twice a year (Mahmoud *et al.* 1975; Grubb 1982). The BAP habitats will be overrun with *A. elatius* and over time, scrub encroachment will lead to woodland. The Highways Agency spends a lot of money on scrub control (i.e. HA 2000; 2005a; 2005b; 2007a; 2007b). The allocated Species-rich grassland / BAP habitats should be cut twice a year, preferably once at the end of the growing season (July – August) and once either in autumn or in spring, followed by once a year, once every two years and only once every three years if financial constraints can't allow for a cut every two years; with removal of the cuttings as soon as possible (i.e. Wells *et al.* 1989; Bobbink & Willems 1993; Schaffers *et al.* 1998; Hovd & Skogen 2005). The money spent on scrub removal can be spent on cutting instead, since scrub removal won't be a problem.

5.5.2 Aspect and species richness and diversity

2) Did south-facing cuttings have greater species richness and diversity than the north-facing cuttings?

In the majority of studies looking into aspect, the greater warmth / radiation on the south-facing slopes increased species richness and increased diversity (i.e. Kutiel 1992; Bruun 2000; Pykala *et al.* 2005). In this study, the Shannon Diversity Index was higher on south-facing slopes but there were no differences in species richness. This may have been influenced by the two most species-rich sites which had 33 and 35 species per site and were north-facing slopes. Most of the south-facing sites had about 20 – 25 species, but the north-facing slopes ranged from only 7 species – 35 species. However, there were more wildflowers found on south-facing slopes. This is a pattern that has been noted in other studies on aspect –

wildflower diversity is often greater on south-facing slopes, which in turn, increases overall diversity (Pahlsson 1974; Kutiel 1992; Rorison *et al.* 1986a; 1996; Kutiel & Lavee 1999; Bennie *et al.* 2006).

5.5.3 Aspect and species composition

3) Did species preferring warm, dry conditions establish on south-facing cuttings and species preferring cold, wet conditions establish on north-facing cuttings?

All the grasses were found on both aspects but they had greater cover on the north-facing slopes, with the exception of *F. ovina* which preferred south-facing slopes. There were more wildflowers found on south-facing slopes such as *C. nigra* and *L. vulgare*. The ordination showed that most of the grasses were on the right of the graph – associated with the north-facing slopes and the wildflowers were on the left of the graph – associated with the south-facing slopes. *C. nigra* prefers south-facing slopes in the sun and *L. vulgare* prefers south-facing slopes (Grime *et al.* 1988). Grime *et al.* (1988) had also noted that *F. rubra* prefers north-facing slopes yet *F. ovina* will grow on both. So, over time, a xeric plant community is developing on south-facing slopes and a mesic community is developing on north-facing slopes (Albertson 1937; Kutiel 1992; Sebastia 2004).

These results show that aspect can be a significant factor influencing plant species composition on roadside verges and should always be taken into consideration when looking at roadside verge habitats. This quote from Kutiel & Lavee (1999) captures the differences in aspect very neatly “North-facing hill-slopes constitute different geoecological systems from south-facing aspects, despite short differences between them”. However, those studies that have looked at grassland plant species composition on roadside verges have rarely looked at aspect differences. Many motorway vegetation studies in Spain found compositional differences, whereas another study in Spain deliberately didn’t look at aspect differences believing they were unimportant (Andres *et al.* 1996, Andres & Jorba 2000, Bochet & Garcia-Fayos 2004; Tormo *et al*. 2006; Matesanz *et al*. 2006). In New Zealand, a number of roadside cuttings were surveyed, but each side of the road was treated the same (Ullmann *et al*. 1995; Wilson *et al.* 2000). Wilson *et al*. (2000) did a comparable study in Wales on roadside verges (the only published scientific paper on a roadside verge survey in England / Wales), on a transect from east – west Wales, but didn't look at the aspect. If only the north-facing slopes were chosen, there would be a much greater proportion of grasses than is actually found on all roadside verges.

5.5.4 Aspect and surface erosion

4) Did south-facing cuttings have more signs of surface erosion than north-facing cuttings? Did the steeper slopes have more signs of surface erosion and slips?

Across all the sites surveyed for geotechnical faults, the only recorded problems were bareground patches and signs of surface erosion – terracing and desiccation. Bareground patches were more associated with south-facing slopes, plus desiccation was found more often on south-facing slopes. Desiccation occurs when the ground is wet and dries quickly. This forms small hexagonal cracks on the soil surface. Since south-facing slopes are warmer and drier, the soil will dry out faster than north-facing slopes. Churchill (1982) also noted that desiccation was greater on south-facing slopes, however, he didn't believe this would influence slope stability. The steeper slopes were on the A38, where there were more sites on slate bedrock. This is an unstable substrate, so bare patches and terracing was common. No signs of slips or larger slope stability problems were noted on any grassland areas across all sites surveyed.

5.5.5 Soil type and species composition

5) Did the chalk soils along the A303 mean that a calcareous community developed?

The A303 runs through chalk substrate and a few sites were clearly very chalky and influencing the species composition. Other sites had thick humus topsoil over the base soil. There was a large amount of variation between the sites and the soil measurements were based on hand-felt texture at the time of the survey. Even so, the soil type influenced 15 % of the variation shown in Figure 5.1 and Figure 5.2. The species associated with chalk were: *C. majus*, *E. acer*, *L. hispidus*, *P. sativa* and *T. repens*. Schaffers *et al.* (2002) showed that the

grassland species composition of roadside verges was influenced by shading and the water level, plus the percentage of calcium carbonate ($CaCO_3$) and the soil pH.
The slate bedrock, mainly found on the A38, also had species associated with them; *C. erythraea*, *P. officinarum, V. riviniana* and *P. sterilis*. The sandy loam and silty clay soils were associated with the weedy, competitive species, typical of MG1 communities. These species are often found on sites with greater organic matter and fertility (i.e. Kutiel 1992; Pywell *et al.* 2003; White *et al.* 2004). Clearly, there are interesting differences in the species composition of plant communities developing over time on roadside verges.

5.5.6 Ellenberg Indicator Values

6) Did the north-facing cuttings have greater Ellenberg Fertility and Moisture Values, and did the south-facing cuttings have greater Ellenberg Light Values?

Although it was expected that there would be greater light loving species on south-facing slopes due to the warmer and drier conditions, aspect didn't influence the Ellenberg Light values in this case (Perring 1959; 1960; Pahlsson 1974; Bennie *et al.* 2006). However, both moisture and fertility values were higher on the north-facing slopes in comparison to the south-facing slopes. Other studies looking at aspect have shown that organic matter and soil depth is greater on north-facing slopes. This could lead to an increase in fertility (Kutiel 1992; Kutiel & Lavee 1999). Numerous studies have measured soil moisture on north-facing slopes and have found that moisture is much greater than south-facing slopes (Rorison *et al.* 1986a; 1986b; Bennie *et al.* 2006; Klimek *et al*. 2007). This has been confirmed by the results of this survey. Some aspect studies have also shown that north-facing slopes have a greater amount of biomass than south-facing slopes due to greater fertility and moisture (Pahlsson 1974; Churchill 1982; Bochet & Garcia-Fayos 2004). Biomass wasn't measured during this survey, however, it was observed that north-facing slopes had greater soil depth and greater aboveground biomass than the south-facing slopes.

5.5.7 Grime's CSR Plant Strategies

7) Did the north-facing cuttings have more competitive species establishing than the south-facing cuttings?

There were more *competitor - competitor-stress-ruderal* species found on the north-facing slopes and there were more *stress - competitor-stress-ruderal* species found on south-facing slopes. Since south-facing slopes are warmer and drier with more bareground, more signs of surface erosion and lower fertility than north-facing slopes, this leads to greater stress (lack of water and greater temperatures) and disturbance (more drought and more desiccation) and these conditions favour the less competitive wildflower species leading to an increase in wildflowers and diversity on south-facing slopes. Whereas since north-facing slopes are colder, wetter and more fertile, with no bareground and surface erosion, this leads to less stress (access to water and lower temperatures) and less disturbance (no drought and no desiccation) and these conditions favour plant growth with an increase in weedy species (i.e. *C. arvense* and *A. elatius*) – and a decrease in diversity (Leps *et al*. 1982; Grime *et al*. 1988; Grime *et al*. 2001; Hunt *et al*. 2004; Williams *et al*. 2005).

5.5.8 Survey methods and the National Vegetation Classification (NVC)

8) Did the NVC classification differ between north-facing and south-facing cuttings?

There were more typical MG1 communities on the north-facing slopes, whereas it was more difficult to fit an NVC classification to the sites on the south-facing slopes. When the species compositions of the sites were looked at in more detail, it became clearer that this was due to the large percentage cover of *A. elatius* and *D. glomerata* on the north-facing slopes. The typical MG1 species include: *A. elatius*, *D. glomerata*, *H. lanatus*, *A. sylvestris*, *C. arvense* and *U. dioica*. These species clumped together on the right of the CCA bi-plot (Figure 5.2). Increases in fertility and moisture on the north-facing slopes are leading to more competitive species. There was a greater mix of NVC classifications on the south-facing slopes including CG (Calcareous) and W (woodland understorey). The mesotrophic classifications were more often found on the north-facing cuttings and the calcicolous and calcifugous classifications were more often on the south-facing slopes. Perring (1958; 1959) and Bennie *et al.* (2006)

showed that on the northern and flatter slopes there was a shift towards mesotrophic grassland communities, whereas typical chalk grassland was restricted to the southern slopes (Bennie *et al.* 2006).

9) Did the roadside verge habitats fit into the NVC classifications?

The majority of the sites had a unique and unusual combination of species that didn't fit into any of the NVC classifications. The number of very poor fits to the NVC, especially on south-facing slopes, shows that the species assemblages on roadside verges do not correspond with the NVC classification. A number of north-facing slopes fitted the NVC classification well, but the majority of the south-facing slopes didn't. Some north-facing sites were given a definite MG1 classification – like site 14 N - but this site had 35 species, another site – 21 N – only had 10 species and was given an MG1 classification. Site 18 N had 33 species with *Clinopodium vulgare*, *Hypericum perforatum* and *P. vulgaris*, but since *A. elatius* was present it was classed as MG1 (Rodwell 1992). The Highways Agency does not value MG1 habitats – it is generally assumed that MG1 is "the roadside verge community" and species poor - these sites would not be classed as "Species-rich grasslands" even though the species found are worth conserving. Some sites had the same species lists – but one had *A. elatius* and the other didn't – one would get MG5 – the other would get MG1 – often with very species-rich flora. Using the NVC classification on these roadside verges is not giving the best picture. It is clumping species-rich grassland into MG1 just because it has some of the indicator species, but it doesn't take into account species richness or diversity.

When the roadside verges are monitored, the most usual method of surveying is a Phase 1 habitat survey (HA 1993). This is very basic and generally classes grassland as semi-improved, improved, tall ruderal, wet grassland etc. In some cases a full species list is completed for the whole site, but the surveys are quick and could easily miss important species. Phase 1 habitat surveys don't classify habitats into BAP classifications i.e. calcareous and dry acid grassland, and it is quite possible that valuable species-rich habitats are missed or misclassified. Since only species-rich grassland habitats are cut once a year, any MG1 sites, or other BAP habitats that have been missed, may only get a cut once every three, six or nine years. *A. elatius* and other weedy species will continue to spread without proper management and the species-rich habitats will be lost (Mahmoud *et al.* 1975; Grubb 1982). These habitats need a botanical survey method that is directly related to the roadside verge habitat.

Roadside verges are new and developing habitats – Novel ecosystems (Hobbs *et al.* 2006; 2009, Williams *et al.* 2009; Marris 2009). The majority of the sites on the A303 are only 22 years old, they haven't had a long time to establish. Even so, new and unusual combinations of species are found. Roadside verges are linear and edge habitats and have many different types of habitats in a close proximity. Woodland, farmland, hay meadows, even heathland, can be just a few metres away (Wester & Juvik 1983; Ulmann *et al.* 1995; Tikka *et al.* 2000; Williams *et al.* 2009). Dispersal of introduced and exotic species has been shown to occur in many roadside habitats. For example, salt tolerant species can spread alongside the road (Thompson *et al*. 1986). In the U.S.A, species typical of roadside verges from Britain are spreading alongside their roadside verges as exotics (Parendes & Jones 1999; Gelbard & Harrison 2003). But if these combinations of species are a common occurrence on roadside verges – should these species assemblages be given a new NVC classification? These habitats need a classification that not only looks at the species composition, but one that looks at how valuable the habitat is, i.e. species richness, diversity and key negative and positive indicator species. This information can be linked back to habitat management, so that the sites that need cutting more frequently than they are presently, can be altered, to prevent scrub encroachment on valuable species-rich grasslands. Full plant species surveys are needed on more roadside verges, especially motorway verges which have never been thoroughly surveyed before, in order to diagnose better species classifications for roadside verges and improve habitat management.

5.5.9 Highways Agency Geotechnical Data Management System (HAGDMS)

10) Did woodland sites have more records of slips and failures than the grassland sites in the HAGDMS?

There were more signs of terracing and desiccation on south-facing cuttings. This was only on a few sites. There were no signs of slips or failures on any grassland site over the whole stretch of the A303, A30 and A38. The use of trees for improving slope stability is the common method employed by road engineers to prevent slips and failures. However, there were signs of slips and failures on the wooded areas, especially on the A30. The results from the HAGDMS show that it is the areas with scrub and scrub encroachment that have more slips; the wooded areas have greater problems with trees dislodging and the grassland areas have problems with rabbit burrows. Using the HAGDMS information has shown that both grassland and woodland habitats seem to do a good job in preventing slips and failures. The problem seems to lay with brambles and scrub encroachment.

A number of studies looking into rooting depths of tree and scrub species have shown that scrub only reaches 0.45 – 0.5 m maximum depth (Greenwood 1996; Norris 2005; Cazzuffi & Crippa 2005). However, grass and wildflower species can grow deeper that this, usually to 0.8 m depth (Schenk & Jackson 2002; Canadell *et al.* 1996). Shrubs such as *C. monogyna* only reach 0.5 m (Greenwood 1996; Norris 2005; Cazzuffi & Crippa 2005). The problem with scrub is two-fold: 1) scrub species like brambles do not have deep root systems, and 2) scrub species do not have a dense canopy cover. The most important factor in reducing surface erosion and rainfall splash is having a dense canopy cover (Boardman 1984; 1991, Bayfield *et al.* 1982; Evans 1990; Morgan 1992; Solé-Benet *et al.* 1997; Mitchell *et al.* 2003). Greenwood (1996) showed that brambles even after 18 months of growth, only had 10 – 15 % ground cover, whereas grasses and wildflowers had 60 % cover. All species only grew to 0.45 m in this time, including the tree species. Morgan (2007) showed that when rain hits the canopy of taller species, the droplets still fall onto the ground at high velocity. However, species that are growing close to the ground, protect the soil surface from rainfall splash. Also, taller species tend to grow in clumps, so cracks and tunnels can develop through the vegetation, where the rainfall is concentrated (Anderson *et al.* 1982; Blight 2003; Morgan 2007). Brambles tend to monopolise areas, preventing growth underneath so bareground patches develop (see Photo 5.7; 5.10). Whereas, woodland and grassland habitats have structurally differentiated canopy layers, with little bareground in between the vegetation. Rain may hit the leaves of trees, but as long as a grassland canopy is underneath, the rainfall splash would be intercepted by the grassland vegetation (Greenwood 1996; Morgan 2007).

5.6 Conclusion and future work

From these results it would seem that grassland habitats are better for slope stabilisation than scrubbed areas. Here we have a dual reason for preventing scrub encroachment by increasing the number of times the habitat is cut in one year – 1) It promotes species-rich grassland habitats, 2) Grassland habitats have less slips and failures associated with them. Grassland habitats should be cut more often, increasing species richness and preventing scrub encroachment which will assist with slope stabilisation. Aspect should be taken into consideration when species composition is investigated. More surveys should be undertaken in areas that have not been surveyed before, in order to create a habitat classification for roadside verges which includes a scale for working out the conservation value of each habitat. The methods for this survey were brief due to time constraints and lack of facilities, i.e. soil texture had been worked out by hand – in future soil samples could be taken, pH could be recorded, along with a measurement of soil depth and vegetation height at each site.

6 Chapter Six: Final Discussion

6.1 Introduction

This chapter links together the results from the BIONICS Embankment, the Mesocosm experiment and the A38 and A303 surveys (from now onwards A303 surveys) with the purpose of making recommendations for the re-creation and maintenance of grassland species composition on roadside verges, in order to improve species richness, diversity and slope stability.

6.2 Species establishment from the seed mixtures

Table 6.1. The species that were commonly found in the BIONICS, Mesocosm and A303 surveys.

	Common Shared species	
	Scientific name	Common name
Shared by all experiments	*Achillea millefolium*	Yarrow
	Alopecurus pratensis	Meadow foxtail
	Cynosurus cristatus	Crested Dogstail
	Daucus carota	Wild carrot
	Holcus lanatus	Yorkshire Fog
	Leucanthemum vulgare	Ox-eye Daisy
	Lolium perenne	Perennial Ryegrass
	Lotus corniculatus	Birdsfoot trefoil
	Phleum bertolonii	Smaller cat's tail
	Plantago lanceolata	Ribwort Plantain
	Rumex acetosa	Common Sorrel
	Trifolium pratense	Red Clover
Bionics and Mesocosm	*Poa trivialis*	Rough Meadow-grass
	Sanguisorba minor ssp. minor	Salad Burnet
	Trisetum flavescens	Yellow Oat-grass
BIONICS and Surveying	*Cirsium arvense*	Creeping Thistle
	Medicago lupulina	Black Medick
	Ranunculus repens	Creeping Buttercup
	Trifolium repens	White Clover
Mesocosm and Surveying	*Agrostis capillaris*	Common bent
	Anthoxanthum odoratum	Sweet vernal-grass
	Centaurea nigra	Common Knapweed
	Conopodium majus	Pignut
	Festuca ovina	Sheep's fescue
	Festuca rubra	Slender creeping red fescue

Table 6.1 shows the species that were shared between the BIONICS Embankment, the Mesocosm experiment and the A303 surveys. *L. perenne*, *C. cristatus*, and *P. bertolonii* were the key grass species common to all and *L. corniculatus, L. vulgare, P. lanceolata, R. acetosa* and *D. carota* were the key wildflower species common to all and that established from the seed mixture. Other key species that established between two of the sites were the grass *T. flavescens* and the wildflowers *T. repens* (not in the sown seed mixture but always sown in the standard grass seed mixture), *S. minor* and *C. nigra*. These species are generalist species with high germination rates and are commonly found in similar experiments (i.e. van Hecke *et al*. 1981; Wells *et al.* 1990; Mountford *et al.* 1993; Oglethorpe & Sanderson 1998; Hopkins *et al*. 1998; Pywell *et al.* 2003; Lindborg 2006; Smith *et al*. 2000; 2008; Lep *et al.* 2007). The species that did not establish were those more associated with lower fertility levels, and species that were less competitive or requiring constant grazing, i.e. *B. media*, *L. hispidus* and *S. dioica* (Grime *et al.* 1988; Smith *et al*. 2000)

Pywell *et al.* (2003) explained that through using species-rich seed mixtures to reclaim land and recreate species-rich grassland, the same species were establishing from these diverse seed mixtures to create a monopoly of grassland habitats all including a similar suite of generalist species. This suite of species could be deliberately used on roadside verges as a mixture of species which will germinate well and produce a quick, dense, ground cover. However, the results from the surveying work showed that the species which were originally sown in the seed mixture were lost over time to natural colonisation. *L. perenne* was common in the BIONICS Embankment and the Mesocosm experiment, yet was only found in 1 % of the quadrats on the A303. However, it must be kept in mind that the purpose of the seed mixture is to create a species-rich grassland habitat in a short space of time. This newly emerging habitat will continue to develop; no seed mixture will contain the exact community that will develop over time (Fagan *et al.* 2008). It can take up to 100 years for a stable species-rich grassland community to develop (Gibson & Brown 1992). Dispersal from the local habitats will occur, but, if just a grass seed mixture is sown without close proximity to any good grassland, this habitat will always remain poor (Wells *et al.* 1989; Crawley *et al.* 1999; Tikka *et al*. 2001; Hansen & Clevenger 2005; Matesanz *et al.* 2006; Fagan *et al*. 2008). Fagan *et al.* (2008) showed that naturally regenerating sites were significantly better when they were in close proximity to species-rich grassland. Roadside verges will cross many different types of habitat so there is no control over the species which colonise (Drake 1990; Wilson *et al.* 1996;

Tikka *et al*. 2001). Therefore in order to create a diverse, species-rich grassland habitat quickly, a grass and wildflower seed mixture should been sown.

In the Mesocosm experiment it was shown that the grass and wildflower plots had greater aboveground biomass than the grasses-only plots, and that the roots could grow down to at least 40 cm. The total root mass was greater in the grasses-only plots in comparison to the grass and wildflower plots. However, the grass roots were smaller and finer, whereas the wildflower roots were bigger, yet lighter. Although the grasses-only plots had greater root mass, these plots had lower aboveground biomass, while the grass and wildflower plots had lower root mass, but greater aboveground biomass. Many studies have shown that greater diversity means a greater use of the three-dimensional space above the ground (Naeem *et al.* 1994; Spehn *et al.* 2000; Spehn *et al.* 2005). This diversity - canopy relationship can also be related to different functional types. Tilman *et al.* (1997) explained that it is functional diversity, not species richness that relates to biomass. A grass seed mixture only contains one type of functional type – grasses – which also have a similar topological lifeform. However, a species-rich grass and wildflower seed mixture contains a number of functional types and hence has greater biomass. In general, wildflowers form horizontal leaf surfaces while grasses have more erect leaf surfaces and functional types can be used to explain vegetation structure (Thompson *et al.* 1996; Spehn *et al.* 2000); in addition Berendse (1981; 1982) and Wardle & Peltzer (2003) showed that the roots of different grass and wildflower species utilise different areas of the soil strata. A quick-growing, thick cover of herbaceous vegetation is required to prevent rainfall from hitting the ground and improving surface erosion and run-off (i.e. Elwell & Stocking 1976; Andres *et al.* 1996; Fullen *et al.* 1998; Blight 2003; Morgan 2007), and greater root biomass can increase soil strength and bind the soil particles together (i.e. Waldron & Dakessian 1982; Anderson *et al.* 1982; Greenwood *et al.* 2004; Norris 2005; Cazzuffi *et al*. 2006; Danjon *et al*. 2007; Tosi 2007). The species which were common across the BIONICS, Mesocosm experiment and A303 surveys (Table 6.1) were a mixture of grasses and wildflowers which can fulfil these requirements. Therefore, a seed mixture containing these species with a range of functional types, should be sown to have good aboveground biomass, good root separation, in order to prevent surface erosion and runoff and increase soil strength.

6.3 The influence of aspect on establishment and species composition

Across the BIONICS Embankment, the Mesocosm experiment and the A303 surveys, a number of key trends could be seen from the influence of aspect on the vegetation and micro-climate processes. Wildflowers were found in greater abundance on the south-facing slopes and there was a greater abundance of grasses on the north-facing slopes. In the BIONICS Embankment and A303 surveys this didn't influence overall species richness, however, in the Mesocosm experiment and A303 surveys this did increase species diversity on south-facing slopes plus, in the Mesocosm experiment, species richness was also greater in the grass and wildflower plots on the south-facing slopes. Many studies have shown that species richness and diversity is higher on the south-facing slopes and this is due to more wildflower species preferring the warmer, drier south-facing aspects (Albertson 1937; Pahlsson 1974; Hutchings 1983; Kutiel 1992; Bruun 2000; Amezaga *et al.* 2004; Pykala *et al.* 2005). This has been confirmed by the results here.

There were however, differences in the individual species responses to aspect. The two species which responded the same were: *L. vulgare* and *C. nigra* which both preferred the south-facing slopes in the Mesocosm experiment and along the A303 cutting. In each experiment, different grasses preferred the north-facing slopes and different wildflowers preferred the south-facing slopes. In the BIONICS embankment *L. perenne* and *C. cristatus* were found all over, yet in the Mesocosm experiment *L. perenne* and *C. cristatus* preferred north-facing plots. *D. carota* was not influenced by any of the treatments in the Mesocosm experiment, yet was commonly found on south-facing slopes along the A303. However, although *L. corniculatus*, *P. lanceolata*, *S. minor*, *M. moscata*, and *D. carota* may only have been significantly found on south-facing aspects in one case, these species are warm-loving species (Grime *et al.* 1988; Hill *et al.* 1999) and show that the increased radiation on south-facing slopes does cause a more xeric plant community to develop, which has been shown in a number of studies (Perring 1959; 1960; Kutiel 1992; Sebastia 2004; Bennie *et al.* 2006).

The differences in the aspect trends can be explained by the differences between the types of experimentation. The BIONICS embankment was of a comparable size to the A303 sites, however, the BIONICS embankment was newly built, and on a farm site, away from other roadside verge communities. The A303 cutting, on the other hand, had 22 years of natural colonisation. The BIONICS embankment and Mesocosm experiment had the same seed mixture, but any species establishing from the seedbank was removed from the Mesocosm, yet natural colonisation occurred on the BIONICS embankment. The Mesocosm plots were only 0.4 m x 0.4 m, unlike the BIONICS embankment where the plots were 18 m x 18 m. Since the Mesocosm experiment was on such a small scale, and yet differences in aspect could be distinguished, it shows how small-scale differences in micro-climate can have an affect on the species composition, even after a small period of time. The differences in the species responses highlight how tiny changes in environmental conditions can influence species germination and establishment over time.

When the Ellenberg Indicator Values were compared, both the BIONICS embankment, the Mesocosm experiment and the A303 surveys confirmed that moisture-loving species established on the north-facing slopes, however, only the BIONICS embankment showed that light values were greater on south-facing slopes. As the north-facing aspect receives less sunlight, the ground takes longer to dry out and tends to be wetter. This, in turn, is influencing the species composition over time so a more mesic community is developing (Perring 1959; 1960; Pahlsson 1974; Churchhill 1982; Kutiel 1992; Kutiel & Lavee 1999; Sebastia 2004; Bennie *et al*. 2006). Both the BIONICS embankment and the A303 surveys showed that fertility values were greater on north-facing slopes. In the Mesocosm experiment, the wetter north-facing slopes increased aboveground biomass in the grass and wildflower plots. Other experiments looking at aspect and biomass have shown that it is the wetter conditions that promote the increase in biomass (Pahlsson 1974; Kutiel & Lavee 1999; Bochet & Garcia-Fayos 2004), plus higher fertility generally means greater biomass (Mountford *et al.* 1993; Hopkins *et al.* 1998; Buckland & Grime 2000; White *et al*. 2004). A number of studies have shown an increase in organic matter, litter accumulation and thickness of soil can all lead to an increase in fertility on north-facing slopes (Pahlsson 1974; Churchill 1982; Kutiel 1992; Kutiel & Lavee 1999).

In the Mesocosm experiment, the aspect influence was affecting belowground properties. Penetrometer resistance, bulk density and moisture contents were all higher on the flat plots, leading to lower root mass (although this wasn't influencing aboveground growth since in the grasses-only mixture, the aboveground biomass was higher on the flat than the south-facing and north-facing aspect). In the first depth (0 – 5 cm), the north-facing plots had greater root mass (219 g m^{-2}) than the flat (107 g m^{-2}) and south-facing plots (112 g m^{-2}). At the 25 – 30 cm depth, where the soil compaction was greater, the aspect effects changed – the south-facing plots had greater root mass (17 g m^{-2}) than the flat plots (9 g m^{-2}) and the north-facing plots (8 g m^{-2}). The north-facing plots had high bulk density and high moisture content, but not high Penetrometer resistance. The south-facing plots had low bulk density and low moisture content, but still high Penetrometer resistance. The soil generally gets harder when it is drier leading to an increase in Penetrometer resistance (Andrade *et al.* 1993; Young *et al.* 1997). A few studies have shown that increasing the temperature of the soil, increases root production (Kaspar & Bland 1992; de Boeck *et al.* 2007). Here, the aspect affects were influencing the moisture content levels and hence influencing the belowground properties.

As it is important to establish a plant community cover as quickly as possible on roadside verges, the seed mixture could be tailored to suit the aspect of the site. A seed mixture containing more grass species could be sown on north-facing sites, whereas a seed mixture containing more wildflower species could be sown on south-facing sites. The seed mixture should contain species that germinate well – so since *L. vulgare* and *C. nigra* grew well on south-facing slopes, plus *D. carota* and *L. corniculatus* which established in all experiments, these wildflower species should be included for south-facing slopes. *C. cristatus* is not included in the standard grass seed mixture (Table 1.1), so should be included since this grows well on north-facing slopes.

6.4 The influence of compaction on establishment and species composition

The influence of compaction on the growth and establishment of plant species in the BIONICS and Mesocosm experiment was noticeable but not particularly damaging. A few differences were noted: In the BIONICS embankment, the total number of grass species was not influenced by compaction, whereas in 2007, the total number of wildflower species was reduced in the south-facing compacted slope, but this effect did not remain into 2008. In the Mesocosm experiment, species richness and diversity was less in the compacted grasses-only plots, whereas species richness and diversity was generally higher in the grasses and wildflower compacted plots. However, south-facing plots generally had greater species richness and diversity, yet with the combination of only one cut in the summer and soil compaction, the diversity was less in the compacted, cut once, south-facing plots. So, although the response of the grass species was different between the BIONICS and Mesocosm experiment, in both the wildflower species were affected by compaction on the south-facing slopes. South-facing slopes are under greater stress from higher temperatures and drought conditions – this combination can reduce the *competitors* and allow the *stress-tolerators* to increase, as was shown from the A303 surveys (Pahlsson 1974; Kutiel & Lavee 1999), however, lessening the cutting regime will allow the more competitive species to dominate (Grime 1990; Rodwell 1992; Bobbink & Willems 1993; Grime 2001). With the combination of only one cut a year (in the BIONICS embankment and in the once cut plots in the Mesocosm experiment) and the compaction effect, the species richness and diversity was reduced.

The influence of compaction did favour some species, and reduce others, in both the BIONICS and Mesocosm experiment. In both, *L. perenne* was reduced by compaction. However, in the BIONICS embankment, compaction reduced *A. millefolium* yet in the Mesocosm experiment, *A. millefolium* was favoured by the compaction treatment. Three key competitive species which colonised the BIONICS embankment from the local seed source were *C. arvense*, *V. sativa* and *R. repens* and these species grew well on the compacted slopes. In the Mesocosm experiment, a number of the less competitive species were reduced by the compaction treatment: *P. bertolonii* and *S. minor*. Therefore, a regular cutting regime would be required on the compacted slopes, to prevent competitive species from becoming established.

A number of experiments have shown that compaction reduces root and shoot growth (i.e. Barley *et al*. 1965; Atwell 1993; Bingham 2001; Montagu *et al.* 2001). However, the compaction treatment made no difference to the aboveground biomass or and little difference to the belowground root biomass in the Mesocosm experiment, even though the soil measurements showed that there was a significant difference in bulk density and Penetrometer resistance between the non-compacted and compacted plots. There was however, higher bulk density and Penetrometer resistance in the flat plots and these plots generally had lower root mass. So, soil strength did lessen the total root biomass over time, but only where the compaction was very great.

In both the BIONICS embankment and the Mesocosm experiment, there is 18 – 30 cm of non-compacted topsoil in which the plant species can grow through before hitting the compacted layer. In the Mesocosm experiment, it was clear that at this depth there was no obvious interface between the topsoil and subsoil and the plant roots grew through the topsoil into the subsoil with no discernable difference, unlike in a number of experiments where a "root-mat" has been observed (Dexter 1986a; 1986b; 1986c). The timing of the effects of compaction in relation to the stage of development of the plant will influence how much the plants growth will be restricted (Bengough *et al.* 1997; Bingham 2001; Young *et al.* 1997; Montagu *et al.* 2001). In the BIONICS embankment, the total number of wildflowers was reduced in the south-facing compacted slopes in 2007, but this trend did not continue into 2008. Clearly, the rooting depth results show that the plant species can grow into the compacted layer. It is possible that the roots hit the compacted layer by June 2007, but by the second year of establishment, the plants compensated for the compaction. Soil is heterogeneous and there are a number of cracks and pore spaces into which the plants can grow (Dexter 1986a; 1986b; 1986c; Bengough *et al.* 1997; Montagu *et al.* 2001; Bingham 2001; Bingham & Bengough 2003). It is clear that the compaction methods used in road construction, does not prevent small pores and cracks from developing into which the year old, mature plant roots can manoeuvre and grow into.

6.5 Cutting regimes and future management recommendations

It was clear from the A303 surveys that scrub encroachment was common in all of the sites – tall, weedy species such as *A. elatius*, *C. arvense* and *S. jacobaea* dominated, and tree and scrub species were found in many quadrats. These species are good invaders and can be reduced by an increase in the cutting regime (i.e. Mountford *et al.* 1993; Greenwood 1996; Crawley *et al.* 1999; Hansson & Fogelfors 1998; Grime 2001; Bakker *et al.* 2002; Pykala 2005). In fact, this was shown in the BIONICS embankment, where the injurious weed *C. arvense* was reduced from common to rare by one cut in September, with the cuttings raked off. In addition *A. sylvestris* and *T. vulgare* were lost completely. In the Mesocosm experiment, the management regime had one cut, four cuts and eight cuts per year. Species richness and diversity was greatest in the plots cut eight times. An increase in the cutting frequency reduced the growth of *L. perenne* and *P. lanceolata*, while *C. cristatus* and *L. vulgare* were favoured by an increase in cutting.

Cutting reduces the frequency of thistles and docks and other competitive weedy species, whilst increasing species richness and diversity, usually by promoting the growth of wildflowers (i.e. Warren *et al.* 1989; Wells *et al.* 1989; Bobbink & Willems 1993; Hansson &

Fogelfors 1998; Bakker *et al*. 2002; Pykala 2005; Smith *et al*. 2008). Roadside verges can be very fertile, and become dominated by injurious weeds and by *A. elatius* and *D. glomerata* – these species are tall and can form dominating monocultures of one life-form (Parr & Way 1988; Grime 1990; Rodwell 1992; Buckland & Grime 2000; Bakker *et al*. 2002; Pykala 2005). The cover of *A. elatius* will only be reduced with regular cutting (Mahmoud *et al*. 1975; Grubb 1982), a minimum of twice a year (Grubb 1982). Cutting promotes dense growth, allowing structural diversity of the canopy and smaller-statured wildflower species can establish (Wells *et al*. 1989; Grime 1990; Pywell *et al.* 2003). The increase in dense canopy cover and diversity resulting from cutting will reduce surface erosion from rainfall (Blight 2003; Morgan 2007) and increase soil strength (i.e. Waldron & Dakessian 1982; Anderson *et al.* 1982; Greenwood *et al.* 2004; Norris 2005; Cazzuffi *et al*. 2006; Danjon *et al*. 2007; Tosi 2007). In addition scrub encroachment will be stopped and the spread of injurious weeds will be controlled.

One cut a year may be appropriate management after a few years of establishment, but at the beginning 2 – 4 cuts should be done in the first year. A number of studies highlight the need for intensive management in the first year of establishment to allow for seedling establishment (Wells *et al*. 1989; Greenwood 1996; Jones & Hayes 1999). At the present time the Highways Agency cuts the road verges every nine years, six years or three years and only in exceptional circumstances are the verges cut once a year. However, the HA also spends money on scrub removal, soil erosion protection methods and controlling the spread of injurious weeds (HA 1994; 2000; 2005a; 2005b). As has been shown by these results, an increase in the cutting regime will prevent scrub encroachment, reduce injurious weeds and increase diversity, which in turn promotes dense canopy cover which reduces surface erosion and runoff. It is suggested that this cutting regime should be changed to: one cut every three years, or every two years for the species poor sites; but one cut a year should be done on the majority of sites. In addition, the species-rich sites should be cut twice a year. It is important that the cuttings are raked off as soon as possible to reduce soil fertility and litter accumulation (Schaffers *et al.* 1998; Bakker *et al.* 2002). It could even be possible to make hay from the cuttings if local landowners were interested. The money spent on scrub removal, reducing the spread of injurious weeds and erosion measures can be spent on cutting instead, since these factors won’t be such a problem. Timing is important for an effective cutting regime. It is important to cut the vegetation after the flower heads have set seed in order for the species to continue to populate. A cut in August or September would be best. For those sites requiring a second cut, it would be preferable to cut around the beginning of the growing season to allow the less competitive, lower canopy species a chance to establish (Well *et al.* 1989; Smith & Jones 1991; Morris 2000; Coulson *et al.* 2001).

6.6 *Rhinanthus minor*

It had been hoped that *R. minor* could have been used as a tool to increase wildflower diversity by reducing the biomass of the competitive grasses, and to assist with the germination of sown species, as has been shown in a number of experiments (i.e. Smith *et al.* 2003; Smith *et al.* 2008; Ameloot *et al.* 2008). However, *R. minor* didn't germinate in the BIONICS embankment, and failed to establish in the first year of the Mesocosm experiment. It was not found in the A303 surveys and when it did germinate in the Mesocosm experiment, it only established in those plots with low biomass. In the Mesocosm experiment, *R. minor* was mainly found in the plots cut 8 times, and was associated with the slopes. There was an indication that *R. minor* was reducing the biomass of *L. perenne* and *C. cristatus* and favouring *F. ovina* and *F. rubra*, but this could have been due to the management treatment, or a combination of the two factors. If *R. minor* was to be used in a seed mixture, then there must be a regular cutting regime, especially around the establishment phase in April. This may be impossible in a roadside verge management plan, so the use of *R. minor* to improve diversity and seedling establishment is limited on roadside verges.

6.7 Surface erosion, soil strength and slope stability

There were no signs of slips or failures on any grassland site over the whole stretch of the A303, A30 and A38. There were a few signs of desiccation on the south-facing slopes due to the warmer, drier conditions, but this was negligible. A dense, thick cover of herbaceous vegetation is needed to prevent rainfall from hitting the ground and improving surface erosion and run-off (i.e. Elwell & Stocking 1976; Andres *et al.* 1996; Fullen *et al.* 1998; Blight 2003; Morgan 2007). The binding effects of rooting systems can improve soil strength and increase slope stability (i.e. Waldron & Dakessian 1982; Anderson *et al.* 1982; Greenwood *et al.* 2004; Norris 2005; Cazzuffi *et al.* 2006; Danjon *et al.* 2007; Tosi 2007). The ground cover on the BIONICS embankment developed quickly, and the biomass from the Mesocosm experiment was much higher in the species-rich grass and wildflower treatment. The root mass was greater in the grasses-only treatment and in both seed mixture treatments the roots went down to 40 cm depth, and would have continued further if possible. A number of studies have shown that complex branching patterns of root systems can improve soil strength, and different species maturing together grow to different depths (Wu *et al*. 1988; Berendse 1981; 1982; Fitter & Stickland 1992; Stokes *et al*. 1996; Wardle & Peltzer 2003; Dupuy *et al*. 2005). Other studies have shown that greater functional diversity means a greater use of the three-dimensional space above the ground, and hence improved ground cover (Naeem *et al.* 1994; Tilman *et al*. 1997; Spehn *et al.* 2000; Spehn *et al.* 2005). Therefore with increased aboveground canopy and roots growing to different depths, a species-rich grassland community can reduce surface erosion and increase soil strength, leading to greater slope stability.

However, uncut roadside verges become dominated by tall, clumpy monocultures of species such as *A. elatius* and *C. arvense* (Grime 1990; Rodwell 1992; Buckland & Grime 2000) and scrub encroachment is common. The HAGDMS database information showed that it was the brambles and scrubby areas that were associated with slips and failures. Bramble and scrub roots only grow to a depth of 0.5 m maximum and has little canopy cover and little understorey (Greenwood 1996; Norris 2005). It has been highlighted that taller plants with little understorey does not intercept rainfall as well as an herbaceous dense canopy. Runoff can be concentrated in the bareground patches between the vegetation (Blight 2003; Morgan 2007). Anderson *et al.* (1982) pointed out that there were deep cracks on poorly vegetated clay areas, but that there were no cracks on dense grass. So, grassland habitats are better at slope stabilisation than the currently held view. Therefore, a management regime needs to be implemented to reduce the taller weedy species, increase diversity / canopy layers in grassland areas and prevent scrub encroachment, which will lead to improved slope stability, especially reducing surface erosion and increasing soil strength.

6.8 National Vegetation Classification

The NVC community on the BIONICS embankment was MG6a but without the addition of seed this community would have been OV25a, a tall herb weed community. In the Mesocosm experiment, where any unwanted species were removed, the NVC classification was MG5a – and at 70 % best fit, this was a good fit. On the A303 survey the NVC classification varied and many sites had a unique and unusual combination of species that didn't fit into any of the NVC classifications. The standard community was MG1 – which was found most commonly on the north-facing cuttings. The Ellenberg Indicator Values for moisture and fertility were greater on north-facing slopes, leading to more grasses (i.e. *A. elatius* and *D. glomerata*) on the north-facing slopes and an MG1 classification. However, scrub encroachment and woodland species were found in many of the quadrats, leading to some of the sites receiving a woodland or open habitat NVC classification, despite being a grassland site. Wilson *et al.* (2000) also noted that roadside verges didn't fit neatly into any NVC classification, although MG1 and OV25 were most common in Britain and MG6 and U4 were most common in New Zealand.

The NVC classification is based on stable, semi-natural, long-term communities, whereas roadside verges are newly establishing communities (Leps *et al.* 1982; Rodwell 1992). Since a seed mixture is added to the soil, and there will also be a local seed source (from a multitude of habitats) and seed in the seed bank, a newly assembled mix of species develops, random and unique for the particular situation at each site (Wester & Juvik 1983; Drake 1990; Tikka *et al*. 2001; Wilson *et al.* 1996; Williams *et al.* 2009). The initial community may be classed as MG5 or MG6 to begin with, but as time goes on and species such as *A. elatius* spread, the classification shifts to MG1 (Rodwell 1992). Here there is the potential for a new classification. The communities developing on roadside verges are not uniform and are quite species rich in a number of cases. They are novel ecosystems, appealing and unique and worthy of more interest (Hobbs *et al.* 2006; Hobbs *et al*. 2009). The MG1 classification is given to any grassland habitat where *A. elatius* is present. This species shouldn't be given such a heavy weight as it is obscuring the value and diversity of roadside verges. Roadside verge vegetation should be re-classified and the MG1 community should be divided into more meaningful categories, relating to species richness and diversity and soil type where possible. There should be a "value" and management aspect to the classification, i.e. *A. elatius* and other weedy species should be classed as negative indicator species and management can be altered to improve species richness and reduce the cover of *A. elatius* and scrub.

A few authors have expressed concern over seed mixtures and establishment. Often the same suite of generalist species are establishing from seed mixtures, creating uniform habitats (Hopkins *et al.* 1998; Pywell *et al*. 2003). Actually, we may be unintentionally creating similar roadside verge habitats across the whole world. For example, Hansen & Clevenger

(2005) found *C. arvense*, *F. rubra*, *L. vulgare*, *M. sativa*, *P. pratense*, *P. pratensis*, *T. officinale* and *T. repens* on transport corridors in Canada. On the highways in Greece, *C. cristatus, D. glomerata, L. perenne, L. corniculatus* and *S. minor* are being sown (Koukoura *et al.* 2007). On West Virginia highways in USA, soils are typically fertilised and seeded with non-native species such as *F. rubra, L. corniculatus*, *L. vulgare* and *D. carota* (Rentch *et al*. 2005), and there are many more examples (Bayfield *et al*. 1992; Andres *et al*. 1996; Matesanz *et al.* 2006; Tormo *et al*. 2006). However, no seed mixture will contain the exact community that will develop over time (Fagan *et al.* 2008) and natural colonisation from local habitats occurs if there is suitable habitat (Crawley *et al.* 1999; Tikka *et al*. 2001; Matesanz *et al.* 2006; Fagan *et al.* 2008). Matesanz *et al.* (2006) showed that the hydroseeded species disappeared after a few years, and as has been shown by the results of the A303 surveys, *L. perenne* was only found in one quadrat, even though this species was the main component of the original grass seed mixture sown when the A303 was built. So, to conclude, although a similar mix of species are being sown on roadside verges around the world, the random assemblage of species from local seed dispersal and natural colonisation, creates novel, “rapidly changing ecosystems” (Marris 2009) that will be different in each location and worthy of further research and classification.

6.9 Future work

More research would be beneficial looking into functional diversity and how this influences rainfall splash, light interception, canopy heights and gaps in the canopy. Does an increase in functional diversity reduce surface erosion and rainfall splash? Mesocosm plots could contain a range of functional types: with just one grass or a mixture of grasses from the HA grass seed mixture; with grasses and a legume such as *L. corniculatus* or *S. minor*; with grasses, legumes and a larger wildflower species such as *L. vulgare* or *D. carota*; with grasses, legumes, tall wildflowers, and a rosette-forming species such as *P. lanceolata* or *R. acetosa*; and finally a species-rich diverse grassland plot. The above and belowground biomass could be measured at the end of experiment. This experiment could include a compaction treatment, with greater compaction than found in the Mesocosm experiment. Soil strength can be tested.

On a larger scale, further research into cutting regimes and species establishment from a seed mixture would be beneficial. For example, have a management treatment including: not cutting allowing scrub encroachment; one cut every two years; one cut a year; two cuts a year; plus a four and eight cut treatment to show how cutting regimes are required to improve seedling establishment, prevent scrub encroachment and increase species richness and diversity. Light interception, canopy heights and above and belowground biomass could also be measured.

6.10 Recommendation of a suitable seed mixture

To create dense ground cover as quickly as possible, species need to be chosen which have quick germination rates, with a range of complementary vegetation structures. The seed mixture needs to include species that can cope well with compaction and include species that can grow on south and north-facing slopes.

The standard grass species mixture includes *L. perenne*, *F. rubra*, *F. brevipila*, *P. pratensis*, *A. capillaris* and *T. repens* (White Clover) (HA 1991). It would be recommended to reduce *L. perenne* and add *C. cristatus* instead, since *C. cristatus* was not reduced in frequency by the compaction treatments. *P. pratensis* and *F. brevipila* are sown in the standard grass seed mixture but was not found in the A303 surveys. These species could be taken out and the grasses *P. bertolonii* and *T. flavescens* added since these species germinated so well in the Mesocosm experiment and the BIONICS embankment. Plus, the addition of two wildflower species would be recommended, i.e. the legumes *L. corniculatus* or *S. minor* which have deep root systems, and *D. carota* which established well across all experiments and had a noticeable deep tap root in the Mesocosm experiment.

Preferably, the addition of finer leaved grasses, rosette-forming species and larger, tap-rooted wildflowers would be a good next step. Species such as *F. ovina* form a dense sward with cutting (Grime 1990). The rosette-forming species – *P. lanceolata* and *R. acetosa* both have dense canopies and they remain wintergreen (Grime *et al.* 1988). Other species which germinated well was the legume *T. pratense*, the tall daisy *L. vulgare* and the tall herb *C. nigra*. All of which were common on the A303 surveys and favoured south-facing slopes. Finally *A. millefolium* established well across all sites and was not reduced by compaction in the Mesocosm experiment.

6.11 Final conclusion of the results of the main chapters

Roadside embankment construction does not influence species richness and diversity detrimentally. A regular cutting regime is required to allow for the establishment of a species-rich and diverse community and at least one cut a year is required to prevent scrub encroachment and to reduce the spread of injurious weeds. Grassland habitats are better at slope stabilisation than previously thought. A seed mixture containing a range of functional types will have greater aboveground biomass, with a denser canopy and heterogeneous root system, which will help to prevent surface erosion and runoff and increase soil strength. The seed mixture needs to include species that can cope well with compaction and include species that can grow on south and north-facing slopes. *L. perenne* should be replaced with *C. cristatus*, and south-facing wildflower species such as *L. corniculatus*, *L. vulgare* and *S. minor* should be included. *R. minor* would only be suitable to use in seed mixtures if the management included a cutting regime to reduce aboveground biomass.

6.12 Final conclusion relating the results of the Thesis to the wider ecological community

The majority of the results discussed during this Thesis can have applicability to the wider ecological community. For example, during this Thesis it was shown that aspect can influence the species composition of UK grassland habitats, yet the closer you are to the equator, the more extreme the aspect differences become. The differences in aspect can be observed in other habitats around the world, where similar patterns can be seen and can be more pronounced. For example, in the Mediterranean climate where there are hot, dry summers and cold rainy winters, a marked contrast has been noticed between north and south-facing slopes in wooded terrain (Armesto & Martinez 1978). The influences of aspect can change vegetation structure at the landscape and habitat level but can also have an evident effect at the species level. For example, bryophytes and lichen abundance can be affected by the edge effects experienced along the tree line of forests (Hylander 2005).

Soil compaction is a serious problem in many systems throughout the world, and is especially detrimental in modern agriculture. Soil compaction is mainly caused by the overuse of heavy machinery and overgrazing, and is especially severe where the moisture content is high. The top layers of the soil are compacted, causing damage to the soil structure, increasing soil strength which reduces the availability of nutrients to the plant. This, in turn, reduces the crop yield and increases the need for adding chemical fertilisers (Soane & Ouwerkerk 1995; Hamza & Anderson 2005). The results from this Thesis have wider implications to assist with this global issue. Compaction did not have such a detrimental impact because there was a 20 cm non-compacted soil layer before the compacted layer, and there were a number of plants which grew through the non-compacted layer and into the compacted layer with little difficulty. In agricultural systems, where surface compaction is a problem, the focus should be on the top 20 cm, finding ways to cultivate the surface layers and using plants with a deep, penetrating tap root to assist with reducing soil compaction (Soane & Ouwerkerk 1995; Hamza & Anderson 2005).

Soil erosion is a widespread problem, especially in areas where there has been large-scale vegetation clearance. These results have shown that an increase in dense, vegetation cover can reduce soil erosion of roadside embankments. This PhD confirms and strengthens the need to increase vegetation cover to prevent surface erosion and can be applied to the global environmental issue. For example, in the Loess Plateau in China, vegetation has been destroyed by human activities. In this semi-arid environment, sudden rainfall events cause wide gullies to develop, washing the soil down the slopes. In this severely eroded region, it is imperative to re-establish vegetation cover as quickly as possible and imperative to prevent the loss of vegetation cover in the long term (Shi & Shao 2000; Zheng 2006). Soil erosion and soil conservation is particularly damaging in agricultural systems around the world. In many areas, vegetation is used as a tool to reduce soil erosion, for example, by using a legume green fallow to improve degraded soil and by sowing fast-growing seeds / weeds into the contours and slopes around field margins (Garcia-Orenes *et al.* 2009; Stevens *et al.* 2009).

The results of this Thesis can be used to assist with the restoration of other habitats, for example, the North Pennines AONB (Area of Outstanding Natural Beauty) Partnership's Hay Time project harvests seed from species-rich upland hay meadows and spreads the seed onto upland hay meadows that have reduced species-richness and diversity but where the fertility has not been increased too detrimentally by chemical fertiliser addition (North Pennines AONB Partnership 2011). A number of the plant species discussed in this Thesis can be found in upland hay meadows, i.e. *T. repens, T. pratense, L. corniculatus, P. lanceolata* and *R. acetosa*.

The botanical surveys from the A303 have shown that a species-rich community can develop and persist in a man-made habitat. We (humans) have affected all habitats on this planet and the urban habitat is no longer separated from the natural environment. Restoration, preservation and biodiversity are key components of a system where people and wildlife are in conflict (Tjallingi 2000). Although urbanisation results in the loss of natural habitats, conversely, it creates new niches for plants and animals and some species flourish (Williams *et al*. 2009; Hobbs *et al.* 2009). This creates a new task for conservationists, ecologists and others to debate: Which urban habitats are important? Which habitats need additional management? What deserves greater attention? (Seastedt *et al.* 2008; Marris 2009). The results from this PhD clearly show that the newly establishing urban habitats should not be ignored and should be celebrated for the clever way in which nature fights back.

This PhD has shown how useful it has been to look at a similar problem, but from different scale perspectives, since better conclusions could be drawn. Seeing comparable patterns developing between the Mesocosm experiment, through to the BIONICS Embankment and up to a landscape-scale has been invaluable to draw effective conclusions. The work placement at the Highways Agency was a key part of this PhD so that the results could be applied in the correct context. In conservation, it is often difficult to find the best approach when a number of different groups are concerned and collaboration and co-operation is needed, with a good idea of the objectives required (Savard *et al.* 2000; Redford *et al*. 2003). During the period of this PhD, ecologists worked alongside civil engineers, who worked alongside academics, who worked alongside stakeholders etc. This PhD can be used as an example for where it is effective having a non bias, all encompassing approach to landscape-scale issues, where human needs and conservation needs do not have to be in conflict, but can be resolved by looking at the whole picture.

7 Reference List

- Akeroyd, J. (1994) *Seeds of destruction? Non-native wildflower seed and British floral biodiversity*. Plantlife, London.
- Akinola, O., Thompson, K. & Buckland, S. M. (1998) Soil seed bank of an upland calcareous grassland after 6 years of climate and management manipulations. *Journal of Applied Ecology*, **35,** 544 – 552.
- Albertson, F. W. (1937) Ecology of mixed prairie in West Central Kansas. *Ecological Monographs*, **7**, 481 – 547.
- Ameloot, E., Martin, H. & Verheyen, K. (2006) *Rhinanthus*: an effective tool in reducing biomass of road verges? An experiment along two motorways, *Belgian Journal of Botany*, **139**, 173-187.
- Ameloot, E., Verlinden, G., Boecks, P., Verheyen, K. & Hermy, M. (2008) Impact of hemiparasitic *Rhinanthus angustifolius* and *R. minor* on nitrogen availability in grasslands. *Plant and Soil*, **311**, 255 – 268.
- Amezaga, I., Mendarte, S., Albizu, I., Besga, G., Garbisu, C. & Onaindia, M. (2004) Grazing intensity, aspect, and slope effects on limestone grassland structure. *Rangeland Ecology & Management*, **57**, 606-612.
- Anderson, M. G., Hubberd, M. G. & Kneale, P. E. (1982) The influence of shrinkage cracks on pore water pressure within a clay embankment. *Quarterly Journal of Engineering Geology*, **15**, 9 – 14.
- Anderson, M. G. & Kneale, P. F. (1980) Pore water pressure and stability conditions on a motorway embankment. *Earth surface processes*, **5**, 37-46.
- Andrade, A. Wolfe, D. W. & Fereres. E. (1993) Leaf expansion, photosynthesis, and water relations of sunflower plants grown on compacted soil. *Plant and Soil*, **149**, 175 – 184.
- Andrén, O, Elmquist, H. & Hansson, A. (1996) Recording, processing and analysis of grass root images from a Rhizotron. *Plant and Soil*. **185,** 259-264.
- Andrés, P. & Jorba, M. (2000) Mitigation strategies in some motorway embankments (Catalonia, Spain). *Restoration Ecology*, **8**, 268-275.
- Andrés, P. V., Zapater, V. & Pamplona, M. (1996) Stabilisation of motorway slopes with herbaceous cover, Catalonia, Spain. *Restoration Ecology*, **4**, 51-60.
- Antonsen, H. & Olsson, P. A. (2005) Relative importance of burning, mowing and species translocation in the restoration of a former boreal hayfield: responses of plant diversity and the microbial community. *Journal of Applied Ecology*, **42**, 337 – 347.
- Armesto, J. J. & Martinez, J. A. (1978) Relations between vegetation structure and slope aspect in the Mediterranean region of Chile. *Journal of Ecology*, **66**, 881 – 889.
- Atwell, B. J. (1988) Physiological responses of lupin roots to soil compaction. *Plant and Soil*, **149**, 175 – 184.
- Atwell, B. J. (1993) Response of roots to mechanical impedance. *Environmental and Experimental Botany*. **33**, 27 – 40.
- Atwell, B. J. & Newsome, J. C. (1990) Turgor pressure in mechanically impeded lupin roots. *Australian Journal of Plant Physiology*, **17**, 49 – 56.
- Ausden, M. & Treweek, J. (1995) Grasslands. *Managing habitats for Conservation* (eds. W. J. Sutherland & D. A. Hill), pp 197 – 229, Cambridge University Press, Cambridge.
- Bakker, J. P., Elzinga, J. A. & Vries, Y. (2002) Effects of long-term cutting in a grassland system: perspectives for restoration of plant communities on nutrient poor soils. *Applied Vegetation Science*, **5**, 107 – 120.
- Bamford, S. J., Parker, C. J. & Carr, M. K. V. (1991) Effects of soil physical conditions on root growth and water use of barley grown in containers. *Soil and Tillage Research*, **21**, 309 – 323.
- Bardgett, R. D., Smith, R. S. Shiel, R. S. Peacock, S. Simkin, J. M., Quirk, H. & Hobbs, P. H. (2006) Parasitic plants indirectly regulate below-ground properties in grassland ecosystems. *Nature,* **439,** 969-972.
- Barker, D. H. (1995) *Vegetation and slopes. Stabilisation, protection and ecology*, Thomas Telford, London.

- Barley, K. P., Farrell, D. A. & Greacen, E. L. (1965) The influence of soil strength on the penetration of a loam by plant roots. *Australian Journal of Soil Research*, **3**, 69 – 79.
- Barley, K. P. & Greacen, E. L. (1967) Mechanical resistance as a soil factor influencing the growth of roots and underground shoots. *Adv. Agron*. **19**, 1 – 43.
- Bayfield, N. G., Barker, G. H. & Yah, K. C. (1992) Erosion of road cuttings and the use of bio-engineering to improve slope stability. *Singapore Journal of Tropical Geography*, **13**, 75 – 89.
- Bayfield, N. G. (1995) Species selection and management for slope revegetation projects. *Vegetation and slopes. Stabilisation, protection and ecology* (eds. D. H. Barker), Thomas Telford, London.
- van Beek, L. P. H., Wint, J., Cammeraat, L. H. & Edwards, J. P. (2005) Observation and simulation of root reinforcement on abandoned Mediterranean slopes. *Plant and Soil*, **278**, 55 – 74.
- Bengough, A. G. & Mullins, C. E. (1990) Mechanical impedance to root growth: a review of experimental techniques and root growth responses. *Journal of Soil Science*, **41**, 341 – 358.
- Bengough, A. G., Croser, C. & Pritchard, J (1997) A biophysical analysis of root growth under mechanical stress. *Plant and Soil*, **189**, 155 – 164.
- Bengough, A. G., Bransby, F. M., Hans, J., McKenna, S. J., Roberts, T. J. & Valentine, T. A. (2006) Root responses to soil physical conditions; growth dynamics from field to cell. *Journal of Experimental Botany*, **57**, 437 – 447.
- Bennie, J., Hill. M. O., Baxter, R. & Huntley, B. (2006) Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of Ecology,* **94,** 355-368.
- Bennie, A. T. P. & Botha, F. J. P. (1986) Effect of deep tillage and controlled traffic on root growth, water-use efficiency and yield of irrigated maize and wheat. *Soil and Tillage Research*, **7**, 85 – 95.
- Berry, P. M., Dawson, T. P., Harrison, P A. & Pearson, R. G. (2002) Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology & Biogeography*, **11,** 453-462.
- Berendse, F. (1981) Competition between plant populations with different rooting depths II. Pot experiments. *Oecologia*, **48**, 334 – 341.
- Berendse, F. (1983) Interspecific competition and niche differentiation between *Plantago lanceolata* and *Anthoxanthum odoratum* in a natural hayfield. *Journal of Ecology*, **71**, 379 – 390.
- Biddle, P. G. (1983) Patterns of soil drying and moisture deficit in the vicinity of trees on clay soils. *Geotechnique*, **33**, 107-126.
- Bingham, I. J. (2001) Soil-root-canopy interactions. *Ann. Appl. Biol*., **138**, 243 – 251.
- Bingham, I. J. & Bengough, A. G. (2003) Morphological plasticity of wheat and barley roots in response to spatial variation in strength. *Plant and Soil*, **250**, 273 – 282.
- Blight, G. E. (2003) The vadose zone soil-water balance and transpiration rates of vegetation. *Geotechnique*, **53**, 55 – 64.
- Boardman, J. (1984) Erosion on the South Downs. *Soil and Water Volume*, **12**, 19 – 21.
- Boardman, J. (1991) Land use, rainfall and erosion risk on the South Downs. *Soil Use and Management*, **7**, 34 – 38.
- Bobbink, R. & Willems, J.H. (1993) Restoration management of abandoned chalk grassland in the Netherlands. *Biodiversity and Conservation*, **2**, 616-626.
- Bochet E. & Garcia-Fayos, P. (2004) Factors controlling vegetation establishment and water erosion on motorway slopes in Valencia, Spain. *Restoration Ecology*, **12,** 166-174.
- de Boeck, H. J., Lemmens, C. M. H. M., Gielen, B., Bossuyt, H., Malchair, S., Carnol, M., Merckx, R., Ceulemans, R. & Nijs, I. (2007) Combined effects of climate warming and plant diversity loss on above- and below- ground grassland productivity. *Environmental and Experimental Botany*, **60**, 95 – 104.
- Boot, R. G. A. & Mensink M. (1990) Size and morphology of root systems of perennial grasses from contrasting habitats as affected by nutrient supply. *Plant and soil*, **129**, 291 – 299.
- Brooks, S. M. & Anderson, M. G. (1995) Modelling the role of climate, vegetation pedogenesis in shallow translational hillslope failure. *Earth Surface processes and landforms*, **20**, 231-242.
- Buckland, S. M., Thompson, K. & Grime, J. P. (2001) Grassland invasions: effects of manipulations of climate and management. *Journal of Applied Ecology* **38,** 301-309.

- Bullock, J. M, Pywell, R. F. & Walker, K. J. (2007) Long-term enhancement of agricultural production by restoration of biodiversity, *Journal of Ecology*, **44**, 6 – 12.
- Cahill, J. F. (2002) Interactions between root and shoot competition vary among species. *OIKOS*, **99**, 101 – 112.
- Caldwell, M. M., Manwaring, J. H. & Durham, S. L. (1996) Species interactions at the level of fine roots in the field: influence of soil nutrient heterogeneity and plant size. *Oecologia*, **106**, 440 – 447.
- Campbell, B. D., Grime, J. P. & Mackey, J. M. L. (1991) A trade-off between scale and precision in resource foraging. *Oecologia*, **87**, 532 – 538.
- Cameron, E. K. & Bayne, E. M. (2009) Road age and its importance in earthworm invasion of northern boreal forests. *Journal of Applied Ecology*, **46**, 28 – 36.
- Canadell, J, Jackson, R. B., Ehleringer, J. R., Mooney, H. A., Sala, O.E. & Schulze, E. D. (1996) Maximum rooting depth of vegetation types at the global scale. *Oecologia*, **108**, 583 – 595.
- Canals, R.M. & Sebastia, M. T. (2000) Soil nutrient fluxes and vegetation changes on molehills. *Journal of Vegetation Science*, **11**, 23-30.
- Casper, B. B. & Jackson, R. B. (1997) Plant competition underground. *Annual Review of Ecological Systems*, **28**, 545 – 570.
- Cazzuffi, D. & Crippa, E. (2005) Contribution of vegetation to slope stability: an overview of experimental studies carried out on different types of plants. *Geotechnical Special Publication*, **128**, 1617 – 1628.
- Cazzuffi, D., Corneo, A. & Crippa, E. (2006) Slope stabilisation by perennial “gramineae” in Southern Italy: plant growth and temporal performance. *Geotechnical and Geological Engineering*, **24**, 429 – 447.
- Chancellor, R. J. (1969) Road verges – the agricultural significance of weeds and wild plants. *Road verges: their function and management*. (eds. J. M. Way), pp. 16 – 19, The Commonwealth Hall, London.
- Chiatante, D., Baraldi, A., Iorio, A. D., Sarnataro, M. & Scippa, G. (2003) Root response to mechanical stress in plants growing on slopes: an experimental system for morphological, biochemical and molecular analysis. *Roots: the dynamic interface between plants and the earth*. (eds. Jun Abe) pp. 427 – 437. Klumer Academic Publishers, Netherlands.
- Churchill, R. E. (1982) Aspect induced differences in hillslope processes. *Earth Surface Processes and Landforms*, **7**, 171 – 182.
- Christen, D. & Matlack, G. (2005) The role of roadsides in plant invasions: a demographic approach. *Conservation Biology*, **20**, 385 – 391
- Clark, L. J., Whalley, W. R., Dexter, A. R., Barraclough, P. B. & Leigh, R. A. (1996) Complete mechanical impedance increases the turgor of cells in the apex of pea roots. *Plant, Cell and Environment*, **19**, 1099 – 1102.
- Clark, L. J., Whalley, W. R. & Barraclough, P. B. (2003) How do roots penetrate strong soil? *Plant and Soil*, **255**, 93 – 104.
- Clark, L. J., Whalley, W. R. & Barraclough, P. B. (2001) Partial mechanical impedance can increase the turgor of seedling pea roots. *Journal of Experimental Botany*, **52**, 167 – 171.
- Cockroft, B., Barley, K. P. & Greacen, E. L. (1969) The penetration of clays by fine probes and root tips. *Australian Journal of Soil Research*, **7**, 333 – 348.
- Cook, A., Marriott, C. A., Seel, W. & Mullins, C. E. (1996) Effects of soil mechanical impedance on root and shoot growth of *Lolium perenne* L., *Agrostis capillaris* and *Trifolium repens* L. *Journal of Experimental Biology*, **47**, 1075 – 1084.
- Craine, J. M., Wedin, D. A., Chapin, F. S. & Reich, P. B. (2003) The dependence of root system properties on root system biomass of 10 North American grassland species. *Plant and Soil*, **250**, 39 – 47.
- Croser, C., Bengough, G. & Pritchard, J. (2000) The effect of mechanical impedance on root growth in pea (Pisum sativum). II. Cell expansion and wall rheology during recovery. *Physiologia Plantarum*, **109**, 150 – 159.
- Danjon, F., Barker, D. H., Drexhage, M. & Stokes, A. (2008) Using three-dimensional plant root architecture in models of shallow-slope stability. *Annals of Botany*, **101**, 8, 1281 – 1293.

- Davies, D. M., Graves, J. D., Elias, C. O., Williams, P. P. J. (1997) The impact of *Rhinanthus* spp. on sward productivity and composition: implications for the restoration of species rich grasslands. *Biological Conservation*, **82**, 87-93.
- Dexter, A. R. (1986a) Model experiments on the behaviour of roots at the interface between tilled seed-bed and a compacted subsoil. 1) Effects of seed bed aggregates size and sub-soil strength on wheat roots. *Plant and Soil*, **95**, 23 -33.
- Dexter, A. R. (1986b) Model experiments on the behaviour of roots at the interface between tilled seed-bed and a compacted subsoil. 2) Entry of pea and wheat roots into sub-soil cracks. *Plant and Soil*, **95**, 135 - 147.
- Dexter, A. R. (1986c) Model experiments on the behaviour of roots at the interface between tilled seed-bed and a compacted subsoil. 3) Entry of pea and wheat roots into cylindrical biopores. *Plant and Soil*, **95**, 149 - 161.
- Dexter, A. R. (2004) Soil physical quality Part 1: Theory, effects of soil texture, density, and organic matter, and effects on root growth. *Geoderma*, **120**, 201 – 214.
- Diaz, S. & Cabido, M. (1997) Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science*, **8**, 463-474.
- Driscoll, R. (1983) The influence of vegetation on the swelling and shrinking of clay soils in Britain. *Geotechnique*, **33**, 2, 93-105.
- Duffey, E., Morris, M. G., Shealil, J., Ward, L. K., Wells, D. A., Wells, T. C. E. (1994) *Grassland ecology and wildlife management*. Chapman and Hall, London.
- Dunnett, N. P., Willis, A. J., Hunt, R. & Grime, J. P. (1998) A 38-year study of relations between weather and vegetation dynamics in road verges near Bibury, Gloucestershire. *Journal of Ecology*, **86**, 610-623.
- Dunnett, N. P. & Grime, J. P. (1999) Competition as an amplifier of short-term vegetation responses to climate: an experimental test. *Functional Ecology*, **13**, 388 – 395.
- Dupuy, L. Fourcaud, T. & Stokes, A. (2005) A numerical investigation into factors affecting the anchorage of roots in tension. *European Journal of Soil Science*, **56**, 319 – 327.
- DPB (2008) Durham Biodiversity Partnership. Transport Corridors Action Plan. http://www.durhambiodiversity.org.uk
- Drake, J. A. (1990) Communities as assembled structures: Do rules govern pattern? *Trends in Ecology and Evolution*, **5**, 159-164.
- Driscoll, R. (1983) The influence of vegetation on the swelling and shrinking of clay soils in Britain. *Geotechnique*, **33**, 93-105.
- Ellenberg, H. & Muller-Dombois, D. (1967) A key of Raunkiaer plant life forms with revised subdivision. *Berichte des Geobotanischen Institutes, ETH Stiftung Rubel*, **37**, 56-73.
- Elliot, R. H. (1908) *The Clifton Park System of Farming and laying down land to grass*. Faber and Faber limited.
- Elwell, H. A. & Stocking, M. A. (1976) Vegetal cover to estimate soil erosion hazard in Rhodesia. *Geoderma*, **15**, 61 – 70.
- Ennos, A. R. (1989) The mechanics of anchorage in seedlings of sunflower, *Helianthus annuus* L. *New Phytologist*, **113**, 185 – 192.
- EWT (2008) Essex Wildlife Trust. Roadside Verges. http://www.essexwt.org.uk
- Evans, P. S. (1971) Root growth of *Lolium perenne* L. II. Effects of defoliation and shading. *New Zealand Journal of Agricultural Research*. **14**, 552 – 562.
- Evans, R. (1990) Water erosion in British farmers' fields – some causes, impacts, predictions. *Progress in Physical Geography*, **14**, 199-219.
- Fitter, A. H. (1991) Characteristics and functions of root systems. *Plant roots, the hidden half.* (eds. Waisel, Y, Eshel, A. & Kafkafi, U.), Marcel Dekker, New York.
- Fitter, A. H. & Stickland, T. R. (1991) Architectural Analysis of Plant Root Systems. 2. Influence of Nutrient Supply on Architecture in Contrasting Plant Species. *New Phytologist*, **118**, 3, 383 – 389.
- Fitter, A. H. & Stickland, T. R. (1992) Architectural Analysis of Plant Root Systems. III. Studies on Plants Under Field Conditions. *New Phytologist*, **121**, 2, 243-248.

- Fullen, M. A. (1991) A comparison of runoff and erosion rates on bare and grasses loamy sand soils. *Soil Use and Management*, **7**, 136 – 139.
- Fullen, M. A. (1992) Erosion rates on bare loamy sand soils in east Shropshire, UK. *Soil Use and Management*, **8**, 157 – 162.
- Fullen, M. A, Zhi, W. B. & Brandsma, R. T. (1998) A comparison of the texture of grassland and eroded sandy soils from Shropshire, UK. *Soil and Tillage Research*, **46**, 301 – 305.
- Garcia-Orenes, F., Cerda, A., Mataix-Solera, J., Guerrero, C., Bodi, M. B., Arcenegui, V., Zornoza, R. & Sempere, J. G. (2009) Effects of agricultural management on surface soil properties and soil-water losses in eastern Spain. *Soil and Tillage Research*, **106**, 117 – 123.
- Garwood, E. A. (1967) Seasonal variation in appearance and growth of grass roots. *Journal of the British Grassland Society*, **22**, 121 – 130.
- Gelbard, J. L. & Belnap, J. (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology*, **17**, 420 – 432.
- Gelbard, J. L. & Harrison, S. (2003) Roadless habitats as refuges for native grasslands: Interactions with soil, aspect and grazing. *Ecological applications*, **13**, 404 – 415.
- Gibson, C. W. D. & Brown, V. K. (1992) Grazing and vegetation change: deflected or modified succession? *Journal of Applied Ecology*, **29,** 120-131.
- Gibson, C. C. & Watkinson, A. R. (1989) The host range and selectivity of a parasitic plant *Rhinanthus minor* L. *Oecologia,* **78**, 401-406.
- Gibson, C. C. & Watkinson, A. R. (1992) The role of the hemiparasitic annual *Rhinanthus minor* in determining grassland community structure. *Oecologia,* **78**, 401-406.
- Gilbert, O. L. & Anderson, P. (1998) *Habitat creation and repair*. Oxford University Press, Oxford.
- Goss, M. J. (1977) Effects of Mechanical impedance on root growth in Barley (*Hordeum vulgare* L.). I. Effects on the elongation and branching of seminal root axes. *Journal of Experimental Botany*, **28**, 96 – 111.
- Gray, D. H. (1995) Influence of vegetation on the stability of slopes. *Vegetation and slopes. Stabilisation, protection and ecology* (eds. D. H. Barker), Thomas Telford, London.
- Greenwood, M. (1996) *Bioengineering: a field trial at Longhorn wood cutting. M20 special publication 128.* UK CIRIA.
- Greenwood, J. R., Norris, J. E. & Wint, J. (2004) Assessing the contribution of vegetation to slope stability. *Geotechnical Engineering*, **157**, 199 – 207.
- Grime, J. P., Hodgson, J. G. & Hunt, R. (1988) *Comparative Plant Ecology*. Unwin Hyman, London.
- Grime, J. P., Willis, A. J., Hunt, R. & Dunnett, N. P. (1994) Climate-vegetation relationships in the Bibury road verge experiments. *Long term Experiments in Agricultural and Ecological Sciences* (eds. R. A. Leigh & A. E. Johnston), pp. 271-285. CAB International, Wallingford.
- Grime, J. P. (2001) *Plant strategies, vegetation processes and ecosystem processes*, Wiley, New York, 2nd ed.
- Grubb, P. J. (1982) Control of relative abundance in roadside *Arrhenatherum*: results of a long-term garden experiment. *Journal of Ecology*, **70**, 845 – 861.
- Hamza, M. A. & Anderson, W. K. (2005) Soil compaction in cropping systems. A review of the nature, causes and possible solutions. *Soil and Tillage Research*, **82**, 121 – 145.
- Hansen, M. & Fogelfors, H. (1998) Management of permanent set-aside on arable land in Sweden. *Journal of Applied Ecology*, **35**, 758 – 771.
- Harmen, H., Williams, P. D., Peters, S. L., Bambrick, M. T., Hopkins, A. & Ashenden, T. W. (2004) Impacts of elevated atmospheric CO_2 and temperature on plant community structure of a temperate grassland are modulated by cutting frequency. *Grass and Forage Science*, **59**, 144 – 156.
- van Hecke, P., Impens, I. & Beheaghe, T.J. (1981) Temporal variation of species composition and species diversity in permanent grassland plots with different fertiliser treatments. *Vegetatio*, **47**, 221-232.
- Hejeman, M., Klaudisova, M., Schellberg, J. & Honsova, D. (2007) The Rengen grassland experiment: plant species composition after 64 years of fertilizer application. *Agriculture, Ecosystems & Environment*, **122**, 259 – 266.

- Highways Agency (1991) *Manual of Contract Document for Highways Works* (MCDW). *Volume 1: Specification for Highways Works. Series 600 Earthworks*. The Stationary Office, London.
- Highways Agency (1992) *Design Manual for Roads and Bridges (DMRB) Volume 10. 1. 2. The Good Roads Guide: New Roads: Planting, Vegetation and Soils.* The Stationary Office, London.
- Highways Agency (1993) *Design Manual for Roads and Bridges (DMRB) Volume 10. 4. 1. The Wildflower Handbook.* The Stationary Office, London.
- Highways Agency (1994) *Design Manual for Roads and Bridges (DMRB) Volume 10. 3. 2. Landscape Management Handbook.* The Stationary Office, London.
- Highways Agency Area 2 (2005a) *Area 2 Trunk Road and Motorways Maintenance Agency. Guidance of the management of the soft estate. Area 2: Grassland Management Programme. Grassland Management Plan.* WS Atkins Consultants Limited.
- Highways Agency Area 2 (2005b) *Area 2 Trunk Road and Motorways Maintenance Agency. Guidance of the management of the soft estate. Area 2: Grassland Management Programme. Appendix A. Area 2 biodiversity: M4 botanical study.* WS Atkins Consultants Limited.
- Highways Agency (2007a) *Area 2 Calcareous grassland improvements (Scheme 01582) Feasibility study – 2nd revision.* InterRoute Area 2, Joint venture between Balfour Beatty and Mott MacDonald Ltd, Highways Agency.
- Highways Agency (2007b) *Manual of Contract Document for Highways Works (MCDW). Volume 1: Specification for Highways Works. Series 3000. Landscape and Ecology.* The Stationary Office, London.
- Hill, M. O., Mountford, J. O., Roy, D. B. & Bounce, R. G. H. (1999) *Ellenberg's Indicator Values for British Plants: ECOFACT.* Vol. 2. Technical Annex. HMSO, London, UK.
- Hill, M. O., Roy, D. B., Mountford, J. O. & Bunce, R. G. H. (2000) Extending Ellenburg's Indicator values to a new area: an algorithmic approach. *Journal of Applied Ecology*, **37**, 3 – 15.
- Hillier, S. (1990) Gaps, seed banks and plant species diversity in calcareous grasslands. *Calcareous grasslands, Ecology and Management* (eds. S.H. Hillier, D.W.H. Walton & D.A. Wells), pp. 57-66. Bluntisham Books, Sheffield.
- Hillier, D. M. & MacNeil, D. J. (2000). *A review of the use of live willow poles for stabilising highway slopes. TRL Unpublished Project Report PR/IS/13/00.* TRL Limited, Crowthorne.
- Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E., Norton, D., Ojima, D., Richardson, D. M., Sanderson, E. W., Valladares, F., Vila, M., Zamora, R. & Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1 – 7.
- Hobbs, R. J., Higgs, E. & Harris, J. A. (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology and Evolution*, **24**, 599 – 605.
- Hodgson, J. G., Grime, J. P., Wilson, P. J., Thompson, K. & Band, S. R. (2005) The impacts of agricultural change (1963-2003) on the grassland flora of Central England: processes and prospects. *Basic and Applied Ecology*, **6**, 107-118.
- Hodkinson, D. J. & Thompson, K. (1997) Plant dispersal: the role of man. *Journal of Applied Ecology*, **34**, 1484 – 1496.
- Hopkins, A., Pywell, R. F., Peel, S., Johnson, R. H. & Bowling, P. J. (1998) Enhancement of botanical diversity of permanent grassland and impact on hay production in Environmentally Sensitive Areas in the UK. *Grass and Forage Science*, **54**, 163 – 173.
- Hovd, H. & Skogen, A. (205) Plant species in arable field margins and road verges of central Norway. *Agriculture, Ecosystems and Environment*, **110**, 257 – 265.
- Hylander, K. (2005) Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. *Journal of Applied Ecology*, **42**, 518 – 525.
- Hudson, N. W. (1957) Erosion control research – progress report on experiments at Henderson Research Station, 1953 – 56. *Rhodesian Agricultural Journal*, **54**, 297 – 323.
- Hulme, M. & Jenkins, G. (1998) *Climate Change Scenarios for the UK: The summary report.* Climate Research Unit of University of East Anglia, Norwich, UK.

- Hunt, R., Hodgson, J. G., Thompson, K., Bungener, P., Dunnett, N. P. & Askew, A. P. (2004) A new practical tool for deriving a functional signature for herbaceous vegetation. *Applied Vegetation Science*, **7**, 163 – 170.
- Hurlbert, S. H. (1984) Pseudoreplication and the design of ecological experiments. *Ecological Monographs*, **54**, 187 – 211.
- Hutchings, M. J. (1983) Plant diversity in four chalk grassland sites with different aspects. *Plant Ecology*, **53**, 179-189.
- Hutchings, M. J. & John, E.A. (2004). The effects of environmental heterogeneity on root growth and root/shoot partitioning. *Annals of Botany,* **94**, 1-8.
- Huston, M. A., Aarssen, L. W., Austin, M. P., Cade, B. S., Fridley, J. D., Garnier, E., Grime, J. P., Hodgson, J., Lauenroth, W. K., Thompson, K., Vandermeer, J. H. & D. A. Wardle (2000) No consistent effect of plant diversity on productivity, *Science,* **289**, 5483, 1255a.
- Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E. & Schulze, E. D. (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia*, **108**, 389 – 411.
- Janssens, F., Peeters, A., Tallowin, J. R. B., Bakker, J. P, Bekker, R. M., Fillat, F. & Oomes, M. J. M. (1998) Relationship between soil chemical factors and grassland diversity. *Plant and Soil*, **202**, 69-78.
- Jefferson, R. G. (2005) The conservation management of upland hay meadows in Britain: A review. *Grass and Forage Science*, **60**, 322-331.
- Jodion, Y., Lavoie, C., Villeneuve, P., Theriault, M., Beaulieu, J. & Belzile, F. (2008) Highways as corridors and habitats for the invasive common reed *Phragmites australis* in Quebec, Canada. *Journal of Applied Ecology*, **45**, 459 – 466.
- Jones, A. T. & Hayes, M. J. (1999) Increasing floristic diversity in grassland: the effects of management regime and provenance on species introduction. *Biological Conservation*, **87**, 381 – 390.
- Joshen Schenk, H. & Jackson, R. B. (2002) Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *The Journal of Ecology*, **90**, 480 – 494.
- Joshi, J. Matthies, D. & Schmid, B. (2000) Root hemiparasites and plant diversity in experimental grassland communities. *Journal of Ecology*, **88**, 634-644.
- Kaspar, T. C. & Bland, W. L. (1992) Soil temperature and root growth. *Soil Science*, **154**, 290-299.
- Kirkham, F. W. & Tallowin, J. R. B. (1995) The influence of cutting date and previous fertiliser treatment on the productivity and botanical composition of species-rich hay meadow on the Somerset levels. *Grass and Forage Science*, **50**, 365-377.
- Kiviniemi, K. & Eriksson, O. (1999) Dispersal, Recruitment and Site Occupancy of Grassland Plants in Fragmented Habitats**.** *Oikos*, **86**, 241-253.
- Klimek, S., Kemmermann, A. R., Hofmann, M. & Isselstein, J. (2007) Plant species richness and composition in managed grasslands: The relative importance of field management and environmental factors. *Biological Conservation*, **134**, 559 – 570.
- van der Krift, T. A. J. & Berendse, F. (2002) Root life spans of four grass species from habitats differing in nutrient availability. *Functional Ecology*, **16**, 198 – 203.
- Kutiel, P. (1992) Slope aspect effect on soil and vegetation in a Mediterranean ecosystem. *Israel Journal of Botany*, **41**, 243-250.
- Kutiel, P. & Lavee, H. (1999) Effect of slope aspect on soil and vegetation properties along an aridity transect. *Israel Journal of Plant Sciences*, **47**, 169-178.
- Lamb, E. G. (2008) Direct and indirect control of grassland community structure by litter, resources and biomass. *Ecology*, **89**, 216 – 225.
- Lamb, E. G. & Cahill, J. F. (2008) When competition does not matter: grassland diversity and community composition. *The American Naturalist*, **171**, 777 – 787.
- Lampurlanés, J. & Cantero-Martínez, C. (2003) Soil bulk density and penetration resistance under different tillage and crop management systems and their relationship with barley root growth. *Agronomy Journal*, **95**, 526 – 536.
- Lauenroth, W. K. & Gill, R. (2003) Turnover of root systems. *Root Ecology* (eds. de Kroon, H. & Visser, E. J. W.), Springer, Germany.

- Laursen, K. (1981) Birds on roadside verges and the effects of mowing on frequency and distribution. *Biological Conservation*, **20**, 59 – 68.
- Lepš, J., Osbornova-Kosinova, J., & Rejmanek, M. (1982) Community stability, complexity and species life history strategies. *Plant Ecology*, **50**, 53-63.
- Lepš, J., Doležal, J., Bezemer, T. M., Brown, V. K, Hedlund, K., Igual M. A., Jörgensen, H. B., Lawson, C. S., Mortimer, S. R., Peix Geldart, A., Rodríguez Barrueco, C., Santa Regina, I., Šmilauer, P. & van der Putten, W. H. (2007) Long-term effectiveness of sowing high and low diversity seed mixtures to enhance plant community development on ex-arable fields, *Applied Vegetation Science*, **10**, 97 – 110.
- Lepš, J. S. & Šmilauer, P. (2003) Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge, U.K.
- Levang-Britz, N. & Biondini, M. E. (2002) Growth rate, root development and nutrient uptake of 55 plant species from the Great Plain Grasslands, USA. *Plant Ecology*, **165**, 117 – 144.
- Lifeontheverge (2010) http://www.lifeontheverge.org.uk
- Lindborg, R. (2006) Recreating grasslands in Swedish rural landscapes – effects of seed sowing and management history. *Biodiversity and Conservation*, **15**, 957 – 969.
- Lutz, H. J. (1936) Runoff and erosion in relation to grassland vegetation. *Ecology*, **17**, 534.
- MacNeil, D. J., Steele, D. P., McMahon, W. & Carder, D. R. (2001) *Vegetation for Slope Stability. TRL Project Report PR/IS/26/2001*. TRL Limited, Crowthorne.
- Mahmoud. A, Grime, J. P. & Furness, S. B. (1975) Polymorphism in *Arrhenatherum elatius* (L.) Beauv. Ex J. & C. Presl. *New Phytologist*, **75**, 269 – 276.
- Marden, M., Rowan, D & Phillips, C. (2005) Stabilising characteristics of New Zealand indigenous riparian colonising plants. *Plant and Soil*, **278**, 95 – 105.
- Marini, L., Fontana, P., Scotton, M. & Klimek, S. (2008) Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. *Journal of Applied Ecology*, **45**, 361 – 370.
- Marris, E. (2009) Ragamuffin Earth. *Nature*, **460**, 450 – 453.
- Marrs, R. H. (1993). Soil fertility and nature conservation in Europe: theoretical considerations and practical management solutions. *Advances in Ecological Research*, **24**, 241–300.
- Masle, J. & Passioura, J. B. (1987) The effect of soil strength on the growth of young wheat plants. *Australian Journal of Plant Physiology*, **14**, 643 – 656.
- Materechera, S. A., Dexter, A. R. & Alston, A.M. (1991) Penetration of very strong soils by seedlings roots of different plant species. *Plant and Soil*, **144**, 297 – 303.
- Materechera, S.A., Alston, A.M., Kirby, J. M. & Dexter, A. R. (1992) Influence of root diameter on the penetration of seminal roots into a compacted subsoil. *Plant and Soil*, **144**, 297 – 303.
- Matesanz, S., Valladares, F., Tena, D., Costa-Tenorio, M. & Bote, D. Early dynamics of plant communities on revegetated motorway slopes from southern Spain: is hydroseeding always needed? *Restoration Ecology*, **14**, 297-307.
- McCully, M. E. (1999) Roots in soil: Unearthing the complexities of roots and their rhizospheres. *Annu. Rev. Plant Physio. Plant Mol. Biol.*, **50**, 695 – 718.
- McDonald, A.W. (1993) The role of seedbank and sown seeds in the restoration of an English flood meadow. *Journal of Vegetation Science*, **4**, 395-400.
- Mitchell, D. J., Barton, A P., Fullen, M. A., Hocking, T. J., Xhi, W. B, & Yi, Z. (2003) Field studies of the effects of jute textiles on runoff and erosion in Shropshire, UK. *Soil use and Management*, **19**, 182 – 184.
- Montagu, K. D., Conroy, J. P. & Atwell, B.J. (2001) The position of localized soil compaction determines root and subsequent shoot growth responses. *Journal of Experimental Biology*, **52**, 2127 – 2133.
- Morgan, R. P. C. (1992) Soil conservation options in the UK. *Soil Use and Management*. **8**, 176 – 180.
- Morgan, R. P. C. (2007) Vegetative-based technologies for erosion control. *Eco- and Ground Bio-Engineering: The use of vegetation to improve slope stability* (eds. Stokes *et al.*), pp. 265 – 272. Oxford University Press, Oxford.

- Mountford J. O., Lakhani, K. H. & Kirkham, F. W. (1993) Experimental assessment of the effects of nitrogen addition under hay cutting and aftermath grazing on the vegetation of meadows on a Somerset peat moor. *Journal of Applied Ecology*, **30**, 321-332.
- Muller, S., Dutiot, T., Alard, D. & Grevilliot, F. (1998) Restoration and rehabilitation of species-rich grassland ecosystems in France: a review. *Restoration Ecology*, **6**, 94 – 101.
- Munguira, M. L., & Thomas, J. A. (1992) Use of road verges by butterfly and burnet populations, and the effect of roads on adult dispersal and mortality. *Journal of Applied Ecology*, **29**, 316-329.
- Naeem, S. Thompson, L. J., Lawler, S. P., Lawton, J. H. & Woodlin, R. M. (1994) Declining biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734-737.
- Nelson, W. W. & Allmaras, R. R. (1969) An improved monolith method for excavating and describing roots. *Agronomy Journal*, **61**, 751 – 754.
- Nepstad, D. C., de Carvalho, C. R., Davidson, E. A., Jipp, P. H., Lefebvre, P. A., Negreiros, G. H., de Silva, E. D., Stone, T. A., Trumbore, S. E. & Viera, S. (1994) The role of deep roots in the Amazonian forests and pastures. *Nature*, **372**, 666 – 669.
- Newman, E. I. (1965) A method of estimating the total length of root in a sample. *Journal of Applied Ecology*, **3**, 139 – 146.
- Nilaweera, N. S. & Nutalaya, P. (1999) Role of tree roots in slope stabilisation. *Bull Eng Geol Env*, **57**, 337 – 342.
- Noble, I. R. & Gitay, H. (1996) A functional classification for predicting the dynamics of landscapes. *Journal of Vegetation Science*, **7**, 329 – 336.
- Norris, J. E. (2005) Root reinforcement by Hawthorn and Oak roots on a highway cut-slope in Southern England. *Plant and Soil*, **278**, 43 – 53.
- NBPG (2008) Northamptonshire Biodiversity Partnership Group. Road Verges Action Plan. http://www.wildlifebcnp.org/old/northants-bap/Roadside%20Verges.htm
- North Pennines AONB Partnership (2011) Hay Time North Pennines. http://www.northpennines.org.uk/index.cfm?articleid=11799
- Oglethorpe, D. R. & Sanderson, R. (1998) Farm characteristics and the vegetative diversity of grasslands in the North of England: a policy perspective. *Biodiversity and Conservation*, **7**, 1333 – 1347.
- Operstein, V. & Frydman, S. (2000) The influence of vegetation on soil strength. *Ground Improvements*, **4**, 81 – 89.
- Oomes, M. J. M. (1992) Yield and species density of grasslands during restoration management. *Journal of Vegetation Science*, **3**, 271-274.
- Oster, M., Ask, K., Romermann, C., Tackenberg, O. & Eriksson, O. (2009) Plant colonisation of ex-arable fields from adjacent species-rich grasslands: the importance of dispersal vs. recruitment ability. *Agriculture, Ecosystems and Environment*, **130**, 93 – 99.
- Pahlsson, L. (1974) Relationship of soil, microclimate and vegetation on a sandy hill. *Oikos*, **25**, 21-34.
- Parendes, L. A. & Jones, J. A. (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. *Conservation Biology*, **14**, 64 – 75.
- Parr, T. W. & Way, M. (1988) Management of roadside vegetation: long-term effects of cutting. *Journal of Applied Ecology*. **25**, 1073 – 1087.
- Perring, F. (1959) Topographical gradients of Chalk grassland. *The Journal of Ecology*, **47**, 447-481.
- Perring, F. (1960) Climatic gradients of Chalk grassland. *The Journal of Ecology*, **48**, 415-442.
- Phoenix, G. K., Johnson, D., Grime, J. P. & Booth, R. E. (2008) Sustaining ecosystem services in ancient limestone grassland: importance of major component plants and community composition. *Journal of Ecology*, **96**, 894 – 902.
- Press, M. C. (1998) Dracula or Robin Hood? A functional role for root hemiparasites in nutrient poor ecosystems. *Oikos*, **82**, 609-611.
- Pykälä, J. (2005) Plant species responses to cattle grazing in mesic semi-natural grassland. *Agriculture, Ecosystems & Environment*, **108**, 109 – 117.

- Pykälä, J., Luoto, M., Heikkinen, R. K. & Kontula. (2005) Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. *Basic and Applied Ecology*, **6**, 25 – 33.
- Pywell, R. F., Bullock, J. M., Hopkins, A., Walker, K. J., Sparks, T. H., Burkes, M. J. W. & Peel, S. (2002) Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology*, **39**, 294-309.
- Pywell, R. F., Bullock, J. M., Roy, D. B., Warman, L., Walker, K. J., Rothery, P. (2003) Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology*, **40**, 65 – 77.
- Pywell, R. F., Bullock, J. M., Walker, K. J., Coulson, S. J., Gregory, S. J. & Stevenson, M. J. (2004) Facilitating grassland diversification using the hemiparasitic plant *Rhinanthus minor. Journal of applied ecology,* **41,** 880-887.
- Quinn, N. N. Morgan, R. P. C. & Smith, A. J. (1980) Simulations of soil erosion induced by human trampling. *Journal of environmental management*. **10**, 155 – 165.
- Redford, K. H., Coppolillo, P., Sanderson, E. W., Da Fonseca, G. A. B., Dinerstein, E., Groves, C., Mace, G., Maginnis, S., Mittermeier, R. A., Noss, R., Olson, D., Robinson, J. G., Vedder, A. & Wright, M. (2003) Mapping the conservation landscape. *Conservation Biology*, **17**, 116 – 131.
- Rice, R. M., Corbett, E. S. & Bailey, R. G. (1969) Soil slips related to vegetation, topography, and soil in southern California. *Water Resources Research*, **5**, 3, 647 – 659.
- Ridley, A. M., Dineen, K., Burland, J. B. & Vaughan, P. R. (2003) Soil matrix suction: some examples of its measurement and application in geotechnical engineering. *Géotechnique*, **53**, 241 – 253.
- Robinson, D., Hodge, A. & Fitter, A. (2003) Constraints on the form and function of root systems. *Root Ecology* (eds. de Kroon, H. & Visser, E. J. W.), Springer, Germany.
- Rodwell, J. S. (1992) *Grasslands and Montane Communities*. Cambridge University Press, Cambridge.
- Ross, S. M. (1986) Vegetation Change on Highway Verges in South-East Scotland. *Journal of Biogeography*, **13**, 109-117.
- Rorison, I. H., Gupta, P. L. & Hunt R. (1986a) Local climate, topography and plant growth in Lathkill Dale NNR. II. Growth and nutrient uptake within a single season. *Plant, cell and environment*. **9**, 57-64.
- Rorison, I. H., Sutton, F. & Hunt, R. (1986b) Local climate, topography and plant growth in Lathkill Dale NNR. I. A twelve year summary of solar radiation and temperature. *Plant, cell and Environment*, **9**, 49-56.
- Russell, E. W. (1973) *Soil conditions and plant growth*. 10th ed. Longman, London.
- Sangwine, A. P. (1996) The management of the roadside verge estate. *Proceedings of Institution of Civil Engineers, Municipal Engineer*, **115**, 197 – 202.
- Savard, J-P. L., Clergeau, P. & Mennechez, G. (2000) Biodiversity concepts and urban ecosystems. *Landscape and urban planning*, **48**, 131 – 142.
- Schaffers, A. P., Vesseur, M. C. & Sykora, K. V. (1998) Effects of delayed hay removal on the nutrient balance of roadside plant communities. *Journal of Applied Ecology*, **35**, 349 – 364.
- Schaffers, A. P. & Sykora, K. V. (2002) Synecology of species-rich plant communities on roadside verges in the Netherlands. *Phytocoenologia*, **32**, 29-83.
- Schenk, H. J. & Jackson, R. B. (2002) Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *The Journal of Ecology*, **90**, 480 – 494.
- Scherer-Lorenzen, M., Palmborg, C., Prinz, A. & Schulze, E-D. (2003) The role of plant diversity and composition for nitrate leaching in grasslands. *Ecology*, **84**, 1539 – 1552.
- Schuurman, J. J. & Goedewaagen, A. J. (1971) *Methods for the examination of root systems and roots*, 2 ed Wageningen: Pudoc.
- Sebastia, M. T. (2004) Role of topography and soils in grassland structuring at the landscape and community scales. *Basic and Applied Ecology*, **5**, 331-346.
- Seel, W. E. & Press, M. C. (1993) Influence of the Host on Three Sub-Arctic Annual Facultative Root Hemiparasites. I. Growth, Mineral Accumulation and Above-Ground Dry-Matter Partitioning, *New Phytologist*, **125**, 131-138.

- Shannon, C. E. & Weaver, W. (1949) *The Mathematical Theory of Communication*, Urbana, pp. 117.
- Shi, H. & Shao, M. (2000) Soil and water loss from the Loess Plateau in China. *Journal of Arid Environments*, **45**, 9 – 20.
- Smethurst, J. A., Clarke, D. & Powrie, W. (2006) Seasonal changes in pore water pressure in a grass-covered cut slope in London Clay. *Geotechnique*, **56**, 523 – 537.
- de Silva, A. P., Kay, B. D. & Perfect, E. (1997) Management versus inherent soil properties effects on bulk density and relative compaction. *Soil and Tillage Research*, **44**, 81 – 93.
- Smith, R. S. & Rushton, S. P. (1994) The effects of grazing management on the vegetation of mesotrophic (meadow) grassland in Northern England. *Journal of Applied Ecology*, **31**, 13-24.
- Smith, R. S., Buckingham, H., Bullard, M. J., Shiel, R. S. & Younger, A. (1996) The conservation management of mesotrophic (meadow) grassland in northern England. 1. Effects of grazing, cutting date and fertiliser on the vegetation of a traditionally managed sward. *Grass and Forage Science*, **51**, 278-291.
- Smith, R. S., Shiel, R. S, Millward, D, & Corkhill, P. (2000) The interactive effects of management on the productivity and plant community structure of an upland meadow, An 8-year field trial. *Journal of applied ecology*, **37**, 6, 1029-1043.
- Smith, R. S., Shiel, R. S., Bardgett, R. D., Millward, D., Corkhill, P., Evans, P., Quirk, H., Hobbs, P. J. & Kometa, S. T. (2008) Long-term change in vegetation and soil microbial communities during the phased restoration of traditional meadow grassland. *Journal of Applied Ecology*, **45**, 670 – 679.
- Snowdon, R. A. (2004) *Environment and Landscape. Environmental Statement. Vegetated reinforced steep slopes, TRL unpublished report PR/CE/177/97*. TRL, Crowthorne.
- Soane, B. D. & van Ouwerkerk, C. (1995) Implications of soil compaction in crop production for the quality of the environment. *Soil and Tillage Research*, **35**, 5 – 22.
- Solé-Benet, A., Calvo, A., Cerdà, A., Lásaro, R., Pini, R. & Barbero, J. (1997) Influences of micro-relief patterns and plant cover on runoff related processes in badlands from Tabernas (SE Spain). *Catena*, **31**, 23 – 38.
- Spehn, E. M., Joshi, J., Schmid, B., Diemer, M. & Korner, C. (2000) Above-ground resource use increases with plant species richness in experimental grassland ecosystems. *Functional Ecology*, **14**, 326 – 337.
- Spehn, E. M. *et al.* (2005) Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monographs*, **75**, 37 – 63.
- Spellerberg, I. F. (1998) Ecological effects of roads and traffic: a literature review. *Global Ecology and Biogeography*, **7**, 317 – 333.
- Stace, C. A. (2010) New flora of the British Isles, Cambridge University Press, Cambridge, UK.
- Stevens, C. J., Quinton, J. N., Bailey, A. P., Deasy, C., Silgram, M. & Jackson, D. R. (2009) The effects of minimal tillage, contour cultivation and in-field vegetative barriers on soil erosion and phosphorus loss. *Soil and Tillage Research*, **106**, 145 – 151.
- Stirzaker, R. J., Passioura J. B. & Wilms, Y. (1996) Soil structure and plant growth: Impact of bulk density and biopores. *Plant and Soil*, **185**, 151 - 162.
- Streeter, D. T. (1969) Road verges – a local responsibility for conservation. *Road verges: their function and management* (eds. J. M. Way), pp. 8 – 10, The Commonwealth Hall, London.
- Stevens, C. J., Dise, N. B., Mountford, J. O. & Gowing, D. J. (2004) Impact of nitrogen deposition on the species richness of grasslands. Science, **303**, 1876 – 1879.
- Stevenson, M. J., Bullock, J. M. & Ward, L. K. (1995) Recreating semi-natural communities: effect of sowing rate on establishment of calcareous grassland. *Restoration Ecology*, **3,** 279-289.
- Stokes, A., Ball, J., Fitter, A. H., Brain, P. & Coutts, M. P. (1996) An experimental investigation of the resistance of model root systems to uprooting. *Annals of Botany*, **78**, 415 – 421.
- Stolzy, L. H. & Barley, K. P. (1968) Mechanical resistance encountered by roots entering compact soils. *Soil science*, **105**, 297-301.
- Sun, G., Coffin, D. P. & Lauenroth, W. K. (1997) Comparison of root distributions of species in North American grasslands using GIS. *Journal of Vegetation Science*, **8**, 587-596.
- Tardieu, F. (1988a) Analysis of spatial variability of maize root density. I. Effect of wheel compaction on spatial arrangement of roots. *Plant and Soil*, **107**, 259 – 266.

- Tardieu, F. (1988b) Analysis of the spatial variability of maize root density. II. Distances between roots. *Plant and Soil*, **107**, 267 – 272.
- Taylor, H. M. & Burnett, E. (1964) Influence of soil strength on the root growth habits of plants. *Soil Science*, **98**, 174 – 180.
- Taylor, H. M. & Gardner, H. R. (1960) Relative penetrating ability of different plant roots. *Journal of Agronomy*, **52**, 579 – 581.
- Thaler, P. & Pages, L. (1999) Why are laterals less affected than main axes by homogeneous unfavourable physical conditions? A model-based hypothesis. *Plant and Soil*, **217**, 151 – 157.
- Thomas, C. (2005) Warwickshire, Coventry and Solihull Local Biodiversity Action Plan. Roadside Verges. www.warwickshire.gov.uk/biodiversity.
- Thompson, P. J., Jansen, L. J. & Hooks, C. L. (1977) Penetrometer resistance and bulk density as parameters for predicting root system performance in mine soils. *Soil Science Society of America Journal*, **51**, 1288 – 1293.
- Thompson, A. G. & Jones, C. (1990) Effects of topography on radiance from upland vegetation in North Wales. *International Journal of Remote Sensing*, **11**, 829 – 840.
- Thompson, K., Hillier, S. H., Grime, J. P., Bossard, C.C. & Brand, S.R. (1996) A functional analysis of a limestone grassland community. *Journal of Vegetation Science*, **7**, 371-380.
- Thurston, J. M. (1969) The effect of liming and fertilisers on the botanical composition of permanent grassland, and on the yield of hay. *Ecological aspects of the mineral nutrition of plants* (eds. I. E. Rorison), Symposium of the British Ecological Society, Blackwell Scientific Publications, Oxford.
- Tikka, P. M., Koski, P. S., Kivela, R. A. & Kuitunen, M. T. (2000) Can grassland plant communities be preserved on road and railway verges? *Applied Vegetation Science*, **3**, 25 – 32.
- Tikka, P. M., Hogmander, H. & Koski, P. S. (2001) Road and Railway verges serve as dispersal corridors for grassland plants. *Landscape Ecology*, **16**, 659-666.
- Tilman, D., Wedin, D. & Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **379**, 718 – 720.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) *Science*, **277**, 1300 – 1302.
- Tjallingii, S. P. (2000) Ecology on the edge: Landscape and ecology between town and country. *Landscape and urban planning*, **48**, 103 – 119.
- Tormo, J., Bochet, E. & Garcia-Fayos, P. (2006) Is seed availability enough to ensure colonisation success? An experimental study in road embankments. *Ecological engineering*, **26**, 224-230.
- Tosi, M. (2007) Root tensile strength relationships and their slope stability implications of three shrub species in the Northern Apennines (Italy). *Geomorphology*, **87**, 268 – 283.
- Ulmann, I, Bannister, P. & Wilson, J. B. (1995) The vegetation of roadside verges with respect to environmental gradients in southern New Zealand. *Journal of Vegetation Science*, **6**, 131 – 142.
- Underwood, C. V. (1969) Management of verges. *Road verges: their function and management* (eds. J. M. Way), pp 26 – 28, The Commonwealth Hall, London.
- Veihmeyer, F. J. & Hendrickson, A. H. (1948) Soil density and root penetration. *Soil science*, **65**, 487 - 493 .
- von der Lippe, M. & Kowarik, I. (2006) Long distance dispersal of plants by vehicles as a driver of plant invasions. *Conservation Biology*, **21**, 4, 986 – 996.
- Waisel, Y, Eshel, A. & Kafkafi, U. (1991) *Plant roots, the hidden half.* Marcel Dekker, New York.
- Waldron, L. J. (1977) The shear resistance of root permeated homogeneous and stratified soil. *Soil Science Society of America Journal.* **41**, 843 – 849.
- Waldron, L. J. & Dakessian, S. (1981) Soil reinforcement by roots: calculation of increased soil shear resistance from root properties. *Soil Science.* **132**, 427 – 435.
- Waldron, L. J. & Dakessian, S. (1982) Effect of grass, legume and tree roots on soil shearing resistance. *Soil Science Society of America Journal.* **46**, 894 – 899.
- Wardle, D. A., Bonner, K. I., Barker, G. M., Yeates, G. W., Nicholson, K. S., Bardgett, R. D., Watson, R. N. & Ghani, A. (1999) Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity and ecosystem properties. *Ecological Monographs*, **69**, 535 – 568.

- Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setala, H., van der Putten, W. H., Wall, D. H. (2004) Ecological linkages between aboveground and belowground biota. *Science*, **304**, 1629 – 1633.
- Warren, M. S. & Stephens, D. E. A. (1989) Habitat Design and management for butterflies. *The Entomologist*, **108,** 123-34.
- Way, J. M. (1976) *Grassed and planted areas by motorways*. The Institute of Terrestrial Ecology, Monks wood experimental station, Huntingdon.
- Way, J. M. (1977) Roadside verges and conservation in Britain: a review. *Biological Conservation*, **12**, 65 – 74.
- Way, J. M. (1979) Roadside verges and their management. *Road verges: their function and management* (eds. Department of Transport), pp. 41 – 44. The proceedings of a symposium organised by the British Ecological Society and TRRL, 11 – 13 September 1978. Transport and Road Research Laboratory, TRRL Supplementary Report 513.
- Weaver, J. E. (1925) Investigations on the root habits of plants. *American Journal of Botany*, **12**, 502 – 509.
- Weaver, J. E. (1958a) Classification of root systems of wildflowers of grassland and a consideration of their significance. *Ecology*, **39**, 3, 393 – 401.
- Weaver, J. E. (1958b) Summary and interpretation of underground development in natural grassland communities. *Ecological Monographs*, **28**, 1, 55 – 78.
- Wells, T. C. E., Cox, R. & Frost, A. (1989) *The establishment and Management of Wildflower Meadows*. Nature Conservancy Council, Peterborough.
- Wells, T. C. E. (1990) Establishing chalk grassland on previously arable land using seed mixtures. *Calcareous grassland ecology and management* (eds. S. Hillier *et al.*), pp. 169 - 170. Sheffield Bluntisham Books.
- Wester, L. & Juvik, J. O. (1983) Roadside plant communities on Mauna Loa, Hawaii. *Journal of Biogeography*, **10**, 307 – 316.
- Westbury, D. B. (2004) *Rhinanthus minor* L. *Journal of Ecology*, **92**, 906-927.
- Westbury, D. B., Davies, A, Woodcock, B. A. & Dunnett, N. P. (2006) Seeds of change: the value of using *Rhinanthus minor* in grassland restoration. *Journal of Vegetation Science*, **17**, 435-446.
- Westbury, D. B. & Dunnett, N. P. (2007) *Rhinanthus minor* and its impact on forb abundance and plant community structure in newly established meadows on a productive site. *Applied Vegetation Science*, **10**, 121 – 129.

- Wester, L. & Juvik, J. O. (1983) Roadside plant communities on Mauna Loa, Hawaii. *Journal of Biogeography*, **10**, 307 – 316.

- White, T. A., Barker, D. & Moore, K. J. (2004) Vegetation diversity, growth, quality and decomposition in managed grasslands. *Agriculture, Ecosystems and Environment*, **101**, 73 – 84.
- Wild, A. (1993) *Soils and the environment*, Cambridge University Press, Cambridge, UK.
- Wilkinson, D. M. (2001) Is local provenance important in habitat creation? *Journal of Applied Ecology*, **38**, 1371 – 1373.
- Williams, N. S. G., Morgan, J. W., McDonnell, M. J. & McCarty, M. A. (2005) Plant traits and local extinctions in natural grasslands along an urban gradient. *Journal of Ecology*, **93**, 1203 – 1213.
- Williams, N. S. G., Schwartz, M. W., Vesk, P. A., McCarthy, M. A., Hahs, A. K., Clemants, S. E., Clorlett, R. T., Duncan, R. P, Norton, B. A., Thompson, K. & McDonnell, M. J. (2009) A conceptual framework for predicting the effects of urban environments on floras. *Journal of Ecology*, **97**, 4 – 9.
- Wilson, J. B. (1988) Shoot competition and root competition. *Journal of Applied Ecology*, **25**, 279-296.
- Wilson, A. J., Robards, A. W. & Goss, M. J. (1977) Effects of mechanical impedance on root growth in Barley, *Hordeum vulgare* L. II. Effects on cell development in seminal roots. *Journal of Experimental Biology*, **28**, 1216 – 1227.
- Wilson, J. B., Ullmann, I & Bannister, P. (1996) Do species assemblages ever recur? *Journal of Ecology*, **84**, 471 – 474.
- Wilson, J. B., Wells, T. C. E., Trueman, I. C., Jones, G., Atkinson, M. D., Crawley, M. J., Dodds & Silvertown, J. (1996) Are there assembly rules for plant species abundance? An investigation in relation to soil resources and successional trends. *Journal of Ecology*, **84**, 527 – 538.

- Wilson, J. B., Steel, J. B., Dodd, M. E., Anderson, B. J., Ullmann, I. & Bannister, P. (2000) A test of community reassembly using the exotic communities of New Zealand roadsides in comparison to British Roadsides. *Journal of Ecology*, **88**, 757 – 764.
- Wijesinghe, D. K., John, E. A. & Hutchings, M. J. (2005). Does pattern of soil resource heterogeneity determine plant community structure? An experimental investigation. *Journal of Ecology,* **93**, 99-112.
- Wu, T. H., Beal, P. E. & Lan, C. (1988) In-situ shear test of soil-root systems. *Journal of Geotechnical Engineering*, **14**, 1376 – 1394.
- Young, I. M., Montagu, K. Conroy, J. & Bengough, A. G. (1997) Mechanical impedance of root growth directly reduces leaf elongation rates of cereals. *New Phytologist*, **135**, 613 – 619.
- Zheng, F-L. (2006) Effect of vegetation changed on soil erosion on the Loess Plateau. *Pedosphere*, **16**, 420 – 427.
- Zimmermann, R. P. & Kardos, L. T. (1961) Effect of bulk density on root growth. *Soil science,* **91**, 280 – 289.