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The development of a methodology for the identification of potential wet grassland restoration sites in south west England

by

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A thesis submitted to the University of Plymouth
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Doctor of Philosophy

Department of Geographical Sciences
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In collaboration with the Environment Agency, English Nature and
the Devon Wildlife Trust

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To my dear friend Heidi, who showed me the true meanings of the words courage, perseverance and friendship.

Author's declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

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Francien

Abstract

The development of a methodology for the identification of potential wet grassland restoration sites in south west England

Francien van Soest

Large scale drainage and pasture improvement in the past and present-day neglect of the floristically diverse wet grasslands in south west England have caused a significant decrease, approximately 92% since 1900, in the total area of this ecologically valuable semi-natural plant community. The plant community, which is locally called Culm grassland, consists of acid purple moor grassland, soft rush meadows and wet heaths. Conservation and restoration of these grasslands requires careful planning and efficient use of resources. This study was aimed at developing strategies for regional planning authorities and nature conservation agencies and developed a management tool for the selection of potential Culm grassland restoration locations and for the prediction of species composition based on the environmental characteristics of a site.

Three separate sections of the research could be distinguished. The first section studied the relationships between the wet grassland location and the landscape topography, catchment hydrology and soil physical characteristics, with the use of Geographical Information Systems. Landscape topography was expressed as the $\ln(a/\tan\beta)$ topographic index, in which 'a' is the upslope area draining through the point for which the index is calculated and 'β' is the local slope angle. Culm grassland sites were generally found on positions with a topographic index larger than eight. A quantification of soil saturation periods was carried out by modelling the surface water dynamics with the hydrological model TOPMODEL, which was based mainly on the topographic index. Soil hydrological characteristics were described by applying the Hydrology Of Soil Types (HOST) classification to the soil map of the area. Results indicated that Culm grassland was mainly associated with poorly drained soils and topographic hollows on level or gently sloping grounds.

The second section investigated the species composition in relation to environmental parameters and grazing regime. A field study involving collection of vegetation, soil and site data was carried out on existing Culm grassland sites. Multivariate statistical techniques were applied to relate vegetation gradients to the environmental parameters.

Results showed that grazing pressure, soil pH and soil water were the factors most responsible for species composition within the Culm grassland communities.

The third section integrated the results into a decision support system, which indicated where potentially suitable restoration sites were located and the species composition that could develop based given the environmental parameters. The procedure was tested by application of the decision rules to an independent area and comparison of the potentially suitable sites to historical data, field observations and land use information. From this study, given readily obtainable soil and topographic data a, good first selection of areas for further Culm grassland development could be made. However, relationships between vegetation and environmental parameters will need more detailed field investigation to obtain completely reliable results.

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PART I

Introduction and background

Chapter 1

Introduction – Culm grassland in context

1.1 Introduction

The research discussed in this thesis investigates site characteristics and vegetation composition of floristically diverse, acid to neutral wet grasslands in south west England, in order to design a methodology for the selection of suitable restoration sites and to predict possible vegetation developments based on environmental gradients. Conservation and restoration of these wetlands is important because of their ecological value and because of their possible functioning in flood prevention and improvement of river quality. The sites were found in a highly fragmented pattern in Devon and Cornwall. At present they cover over 4000 ha, but it is estimated that around 1900 over 50.000 ha of this habitat existed (Devon Wildlife Trust, 1992, in Wolton, 1992). Nationally this habitat is called Rhôs pasture and locally it is referred to as Culm grassland, which is the name used in this thesis.

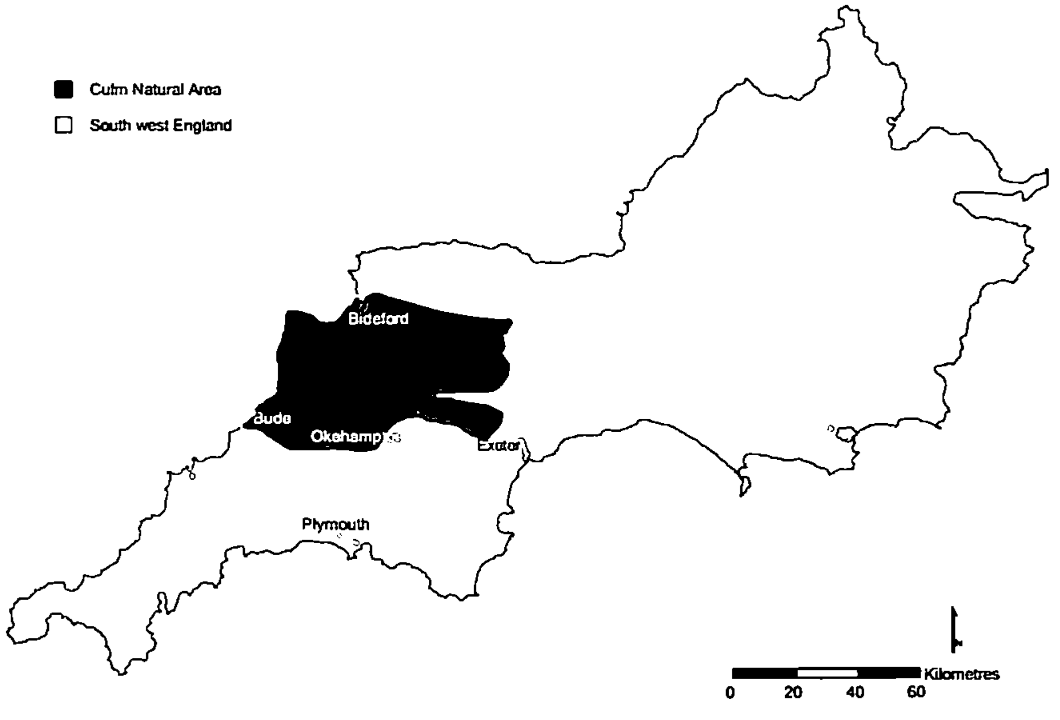


Figure 1.1 Location of the Culm Natural Area

It is one of the main vegetation habitats in the Culm Natural Area (CNA) (Hughes and Tonkin, 1997), which is one of the 76 terrestrial Natural Areas, defined by English Nature (Figure 1.1). The CNA follows largely the boundaries of the Culm Measures geological formation, which is characterised by folded shales and sandstone (section 3.4). The main soil associations in the area are the poorly draining Halstow and Hallsworth 1 and 2 associations and the well draining Neath, Denbigh 1 and Manod associations, which are described in section 3.5. The semi-natural habitat is found in the area due to poorly draining soils and benefits from a number of traditional agricultural management practices. However, pasture improvements in the past and present-day neglect have caused large areas to disappear. Further background information to the study and its research context will be given in the next section. Section 1.3 discusses the importance of the project, gives an overview of the aims and objectives and concludes with an outline of the rest of the thesis.

1.2 Research context

Worldwide, many natural or semi-natural habitats are under threat, due to urbanisation, pollution, increased use of land for industry, increasing intensification of agriculture over the second half of the twentieth century. On the other hand, the recent crisis in agriculture in Europe has caused semi-natural habitats to disappear, due to neglect of marginal farmland. Increasing awareness of the rapid decline of important habitats in the last few decades has changed the attitude of society towards natural habitats, although considerable damage has already been done. In 1992, at the UN Conference on Environment and Development in Rio de Janeiro, the Convention of Biological Diversity was presented and since then has been signed by over 160 countries (Swanson, 1997). Part of the agreement involved the development of national strategies for the conservation of biological diversity and the sustainable use of biological resources, which was written up in Article 6 of the Convention (HMSO, 1994). The UK government responded to this by drawing up a national Biodiversity Action Plan (BAP), which gave a general overview of the important (semi-) natural habitats and the endangered species of the UK (HMSO, 1994). Objectives and targets for purple moor grass and rush pasture, both part of the Culm grassland plant communities, were covered. In south west England, a regional BAP was prepared to make the implementation of the national plan easier (South-West Biodiversity Partnership, 1997). The plan does not cover Culm grasslands as such, but does refer to species occurring on the sites, like the marsh fritillary butterfly and the southern damselfly.

In the Devon and Cornwall BAPs, the importance and objectives for the habitat studied in this thesis were presented. The following objectives were listed in the Devon BAP (Devon Biodiversity Partnership, 1998):

1. To ensure there is no further loss of Rhôs pasture within its three major zones: The Culm Measures, Dartmoor or Blackdowns
2. To ensure all remaining Rhôs pasture sites greater than 0.5 ha in size are secured under sustainable management regimes, which perpetuate the species they support
3. To expand the area of Rhôs pasture habitat by appropriate means, in order to buffer, link and expand existing sites
4. To establish positive links between the sustainable management of Rhôs pasture and the economic diversification of the areas in which it occurs, and to foster greater public awareness and enjoyment of this habitat and its wildlife.

Similarly, the Cornwall BAP (Cornwall Biodiversity Initiative, 1998) listed the following objectives specifically aimed at Culm grassland:

1. Completion of a Cornwall Inventory of Culm grassland
2. Maintenance of the existing resource of Culm grassland habitat, particularly sites > 0.5 ha
3. Ensuring positive management of all Culm grassland sites
4. Identification of suitable sites and promotion of their re-creation
    - Possible sites for re-creation were to be identified and included as part of the Culm sites inventory, where they must be clearly distinguished from the existing sites.
    - Experimental / demonstration sites were to be set up

In this study, the possibilities for expansion of the total Culm grassland area and the relationships between the plant communities and the environmental and management conditions were investigated.

The use of land for agriculture has not always caused a detrimental loss for nature in England. Ingrouille (1995) stated that the landscape was at its most diverse during the 18th and 19th century. Remnants of older landscapes and vegetation survived, because in those times agricultural improvements did not yet occur on a large scale. The resulting pattern was a mosaic of woodland, heathland, wetland, moorland, meadows and agricultural fields. Also the agricultural landscape had a much higher floral and faunal diversity than at present. Land used for agriculture in the south west England mainly consisted of permanent grassland used for cattle and sheep grazing. On less fertile, acidic soils, large heathland areas were maintained by grazing and burning (Nature

Conservancy Council, 1984). Over the last sixty years, however, agriculture has changed radically. Farm modernisation and agricultural improvement have taken place on a large scale to increase food production, decrease labour intensity and increase living standards (Baldock, 1990). Due to intensification of farming, the production of the land has increased and large areas with low production levels went out of production caused by unequal competition (Baldock, 1990). In Europe, the percentage of land occupied by agriculture in 1987 varied from 43% to 81% (Baldock, 1990), with the UK as the second highest with 75.8% (EC commission, 1988 in Baldock, 1990). As a result the species-rich, unimproved grasslands of North Devon, of which the Culm grasslands are part, have been improved by drainage, reseeding and the use of herbicides.

Conventional agriculture and nature often have conflicting requirements. Natural vegetation thrives best under unimproved circumstances, but for agriculture, changes are often necessary to increase yield. Semi-natural vegetation often needs a certain level of management e.g. low-intensity grazing or occasional burning. However, the change from extensive and mixed farming to more specialised and intensive farming, with large amounts of chemical input, has created more uniform habitats with little value for wildlife (Baldock, 1990). These large habitat losses in Europe have caused a decline in wildlife species. On the other hand, if land is not managed at all and sites are neglected, shrub invasion could take place, which would also cause a serious threat to the existence of semi-natural habitats (Ingrouille, 1995). The recent farming crisis, caused partially by livestock diseases like BSE and Foot and Mouth disease, has forced many farmers out of business. Therefore, grazing pastures have been abandoned and semi-natural plant communities are being threatened. For other farmers the same crisis has caused them to look for other sources of income, such as agri-environmental schemes and thus take advantage of conservation payments to ensure some income (Morris and Potter, 1995). Management agreements that apply to Culm grassland farmers are the Countryside Stewardship (MAFF, 1998) and the Wildlife Enhancement Schemes (English Nature, 1991), which are especially set up for sites classified as Sites of Special Scientific Interest (SSSI). Both schemes were designed to financially support wildlife-friendly management. Since the last major reform of the CAP (Common Agricultural Policy) in 2000, the European Union permits 20% of the subsidies paid out under this policy to be transferred to environmental and rural development schemes. In 2001, the UK government used 2,5% for this purpose and aims to increase the amount to 4,5 % in 2006. A recently published report of the Policy commission on the future of farming and food, advised a further increase of this percentage (DEFRA, 2002).

Marshes, fens and wet grasslands are among the most threatened semi-natural habitat types. The main causes of habitat loss are agricultural improvement, drainage and reclamation. These wetlands were not only threatened by the activities on the site itself, but also by the management of the surrounding land. Drainage of nearby land can cause the groundwater table to lower and the use of large amounts of fertiliser could cause eutrophication of the water flowing into these wetlands, causing the nutrient levels to rise and the vegetation to change in response. No overall figures for the decrease in area of these wetlands are available for the whole of Europe, but numbers of 10,000 ha per year in France and 1,000 to 1,200 ha of drainage of wetlands in Belgium are mentioned in Baldock (1990). Baldock (1984) reported an annual loss of 4,000 to 8,000 ha of damp grassland and marsh per year in England and Wales. Culm grassland is one such species-rich, wet grassland and wet heath habitat found in south west England. The major threats to Culm grassland existence are agricultural improvement of land, afforestation, abandonment and neglect, inappropriate management, fragmentation and isolation of sites, pond creation and mineral workings (Devon Biodiversity Partnership, 1998).

From historical maps, only about 8% of the original area of Culm Grassland present around 1900 was estimated to remain in 1992 (Devon Wildlife Trust, 1992 in Wolton, 1992). Between 1984 and 1989, 48% of the total area of Culm grassland was lost, of which 87% was due to agricultural improvement (Devon Wildlife Trust, 1992 in Wolton, 1992). Currently, another major threat is neglect of the site (Hughes and Tonkin, 1997). The Biodiversity Plans of both Cornwall and Devon include the conservation of Culm grassland as one of their major tasks. Both plans state that the aim is to maintain the area of remaining Culm Grassland and increase the area by recreation and restoration. The main possibilities for nature conservation organisations to reach the objectives are through management schemes, like the Countryside Stewardship scheme, which compensates farmers for their adapted management practices. A number of sites have a SSSI status, on which through WES (Wildlife Enhancement Scheme) agreements the management can be beneficial for Culm grassland. Other sites are nature reserves, owned and protected by nature conservation organisations.

1.3 Research outline

1.3.1 Project description and importance

The protection and conservation of (semi-) natural habitats is of great importance (Warren and Goldsmith, 1974). Scientific research can help to provide a better understanding of the functioning of the system and to 'direct' the management strategy. In this study, relationships between vegetation, soil, hydrology and topography of the wet, species-rich grasslands in the Culm Natural Area are investigated to obtain insight into selecting suitable locations for restoration of this plant community. The knowledge of ecosystem functioning is crucial to habitat management and restoration and recreation of suitable vegetation habitats (O'Connor, 1974). Ratcliffe (1977a) described a grading system to assess the ecological importance of sites. A number of criteria were used: size, diversity, naturalness, rarity, fragility, typicalness, recorded history, position in an ecological/geographical unit, potential value and intrinsic appeal. Sites were graded from 1-4, with grade 1 and 2 sites of (inter)national importance, which were presented as key sites, and grade 3 and 4 SSSI sites of regional importance. No key sites were listed in the Culm Natural area (Figure 1.1) and some SSSI sites of grade 3 or 4 existed in the region (Ratcliffe, 1977b). From this statement it could be concluded that (semi-) natural sites present in the area might have a limited conservation value. Another reason for the relatively small interest in the conservation of Culm grassland could be that the sites are not as 'attractive' as other habitats such as chalk grassland. Further, Culm grassland sites are less diverse than, for example, chalk grasslands, which have a natural species richness (Ratcliffe, 1977a). On the other hand, Ratcliffe (1977a) also mentioned the enormous importance of the presence of a network of (semi-) natural and artificial ecosystems to link other 'superior' habitats.

Also, many other reasons exist for the conservation and restoration of Culm grassland:

1. Culm grassland is a rare habitat both nationally and regionally (Devon Biodiversity Partnership, 1998). However, nature conservation agencies have only fairly recently recognised this as a valuable habitat and it has not been mentioned by Ratcliffe (1977a and b).
2. A number of threatened species of regional, but also of national importance are found here. Preserving the habitat is crucial to their survival in the area (Hughes and Tonkin, 1997).
3. The wet grasslands continue to be productive in times of drought. These wetter sections of the farmland can provide fresh grass and water to the cattle, if other areas are dried out (A. Cox, pers. comm.).
4. The sites could provide storage of excess water, forming a natural barrier against floods. The storage of water in these fields slows down the discharge of water to the river. The streams respond therefore slower to an event of heavy rain, spreading the peak over a longer period of time (S. Thurley, pers. comm.).

5. The wetlands could function as nutrient and sediment traps. When water is drained quickly from arable land and improved pasture, large amounts of sediment and attached nutrients enter the stream. The wet grasslands form a buffer zone retaining the coarser part of the sediment and keeping the rivers clear. This mechanism is of major importance to river quality and its ecological functioning (Blackwell *et al.*, 1999; S. Thurley, pers. comm.).

The major organisations in the area concerned with the conservation and restoration of Culm grasslands are the Environment Agency, English Nature and the Devon and Cornish Wildlife Trusts. Their major objectives were the ones listed in the discussion on the Biodiversity Action Plans in the previous section. English Nature has published some management guidelines, which mainly consisted of summer cattle grazing and occasional burning (Wolton, 1992). Further management details follow in Chapter 2.

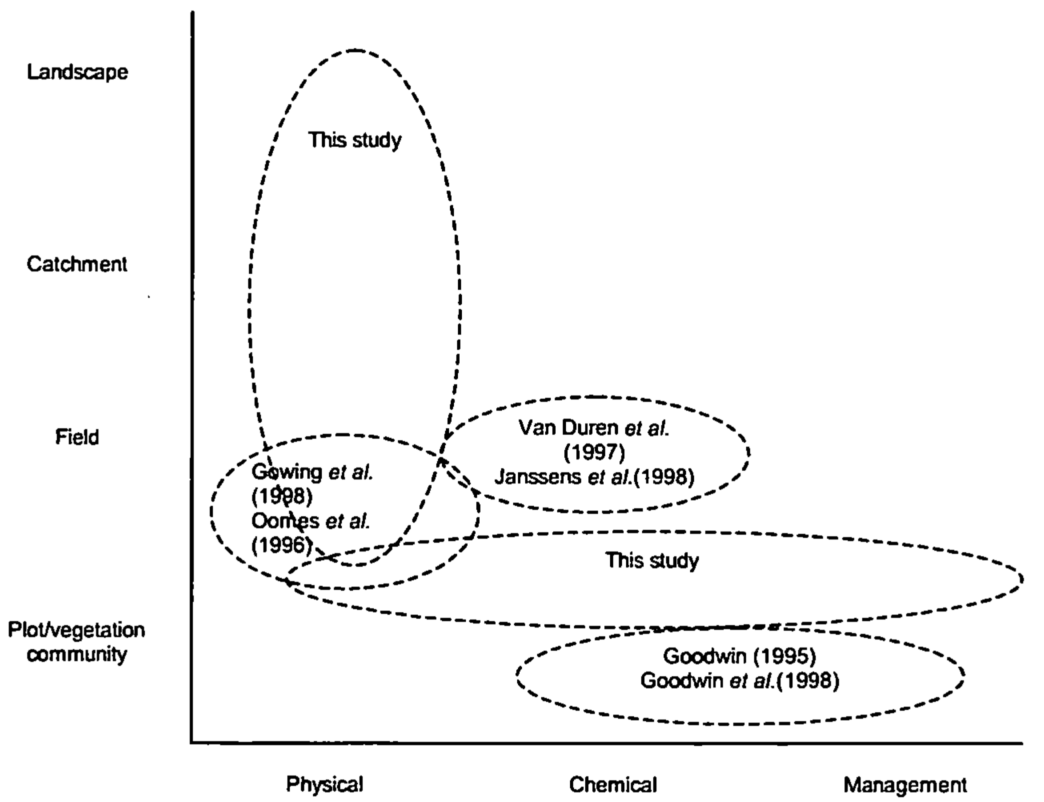


Figure 1.2 Diagram showing the different scales and subjects of wetland investigation

Little research so far has focused on the Culm grassland communities of southwest England, with the exception of work by, for example, Goodwin (1995), Goodwin *et al.* (1998) and Tallowin and Smith (*in press*). However, research on various aspects such as wetness and nutrient requirements of comparable wet grasslands elsewhere provided insight into the most important processes and relationships. Chapter 2 presents a review of the published literature.

In many research papers, such as Van Duren *et al.* (1997), Goodwin *et al.* (1998) and Janssens *et al.* (1998), relationships between nutrient levels and vegetation have been studied. Much less is known, however, about the response of the vegetation to hydrological changes. Further, most hydrological studies in relation to vegetation, such as Gowing *et al.* (1998) and Oomes *et al.* (1996) have focussed on processes operating at the plot or field scale. In this research project, relationships between hydrology, soil characteristics and vegetation are investigated at the regional and catchment scale. Figure 1.2 provides an overview of the focus on the studies mentioned above and indicates how these relate to the study presented in this thesis. The general characteristic of this research is that it was conducted at a regional scale, with a large number of sites to make sure the results would be representative for the area, whereas the other studies have focused on detailed process information for a specific site or plant community.

The Culm grassland habitat consists of a diverse set of plant communities (Wolton, 1992). Various techniques of vegetation analyses can be used to divide the grassland community into sub-community types based on floristic composition. The differences between the communities depend on a number of environmental and biotic factors, such as nutrient availability, water availability and land management, but also nearby presence of species and species interaction. The relationship between the species composition and environmental factors is the key to understanding the functioning of the system and to the prediction of what vegetation developments can be expected when alteration of the system or of the land use takes place. The use of Geographical Information Systems (GIS) provides a useful tool for landscape studies and was therefore one of the major instruments in this study. The spatial organisation of data and the possibilities for querying the information and the derivation of relationships between the various factors facilitates the analysis of the data. It also provides a number of possibilities for hydrological modelling. Understanding the hydrological functioning of a catchment is an important component of vegetation research, especially when studying wetlands (Wheeler, 1999). Therefore, in this thesis, topographical and hydrological properties were taken as a base for researching the ecology of Culm grassland.

1.3.2 Research aim and objectives

This study aims to derive a better understanding of the position of Culm Grassland within the landscape, based on the physical characteristics of the landscape (e.g. slope, soil type, hydrology) and to describe the plant communities in relation to their environmental characteristics. The different scales at which the work is conducted are important (Figure 1.2). General characteristics and conditions for the Culm grassland habitat as a whole were studied at a regional scale. The variations in species composition within the habitat, however, are related to more local variations in the environment and therefore need to be studied on a more detailed scale. Further, a methodology was developed for the designation of potential restoration sites for Culm grassland based on landscape features and an estimation was made of the vegetation trends that could be expected under given environmental characteristics and management practices. Although this project focused on this specific type of vegetation, the methodology should in principle also be suitable for other habitats, in which occurrences might be controlled by other landscape features. To address the aim of the study the following objectives were formulated:

1. **To describe the topographical characteristics of Culm Grassland at a regional scale for the whole Culm Natural Area**

   The relationships between the location of the remaining Culm grassland sites, topographic features (slope and position) and soil type were studied at a landscape scale. A GIS was set up to combine all the available information and derive the relationships between the variables.

2. **To investigate the occurrence of Culm Grassland in relation to catchment hydrology and soil water regime at a catchment scale.**

   The location of Culm grassland was expected to depend largely on hydrological properties. The length of the wet season, the soil moisture regime and water table depth could be of major importance. A catchment study was carried out which used hydrological modelling based on topographic features to describe the hydrodynamics. Results were verified with field measurements. The outcome was then related to the location of Culm sites and provided an indication of sites with a similar hydrological pattern. In this thesis the terms soil water and soil moisture are used interchangeably.

3. **To describe the Culm grassland plant communities and to determine the major environmental gradients that control their nature at a field or quadrat scale.**

   Information on the species composition of the various sites was used to group vegetation samples into plant communities and a detailed field study was carried out to describe the vegetation and obtain information on the soil properties of the groups. From these analyses, a general overview is provided of the factors important to Culm grassland. Further insight is obtained on the use of the available data and the scale on which the information should be gathered.

4. **To integrate these findings into a decision support system (DSS), to aid in the identification of potential restoration sites at a regional or catchment scale.**
An important part of the study was the establishment of a system to indicate potential Culm grassland restoration and re-creation sites. The major base for this decision support system was the hydrological functioning of the catchment, although some of the research deals with soil properties. The result gives an indication of potential sites to be transformed into Culm grassland and thus provides guidelines as to where restoration practices should be concentrated. A key component of the final stage will be the utilisation of verification procedures for independent corroboration of the site locations identified. Special attention was given to the problems occurring due to the different scales at which the work was carried out.

1.3.3 Thesis outline

This thesis is divided into four parts, each focusing on a different aspect of the study. Figure 1.3 gives an overview of the outline. The first part gives a general introduction into the subject and provides background information on research already conducted in this field and on the study area. In this first chapter the wider context of the research is set and the aim and objectives of the study are defined. Chapter 2 presents a literature review on species-rich wet grasslands, covering their main plant communities, location, physical and chemical environmental conditions, management and the restoration and rehabilitation strategies. The study area is introduced in Chapter 3 to provide the environmental context in which the work was conducted. The second part of the thesis will present the research on topographical and hydrological characteristics of Culm grassland sites conducted at a regional and catchment scale. Chapter 4 introduces the GIS and modelling techniques that were used for this part of the study. In Chapter 5, the results of the GIS study, investigating the relationship between Culm grassland location and landscape topography and soils, are presented and discussed. The hydrological modelling techniques are discussed in Chapter 6. The wetness of the catchment was determined using topography-based models and a soil classification system based on soil hydrology. The third part of the thesis is concerned with a description of Culm grassland plant communities and their relationships to environmental and management characteristics. Chapter 7 presents the field and laboratory techniques that were used for this part of the study. The results will be presented and discussed in Chapter 8. The last part of the thesis concludes the research, by integrating the results of Part 2 and 3 into a management tool that aims to help in the planning of the restoration and expansion of Culm grassland vegetation in the region. The final chapter, Chapter 10, gives some conclusions and recommendations for future work.

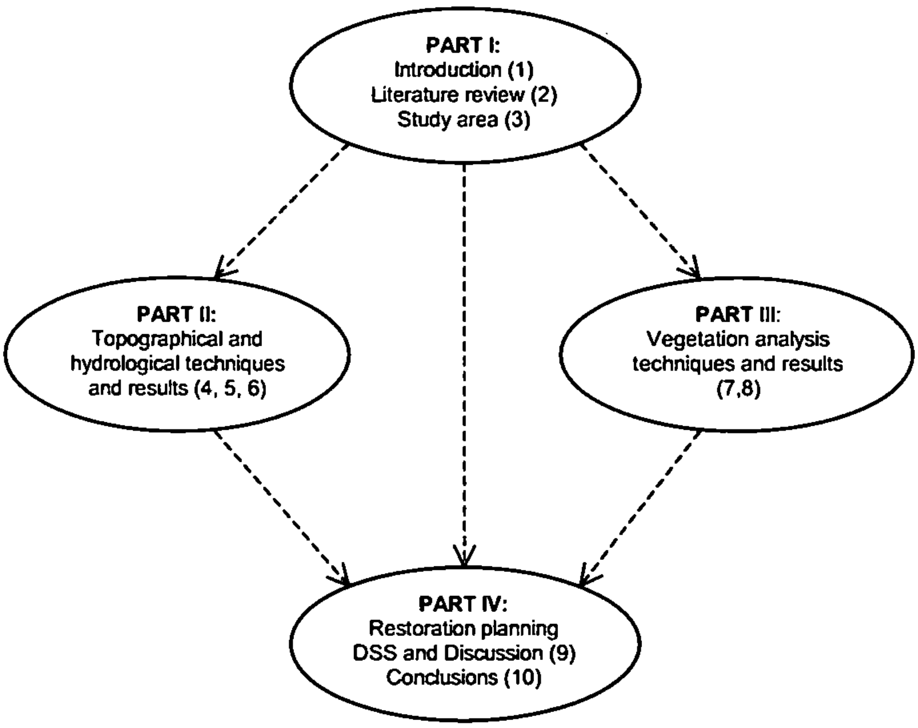


Figure 1.3 Overview of the thesis structure. Chapter numbers between brackets.

Chapter 2

Culm grasslands: a literature review on vegetation, environmental characteristics, management and restoration

2.1 Introduction

After discussing the wider context of the research in the previous chapter, this chapter reviews the literature published on the distribution of wet species-rich grasslands in Europe, focusing on Britain and in particular south west England. More specifically, it describes the plant communities in the Culm Natural Area in relation to other comparable communities in Europe. The chapter also describes research investigating the environmental characteristics associated with the wet, species-rich grasslands, the way they are managed and the previous research on restoration of these habitats. It aims at providing a broad overview of the research issues important to Culm grassland location and species composition. Section 2.2 introduces the plant communities, defines Culm grassland and gives a description of the communities in the phytosociological classification. Section 2.3 relates this vegetation type to similar communities in the Atlantic zone in Europe. Section 2.4 examines factors controlling the location of Culm grassland, such as hydrology, chemical factors and management. Restoration strategies are also reviewed.

2.2 Vegetation

2.2.1 Culm Grassland in south west England

The wet, unimproved, species-rich grasslands studied in this thesis are an association of wet heaths, soft rush meadows and acid purple-moor grassland (Goodwin, 1995). They are located on the Culm measures geological formation in south west England and are locally referred to as Culm grassland. Nationally they are known as Rhôs pasture, after the Welsh word for 'a wet, often heathy grazing pasture'. The vegetation can be described as a mosaic of the following five National Vegetation Classification (NVC) communities: M16b, M23a, M24c, M25c and M27c (Devon Biodiversity Records Centre, 1998; Wolton, 1992) as described by Rodwell *et al.* (1991). The communities are *Erica tetralix - Sphagnum compactum* wet heath (M16), *Juncus effusus/acutiflorus - Galium palustre* rush pasture (M23), *Molinia caerula - Cirsium dissectum* fen-meadow (M24), *Molinia caerulea - Potentilla erecta* mire (M25) and *Filipendula ulmaria - Angelica sylvestris* mire

(M27). Characteristic species are *Erica tetralix* (cross-leaved heath), *Calluna vulgaris* (heather), *Molinia caerulea* (purple moor grass), *Juncus effusus* (soft rush) and *Juncus acutiflorus* (sharp-flowered rush), *Holcus lanatus* (Yorkshire fog), *Galium palustre* (marsh bedstraw), *Carex panicea* (carnation sedge), *Cirsium dissectum* (meadow thistle), *Anthoxanthum odoratum* (sweet-vernal grass), *Luzula multiflora* (heath wood-rush), *Filipendula ulmaria* (meadow sweet), *Angelica sylvestris* (angelica), *Epilobium hirsutum* (great willowherb), *Lychnis flos-cuculi* (ragged robin) and others (Rodwell *et al.*, 1991).

The occurrence of these plant communities in mid-Devon is due to a combination of the mild, damp climate and low permeability soils (Wolton, 1992). The communities occur mainly on acid to neutral soils or peats, with water regimes that vary between moist to seasonally waterlogged (Table 2.1) (Rodwell *et al.*, 1991). Small differences in environmental and biotic factors determine the locations where the different plant communities can be found.

NVC community	Description	Conditions
M16	*Ericetum tetralicis* wet heath	Periodically waterlogged shallow peat & humic mineral soils
M23	*Juncus-Galium* rush pasture	Moist, acid to neutral gley soils, often humic at the top
M24	*Cirsio-Molinietum* fen-meadow	Moist to dry, neutral peat soils and peaty mineral soils
M25	*Molinia-Potentilla* mire	Moist, but well aerated peat soils & and peaty mineral soils
M27	*Filipendula- Angelica* mire	Moist, reasonably rich, neutral soils

Table 2.1 Culm grassland NVC communities and their environment as described by Rodwell et al. (1991)

Following the continental phytosociological vegetation classification (Braun-Blanquet and the Zurich-Montpellier School), as described by Rieley and Page (1990) wet grasslands are classified in the *Molinio – Arrhenatheretea* class in the *Molinietalia* order. Three alliances can be distinguished:

- *Calthion palustris*, on soils with high organic matter content and a water table at or just below surface level for most of the year. Characteristic species include *Caltha palustris, Lotus uliginosus, Carex disticha, Scirpus sylvaticus, Lychnis flos-cuculi, Crepis paludosa.*
- *Filipendulion*, on humus-rich, damp soils high in nitrogen, mostly along streams, rivers and drainage channels, subject to periodic flooding. Characteristic species are *Hypericum tetrapterum, Lythum salicaria, Stachys palustris, Eupatorium cannabinum, Epilobium hirsutum, Calamagrostis canescens* and *Phalaris arundinacea.*

- *Junco – Molinion*, on more acid soils in the transition between wet peat-forming associations and terrestrial associations. Characteristic species are *Succisa pratensis, Parnassia palustris, Danthonia decumbens* and *Molinia caerulea.*

Wet heaths are described as belonging to the *Ericetalia tetralicis* order in the *Oxycocco-Sphagnetea* class (Rieley and Page, 1990). The alliance Ericion tetralicis has *Erica tetralix, Trichophorum cespitosum, Juncus squarrosus, Sphagnum compactum, Sphagnum tenellum, Gymnocolea and Zygogonium ericitorium* as characteristic species.

Figure 2.1 shows the zonation and succession of five Culm NVC communities. This figure has been compiled from information given for every community by Rodwell *et al.* (1991; 1992a; 1992b), in an attempt to schematise the complex relationships between the plant communities. The typical Culm grassland communities are indicated in grey and environmental gradients with associated plant communities are indicated by arrows with plus and minus signs to indicate an increase or decrease of the environmental factor. Generally, when soil water content increases the vegetation develops into more swamp-like communities or wet heaths. Decreasing soil water or increasing nutrients results in communities dominated by grasses. If the vegetation is not grazed or mown, shrubs and trees invade and communities change towards woodlands. However, the boundaries between the plant communities are gradual and the development of a specific plant community depends on the combined effect of various environmental parameters and the presence of characteristic species nearby.

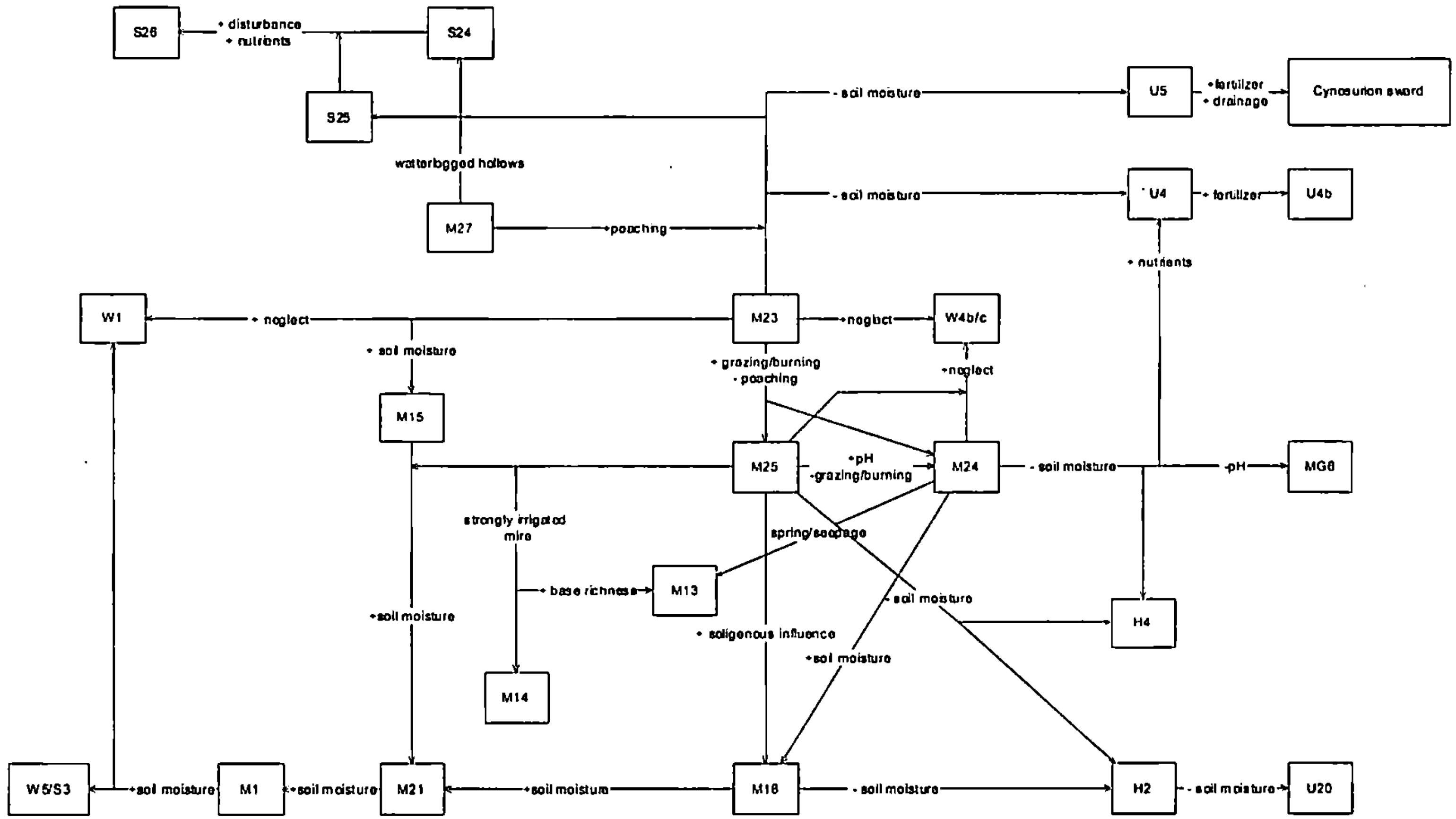


Figure 2.1 Overview of the Culm grassland communities (grey) related to other NVC communities (Rodwell, 1991;1992a, 1992b). – decrease, + increase

H2 = Calluna vulgaris - Ulex minor heath, *H4 = Ulex galli –Agrostis curtisii* heath, *M1 = Sphagnum auriculatum* pool, *M13 = Schoenus subnodulosus* mire, *M14 = Schoenus – Narthecium* mire, *M15 = Scirpus – Erica* wet heath, ***M16 = Erica tetralix – Sphagnum compactum* wet heath**, *M21 = Narhecio – Sphagnetum* bog, ***M23 = Juncus effusus/acutiflorus – Galium palustre* rush-pasture**, ***M24 = Molinia caerulea – Cirsium dissectum* fen-meadow**, ***M25 = Molinia caerulea – Potentilla erecta* mire**, ***M27 = Filipendula ulmaria – Angelica sylvestris* mire**, *MG6 = Lolium perenne – Cynosurus cristatus grassland, S3 = Carex paniculata swamp, S24 = Phragmites australis – Peucedanum palustre tall-herb fen, S25 = Phragmites australis – Eupatorium cannabinum tall-herb fen, S26 = Phragmites australis – Urtica dioica tall-herb fen, U4 = Festuca ovina – Agrostis capillaris Galium saxatile grassland, U20 = Pteridium aquilinum – Galium saxatile community, W1 = Salix cinerea – Galium palustre* woodland, *W4b/c = Betula pubescens – Molinia caerulea* woodland, *W5 = Alnus glutinosa – Carex paniculata* woodland

2.2.2 Wet, species-rich grasslands and wet heaths in the European Atlantic zone

As described in section 2.2.1, Culm grassland is principally defined by five distinct NVC communities (Wolton, 1992; DBRC, 1998). In other parts of Europe, where the same or associated communities are found, they are mostly referred to under different names (e.g. phytosociological or local names). The most likely places to find similar wet grassland and heath communities are at locations with comparable hydrological and chemical conditions, with similar forms of extensive management.

A damp climate is an important factor in the occurrence of the wet grasslands in Britain and rest of the Atlantic zone. Heathland is mainly found in temperate, oceanic climatic conditions and thus, in Europe, large areas of lowland heath occur in the Atlantic zone (Gimingham and De Smidt, 1983). The Atlantic zone stretches from north west Portugal and Spain along the western side of France, the whole of Britain, Belgium and the Netherlands through Denmark into south west Norway (Figure 2.2). The Atlantic zone corresponds largely with the Köppen classification of mild temperate rainy climates, with no distinct dry season (Cf) (Trewartha and Horn, 1980).

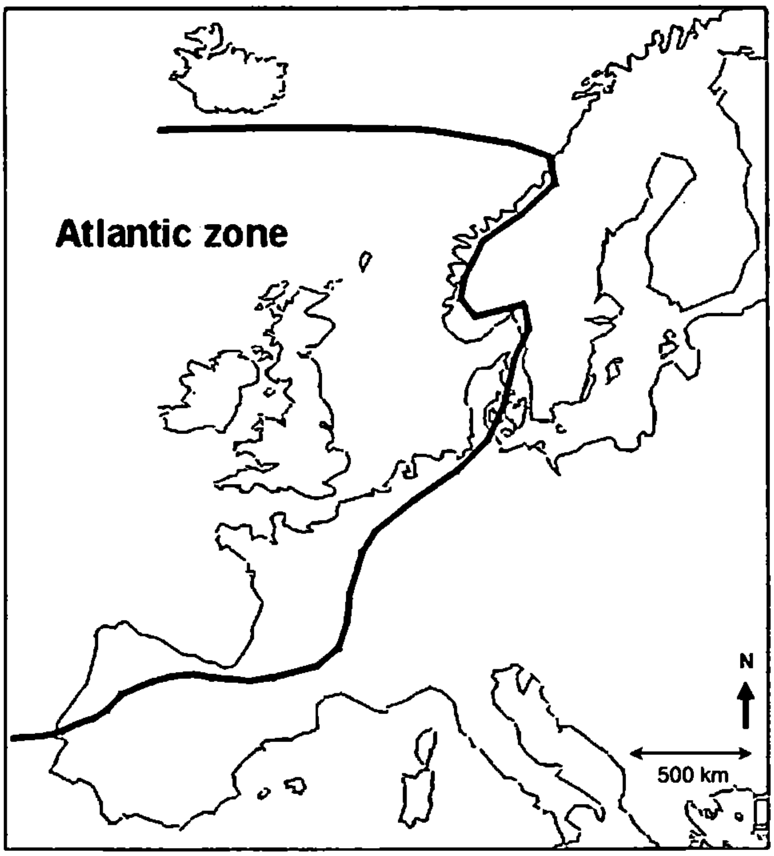


Figure 2.2 Map of the Atlantic zone (after Polunin and Walters, 1985)

Polunin and Walters (1985) stated that the moist climate of the Atlantic, with comparatively mild winters, results in a rich growth of vegetation, which can be used for feeding livestock throughout the year. In the northern areas of the Atlantic zone, grasslands are found on the range from sea level to montane areas, while in southern parts they are mostly restricted to montane regions.

Vegetation similar to Culm grassland is known to be found in southern Wales (Dyfed, Powys and Glamorgan) and south west Scotland (Dumfries and Galloway) (Wolton, 1992). However, no information on the exact location of these sites was available. In Wales large areas of *Molinia* and *Juncus* pastures exist. These include the NVC communities M22, M23, M24, M25 and M26, respectively: *Juncus subnodulosus – Cirsium palustre* fen-meadow, *Juncus effusus/acutiflorus – Galium palustre* pasture, *Molinia caerulea – Cirsium dissectum* fen-meadow, *Molinia caerulea – Potentilla erecta* pasture and *Molinia caerulea - Crepis paludosa* pasture. About 31,000 ha of lowland wet pasture and about 49,000 ha of similar vegetation in the uplands were mapped in Wales (Blackstock *et al.*, 1997). Outside Britain, similar plant communities are known to be found in Brittany, France and are expected to exist in western Ireland, north west Spain and northern Portugal (Wolton, 1992; E. Williams, pers. comm.), although information from literature is scarce. In the Netherlands, large areas of groundwater-fed fen-meadows are found. However, many are now degraded sites due to fertilising and drainage. Several studies have been conducted on these systems, e.g. Oomes *et al.* (1996) studied a former *Junco - Molinion* grassland and Berendse *et al.* (1992) described a study on the restoration of wet species-rich grasslands, with characteristic species like *Ajuga reptans, Lychnis flos cuculi, Cardamine pratensis*, *Ranunculus repens* and *Thalictrum flavum*. These species can also be found in Culm grasslands. However, it is not clear whether the plant communities would be classified as one of the five Culm grassland NVC-communities, as defined in section 2.2.1.

2.2.3 Distribution and fragmentation

The Culm grassland sites are found in a highly fragmented pattern, which has important implications for conservation and restoration of the habitat. Two theories need to be considered here: the island biogeography theory of MacArthur and Wilson (1967) and the metapopulation theory described by Hanski (1999). The island biogeography theory is based on the equilibrium between species immigration and extinction on oceanic islands. The immigration rate depends on the distance to other islands and the extinction rate depends on the size of the island (Kent, 1989; Begon *et al.*, 1990). The same theory has been applied in nature conservation to study fragmented plant communities. The theory predicts that the larger the size of a patch or fragment, the higher the number of species (Begon *et al.*, 1990; Whittaker, 1998, Lomolino, 2000; 2001). Many researchers have studied this theory for different plant communities (e.g. Benayas *et al.*, 1999; Haig *et al.*, 2000). However, due to complicated ecological mechanisms and response of species to climatic conditions and human impact that intervene with the theory, little evidence has been found that the island biogeography theory was valid. The metapopulation theory became increasingly important in the late 1980s. Although based on similar principles to the island biogeography theory, and dealing similarly with spatially patchy and fragmented semi-natural vegetation, these models focus on individual species responses and population ecology instead of communities (Hanski, 1999). Unlike in the island biogeography theory, no permanent mainland community, which prevents global extinction is assumed and therefore it is more relevant to endangered species in a fragmented landscape (Hanski, 1999). The importance of this theory is the regional view it promotes. Restoration of habitats and re-introduction of species should be considered not just on a local scale, but should take the presence of species in neighbouring fragments and the distance between these fragments into account. Hence, the importance of regional planning of restoration activities encouraged by methods such as the one presented in this thesis is underlined. However, the presented research was limited to plant communities and no species interactions and population dynamics of species at higher trophic levels were studied.

2.3 Previous research on the wet, species-rich grassland environment and management and restoration strategies

2.3.1 Introduction

Wet terrestrial ecosystems can be divided into three broad categories: permanent wetland, which includes Culm grassland, seasonal wetlands, where seasonal changes in the water table drive changes in vegetation, and fluctuating wetlands, where long-term changes in the water table control the species composition (Wheeler, 1999). These water dynamics are controlled by a number of factors, involving topography, geology, soil type, climate and management. The water regime and soil characteristics are of major importance to nutrient availability to the vegetation and together with species dynamics these abiotic factors together determine largely where a species can establish itself. For example, a multidisciplinary research programme of the European Community: FAEWE - Functional Analysis of European Wetland Ecosystems, showed that wetland community

diversity is mainly controlled by hydrodynamics and topography, whereas the degree of species richness, i.e. the number of species within the community, is mainly determined by nitrogen and phosphorus availability and above-ground plant biomass (Clément and Maltby, 1996). A survey, which examined vegetation-environment relationships within East-Anglian fens reported that base-richness, soil-fertility and water-level were the most important factors determining species composition (Wheeler and Shaw, 1995).
The most important abiotic parameters and related processes are discussed in the following sections. It describes the physical (section 2.3.2) and chemical environment (section 2.3.3) of Culm grassland and related communities and deals with the management practices needed to maintain the vegetation (section 2.3.4) together with restoration strategies to re-establish lost communities (section 2.3.5).

2.3.2 Relationships between the occurrence of wet grasslands and the physical environment

The hydrodynamic functioning of an area is one of the most important factors determining the location of wetland vegetation and often influences other crucial factors such as pH and nutrient availability. Several studies have looked at the relationships between species composition and hydrology at plot or field level. A recent study conducted by Gowing *et al.* (1998) used ditch-drained wetlands on the Somerset levels to study the effects of manipulating the water table on species composition. A strong correlation between plant distribution patterns and water regimes was found. Species like *Polygonum amphibium, Eleocharis palustris, Carex disticha, Carex nigra, Filipendula ulmaria* and *Juncus effusus* were found to be less tolerant to drought stress than *Centaurea nigra, Dactylis glomerata* and *Stellaria graminea*.

The effects of raising the water table on vegetation change were examined by Oomes *et al.* (1996). They reported a more rapid establishment of species indicative of wet conditions and the same species became dominant independent of the vegetation management. A decrease in species diversity of the 'wet' plots compared to the 'dry' plots after raising the water table was reported by Mountford *et al.* (1997). Significant effects of raising the water table were also observed for individual species, e.g. an significant increase in *Agrostis stolonifera* and *Caltha palustris* and an increase of *Carex nigra*, *Carex riparia*, *Glyceria fluitans*, *Ranunculus flammula*, *Ranunculus repens* and *Scenecio aquaticus*. A decrease in *Cynosurus cristatus*, *Festuca rubra*, *Holcus lanatus* and *Luzula campestris* was found. Declines were also reported for *Cirsium dissectum, Filipendula ulmaria* and *Plantago lanceolata*.

Other research has focused at a smaller scale on wetland functioning and the relationships between hydrological factors and species composition. For example, in the Netherlands, many studies focused on the relationship between wetlands and groundwater flow systems. Drainage of the land has changed water regime of large areas of land. Longer dry periods in the year and lower water tables have threatened the existence of many wetlands. Other important aspects were changes in the water flow system and therefore the change of the source of the water. Kloosterman *et al.* (1995) showed that the change in groundwater flow due to pumping of groundwater for drinking water supply and for agriculture has replaced the deep unpolluted calcium carbonate rich groundwater flow with shallower polluted water flows. This caused the characteristic brook-valley vegetation to change towards species-poor plant communities. Wassen *et al.* (1996) compared the relationship between vegetation composition and hydrological flow patterns between natural and artificial hydrological regimes of river plains. They found a similar relationship to Kloosterman *et al.* (1995): low-productive fens were mainly fed by calcium- and base-rich, nutrient-poor groundwater. In the 'natural' valleys, large areas of these fen systems existed in groundwater discharge areas, whereas in the artificial system, this type of fen is confined to small areas fed by calcareous groundwater. The artificial drainage of the valleys caused the hydrology to change drastically and therefore the vegetation also altered. Swetnam *et al.* (1998) used a GIS system to link a hydrological model (DITCH) to a database with plant requirements and a map with plant communities. Based on the hydrological situations and the hydrological requirements for certain plants the changes in vegetation and communities were predicted.

Relating the occurrence of individual species in plant communities to environmental parameters is a difficult and time-consuming task. Ellenberg (1988) defined 'F-values', which indicate the hydrological preferences and tolerances of individual species, for a large number of species in Central Europe. Although these values do not give an absolute value for the soil water requirements, a qualitative indication is provided, which makes it possible to compare the demands between the species. From a study on the water regime requirements of British wetland vegetation in which the moisture classification of Ellenberg was used, it appeared that Ellenberg's F–values were valid for a range of British species and situations (Mountford and Chapman, 1993). Their study, however, was conducted for *Alopecurus pratensis – Sanguisorba officinalis* flood meadow (NVC: MG4), *Centaurea nigra – Cynosurus cristatus* meadow (MG5) and *Cynosurus cristatus – Caltha palustris* flood pasture (MG8), which are all wet grasslands but have different species from the Culm grassland communities. Hill *et al.* (1999) applied Ellenberg's indicator value to the most important British plant species. A quantification of the water level requirements of 307 British wetland plants was published in a report by English Nature (Newbold and Mountford, 1997). Water table levels are listed in three ranges, the preferred level and 'dry' and 'wet' levels likely to stress the plants.

Papatolios (1994) and Maltby *et al.* (1996) studied the wetland systems of Kismeldon Meadows and Bradford Mill in the Culm Natural Area in Devon. The vegetation at Kismeldon meadows consists mainly of oligotrophic humid grasslands of which sections are similar to Culm grassland, while at Bradford Mill, eutrophic humid grasslands dominate (Maltby *et al.*, 1996). Both sites are located along the river in the Upper Torridge catchment. The wetlands are maintained by high precipitation input and slow discharge of groundwater due to low soil permeability (ranging from 10^{-5} – 10^{1} m day^{-1}). The water balance was found to be dominated by surface water, but groundwater was important in wetland maintenance in the drier times of the year (Papatolios, 1994). These results have important consequences for the research presented in this thesis. The topographical and hydrological techniques used in the second part of the thesis were selected because of the importance of surface water hydrology.

2.3.3 Chemical environment of wet grasslands

A number of studies have been conducted into the chemical environment of wet species-rich grasslands and wet heaths. Research focusing on these plant communities in south west England was carried out by Hayati and Proctor (1990), Van Oorschot (1994) and Goodwin *et al.*(1998). They found that nutrient availability and other chemical as well as physical factors influence species composition. Duffey *et al.* (1974) mentioned a rapid change in floristic composition towards grass-dominated swards with hardly any other species present, caused by fertiliser application.

The main nutrients released from organic matter decomposition are carbon, nitrogen, phosphorus and sulphur, and mineral weathering is the main source of cationic nutrients like potassium, magnesium and calcium. Although weathering of the soil material beneath the vegetation is important, many wetlands receive water from outside bringing in nutrients from other areas and therefore the chemistry of surrounding areas can be also of great importance (Wheeler, 1995). Wheeler (1999) mentioned the increased nutrient availability to the plant roots, due to the increased quantity and rate of solute supply caused by the movement of water.

Grime *et al.* (1996) described the so called C-S-R model, which classifies species into three extreme survival strategies or combinations of these. The strategies are based on the species response to two external factors, stress and disturbance. Stress consists of factors that restrict the photosynthetic reproduction, like shortage of nutrients, water or light. Disturbance consists of (partial) destruction of plant biomass, which is caused by activities like grazing, mowing or burning or processes like soil erosion or wind-damage. The 'competitors' (C) benefit from low stress and low disturbance. The 'stress-tolerators' (S) have a strategy to deal with high levels of stress, but little disturbance and are often found in (semi-) natural conditions where nutrients or water are limited. The 'ruderals' (R) tolerate high levels of disturbance, but low intensities of stress (Grime *et al.*, 1996). Many semi-natural grasslands have slow-growing species that benefit from their ability to survive towards the lower limit of their edaphic range and could thus be qualified as 'stress-tolerators'. In fertile soils fast growing species will dominate (Rorison, 1971). Important limiting factors in flooded soils are often available nitrogen and phosphorus (Mitsch and Gosselink, 1993). Other important factors are potassium, pH, calcium and magnesium content and redox potential, which could control the release of phytotoxins like Fe^{2+}, Mn^{2+}, S^{-} (Wheeler, 1999). The role of major nutrients and other chemical parameters are discussed below.

Nitrogen

The most limiting nutrient in wetlands is often nitrogen (Mitsch and Gosselink, 1993): availability depends on the length of time that the soils are flooded in the year. Nitrogen mineralisation is the process of the transformation of organically bound nitrogen to inorganically bound ammonium-nitrogen during organic matter degradation (ammonification). This process can be continued by nitrification under aerobic conditions, in which the ammonium is oxidised to nitrite and nitrate. Vegetation can take up both the nitrate and ammonium. Ammonification can take place both under anaerobic and aerobic conditions. However, under flooded conditions (reduced) the major process is denitrification, resulting in a loss as N_2O and N_2, which are important greenhouse gasses. The nitrification does not take place at all or only in very small amounts and part of the ammonium is immobilised by binding to negatively charged soil particles. Available nitrogen is therefore often a limiting factor in wetlands.

A large number of studies have looked at nitrogen availability through mineralisation in species-rich grasslands. Drainage of a site generally increases the N-mineralisation, e.g. Berendse *et al.* (1994) reported 201 kg N $ha^{-1}year^{-1}$ for a dry site and 158 kg N $ha^{-1}year^{-1}$ for a wet site in the centre of The Netherlands. However, the period of highest mineralisation was different between the sites: April to June for the dry site and June to August for the wet site. Van Duren *et al.* (1997) reported a change from K limitation to N limitation due to a decrease in N-mineralisation when increasing the groundwater table.

Between the various Culm grassland communities, different levels of nitrogen are found. The wet grasslands in Wales studied by Blackstock *et al.* (1998) revealed higher levels of inorganic N in soils under *Molinia – Crepis paludosa* mire compared to those under *Juncus – Galium palustre* rush-pasture. Goodwin (1995) reported higher ammonium-nitrogen levels than nitrate-nitrogen, possibly due to a relatively low pH and high soil moisture content, with values varying between 0.5 and 4 mg kg^{-1} (air dry soil) for nitrate-nitrogen and between 1 and 8 mg kg^{-1} (air dry soil) for ammonium-nitrogen. The FAEWE Functional Analysis of European Wetland Ecosystems study reports on a positive relationship between plant production and N-mineralisation. Sites that had received high P inputs in the past were now mainly N-limited, whereas other sites that had not received any nutrients were both P- and N- limited (Van Oorschot, 1994).

Phosphorus

Phosphorus is one of the major nutrients controlling vegetation growth (Mitsch and Gosselink, 1993). Most of the phosphorus in the soil is bound to organic matter and mineral sediments. Orthophosphate (PO_4^{3-}, HPO_4^{2-}, $H_2PO_4^{-}$) is the main inorganic form of phosphorus and the only form which can be taken up by the plant. The following mechanisms make large amounts of phosphorus unavailable for plant uptake:

- Precipitation with ferric iron, calcium and aluminium under oxidised conditions.
- Adsorption to clay particles, organic peat and ferric and aluminium hydroxides and oxides.
- Incorporation into the living biomass.

Phosphates can be released from these pools for plant uptake under anaerobic conditions (Mitsch and Gosselink, 1993). Slow release of the mineral-bounded phosphates maintaining an equilibrium with the soil solution also makes phosphates available for vegetation (George, 1992).

Janssens *et al.* (1998) compared a number of grassland systems in Europe. They found a close relationship between phosphorus content and plant diversity. For phosphorus values above 50 mg kg^{-1} soil (acetate and EDTA extraction) a maximum diversity of 20 species per 100 m^2 was found. Below this limit, the number of species could reach 50-60 per 100m^2. Hayati and Proctor (1990) reported that the highest concentrations of extractable phosphorus and ammonium-nitrogen were found in the species-poor parts of the wet heath sites that they studied in Devon. Wheeler *et al.* (1992) reported values of total phosphorus between 100 and 3900 mg kg^{-1} soil, measured in 86 rich-fen soils in lowland England and Wales. Goodwin *et al.* (1998) compared the available soil phosphorus content and the uptake between an improved pasture and a *Cirsio - Molinietum* fen-meadow, which were both part of the Culm grasslands. The available phosphorus content in both grasslands was between 1-6 mg kg^{-1} soil (Olsen P extraction), but was generally higher in the improved pasture. Total phosphorus levels were 545 mg kg^{-1} soil on the unimproved site, compared to 790 mg kg^{-1} soil on the improved site.

Other chemical factors

For potassium, a similar relationship between species diversity and nutrient content of the soil is found as for phosphorus. Janssens *et al.* (1998) reported a maximum number of species was observed in soils with between 15 and 20 mg potassium per 100 g soil. A much higher value was reported by Van Duren *et al.* (1997), who measured a mean value of 2400 mg K kg^{-1} soil for an undrained species-rich fen. Potassium contents of the top 5 cm of soil under Culm grasslands were found to vary between about 200 and 500 mg kg^{-1} (Goodwin, 1995). Blackstock *et al.* (1998) studied chemical soil characteristics in wet grasslands in Wales. They found higher soil pH (water) (6.03 versus 4.19) and Ca-levels (315.0 versus 30.2 mmolc kg^{-1}), greater base saturation (100 versus 47%) and lower exchangeable acidity (0.6 versus 55.5 mmolc kg^{-1}) in soils under *Molinia – Cirsium dissectum* fen-meadows than under *Molinia – Potentilla erecta* wet grassland. Goodwin (1995) found mean pH (water) values for Culm grassland between 3.71 and 4.33 for the top 5 cm and a value of 5.59 for an improved site. Calcium concentrations were measured between 200 and 480 mg kg^{-1} and Mg-levels between 130 and 200 mg kg^{-1}. Table 2.2 gives an overview to summarise the values presented in the previous section.

NO_3^- mg kg^{-1}	NH_4^+ mg kg^{-1}	PO_4^{3-} mg kg^{-1}	K mg kg^{-1}	Ca mg kg^{-1}	Mg mg kg^{-1}	pH (water)
0.5 - 4	1-8	1-6	200 - 500	200 - 480	130 - 200	3.7 - 4.3

Table 2.2 Overview of the nutrient levels and pH measured on Culm grassland recorded by Goodwin (1995)

2.3.4 Historical ecology and management practices

Little has been published on the land use history of the Culm Natural Area. However, in many locations agricultural land use in the area was restricted by poorly draining soils (Findlay *et al.*, 1984). As mentioned in Chapter 1, the diverse landscape of the 19^{th} century consisted of a mosaic of woodland, heathland, wetland, moorland, meadows and agricultural fields. The agricultural landscape slowly developed over millennia of human use and had a much higher floral and faunal diversity than at present (Ingrouille, 1995). In south west England, agricultural land use mainly consisted of permanent grassland used for cattle and sheep grazing and large heathland areas were maintained by grazing and burning (Nature Conservancy Council, 1984). From the beginning of the twentieth century, but especially from the second World War onwards, agriculture has changed radically and large scale pasture improvements have taken place. Only some marginal farmland was not improved, because the costs outweighed the benefits. On these sites the traditional management of low intensity grazing was often continued.

To maintain a semi-natural grassland habitat, management practices like grazing, mowing or burning are needed to avoid the succession of the vegetation into coarser grasslands, shrub or woodland. Such practices also remove plant material containing nutrients and favours less competitive species allowing more of the slower-growing perennials and species of smaller stature to survive (Benstead *et al.*, 1997). By removing the nutrients, stress-tolerating species get a better chance to develop. However, if excessive intensities of grazing, mowing or burning are applied, the level of disturbance causes 'ruderal' species to take over or vegetation to disappear altogether (Grime *et al.,* 1996). Most lowland heaths will follow succession into tree and shrub vegetation without human management (Gimingham and De Smidt, 1983). Wolton (1992) described the ideal management for Culm grassland. A number of management practices are beneficial for the communities: Grazing by cattle between late May and late September is suggested by Wolton (1992), with stocking levels equivalent to about one suckler cow per 0.8 ha. If adequate results cannot be achieved with grazing due to field conditions that are too wet, increasing the risk of severe poaching, burning of *Molinia*-dominated fields and cutting of rush-dominated field is important in addition to grazing.

Duffey *et al.* (1974) described the three most important aspects of grazing: defoliation of the sward, removal of nutrients in plant material and return in the form of dung and urine and physical damage due to trampling of the vegetation. Grazing animals select certain species for consumption, while never eating others, thereby affecting the species composition of the sward. This selection procedure is affected mainly by the presence of other species and the time of year. The redistribution of nutrients is determined by the pattern of dung and urine distribution in the field. Nitrogen and potassium are mainly returned by urine, while phosphorus and calcium are mainly present in dung. This has diverse effects on vegetation composition. Trampling of animals causes soil compaction, resulting in reduced aeration, water penetration and regrowth (Duffey *et al.*, 1974). Especially on wet marshes, the soil is susceptible for trampling and this would therefore form a risk, if Culm grassland sites were too intensively grazed. Amiaud *et al.* (1996) investigated the importance of grazing on wet grasslands along the Atlantic coast of France. They found a significant decrease in floristic diversity when grazing was absent and a dominance of the species *Agrostis stolonifera* and *Elymus repens*. Grant *et al.* (1996) also reported an increased floristic diversity on grazed compared to ungrazed plots. Grazing caused the cover of *Molinia* to decrease and the cover of other broad-leaved grasses to increase. However, a study conducted in the Jet catchment in France revealed no decrease in species richness in the first 20 years of abandonment (Regimebeau and Clément, 1996). The importance of grazing and mowing is also clear from research done in the Torridge catchment in Devon (UK) and the Shannon catchment in Ireland. Clément and Maltby (1996) found the highest species diversity in moist oligotrophic grasslands that were extensively grazed or mown.

Unsustainable grazing management can cause severe damage to soil and vegetation. Excessive numbers of livestock cause a drop in forage quality and productivity and if the animals access the land too early in the year, early and medium-late flowering grasses have no chance to develop flowers and seeds (Looman, 1983). Wetness of the land can also cause severe problems, poaching of the soil can cause porosity of the soil to decrease (Taboada and Lavado, 1993) and the bulk density of the topsoil to increase (Ferrero, 1991). The decrease in pore volume decreases oxygen availability to plant roots.

Cutting or mowing of vegetation is used to remove nutrients from the site or to clear the vegetation and to give less dominant species a chance to grow. In some grasslands, mowing is used to obtain fodder or hay to feed animals in winter. One example is *Molinio – Arrhenatheretea* (Looman, 1983). The main difference between the effect of mowing and grazing is that mowing is an unselective method clearing all present species, while grazing is a selective method in which the preferences of the livestock determine which species are eaten (Looman, 1983).

Burning of grasslands is mostly used to clear shrubs off the land or prevent one species from dominating. In heathland, burning is used to rejuvenate old heather shrubs or to increase nutrient cycling in the system (Gimingham and De Smidt, 1983). The nutrients available from the ashes are directly available for the plants, but are often leached with rainwater or are blown away (Forgeard and Frenot, 1996).

2.3.5 Restoration and rehabilitation techniques

This section describes research on restoration and recreation of wetlands. Although the vegetation type studied in this thesis consists mainly of wet grasslands, fen-meadows and wet heaths, this section will, when relevant, also deal with restoration techniques used in related vegetation types like fens and bogs. Habitat restoration is recognised in both the Cornwalland the Devon Biodiversity Action Plans as an important method to buffer, link and expand existing sites (Cornwall Biodiversity Initiative, 1998; Devon Biodiversity Partnership, 1998).

Restoration by 'repair' and by 'rebuilding' are the two main strategies to restore habitat conditions (Wheeler, 1995). Restoration by repair restores the essential conditions directly and is more suitable for small-scale damage. Restoration by rebuilding restores the ecosystem to an earlier stage and lets the system redevelop more naturally. This strategy is suitable for larger scale damage. A model of grassland ecosystem degradation and the possible pathways of restoration after Aronson *et al.* (1993) is presented by Muller *et al.* (1998), in which a distinction between different grades of degradation of the ecosystem is made. Low degradation levels should permit passive restoration. More severe degradation levels require more intervention to the system to restore it to the original state. If certain thresholds of irreversibility are crossed, the system cannot be restored into its previous state but a new ecosystem could still be created. Grootjans and Van Diggelen (1995) stated that the best chances for fen system restoration lie in focusing on the restoration of the least damaged systems. Gilbert and Anderson (1998) presented a schematic approach to habitat creation and restoration, covering the whole process from setting the objectives to monitoring the results. They distinguish four types of habitat creation:

- Natural colonisation – natural processes determine the habitat development on an unmodified site.
- Framework habitat creation – physical and chemical conditions are adjusted to the desired pattern, but plant communities should develop through natural colonisation
- Designer habitat creation – complete landscaping, including planting of trees and shrubs and sowing of grassland species, to a predetermined design
- Political habitat creation – habitat creation for educational and propaganda purposes, not meant to resemble any specific natural habitat

The work in this thesis is aimed at the first two types of habitat creation, where the habitat is re-established through natural colonisation. By selection of naturally favourable locations, the basic conditions should be suitable for the restoration of Culm grassland.

Only small amendments might be needed to restore field characteristics to the unmodified state.

Depending on the cause of wetland degradation, various restoration strategies are applied. Fojt (1995) distinguished 'internal' and 'external' threats. A major 'internal' threat is the neglect of the fen or bog system, which may lead to overgrown vegetation. Degraded wetland sites may have been drained or fertilised in the past to improve their agricultural potential. 'External' threats are changes in land use and water use of nearby locations. Drainage of the surrounding area may influence the water regime of the wetland and fertilising nearby farmland may increase the nutrient level of the water flowing into the wetland. If 'internal' threats are the main problem, restoration can focus on the affected area only. 'External' threats are more complicated is to deal with, as land use in the surrounding area needs to be changed to improve the wetland site.

Importance of the soil seedbank

Together with the migration of species from neighbouring sites (Section 2.2.3), restoration of degraded plant communities often depends on the presence of species in the soil seed bank. However, the management of the site is very important in maintaining the size of the seed bank and the species' proportions (Maas and Schopp-Guth, 1995). Lowest species richness was found in the seedbank of wetlands with a history of hydrological modification and other disturbances (Brock and Britton, 1995). Typical fen species, like *Succisa pratensis*, *Viola palustris* and *Potentilla erecta* have a transient or short-term persistent seedbank. The proportion of fen plants in the seed bank of *Molinia* and *Schoenus ferrugineus* communities in southern Germany, was reported to have declined to less than 4 % ten years after intensification of agricultural management (Maas and Schopp-Guth, 1995). McDonald *et al.* (1996) investigated the importance of the seed bank for the restoration of species-rich flood-meadows. They found that the seed bank of an ancient flood-meadow consisted largely of transient (viable in the soil for less than one year) and short-term persistent (viable for 1 to 5 years) species. When species disappear due to improvements, most of them will not re-establish after the traditional management has been reinstated. The impact of different grazing animals was also investigated. It was concluded that a larger seed bank was formed under cattle grazing, as compared to sheep grazing or no grazing. This was probably caused by disturbance of the topsoil by cattle, whereas sheep tend to maintain a dense closed turf (McDonald *et al.*, 1996). Bakker and Berendse (1999) mention that often only half the species present in the vegetation also occur in the seed bank and the ones present are the 'non-target' species with long-term persistent seed banks. Therefore, restoration practices cannot just rely on the presence of species in the seed bank. Reintroduction of species by sowing a seed mixture or the establishment of species through seed dispersal of nearby plant communities is therefore crucial.

Manipulation of nutrient levels

A large number of studies have been carried out to investigate the effects of eutrophication of wet grassland and fen-meadow systems and on potential restoration techniques. Koerselman and Verhoeven (1995) presented an overview of the impacts of the various techniques on N and P availability (Table 2.3).

Measures	N	P
Reduce nutrient inputs	Yes	Yes
Restore high groundwater level	Yes	No*
Sod removal	Yes	Yes
Mowing	Yes**	Yes
Restore discharge of clean Ca/Fe-rich groundwater	No	Yes

*Table 2.3 Measures to reduce nutrient availability (derived from Koerselman and Verhoeven, 1995). *This could increase P availability. **Only reduces N availability significantly if amount of harvested material exceeds the N input from deposition.*

Restoration of Culm grassland sites is mostly achieved by reducing the nutrient inputs and occasionally mowing the site. Neglected sites are often cleared of shrubs and trees first and then burning of the plant material takes place. When site clearance is finalised a low intensity grazing scheme can be implemented (Wolton, 1992).

The reduction of nutrient inputs is crucial to obtain nutrient-poor conditions for restoration. Yet often this measure is not sufficient and additional measures need to be taken. Increasing the level of the groundwater table can reduce N mineralisation and stimulate denitrification (Grootjans and Van Diggelen, 1995), but this could increase the P availability. In an experiment on phosphate release and sorption under aerobic and anaerobic conditions, more P was released to the soil solution under the latter (Patrick and Khalid, 1974). Removal of the nutrient-rich topsoil is an effective measure in removing N and P, but could also take away the seed bank and destroy existing plant communities. Mowing and harvesting does remove P and N by taking away plant material, but for N, this often does not exceed the amount deposited from the air. Phosphorus availability can be reduced by discharge of Fe- and Ca-rich groundwater in the fen-ecosystem, as these cations help to bind the phosphates (Patrick and Khalid, 1974; Koerselman and Verhoeven, 1995)

Berendse *et al.* (1992) conducted a long-term experiment to compare restoration strategies on species-rich meadows in the centre of the Netherlands. Three experiments were set up to evaluate the effectiveness of techniques to remove an excess of nutrients from the grassland systems. The first experiment compared unfertilised with fertilised plots. The second compared effects of mowing and removing harvested material between no fertiliser with low fertiliser plots. The third compared four levels of nutrient removal by mowing and removing the harvested material and a separate treatment of removing 5 cm of topsoil on soils with three different water regimes. The experiment revealed that mowing and hay removal decreased the above-ground biomass, but after nearly two decades did not increase species diversity. Sod removal led to an increase in the diversity compared to the plots that were only mown. Also a number of rare species became established in these plots (Berendse *et al.*, 1992).

In northern Germany, a study by Schrautzer *et al.* (1996) compared management measures to restore strongly degenerated *Lolio-Potentillion* wet grasslands and abandoned wet meadows to mesotrophic *Calthion* wet grasslands. The results indicated that, due to partially irreversible abiotic and biotic changes, none of the techniques succeeded sufficiently. However, by changing the management of abandoned wet meadows into an unfertilised and mowed system, the sites developed into eutrophic *Calthion* systems. They concluded that restoration techniques should therefore focus on the preservation and maintenance of near-natural *Calthion* ecosystems (Schrautzer *et al.*, 1996).

Other experiments were set up to analyse the impact of drainage and rewetting of wetlands on vegetation composition. Van Duren *et al.* (1997) studied nutrient limitations in drained and undrained poor fens. They found N to be the limiting nutrient for plants in the undrained fen, while for the drained site K was the limiting factor. Rewetting the peat did not change the nutrient limitations on a short time scale. This indicates that restoring vegetation on peat lands by rewetting does not automatically lead to successful restoration.

2.4 Summary

This chapter gave a review of the literature available on Culm grasslands and associated plant communities in the rest of the United Kingdom and Europe. A short summary of the most important aspects to this study is given in this section.

Culm grasslands are wet, unimproved floristically diverse grasslands consisting of the following National Vegetation Classification communities: *Erica tetralix - Sphagnum compactum* wet heath (M16), *Juncus effusus/acutiflorus - Galium palustre* rush pasture (M23), *Molinia caerula - Cirsium dissectum* fen-meadow (M24), *Molinia caerulea - Potentilla erecta* mire (M25) and *Filipendula ulmaria - Angelica sylvestris* mire (M27). This highly fragmented habitat in is found in the Culm Natural Area in south west England, but also in several other areas across the Atlantic zone. The area of Culm grassland was significantly reduced, due to drainage and pasture improvement during the second half of the twentieth century. Currently, the habitat is threatened by neglect. Regional planning is needed to maintain this plant community in south west England. The degree of fragmentation and the distance between sites are important aspects to consider in this planning process.

Hydrodynamic functioning of an area determines the location of wetlands and influences chemical processes and species composition. Earlier research performed on Culm grassland sites in south west England showed that the water balance of the sites was dominated by surface water. Most limiting nutrient in wetlands is often nitrogen, due to the denitrification process. A negative correlation between species diversity and both phosphorus and potassium availability was found by some workers.

Management practices, such as grazing, mowing and burning are needed to avoid succession into shrub- or woodland. Restoration of a habitat can be performed by improving degraded sites or by creating new sites. To obtain nutrient poor conditions inputs need to be reduced and nutrients could be removed by mowing, removal of the topsoil or by stimulating denitrification by increasing the groundwater table. Restoration of plant communities depends often on the presence of species in the nearby area or in the soil seed bank.

From the literature in this chapter is clear that careful planning of management practices and restoration activities is crucial to maintain and enlarge the area of (semi-) natural habitats. The research presented in this thesis adds information and insight into the parameters important for Culm grassland location and composition in particular and into the approach that could be adopted in general to planning habitat conservation and selecting target areas on a regional scale. The resulting maps with suitable Culm grassland restoration locations can be used together with other spatial information, such as land cover data, present occupation patterns, infrastructure and the location of other valuable habitats, in the regional and national policy making process. From the combination of these data with non-spatial and socio-economic data, a clear picture is formed on which areas could be used for Culm grassland restoration and how to connect existing sites. Integration of this information in and early stage of the policy making, enables the optimal use of resources. For other habitats a similar approach could be adopted.

Chapter 3

The Culm Natural Area: location, characteristics and land use

3.1 Introduction

Following the introduction and the literature review (Chapters 1 and 2), the general characteristics of the study area will be described in this chapter. Although Culm grassland sites are found in a few other locations in the south west, the chosen boundary for this research is the Culm Natural Area (Figure 1.1) as was defined by English Nature (Hughes and Tonkin, 1997). The Natural Areas approach has been part of English Nature's 'Strategy for the 1990s' (English Nature, 1993). A total of 120 terrestrial and marine Natural Areas were defined based on the distribution of wildlife and natural features and on the pattern of land use and human history of each area. The areas cover the whole of England and were identified to provide a more effective framework than administrative boundaries for planning and achievement of nature conservation (Hughes and Tonkin, 1997). Since part of the aim of this thesis was to design a management tool to aid nature conservation and environmental organisations in the planning of the expansion of the existing Culm grassland area, the Culm Natural Area was chosen as the study area. This chapter describes the most important characteristics of the area. Section 3.2 describes the location and presents photographs of Culm grassland sites. In section 3.3, the climate will be described. The chapter continues with a description of the main characteristics of the geology (section 3.4), soils (section 3.5) and hydrology (section 3.6) of the area. Finally, a description of the major land use types is given in section 3.7.

3.2 Location and appearance

As was mentioned in Chapter 1 and the previous section, Culm grassland in south west England is mainly found within the Culm Natural Area. The name for the Culm Natural area is taken from the Culm Measures geological formation (Section 3.4). The word 'Culm' comes from an old mining term for rock containing occasional thin coal seams, which occur in the area. The area stretches roughly from Barnstaple, north Devon along the Somerset border to Tiverton and from Exeter to the west coast in north Cornwall (Figure 3.1). Grid references are approximately SX (210,000; 80,000) to SS (290,000; 130,000) and the area covers about 3500 km^2. The boundary follows the edges of the Culm Measures geological formation, which will be described in section 3.3.

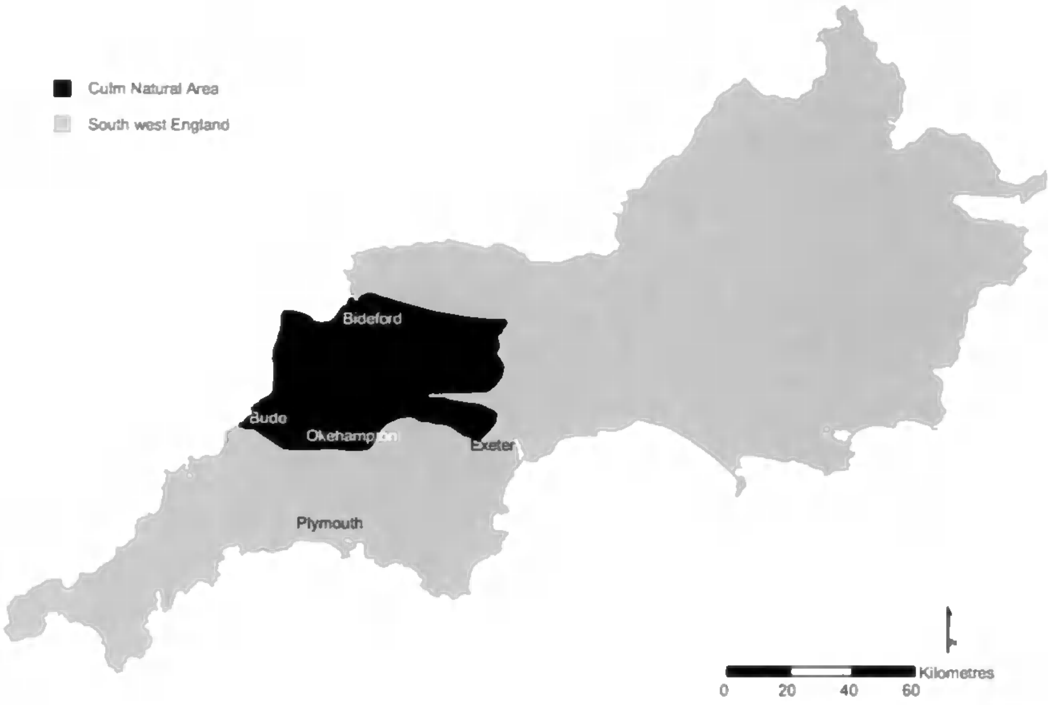


Figure 3.1 Location of the Culm Natural Area

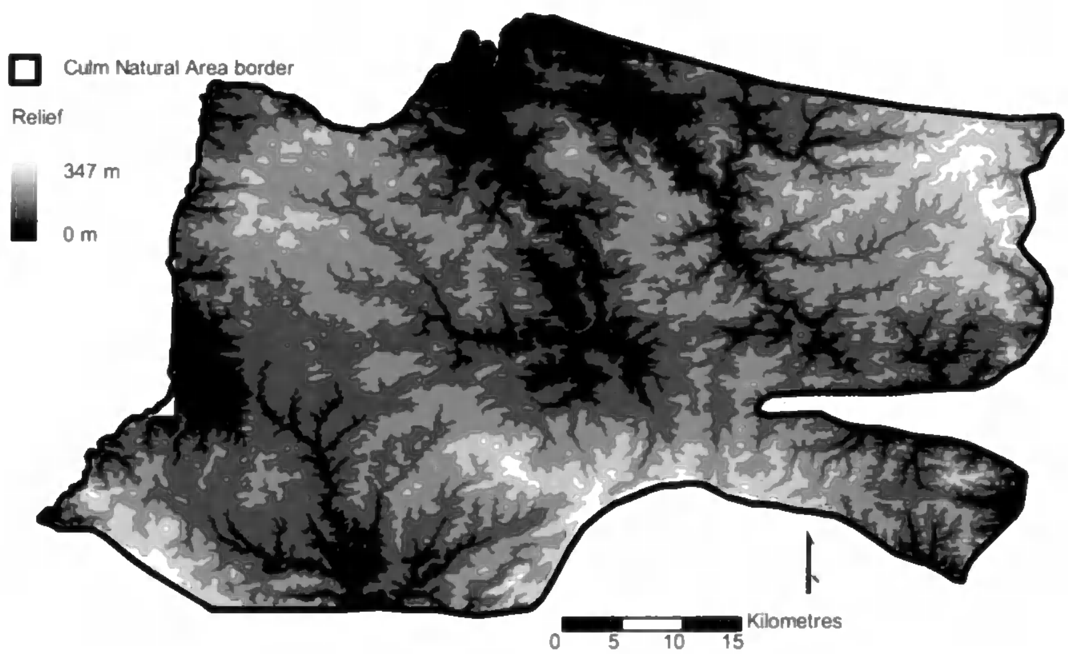


Figure 3.2 Relief of the Culm Natural Area

The relief in the area consists mainly of rolling hills with slope angles between 0 and 12 degrees and an altitude varying between 0 m at the coast to about 500 m towards Dartmoor (Figure 3.2).

Culm grassland sites are found in a very scattered pattern spread over the whole area and cover only 2% of the total Culm Natural Area (Hughes and Tonkin, 1997; DBRC, 1998). Part 2 of the thesis will describe the distribution in more detail. To give an impression of Culm grassland sites four photographs are presented in Plate 3.1 to 3.4.

Plate 3.1 Fieldwork in a typical Culm grassland site in flower (July 1999)

Plate 3.2 A Culm grassland site dominated by rushes (Winter 2000)

Plate 3.3 Culm grassland site on a plateau (Winter 2000)

Plate 3.4 Field visit with the collaborating organisations (June 2000)

3.3 Climate

The climate in the region is generally defined as 'oceanic', which means that rainfall and temperature in the area are strongly influenced by the sea. Following Köppen's classification system, it can be described as a mild temperate rainy mesothermal climate, with no distinct dry season, coded as Cf (Trewartha and Horn, 1980). Rainfall in the area is mainly determined by topography: low-lying areas have generally lower amounts of rainfall than the more upland regions, like e.g. Dartmoor and Exmoor. The Culm Natural Area has an annual precipitation average of 1000-1400 mm (Meteorological Office, 1983). As was mentioned before, the hydrology of the sites is mainly determined by surface water. Therefore, together with other climatic and non-climatic factors, high precipitation is an important factor for the presence of Culm grassland in the area.

The temperature regime in south west England is also mainly determined by proximity to the sea. The temperature of seawater changes slowly over the year. Air masses coming from the Atlantic have a large influence on temperature. Coastal areas therefore have relatively mild winters and fresh summers. Although the whole area has a mild climate, inland, the temperature is mainly affected by altitude. The low-lying and coastal areas have an annual mean temperature of about 11 °C, compared to 8 °C on Dartmoor. February is on average the coldest month in the area with mean monthly temperatures at around 1.5 °C inland in Devon. The warmest months are July and August, with mean temperatures around 19 to 21 °C (Meteorological Office, 1983).

The relative humidity of the air is the ratio of amount of water vapour in the air and the maximum amount that could be contained by the air at a given temperature. This mainly depends on the seasonal and diurnal temperature regimes. An average relative humidity of around 80% is recorded for south west England. Highest values up to around 90% are found at night and in winter (Meteorological Office, 1983).

The average number of sunshine hours depends on latitude and altitude, but also topography can be important. The average value for the period from 1951 to 1980 at Hartland Point was around 1660 hours decreasing towards Exeter to 1512 hours (Meteorological Office, 1983).

Changing climatic conditions could have implications for the occurrence of Culm grassland. If the climate would become more humid, waterlogged conditions might occur in a larger area for a longer period of time, which could increase the area suitable for wetland habitats. However, this also depends on soil drainage characteristics. Increased temperatures could potentially affect the species composition due to competition by species adapted to warmer climates.

3.4 Geology

The Culm Measures geological formation, as defined in Section 3.2, is located between Dartmoor, Exmoor, the West Coast and Tiverton. It covers about half of Devon and stretches into the northern part of Cornwall. The formation consists of folded non-calcareous shales and sandstones, which were formed during a marine environment in the Carboniferous period (Durrance and Laming, 1982). At the end of the Devonian and the beginning of the Carboniferous period, a combination of more rapid subsidence of the seabed and reduced sediment supply compared with previous periods, resulted in a deepening of the sea. On the edges of the Culm Measures, sediments of the Lower Carboniferous (345-325 Ma) were found, mainly consisting of shallow water sandstones at the edges and shales, thin deep-water limestones and cherts, which were deposited under marine conditions. The rest of the area consists of sediments deposited in the Upper Carboniferous (325-280 Ma) period, filling the trough with sandstones and shales (Durrance and Laming, 1982). The Variscan orogeny, which had its peak during the late Carboniferous, caused the sedimentary rocks to fold. Folding of the bedrock can affect the hydrology by constraining groundwater flow in the directions of the folded sandstone aquifers.

The stratigraphic successions of the Culm Measures are formed by the Lower Culm Group and the Upper Culm Group (Figure 3.3). The Lower Culm Group is characterised by the first appearance of the widespread black or dark grey shales. The main fraction of the group consists of interbedded limestone and shale or cherts and the topmost section of the Lower Culm consists of a thin sequence of grey shales (Durrance and Laming, 1982). In north and central Devon, the Crackington and the Bude Formations of the Upper Culm Group are found. The Crackington Formation consists of poorly sorted quartz medium to fine-grained sandstones, with a clay matrix (graywacke) interbedded with dark grey or black shales. The material of this formation is rather impermeable (Findlay *et al.* 1984).

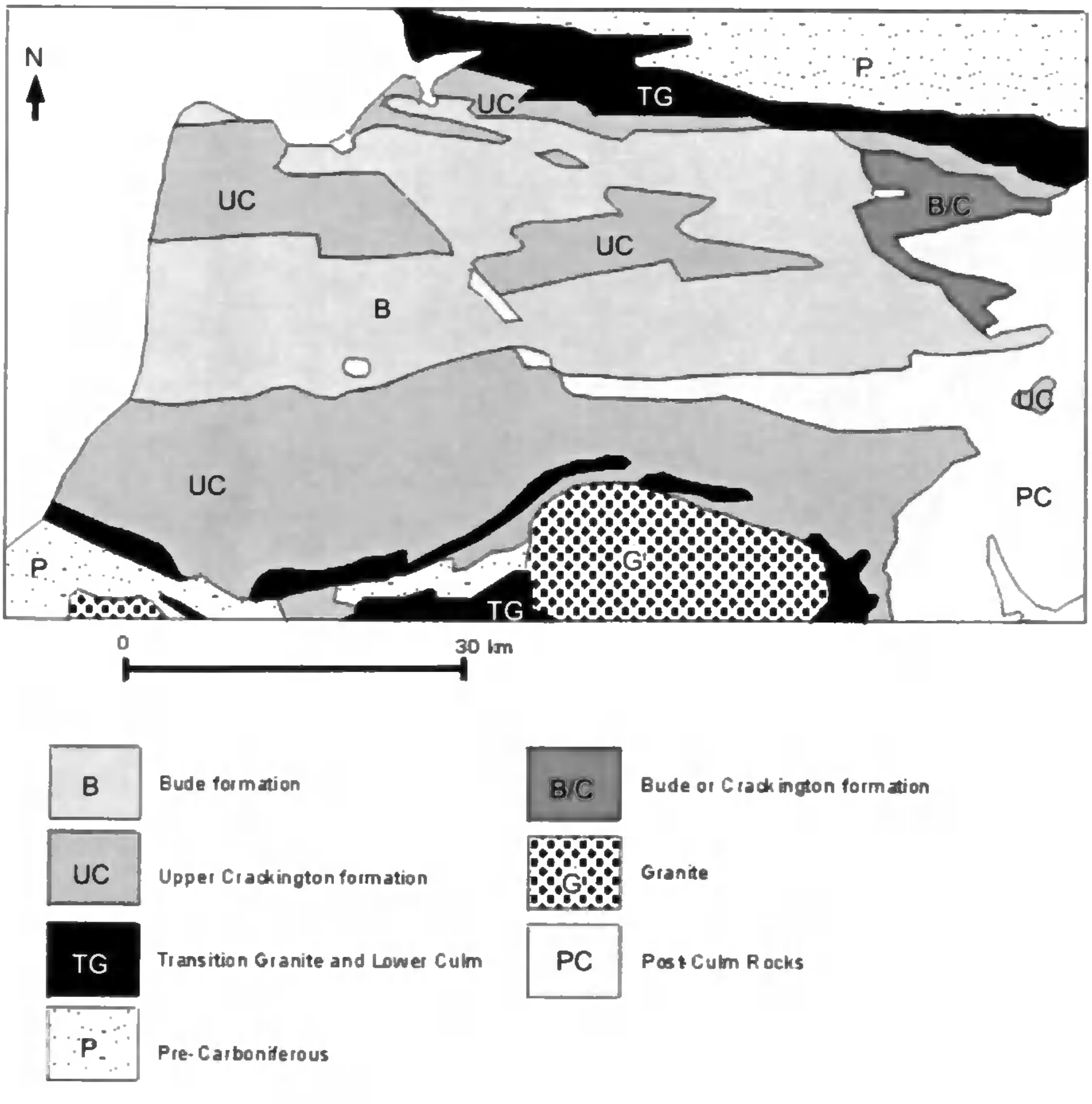


Figure 3.3 Geology of the Culm Measures (Bude and Crackington formations and transition between Granite and Lower Culm) and the surrounding area (Granite, Post Culm Rocks and Pre-Carboniferous). (Durrance and Laming, 1982).

The Bude Formation appears to be younger than the Crackington Formation and is characterised by massive sandstone beds interbedded with thin extensive sheet features of sandstones, siltstones and shales (Durrance and Laming, 1982). The saturated hydraulic conductivity of the bedrock is likely to be higher than that of the Crackington formation. In the southern part of the Culm measures, the Ugbrooke sandstones are found. This formation is fairly similar to the Crackington Formation, but contains feldspar and is in many areas structureless with very little shale (Durrance and Laming, 1982).

Quaternary head is deposited on top of the Carboniferous Bude and Crackington formations. These deposits consist of unstratified or crudely stratified material, which were transported by solifluction in the periglacial environment during the Pleistocene periods (Findlay *et al.*, 1984). Alternating conditions of freeze and thaw caused the soil material to move down slope. Most of the Carboniferous rocks on the Culm Measures are covered by 1 to 4 m thick head, with thinner sections on slopes and thicker layers of material collected at the base of the slope. The material has only moved short distances because of short, moderately steep slopes. Therefore, no large differences exist between material of the top layer and the underlying rocks and the head deposits barely influence the hydrology.

3.5 Soils

This section describes the most important soil associations and soil series in the area. On the sandstone and shale layers (Section 3.4) of the Culm Measures, soils varying from impermeable clays to freely draining brown earths have developed. Figure 3.4, derived from Findlay *et al.* (1984), gives a schematic overview of the toposequence of the soil associations. The poorly drained stagnogley soils of the Halstow, Hallsworth 1 and Hallsworth 2 associations are mainly found on the flat plateaux and the valley bottoms. The well drained Neath, Manod and Denbigh 1 associations are situated on the slopes. A drawback to the use of soil associations is that for the purpose of generalisation of the soil information on smaller scale maps, like the 1:250,000 map, soil series with varying characteristics might be grouped into one association.

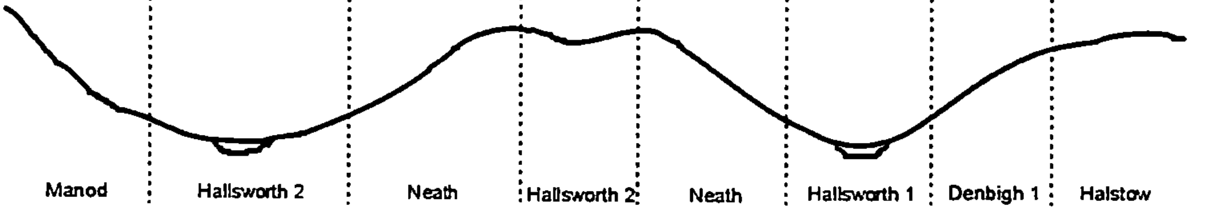


Figure 3.4 Soil associations transect on the Culm Measures derived from Findlay et al. (1984)

Table 3.1 gives a summary of the characteristics of the soil associations and its associated soil series. For the occurrence of Culm grassland, wet conditions are needed and poorly draining soils support waterlogged conditions. The most important poorly draining soil associations in the area are the Halstow and Hallsworth 1 and 2 assocations. The Halstow association mainly consists of Halstow, Hallsworth and Tedburn series as described in Tables 3.1 and 3.2. It is an association of non-calcareous pelosols and pelo-stagnogley soils, which are found on crests and gentle or moderate slopes over Carboniferous shale. In some places with a thicker surface horizon, soils of the Cherubeer series are found in stead of the Halstow series. The Hallsworth 1 and 2 associations are both found in valleys and on broad ridge crests. The major soils of the Hallsworth 1 association are pelo-stagnogley soils which are slowly permeable. The two most important are of the Hallsworth and Tedburn series (Tables 3.1 and 3.2). Other soils are of the Dale and the Cegin, Greyland, Brickfield series, which have a slightly coarser texture. Soils of the Onecote series with a humose topsoil are also found mostly between Okehampton and Holsworthy. The Hallsworth 2 association consists of stagnogley soils with large variation in texture. The major soils are Hallsworth and Brickfield (Tables 3.1 and 3.2), but the clayey Tedburn, fine silty Cegin, the fine loamy over clayey Greyland and the Onecote series are also found (Findlay *et al.*, 1984).

The poorly draining soils are mostly used for permanent pasture supporting dairy, beef cattle and sheep. Fields of the Hallsworth associations are often rushy or covered by coniferous forests, deciduous woodland or *Molinia* moor. Soils are susceptible for damage by trampling or use of machinery. Therefore, the use for crop growth is restricted and stock densities need to remain low, which favours the development of semi-natural plant communities. The soils of the Halstow association are better suited for crop production, but yields are limited and most of the soils are used for grassland (Findlay *et al.*, 1984).

	Soil series	Characteristics	Wetness class
POORLY DRAINING SOIL ASSOCIATIONS			
HALSTOW			
Position	Crests and gentle or moderate slopes over Carboniferous shale		
	Soil series	**Characteristics**	**Wetness class**
	Halstow	Non-calcareous pelosols, slightly mottled above 40 cm, clay or (silty) clay loam topsoil, immediate subsoil most clayey. Waterlogged for long periods in winter.	IV
	Hallsworth	Pelo-stagnogley soils, often gleyed to the surface, clay or (silty) clay loam topsoil, immediate subsoil most clayey. Waterlogged for long periods in winter.	V
	Tedburn	Pelo-stagnogley soils, often gleyed to the surface, clay or (silty) clay loam topsoil, immediate subsoil most clayey. Rock within 80 cm of surface. Waterlogged for long periods in winter.	V
HALLSWORTH 1			
Position	On gentle footslopes and basins and broad ridge crests over Carboniferous shales or shaly Head		
	Soil series	**Characteristics**	**Wetness class**
	Hallsworth	Pelo-stagnogley soils, often gleyed to the surface, clay or (silty) clay loam topsoil, immediate subsoil most clayey. Waterlogged for long periods in winter.	V
	Tedburn	Pelo-stagnogley soils, often gleyed to the surface, clay or (silty) clay loam topsoil, immediate subsoil most clayey. Rock within 80 cm of surface. Waterlogged for long periods in winter.	V
HALLSWORTH 2			
Position	In shallow valleys and on broad ridge crests over Carboniferous Bude Formation		
	Soil series	**Characteristics**	**Wetness class**
	Hallsworth	Pelo-stagnogley soils, often gleyed to the surface, clay or (silty) clay loam topsoil, immediate subsoil mostly clayey. Waterlogged for long periods in winter.	V
	Brickfield	Stagnogley soils, often gleyed to the surface, fine loamy topsoil, immediate subsoil mostly clayey. Waterlogged for long periods in winter.	V
WELL DRAINING SOIL ASSOCIATIONS			
NEATH			
Position	Mainly found over Carboniferous sandstone with subordinate shale on convex ridges and slopes		
	Soil series	**Characteristics**	**Wetness class**
	Neath	Brown earths, permeable and well drained, brown clay upper horizons with fine sandstone and siltstone fragments. Below about 50 cm depth stone content increases	I
	Nercwys	Stagnogleyic brown earths, mottled less permeable, clay loam subsoils	III
DENBIGH 1			
Position	Mainly found over Palaeozoic rocks on slopes and ridges		
	Soil series	**Characteristics**	**Wetness class**
	Denbigh	Fine loamy typical brown earths with a blocky structure on solid or shattered rock within 80 cm depth, free draining.	I
	Manod	Typical brown podzolic soils, permeable clay loam with a dark topsoil over ochreous subsoil, granular structure. Solid or shattered rock is found within 80 cm depth. The soil is free draining.	I
MANOD			
Position	Mainly found over Palaeozoic mudstone, siltstone or slate on steep slopes		
	Soil series	**Characteristics**	**Wetness class**
	Manod	Typical brown podzolic soils, permeable clay loam with a dark topsoil over ochreous subsoil, granular structure. Solid or shattered rock is found within 80 cm depth. The soil is free draining.	I
	Denbigh	Fine loamy typical brown earths with a blocky structure on solid or shattered rock within 80 cm depth, free draining.	I
	Powys	Unmottled, fine loamy soils on solid or broken rock within 30 cm depth	I

Table 3.1 Overview of soil associations and their major soil series found on the Culm Measures after Findlay et al. (1984).

Halstow	Hallsworth series:	Tedburn series:	Brickfield series:
0-25 cm Ap *Brown, slightly mottled, lightly stony clay loam or clay.*	0-20 cm Apg *Dark greyish brown, slightly stony clay loam or clay.*	0-20 cm Ahg *Dark grey, slightly mottled, slightly stony clay loam or clay*	0-20 cm Ap *Very dark greyish brown, slightly stony clay loam.*
25-40 cm Bw(g) *Yellowish brown, mottled, slightly or moderately stony silty clay or clay; moderate coarse subangular blocky or prismatic structure.*	20-50 cm Bg *Yellowish brown with many ochreous mottles, slightly stony clay; moderate coarse prismatic structure.*	20-50 cm Bg *Grey with many ochreous mottles, slightly stony clay or silty clay; strong coarse prismatic structure*	20-50 cm Bg *Greyish brown with many ochreous mottles, slightly stony clay loam; moderate medium subangular blocky structure.*
40-70 cm Bg *Grey, mottled, slightly stony clay or silty clay; weak coarse prismatic structure.*	50-100 cm BCg *Greyish brown, mottled, slightly stony clay; moderate coarse prismatic structure; high packing density.*	50-100 cm BCg or Cr *Grey with many ochreous mottles, very stony clay; weak coarse angular blocky or massive structure or shale* in situ	50-100 cm BCg *Grey, mottled, moderately stony clay loam; weak coarse subangular blocky or prismatic structure; high packing density.*
70-100 cm Cr *Grey, shale* in situ.			

Table 3.2 Typical soil profiles of the Halstow, Hallsworth, Tedburn and Brickfield series (Findlay et al., 1984; Harrod, 1988).

Other, better draining soil associations found in the area are the Neath, Denbigh 1 and Manod associations. The well drained Neath association comprises fine loamy brown soils over sandstone, with the Neath and Nercwys soil series (Table 3.1) as the most important ones. This association is mainly found on convex ridges and slopes. Other series found in this association are Cherubeer: stagnogleyic brown earths, Halstow and Hallsworth (both described in Table 3.1 under the Halstow association). The Denbigh and Manod soil series are the major representatives of the brown, stony, well-drained Denbigh 1 association, which, like the Neath association, is found on slopes and ridges. Well-drained Denbigh soils are found on places where the shaley parent rock has been sheared and is less weatherable. Other soils that occur are the shallower Powys soils, the siltier Barton series and the stagnogleyic Sannan soils. The Manod association is found on steep slopes and consists of the free-draining fine loamy Manod, Denbigh and Powys soils, which are described in Table 3.1. Like the land use on the poorly draining soils, these soils are often used for permanent pasture. However, due to good drainage there is little risk of trampling and therefore stock densities can be higher and grazing animals can stay in the field for a longer period of the year (Findlay *et al.*, 1984).

3.6 Hydrology

Hydrology is mainly determined by the amount of precipitation, losses due to evaporation and evapo-transpiration by the vegetation and the permeability of geological formations and soils. In the CNA, three major rivers originate from a large number of smaller streams: the Tamar, draining the south western part of the area southwards and the Torridge and

Taw, both draining north and receiving the water from the central and north eastern side. The zones with relatively impermeable slates and shales are deeply dissected by streams, whereas the more persistent sandstone or chert bands form ridges only dissected by small streams that form in the weaker cross-faults (Findlay *et al.,* 1984). As described in section 3.5, the soils in the area vary from impermeable stagnogley soils to freely draining brown earths. Permeable soils enable the water to infiltrate into the deeper groundwater and drain towards the stream. The impermeable soils cause the water to drain by shallow subsurface flow or overland flow. To improve the agricultural value of the poorly drained soils, drainage techniques were applied to the fields at a large scale in the sixties and seventies, generally reducing the wetness class by one grade. Techniques such as mole draining and subsoiling are common (Findlay *et al.,* 1984). Draining of soils at water contents greater then field capacity decreases the time taken for the water to flow from the soil surface to the river, causing the river to respond quicker to a rainfall event (Robinson and Beven, 1983). This could cause an increase in floods. A lower wetness class means less wet fields and saturation for a shorter time period (Findlay *et al.*, 1984). Although low wetness classes are favourable for agriculture, they have significant adverse effects for natural vegetation.

3.7 Land use

The combination of a wet climate in south west England, with a large area of relatively impermeable soils, causes much of the land to be used for stock rearing and dairy-farming. The high rainfall, together with the mild climate enables, grass growth throughout an extended season (Findlay *et al.,* 1984). In Devon, 77% of the total area is used for agriculture. Of this, 33% is taken up by tillage, including all arable crops, fallow land and grassland of four years old or less, 56% for permanent grassland and 7.3% for rough grassland (Findlay *et al.,* 1984). However, these figures include Dartmoor and the South Hams. For a part of the Culm Natural Area, data from the land cover map of Great Britain (NERC, 1990) were available, which showed that approximately 13% of the area is covered by wood or shrubland, 78% can be classified as grazing pasture or semi-natural vegetation, 7% is used as arable land and the rest is covered by open water or urban areas.

High levels of production and intensive farming were encouraged by the Common Agricultural Policy (CAP) that was designed in 1958 to secure food production and income for farmers (Barnes and Barnes, 1999). The associated increase in land drainage and agricultural improvement by increased use of fertilisers over the last decades has resulted in a rise in production levels, but also in a decrease in the area of natural and semi-natural vegetation. Further, the increase in fertiliser use has caused larger amounts of nutrients to leach to the groundwater and subsequently surface water and has thereby altered the natural environment in surrounding areas, as was mentioned in Chapter 1. Reforms of the European agricultural policies in the early 1990s aimed to reduce the large stocks by weakening the link between production and income support. However, due to the BSE crisis consumption dropped dramatically and cattle farmers lost a large part of their income, which forced some of them to go out of business (Barnes and Barnes, 1999). During the first half of 2001, Foot and Mouth Disease followed, which worsened the financial situation for many farmers. The abandonment of farmland could cause semi-natural plant communities to be neglected, which might result in shrub invasion. Valuable low intensity grazing meadows could then disappear.

A few other important natural plant communities exist in the CNA, which are outlined below, but will not be included in the study. For example, small sections of broad-leaved woodlands are found. They mainly occur on the steep slopes with deep, well-drained soils. These woods have formerly been used for coppice, but coppicing is rarely practised now (Findlay *et al.,* 1984). The major species found in these forests are *Quercus petraea* (sessile oak), *Quercus robur* (pedunculate oak), *Sorbus aucuparia* (rowan), *Ilex acquifolium* (holly) and *Corylus avellana* (hazel) and the ground-covering species like *Vaccinium myrtillus* (bilberry), *Calluna vulgaris* (heather), *Melampyrum sp.* (cow-wheat) and *Solidago virgaurea* (golden rod) (Hughes and Tonkin, 1997). Further, the sea cliffs and slopes comprise another important habitat in the area. Due to the constant spray of salt water and strong winds, only hardy salt-tolerated species can grow here, such as lichens and woody perennials (Hughes and Tonkin, 1997).

PART II

Topography and hydrology

Chapter 4

Techniques for topographical and hydrological analyses

4.1 Introduction and study outline

The second part of the thesis is concerned with the relationships between Culm grassland location and topography and soil hydrology. It addresses the first part of the aim of the study: 'to come to a better understanding of the position of Culm grassland within the landscape'. When planning restoration activities, a thorough investigation of environmental parameters affecting the occurrence and composition of Culm grassland is required to obtain insight into the most important factors that need to be considered. As discussed in Chapter 2, other research conducted on the relationships between various environmental characteristics and Culm grassland vegetation or similar wet grassland vegetation types, has focused on a few parameters in detail at a few specially selected sites (e.g. Papatolios, 1994; Goodwin *et al.*, 1998; Tallowin and Smith, *in press*). These studies acquired very important and detailed information on the environmental conditions of these habitats and crucial insight was gained into the response of the vegetation to environmental changes. However, the unique character of their study sites makes it difficult to extrapolate their conclusions to a wider area. In contrast, the study presented in this thesis aimed to identify characteristics of Culm grassland occurrence in general, and to specify environmental conditions needed for the development of the various Culm grassland types. It was therefore important to take a wider perspective and include a whole range of sites and landscape features. All Culm grassland sites that were located within the Culm Natural Area and previously identified by the Devon Wildlife Trust, were used in this thesis to derive the relationships between topography and hydrology and the location of the sites. The location, size, management and species composition of the sites varied largely, but all sites were included without exception for this part of the study to make sure the whole range of sites were enclosed. The synthesis of various environmental factors in combination with habitat location and species composition data, studied at a range of scales is an innovative step forward in habitat conservation and restoration research and provides a new approach to bio-geographical data integration.

This part of the thesis addresses the first two objectives that were presented in Chapter 1, which are re-stated below:

1. **To describe topographical characteristics of Culm Grassland at a regional scale for the whole Culm Natural Area**

2. **To investigate the occurrence of Culm Grassland in relation to catchment hydrology and soil water regime at a catchment scale.**

This chapter introduces the techniques that were used to study these aspects. A detailed description of the methods used to investigate the relationships between Culm grassland location and landscape topography is given in Section 4.2. The hydrological techniques used to study the relationships between Culm grassland location and the moisture regime are presented in Section 4.3. The results will be presented and discussed in Chapters 5 and 6.

4.2 Regional scale relationship between Culm grassland location, soil and topography

4.2.1 Introduction

As was mentioned in the previous section and in Section 1.3, the first objective of the thesis was to describe the topographic features and soil characteristics of Culm grassland at a regional scale. It was decided to commence the research with the investigation of the relationship between landscape topography and the location of the wet grassland sites, because earlier research on a site in the Upper Torridge catchment, situated in the north western part of the study area, indicated that the water balance of this site was mainly determined by the surface water component (Papatolios, 1994). The patterns of surface water flow depend largely on the topography of the area and it was therefore expected that topography could be used to indicate the relative wetness of the landscape. Further, soil physical properties could play an important role in determining the drainage characteristics of a catchment and reports produced by the Soil Survey of England and Wales mentioned *Molinia caerulea* wet heaths and rush pastures found on the poorly draining soils (Harrod, 1978; 1987; 1988). Hence, the relationships between vegetation occurrence and soil units were also studied.

The most suitable tool to investigate the topographical and soil characteristics of Culm grassland sites was a Geographical Information System (GIS). GIS establish relationships between various spatial parameters, for example how agricultural land use is related to soil types and the distance to streams. The use of GIS and digital maps offered potentially a good base for the set up of a decision support system (DSS), concerned with Culm grassland restoration locations, presented in the last part of this thesis. Before more detailed research could be carried out, the potential for using digital topography and soil maps and GIS as a tool in designing a system for the identification of potential restoration sites had to be investigated. The suitability of using a GIS was tested by investigating the relationships between Culm grassland location and topography and basic soil information. The description of the available data sets will be presented in Section 4.2.2 and GIS techniques that were applied will be described in Section 4.2.3. The results provided the basis for further hydrological modelling as will be described in section 4.3.

4.2.2 Description of data sets

An important factor determining the success of the study was the availability of existing data sets. The scale at which the work was conducted required the use of existing digital data sets to be able to set up a DSS that was valid for as much of the Culm Natural Area as possible. The following digital data sets were available and suitable for use in this study:

1. Culm grassland location map

The digital map with the locations of the Culm grassland sites was obtained from Devon Wildlife Trust (DBRC, 1998). The sites were identified mostly from aerial photo interpretation and were verified by field surveys. A total of 790 sites were indicated on 1:25.000 topographic maps, which covered the Devon side of the Culm Natural Area. The sites were found in a highly fragmented pattern across the area (Figure 4.1). These sites, however, were remnants of much larger areas and therefore care has to be taken when using these to identify the characteristics of the full range of sites. This issue is addressed in more detail in Section 5.4. The Culm grassland sites in Cornwall were not available in digital format and could therefore not be included in the analysis. The implications are discussed in Section 5.4.

2. **Ten metre interval contour maps, scale 1:50,000, covering the Culm Natural Area.**

The following thirteen digital sheets of Ordnance Survey 1:50,000 Land Form Panorama Contour map (OS, 1999; 2000) were combined into one map and used to derive a Digital Elevation Model (DEM): Sheet SX08, SX28, SX48, SX68, SX88, SS20, SS40, SS60, SS22, SS42, SS62 and SS82. Both the contour map and the DEM of the Culm Natural Area are presented in Figures 4.2 and 4.3. The conversion from contour lines into a hydrologically correct Digital Elevation Model was carried out using the TOPOGRID command in ArcInfo, which is based on a model of Hutchinson (1988). Spot-heights and location of lakes were taken into account in the interpolation. A cell size of 50 m was chosen to make sure the file size of the DEM would not be too large but enough detail was still available to describe the topography. Ordnance Survey uses the same resolution for DEM maps at this scale. Two separate halves of the DEM were derived from the contour map and later joined into one grid. To make sure the edges of the DEM were as reliable as the centre of the grid, a margin of 500 metres around the outside of the DEM was omitted. The outline of the Culm Natural Area was used to crop the DEM to the size of the study area. The resulting DEM could be used to derive topographic features such as slope, curvature and order of the streams.

3. **Soil maps**

Two soil maps at a scale of 1:25.000 were available for the area covered by the Culm grassland sites. The SS30 Holsworthy sheet (Harrod, 1978) and the SS61 Chulmleigh sheet (Harrod, 1981). Further, a 1:50,000 soil map of the Wolf, Thrushel, North Lew and Carey catchments (Harrod, 1988) was available. The SS30 sheet, which covers an area of 100 km^2 around Holsworthy, was digitised for this analysis with the permission of the Soil Survey & Land Research Centre. The 1:50,000 soil map was digitised by the Soil Survey & Land Research Centre based at Cranfield University. The two digital maps are presented in Figures 4.4 and 4.5. The SS61 sheet was not digitally available.

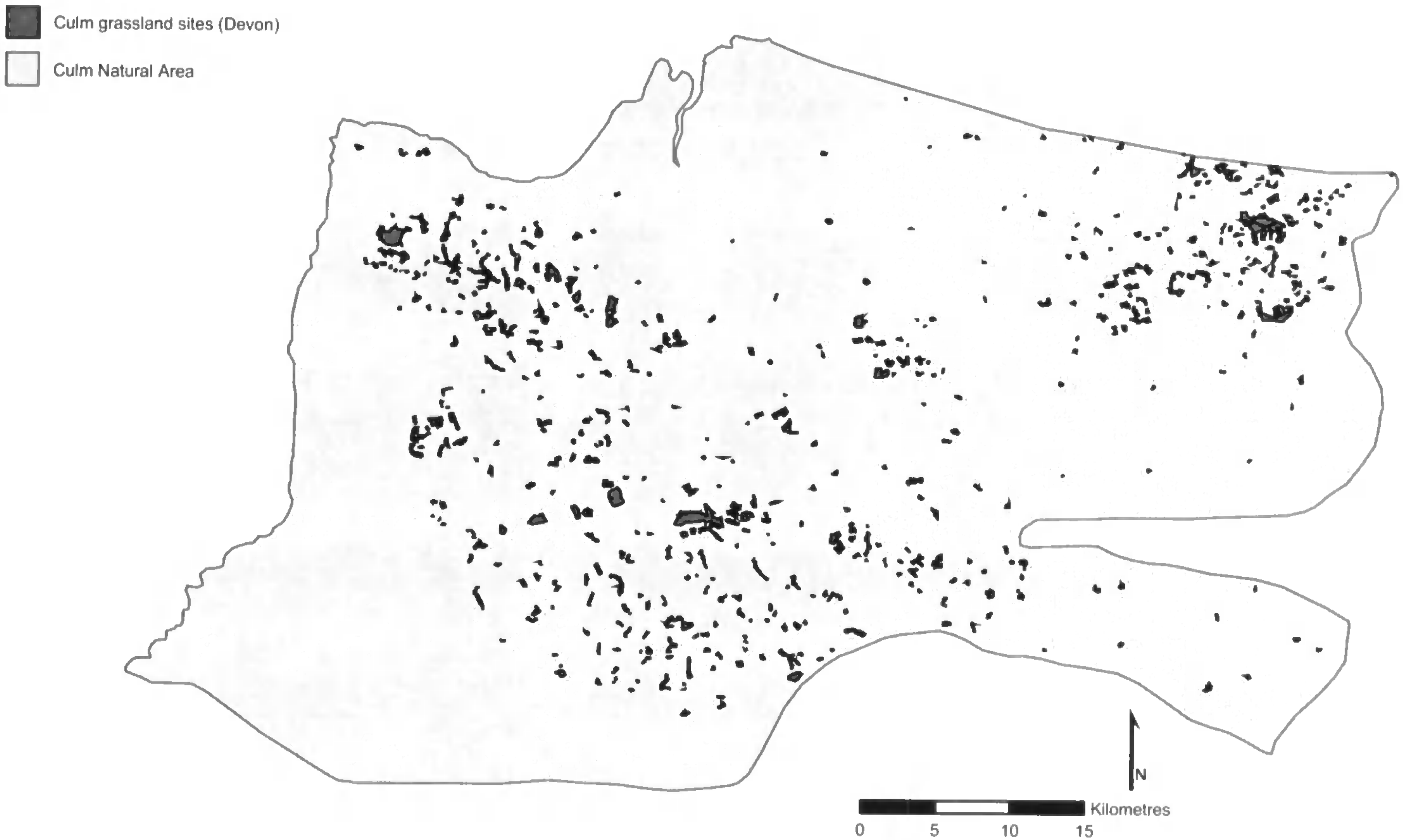


Figure 4.1 Location of the Culm grassland sites in Devon. Source: Devon Biodiversity Records Centre Culm grassland database (DBRC, 1998)

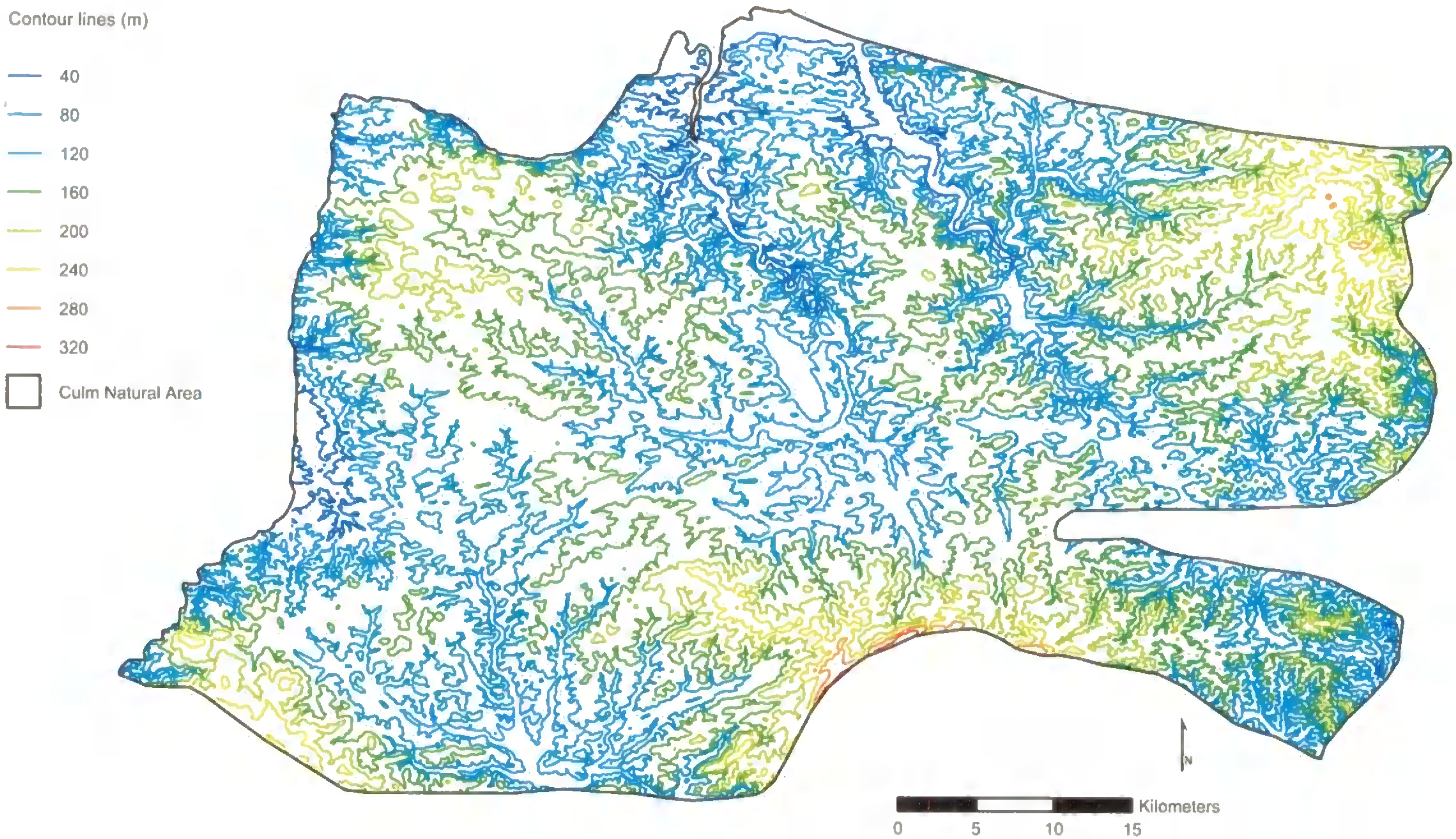


Figure 4.2 Contour lines for the Culm Natural Area (O.S., 1999; 2000)

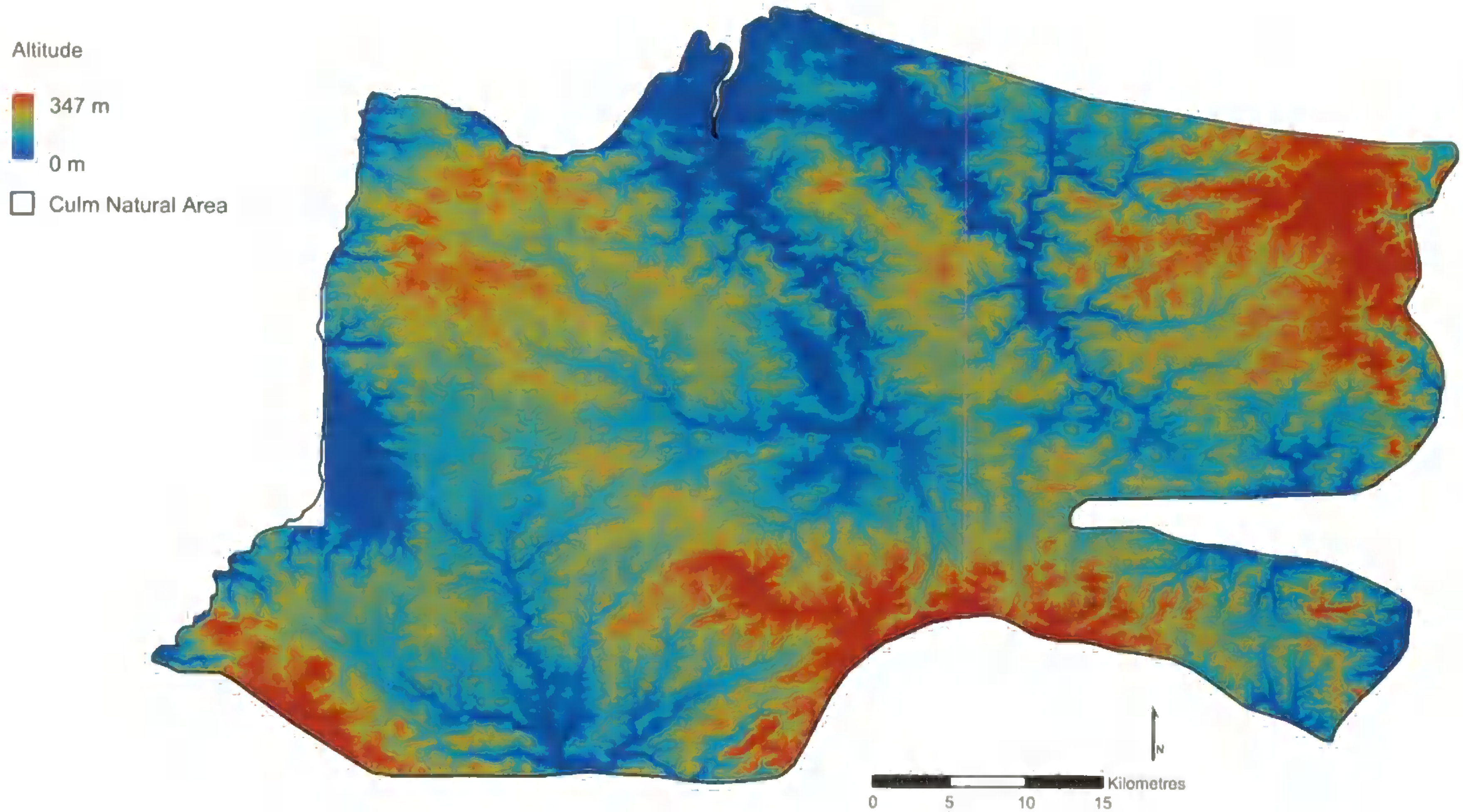


Figure 4.3 Digital Elevation Model (DEM) for the Culm Natural Area

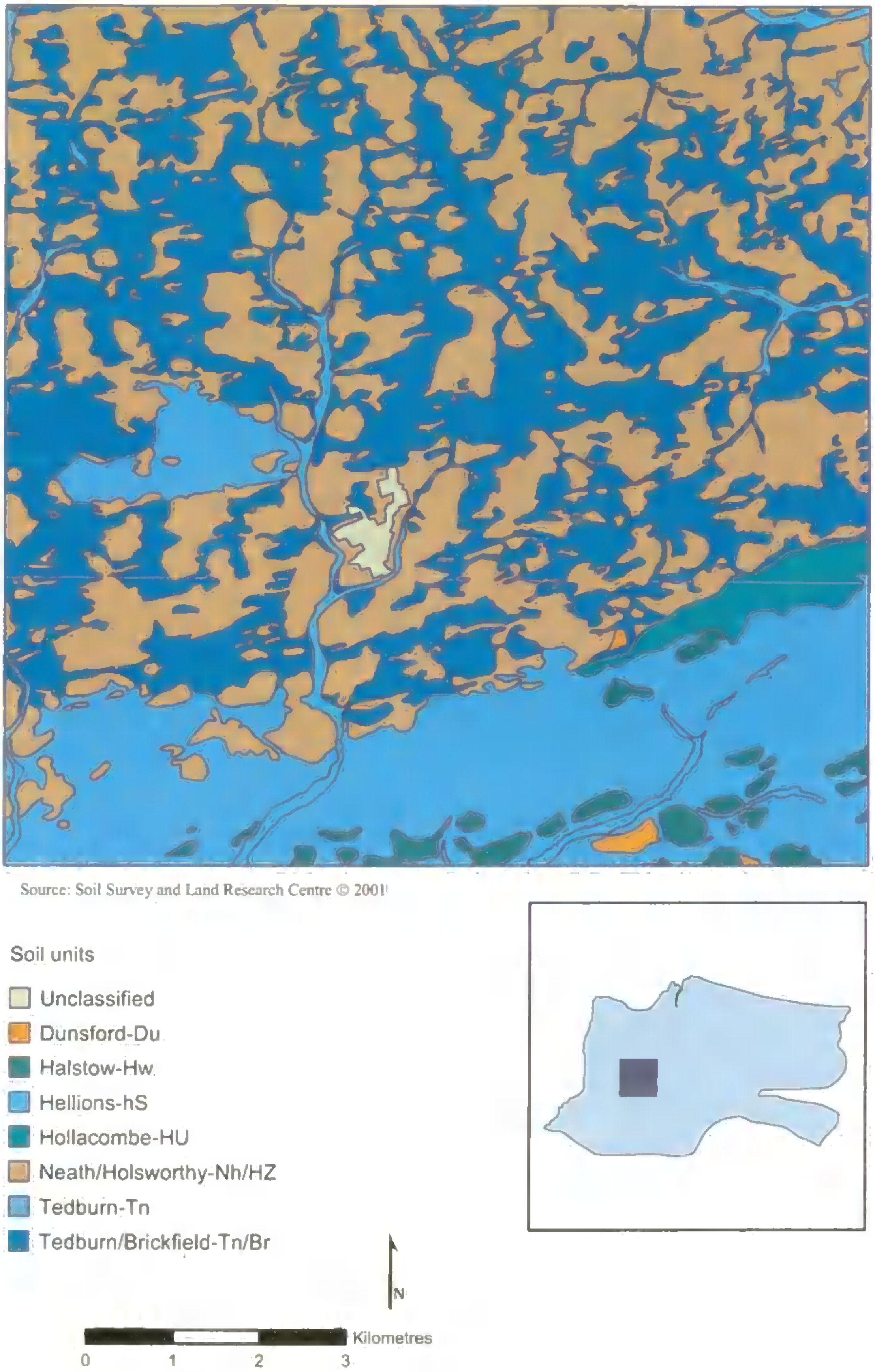


Figure 4.4 Soil map (1:25,000) of the Holsworthy area, sheet SS30 (Harrod, 1978)

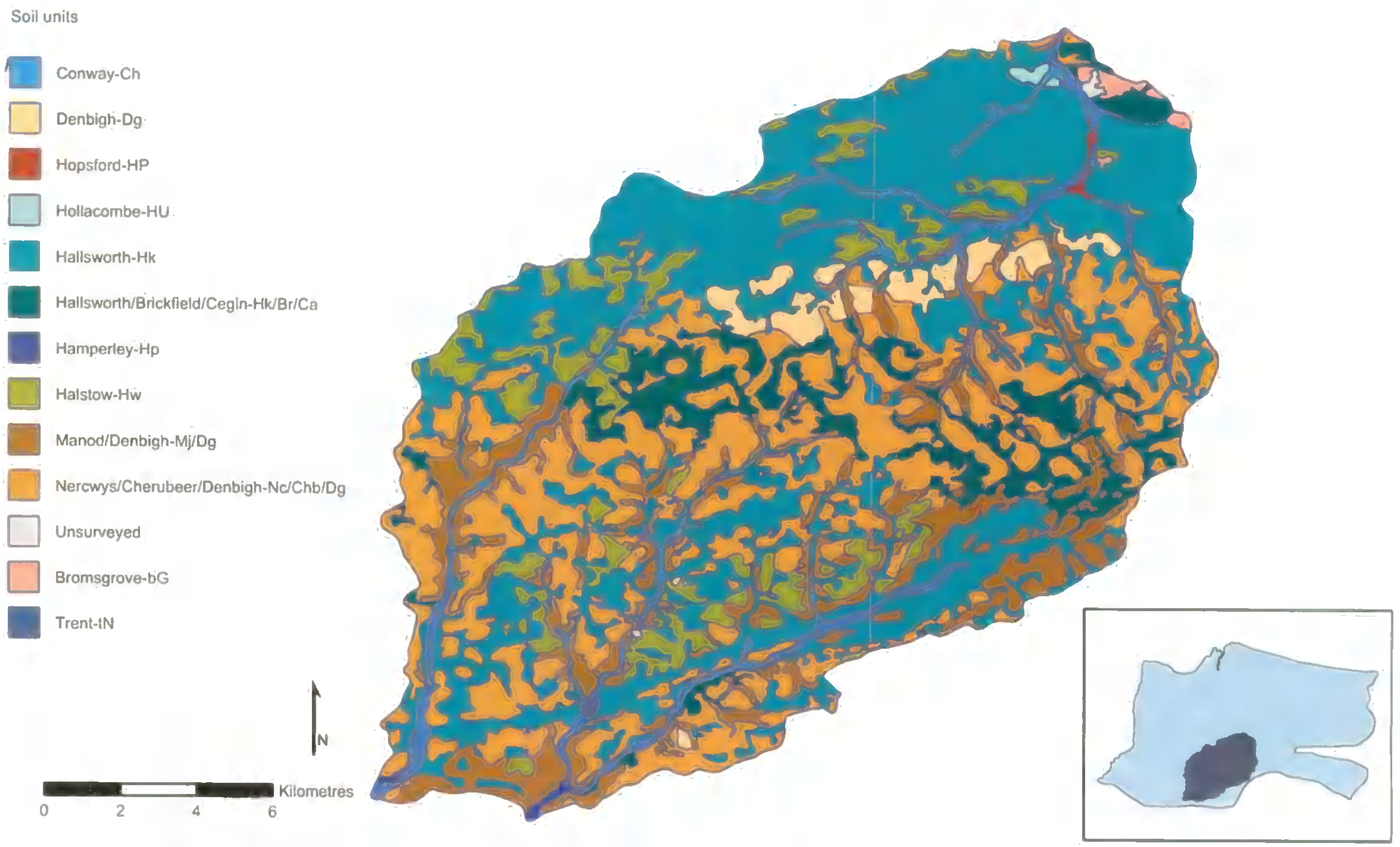


Figure 4.5 Soil map (1:50,000) of the Wolf, Thrushel, Carey and North Lew catchments (Harrod, 1988)

4.2.3 Topography and soil characteristics

To analyse the topographic features of the landscape, the DEM was used as a base map from which other maps were derived. A slope map was created which identified the maximum rate of change in value from each cell to its neighbours. The slope for each cell was calculated from the three by three cell neighbourhood using the average maximum technique (Burrough and McDonnell, 1998; Johnston, 1998). A grid representing the curvature of the landscape was created, indicating which parts of the landscape are concave, convex or flat. In calculating the curvature, once again, a three by three neighbourhood was taken into account. The direction of flow and the upslope contributing area were used to indicate patterns of water movement through the landscape. For each cell of the DEM, the most likely direction of flow, based on surface topography, was calculated. From this raster map, a new grid was derived, which showed the amount of water flowing through each cell, expressed as number of upstream cells.

A stream network was derived from the flow accumulation grid by selecting all cells which have more than 100 upstream cells (Jenson and Domingue, 1988). The order of streams was assigned using Strahler's method in which all headwater streams are referred to as first order streams. When two first order links intersect, the down slope stream is assigned an order of 2. When two second order streams intersect, the down slope stream is assigned an order of 3, etc. Only when two streams of the same order intersect will the order increase (ESRI, 1999). The location of Culm grassland was studied in relation to the stream network. From the grids with the direction of the flow and a grid, which indicates all points where streams join, a grid was derived indicating all the watersheds at the lowest level. By assigning the stream order to all these micro-watersheds, a distinction was made between headwater watersheds and watersheds, which were located closer to the main streams.

All raster maps that were created gave information on the landscape features found in the area. To be able to describe the characteristics of the landscape at the Culm grassland sites, the grids were overlaid with the digital Culm grassland map. For most grids, a classification was needed and the frequencies of the categories of both the total Culm Natural Area and the Culm grassland sites were compared, using the χ^2 test statistic. The actual number of cells (i.e. frequencies) in each category were derived from the Culm grassland sites and the expected number of cells from the total Culm Natural Area. Due to the differences in the total number of cells, the expected numbers were calculated based on the number of Culm grassland cells. The frequencies were transferred to distributions and displayed in column charts for visual comparison. Maps were also visually examined.

An overlay of the SS30 soil map with the Culm grassland sites was made to determine whether Culm sites were associated with particular soil types. Areas of each soil type under Culm grassland were calculated and compared to the total soil map area using χ^2 test.

4.3 Hydrological modelling

4.3.1 Modelling of catchment hydrology and model selection criteria

To explain the location of existing Culm sites and to be able to predict sites where Culm grassland is likely to develop, knowledge of the 'wet' and 'dry' areas in the landscape was needed. Although a range of plant species is found on Culm grassland sites which are adapted to various environmental conditions, generally these wet grassland sites are associated with relatively wet locations. However, a quantification of the term 'wet' is needed. To model wetness patterns and duration of soil saturation, a catchment study was carried out. This part of the study did not aim to describe the hydrological processes in great detail or to obtain very precise information on the various components of the water balance, but sought to develop a picture of relative wetness patterns in the catchment. A large number of models exist for simulation of catchment hydrology, varying from very basic to very detailed and from the very small scale (<1 km^2) to regional scale (>100 km^2), but all are based on the components of the water balance. Essentially, the models can be divided into deterministic models, which simulate the physical processes that transform precipitation into runoff in the catchment, and stochastic models, which describe hydrological time series of measured variables and take into account the probability distribution of the variables (Ward and Robinson, 1990; Shaw, 1994).

A number of criteria were set up for the model selection:

1. The model should be suitable for medium sized catchments (1 - 100 km^2).

The two catchments that were used in the modelling study are the Wolf catchment (± 11 km^2) and the Thrushel catchment (± 56 km^2). These catchments were selected because of the availability of discharge, rainfall, topographical and soil data.

2. The model should simulate surface water and shallow sub surface flow characteristics.

Previous research indicated that surface water was a major component of the water balance of Culm grassland (Papatolios, 1994). Earlier in this study, strong topography-vegetation relationships were found, indicating a potential for surface water modelling based on landscape topography.

3. Topography and physical soil characteristics should be included in the model inputs and the model should indicate soil water content or soil water characteristics of the topsoil, flow patterns and number of days with saturated soils.

The initial GIS study indicated topography and soil were important factors. Chapter 5 describes the results.

4. Model results should be suitable for linkage to a GIS system to allow comparison with Culm grassland locations.

Linking the catchment model to a GIS provides important advantages, because digital spatial data can be used as input into the model and the model output can be presented in the GIS system to be used in further spatial analysis. Only in a few advanced systems is a model actually incorporated in the GIS, but mostly the data can be transferred between the model and the GIS.

5. The model input requirements should not demand large detailed data sets.

The scale of the study does not allow extensive data collection and if the resulting DSS is to be applied by environmental and conservation agencies, data need to be readily available. The use of detailed field data, which need to be collected for every catchment, would require significant resources that would mostly not be available.

Three approaches that met these criteria were selected: the use of a topographic index (Section 4.3.2), modelling of the catchment hydrology with the use of TOPMODEL (Section 4.3.2) and the classification of soils with the Hydrology Of Soil Types classification (HOST) (Section 4.3.3).

4.3.2 The topographic index and TOPMODEL

In this study the relationships between Culm grassland location, topography and surface water characteristics were further investigated with the aid of a topographic index and

TOPMODEL. Kirkby (1975) described the following topographic index, which represents the chance of any point in the catchment to develop saturated conditions:

$$a/\tan\beta \qquad \textit{Equation 4.1}$$

In which:

a = upslope contributing area per unit contour (m^2)

β = local slope angle (°)

With this index, hydrology is described purely on the basis of catchment topography and no other hydrological processes are taken into account. It functions on the principle that the more land is situated above a particular point, and the gentler the slope at that point, the more water should collect in that position. O'Loughlin (1981, 1986) presented a similar relationship between wetness and topography, expressed as:

$$Q_b/Sb \geq T \qquad \textit{Equation 4.2}$$

In which:

b = the length of the contour element (m)

Q_b = the local drainage flux ($m^3\,day^{-1}$)

S = the local hillslope gradient ($m\,m^{-1}$)

T = the soil transmissivity ($m^2\,day^{-1}$)

This relationship assumes local saturation at any point in a catchment will occur whenever the drainage flux from upslope exceeds the capacity of the soil profile to transmit the flux (Moore *et al.*, 1988). Beven and Kirkby (1979) embedded the a/tanβ topographic index in TOPMODEL, a semi-distributed rainfall-runoff model, in the form of:

$$\ln(a/\tan\beta) \qquad \textit{Equation 4.3}$$

or

$$\ln(a/T_0\tan\beta) \qquad \textit{Equation 4.4}$$

to include transmissivity of the soil (T_0).

The ln (a/tanβ) index was calculated for the Carey, Wolf, Thrushel and Lew catchments with GRIDATB (Beven *et al.*, 1994), which was adapted for this study to use a DEM of 2000*2000 cells. The 50 m resolution DEM, cropped to the size of the catchment, was used as input into the GRIDATB program. The output raster map with the topographic index values was compared to the location of Culm grassland sites in the area by using the χ^2 test and visual comparison of the distribution graphs and maps.

A further description of catchment hydrology was obtained with the use of TOPMODEL. TOPMODEL is based on the following simplifications (Beven, *et al.*, 1994):

1. The dynamics of the saturated zone can be approximated by successive steady state representations
2. The hydraulic gradient of the saturated zone can be approximated by the local surface topographic slope, tanβ
3. The distribution of downslope transmissivity with depth is an exponential function of storage deficit or depth to the water table.

The model is widely accepted and has been tested in many studies (e.g. Beven *et al.*, 1984; Hornberger *et al.*, 1985; Wood *et al.*, 1988 and Ambroise *et al.*, 1996) and has been linked to grid-based GIS such as GRASS (Chairat and Delleur, 1993) and WIS (Romanowicz *et al.*, 1993). Inputs to the model were rainfall, potential evapo-transpiration and discharge data. In this thesis, TOPMODEL was applied to the Wolf and Thrushel catchment, because for these basins the necessary data were available and no additional field measurements needed to be conducted. The climatic and discharge data were obtained from the Environment Agency.

TOPMODEL (Beven *et al.*, 1995), was used to simulate river discharge and period of soil saturation. For both catchments, two periods were modelled on a daily basis. Daily rainfall data were available from local meteorological stations at Roadford, which was used for the Thrushel catchment, and at Higher Brockscombe, which was used for the Wolf catchment. Evaporation data were derived from the MORECS (Meteorological Office Rainfall and Evaporation Calculation System) database supplied by the Environment Agency. No detailed measurements on evaporation (E) were available, but values were estimated in mm day^{-1} from monthly values with the following equation (Beven *et al.*, 1995):

$$E = E_{min} + 0.5 * ((E_{max} - E_{min}) * (1 + \sin(2\pi * (Julianday / 365 - 0.5\pi))))$$ *Equation 4.5*

The topographic index maps for the Wolf and Thrushel catchments were calculated from a DEM with 20 by 20 m cells, which was derived from the 1:50,000 contour map (Section 4.3.1). The model was run for a high discharge period (Thrushel: 5/10/95 to 29/6/96; Wolf: 12/10/95 to 25/06/96) and a low discharge period (Thrushel: 1/7/96 to 13/10/96; Wolf: 26/06/96 to 22/10/96). The rainfall for both stations in 1995 and 1996 was lower than the long-term average rainfall recorded (Table 4.1). However, in the 1995 - 1999 period, for which all data were available, the rainfall amounts of the year 1995/1996 were comparable with the long-term average. Further, rainfall was assumed to be uniform over the catchment, because of the limited number of rainfall measuring stations in the area. Thereby, a small error in the order of 3% was introduced, which was calculated from the difference in rainfall between the rainfall station at the outflow point of the catchment and the a station more centrally located in the catchment. However, this error was not expected to affect the results significantly.

	1995	1996	Long term average
Wolf	1079	1108	1183 (year 1977-1999)
Thrushel	1021	1058	1136 (year 1988-1999)

Table 4.1 Rainfall (mm year^{-1}) in the Wolf and Thrushel catchments

In 1995, the minimum and maximum evaporation values were 0.38 mm d^{-1} and 3.46 mm d^{-1} and for 1996 the minimum and maximum values were 0.58 mm d^{-1} and 3.13 mm d^{-1} (EA, 2000b). The estimation of soil saturation patterns was achieved by fitting the river discharge curves to the measured discharge of the Rivers Thrushel and Wolf. The model was run with a number of different parameters until the optimum parameter set had been found. The parameter sets used for the two study catchments and the two modelling periods will be presented later in this thesis in Table 6.5 (Section 6.4.1). A saturation index was calculated by the total number of days of saturation divided by the total number of simulation days. Results of the study were related in a GIS to the wet grassland locations and distributions of the saturated zones for the wetlands and were compared to the total frequency distribution in the catchment, using χ^2 tests.

4.3.3 Hydrology of Soil Types (HOST)

The surface water hydrology of a catchment largely depends on soil physical and shallow groundwater characteristics. More information on soil hydrological functioning was needed to provide a base for the DSS set up. Therefore the Hydrology Of Soil Types (HOST) classification system (Boorman and Hollis, 1990; Boorman *et al.*, 1991; 1995) was applied to the 1:50,000 soil map of the Carey, Wolf, Thrushel and North Lew basins (Harrod, 1988). HOST was designed to classify the units of the 1:250,000 scale soil map (Soil Survey of England and Wales, 1983). The classification distinguishes 29 HOST categories, based on six soil-hydrological characteristics: **(i)** soil hydrogeology (distinction between permeable, slowly permeable and impermeable substrates), **(ii)** depth to aquifer or groundwater, **(iii)** presence of a peaty topsoil, **(iv)** depth to a slowly permeable layer, **(v)** depth to gleyed layer and **(vi)** integrated air capacity, which is the average percentage air volume over a depth of 1 m.

HOST categories were assigned to the map units of the soil map for the area. A problem existed in the difference in scale of the original HOST classification, which was designed for the 1:250,000 soil map, and the scale of the soil map it would be applied to. The problem was solved by comparing the HOST class distributions for the units of the 1:250,000 soil map to the profile descriptions of the identically named soil series of the 1:50,000 map. The soil series always corresponded with the largest HOST class within the map unit. If no identically named soil unit existed, a different unit, which included the particular soil series, was selected and the HOST class was assigned based on the profile description.

Table 4.2 describes the HOST categories found in the study area. Distributions of the HOST classes under Rhôs pasture sites and the total study area were compared in a GIS to find preferential positions. χ^2 tests were carried out to assess the significance of the differences between the distributions.

The outcomes of the topographical and hydrological analyses are presented in Chapters 5 and 6. These results determined which methods were used to select suitable Culm grassland restoration sites. Integration of the methods to describe hydrology and the results of the vegetation analyses (Part 3) are presented in Chapter 10.

HOST	Description
3	No impermeable or gleyed layer within 100 cm.
	Substrate hydrogeology: weakly consolidated, macroporous, by-pass flow uncommon.
	Groundwater or aquifer normally present at >2 m
8	Impermeable layer within 100 cm or gleyed layer at 40-100 cm.
	Substrate hydrogeology: unconsolidated, microporous, by-pass flow common.
	Groundwater or aquifer normally present at ≤2m.
9	Gleyed layer within 40 cm.
	Substrate hydrogeology: unconsolidated, microporous, by-pass flow common.
	Groundwater or aquifer normally present at ≤2m.
	Saturated hydraulic conductivity < 1 m day^{-1}.
10	Gleyed layer within 40 cm.
	Substrate hydrogeology: unconsolidated, microporous, by-pass flow common.
	Groundwater or aquifer normally present at ≤2m.
	Saturated hydraulic conductivity ≥1 m day^{-1}.
17	No impermeable or gleyed layer within 100 cm.
	Substrate hydrogeology impermeable.
	No significant groundwater or aquifer.
21	Impermeable layer within 100 cm or gleyed layer at 40-100 cm.
	Substrate hydrogeology: slowly permeable.
	No significant groundwater or aquifer. Integrated air capacity ≤ 7.5%
24	Gleyed layer within 40 cm.
	Substrate hydrogeology: slowly permeable.
	No significant groundwater or aquifer.
97	Unsurveyed

Table 4.2 HOST classes found in the study area (Boorman et al., 1995)

Chapter 5

Culm grassland site characteristics and landscape topography

5.1 Introduction

Culm grassland sites in the south-west of England are found in a scattered pattern across the Culm Natural Area (CNA) (Chapter 2). The location of these grasslands largely depends on wet or moist soil conditions for large periods of the year (Wolton, 1992), which is mainly related to climatic factors, soil characteristics and topography on a regional scale. The first objective of this study was to determine the characteristics of the Culm grassland environment on the landscape scale. Examining the relationships at this level was important because part of the aim of the study was designing a Decision Support System (DSS), which would function at the same scale at which policy decisions are made. The criteria for the identification of potential restoration sites needed to be valid for the total CNA and had to make use of easily obtainable data at a landscape scale. Therefore, it was very important that this study identified relationships valid for a whole range of sites found in the region and did not just focus on one or a few isolated sites, which could have resulted in decision-making rules unique to the studied sites.

Rainfall and temperature in the area vary from the coast to further inland areas (Section 3.3). Everywhere in the region annual precipitation exceeds the evapotranspiration, resulting in an annual water surplus (Findlay *et al.*, 1984). The spatial variability of excess water on a regional to national scale is mainly determined by climatic factors. The hydrological processes on a local to regional scale and the distribution of soil water within the area, however, depend largely on geology, soil conditions and topographic factors. This chapter describes the characteristics of the Culm grassland sites (Section 5.2) and the relationships between Culm grassland location and topographic factors (Section 5.3). A short discussion of the results follows in Section 5.4. Topographic information for the area was available from digital Ordnance Survey 1:50,000 contour maps with 10 m interval contour lines. The information was combined with the Culm grassland locations in a GIS to investigate the importance of topographic factors. Detailed comparisons between the sites and the total study area were made and the significance of the differences in distribution of the topographic parameters was tested with the χ^2 test, which compares observed to expected frequencies.

5.2 Site characteristics of Culm grassland

5.2.1 Culm grassland fragment size and distribution

Figure 5.1 shows the distribution of Culm grassland sites at the Devon side of the CNA. The Cornish sites were not digitally available and were therefore not used for the GIS analysis. There are 789 fragments of Culm grassland on the Devon Wildlife Trust (DWT) database, which were mapped with the aid of aerial photographs, topographic maps and field observations (Section 4.2.2). Inevitably, some sites, especially smaller ones, were missed and other sites with 'non-Culm' plant communities might have been included. Also, the data were gathered by a large number of people, which caused inconsistencies. However, this extensive data set was the best result that could be achieved with the resources available to the Wildlife Trust. It was an essential input for the work presented in thesis and given the size and the extent of the data set small errors were likely to be of little significance.

The sites had variable characteristics, in terms of size, ownership and management. A histogram with the number of sites per area group is presented in Figure 5.2. The average size of the fragments was approximately 5.1 ha (median: 2.5 ha), but sizes varied from 80 m^2 to 185 ha. 3.9 % of the sites were smaller than the grid cell size of 2500 m^2 used in the GIS and those sites were therefore represented by a single value for the topographic data analysis. On a field scale, the sites, however, were unlikely to be uniform. This small percentage of the total number of fragments, which would be even smaller when expressed as area percentage, was unlikely to affect the results significantly. The scale at which the work was completed meant that it was inevitable that some of the detail observed in the field would be lost in the GIS. A smaller grid cell size could not be used, because of limited computer capacity.

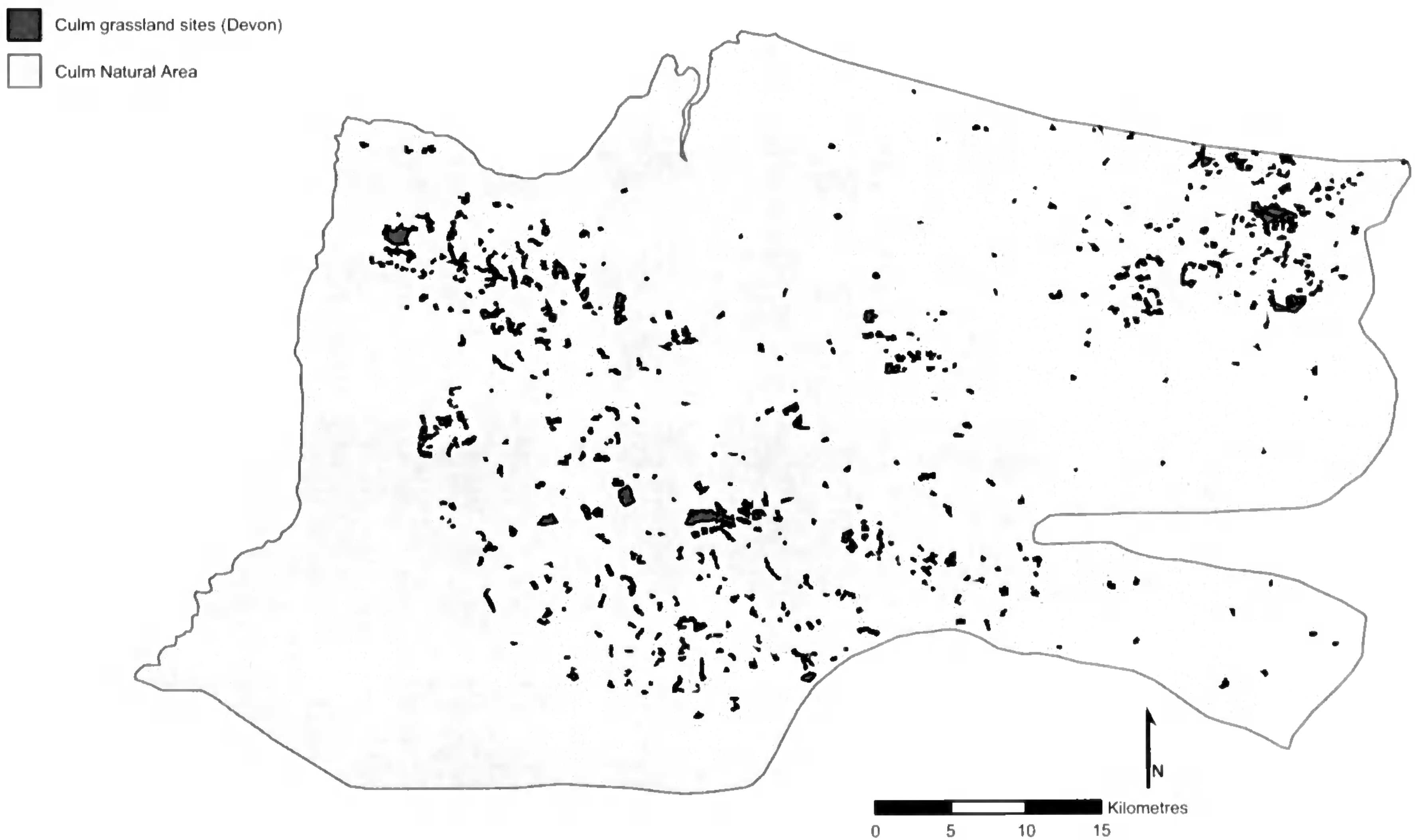


Figure 5.1 Location of the Culm grassland sites in Devon. Source: Devon Biodiversity Records Centre Culm grassland database (DBRC, 1998)

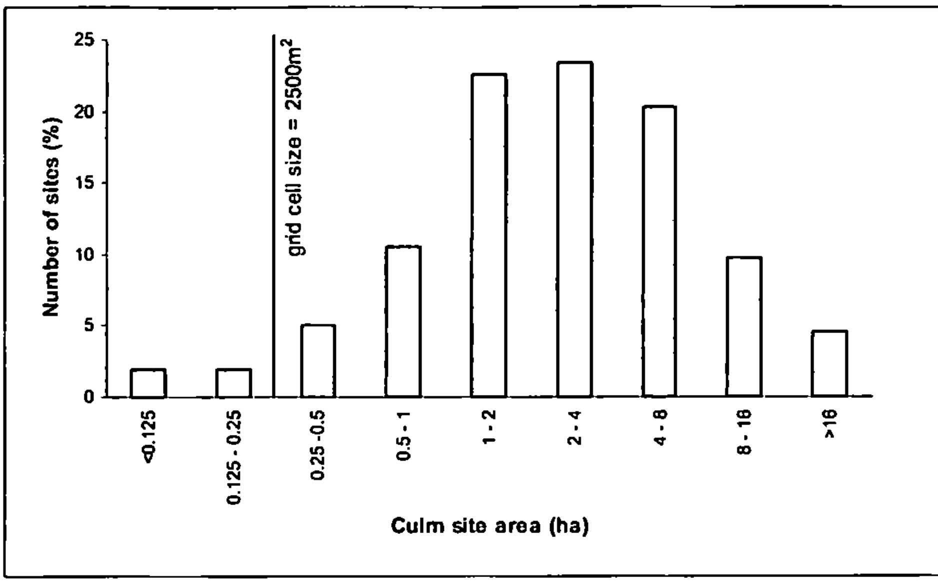


Figure 5.2 Histogram of the percentage of sites in each area group

5.2.2 Vegetation records related to site area

The information on vegetation available for this study existed for 359 of the sites of the database of the DWT (Section 4.2.2). However, there was a large variation in the quality of the data. Vegetation of the sites had been surveyed during the 1980s for different purposes, by various botanists and with diverse sampling strategies. The original mapping and surveying of the sites was carried out to obtain an overview of the Culm grassland sites that were left in Devon (DBRC, 1998). Only a small number were owned by conservation organisations like the Wildlife Trust and English Nature and were benefiting from management practices focused on Culm grassland conservation and maintenance of biodiversity. The rest of the sites were privately owned and only some of these were protected under various management agreements, like the Countryside Stewardship Agreement (CSA).

The number of species listed per site varied from 1 to 112, with an average of 24. Although the varying data quality could affect the results of further floristic data analysis, it was the most extensive database available on Culm grassland and would provide a base for further sampling strategies. To find whether a correlation existed between the number of species listed per site and the area, the correlation coefficient was calculated with Spearman's rank test. This non-parametric test was selected because the data were not normally distributed. A significant ($p < 0.001$) but very weak positive correlation between number of species and site area was found ($r_s = 0.252$) (Figure 5.3). The average number of species found was 12 ha^{-1}, with a minimum of < 1 ha^{-1} and a maximum of 289 ha^{-1}.

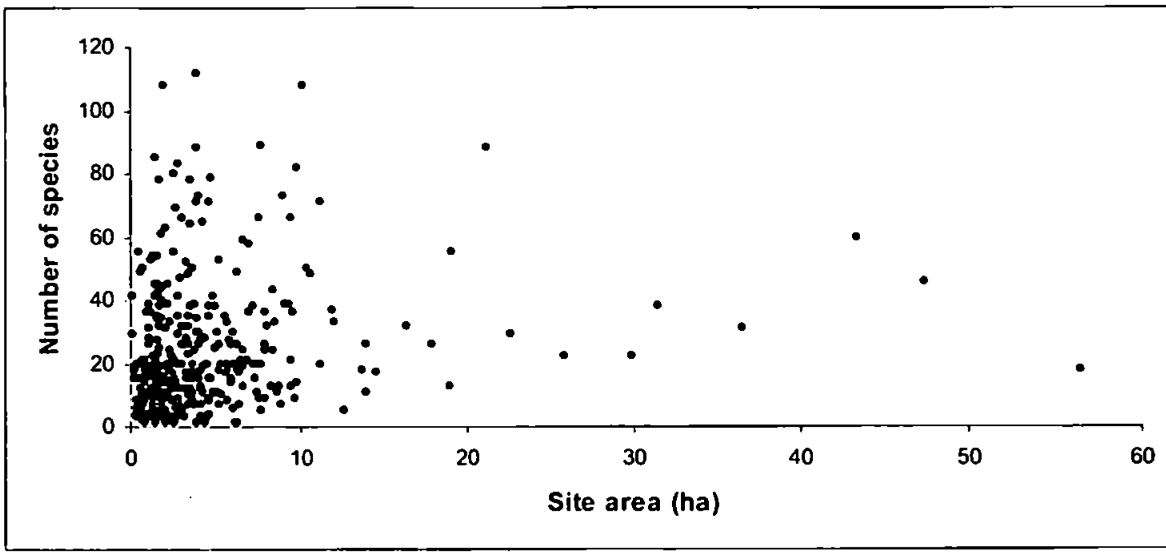


Figure 5.3 Scattergram of the number of species per site and the site area (one outlying value removed from graph for clarity, but not from the analysis)

To study the effect of the larger sites on the correlation between the site area and the number of species, the sites larger than 10 ha were removed from the analysis. Figure 5.4 shows the results. Although the data points appear scattered over the whole graph, Spearman's ranked correlation test still indicates a significant positive correlation (r_s = 0.207, $p < 0.001$). This correlation is most likely due to the very high number of observations (332) and related high number of degrees of freedom, which is expressed by the very low correlation coefficient.

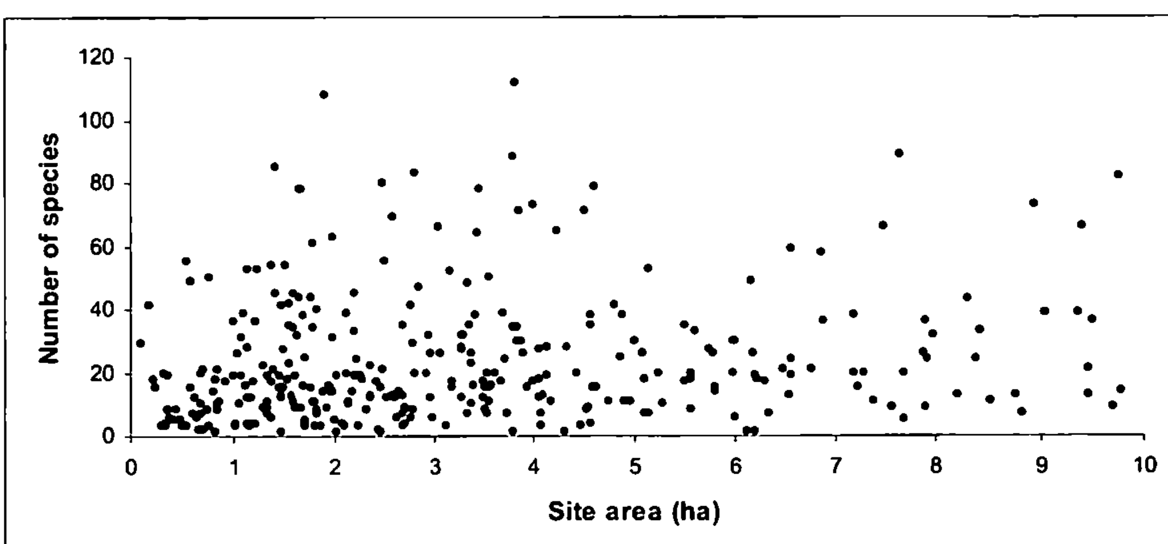


Figure 5.4 Scattergram of the number of species per site and the site area of sites smaller than 10 ha

5.3 Culm grassland in relation to topography

5.3.1 Introduction

Landscape topography is of major importance to catchment hydrology (Moore and Grayson, 1991; O'Loughlin, 1981, 1986; Moore *et al.*, 1988; Quinn *et al.*, 1991) and determines the occurrence of wet and dry areas in the catchment. The location of wetlands is directly related to areas that are saturated for large periods of the year. Relationships between site location and topography were investigated, to examine the possibilities for using digital elevation data to determine potentially suitable Culm grassland restoration sites. All topographic parameters were derived from a Digital Elevation Model (DEM) for the area. Relationships of the location of Culm grassland sites with elevation (Section 5.3.2), slope (Section 5.3.3), upslope contributing area (Section 5.3.4), slope curvature (Section 5.3.5) and the watershed order (Section 5.3.6) were studied. A few sites of the DWT database were situated just outside the Culm Natural Area (CNA) boundaries and, but for the analyses, only the sites within the CNA were taken into account.

All values for the topographic parameters presented in this chapter under Culm grassland were compared to the total CNA. Continuous data were classified into categories and the observed frequencies of cell values under Culm grassland in each category were compared to the expected frequencies based on the distribution for the total CNA. This approach assumed that if the location of the sites was not influenced by topography, the sites would be randomly distributed over the area and observed and expected frequencies could be expected to be equal. For the selection of the categories it was not possible to construct a continuous distribution. Classes were chosen after some experimentation on the results. Significance of the differences was tested with χ^2 tests. A further explanation is given in Section 5.3.2.

5.3.2 Altitude

The altitude of the CNA is presented in Figure 5.5 and ranges from sea level to 347 m. The distribution of altitudes under Culm grassland sites was compared to the distribution for the entire CNA. The results are presented in Figure 5.6. Table 5.1 presents the results of a χ^2 test comparing the observed altitude distribution (O) under Culm grassland sites to the expected distribution (E) based on the distribution of altitude classes in the CNA. The column with (O-E) represents the differences between the observed and expected values and the sum of $(O-E)^2/E$ gives the χ^2 test statistic.

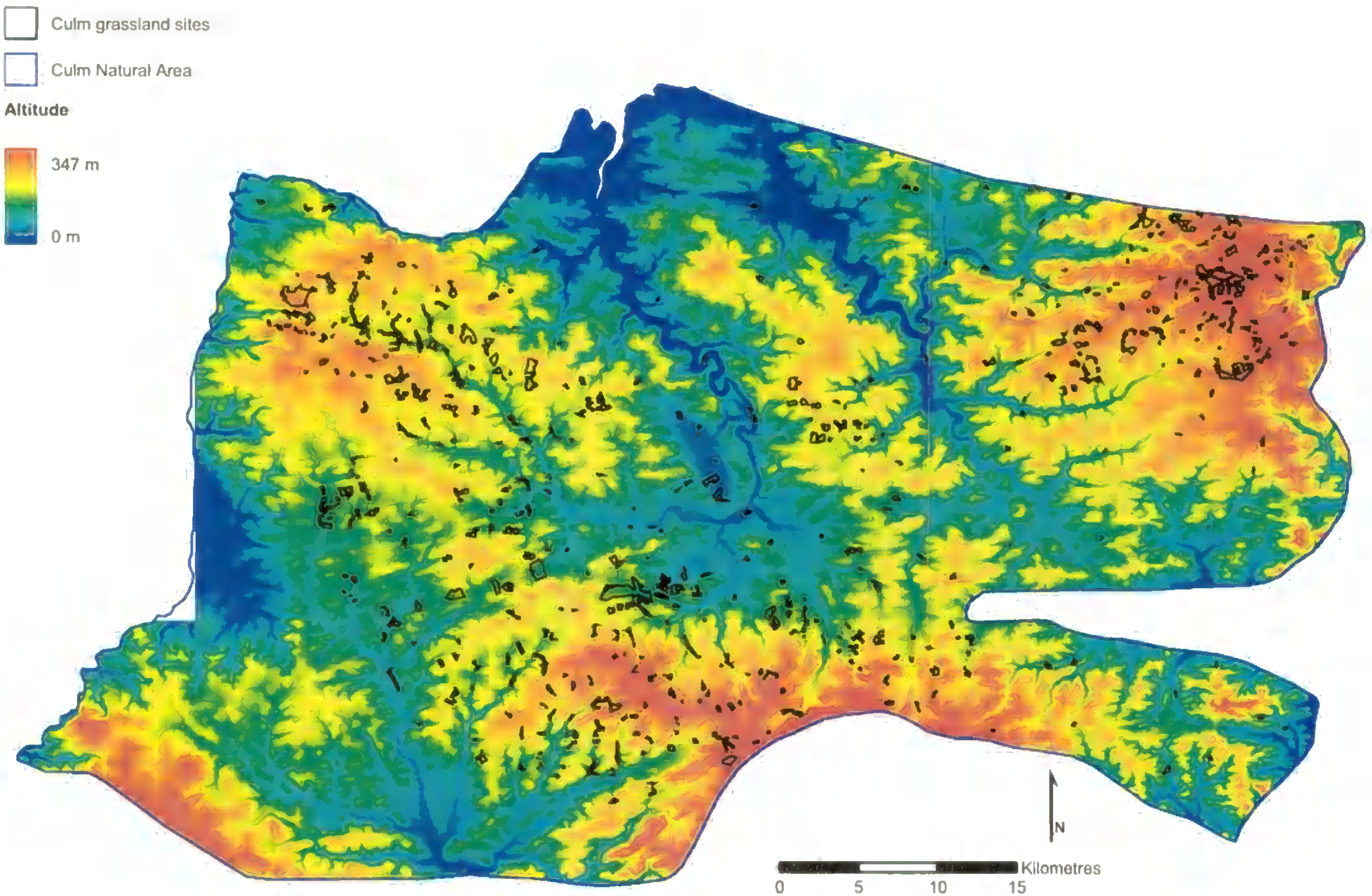


Figure 5.5 Altitude distribution of the Culm Natural Area and of the Culm grassland sites

The explained variance is calculated from the $(O-E)^2$ variance per category divided by the sum of all variances (Shaw and Wheeler, 1994). A significantly different distribution under Culm grassland sites was found ($p < 0.001$), with Culm grasslands showing a preference for the higher altitudes in the area. The difference was mostly explained (51.8%) by the presence of less sites in the range from 50-100 m and more sites in the range from 200–250 m (28.6% of the variance). Of the total area under Culm grassland, 56% is found at altitudes higher than 150 m compared to 41% of the area of the CNA.

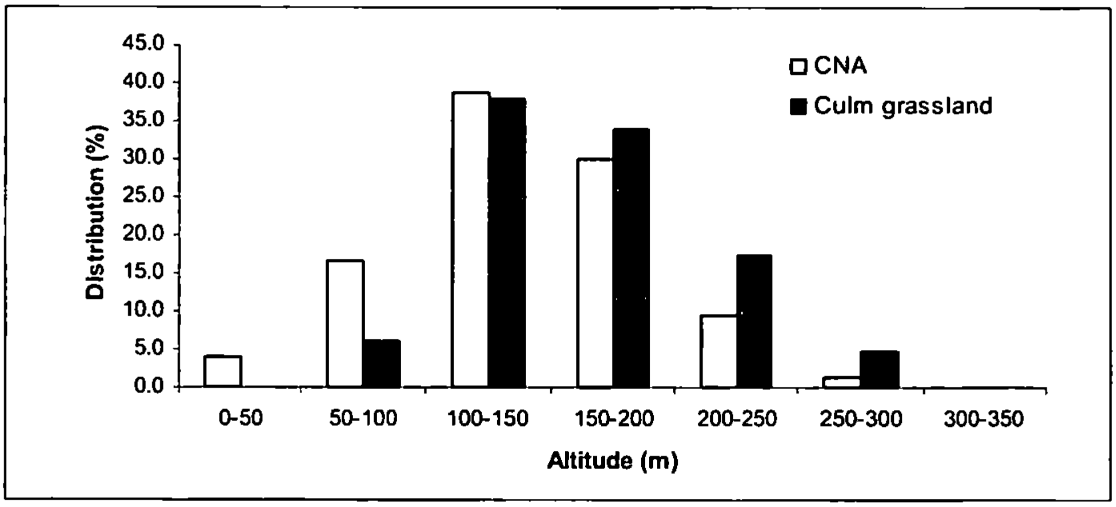


Figure 5.6 Altitude distribution of Culm grassland sites compared to the overall distribution of altitude in the Culm Natural Area (CNA)

Altitude (m)	Observed (O)	Expected (E)	(O-E)	$(O-E)^2/E$	*Explained variance (%)*
0-50	18	604	-586	568.3	6.8
50-100	898	2509	-1611	1034.6	51.8
100-150	5746	5848	-102	1.8	0.2
150-200	5132	4526	606	81.2	7.3
200-250	2617	1419	1198	1010.8	28.6
250-300	718	209	509	1240.4	5.2
300-350	0	14	-14	13.8	0.0

Table 5.1 Results of the χ^2 tests for comparing the altitude distribution under Culm grassland sites to the altitude in the total Culm Natural Area. $\chi^2 = 3951$. $p < 0.001$.

5.3.3 Slope

Surface gradients are an important factor influencing soil water patterns and hydrological pathways (Beven, 1986; Anderson and Burt, 1990). Together with other factors like physical soil characteristics, vegetation cover and human impact, the slope determines the amount and type of overland flow and subsurface stormflow (Anderson and Burt, 1990) and therefore also the extent of saturated zones in the catchment (O'Loughlin, 1986). Also, groundwater flow is affected by the surface gradient if the shallow subsurface flow is parallel to the land surface. Hence, the surface gradient was expected to be an important discriminator for wetland location and therefore the relationship between the two was studied.

Figure 5.8 shows the slope angle (°) derived from the DEM, with the Culm grassland sites overlaid on top. Culm grassland sites were found to be associated with flat or gently sloping areas. This is confirmed by comparing the distributions found under Culm grassland to the slope distribution found in the total CNA. Figure 5.7 presents both distributions and a clear preference for the lower slope angles can be observed. Approximately 76% of the sites were found on slopes less than 4°, whereas 52% of the slope angles of the CNA fell into this category. The difference in distributions was tested with a χ^2-test (Table 5.2) and proved to be significant ($p < 0.001$). The difference was mostly explained (55.8%) by more sites in the range from 1-3° and less sites in the range from 6-9° (12.4% of the variance).

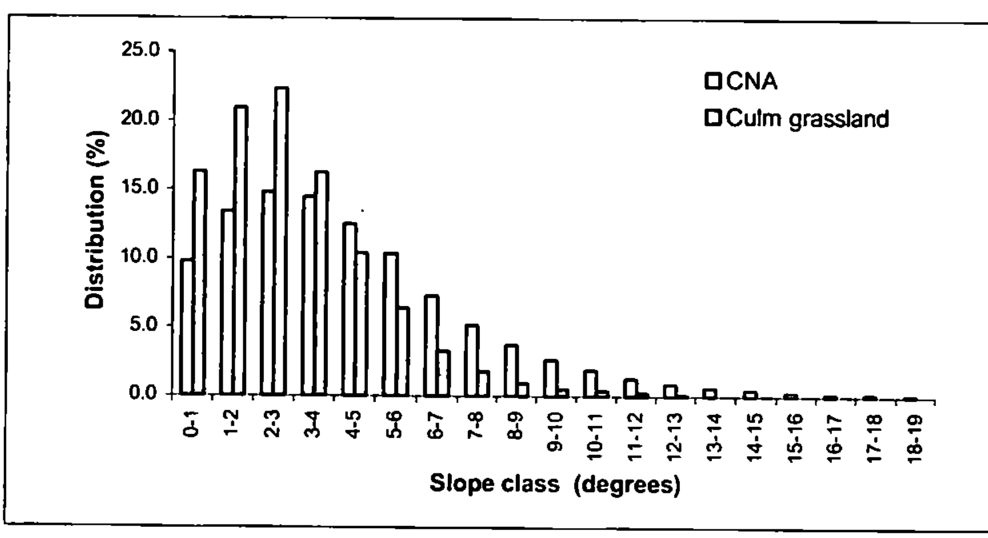


Figure 5.7 Slope distribution (percentage) under Culm grassland compared to the overall distribution in the Culm Natural Area (CNA)

Slope class (°)	Observed (O)	Expected (E)	(O-E)	$(O-E)^2/E$	*Explained variance (%)*
1-3	9016	5743	3273	1865.0	55.8
3-6	5001	5634	-633	71.2	2.1
6-9	905	2446	-1541	971.1	12.4
9-12	185	882	-697	551.2	2.5
12-15	21	297	-276	256.0	0.4
15-18	1	89	-88	87.0	0.0
18-21	0	27	-27	27.1	0.0
21-24	0	8	-8	7.6	0.0
24-27	0	2	-2	2.3	0.0

Table 5.2 Results of the χ^2 tests for comparing the slope class distribution under Culm grassland sites to the total Culm Natural Area. $\chi^2 = 3839$. $p < 0.001$.

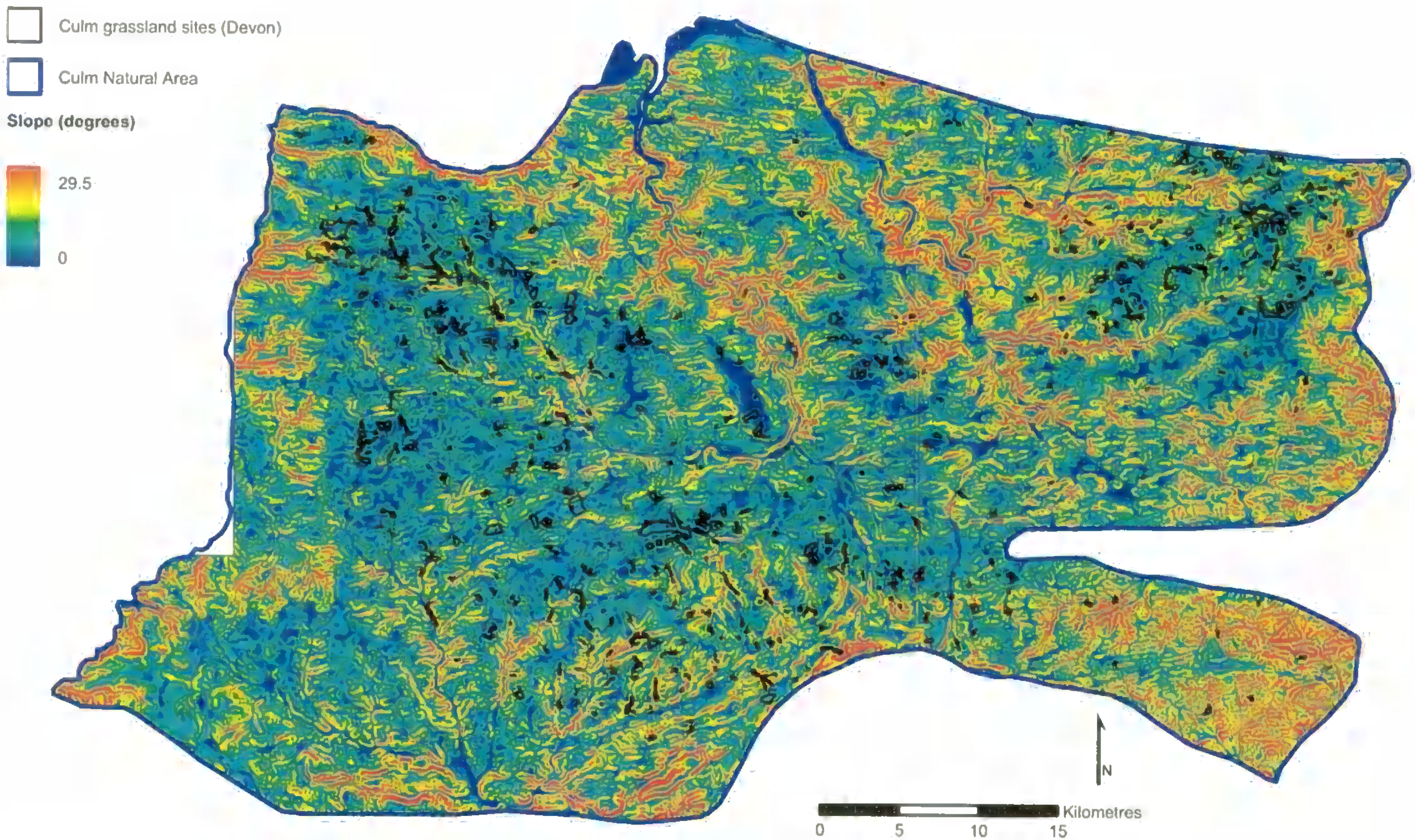


Figure 5.8 Slope (degrees) distribution of the Culm Natural Area and of the Culm grassland sites. The chosen colour scheme is non-linear, because of the skewed nature of the data.

5.3.4 Upslope contributing area

The upslope contributing area gives an indication of how much of the land is expected to drain through a specific point (Anderson and Burt, 1990; Burrough and McDonnel, 1998). For each location in the catchment the upslope area from which the water will drain through this location can be calculated. This area can be regarded as a sub-catchment within the bigger catchment and assumes that water drainage is purely controlled by topography. This topographic factor has been incorporated in several catchment hydrology models (O'Loughlin, 1986; Quinn *et al.*, 1995), as a measure of the amount of water received by a certain point, if rainfall in the area was uniform. It was therefore expected that an association of Culm grassland with wet locations in the landscape would be demonstrated with a large amount of sites situated on positions with high upslope contributing areas compared to the proportion of high upslope contributing areas in the total CNA.

Figure 5.9 presents the location of the Culm sites in relation to the distribution of the upslope contributing area. Figure 5.10 shows a preference of Culm sites for areas which have more than 10,000 m^2 upslope contributing area. Table 5.3 shows that the distributions for Culm grassland sites and the CNA were found to be significantly different (χ^2: $p < 0.001$). Of all the sites, 50 % were found in areas with over 10,000 m^2 upslope contributing area, which only covers 30% of the total CNA (Figure 5.5). The difference was mostly explained (70.1%) by fewer sites with an upslope contributing area of 2500 m^2 or less and more sites with an upslope contributing area of 1–2 ha (19.6% of the variance) and larger than 25 ha (11.2% of the variance). Grid cells with an upslope contributing area of more than 25 ha were classified as drainage channels, although the streams in this area are generally narrower than 50 m (grid cell width). The Culm grassland sites in this category should thus be interpreted as being situated adjacent to streams.

Upslope area (ha)	Observed (O)	Expected (E)	(O-E)	$(O-E)^2/E$	*Explained variance (%)*
0	1969	3518	-1549	681.7	48.9
0 - 0.25	1743	2761	-1018	375.6	21.2
0.25 - 0.5	1588	2021	-433	92.7	3.8
0.5 - 1	2316	2333	-17	0.1	0.0
1 - 2	2436	1765	671	254.8	9.2
2 - 4	1677	964	713	528.3	10.4
4 - 8	973	515	458	407.2	4.3
8 - 16	597	297	300	302.1	1.8
16 - 25	276	143	133	124.3	0.4
> 25	1554	812	742	677.5	11.2

Table 5.3 Results of the χ^2 tests for comparing the upslope contributing area distribution under Culm grassland sites to the total Culm Natural Area. $\chi^2 = 2767$. $p < 0.001$.

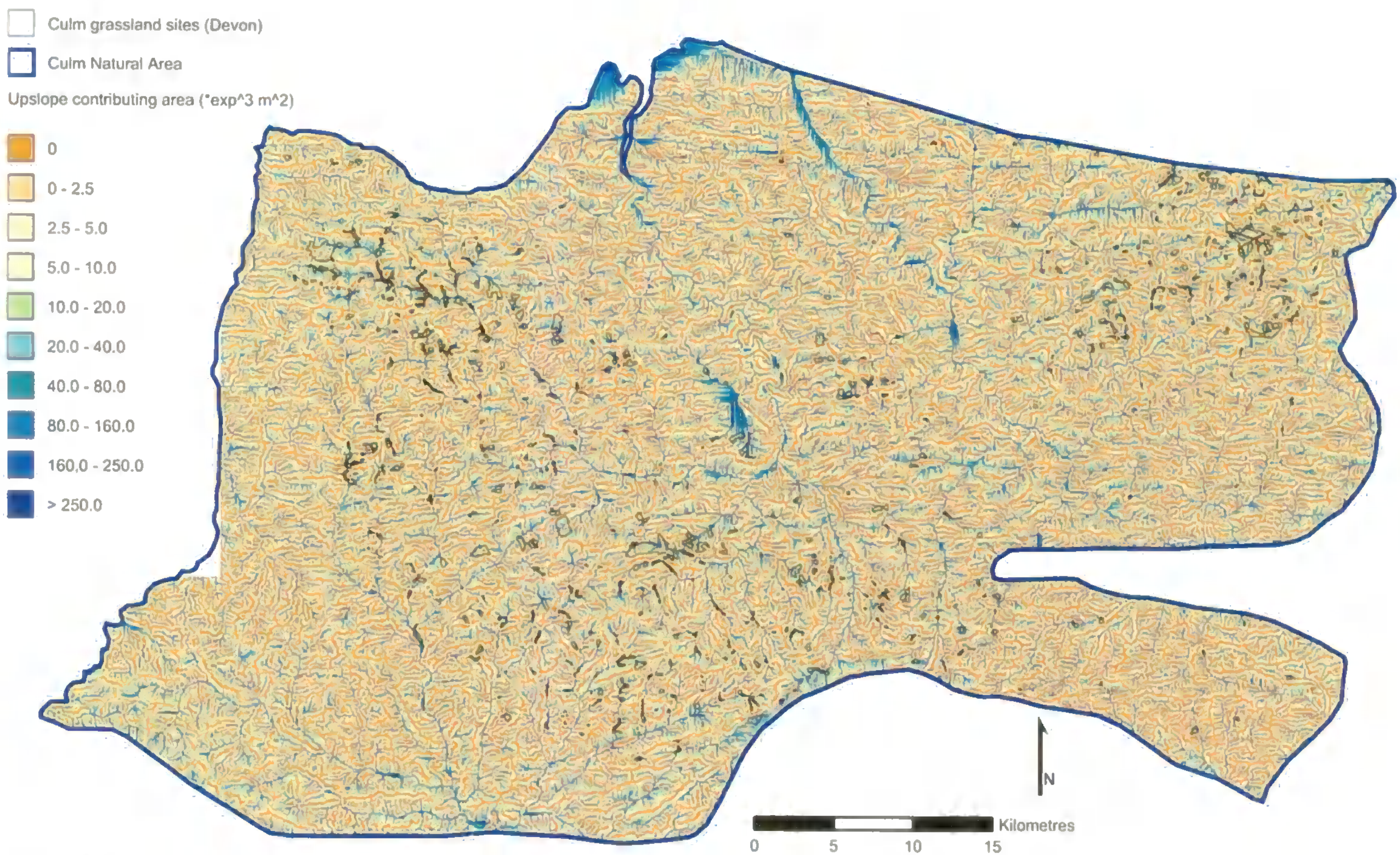


Figure 5.9 Upslope contributing area of the Culm Natural Area and of the Culm grassland sites

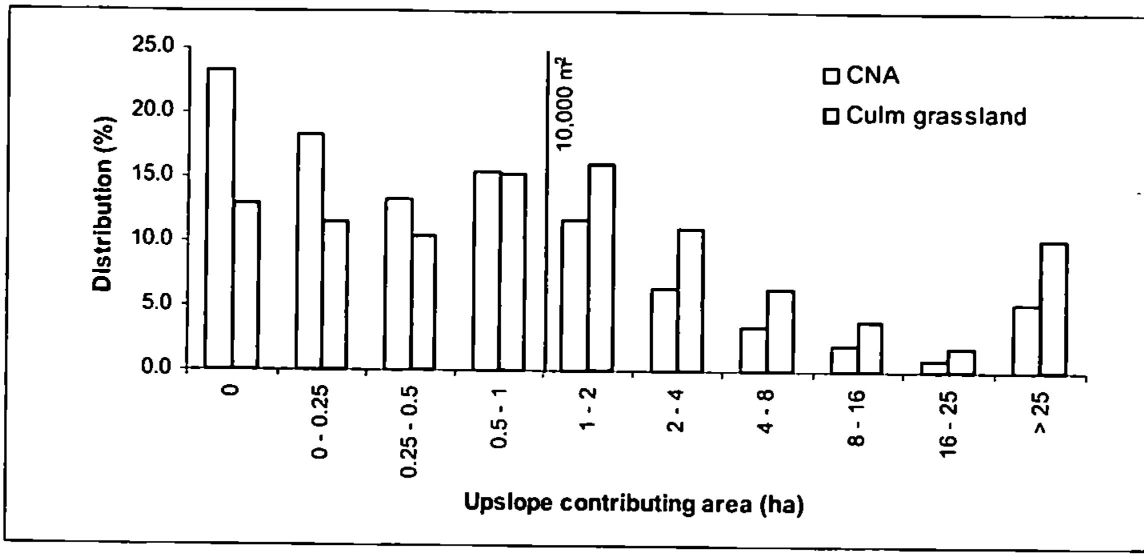


Figure 5.10 Upslope area distribution (m^2) under Culm grassland compared to the overall distribution in the Culm Natural Area (CNA)

5.3.5 Curvature

The curvature of the land surface is another important aspect determining the water flow in the landscape. It determines where converging and diverging water flows appear, which are related to respectively 'wetter' and 'drier' conditions. The curvature was calculated from the DEM and, as before, values for Culm grassland sites were compared to values for the total CNA. Negative values for the curvature indicated that the cell is upwardly concave at that point and positive values indicate an upward convexity (ESRI, 1999). A curvature of zero indicated a straight slope. In this case, profile and plan curvature were considered together. Figure 5.11 and Figure 5.12 show the results. As was expected for wetland sites, a preference for concave areas was found, 66% compared to 45% for the total CNA. The distributions of the straight slopes were similar and fewer sites than expected were found on convex areas. Table 5.4 shows that a significant difference between the two distributions was found with a χ^2 test ($p < 0.001$).

Curvature	Observed (O)	Expected (E)	(O-E)	$(O-E)^2/E$	*Explained variance (%)*
concave	9932	6737	3195	1515.6	47.1
flat	549	363	186	95.8	0.2
convex	4648	8030	-3382	1424.2	52.7

Table 5.4 Results of the χ^2 tests for comparing the curvature distribution under Culm grassland sites to the total Culm Natural Area. $\chi^2 = 3036$. $p < 0.001$.

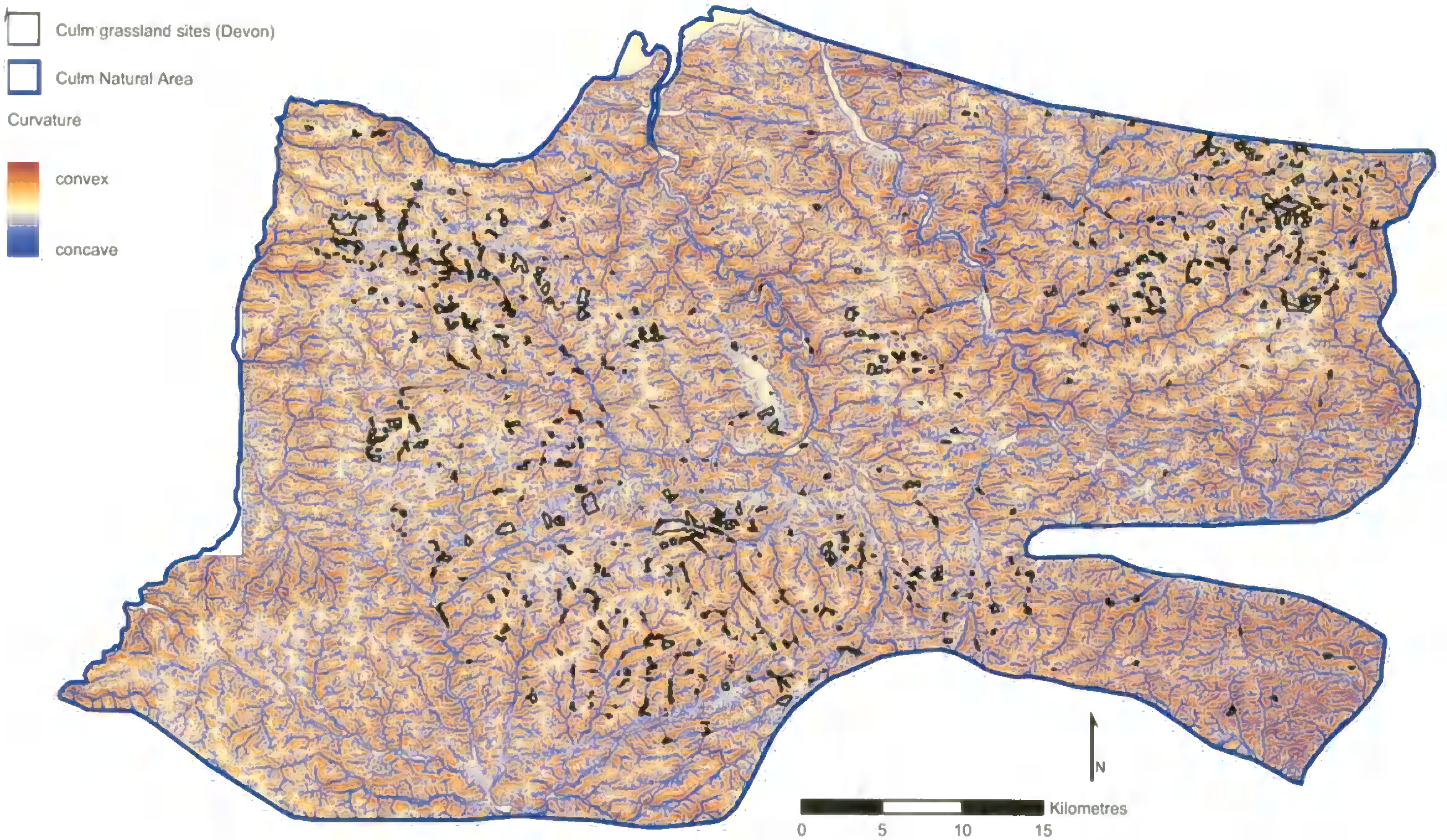


Figure 5.11 Curvature of the Culm Natural Area and of the Culm grassland sites

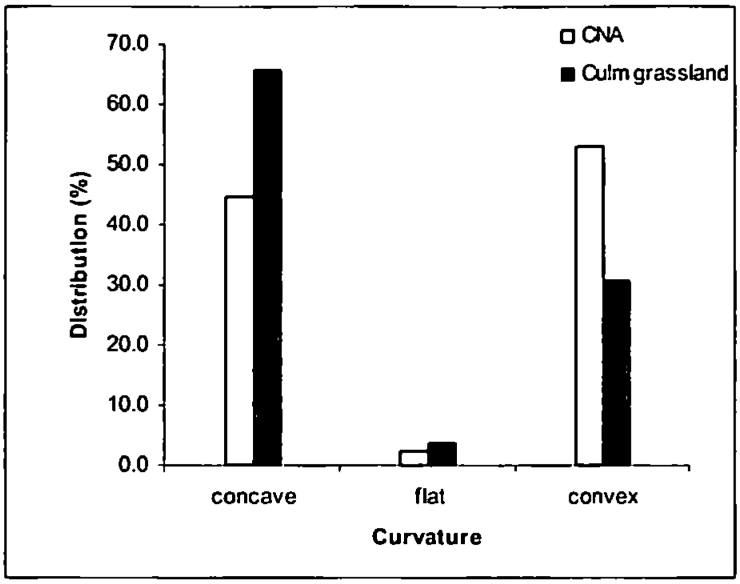


Figure 5.12 Curvature of the landscape under Culm grassland compared to the overall distribution in the Culm Natural Area (CNA)

5.3.6 Stream and watershed order

Culm grassland sites were mostly referred to by local conservationists as a headwater vegetation type. This was confirmed by visually examining Figure 5.9, which showed the Culm grassland sites in relation to the drainage network. To investigate whether this could be determined from the digital elevation data, the catchments were classified according to the order of the streams (Figure 5.16). The catchment order was derived from the order of the streams which were assigned using Strahler's method (Figure 5.13). In this method, the stream order increases when streams of the same order join. The intersection of two first order stream will create a second order stream, whereas when a first and a second order stream join, the stream remains a second order stream rather than create a third order stream (Strahler, 1957; 1975). Strahler's method was given preference to Shreve's method (Figure 5.14), in which all streams with no tributaries are assigned an order of 1 and when two streams intersect, their orders are added and assigned to the downstream section (Shreve, 1966). Comparison between stream orders with Shreve's method would have been more complicated because of the large difference in magnitudes that are possible. Shreve's method could be regarded as a measure for the drainage density and Strahler's method as a measure for discharge.

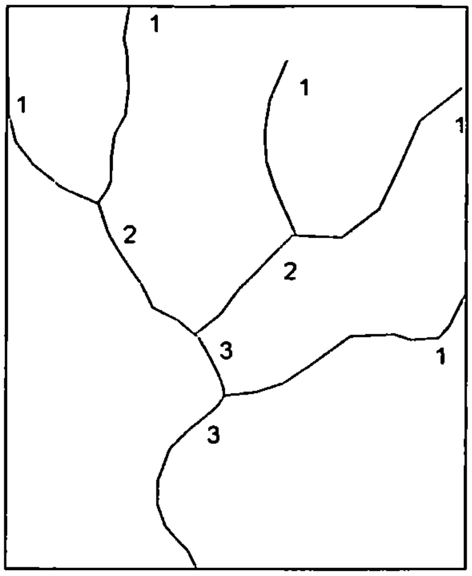


Figure 5.13 Strahler's stream order method, which was used in this thesis

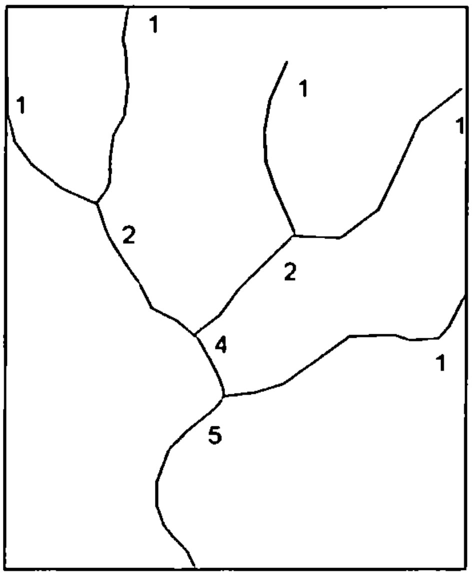


Figure 5.14 Shreve's stream order method

Figure 5.16 shows Culm grassland sites in relation to catchment order. Generally the sites are found in locations with low order catchments. The result of the χ^2 test (Table 5.5) to compare the distributions under the sites with the total CNA confirms this observation, indicating a significant difference in distribution ($p < 0.001$). Most of the variance is explained by more Culm grassland sites in watersheds of the order 2 and less in the order 3 to 6. However, visually, there is not much difference between the histograms for the sites and for the whole CNA (Figure 5.15).

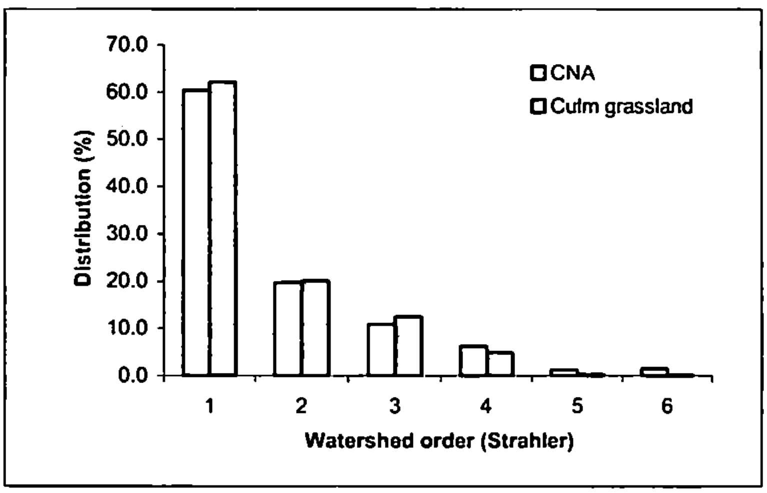


Figure 5.15 The order of the watersheds (Strahler's method) of the landscape under Culm grassland compared to the overall distribution in the Culm Natural Area (CNA)

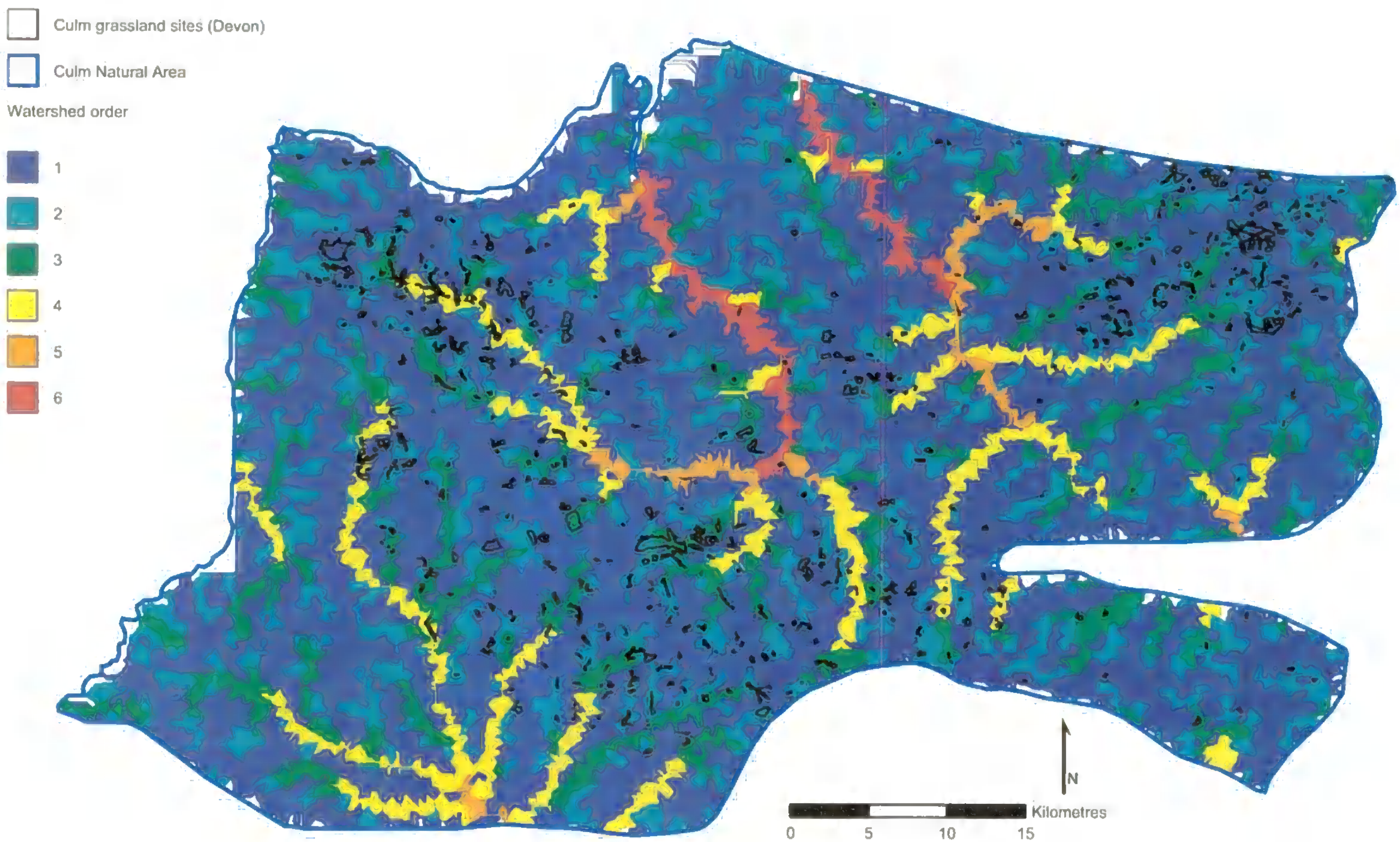


Figure 5.16 Order of the watersheds (Strahler's mthod) of the Culm Natural Area and of the Culm grassland sites

Watershed order	Observed (O)	Expected (E)	(O-E)	$(O-E)^2/E$	*Explained variance (%)*
1	9396	9129	267	7.8	28.9
2	3041	2976	65	1.4	1.7
3	1878	1635	243	36.1	24.0
4	734	952	-218	49.8	19.3
5	33	190	-157	130.1	10.1
6	30	229	-199	173.3	16.1

Table 5.5 Results of the χ^2 tests for comparing the watershed order distribution under Culm grassland sites to the total Culm Natural Area. $\chi^2 = 399$. $p < 0.001$.

5.4 Discussion

The results presented in this chapter showed a clear preference of Culm grassland for specific topographic positions. The distributions observed under the Culm grassland sites were compared to the distribution in the total CNA, by visually examining maps and histograms and by testing the data with χ^2 tests. Although all tested factors were significantly different, χ^2 tests are not as powerful as the parametric or non-parametric tests comparing two sets of data. For this study, no other statistical test could be used, because the large number of grid cells (over 10^6) meant that the data could not be treated as individual numbers and therefore had to be converted to a limited number of categories. Therefore, no continuous data set was available and a frequency table had to be created to generate a suitable format for statistical analysis.

One limitation of the study is that it was entirely based on existing sites. Large areas of Culm grassland have disappeared, due to agricultural improvement, mainly drainage, and therefore the sites that remained were probably the most difficult ones to improve. This implies that only a limited range of original Culm grassland sites has been studied in this research. No historical information on Culm grassland location was available. However, historical maps from the beginning of the twentieth century (e.g. OS, 1907) indicate locations of generally marshy areas. The lack of information of the former extent of Culm sites might result in an under-estimation of the sites suitable for Culm grassland restoration. It is likely that the prediction of potentially suitable restoration locations involved mainly the sites at the wetter end of the spectrum. However, as these sites were the least useful for agriculture they are the most likely to be reverted to (semi-) natural plant communities. For habitat restoration, the gradient and spectrum of sites from wet to dry land is also important for maintaining biodiversity. Although the historical maps indicating marshland could not be used in designing decision rules for Culm grassland restoration, they could be used for testing the final Decision Support System. In the last part of the thesis, more details on the use of historical maps for verification of the selection of potentially suitable locations are presented. Further, the Cornish Culm grassland sites were not digitally available and were therefore not included in the analysis. However, for the total distribution of the parameters the total CNA including the Cornish side was used. The distribution of the topographical parameters in Cornwall was, however, similar to Devon and therefore the inclusion of the Cornish part of the CNA did not cause problems.

This part of the study was conducted to investigate general landscape topography characteristics of Culm grassland sites. The scale at which the work was conducted meant that not all detailed information observed at the field scale could be taken into account. Certain generalisations had to be made and some of the topographic characteristics could not be taken into account. For example, most Culm grassland sites occur on slopes of less than 4° and therefore this could be one of the discriminators for suitable restoration sites. However, some of the existing Culm grassland sites are found on areas with slopes larger than 4°, but they would be excluded because they do not meet the criteria. As a result, the selection will therefore be a general indication of preferential sites and does not imply that the sites are the only suitable restoration locations. A more detailed explanation of how this is dealt with in the set up of the DSS will follow in Chapter 9.

A further problem was that the DEM used in this study is a representation of the landscape, based on the interpolated of 10 m interval contour lines on a 50 m cell basis. To create a hydrologically correct DEM and to be able to derive hydrological parameters, all depressions were removed from the DEM. Local depressions present in the landscape are thus not represented in the DEM, but could be of major importance to vegetation patterns.

Another aspect related to this problem is the generalisation made by the decision to use a resolution of 50 m, excluding local variation within the diameter of a grid cell. If the whole region is considered, a uniform area of 2500 m^2, represented by one grid cell, is a reasonable assumption and the information from a map with this resolution can be regarded as very detailed. The same cell size was used by Dunn *et al.* (1998) for the hydrological modelling of a catchment of 548 km^2, by deriving similar topographic characteristics as were derived in this study. On the other hand, from the perspective of plant communities, large variations can occur on a scale of metres and therefore more detailed information would be desirable. This part of the study, however, aimed to study relationships between vegetation, topography and soils at the landscape scale and consequently a certain level of generalisation was needed. The overall results are unlikely to be considerably affected by small-scale variation, because the size of the sites that might have been missed are insignificant as compared to the total area of Culm grassland present in the region.

Further, the choice of 50 m cell size was based on the resolution of the original data and the available computer capacity. Increasing the resolution would have led to much longer calculation times and would have resulted in very detailed information that would have been difficult to interpret at the landscape scale. For a detailed process study, a finer resolution would have been necessary, but the detail of the resolution that can be achieved from 10 m interval contour lines is limited. Quinn *et al.* (1995) discussed the problems of DEM resolution on flow patterns in a catchment. DEMs of small catchments with a 50 m resolution tended to hide small streams in larger grid cells. It has to be considered, however, that computer-calculating time would increase exponentially when increasing the resolution. On the other hand, working with coarse resolutions could be desirable, especially if different spatial data sets need to be compared. Bian (1997), for example, showed the use of aggregation of spatial data to match biomass and elevation data. With the use of a very fine resolution, patterns only matched crudely. However, aggregation of the raster maps to create a coarser resolution resulted in corresponding operational scales, enabling comparisons between the two data sets to be made.

The results, presented in this chapter, have shown the potential to use a GIS to relate Culm grassland to digital elevation data. A 1:50,000 DEM provided suitable input data to derive topographical characteristics at a landscape scale. However, although the topographical relationships all showed significant results, topography is not the only driving parameter. More detailed information on the relationships between the position of Culm grassland and catchment hydrology is needed to be able to use topographical and soil information as base maps for further Culm grassland re-creation. Chapter 6 will, therefore focus on wetland location in correspondence to catchment hydrology and soil water patterns.

Chapter 6

Hydrological characteristics of Culm grassland

6.1 Introduction

The results presented in Chapter 5 demonstrated the importance of landscape topography for the location of Culm grassland sites. General topographic parameters were studied and sites were found on locations characterised by a topography related to 'wet conditions'. Favourable positions could be described by gentle slopes, on concave areas and locations with a medium to large sized upslope contributing area. This chapter addresses the second objective of the thesis to study Culm grassland location in relation to catchment hydrology. The relationships between the wetland sites and catchment hydrology are explored further in this chapter by studying those topographic parameters that are more directly related to catchment hydrology. The study was caried out in the watersheds of the Wolf, Thrushel, Carey and North Lew, which cover a section in the southern part of the Culm Natural Area (Figure 6.1). This area was chosen because of the availability of a 1:50.000 soil map and hydrological information for a number of gauging stations in the area. Further, the area was considered representative for the distribution of Culm grassland sites, because many are situated in the area and sizes of the sites are variable (Figure 6.1).

Section 6.2 describes the topography using a topographic index representing 'dry' and 'wet' landscape locations. This will be extended into a soil-topographic index by including soil drainage characteristics in Section 6.3. These two indices are used as a relative indication of soil water patterns. Section 6.4 will quantify the duration of soil saturation by applying the hydrological model TOPMODEL, to simulate river discharge and soil saturation for two simultaneous periods. This modelling exercise was conducted for the Wolf and Thrushel catchments only, because no discharge data were available for the other two catchments. A different approach to classifying the hydrological catchment characteristics was adopted by application of the Hydrology Of Soil Types (HOST) classification to the Wolf, Thrushel, Carey and North Lew watersheds, which will be presented in Section 6.5. A discussion of the results presented in this chapter follows in Section 6.6.

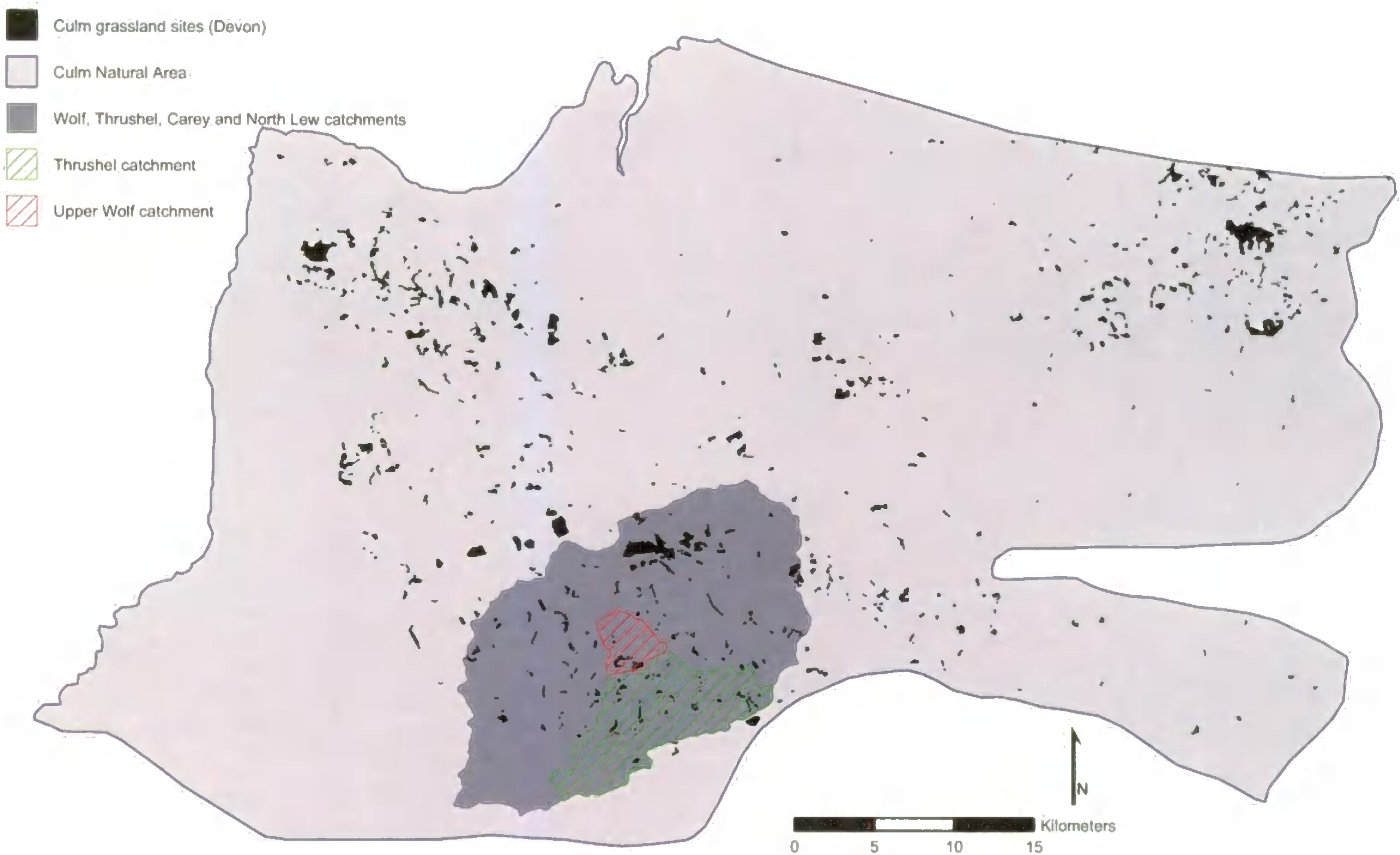


Figure 6.1 Location of the Wolf, Thrushel Carey and North Lew catchments. Shaded areas were used for the TOPMODEL modelling exercise.

6.2 Topographic index

As described in Chapter 4, Kirkby (1975) first introduced the $a/\tan\beta$ topographic index to provide an indication of the potential of any point in a catchment developing saturated conditions. In this equation, a is the upslope contributing area and β is the local slope angle. The logarithmic form of the index:

$$\textit{Topographic index}: \ln(a/\tan\beta) \qquad \textit{Equation 6.1}$$

was incorporated into the hydrological model TOPMODEL (Beven *et al.*, 1994) and has been widely used by many researchers (e.g. Quinn *et al.*, 1991; Kim and Delleur, 1997; Rodhe and Seibert, 1999).

In this study, the $\ln(a/\tan\beta)$ topographic index was calculated for the Wolf, Thrushel, Carey and North Lew catchments, which were selected on the basis of the availability of topographic, soil, river discharge and climate data. Calculations were made based on the GRIDATB module (Beven *et al.*, 1994) adapted for gridsize of 2000 by 2000 cells, using the DEM with 50 by 50 m cells as input data. The results are presented in Figure 6.2 and 6.3. The Culm grassland sites were overlaid on top of the topographic index map and distributions of the sites were compared to the total catchment area in a similar manner as in Chapter 5. Culm grassland sites occupied 2.7% of the total area of 29,946 ha of the Wolf, Thrushel, Carey and North Lew catchments.

Figure 6.2 presents a graphical comparison of the distributions and shows a shift for Culm grassland sites towards the higher topographic index values when compared to the total catchment. Preferences for sites with an index higher than nine were found. This indicated that Culm grassland sites were mainly found on locations where the upslope contributing area was high or the slope angle low. The frequencies of cells in each category were also compared with the aid of a χ^2 test, which indicated a significant difference ($p < 0.001$) between topographic indices found for Culm grassland and for all catchments together. Table 6.1 shows that most of the variance can be explained by significantly fewer sites in the 6-7 and 7-8 classes and significantly more in the 9-10 and 10-11 classes. These results indicate that Culm grasslands were related to topographic locations associated with wet conditions and that these relationships can be derived from digital elevation data.

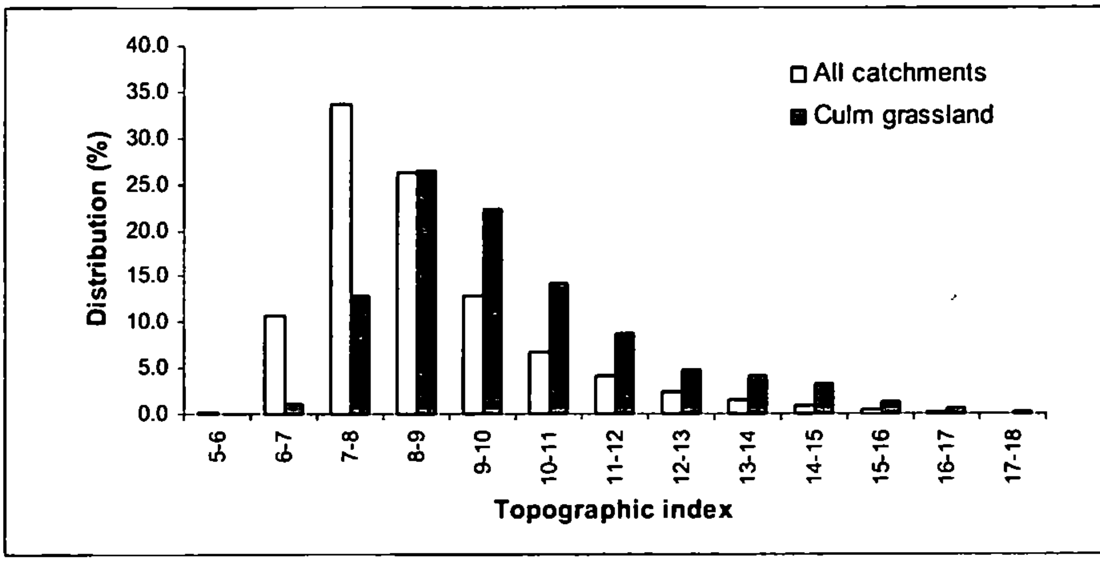


Figure 6.2 Ln(a/tanβ) topographic index distribution under Culm grassland compared to the Wolf, Thrushel, Carey and North Lew catchments

Ln(a/tanβ)	Observed (O)	Expected (E)	(O-E)	$(O-E)^2/E$	*Explained variance (%)*
5-6	0	8	-8	8	0.0
6-7	38	342	-304	270	12.8
7-8	411	1077	-666	412	61.4
8-9	845	838	7	0	0.0
9-10	712	411	301	220	12.5
10-11	453	221	232	245	7.5
11-12	279	130	149	170	3.1
12-13	156	76	80	83	0.9
13-14	133	47	86	156	1.0
14-15	102	29	73	184	0.7
15-16	45	15	30	57	0.1
16-17	24	8	16	35	0.0
17-18	9	3	6	13	0.0
> 18	1	2	-1	0	0.0

Table 6.1 Results of the χ^2 tests for comparing the topographic index distribution of Culm grassland sites the Wolf, Thrushel, Carey and North Lew catchments. Observed and expected values are in number of grid cells of 2500 m^2. $\chi^2 = 1851$, $p < 0.001$.

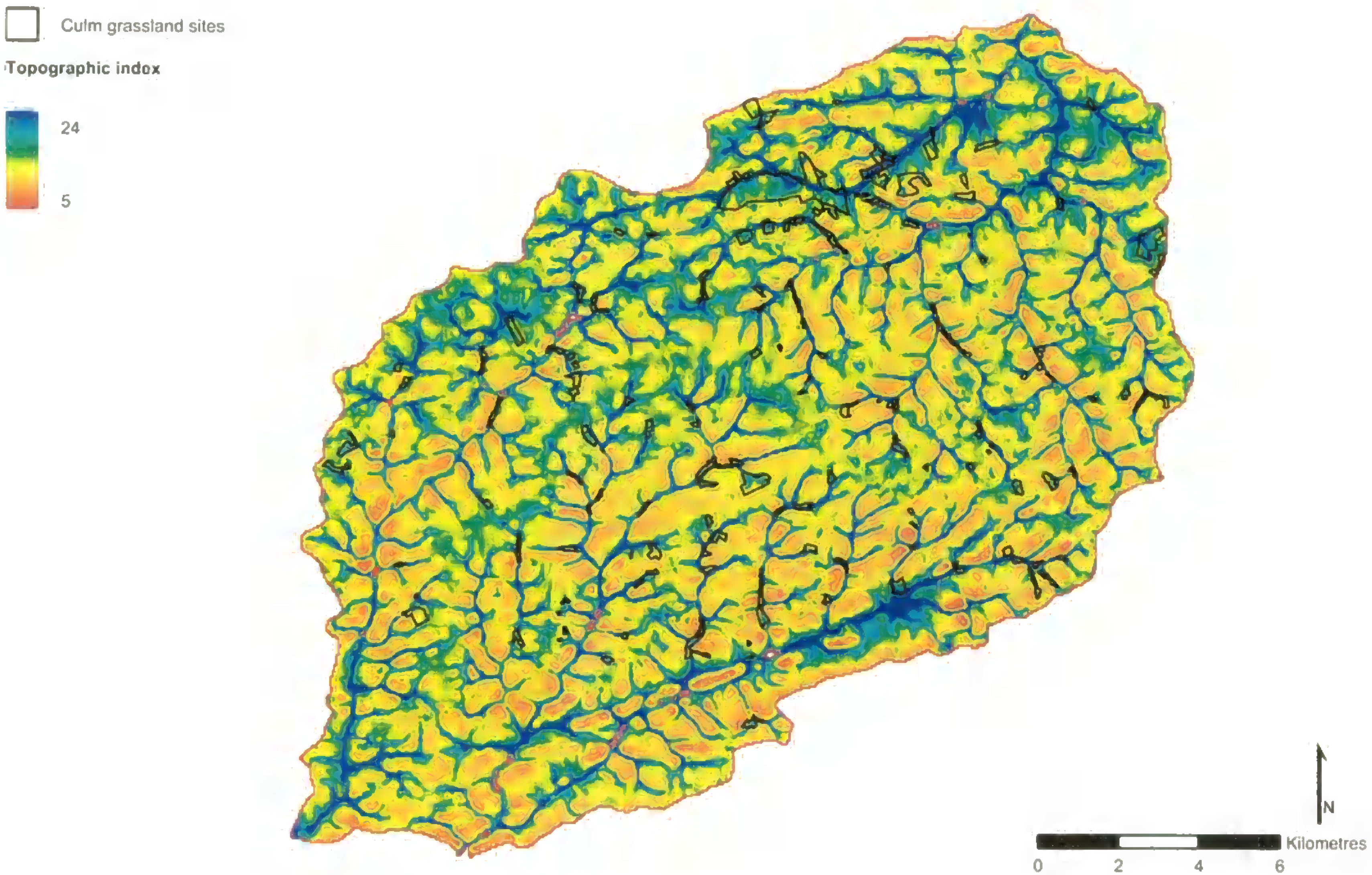


Figure 6.3 Ln(a/tanb) topographic index for the Wolf, Thrushel, North Lew and Carey catchments

6.3 Soil-topographic index

The results presented in Section 6.2 showed that Culm grassland sites were related to locations with higher topographic index values. The analysis, however, does not take any soil characteristics into account. Drainage characteristics of soils are of major importance to soil moisture patterns in a catchment. At opposite extremes are sand and clay soils, with sandy soils draining excess water quickly, and clay soils, which are generally more slowly draining (Rowell, 1994). Between these two extremes, exists a range of many different soils with a large variation in drainage characteristics, which do not only depend on soil texture but also soil structure and organic matter content. The soil map of the Wolf, Thrushel, Carey and North Lew catchments with the location of the Culm grassland sites is presented in Figure 6.4. Table 6.2 presents an overview of all map units and the characteristics of the soils.

Soil series	Name	Texture	Estimated vertical Ksat values for the whole profile (m day^{-1})
tN	Trent	clayloam	10^{-2}
Mj/Dg	Manod/Denbigh	stony clayloam	10^{-2}
Nc/Chb/Dg	Neath/Cherubeer/Denbigh	stony clayloam	10^{-2}
Hk/Br/Ca	Hallsworth/Brickfield/Cegin	stony clayloam – clay	10^{-3}
Hk	Hallsworth	(stony) clayloam – clay	10^{-3}
Hw	Halstow	(stony) clayloam – clay	10^{-3}
Ch	Conway	silty clayloam – clay	10^{-3}
HU	Hollacombe	(stony) clayloam – clay	10^{-3}
bG	Bromsgrove	(stony) sandy loam	10^{-1}
U	Unsurveyed	-	-
HP	Hopsford	stony clayloam	10^{-2}
Dg	Denbigh	stony clayloam	10^{-2}
Hp	Hamperley	stony clayloam	10^{-2}

Table 6.2 Characteristics of the 1:50,000 soil map of the Wolf, Thrushel, Carey and North Lew catchments (Harrod, 1988). Ksat values estimated from Davis and De Wiest (1966).

The soil map shows that most Culm grassland sites were found on the Hallsworth, Hallsworth/Brickfield/Cegin and the Conway map units (Figure 6.4). These soils are generally associated with a clay loam to clay texture with impeded drainage (Harrod, 1988). Typical soil profiles of the map units are described below in Table 6.3:

Hallsworth series: (Hk and Hk/Br/Ca map units)	*Tedburn series: (Hk map unit)*	*Brickfield series: (Hk/Br/Ca map unit)*	*Cegin series: (Hk/Br/Ca map unit)*
0-20 cm Apg *Dark greyish brown, slightly stony clay loam or clay.*	0-20 cm Ahg *Dark grey, slightly mottled, slightly stony clay loam or clay*	0-20 cm Ap *Very dark greyish brown, slightly stony clay loam.*	0-20 cm Apg *Dark greyish brown, slightly stony silty clay loam.*
20-50 cm Bg *Yellowish brown with many ochreous mottles, slightly stony clay; moderate coarse prismatic structure.*	20-50 cm Bg *Grey with many ochreous mottles, slightly stony clay or silty clay; strong coarse prismatic structure*	20-50 cm Bg *Greyish brown with many ochreous mottles, slightly stony clay loam; moderate medium subangular blocky structure.*	20-50 cm Bg *Light brownish grey, mottled, slightly stony silty clay loam; moderate coarse prismatic structure.*
50-100 cm BCg *Greyish brown, mottled, slightly stony clay; moderate coarse prismatic structure; high packing density.*	50-100 cm BCg or Cr *Grey with many ochreous mottles, very stony clay; weak coarse angular blocky or massive structure or shale* in situ	50-100 cm BCg *Grey, mottled, moderately stony clay loam; weak coarse subangular blocky or prismatic structure; high packing density.*	50-100 cm BCg *Light grey with many ochreous mottles, moderately stony silty clay loam; strong coarse prismatic structure becoming massive with depth*
Greyland series: (Hk/Br/Ca map unit)	***Conway series: (Ch map unit)***	***Trent series: (Ch map unit)***	***Fladbury series: (Ch map unit)***
0-25 cm Ah *Dark greyish brown, slightly mottled, slightly stony clay loam.*	0-20 cm Apg *Dark greyish brown, stoneless silty clay loam.*	0-25 cm Ap *Dark brown, stoneless clay loam.*	0-15 cm Apg *Dark greyish brown, mottled, stoneless clay*
25-50 cm Bg1 *Pale olive, mottled, slightly stony clay loam; moderate coarse angular blocky.*	20-80 cm Bg1 *Light brownish grey, mottled, stoneless silty clay loam; moderate coarse prismatic structure.*	25-50 cm Bw *Brown, stoneless clay loam; moderate coarse subangular blocky structure.*	15-60 cm Bg *Greyish brown with many ochreous mottles, stoneless clay; strong coarse prismatic structure*
50-80 cm Bg2 *Light grey, mottled, moderately stony clay; weak coarse prismatic structure; high packing density.*	80-120 cm Bg2 *Light grey with many ochreous mottles, stoneless silty clay loam; moderate coarse prismatic structure.*	50-100 cm Bg *Yellowish brown, mottled, stoneless clay loam or sandy loam; weak medium angular blocky structure.*	60-100 cm Cg *Grey, mottled, stoneless clay; moderate angular blocky or massive structure*
80-100 cm BCg *Light grey, mottled, moderately stony clay; massive structure; high packing density.*			

Table 6.3 Typical soil profiles of the Hallsworth, Hallsworth/Brickfield/Cegin and the Conway map units (Harrod, 1988).

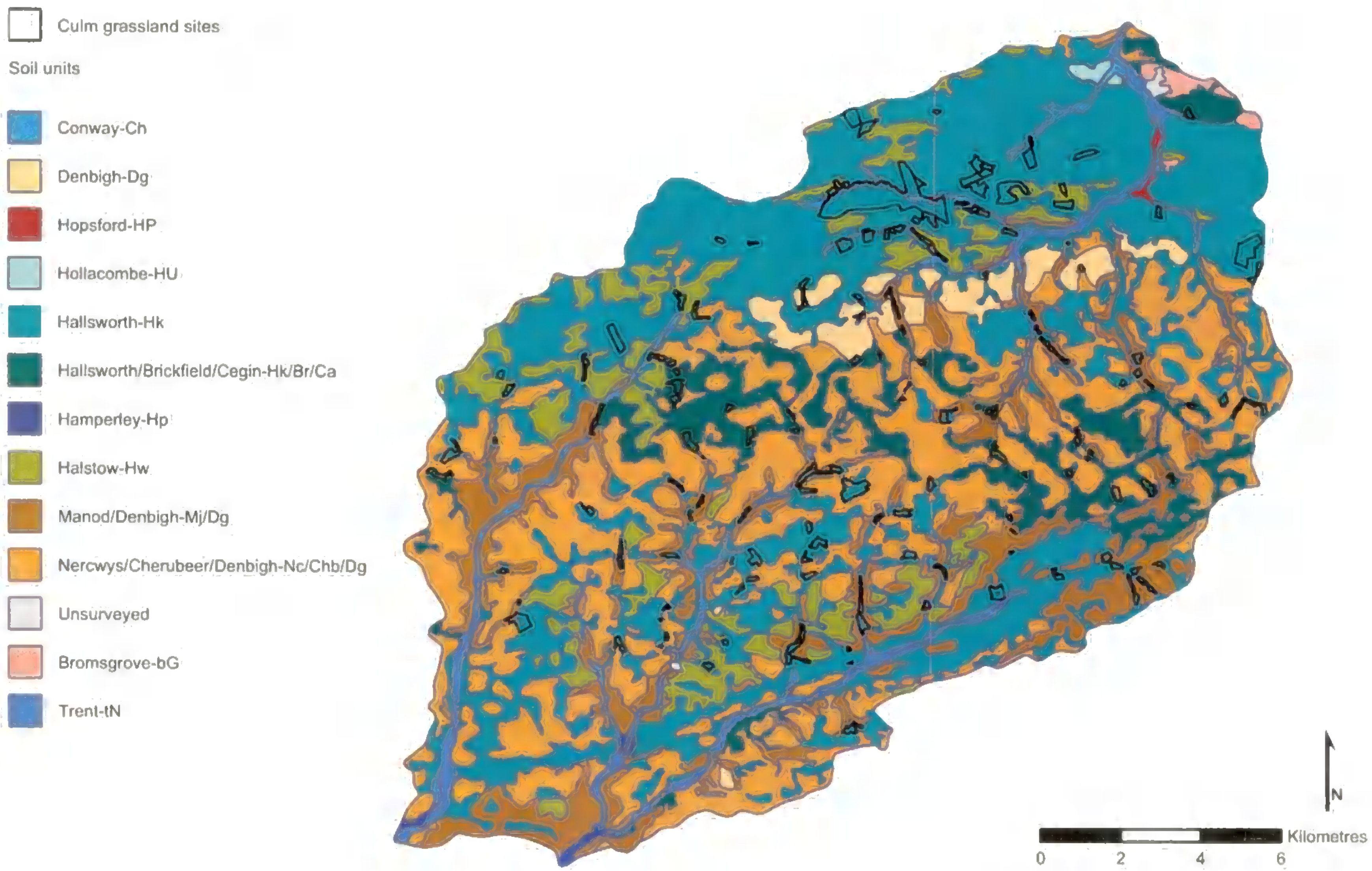


Figure 6.4 Soil map (1:50,000) of the Wolf, Thrushel, Carey and North Lew catchments (Harrod, 1988)

The transmissivity (T_0) of the soil can be included in the topographic index, creating the soil topographic index (Beven *et al.*, 1994), by changing the equation to:

$$\textit{Soil topographic index} = \ln(a / T_0 \tan\beta) \qquad \textit{Equation 6.2}$$

The transmissivity is the saturated hydraulic conductivity multiplied by the saturated depth of the soil (Marshall and Holmes, 1988). The saturated conductivity of the soils in the study area was estimated from the literature based on the texture of the soils (Davis and De Wiest, 1966). Estimations can be used as a guide to distinguish the hydrological properties of the different soil types. In this study, no distinctions between the depths of the soil types are made because these do not differ substantially for the soil types found in the area. No abrupt changes in texture, which could determine the active depth of the soil, existed for the profiles described by Harrod (1988), (Table 6.3). Potential differences between the transmissivity value of the topsoil and subsoil, e.g. caused by biological activity, were also not taken into account. Further, due to the crude estimation of the saturated hydraulic conductivity, no significantly better estimation of the actual transmissivity value could be gained by using different values for the soil depth. For all soils, the depth was set to 1 m, which corresponded to the depth of the parent materials for most of the soil profiles (Harrod, 1988). Therefore, the transmissivity value under saturated conditions was equal to the saturated hydraulic conductivity.

The results of this analysis are shown in Figure 6.5 and Figure 6.6. As in Section 6.2, a shift of the Culm grassland sites towards the higher soil-topographic index values can be observed in comparison to the values for the whole area. The distribution of the soil-topographic index for the whole soil map area showed that the number of cells in the category from 13 to 14 is lower than expected according to a normal distribution. This was probably due to the relationship between topography and soil characteristics. Low topographic indices are often related to ridges or steep slopes which have naturally better draining soils with a high soil transmissivity value (T_0) and thus a low $\ln(T_0^{-1})$. High topographic indices are generally found on flat valley bottoms and plateaux which are often associated with soils with impeded drainage and thus a high $\ln(T_0^{-1})$ (Whipkey and Kirkby, 1978; Church and Woo, 1990). Therefore, the observation of a low number of cells with mid-range soil topographic index values was according to the expectations.

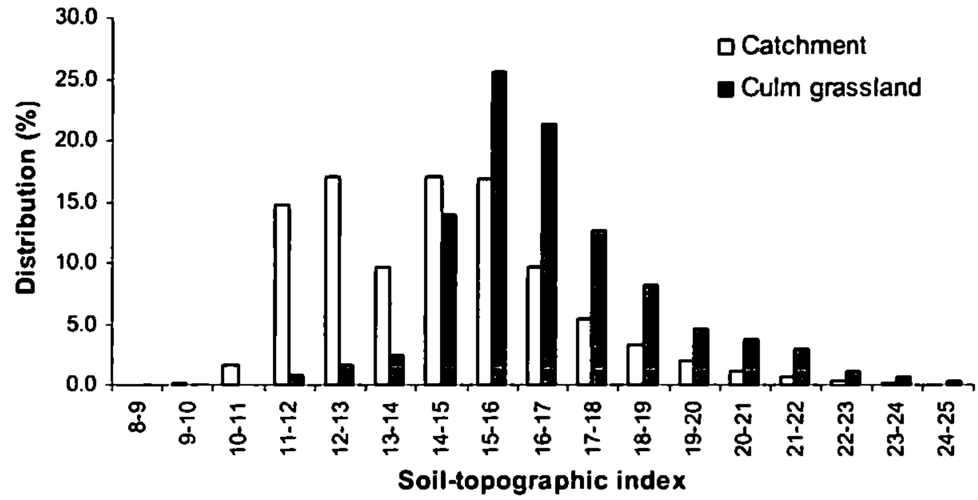


Figure 6.5 Ln(a/T0tanβ) soil-topographic index distribution under Culm grassland compared to the Wolf, Thrushel, Carey and North Lew catchments

Table 6.4 shows the results of the χ^2 analysis. A significant difference was found between the soil topographic index of Culm grassland sites and the indices for the total soil map area ($p < 0.001$). Most of the difference could be explained by significantly less sites in the 11 to 13 category and significantly more in the category from 15-18.

$Ln(a/T_0tan\beta)$	Observed (O)	Expected (E)	(O-E)	$(O-E)^2/E$	*Explained variance (%)*
8-9	0	1	-1	1	0.0
9-10	0	5	-5	5	0.0
10-11	1	52	-51	50	0.3
11-12	26	474	-448	424	24.2
12-13	53	548	-495	447	29.4
13-14	77	308	-231	173	6.4
14-15	446	549	-103	19	1.3
15-16	822	541	281	145	9.5
16-17	686	308	378	465	17.2
17-18	405	174	231	306	6.4
18-19	262	106	156	229	2.9
19-20	146	63	83	108	0.8
20-21	121	39	82	169	0.8
21-22	93	22	71	234	0.6
22-23	38	10	28	84	0.1
23-24	21	4	17	61	0.0
24-25	9	1	8	39	0.0
> 25	1	1	0	0	0.0

Table 6.4 Results of the χ^2 tests for comparing the topographic index distribution of Culm grassland sites the Wolf, Thrushel, Carey and North Lew catchments. Observed and expected values are in number of grid cells of 2500 m^2. $\chi^2 = 2960$, $p < 0.001$.

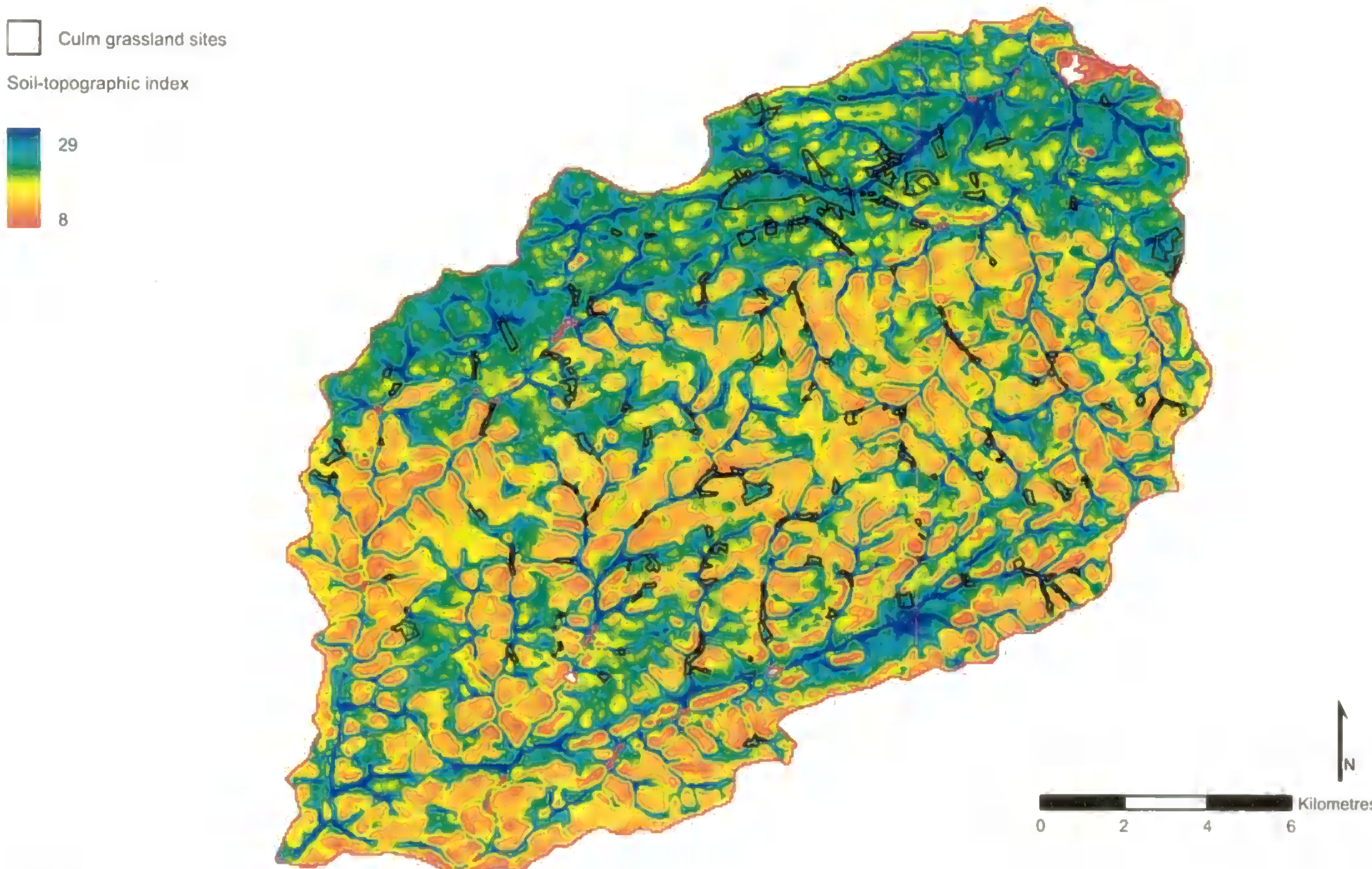


Figure 6.6 Soil - topographic index for the Wolf, Thrushel, Carey and North Lew catchments.

6.4 TOPMODEL results

Simulation of soil saturation areas in two study catchments was conducted with the aid of TOPMODEL, a semi-distributed surface water model based on the ln(a/tanb) topographic index (Beven *et al.*, 1994) (Chapter 4). The period from mid-October 1995 to mid-October 1996, was modelled for the Wolf and Thrushel catchments and the simulation was split into two periods: October 1995 to June 1996 with relatively high rainfall and discharge levels, and June 1996 to October 1996 with relatively low rainfall and discharge levels. As mentioned in Chapter 4, this modelling period was selected because all necessary input data were available and rainfall was closest to the average value for both catchments. The data input and the modelling parameters will be described in section 6.4.1 and section 6.4.2 discusses the resulting saturated zones.

6.4.1 Data input and modelling parameters

The TOPMODEL input data for the Wolf and Thrushel catchments consisted of discharge, rainfall, evaporation and topographic index information. The topographic index maps for the two catchments were calculated from a DEM with 20 by 20 m cells, which was derived from the 1:50,000 contour map (Chapter 4). Discharge and rainfall data on a daily time-scale were obtained from the Environment Agency (EA, 2000a). For both Wolf and Thrushel, minimum and maximum evaporation data were derived from the MORECS (Meteorological Office Rainfall and Evaporation Calculation System) database supplied by the Environment Agency (Chapter 4).

No detailed measurements on evaporation (E) were available, but values were estimated from monthly values with the following equation (Beven *et al.*, 1995):

$$E = E_{\min} + 0.5 * ((E_{\max} - E_{\min}) * (1 + \sin(2\pi * (Julianday/365 - 0.5\pi)))) \qquad \textit{Equation 6.3}$$

In 1995, the minimum and maximum evaporation values were 0.38 mmd^{-1} and 3.46 mmd^{-1} and for 1996 the minimum and maximum values were 0.58 mmd^{-1} and 3.13 mmd^{-1} (EA, 2000b).

The estimation of soil saturation patterns was achieved by fitting the river discharge graphs to the measured discharge of the rivers Thrushel and Wolf. The model was run with a number of different parameters until the optimum parameter set had been found. Results achieved with the different parameter sets were judged by visual comparison of the discharge curves. Table 6.5 presents the parameter sets used for the two study catchments and the two modelling periods.

		Oct. 1995 – June 1996		June – Oct. 1996	
		Thrushel	Wolf	Thrushel	Wolf
m	Exponential storage parameter (m)	0.008	0.01	0.025	0.017
T_0	Ln (Mean soil transmissivity in m^2/h)	0.8	0.5	0.5	1
Td	Time delay per unit (h)	25	18	100	40
CHV	Main channel routing velocity (m/h)	250	200	500	200
RV	Internal subcatchment routing velocity (m/h)	250	200	500	200
SRmax	Available water capacity root zone (m)	0.025	0.03	0.04	0.03

Table 6.5 TOPMODEL parameters

The parameter *m* is a scaling parameter which determines the transmissivity of the soil profile together with the soil transmissivity under saturated conditions, expressed as in equation 6.4 (Beven *et al.*, 1994):

$$T_{D_i} = T_{0_i} e^{-D_i/m}$$ *Equation 6.4*

In this equation D_i is the local storage deficit (m). Beven *et al.* (1994) state that the exponential storage parameter (*m*) can be interpreted physically as the active depth of the soil profile. The soil transmissivity (T_0) can be derived from the saturated hydraulic conductivity multiplied by the saturated depth of the soil. A high T_0, combined with a low m value results in a slowly draining soil profile and a fast-draining soil profile can be represented by a low T_0 combined with a high value for *m*.

The *m* values used for modelling the discharge of the Wolf and Thrushel catchment are in the same range as the values presented by Beven *et al.* (1984) and Beven (1987) for medium-sized UK catchments (8 to 36 km^2). The T_0 values used for the modelling are relatively high compared to the saturated hydraulic conductivity values estimated for the soils in the catchment, which range from 0.1 to 0.001 $mday^{-1}$. This could be explained by a higher lateral downslope transmissivity than might be expected from small-scale vertical hydraulic conductivity due to preferential flow pathways (Beven *et al.*, 1994). Another reason could be that a large transmissivity value compensates for an overestimation of the upslope contributing area (*a*) of the $a/T_0\tan\beta$ index (Beven *et al.*, 1994). The effective *a* value could be much smaller than the upslope contributing area due to variability in upslope recharge rate, as the effective area does not always extend all the way to the catchment divide. This could be a problem, particularly in drier catchments (Beven *et al.*, 1994). Also for the modelling exercise, the T_0 values for both catchments are different in the wet and dry seasons. The values should have been the same because soil properties are identical. Transmissivity values are likely to change if cracking of the soil occurs to substantial depth due to drying out of the soil. However, this process was not observed during field visits. Harrod *et al.* (1988) report occasional cracking of the topsoil of the Hallsworth soils. However, this does not extent into the subsoil and only occurs in degraded soils.

The values for the main channel routing velocity and the internal subcatchment velocity have little effect on the results, as long as both routing velocities are large enough to reach the catchment outlet in one time-step (1 day). The length of the main channel of the Thrushel catchment was approximately 12 km and the main channel of the Wolf catchment approximately 3 km. With a modelling time step of 1 day and a routing velocity of respectively 200 mh^{-1} and 250 mh^{-1}, this meant that the water takes less than one time step to reach the outlet in the Wolf catchment and two time steps to reach the Thrushel outlet. Using lower routing velocity values meant that simulated discharge peaks lagged the observed peaks. The difference between winter and summer routing velocities for the Thrushel catchment could be explained by a delay due to soils retaining the water in an unsaturated state.

The root zone storage was used to calculate the actual evapotranspiration from the potential evaporation data and therefore reduces the amount of water that is discharged by the river. The root zone storage depends on the depth of the root zone and the difference in water content between field capacity and wilting point. To give an impression of a reasonable magnitude of this storage parameter a comparison is made with values reported for Dutch loam and clay soils. For a root zone of between 10 to 20 cm and a volumetric moisture content of 10 to 20% (Koorevaar *et al.*, 1983), root zone storage capacity values of between 0.01 and 0.04 m are reasonable. However, this storage parameter is dependent on physical soil properties that have a high spatial variability, which was not taken into account.

6.4.2 Discharge results

The discharge of the river Wolf and Thrushel was simulated with TOPMODEL for the periods October 1995 to June 1996 and June 1996 to October 1996. In the first period (autumn to spring), from visual examination the results of the discharge modelling for the Wolf catchment showed a close match with the observed discharge (Figure 6.7). From the beginning of October to mid-February, discharge peaks were of the appropriate amount and the timing was found to be accurate. Baseflow corresponded generally to the observed level. From March to April, the simulated discharge peaks were only about a third of the flux of the observed ones. In May, the simulation of the peaks was two to two and a half times the observed discharge.

A similar picture was found for the Thrushel catchment in the same period (Figure 6.8). A close match of baseflow was generally found for the whole modelling period. Timing of discharge peaks was generally simulated accurately. However, for the first two months, the simulated peaks were approximately double the height of the observed ones. From mid-December to mid-February the stage of the discharge peaks was found to be accurate. From March onwards, not all peaks were simulated and some were only half the flux of the observed peaks.

During the second modelling period, June – October 1996, the modelling results of discharge peaks for the river Wolf were less accurate than for the first period (Figure 6.9). The first discharge peaks were not simulated at all and the baseflow level was about twice the observed level.

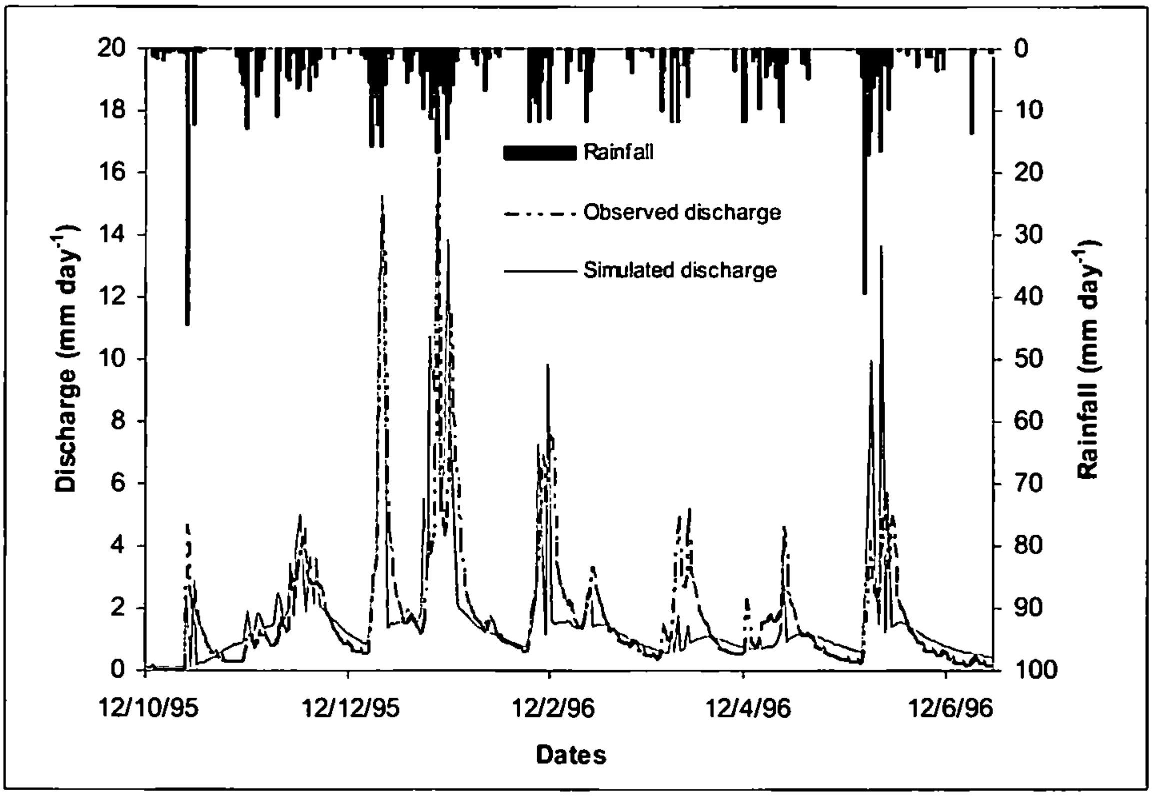


Figure 6.7 Wolf rainfall observed and simulated discharge 1995/1996

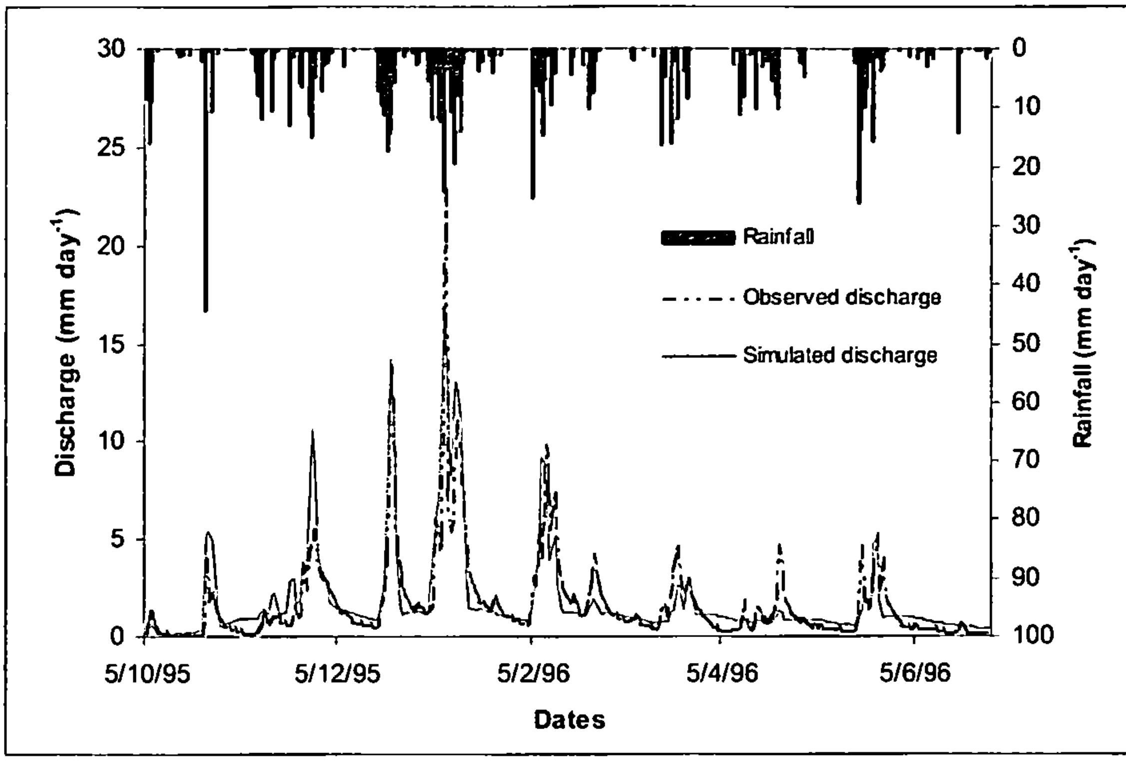


Figure 6.8 Thrushel rainfall observed and simulated discharge 1995/1996

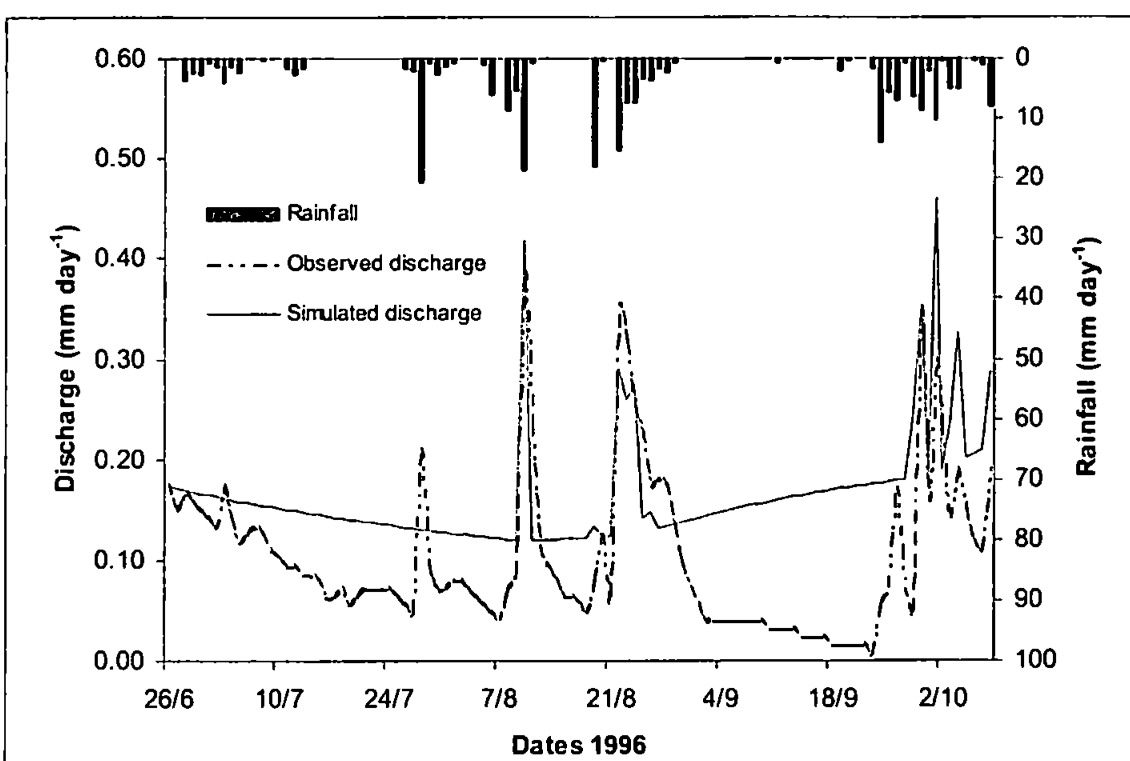


Figure 6.9 Wolf rainfall observed and simulated discharge 1996

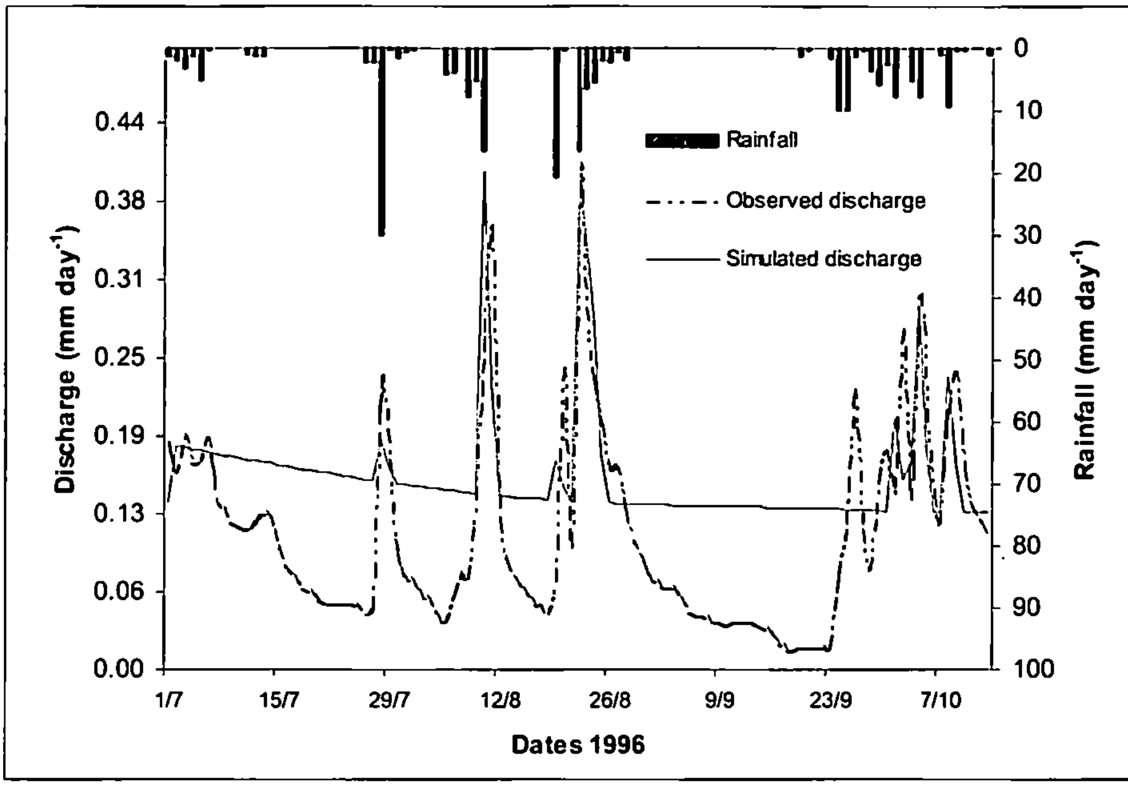


Figure 6.10 Thrushel rainfall observed and simulated discharge 1996

Figure 6.10 shows that the simulated baseflow for the river Thrushel was also too high, approximately three to four times the observed level. The timing of the peaks was slightly too early and not all peaks were simulated. The flux of the peaks was found to match the observed values closely. The results described above are discussed in Section 6.6.

The results described above can be explained by the transportation of water under varying soil water contents. In soils with a high water content, which are more likely to occur in winter, the transportation of water is more dependent on topography than in soils with low water contents (Meyles *et al.*, *in press*).

6.4.3 Soil saturation in relation to Culm grassland sites

Figures 6.11 and 6.12 show the percentage of time of soil saturation in the October 1995 to June 1996 modelling period. From the maps with the saturated zones for both the Wolf and the Thrushel catchments, it was clear that no Culm grassland sites were found on locations with the lowest saturation indices. This confirms the expectations that Culm grassland sites are located at the 'wet' locations in the landscape. During the summer months, soil saturation was found less frequently and Culm grassland was found on the total range of soil saturation indices (Figure 6.13 and 6.14).

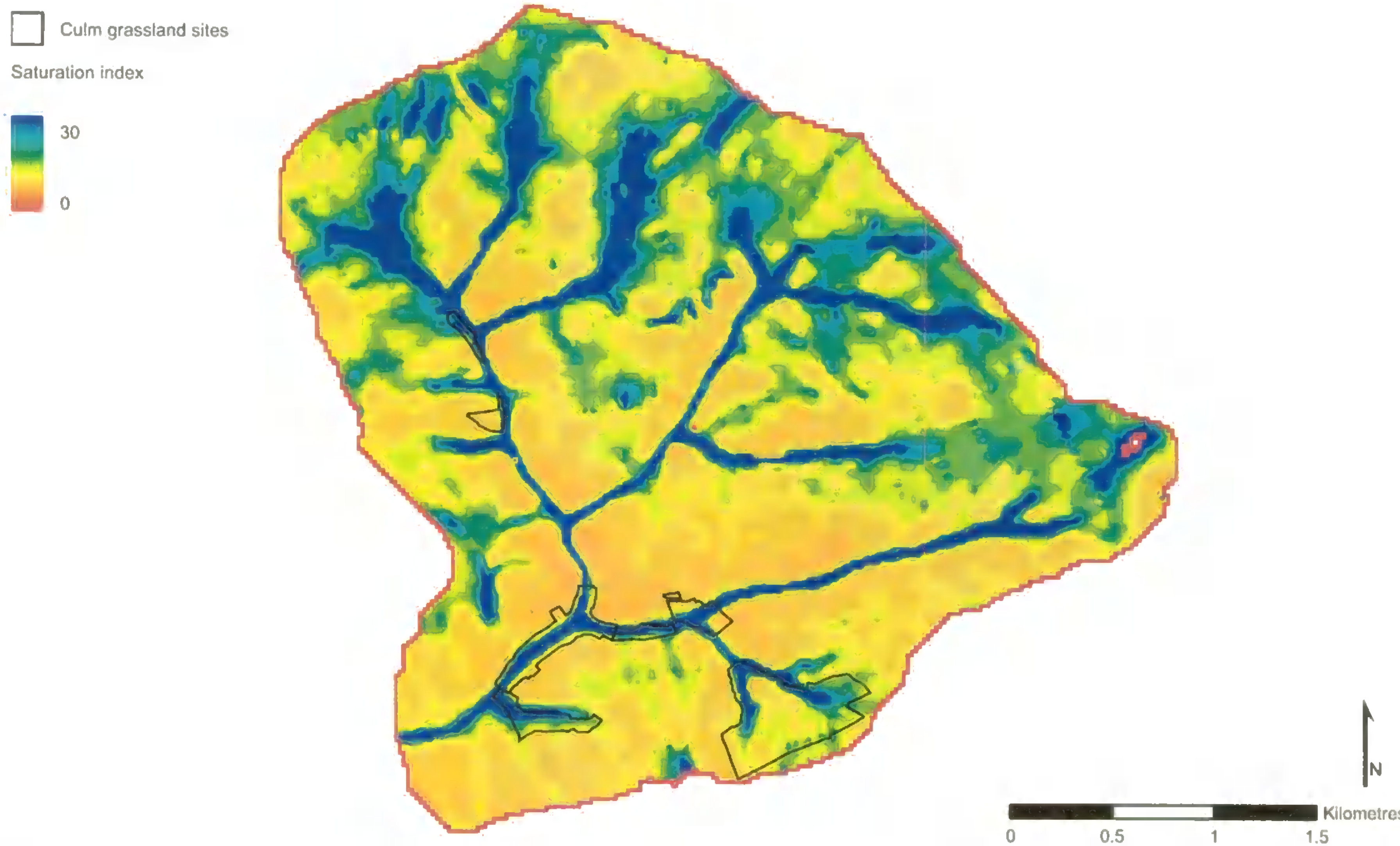


Figure 6.11 Soil saturation index for the Wolf catchment, October 1995 - June 1996

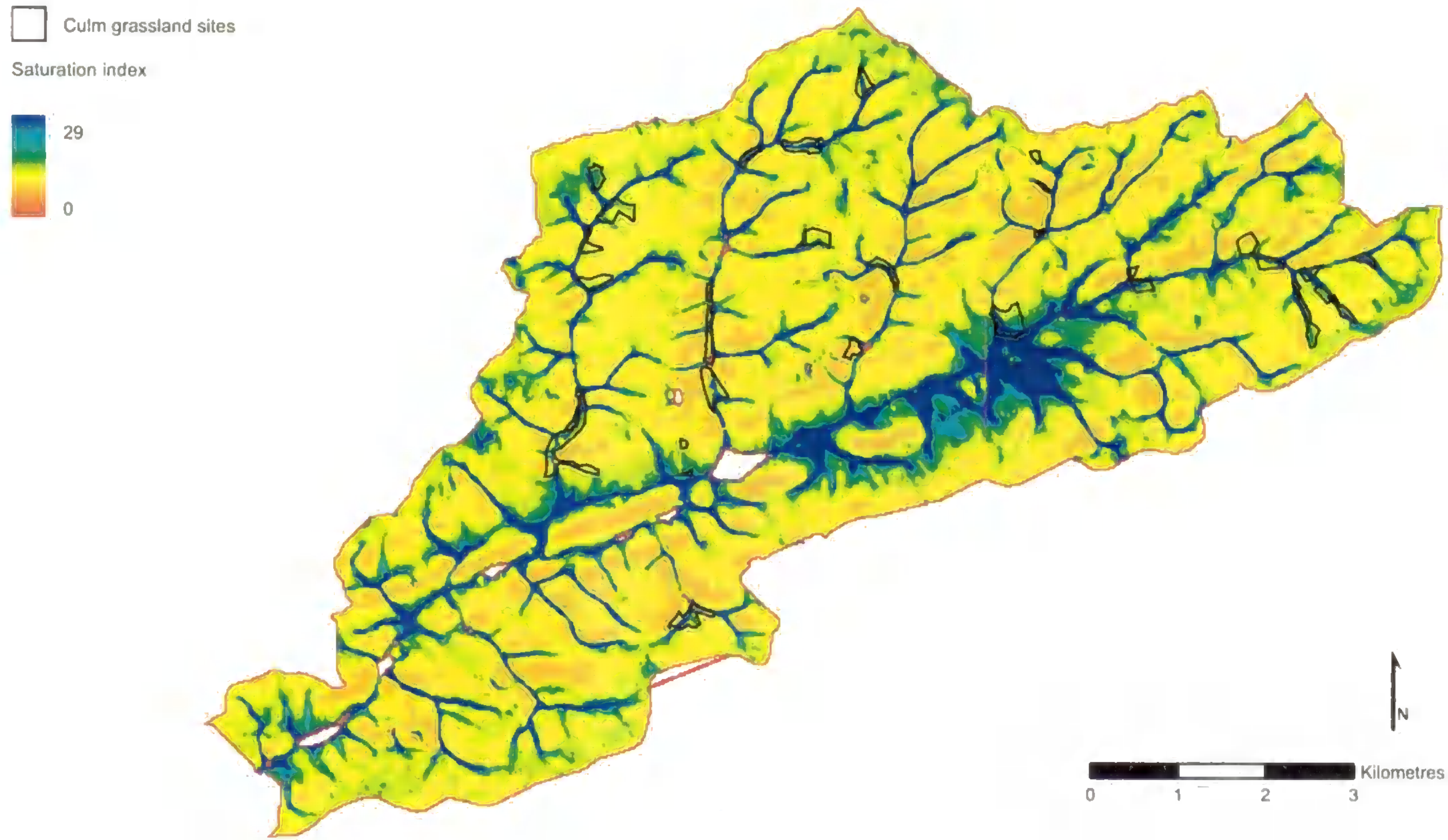


Figure 6.12 Soil saturation index for the Thrushel catchment, October 1995 - June 1996

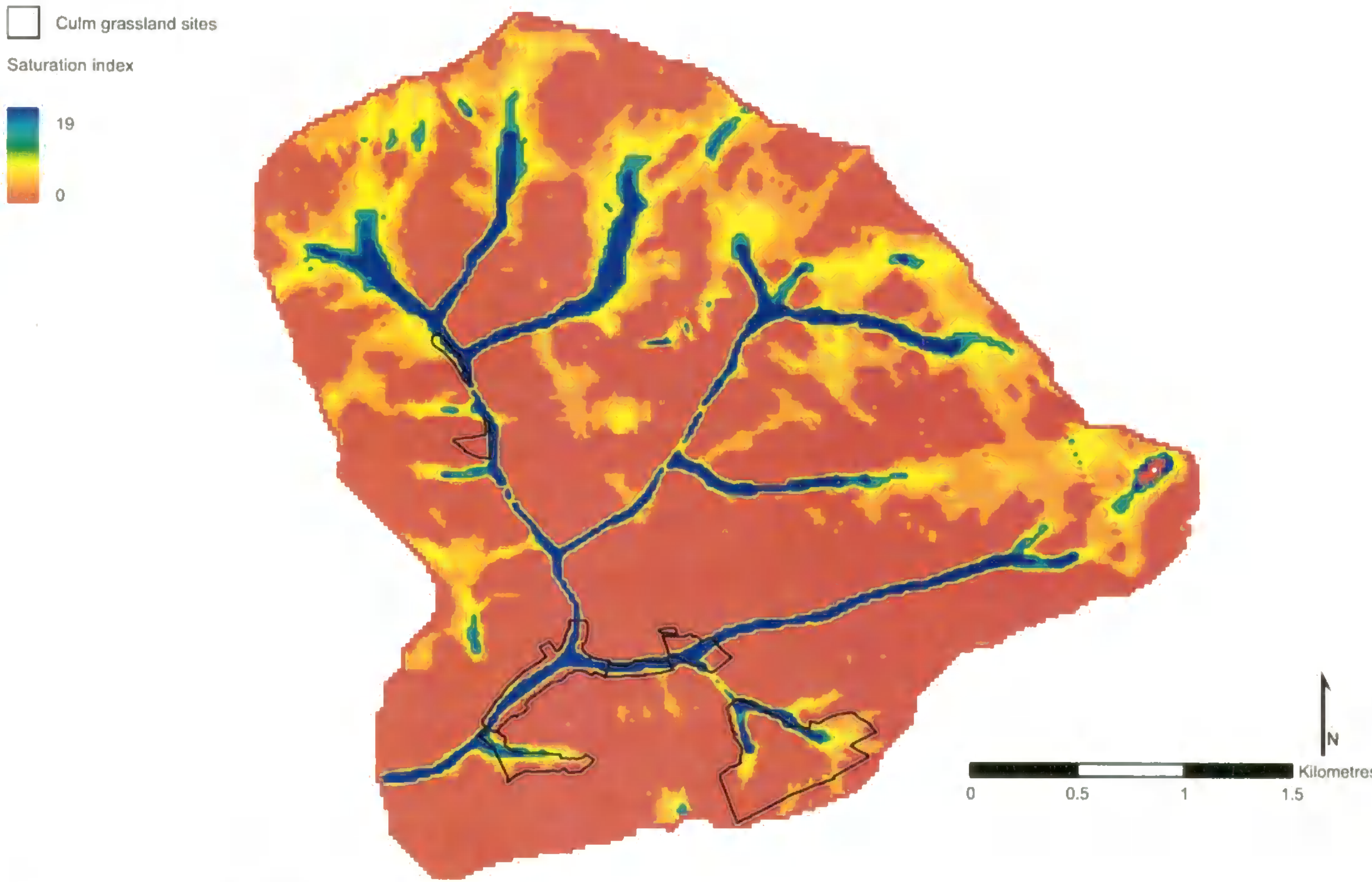


Figure 6.13 Soil saturation index for the Wolf catchment, June - October 1996

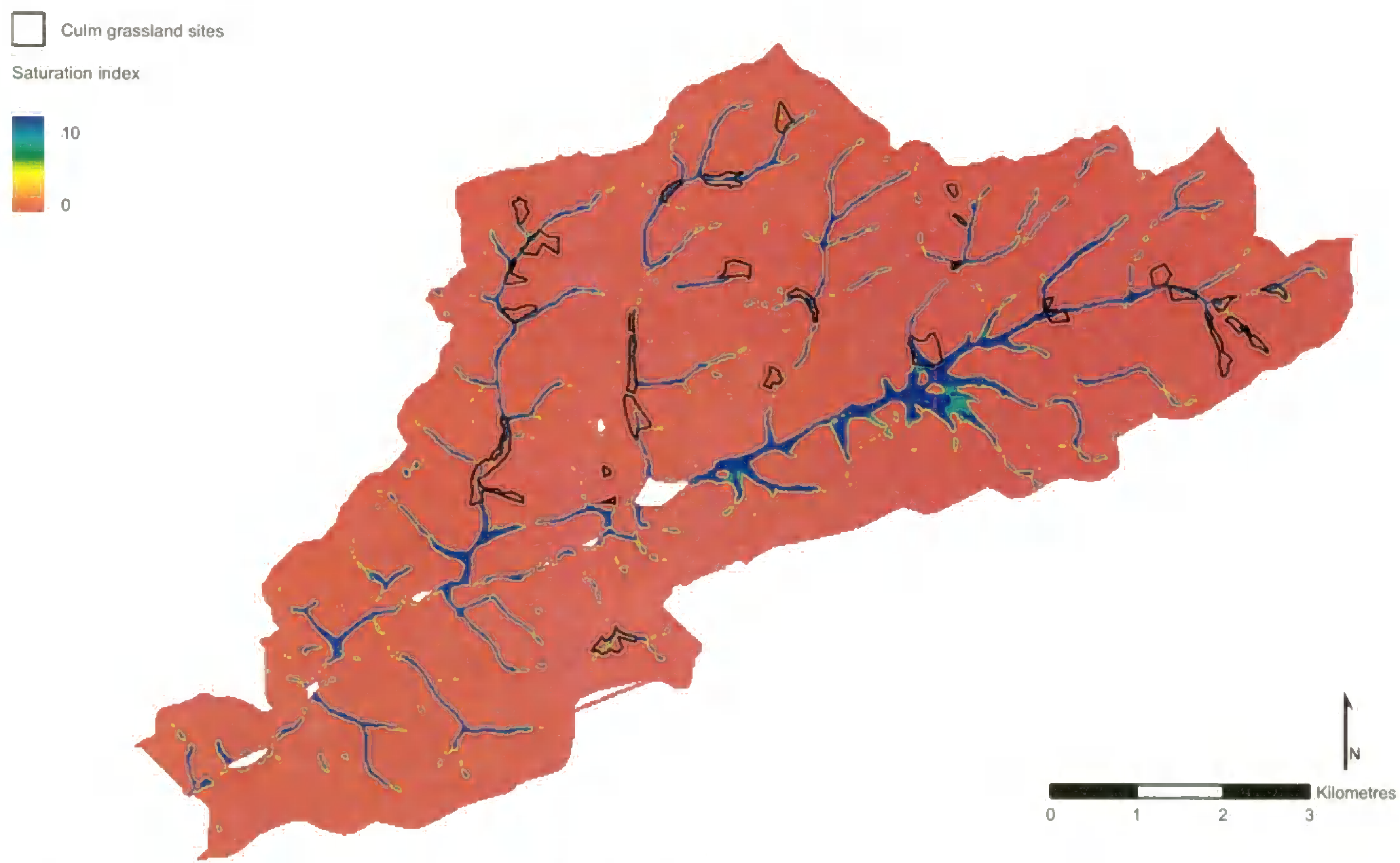


Figure 6.14 Soil saturation index for the Thrushel catchment, July - October 1996

The results described in Section 6.4.2 show a reasonable agreement with the discharge simulation during the period with high discharge levels. During the low discharge periods however, simulation of the baseflow fails. The soil saturation periods presented in Figure 6.11 to 6.14 seem to be an underestimation of the situation in the field, where standing water was observed even in the summer after a long dry period. However, field observations were made only in Culm grassland sites and do not represent other areas of the catchments, which could show an overestimation of the soil saturation period. Other factors important to catchment hydrology, like a spatially variable soil hydraulic conductivity, should be taken into account to model the saturation patterns accurately.

The results of this modelling exercise are therefore only of limited value and can only be used as an indication for wetness differences. No absolute soil saturation data can be related to the location of the wet grassland sites. In that respect the modelling of soil saturation duration with TOPMODEL does not improve the results compared to the topographic index presented in section 6.2, as the modelling results are directly based on the index distribution. TOPMODEL was therefore not used any further in this research.

A major disadvantage existed, in that TOPMODEL assumes homogenous soils for the whole catchment, which was not realistic, as was shown in Section 6.3. A solution to this problem could have been to use the soil-topographic index as input into TOPMODEL and while setting the transmissivity value in the program to 1. However, in this case no detailed transmissivity values were available for the soils in the area and measurements required too many resources. Therefore, it was not expected that the results would improve substantially and result in a realistic soil saturation pattern. Further analysis was therefore restricted to wetness indices with and without soil transmissivity values and no simulations of actual saturation patterns were undertaken.

6.5 HOST

A different approach to describing the hydrological characteristics of the study area was based on the drainage characteristics of the soils in the area. The Hydrology Of Soil Types (HOST) classification as described by Boorman *et al.* (1995) was used to classify the 1:50,000 soil map of the Wolf, Thrushel, Carey and North Lew catchments for the area (Harrod, 1988) (Figure 6.4) according to hydrological behaviour (Figure 6.16). This classification was based on conceptual models of the hydrological processes that occur in the soil and substrate. The resulting scheme consists of 29 different classes varying from groundwater-dominated systems to surface water-dominated systems (Chapter 4). Table

6.3 describes the HOST classes found in the study area. Distributions of the HOST classes under Culm grassland sites and the total study area were compared in a GIS to find their preferred positions. As before, χ^2 tests were carried out to assess the significance of the differences between the distributions.

HOST	Description
3	No impermeable or gleyed layer within 100 cm. Substrate hydrogeology: weakly consolidated, macroporous, by-passs flow uncommon. Groundwater or aquifer normally present at >2 m.
8	Impermeable layer within 100 cm or gleyed layer at 40-100 cm. Substrate hydrogeology: unconsolidated, microporous, by-pass flow common. Groundwater or aquifer normally present at ≤ 2m.
9	Gleyed layer within 40 cm. Substrate hydrogeology: unconsolidated, microporous, by-pass flow common. Groundwater or aquifer normally present at ≤ 2m. Saturated hydraulic conductivity < 1 m day^{-1}.
10	Gleyed layer within 40 cm. Substrate hydrogeology: unconsolidated, microporous, by-pass flow common. Groundwater or aquifer normally present at ≤ 2m. Saturated hydraulic conductivity ≥ 1 m day^{-1}.
17	No impermeable or gleyed layer within 100 cm. Substrate hydrogeology impermeable. No significant groundwater or aquifer.
18	Impermeable layer within 100 cm or gleyed layer at 40-100 cm. Substrate hydrogeology: slowly permeable. No significant groundwater or aquifer. Integrated air capacity > 7.5%.
21	Impermeable layer within 100 cm or gleyed layer at 40-100 cm. Substrate hydrogeology: slowly permeable. No significant groundwater or aquifer. Integrated air capacity ≤ 7.5%
24	Gleyed layer within 40 cm. Substrate hydrogeology: slowly permeable. No significant groundwater or aquifer.
97	Unsurveyed.

Table 6.6: HOST classes found in the study area (Boorman et al., 1995)

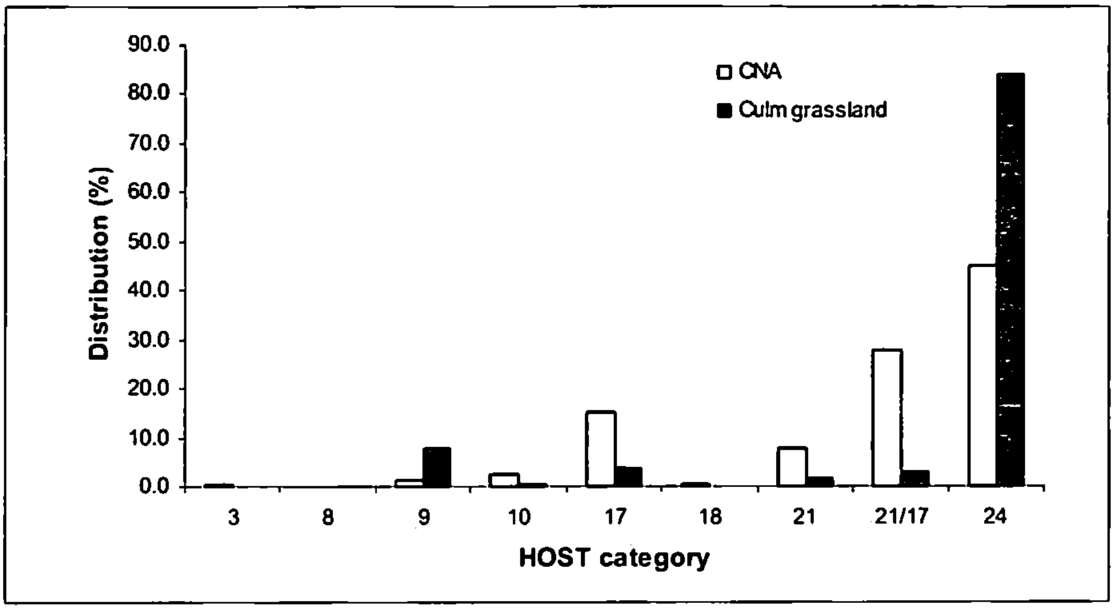


Figure 6.15 HOST class distributions under Culm grassland sites compared to the Wolf, Thrushel, Carey and North Lew catchments

Figure 6.15 shows that the majority of Culm grassland sites were found on soils with a HOST class of 24. Table 6.7 presents the results of the χ^2 tests performed on the data. A significant difference between the HOST classes for Culm grassland sites and the total catchment area was found ($p < 0.001$). Most of the difference can be explained by the large area of Culm grassland sites within class 24 and the small area on class 17 and 21/17. Significantly more sites were also found within class 9 than was expected. However this HOST category only covers a relatively small section of the soil map.

HOST category	Observed (O)	Expected (E)	(O-E)	$(O-E)^2/E$	*Explained variance (%)*
3	0	12	-12	11.9	0.0
8	0	4	-4	3.7	0.0
9	253	45	208	971.6	1.8
10	10	76	-66	57.4	0.2
17	119	482	-363	273.3	5.5
18	0	7	-7	7.3	0.0
21	49	244	-195	155.7	1.6
21/17	92	890	-798	715.9	26.6
24	2687	1447	1240	1063.1	64.3
97	0	3	-3	3.3	0.0

Table 6.7: HOST class distributions under Culm grassland sites compared to the total study area. Observed and expected values are in number of grid cells of 2500 m2. $\chi 2 = 3236$. $p < 0.001$.

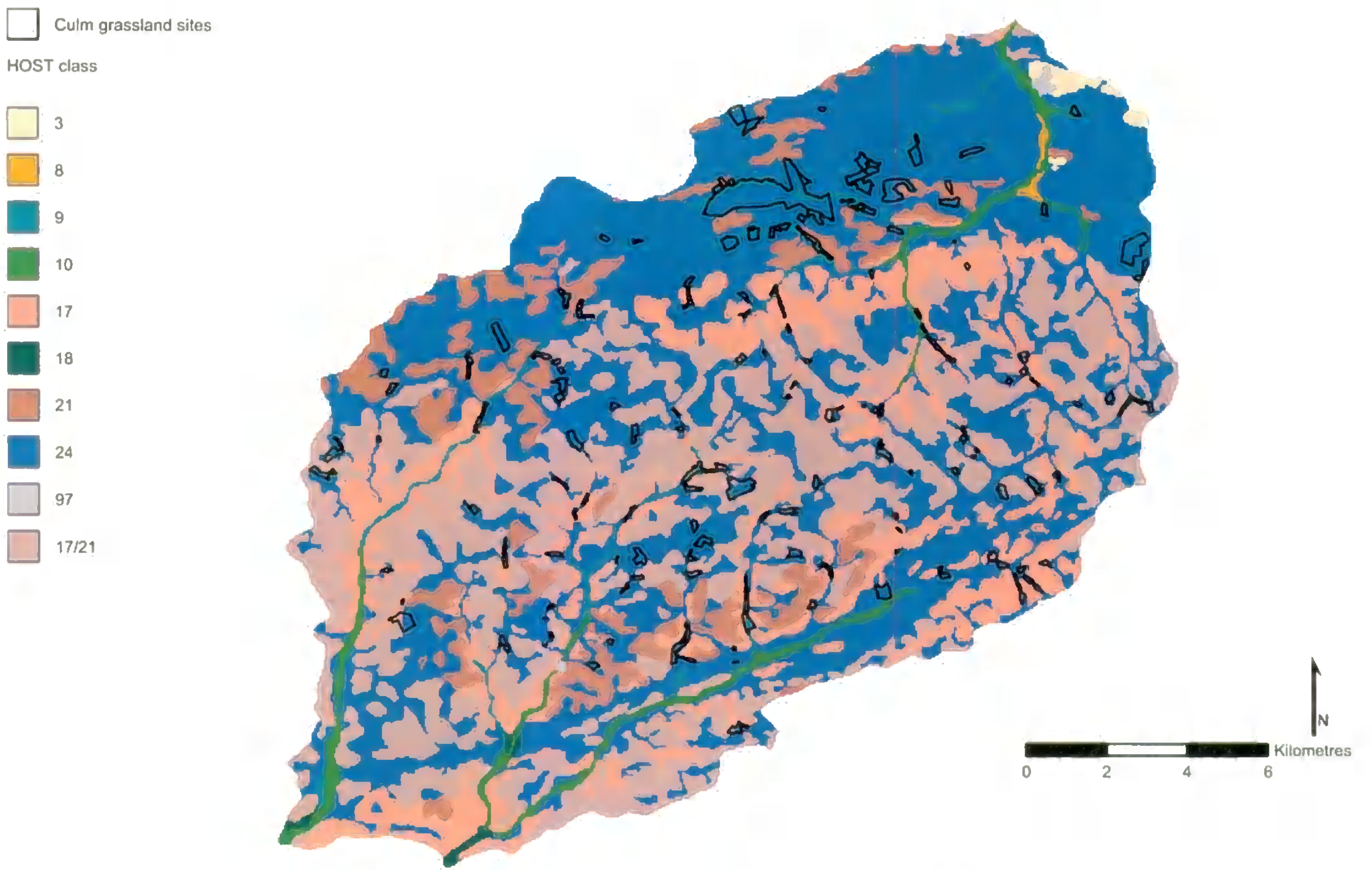


Figure 6.16 HOST classification of the 1:50,000 soil map of the Wolf, Thrushel, Carey and North Lew catchments

6.6 Discussion

The results described in this chapter focused on the relationship between Culm grassland location and hydrology. Four different approaches in describing the hydrological characteristics of the landscape or catchment, namely the topographic index, the soil-topographic index, soil saturation pattern modelling with TOPMODEL and classification of the soils in the study area with the HOST classification were explored to find a method that best explained the location of Culm grassland sites.

The topographic index classification of the Wolf, Thrushel, Carey and North Lew watersheds showed clearly the relationship between Culm grassland location and topographic indices higher than 8. Of the total area covered by Culm grassland, 86% was classified in this category. These results showed that relationships between Culm grassland location and landscape hydrology could be derived from digital elevation data and indicated a clear preference for 'wet' locations. However, the results could not completely explain the patterns of Culm sites found in the area and only relative information on the 'wetness' of the sites was obtained.

To improve the explanation for the distribution of Culm grassland sites, the topographic index was extended with the transmissivity of the soil, resulting in the soil-topographic index. The transmissivity was derived from the saturated hydraulic conductivity, which was estimated from the texture of the soils, based on values reported in the literature. This technique provided only a crude estimation of the drainage characteristics of the soil. However, no better information was available and also this study aimed to use readily available data to ensure that the proposed methodology would be accessible for a wide range of potential users. The estimation of the lateral soil transmissivity from the saturated hydraulic conductivity could cause an underestimation of the real value. Saturated hydraulic conductivity values are generally estimated for a relatively small sample (Klute and Dirksen, 1986; Vepraskas *et al.*, 1991) of the soil and measure the vertical conductivity. Many authors have shown that the existence of preferential flow pathways could cause the transmissivity to be many times higher (e.g. Gilman and Newson, 1980; Anderson and Burt 1990; McDonnell, 1990; Brown *et al.*, 1999; Deeks *et al.*, 1999), but these are not accounted for in TOPMODEL. Other flow mechanisms like the kinematic wave theory, which explains the quick response of stream discharge after a rainfall event (Rasmussen *et al.*, 2000; Williams *et al., in press*) are also not included in the TOPMODEL framework, but could be of major importance in the distribution of soil water in the catchment.

Culm grassland sites were found to have a preference for locations with a soil-topographic index larger than 15 and 81% of the Culm grassland area was situated in this category. However, by using the soil-topographic index, the area of Culm sites within the selection criteria decreased from 86% to 81% and the total area in the study area meeting these criteria decreased from 56% to 40% of the total. The soil-topographic index thus provided a much more selective criterion than the topographic index on its own and would therefore be better suited as a decision-making rule in the DSS, which is discussed in Chapter 10.

To quantify the soil saturation patterns in the catchment, the hydrological model TOPMODEL was used for the Wolf and Thrushel watersheds. For this modelling exercise, the soils were assumed to be homogeneous, which caused an overestimation of the number of saturation days in some areas and an underestimation in other areas. The latter became clear when comparing the results with field observations in Culm grassland sites where saturated conditions were found even after a dry period of two weeks in the middle of summer. The real soil transmissivity value will be higher than the estimated one for the better draining soils or lower for the poorly draining soils in the area. The use of an average value for transmissivity reflects the overall catchment conditions well if the aim is to study the discharge of the streams. Where the aim is to study soil saturation patterns, such an average value is not suitable and TOPMODEL could therefore not be used. The major reasons for the poor performance were that the model is only semi-distributed and thus does not produce spatial output that resembles reality. Further, the modelling exercise is mainly a matter of curve fitting and the parameters used have therefore no real physical meaning.

The topographic index maps used for the hydrological modelling were derived from a DEM with 20 by 20 m gridcells. This resolution was chosen to obtain as detailed information as possible. In some parts of the maps, however, problems with the interpolation from the contour maps existed, especially where contour lines were far apart. Not enough information was present at the 1:50,000 scale to interpolate properly between the contour lines. Nodes on the contour lines showed a distortion, especially where the node represents a convex area. Figure 6.17 gives an example of this distortion, by comparing the topographic index for 25 m by 25 m to 50 m by 50 m grid cells. In the 25 m resolution map this effect can be observed from 'fingering' pattern. However, inaccuracies due to interpolation were not expected to affect the modelling results significantly, because the topographic index distributions on which TOPMODEL is based for both the resolutions were similar (Figure 6.18 and 6.19).

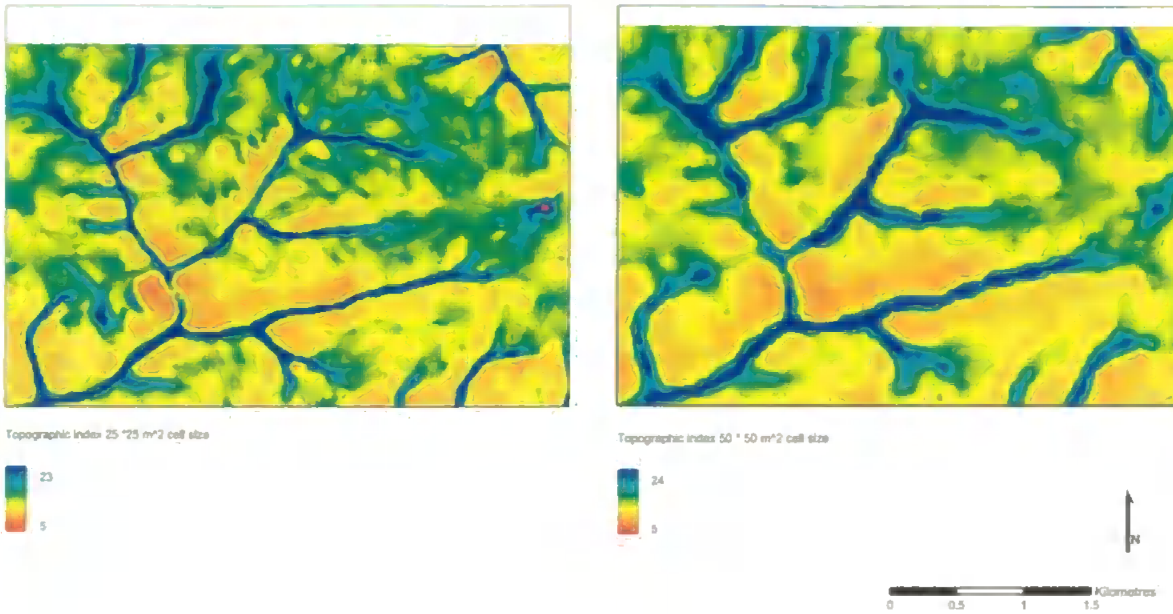


*Figure 6.17 Comparison of the topographic index based on 25 m * 25 m and 50 m * 50 m grid cells*

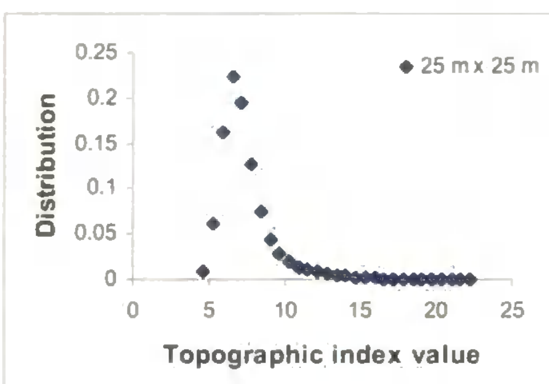


Figure 6.18 Topographic index distribution 25m x 25m grid cells

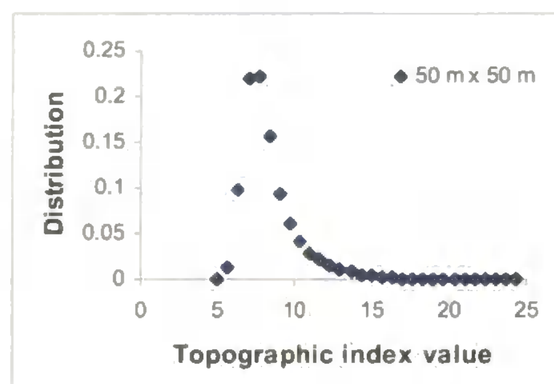


Figure 6.19 Topographic index distribution 50m x 50m grid cells

Another drawback of the modelling is that the river discharge and soil saturation were only simulated for a limited time period. The model period might not reflect average conditions in the catchment. Fitting the simulated discharge curve to the observed curve was largely a matter of trial and error to obtain an optimal parameter set. Although values were generally found to be realistic (Section 6.4.2), few field values were available for verification from this research project or other studies. To perform the hydrological modelling in enough detail to obtain reliable results, much more field information should be incorporated in the model and field verifications are needed. Such an amount of detailed work would be too resource-intensive to fit into this study and would not add substantially to the information already available. Furthermore, if detailed hydrological modelling was to be incorporated into a decision-making framework, it would be difficult to generate satisfactory results for a large area. Also, specialist knowledge would be needed to operate the model and this would cause a significant hurdle for conservation organisations. Therefore, it was decided to abandon hydrological modelling for the set up of a DSS and only to include simple classification systems of landscape topography and soils.

The application of the Hydrology Of Soil Types classification gave very useful results. It was found that 92% of the total Culm grassland area was situated on soils with HOST class 9 or 24 compared to the 46% of the total area. These results indicate that the HOST classification could form a very useful selection criterion for the decision where Culm grassland sites should be restored. The HOST classification was originally designed for use at the 1:250,000 scale soil map, for each map unit the HOST categories were listed (Boorman *et al.*, 1995) Most map units were classified by more than one HOST category and were therefore difficult to use directly for the map units of the 1:50,000 scale soil map. However, by comparing the soil series profiles present in each map unit with the listed HOST categories, a reliable decision on the HOST class could be made. In the HOST classification, different physical characteristics of the soil profile and the substrate important for the hydrology of an area are taken into account. The classification was therefore more sophisticated than the soil map classification based on the transmissivity of the soils and was thought to be more useful for the purpose of this study. Dunn and Lilly (*in press*) and Dunn *et al.* (*in press*) used the HOST classification as an indication of hydrologically similar units to use as input into a catchment scale hydrological model. On the other hand, the assumption of uniform soil hydrological functioning for soils with similar flow paths and hydrological mechanisms is a simplification not necessarily corresponding to reality (Dunn and Lilly, *in press*).

PART III

Culm grassland ecology

Chapter 7

Examination of relationships between vegetation and environmental factors in Culm grassland – Techniques

7.1 Introduction

In Part 3 of the thesis, relationships between Culm grassland vegetation and environmental characteristics are presented. The relationships between Culm grassland and its environment were studied at the plot scale, instead of at the catchment or regional scales, like the work presented in Part 2. Part 2 of the thesis has introduced methods to relate Culm grassland location to environmental factors at a regional and catchment scale and presented the results of the topographical and hydrological analysis. In this part, a much more detailed approach is presented, concerned with the effect of soil and management parameters directly on species composition. The major aim was to address Objective 3 of the thesis:

To describe the Culm grassland plant communities and determine the major environmental gradients.

This chapter describes the methodology that was used to investigate Culm grassland ecology. The methodology was based on the Culm grassland database of the Devon Wildlife Trust, which contained species information for a large number of sites on the Devon side of the Culm Natural Area. Section 7.2 gives a description of the data set and the techniques used to group the sites. A field survey, referred to as 'the 1999 survey', was designed to determine the environmental characteristics of the sites. The strategy that was adopted, including details on the field and laboratory methods, are described in Section 7.3. The section not only describes the methodology, but also includes the results of the study. Analysis of the results uncovered a few problems with the data set and therefore the findings were used as a basis for a second field survey, referred to as 'the 2000 survey'. In contrast to the 1999 survey, the 2000 survey included species data collected at the same location and time as the environmental information and the results are incorporated in the decision-making tool presented in Part 4. Many details of this second survey are similar to the 1999 survey, but a short overview will be presented in Section 7.4. Results of the 2000 survey will be presented in detail in Chapter 8.

7.2 Botanical analysis of the Devon Wildlife Trust database

Digital vegetation data for approximately half of the 790 Culm grassland fragments in Devon were available in the Devon Wildlife Trust the database. The data set was compiled from information collected by a large number of volunteers working for the Trust and data were assembled during various parts of the field season and over a number of years. The initial vegetation survey was completed in 1989, but updates of the database have taken place regularly since that time. The floristic data consisted of species lists with presence/absence data for each site. A selection procedure was followed to eliminate unsuitable information, resulting in the exclusion of 98 sites, which were indicated as plant communities associated with, but not included in the Culm grassland communities. *Betula - Molinia* woodland, for example, is found on equally wet soils and could develop when the sites are not grazed. Other sites that were eliminated were those that could not be related to specific fragments, because no grid reference was linked to the vegetation information and the site consisted of more than one fragment. The data from the resulting 359 suitable sites were used for a botanical and phytosociological analysis. A detailed examination of the species lists resulted in a total of 200 species. Species classified only to plant family level were either left as they were, deleted from the list or assigned to the most likely species group present on the site, depending on the difficulty of the decision.

Two-Way Indicator Species Analysis (TWINSPAN), a divisive polythetic classification method, (Hill, 1979a; Kent and Coker, 1992) was carried out to group the data into classes with similar species composition. This method is probably the most widely used method for classification of plant community data (Kent and Coker, 1992; Waite, 2000). TWINSPAN divides the vegetation recording units (fields/quadrats) into groups based on similarity of the species composition. Pseudospecies are identified, which combines presence/absence species information with abundance data. For the DWT data, only presence/absence data were available and thus the pseudospecies concept was not applied. Seven major groups were distinguished from the DWT dataset (1 to 7), which are presented in Table 7.1. The number of samples in each group are given in Table 7.2.

	Plant community groups						
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Salix sp.	V	I	I	II	II		II
Filipendula ulmaria	III	I	III	III	IV	IV	III
Molinia caerulea	II	IV	V	IV	III	IV	I
Juncus acutiflorus	II	III	V	III	IV	IV	II
Angelica sylvestris	II	II	V	IV	IV	V	III
Juncus effusus	II	II	IV	III	V	IV	
Valeriana officinalis	II	I	III	I	III	IV	I
Deschampsia caespitosa	II	I	II	II	III	V	II
Alnus glutinosa	II	I	I	I	II	IV	
Succisa pratensis	I	IV	V	III	IV	IV	
Cirsium palustre	I	II	IV	III	IV	V	
Lotus pendunculatus	I	II	IV	III	IV	III	II
Ulex europaeus	I	II	II	I	II	III	
Potamogeton polygonifolius	I	II	I	I	I	I	
Rubus fruticosus agg.	I	II	I	II	III	IV	
Lychnis flos-cuculi	I	I	IV	II	IV	III	II
Mentha aquatica	I	I	III	II	III	IV	
Dactylorhiza praetermissa	I	I	II	I	I	I	
Salix cinerea	I	I	II	I	II	II	II
Betula pubescens	I	I	I		I	I	I
Betula pendula/pubescens	I	I	I	I	I		
Caltha palustris	I	I	I	I	I	II	I
Carex laevigata	I	I	I	I	I	I	
Carex paniculata	I	I	I	I	I	I	IV
Cirsium arvense	I	I	I	I	II	II	
Corylus avellana	I	I	I	I	II	IV	II
Crataegus monogyna	I	I	I		I	III	II
Dryopteris dilatata	I	I	I		I	III	
Glyceria fluitans	I	I	I	I	I	IV	
Hypericum undulatum	I	I	I	I	I		
Iris pseudacorus	I	I	I	I	I	I	II
Oenanthe crocata	I	I	I	I	II	II	IV
Quercus petraea/robus	I	I	I	I	I		I
Salix aurita	I	I	I	I	I		II
Sparganium erectum	I	I		I	I	I	II
Epilobium hirsutum	I		I	I	I		II
Lycopus europaeus	I		I	I	I	I	II
Solanum dulcamara	I		I	I	I	II	I
Fraxinus excelsior	I				I	II	I
Phalaris arundinacea	I			I	I		III
Scirpus sylvaticus	I			I	I	I	III
Calluna vulgaris		IV	II	I	I	I	
Erica tetralix		IV	I	I	I	I	
Carex panicea		III	V	I	II	I	
Cirsium dissectum		III	IV	II	II	II	
Potentilla erecta		III	IV	II	III	V	
Narthecium ossifragum		III	II	I	I		

Table 7.1 Vegetation groups derived from the DWT database. Species frequencies: I = 1-20%, II = 21-40%, III = 41-60%, IV = 61-80% and V = 81-100%.

	Plant community groups						
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Serratula tinctoria		III	II	I	II	I	II
Holcus lanatus		II	IV	II	IV	IV	I
Ranunculus flammula		II	IV	I	III	V	
Achillea ptarmica		II	III	II	III	IV	
Anthoxanthum odoratum		II	III	I	III	II	
Carex viridula ssp. oedocarpa		II	III	I	I		
Viola palustris		II	III	I	II	IV	I
Carex echinata		II	II	I	I		
Dactylorhiza maculata		II	II	I	I	I	
Hydrocotyle vulgaris		II	II	I	I	II	
Luzula multiflora		II	II	I	II	I	
Pedicularis sylvatica		II	II	I	I	I	
Salix repens		II	II	I	I		
Scutellaria minor		II	II	I	I	II	
Ulex gallii		II	II	I	I		
Anagallis tenella		II	I	I	I	I	
Eriophorum angustifolium		II	I	I	I		
Pteridium aquilinum		II	I	I	II	III	
Galium palustre		I	III	II	III	V	I
Rumex acetosa		I	III	I	III	V	I
Agrostis canina/capillaris		I	II	I	II		
Agrostis stolonifera		I	II	I	II	II	
Cardamine pratensis		I	II	I	II	III	
Carex nigra		I	II	I	I	I	
Centaurea nigra		I	II	I	V	IV	
Cynosurus cristatus		I	II	I	III	II	
Epilobium palustre		I	II	I	II	I	
Festuca rubra agg.		I	II		II	II	
Juncus bulbosus		I	II	I	I	I	
Juncus conglomeratus		I	II	I	I	II	
Lathyrus linifolius		I	II	I	II	II	
Plantago lanceolata		I	II	I	IV	III	
Prunella vulgaris		I	II	I	III	IV	
Ranunculus acris		I	II	I	II	III	
Ranunculus repens		I	II	I	III	IV	
Senecio aquaticus		I	II	I	III	IV	
Achillea millefolium		I	I	I	II	III	
Agrostis canina		I	I	I	II	I	
Agrostis capillaris		I	I	I	II	II	
Ajuga reptans		I	I	I	II	IV	
Athyrium filix-femina		I	I		I	II	
Betula pendula		I	I	I	I	IV	
Blechnum spicant		I	I		I	IV	
Carex binervis		I	I	I	I		
Carex flacca		I	I	I	I	II	
Carex hostiana		I	I	I	I		
Carex pilulifera		I	I				
Carex pulicaris		I	I	I	I		

Table 7.1 (contnd.) Vegetation groups derived from the DWT database. Species frequencies: I = 1-20%, II = 21-40%, III = 41-60%, IV = 61-80% and V = 81-100%.

Species	Plant community groups						
	1	2	3	4	5	6	7
Carex rostrata		I	I		I		
Cerastium fontanum		I	I		II	IV	
Chamerion angustifolium		I	I	I	I	I	
Cirsium vulgare		I	I		I	I	
Dactylis glomerata		I	I	I	II	II	
Dactylorhiza sp.		I	I	I	I		
Danthonia decumbens		I	I		I		
Digitalis purpurea		I	I	I	I	III	
Epilobium parviflorum		I	I		I		
Erica cinerea		I	I	I			
Eupatorium cannabinum		I	I	I	II	I	
Euphrasia officinalis agg.		I	I		I	I	
Fagus sylvatica		I	I	I	I	II	
Festuca ovina agg.		I	I	I	I		
Festuca ovina/rubra		I	I	I			
Frangula alnus		I	I	I	I	I	
Galium aparine		I	I	I	I	I	II
Galium saxatile		I	I	I	I		
Galium uliginosum		I	I	I	II	I	
Genista anglica		I	I	I	I		
Holcus mollis		I	I		I	II	
Hypericum elodes		I	I	I	I	I	
Hypericum pulchrum		I	I		I	II	
Hypericum tetrapterum		I	I	I	II	III	
Hypochaeris radicata		I	I	I	II	III	
Juncus articulatus		I	I	I	II	II	
Juncus bufonius agg.		I	I	I	I	I	
Lathyrus pratensis		I	I	I	II	II	
Leontodon autumnalis		I	I		I	I	
Leucanthemum vulgare		I	I		I	II	
Lotus corniculatus		I	I	I	II	IV	
Luzula campestris		I	I		I	I	
Mentha arvensis		I	I		I	II	
Menyanthes trifoliata		I	I	I	I	I	
Nardus stricta		I	I		I		
Pedicularis palustris		I	I		I		
Persicaria hydropiper		I	I	I	II	III	
Phleum pratense sens.lat.		I	I		II	I	
Poa pratensis sens.lat.		I	I		I	I	
Poa trivialis		I	I	I	I	I	I
Polygala serpyllifolia		I	I				
Potentilla anserina		I	I	I	II	III	
Potentilla palustris		I	I	I	I	I	
Potentilla reptans		I	I	I	II	II	
Prunus spinosa		I	I		I	II	I
Pulicaria dysenterica		I	I	I	III	II	
Quercus petraea		I	I	I	I	I	

Table 7.1 (contnd.) Vegetation groups derived from the DWT database. Species frequencies: I = 1-20%, II = 21-40%, III = 41-60%, IV = 61-80% and V = 81-100%.

	Plant community groups						
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Quercus robur		I	I	I	I	III	
Ranunculus ficaria		I	I		I	I	
Ranunculus omiophyllus		I	I		I	I	
Rosa canina agg.		I	I		I	II	
Rumex acetosella		I	I	I			
Rumex crispus		I	I	I	I	I	
Salix caprea		I	I		I	III	
Stachys officinalis		I	I	I	II	III	
Stellaria graminea		I	I		I	I	
Stellaria uliginosa		I	I	I	II	III	
Taraxacum officinale agg.		I	I		II	II	
Trifolium medium		I	I	I	I	I	
Trifolium pratense		I	I		II	III	
Trifolium repens		I	I	I	II	I	
Veronica scutellata		I	I	I	I	I	
Vicia cracca		I	I	I	I	I	
Viola riviniana		I	I			IV	
Wahlenbergia hederacea		I	I	I	I	I	
Callitriche stagnalis sens.lat.		I		I	I	I	
Drosera rotundifolia		I					
Oxalis acetosella		I			I	IV	
Pinguicula lusitanica		I				I	
Senecio jacobaea		I			I	I	
Cardamine flexuosa			I		I	III	I
Carex ovalis			I	I	I		
Carum verticillatum			I	I	I		
Centaurium erythraea			I	I	I	I	
Dryopteris affinis			I			III	
Equisetum fluviatile			I	I	I	I	
Equisetum palustre			I	I	I	I	
Galeopsis tetrahit agg.			I	I	I	I	
Geranium robertianum			I			IV	
Ilex aquifolium			I	I		II	
Lolium perenne			I		II	I	
Lonicera periclymenum			I		I	III	
Lysimachia nemorum			I		I	III	
Lythrum salicaria			I	I	I		
Myosotis secunda			I	I	I		I
Potentilla sterilis			I		I	I	
Rumex obtusifolius			I	I	I	I	
Rumex sanguineus			I		I	II	
Urtica dioica			I	I	II	III	II
Veronica chamaedrys			I		I	II	
Arrhenatherum elatius					I	I	I
Carex remota					I	II	
Chrysosplenium oppositifolium					I	III	I
Circaea lutetiana					I	III	

Table 7.1 (contnd.) Vegetation groups derived from the DWT database. Species frequencies: I = 1-20%, II = 21-40%, III = 41-60%, IV = 61-80% and V = 81-100%.

	Plant community groups						
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Crepis capillaris					I	I	
Dryopteris filix-mas agg.					I	II	
Hedera helix						IV	I
Heracleum sphondylium				I	I	II	I
Hyacinthoides non-scripta					I	I	I
Polypodium vulgare agg.					I	III	
Primula vulgaris					I	III	
Silene dioica				I	I	IV	
Stachys palustris				I	I	I	
Stachys sylvatica				I	I	II	
Stellaria holostea					I	II	

Table 7.1 (contnd.) Vegetation groups derived from the DWT database. Species frequencies: I = 1-20%, II = 21-40%, III = 41-60%, IV = 61-80% and V = 81-100%.

These groups were used as the strata to set up a stratified random sampling scheme for the collection of environmental and soil data. Selecting a number of sites from each vegetation class ensured that the sampling included as much of the variation in the vegetation composition of the sites as was possible. The following criteria were used for site selection:

1. A spread of selected sites over the whole Culm Natural Area.
2. Easy access to the site.
3. Permission of the owner to enter the site.
4. A minimum of 3 sites for each stratum.

Field data were collected during two field seasons: July/August 1999 and June 2000. Techniques and results of the 1999 survey will be presented and discussed in the next section. The design of the follow-up 2000 survey carried out to deal with the problems that arose from the 1999 survey will be presented in Section 7.4. For the design of the decision support system presented in Part 4 of the thesis, the results of the 1999 survey were discarded in favour of the data from the 2000 survey.

7.3 Vegetation – environment relationships: the 1999 field survey

7.3.1 Sampling design

In total, 29 fields were selected for the collection of environmental data in July and August 1999. Limited resources dictated largely how many sites could be visited. However, 29 sites (8% of the total) were considered representative of the range of sites found. The number of sites for each vegetation group was adapted to the size of the stratum. However, due to the great range in size of the strata, the number of sites selected for each stratum were not allocated on a *pro rata* basis (Table 7.2). A minimum of two and a maximum of four soil samples were taken in each field, depending on the size and the visible variation present in the field. A total of 95 locations were sampled and sampling locations were selected in the field based on vegetation and topographic differences. The aim was to cover the whole range of vegetation in the different topographic locations was. However, no samples were taken from group 7 because only a few fields were classified as this group and it also included all the odd samples.

Vegetation group	1	2	3	4	5	6	7
Number of samples in DWT database	19	77	64	122	51	19	7
Number of field samples 1999	9	22	13	18	23	10	0

Table 7.2 Number of samples for each vegetation group in the Devon Wildlife Trust and number of field samples taken 1999

The next section presents the techniques used for the sampling and analyses performed in the field.

7.3.2 Field analyses and soil sampling

As described in Section 7.2, soil samples were collected at a number of locations in every field to obtain an average value for each parameter, which could be linked to the vegetation information present for each field. To describe general field characteristics, slope was measured with a hand-held clinometer and aspect was derived from a topographic map. To obtain insight into the general soil properties, a soil core was extracted at every location, enabling soil profiles down to 120cm depth to be described based on depth, texture, colour and mottles. Further, drainage characteristics, which are of major importance for wetland development, were determined. At one location in every field, a vertical soil core of 942 cm^3 (10cm diameter and 12 cm length) was taken for saturated conductivity and bulk density measurements. The techniques to measure these two parameters in the laboratory will be described in the Section 7.3.3. A description of the measurement of the volumetric soil water content is given below. Although this factor is highly variable through time, the purpose was to obtain relative differences between the fields. To reduce the time-effect, the field measurements were taken over as short a time-span as possible.

Volumetric soil water content

Soil water readings were taken with a theta probe (Delta -T Devices) at 5 cm depth on 4 sides of a 20 by 20 cm soil pit. The theta probe measures the volumetric soil water content (θ_v) by determining the apparent dielectric constant (ε) using the following equation:

$$\theta_v = \left(\sqrt{\varepsilon - a_0}\right) / a_1$$ *Equation 7.1*

In this equation a_0 and a_1 are curve-fitting parameters. A signal is sent out and the difference of the amplitude of the returning wave is measured to determine the dielectric constant. The theory is based on the fact that the dielectric constant of water is much greater than that of soil and air. Therefore, the dielectric constant of the soil depends largely on its water content (Roth *et al.,* 1992; Whalley, 1993; White *et al.,* 1994). This parameter is also affected by the organic matter content and therefore different calibration curves are used for mineral and organic soils. Due to the large variation of soils in the area, it was decided to use the parameters suggested in the manual and not to calibrate the probe on a sample from the area. The values are presented in Table 7.3.

	a_0	a_1
Mineral soils	1.6	8.4
Organic soils (specified as >7% organic carbon)	1.3	7.7

Table 7.3 Parameters used to calculate the soil water content

Soil water content (θ) was calculated from the output voltage (V), by using the following equation:

$$\theta = \frac{\left(1.07 + 6.4V - 6.4V^2 + 4.7V^3\right) - a_0}{a_1}$$ *Equation 7.2*

The parameter values in Table 7.3 were applied depending on the organic carbon content of the soil, for which the methodology will be described in Section 7.3.3.

7.3.3 Laboratory analyses

The soil samples collected for the 1999 survey were analysed for both physical and chemical properties. Physical parameters, that were measured to describe soil drainage characteristics, were texture, saturated hydraulic conductivity, bulk density and porosity. The following chemical parameters were measured: soil acidity, total carbon and nitrogen content, available phosphorus, available, potassium, calcium, magnesium and sodium. These parameters were measured because they determine the nutrient richness of the soil and therefore influence the species composition. To ensure that representative sub-samples were used for the measurements and chemical extraction solutions would get in contact with all soil material, bulk soil samples for the texture analysis and the chemical analyses were air dried first and sieved through a 2 mm sieve,

Texture

Both chemical and physical behaviour of soils is largely determined by texture. Generally, coarse sandy soils warm up quickly in spring and drain easily, but also provide a poor supply of nutrients and have a poor ability to hold water. Clay soils on the other hand generally provide a good supply of nutrients retain water easily, but have poor drainage properties (Rowell, 1994).

To measure the percentages of sand, silt and clay, a scoop of soil was boiled with hydrogen peroxide to remove the organic matter. The foamy layer of organic material that formed on top of the solution was removed. A small amount of the mineral residue was dispersed into a water tank into which a mixture of 8% sodium hexametaphosphate and sodium carbonate was dissolved. The sample was analysed on the Mastersizer X (Malvern Instruments Ltd.), which uses the angle of light diffraction of a Laser beam to determine the particle sizes present in the sample. This is based on the theory that the diffraction angle is inversely proportional to particle size. Particle size distributions are determined by magnifying the scattered beam with a 45 mm lens (for the silt and clay fractions) and a 100 mm lens (for the coarser sand particles) and analysing the light signal on a photosensitive detector.

Saturated hydraulic conductivity

Soils under Culm grassland are characteristically very slowly permeable or rather impermeable and are often saturated for large periods of the year (Harrod, 1987). The saturated hydraulic conductivity is a measure of the ability of the soil to transport water under saturated conditions (Koorevaar *et al.*, 1983). It was measured for the upper 12 cm of the soil, sampled with a soil core of 10 cm in diameter. The conductivity was measured with a falling head permeameter (Klute and Dirksen, 1986; Young, 1991). The cores were saturated by soaking them for at least 24 hours in a water bath of with the water-level flush with the top of the core. Saturated soil cores were enclosed in a watertight cell and a column of water was set on top of the soil column. The time and volume of the water running through the core were measured.

Saturated conductivity was calculated in cm s^{-1} with the following equation (Klute and Dirksen, 1986):

$$K = \frac{a * l}{A}\left[\frac{\log_e H_0 - \log_e H_1}{t}\right]$$ *Equation 7.3*

In which:

a = area of manometer tube in cm^2

l = length of sample in cm

A = area of sample in cm^2

H_0 = initial head in cm

H_1 = final head in cm

t = time in s

Bulk density and porosity

The pores in the soil hold water, allow drainage of excess water and ensure that oxygen can reach plant roots and carbon dioxide to be removed from the soil. The porosity depends on the dry bulk density of the soil and the particle density (Rowell,1994). Porosity of the topsoil was determined by measuring the weight of the saturated soil cores used for the saturated conductivity measurements. Cores were oven-dried and weighed again. The difference between the wet and dry core was the amount of water in the core, when all pores are filled. A small error is introduced, however, because the adsorbed water within the clay particles is also reduced. The weight of the water was converted into a volume by dividing with the density of water. Porosity was calculated by dividing the pore volume by the total volume of the core. Bulk density was determined by measuring the core dry weight and dividing this by the core volume.

pH

A number of processes in soils that are important for plant nutrient uptake are affected by the acidity of the soil. For example, lowering the pH decreases the exchangeable calcium and magnesium cations concentration and increases the amount of exchangeable aluminium cations. Also phosphate solubility is reduced under more acidic conditions and the activity of many soil organisms is reduced resulting reduced mineralisation and decreased availability of nitrogen, phosphorus and sulphur (Rowell, 1994). The samples collected in 1999 were analysed for pH-$CaCl_2$. Approximately 10 g air dry soil, 25 ml water and 2 ml 0.125 M calcium chloride were stirred thoroughly in a beaker and a pH-probe was left for 30 seconds in the suspension before taking a reading (Rowell, 1994).

Total carbon and nitrogen content

Total carbon and nitrogen are a measure of the amount of organic matter present in the soil. On average, organic matter contains 58 mass % of carbon (Rowell, 1994). The C:N ratio of the organic material determines the speed of the mineralisation process (White,1997). The higher the C:N ratio, the longer it takes to decompose the organic matter. Total carbon and nitrogen content were determined with the LECO CNS-2000. From the air-dry soil sample, 0.2 g was weighed into a ceramic sample holder. The samples were placed in a combustion chamber, where the furnace and the flow of oxygen cause the sample to combust. This process converts all elemental carbon and nitrogen into CO_2 and N_2. An infrared cell determines the carbon content and a thermal conductivity cell measures the nitrogen content.

Phosphorus availability

Phosphorus is one of the major macronutrients required for plant growth (Mitsch and Gosselink, 1993). Phosphorus availability is often a limiting factor in species-rich grasslands and heathlands (Marrs *et al.*, 1991; Gough and Marrs, 1990). A detailed study of P availability in Culm grassland soils was conducted by Goodwin *et al.* (1998), who found lower values on an unimproved Culm grassland site compared to an improved site when using Olsen's bicarbonate method. This was not confirmed, however, by using a technique, which extracts available phosphorus by centrifuging the soil solution. In this study, available phosphorus content was measured using Olsen's method (Rowell, 1994), which is most widely used by other researchers. With this method, phosphorus is extracted under a pH of 8.5, which is not directly comparable with the more acidic soils typical of Culm grassland. However, the Olsen's bicarbonate method is the most frequently used on a wide range of soils and the use of the same technique ensures comparability with other studies.

Available phosphorus was extracted from 2 g air dry soil sample with 40 ml 0.5 M sodium bicarbonate at pH 8.5 and leaving the samples overnight. The extract was filtered and 5ml was put into a boiling tube with 20 ml of ammonium molybdade, 5 ml ascorbic acid and 1 ml of 1.5 M sulphuric acid for blue colouring and neutralisation of the sample. Calibration ranges of 1, 3, 5 and 7 mg PO_4-P l^{-1} for the 1999 samples and 0.05, 0.1, 0.5, 1 and 3 mg PO_4-P l^{-1} were set up for the 2000 samples. Light absorption was measured on the Specord M500 (Zeiss).

Available calcium, magnesium, potassium and sodium

Available calcium, magnesium, potassium and sodium concentrations were determined by weighing 2 grams of air dry soil (<2 mm) into a bottle and adding 50 ml of 1 M ammonium-acetate at pH 7. The samples were shaken thoroughly and then left for 24 hours (Rowell, 1994). Ammonium ions replace the exchangeable cations. Samples were filtered into volumetric flasks and the amount was topped up to precisely 50 ml. Potassium and sodium concentrations were determined on a flame photometer by flame emission. Samples with concentrations higher than 10 ppm were diluted 20 times. Calcium and magnesium concentrations were measured by diluting 1 ml of the extract with 9 ml of water. Lanthanum chloride (0.1 ml of 10%) is added to remove interference of elements such as phosphate, aluminium and silicon. Concentrations were measured by absorption on the SpectrAA 100/200.

7.3.4 Statistical techniques

To compare the soil and field characteristics of the six vegetation groups (1 to 6) that were derived from the Devon Wildlife Trust database, descriptive statistics on the environmental data were carried out. The relationships between species composition and environmental factors (including the topographic index presented in Part 2) were examined using Detrended Correspondence Analysis (DCA) (Hill, 1979b; Hill and Gauch, 1980) and Canonical Correspondence Analysis (CCA) (Ter Braak, 1986, 1987; Ter Braak and Smilauer, 1997). DCA and CCA are both ordination techniques that are widely used in ecological research. Reciprocal averaging or correspondence analysis lies at the base of both methods, which is based on a weighted averaging technique (Kent and Coker, 1992; Waite, 2000). Weights evenly distributed on a scale from 0 to 100 are assigned to all species (species scores) and average scores for each quadrat are calculated based on the presence/absence of species multiplied by the species scores and divided by the total number of species. The resulting values are rescaled from 0 to 100 to obtain the quadrat scores. The quadrat scores are used to calculate a new set of species scores. The process is repeated until the species and quadrat do not change any longer (Kent and Coker, 1992; Waite, 2000). DCA also includes 'detrending' to reduce both the 'arch' and 'axis compression' effects (Hill, 1979; Kent and Coker, 1992). The results are presented as ordination diagrams with the axes pointing in the direction of the largest variation. The main difference between DCA and CCA is that CCA includes environmental data in the analysis using multiple regression techniques (Ter Braak, 1986; 1987). For the DWT survey vegetation data were recorded at field scale instead of quadrat scale. Therefore, DCA and CCA were carried out for the 29 fields sampled in the 1999 survey. Environmental data were collected on more than one location in each field and thus average values for each field were used in the CCA.

7.3.5 Results and discussion of the 1999 field survey

The results of the 1999 survey are described only briefly in this section. It was decided not to include full details, but only to show those results relevant to the decision to repeat the field survey in 2000. The data collected during the 1999 survey were not used any further in this thesis and therefore a concise account of the results was considered sufficient and no significance testing was carried out.

Figure 7.1 presents the fields that were sampled for the 1999 survey. Figure 7.2 to 7.13 show the average values of the 12 environmental parameters that were measured recorded for the 6 vegetation groups that were derived from the DWT database. The bars indicate the standard error. The major observations that could be made from these results were that vegetation groups 2 to 4 were found on the lowest gradients. Soil water and bulk density values showed little variation between the vegetation groups and although the saturated hydraulic conductivity values were lowest for vegetation group 3, the large variation in the data meant that little could be concluded from this. Group 5 and 6 were associated with the highest soil acidity values and group 3 and 6 had the lowest total carbon and nitrogen contents. However, the variation of the values measured in group 6 were rather high. For available phosphorus and potassium, results showed groups 1 to 3 and 6 to be the lowest. The available sodium content of all groups was fairly equal and the same counted for the available calcium content, with the exception of group 5, which had a very high average value caused by one outlier. Group 5 was associated with the highest magnesium content. The texture of all samples was fairly uniform and consisted of sandy, silty loam to silty loam.

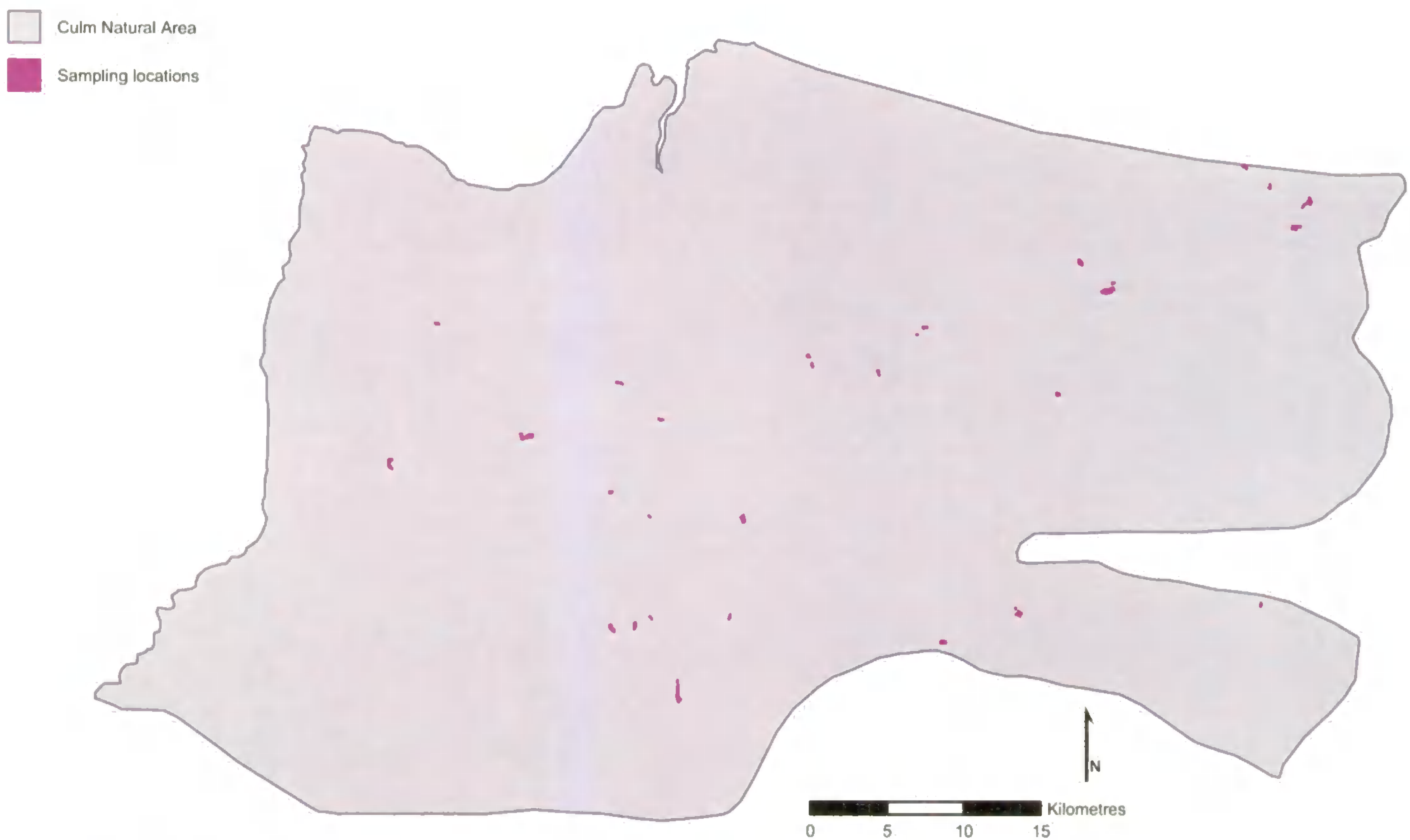


Figure 7.17 Sampling locations 1999

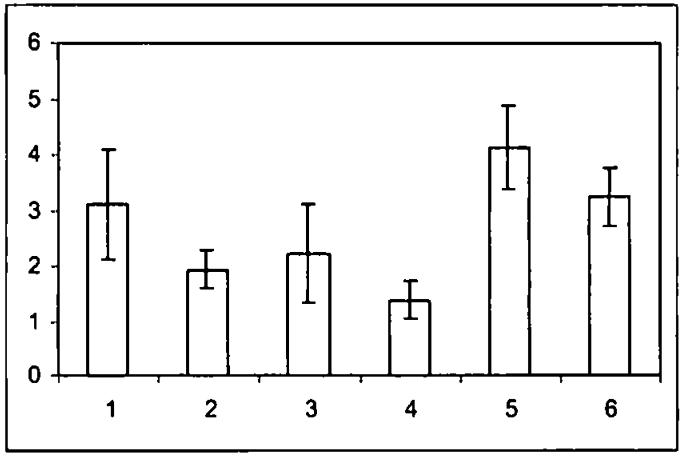


Figure 7.2 Local gradient (degrees) – 1999 survey

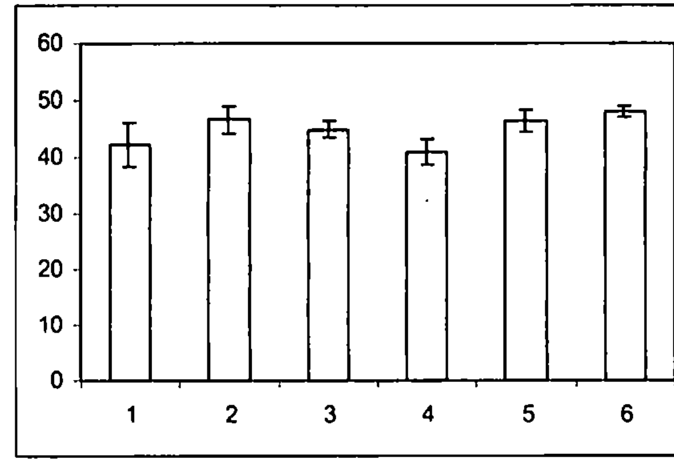


Figure 7.3 Volumetric soil water content (%) – 1999 survey

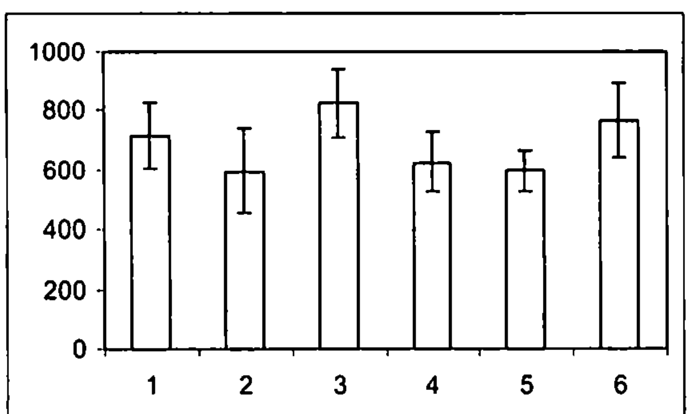


Figure 7.4 Bulk density (kg m^{-3}) – 1999 survey

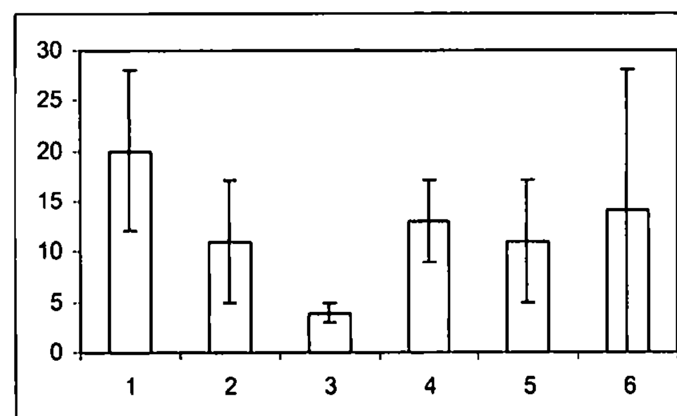


Figure 7.5 Saturated hydraulic conductivity- Ksat (m day^{-1}) – 1999 survey

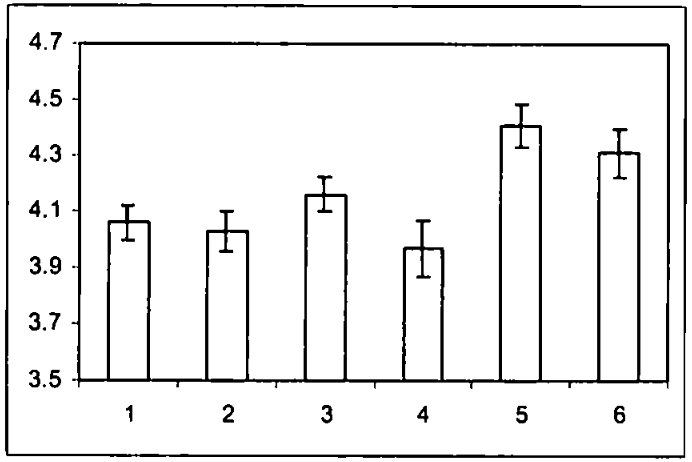


Figure 7.6 Soil acidity pH – $CaCl_2$ – 1999 survey

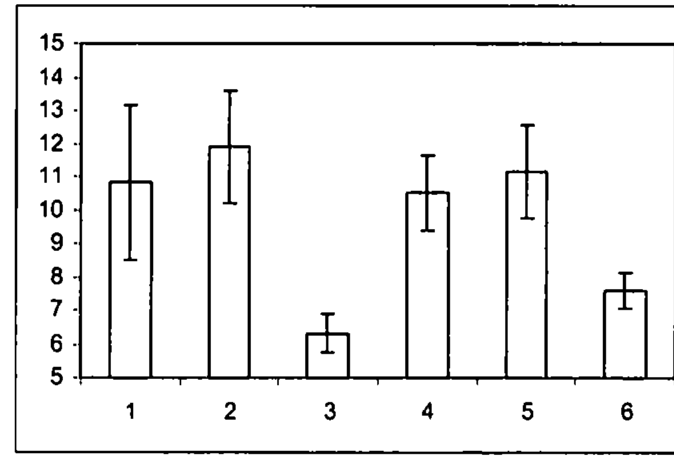


Figure 7.7 Carbon content (%) – 1999 survey

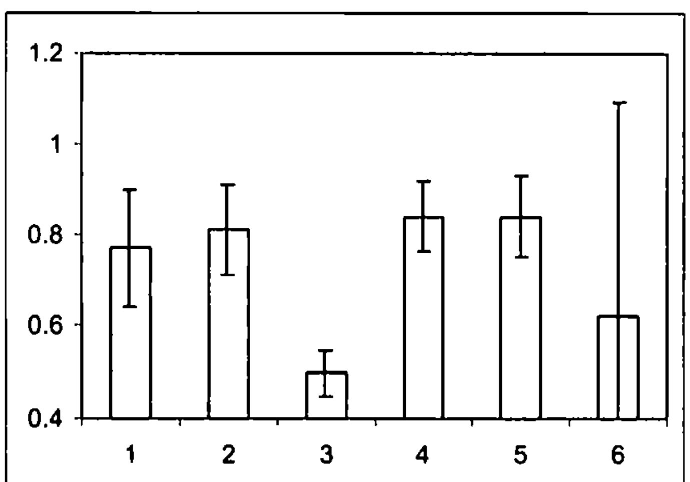


Figure 7.8 Nitrogen content (%) – 1999 survey

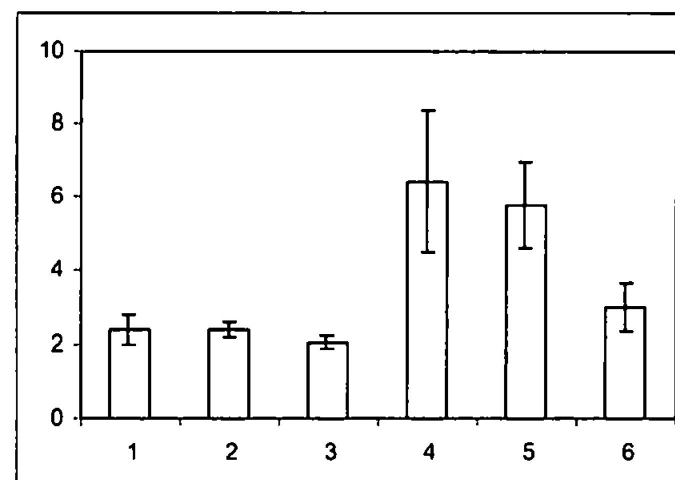


Figure 7.9 Available phosphorus content (g kg^{-1} air dry soil) – 1999 survey

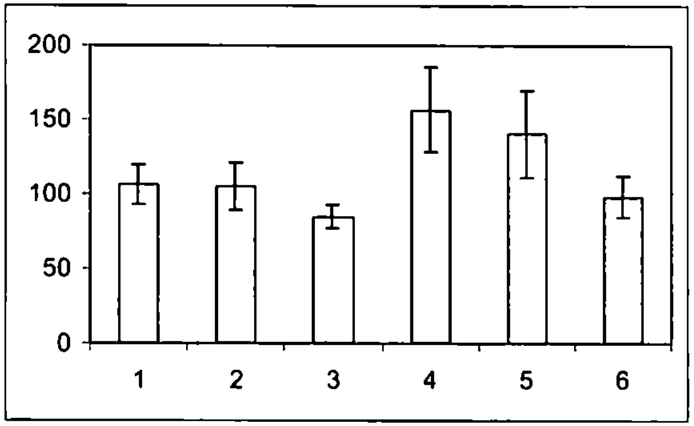


Figure 7.10 Available potassium content (g kg^{-1} air dry soil) – 1999 survey

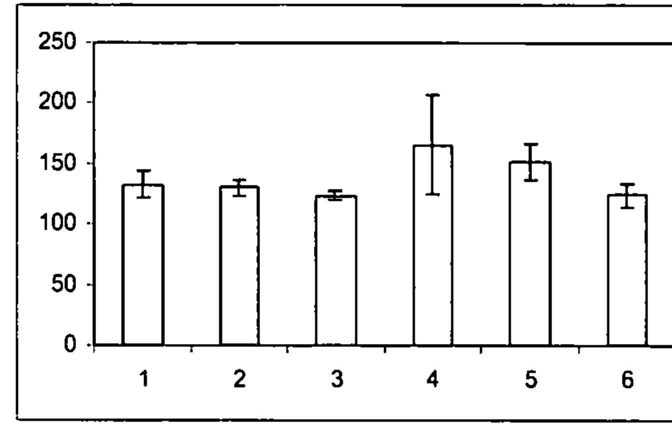


Figure 7.11 Available sodium content (g kg^{-1} air dry soil)- 1999 survey

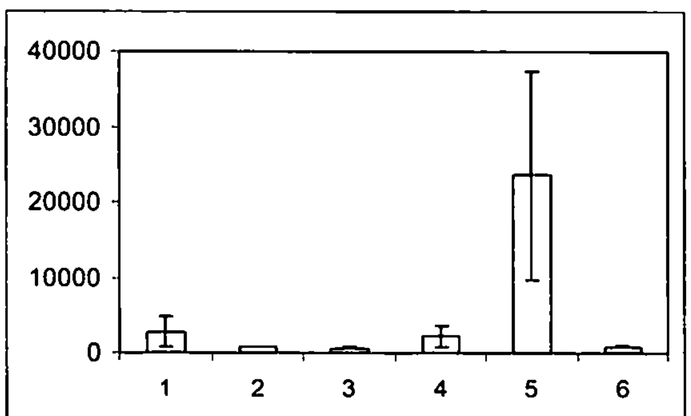


Figure 7.12 Available calcium content (g kg^{-1} air dry soil) – 1999 survey

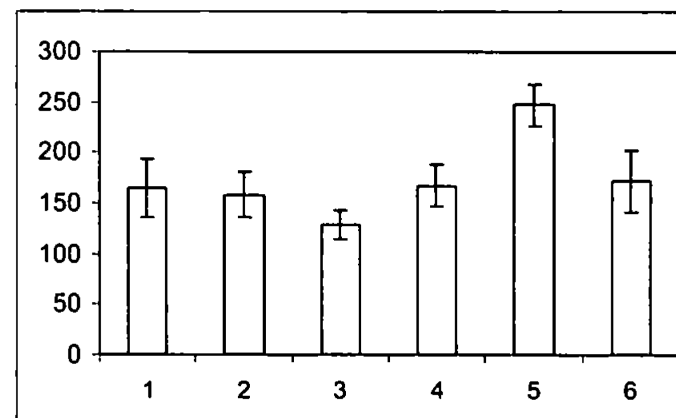


Figure 7.13 Available magnesium content (g kg^{-1} air dry soil) – 1999 survey

To find the overall variation within the vegetation data set, DCA was carried out. Two outliers were removed from the data and the resulting graphs are presented in Figure 7.14 and 7.15. The ordination graphs show fairly clearly the separate TWINSPAN groups. However, overlap between most groups does exist in the middle of the graph (Figures 7.16 and 7.17). As expected the separate groups were most clearly visible along the first ordination axis. Normally, no polygons can be defined by two points or less. Therefore, the polygon of group 1 has been drawn to indicate the connection of the samples.

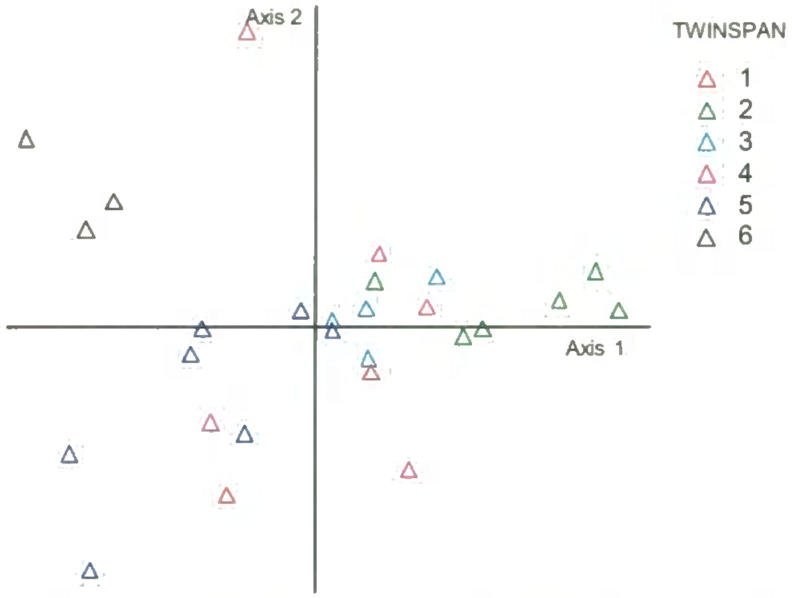


Figure 7.14 DCA results axes 1 and 2, two outliers have been omitted

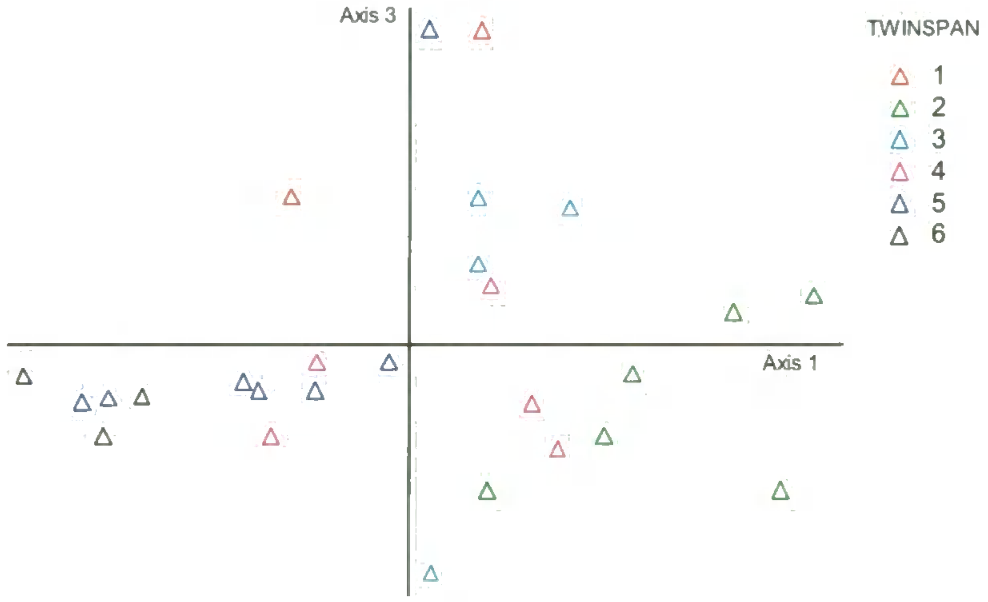


Figure 7.15 DCA results axes 1 and 3, two outliers have been omitted

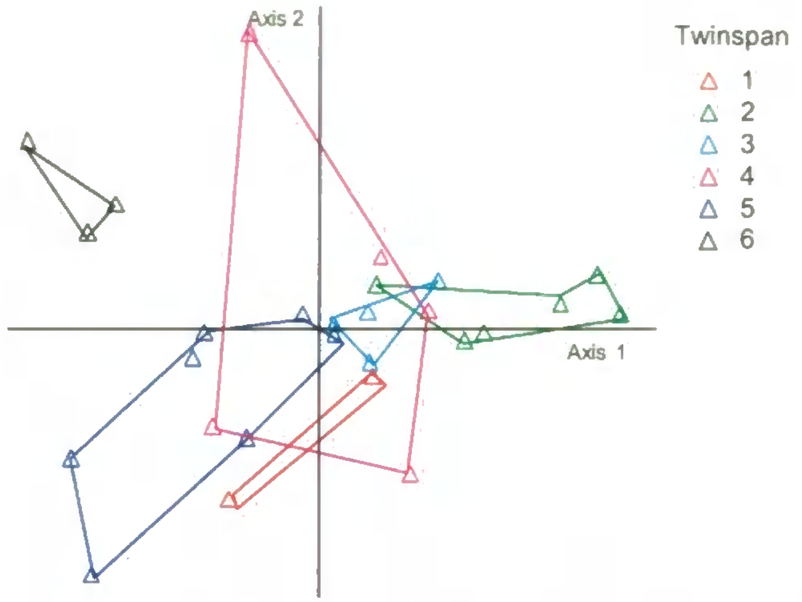


Figure 7.16 Polygons defining the TWINSPAN groups presented in the DCA ordination graph, axes 1 and 2, two outliers have been omitted

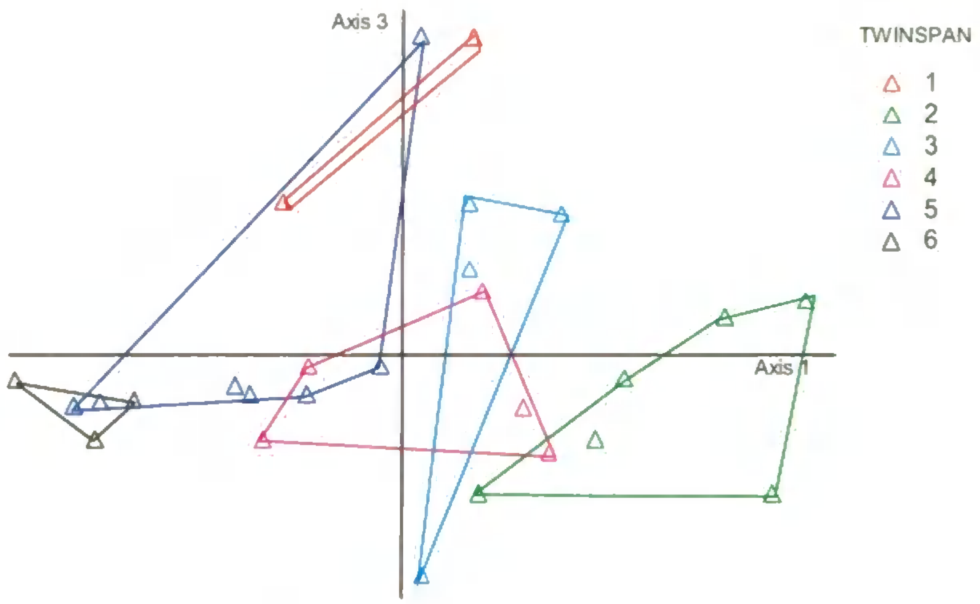


Figure 7.17 Polygons defining the TWINSPAN groups presented in the DCA ordination graph, axes 1 and 3, two outliers have been omitted

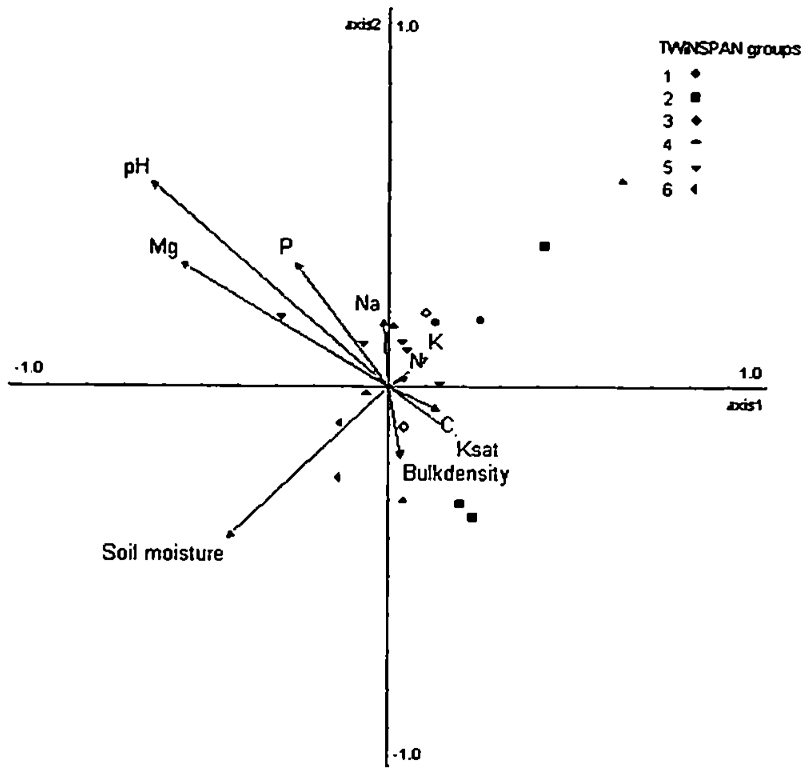


Figure 7.18 CCA results axes 1 and 2, all samples and variables included

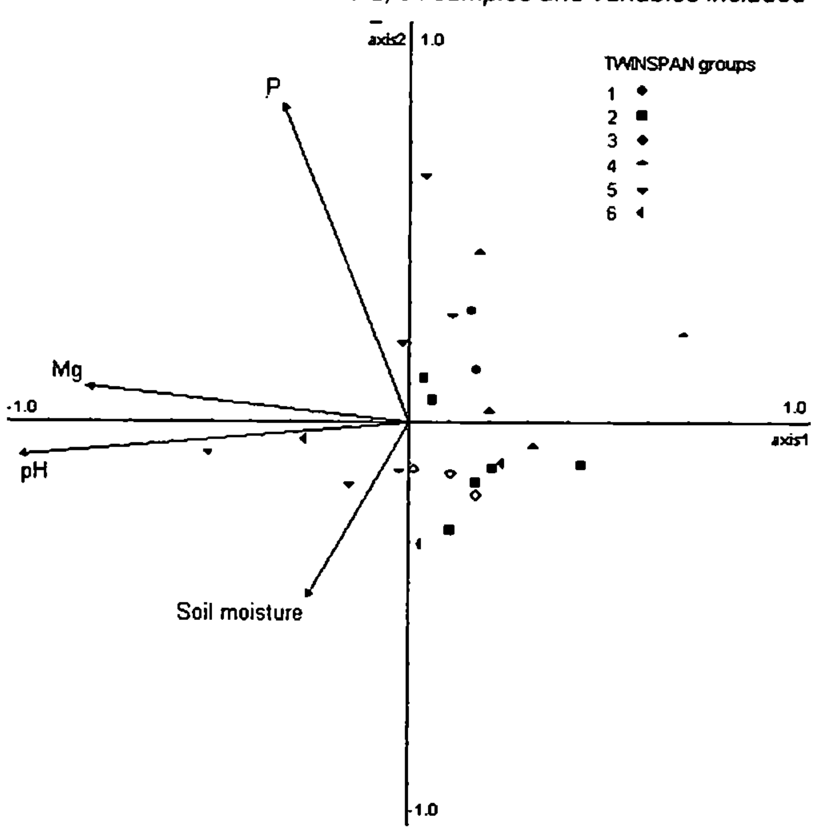


Figure 7.19 CCA results axes 1 and 2, 1 sample and 8 variables have been omitted

Figure 7.18 presents the sample scores derived from the CCA, with all samples and environmental variables included. TWINSPAN groups are indicated with different symbols and the directions and magnitudes of the environmental variables are indicated by arrows. To improve the analysis, noise had to be minimised and therefore one sample and eight environmental variables were removed from the data set. Figure 7.19 shows the results. The CCA graphs showed a very high, significant correlation of the pH ($r = -0.922$) and magnesium content ($r = - 0.766$) with the first axis of the floristic data. Further, a significant correlation of phosphorus ($r = -0.724$) with the second axis of the floristic data was shown. A correlation of soil moisture ($r= -0.396$) with the same axis was found to a lesser extent. Soil water is, therefore, of less significance than pH, magnesium and phosphorus. Both figures show clearly that all TWINSPAN groups were completely overlapped with each other and also the groups were concentrated in the centre of the graph, even after removing the most extreme outlier. Another observation was that the environmental arrows mainly pointed away from the samples, which indicated a negative association between the sample vegetation and the environmental parameters.

From these results it was concluded that the field vegetation records and the averaged soil sampling did not match sufficiently. Two reasons could be given for this:

1. The averaging of the environmental information for each field gave too generalised information to explain the vegetation composition. Although it was tried to cover the full topographical and vegetational variation within each field, the presence of extreme variations within each field (e.g. fairly dry sandy soils together with local hollows filled with peat) probably caused the average value to be of limited use for the description of soil characteristics. Vegetation in these fields also showed large variation, but due to lumping the data recorded in various plant communities within the field into records for the total field, differences between plant communities were not reflected in the vegetation records.
2. The quality of the DWT vegetation data was highly variable and for some fields rather limited. For some sites only a few species were listed for each field, whereas for other sites detailed records were available. The reasons for this high variability in the data quality could have been that data were recorded by many different people, with varying botanical skills. Furthermore, in some fields possibly only the key species were listed, because of the collection of data for a different purpose. Surveying has taken place during different parts of the field season and over various years. Although the data set provides substantial information on Culm grassland sites in Devon, for the purpose of this study the material was probably not suitable except for designing a

sampling strategy and determining the range of variation present in the Culm grassland communities.

The DWT vegetation data were thus of insufficient detail and consistency to allow linkages to be made between vegetation and soil/environmental conditions. From the above became clear that secondary data of the kind collected for general purposes by nature conservation organisations are unlikely to be useful for a rigorous investigation. Detailed ecological research requires careful planning of the sampling strategy to ensure the impact of unknown factors is minimised.

For the reasons described above, it was decided to repeat the field sampling during the summer of 2000 and include a vegetation survey at every sampling location. A description of the sampling strategy is given below.

7.4 Repetition of field measurements: the 2000 field survey

In June 2000, the sampling was repeated at 21 of the original 29 of the 1999 field survey sites. The other eight were not revisited, either because access to some of the fields was denied or the sites were inaccessible or no permission could be obtained from the owner. Therefore, four new sites in Devon were added to the selection and five Cornish SSSI were also included to extend the survey into the Cornish side of the Culm Natural Area. The new sites were not part of the initial DWT data stratification. Figure 7.20 shows the locations of the sites visited for the 2000 survey. At the 30 sites, once again between 2 and 4 soil samples were taken, leading to a total of 97 soil sampling locations. General field descriptions, including local gradient, aspect and soil depth, were made for every sampling point. As in 1999, slope was measured with a hand-held clinometer, but for measurement of the aspect a compass was used. Measurement of soil depth was added to the list of field measurements, because of its importance for the plant rooting depth and thus its influence on plant species. Soil depth was measured on the four corners and in the middle of the vegetation quadrat. Soil water measurements were also repeated and the same technique was used as before (Section 7.3.2). Further, unlike during the 1999 survey, grazing pressure was added to the list of parameters measured in the field. A subjective scale of 0 to 5 was used, based on:

- Physical evidence of browsing activity or cropping of the sward
- Evidence of trampling and poaching
- Presence of faecal units

The grazing pressure was valued 0, if no evidence of grazing was found at all and a value of 5 was allocated for the highest grazing pressure.

A detailed vegetation description of a 4 m^2 quadrat around each sampling point was also made during the 2000 field survey and vegetation data for the 97 locations were collected with the aid of a professional botanist. Abundance of species were listed, based on the DAFOR scale, with on one end of the spectrum **Dominant** - ultimate class, only 1 or 2 species can be called dominant otherwise they are called abundant, and at the other end **Rare** - less than 5% cover, 1 to 3 individuals (Mike Cook, pers. comm.). The DAFOR scale gives a subjective estimation of the abundance of plant species. However, the resources available demanded a rapid approach and the relative differences between the quadrats are still clear because the same people collected all data. Wherever possible, the samples were taken at the same positions as the year before.

At every sampling, point a bulk soil sample was collected and taken back to the laboratory for further analysis. Table 7.4 gives an overview of the measurements that were repeated in the 2000 field season.

Laboratory measurements	1999	2000
Texture	+	-
Saturated hydraulic conductivity	+	-
Bulk density	+	-
Soil acidity	+	+
Total carbon and nitrogen content	+	+
Phosphorus availability	+	+
Calcium, magnesium, potassium and sodium availability	+	+

Table 7.4: Overview of laboratory measurements conducted in the first and second season of the research

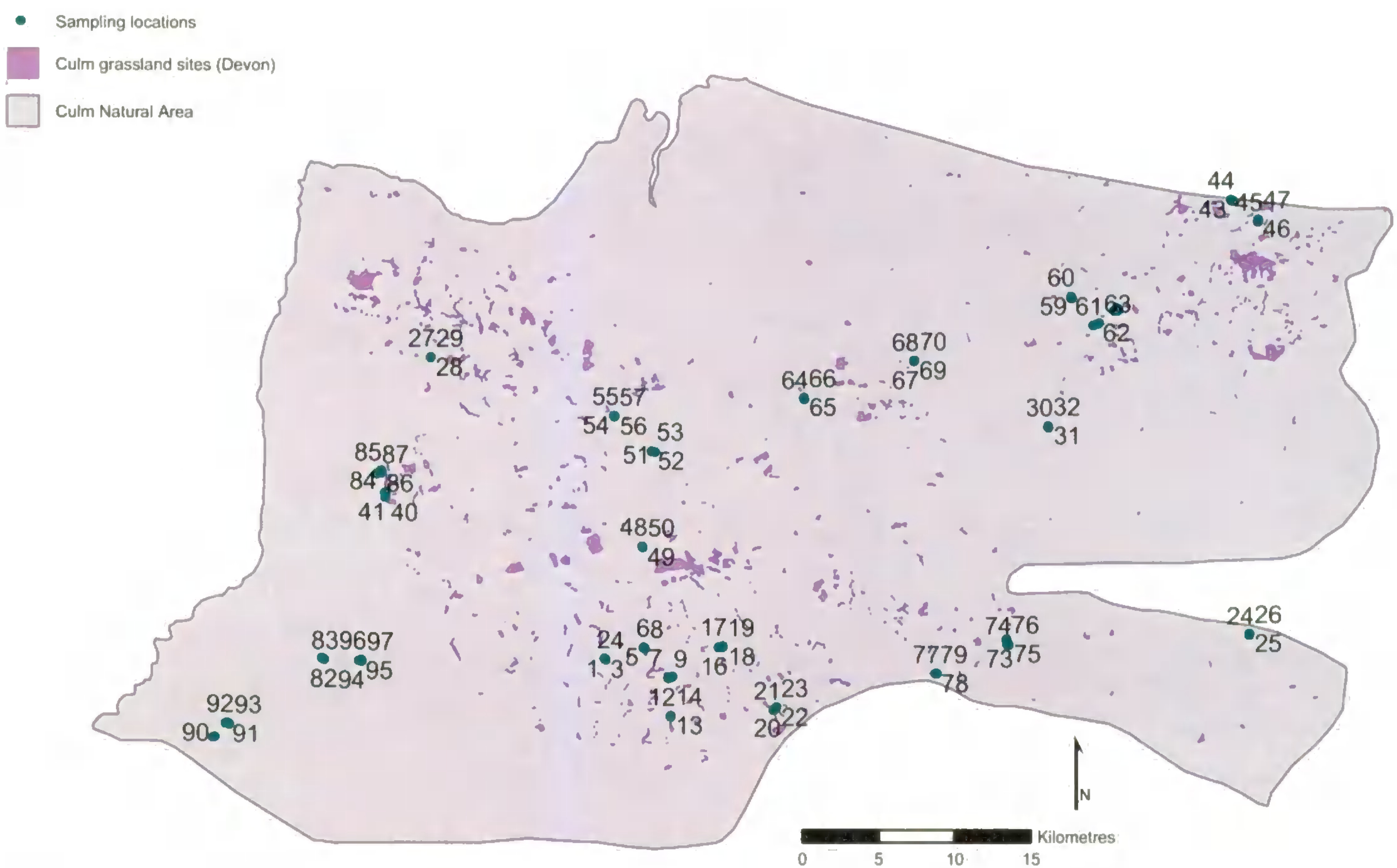


Figure 7.17 Sampling locations June 2000

In 2000, particular emphasis was placed on measurements of soil chemistry, because most variation was found in the 1999 survey for those parameters. The techniques used for the analyses were identical to the year before and are described in Section 7.3.3. Texture, saturated conductivity and bulk density measurements were not repeated in 2000, because the results of the 1999 survey did not show much difference in texture and high variability of the saturated conductivity and bulk density of the topsoil caused obscuring of the potential differences between the vegetation groups. Further, from field observations these parameters were considered of minor importance for determining variability within Culm grassland vegetation. To link the work presented in Part 2 with the research in this part, the topographic index was derived for each sampling point from the GIS maps. As was mentioned before, the topographic index indicated wetness patterns on a landscape level. However, the topography measured at regional scale (grid resolution of (50m) do not necessarily reflect the topography that would be measured at the local scale, due to generalisations. It was therefore unlikely that high correlations between local vegetation communities and regionally measured wetness patters were found. Statistical analysis was performed to investigate the correlation of the floristic data with the environmental data collected from the field sampling and the topographic index value.

Data analysis

Two-Way Indicator Species Analysis – TWINSPAN (Hill 1979a) was again used to define plant community types, based on the newly collected vegetation data. To compare the significance of the differences of environmental data in the different plant community groups, Mann Whitney's U test was used. This is a non-parametric test comparing the medians of two sets of data (Waite, 2000). Ordination of the vegetation data was performed by repeating DCA and relationships between species composition and environmental parameters were established by CCA. For the 2000 survey, both vegetation and environmental data were collected for each quadrat. Therefore quadrat data were used for DCA and CCA, instead of field data as was used for the 1999 survey. Results of the 2000 survey will be presented in detail in the next chapter.

Chapter 8

Vegetation - environment relationships in Culm grassland

8.1 Introduction

This chapter presents the results of the 2000 field survey, the vegetation and soil analysis and the relationships between vegetation and the environment. The problems that arose from the 1999 survey were discussed in Chapter 7 and the adjustments to the approach were also introduced. During the 2000 survey, paired vegetation and soil samples were collected at the same locations. Locations were selected after careful analysis of the DWT data in 1999. The sampling strategy was set up to cover as much variation in vegetation as possible with the limited resources available and to collect a data set suitable to address the third objective of the thesis, presented in Section 1.3 and 7.1. Section 8.2 will give an overview of the Culm grassland vegetation classified with the use of two way species indicator analysis into seven groups. In the same section, a comparison with the National Vegetation Classification (NVC) is made. The environmental characteristics of Culm grassland as a whole and for the separate groups are described in Section 8.3 and the results are compared to other research outcomes in similar plant communities. The techniques that were used to obtain the results were explained before in Section 7.3. In Section 8.4, vegetation data and environmental characteristics are related using ordination techniques to identify the factors and gradients responsible for the variation in species composition. The chapter finishes with a short discussion of the results and the techniques applied (Section 8.5).

8.2 Culm grassland vegetation

This section describes the vegetation composition of Culm grassland at the 97 locations sampled in June 2000. Species abundance was listed on the DAFOR (Dominant, Abundant, Frequent, Occasional, Rare) scale (Kent and Coker, 1992) within 4 m^2 quadrats around each sampling point. Seven vegetation groups or community types A to G were distinguished using Two-way Indicator Species Analysis (TWINSPAN), a divisive polythetic classification method (Hill, 1979a). An overview of the results is presented in Appendix A, using the same presentation technique as was used for the National Vegetation Classification (NVC) floristic tables (Rodwell *et al.*, 1991). Species occurring with a frequency of IV or V are the constant species of a group, a frequency of III corresponds with common species, II with occasional and I with scarce. Abundance is indicated between brackets on a scale from 1-5 instead of 1-10 as is used by Rodwell *et al.* (1991; 1992a and b). Below follows a description of the groups listing the constant and commonly present species for each group. Each group is compared to the NVC communities by using TABLEFIT (Hill, 1996). The TABLEFIT results for each sample are presented in Appendix B. An overview of the constant and common species for each group is given in Table 8.1.

Group A:

Compared to the NVC communities, plant community group A shows most resemblance with M24c *Molinia caerulea – Cirsium dissectum* fen-meadow *Juncus acutiflorus – Erica tetralix* sub-community, which is associated with moist to fairly dry peats and peaty mineral soils (Rodwell *et al.*, 1991). This habitat is transitional between mires on the one hand and grasslands and dry heaths on the other. Soil conditions should be neutral and moderately mesotropic for this plant community to develop and maintenance of the community occurs through grazing and mowing (Rodwell *et al.*, 1991). A few quadrats of group A can be classified as *Molinia caerulea – Potentilla erecta* mire *Anthoxanthum odoratum* sub-community (M25b) and *Scirpus cespitosus – Erica tetralix* wet heath *Carex panicea* sub-community (M15a), which form both on more acidic soils with a higher moisture content under cooler climatic conditions. Grazing and burning are the most important management practices for maintaining these communities (Rodwell *et al.*, 1991). *Nardus stricta – Galium saxatile* grassland *Carex panicea – Viola riviniana* sub-community (U5c) is also found in group A, although the quality of the fit was rather poor. This community is associated with moist peaty mineral soils, which are base-poor and infertile, and is mostly found in the cool and wet climatic conditions of northern Britain (Rodwell *et al.*, 1992).

Group B:

Group B also corresponds best with *Molinia caerulea – Cirsium dissectum* fen-meadow *Juncus acutiflorus – Erica tetralix* sub-community (M24c). This group however tends more towards M23a *Juncus acutiflorus – Galium palustre* rush – pasture. This community is found under slightly moister conditions than M24c on moderately acid to neutral peaty and mineral soils. Like M24c, the community benefits from grazing and occasionally mowing to prevent succession into woodland (Rodwell *et al.*, 1991). *Molinia caerulea – Potentilla erecta* mire *Anthoxanthum odoratum* sub-community (M25b) is also found in group B (for habitat description see group A).

Group C:

Group C is very similar in composition to group A. It also resembles M24c, with some quadrats corresponding with M25b. However, group C shows less typical *Molinia caerulea – Cirsium dissectum* characteristics. *Carex panicea* is not one of the dominant species and *Cirsium – dissectum* occurs less frequently. Other communities found in this group are *Juncus acutiflorus – Galium palustre* rush – pasture (M23a) and *Carex echinata - Sphagnum recurvum/auriculatum* mire *Juncus acutiflorus* sub-community (M6d), which is found on peat and peaty gley soils with a rather base-poor water supply. It is generally found in the uplands and not likely to be found in large parts of the Culm Natural Area.

Group D:

Group D can be described as a combination of *Molinia caerulea – Cirsium dissectum* fen-meadow *Juncus acutiflorus – Erica tetralix* sub-community (M24c) and *Molinia caerulea – Potentilla erecta* mire *Angelica sylvestris* sub-community (M25c). M25c differs from M25b, found in group A, B and C, in co-dominance by *Angelica sylvestris* instead of *Anthoxanthum odoratum* and is found on wetter, less acidic soils with a higher base-richness (Rodwell *et al.*, 1991).

Group E:

The majority of the quadrats in group E can be classified as *Juncus acutiflorus – Galium palustre* rush – pasture (M23a), which is related to moist conditions and moderately acid to neutral peaty and mineral soils. Its other sub-community, *Juncus effusus –Galium palustre* (M23b), occurs also in this group. *Filipendula ulmaria – Angelica sylvestris* mire with two sub-communities *Juncus effusus – Holcus lanatus* (M27c) and *Valeriana officinalis – Rumex acetosa* (M27a) is also found. This community is typically found on moist, reasonably rich, neutral soils in areas protected from grazing (Rodwell *et al.*, 1991). A few quadrats tend towards *Molinia caerulea – Cirsium dissectum* fen-meadow *Juncus acutiflorus – Erica tetralix* sub-community (M24c), *Molinia caerulea – Potentilla erecta* mire *Angelica sylvestris* sub-community (M25c) and *Holcus lanatus – Deschampsia cespitosa* (MG9). The latter occurs on permanently moist, gleyed and periodically inundated circumneutral soils and is found in patches associated with a wide range of plant communities (Rodwell *et al.*, 1991).

Group F:

Group F is similar in composition as group E, M23a is the major NVC community and occurs together with M23b, M27a and M27c (described under Group E). *Angelica sylvestris* is, however, not one of the constant species and also *Valeriana officinalis,* *Achillea ptarmica, Galium aparine* and *Molinia caerulea* occur less frequently. Other species, notably *Poa trivialis, Ranunculus repens, Stellaria uliginosa* and *Lychnis flos-cuculi* are most more often or only in group F. Based on the vegetation in one quadrat, this group is leaning slightly towards *Iris pseudacorus – Filipendula ulmaria* mire (M28). This community is related to most, more nutrient-rich soils (Rodwell *et al.*, 1991). *Iris pseudacorus* does, however, not occur in group F.

Group G:

The majority of the quadrats of group G can be classified as *Filipendula ulmaria – Angelica sylvestris* mire *Juncus effusus – Holcus lanatus* sub-community (M27c). Also, large resemblance with *Juncus effusus – Galium palustre* (M23b) is found, which benefits more from grazing. One quadrat can be classified as *Iris pseudacorus – Filipendula ulmaria* mire *Juncus effusus – Juncus Acutiflorus* sub-community (M28a) and two others are classified as swamp communities: S3 and S14c. The quality of fit is however not very high. *Holcus lanatus – Juncus effusus* rush-pasture *Iris pseudacorus* sub-community (MG10C) is also found in two quadrats, indicating permanently moist soils. This sub-community appears typically on periodically flooded alluvium and is limited to the extreme west of England and Wales (Rodwell *et al.*, 1992a).

Group	*Constant species*	*Common species*
A	*Agrostis canina sens str., Molinia caerulea, Carex panicea, Potentilla erecta, Dactylorhiza maculata*	*Anthoxanthum odoratum, Festuca rubra sens.str., Holcus lanatus, Carex pulicaris, Carex viridula ssp. oedocarpa, Juncus acutiflorus, Cirsium dissectum, Cirsium palustre, Lotus pedunculatus, Succisa pratensis, Calliergon sp., Pseudoscleropodium purum, Rhytidiadelphus squarrosus, Thuidium tamariscinum, Sphagnum spp..*
B	*Anthoxanthum odoratum, Holcus lanatus, Juncus acutiflorus, Lotus pedunculatus, Calliergon sp.*	*Agrostis canina sens.str., Cynosurus cristatus, Carex flacca, Carex panicea, Juncus conglomeratus, Cirsium palustre, Potentilla erecta, Ranunculus flammula.*
C	*Agrostis canina sens.str, Anthoxanthum odoratum, Holcus lanatus, Molinia caerulea, Juncus acutiflorus, Potentilla erecta, Lotus pedunculatus*	*Luzula multiflora, Cirsium palustre, Galium palustre, Rumex acetosa, Succisa pratensis, Viola palustris, Eurhynchium praelongum, Pseudoscleropodium purum, Rhytidiadelphus squarrosus.*
D	*Molinia caerulea, Juncus effusus, Angelica sylvestris, Cirsium palustre, Potentilla erecta, Valeriana officinalis*	*Agrostis canina sens.str., Juncus conglomeratus, Galium palustre, Lotus pedunculatus, Eurhynchium praelongum, Sphagnum spp.*
E	*Juncus acutiflorus, Angelica sylvestris, Cirsium palustre, Lotus pedunculatus, Rumex acetosa, Valeriana officinalis, Eurhynchium praelongum.*	*Holcus lanatus, Molinia caerulea, Juncus conglomeratus, Juncus effusus, Achillea ptarmica, Filipendula ulmaria, Galium aparine, Galium palustre.*
F	*Agrostis canina sens str., Holcus lanatus, Poa trivialis, Juncus acutiflorus, Juncus effusus, Lotus pedunculatus, Cirsium palustre, Filipendula ulmaria, Galium palustre, Ranunculus repens, Rumex acetosa, Stellaria uliginosa, Eurhynchium praelongum*	*Lychnis flos-cuculi, Brachythecium sp.*
G	*Juncus effusus, Filipendula ulmaria, Ranunculus repens, Eurhynchium praelongum*	*Holcus lanatus, Poa trivialis, Cirsium palustre, Galium palustre, Lotus pedunculatus, Mentha aquatica, Myosotis secunda, Oenanthe crocata, Stellaria uliginosa, Brachythecium sp.*

Table 8.1 Overview of the constant and common species for each plant community group.

From the discussion above, it is clear that most vegetation groups resemble the NVC communities M23, M24, M25, M27 to a certain extent. However, the NVC M16 *Erica tetralix – Sphagnum compactum* wet heath community does not seem to be represented in the vegetation groups. Nevertheless, its constant species are present in the other vegetation groups. *Calluna vulgaris* is found in group A, C and D; *Erica tetralix* is found in group A; *Molinia caerulea* is found in all groups, except E and G and *Sphagnum spp.* is found in A, C and D.

8.3 Environmental characteristics of Culm grassland

8.3.1 Introduction

In this section the environmental characteristics of the seven Culm grassland vegetation groups defined in Section 8.2 are described. Slope, soil depth, soil water content, pH, total carbon, total nitrogen, C/N-ratio, available phosphorus, potassium, sodium, calcium and magnesium were the parameters measured for each sample. The results are presented for each environmental parameter in a graph, indicating the mean and standard error of the data, and in a table, indicating significant differences between the median values of the groups. Appendix C also presents the mean, median and standard error by vegetation group. Significance between groups was tested with the non-parametric Mann-Whitney U test, which compares the median values of the samples. The null hypothesis for this test is that there is no significant difference between the groups and the alternative hypothesis is that there is a significant difference between the groups. The results of Mann-Whitney's U test (MW) are presented in a matrix as follows:

EXAMPLE:

	A	B	C
A		significantly different at 0.05	not significantly different
B	0.025		significantly different at 0.05
C	0.678	0.001	

The left half of the matrix indicates the chance that the null hypothesis is true (p – values) and the right half gives the interpretation of the results. A grey rectangle indicates a significant difference between median values of two groups. Section 8.3.2 describes the physical characteristics and Section 8.3.3 describes the chemical parameters. A total of 97 samples were taken, but the number of samples differ for vegetation each group. Numbers are given in Table 8.2.

Group	A	B	C	D	E	F	G
N	12	15	15	7	19	13	16

Table 8.2: Number of samples (N) for each vegetation group

8.3.2 Physical characteristics

Slope, soil depth and the volumetric soil water content were the physical parameters determined for every sampling point during the 2000 field season. The results are presented below for each variable.

Slope

In Figure 8.1 the average slope and standard errors of the vegetation groups are presented. The overall average value is 2.74° ± 0.21. The highest average value of 3.67° ± 0.49 is found in group B and the lowest average value of 2.17° ± 0.32 in group A.

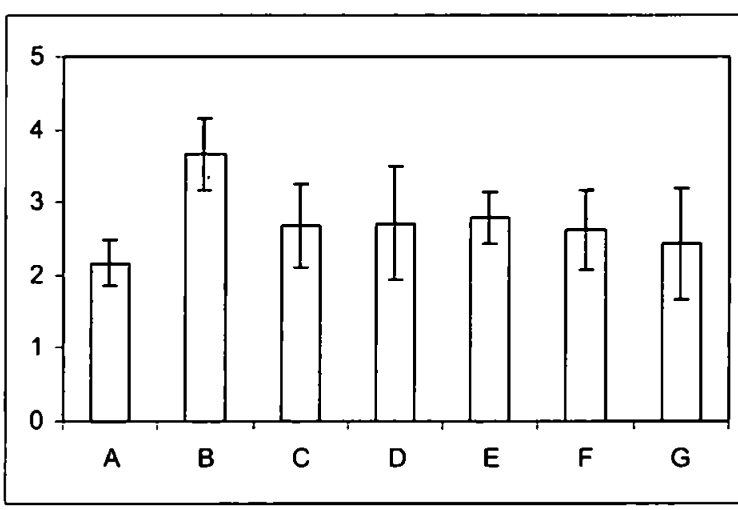


Figure 8.1 Slope (degrees) for each vegetation group

	A	B	C	D	E	F	G
A							
B	0.022						
C	0.689	0.179					
D	0.895	0.225	0.972				
E	0.242	0.210	0.712	0.746			
F	0.523	0.243	0.981	0.968	0.846		
G	0.319	0.042	0.445	0.336	0.154	0.489	

Table 8.3 Mann Whitney (p-values) results of the gradients for each vegetation group

Table 8.3 gives an overview of the slope differences between the vegetation groups. Significant differences were only found between A and B (MW: p = 0.022) and B and G (MW: p = 0.042), with group B having a larger gradient than group A and G.

Soil depth

Figure 8.2 presents the average soil depth for each group compared to the overall average. The average depth for all sampling locations was 59.0 cm ± 1.8. Group A had a lowest average of 49.8 cm ± 4.9 and D a highest average of 67.9 cm ± 3.5.

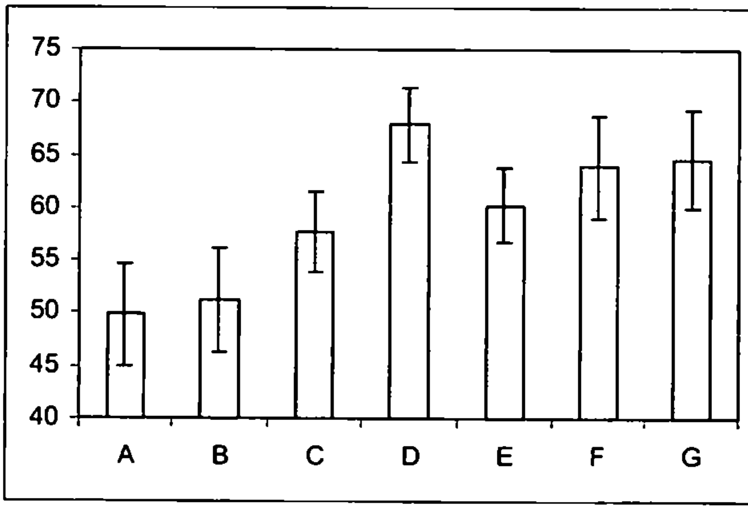


Figure 8.2 Soil depth (cm) for each vegetation group

Table 8.4 shows that group A was found to be significantly lower than group D, E, F and G, with p-values respectively 0.021, 0.050, 0.027 and 0.025. Group B is also found to be significantly lower than G (MW p-value: 0.023)

	A	B	C	D	E	F	G
A							
B	0.735						
C	0.234	0.392					
D	0.021	0.085	0.072				
E	0.050	0.271	0.525	0.220			
F	0.027	0.058	0.113	1.000	0.162		
G	0.025	0.023	0.060	0.544	0.053	0.836	

Table 8.4 Mann Whitney (p-values) results of the soil depth for each vegetation group

Soil water content

The range of plant communities within Culm grassland varies from wet heaths to mire systems, corresponding with a moisture gradient from moist to saturated for most of the year (Rodwell *et al.*, 1991). Therefore soil moisture is expected to be one of the major factors determining the difference in vegetation composition. Soil moisture was measured as a volume percentage with a Theta Probe (see Chapter 4). Figure 8.3 gives an overview of the top soil volumetric soil moisture contents for the groups.

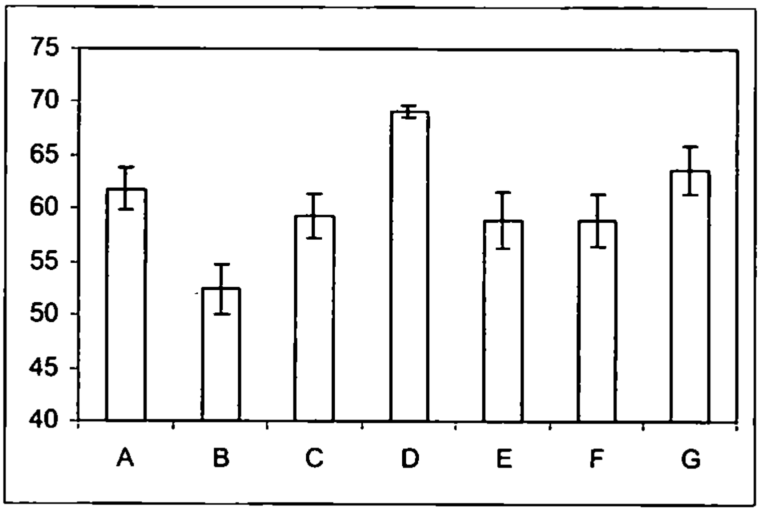


Figure 8.3 Soil moisture content (volume %) at 5 cm depth for each vegetation group

The overall average soil moisture content was 59.8% ± 1.0, which corresponded to the soil water content of between 45 and 60 % found on Culm grassland by Goodwin (1995). Table 8.5 shows the significance of the differences between the vegetation groups. Group B is significantly lower than group A, C, D and G and group D is found to be significantly higher than group all other groups.

	A	B	C	D	E	F	G
A							
B	0.010						
C	0.510	0.042					
D	0.003	0.001	0.002				
E	0.589	0.077	0.948	0.034			
F	0.415	0.072	0.854	0.011	0.865		
G	0.183	0.003	0.102	0.024	0.396	0.151	

Table 8.5 Mann Whitney (p-values) results of the soil moisture for each vegetation group

8.3.3 Chemical characteristics

This section presents the results of the chemical analysis of the soil samples. Samples were taken of the top 10 cm of soil. Acidity, total organic carbon and nitrogen, C/N-ratio, available phosphorus, potassium, sodium, calcium and magnesium were measured for all samples.

Soil pH

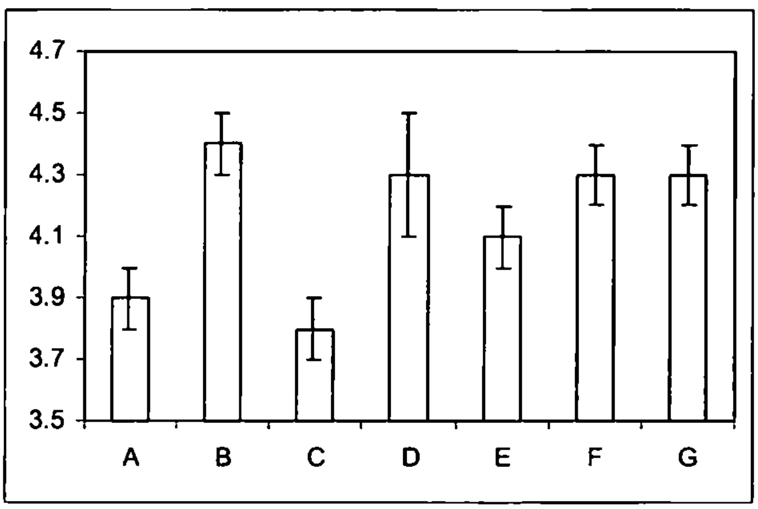


Figure 8.4 pH – $CaCl_2$ for each vegetation group

Figure 8.4 shows the results of the pH measurements for the second field season. An overall average of 4.1 ± 0.03 was found, which is similar to the value of 4.3 found for Culm grassland by Goodwin (1995). Tallowin and Smith (*in press*) reported a pH (H_2O) of 5.2, but for an intact *Cirsio-Molinietum* fen-meadow. A pH of 3.84 was found by Pywell *et al.* (1994) for a wet heath community. Table 8.6 indicates the significant differences between the vegetation groups. Group A was found to be significantly lower than B, D, F and G. Group B was higher than C and E and C is significantly lower than D, E, G and F. Group E was lower than F and G.

	A	B	C	D	E	F	G
A							
B	0.000						
C	0.464	0.000					
D	0.025	0.944	0.024				
E	0.320	0.002	0.033	0.073			
F	0.002	0.475	0.000	0.874	0.014		
G	0.003	0.477	0.001	0.789	0.016	0.965	

Table 8.6 Mann Whitney (p-values) results of the pH for each vegetation group

Total organic Carbon and Nitrogen and the C/N ratio

An overview of the organic matter characteristics of the soil is given in this section. Figure 8.5, 8.6 and 8.7 present the values for the total organic Carbon content, the total organic Nitrogen content and the C/N ratio. Overall average values for C, N and C/N are respectively 12.11, 0.89 and 12.7%. Goodwin (1995) reported average organic matter values of 20.9 and 28.2% (corresponding to 12.5 and 16.8% organic C) on two *Erica tetralix – Sphagnum compactum* wet heath (NVC M16) sites. The first value is similar to group A to C and E to G and the second to group D. Pywell *et al.* (1994) reported a soil organic matter content under a wet heath vegetation of 46.9%. A total organic nitrogen content of 1.89% was found by Van Duren *et al.* (1998) in a *Cirsio-Molinietum* fen-meadow.

	A	B	C	D	E	F	G
A							
B	0.060						
C	0.354	0.407					
D	0.011	0.002	0.041				
E	0.256	0.395	0.959	0.008			
F	0.446	0.259	1.000	0.014	0.863		
G	0.416	0.012	0.465	0.016	0.150	0.203	

Table 8.7 Mann Whitney results (p-values) of the carbon content for each vegetation group

	A	B	C	D	E	F	G
A							
B	0.196						
C	0.845	0.455					
D	0.008	0.002	0.048				
E	0.984	0.165	0.742	0.010			
F	0.807	0.123	0.712	0.019	0.715		
G	0.210	0.016	0.567	0.030	0.274	0.334	

Table 8.8 Mann Whitney results (p-values) of the nitrogen content for each vegetation group

	A	B	C	D	E	F	G
A							
B	0.007						
C	0.092	0.533					
D	0.471	0.011	0.037				
E	0.009	0.521	0.061	0.007			
F	0.011	0.519	0.102	0.013	0.631		
G	0.006	0.678	0.921	0.012	0.108	0.141	

Table 8.9 Mann Whitney results (p-values) of the C/N ratio for each vegetation group

Significantly higher carbon and nitrogen contents were found in group D compared to the other groups (Table 8.7 and 8.8). Furthermore, group B was found to be significantly lower than group G. Table 8.7 and Figure 8.9 show that group A and D have significantly higher C/N ratios than B, E, F, G.

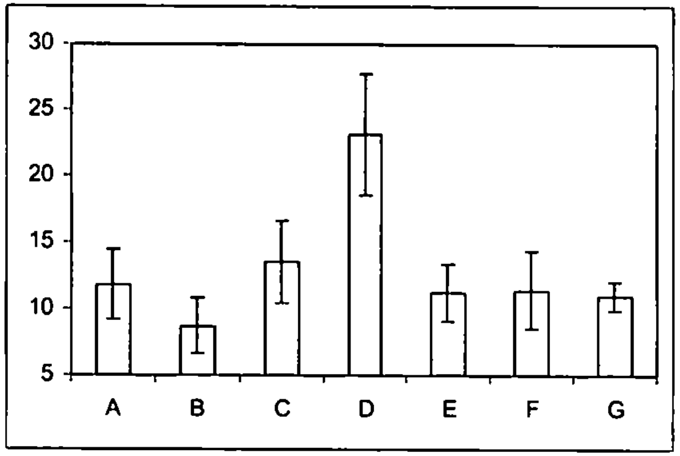


Figure 8.5 Total organic carbon content (%) for each vegetation group

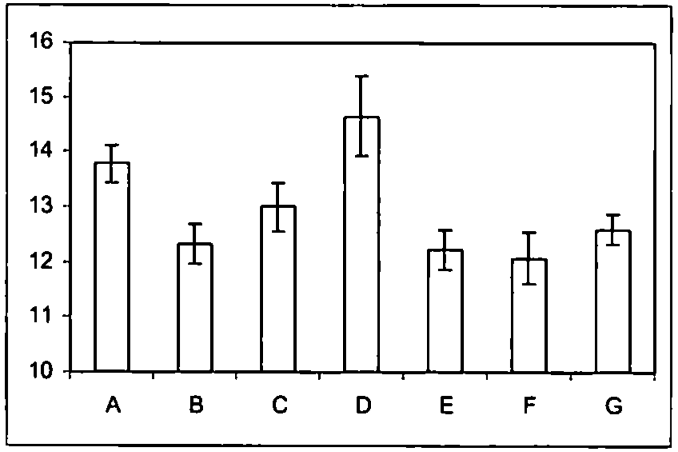


Figure 8.7 C/N ratio for each vegetation group

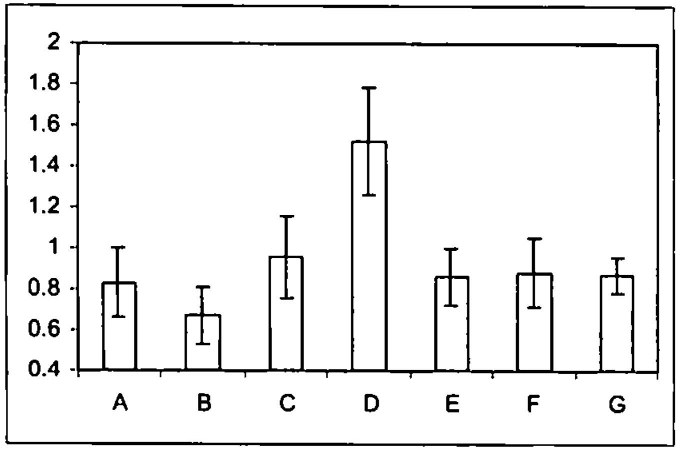


Figure 8.6 Total organic nitrogen content (%) for each vegetation group

Phosphorus availability

Phosphorus is considered to be one of the most important limiting factors for fen-meadow and wet heath communities. This parameter was also found to be highly correlated with the second ordination axis of the 1999 survey. Gough and Marrs (1990) suggest target level of extractable phosphorus of 5-10 mg kg^{-1} air dry soil. Janssens *et al.* (1998) related phosphorus levels to species diversity and report a limit of 50 mg kg^{-1} air dry soil for grasslands in general, above which less than 20 species per 100 m^2 were found (extraction with acetate-EDTA). Figure 8.8 presents the values found for Culm grassland. The overall average is 5.13 mg kg^{-1} ± 0.74, which is comparable to the highest value of 4.65 ± 0.16 mg kg^{-1} as reported for a *Cirsio-Molinietum* fen-meadow by Goodwin *et al.* (1998). Tallowin and Smith (*in press*) found a value of 8.8 mg kg^{-1} air dry soil on a site with similar vegetation. The overall average, however, is strongly affected by the high average value for group G. Removal of the values measured for group G, resulted in an overall average of 3.77 mg kg^{-1}.

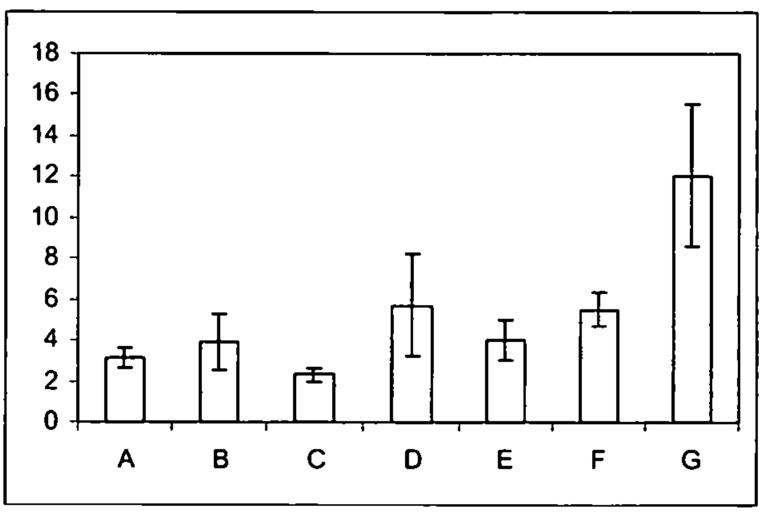


Figure 8.8 Phosphorus availability (mg kg^{-1} air dry soil) for each vegetation group

	A	B	C	D	E	F	G
A							
B	0.608						
C	0.272	0.507					
D	0.642	0.324	0.121				
E	0.984	0.521	0.103	0.603			
F	0.399	0.250	0.043	1.000	0.266		
G	0.022	0.010	0.001	0.193	0.016	0.076	

Table 8.10 Mann Whitney results (p-values) of the phosphorus availability for each vegetation group

Table 8.10 indicates a significantly higher available phosphorus content for group G in comparison with A, B, C and E. Phosphorus availability in group F is found to be significantly higher than of group C.

Potassium, sodium, calcium and magnesium

The other soil chemical elements measured were potassium, sodium, calcium and magnesium. Figure 8.9 shows the potassium contents of the plant community groups. The overall average value is 247.3 ± 27.0 mg/kg air dry soil. Goodwin *et al.* (1998) reported an average value of 334 mg/kg and Tallowin and Smith (*in press*) a value of 209 mg/kg, both on a *Cirsio-Molinietum* site. Table 8.11 presents the significance of the difference between the vegetation groups and shows that group D is significantly higher than A and B, a median of 181.4 versus 154.1 and 125.2 mg/kg air dry soil.

Figure 8.10 presents the sodium content of the groups. An average of 187.4 mg/kg air dry soil ± 56.0 was found. A lower value of 128 ± 0.51 mg/kg was found by Tallowin and Smith (*in press*). Group A and E have high standard errors caused by a few outliers in the data. Table 8.12 presents the significance of the differences between the groups and group E is found to be significantly lower than group A.

Calcium contents are presented in Figure 8.11. The average value of 1395 mg/kg air dry soil found is much higher than the 208 mg/kg reported by Goodwin *et al.* (1998). A yet higher value of 2828 mg/kg was however reported by Tallowin and Smith (*in press*). Van Duren *et al.* (1998) found a calcium level of 144.5 meq/kg. Group A was found to be significantly different from B, D, F and G. Group C was significantly lower than D and G and group E was significantly lower than G (Table 8.13).

Magnesium contents are presented in Figure 8.12. The average value is 469 mg/kg air dry soil, but the median is 183 mg/kg air dry soil. The difference is caused by a few outliers in group D. The median is comparable to the value of 120 – 220 mg/kg air dry soil found by Goodwin (1995). Tallowin and Smith (*in press*) found a much higher value of 1286 mg/kg. No significant differences were found between the groups (Table 8.14).

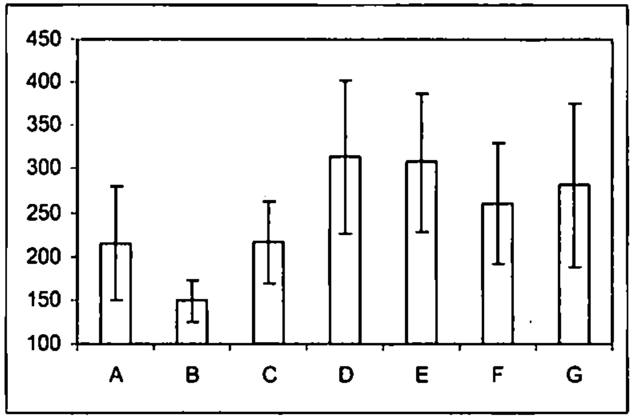


Figure 8.9 Potassium content (mg kg^{-1} air dry soil) for each vegetation group

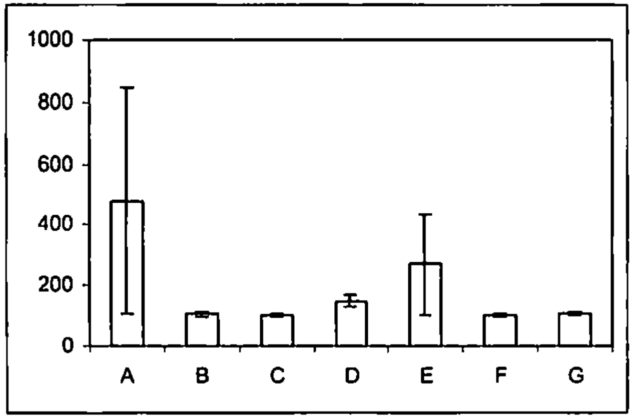


Figure 8.10 Sodium content (mg kg^{-1} air dry soil) for each vegetation group

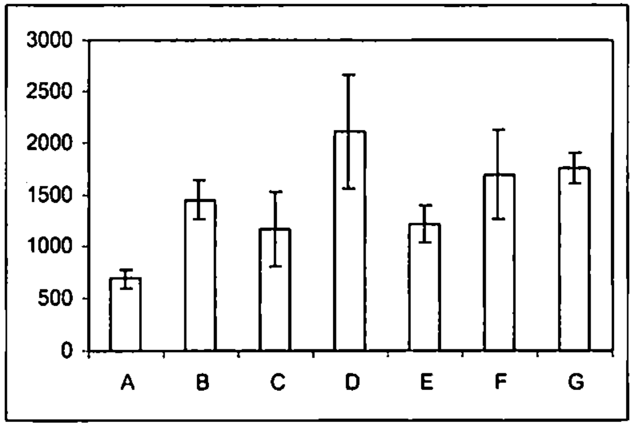


Figure 8.11 Calcium content (mg kg^{-1} air dry soil) for each vegetation group

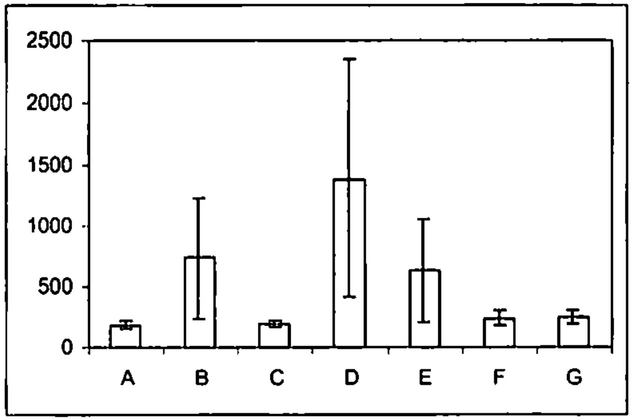


Figure 8.12 Magnesium content (mg kg^{-1} air dry soil) for each vegetation group

	A	B	C	D	E	F	G
A							
B	0.113						
C	0.678	0.481					
D	0.047	0.005	0.105				
E	0.612	0.066	0.252	0.418			
F	0.978	0.231	0.645	0.235	0.645		
G	0.472	0.649	0.984	0.057	0.240	0.584	

Table 8.11 Mann Whitney results (p-values) of the potassium content for each vegetation group

	A	B	C	D	E	F	G
A							
B	0.367						
C	0.450	0.901					
D	0.291	0.057	0.078				
E	0.049	0.445	0.755	0.094			
F	0.165	0.747	0.854	0.057	0.788		
G	0.626	0.678	0.649	0.133	0.313	0.469	

Table 8.12 Mann Whitney results (p-values) of the sodium content for each vegetation group

	A	B	C	D	E	F	G
A							
B	0.000						
C	0.213	0.016					
D	0.013	0.324	0.057				
E	0.065	0.176	0.349	0.119			
F	0.003	0.580	0.065	0.428	0.337		
G	0.000	0.118	0.001	0.867	0.016	0.091	

Table 8.13 Mann Whitney results (p-values) of the calcium content for each vegetation group

	A	B	C	D	E	F	G
A							
B	0.294						
C	0.903	0.431					
D	0.069	0.290	0.091				
E	0.919	0.315	0.808	0.106			
F	0.807	0.645	1.000	0.113	0.908		
G	0.501	0.737	0.594	0.102	0.856	0.878	

Table 8.14 Mann Whitney results (p-values) of the magnesium content for each vegetation group

8.4 Relationships between vegetation composition and environmental characteristics

8.4.1 Introduction

Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) (Ter Braak, 1986; 1987; Ter Braak and Smilauer, 1997) ordination techniques (Hill, 1979b; Kent and Coker, 1992; Waite, 2000) were applied to find the environmental variables explaining most of the variation within the vegetation data. DCA was conducted in the computer package PC-Ord (McCune and Mefford, 1999) and CCA in CANOCO (Ter Braak and Smilauer, 1997). The data set included both the botanical data set and the environmental data set as described in section 8.3. Grazing pressure, estimated on a 0-5 scale, and a topographic index value, derived from a GIS map, were extra environmental factors included in the analysis.

The CCA ordination method was designed for normally distributed environmental data, being based on the multiple regression model. Of all environmental variables pH was the only parameter with a significantly normal distribution (accept H0: data are normally distributed, Anderson Darling: $p = 0.885$). The distributions of the environmental variables were normalised by transforming the data. Four different transformations, log, square root, arcsinus and arcsinus square root, were applied to each of the other variables and the best fit was used for CCA. The following parameters were not transformed at all, because it did not improve the distributions: slope, soil depth, soil water, pH, sodium content and grazing intensity. The other variables, topographic index, total carbon content, total nitrogen content, C/N ratio, available phosphorus, potassium, calcium and magnesium content, were transformed with a log transformation. Only calcium transformed into a significantly normal distribution (Anderson Darling: $p = 0.297$) and available phosphorus nearly reached a significantly normal distribution (Anderson Darling: $p = 0.035$). The other factors improved compared to their original distribution but did not become significantly normal.

For soil depth and soil water content, a few missing values existed. Both DCA and CCA cannot calculate with an incomplete data set and therefore missing data need to be given a value. Average values were assigned to the missing soil depth measurements. In three cases, a note was made in the field that soil moisture could not be measured due to too wet conditions and soil saturation was reported. In those situations, the maximum soil water content was used. Where the soil water content was not clear, the average value was used.

Results of the DCA analysis are presented in Section 8.4.2 and results of the CCA analysis are described in Section 8.4.3.

8.4.2 Detrended correspondence analysis

Detrended Correspondence Analysis was carried out a number of times to reach an optimum result. The results of the analyses are presented in this section and reasons for adjustments of the data set are given. For all analyses, results were plotted in relation to the first two dimensions of maximum variation, with the TWINSPAN classification superimposed. Environmental variables were presented in the same graphs, pointing from the centre of the graph towards positive change in value. Although the environmental variables are not used in the ordination of the samples, presenting them in the same graphs gives a clear overview of the factors most responsible for the variability in the vegetation composition.

Figure 8.13 shows the seven TWINSPAN groups standing out very clearly and shows that grazing is associated most strongly with axis 1 and soil moisture with axis 2. The trends are reflected by the vegetation groups as defined from the Two-way Species Indicator Analysis: Low grazing levels are associated with group G and move via E and F and B, C and D into A. For soil moisture a sequence from top to bottom is found, with relatively dry soils corresponding with group B, F and G changing into wetter soils corresponding with A, C and E and into the wettest soils with group D.

Table 8.15 presents the correlation of the environmental variables with the ordination axes. The results show axis 1 to be correlated most strongly with grazing pressure, axis 2 to have the highest correlation with pH, soil moisture content and C/N-ratio and axis three to have the strongest correlation with the topographic index.

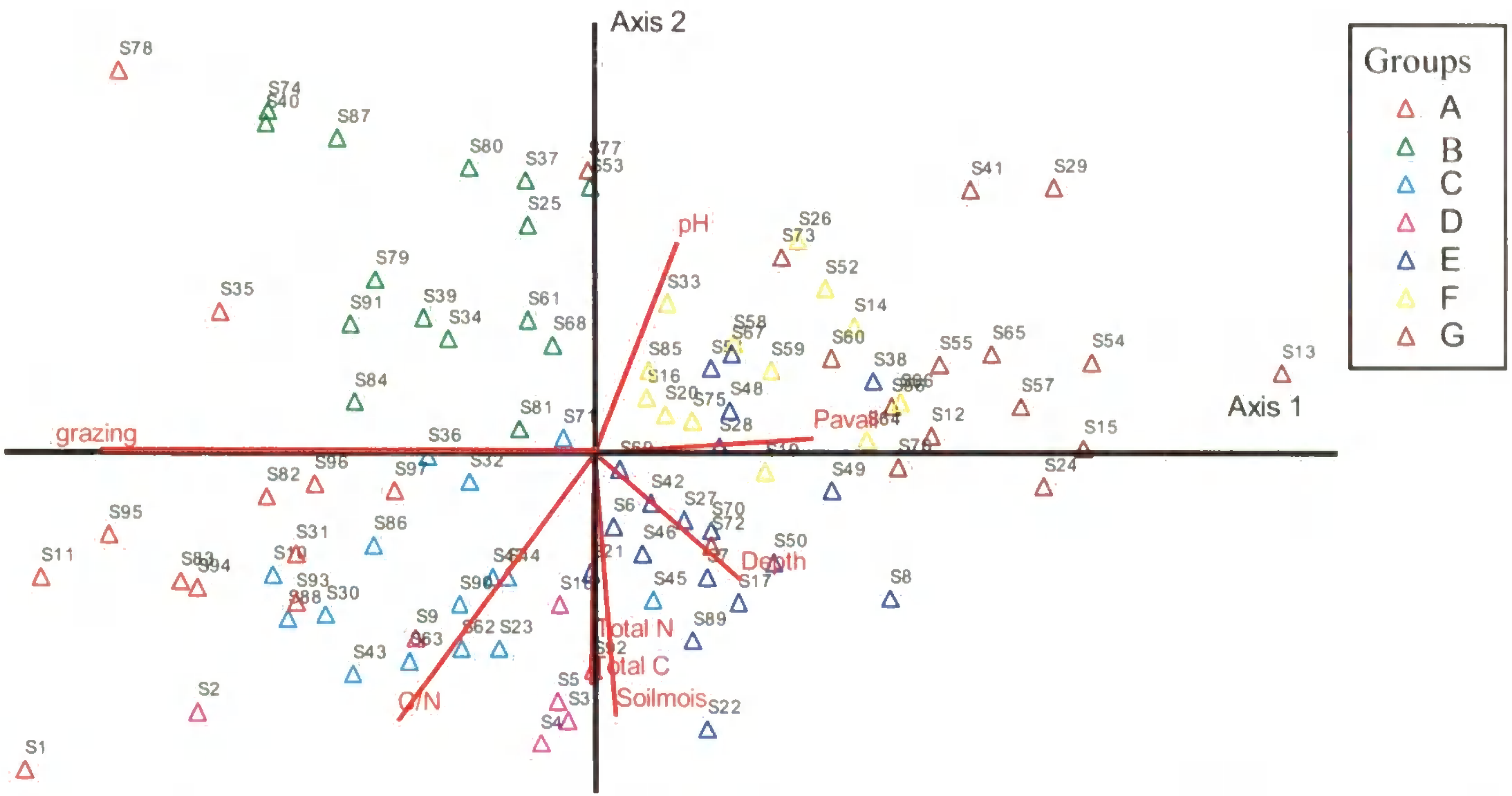


Figure 8.13 Results of the detrended correspondence analysis. R^2 cut-off level for showing the environmental variables 0.100 and length of arrows at 250%.

	axis 1	axis 2	axis 3
Slope	-0.040	**0.158**	0.041
Soil depth	**0.250**	-0.079	-0.042
Soil moisture	0.081	**-0.271**	-0.066
pH	**0.161**	**0.293***	-0.102
Na	**-0.158**	-0.103	-0.075
Topographic index	0.024	-0.073	**0.206**
Total C	-0.011	**-0.246**	-0.022
Total N	0.053	**-0.236**	0.002
C/N	**-0.259**	**-0.272**	-0.055
P available	**0.229**	0.089	-0.003
K	0.024	-0.112	0.093
Ca	**0.221**	0.123	-0.062
Mg	-0.005	-0.074	0.009
grazing	**-0.480***	-0.052	**-0.207***

Table 8.15 Kendall's τ correlation coefficients of normalized environmental data with the first three axes of the detrended correspondence analysis. Critical value at a two-tailed 0.05 significance level 0.135 (N = 97). Significant correlation printed in bold font. * Strongest correlation.

Outlier analysis in PC-Ord (McCune and Mefford, 1999) of the species data set using Euclidean distances indicated samples 40 and 78 as outliers. These were therefore removed from the data set for further DCA. Further, sample 13 was removed because it was considered an outlier by visually examining the graphs (see Figure 8.13). The same analysis procedure as described before was conducted and results are presented in Figure 8.14. Similar trends as described before can be distinguished from the graphs. However, trends are not shown as clearly as before especially for the relationship with soil moisture.

Table 8.16 presents the correlation between the axis and the environmental variables. It shows that grazing pressure, soil moisture content and the pH were correlated most strongly with axis 1, 2 and 3 respectively.

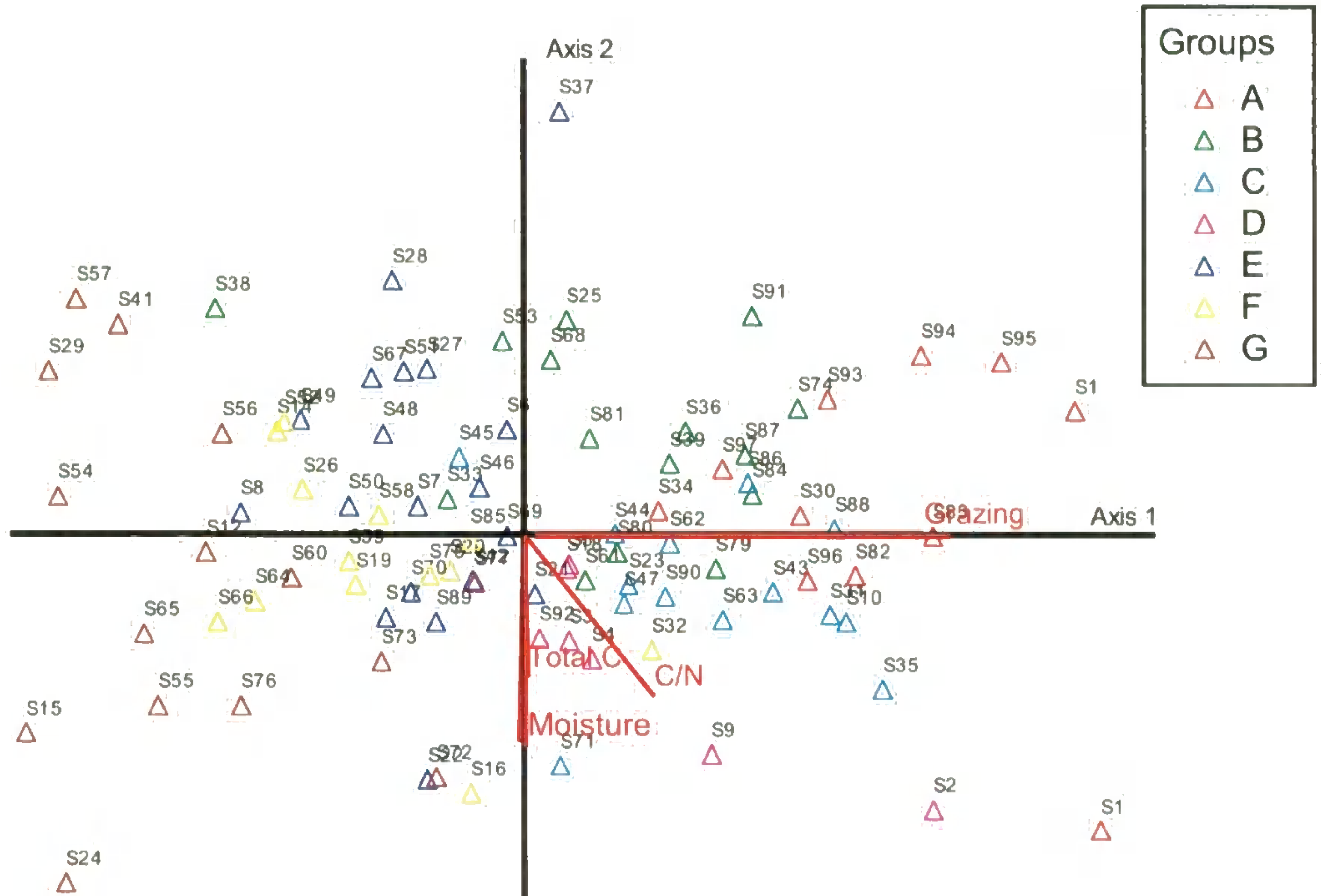


Figure 8.14 Results of the detrended correspondence analysis after removing the outliers (13, 40 & 78). R^2 cutoff level for showing the environmental variables 0.100 and length of environmental variables at 250%.

	axis 1	Axis 2	axis 3
Slope	-0.015	0.110	0.083
Soil depth	**-0.248**	-0.092	-0.028
Soil moisture	-0.056	**-0.296***	-0.105
pH	**-0.211**	-0.042	**0.274***
Na	**0.142**	**-0.185**	-0.004
Topographic index	-0.039	0.097	-0.118
Total C	-0.000	**-0.244**	-0.107
Total N	-0.044	**-0.240**	-0.100
C/N	**0.217**	**-0.231**	**-0.138**
P available	**-0.190**	-0.003	0.107
K	-0.042	-0.002	-0.105
Ca	**-0.222**	-0.094	0.133
Mg	-0.017	-0.062	-0.010
grazing	**0.442***	0.000	0.065

*Table 8.16 Kendall's τ correlation coefficients of normalized environmental data with the first three axes of the detrended correspondence analysis after removing the outliers (13, 40 & 78).Critical value at a two-tailed 0.05 significance level 0.137 (N = 94). Significant correlation printed in bold font. *Strongest correlation.*

Figures 8.15 and 8.16 are the result of removing sample point 37 from the data set. As can be observed from Figure 8.14 sample 37 influences the spread of data on the second axis quite strongly.

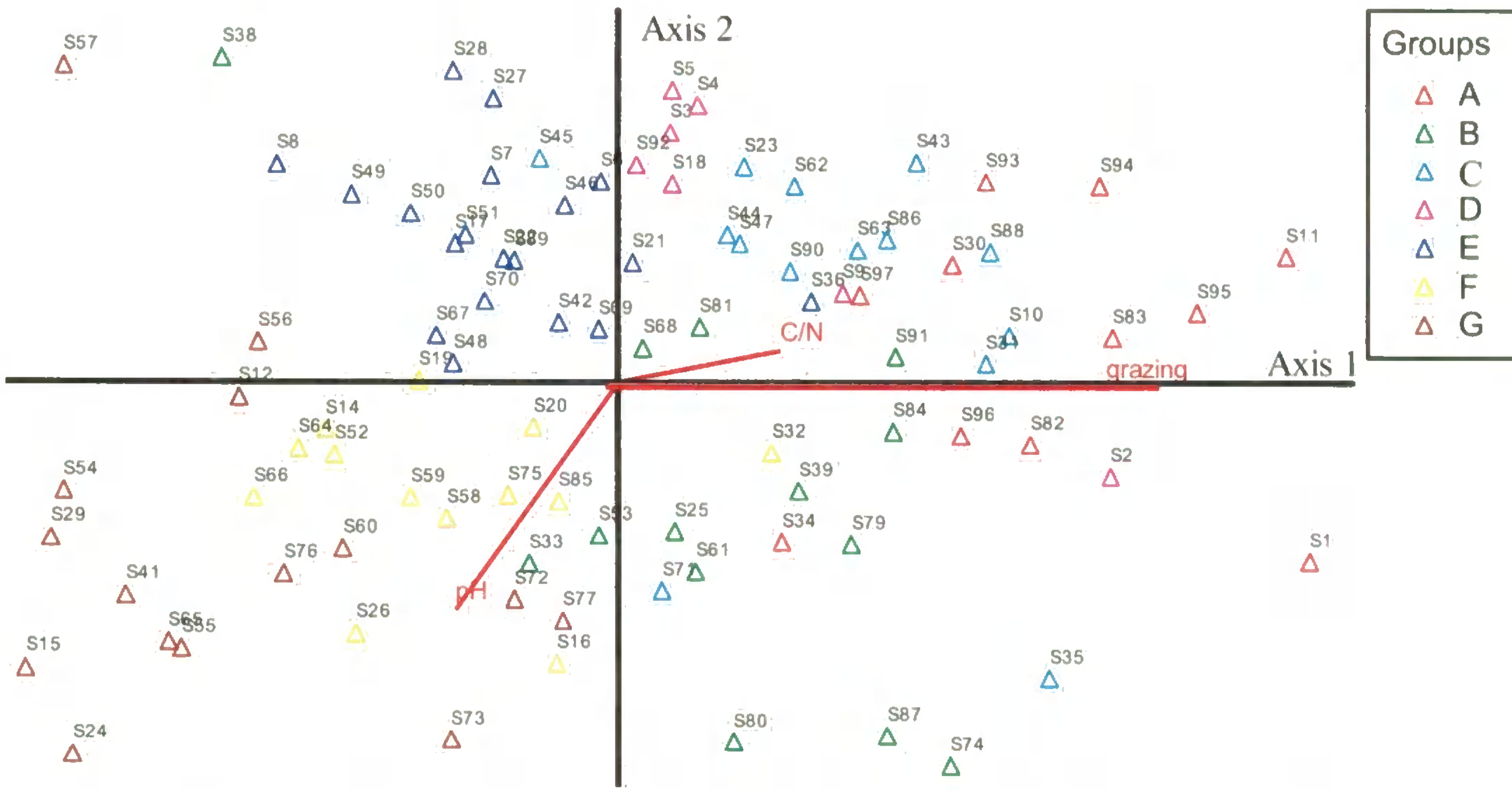


Figure 8.15 Results of the detrended correspondence analysis after removing the outliers (13, 37, 40 & 78) presented on axis 1 and 2. R^2 cutoff level for showing the environmental variables 0.100 and length of environmental variables at 250%.

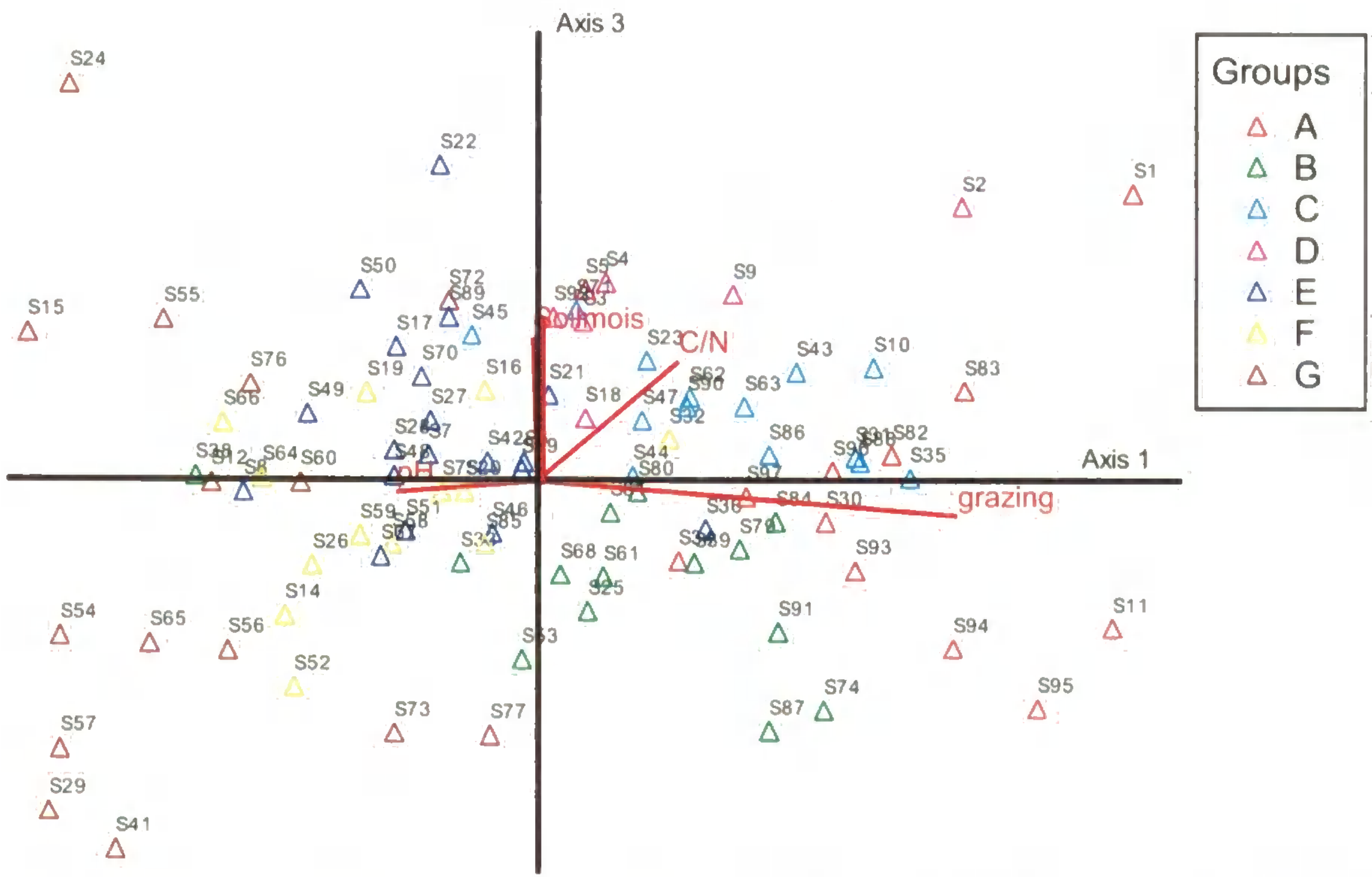


Figure 8.16 Results of the detrended correspondence analysis after removing the outliers (13, 37, 40 & 78) presented on axis 1 and 3. R^2 cutoff level for showing the environmental variables 0.100 and length of environmental variables at 250%.

Removal of this sample point results in soil water to be shifted from the second axis to the third axis, but patterns remain the same (Figure 8.16). Acidity is in this case the most important factor on the second axis. However, the trend goes diagonally across the graph. Group F and G are associated with higher pH values, B and E with the middle ranges and A, C and D with the lower values (Figure 8.15). These trends are presented, once again, in Figure 8.17, which outlines the outside border of each TWINSPAN group in a graph with the first two ordination axes, to make the observed patterns clearly visible. To show how the plant community groups are situated in the ordination graph and to give an indication of the spread of the data, the average sample scores and standard errors on axis 1 and 2 are presented in Figure 8.18. The correlation coefficients between the axes and the environmental variables are presented in Table 8.17.

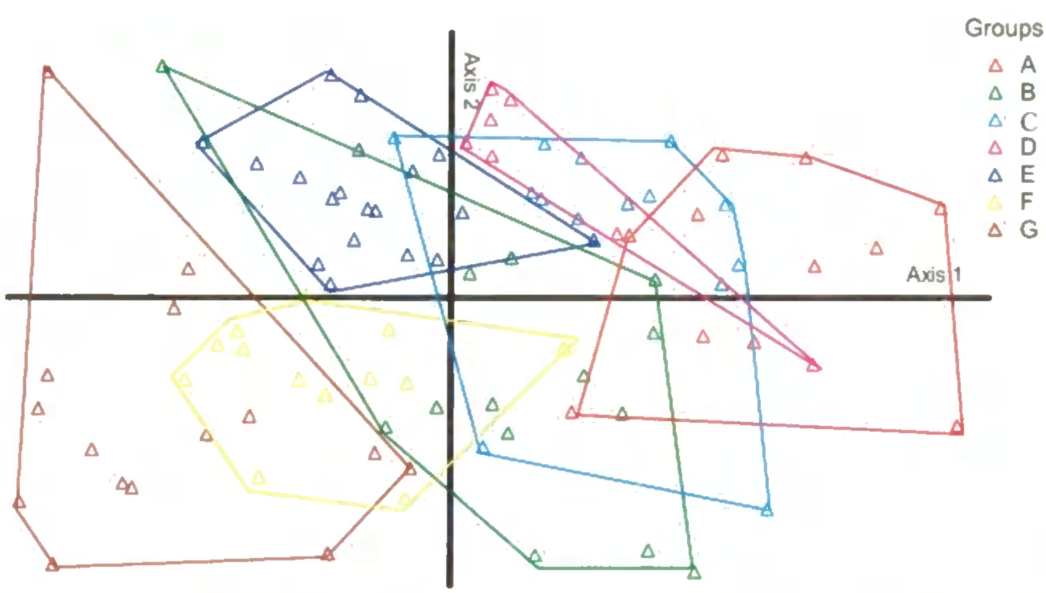


Figure 8.17 Polygons defining TWINSPAN groups presented in the DCA ordination graph, axis 1 and 2.

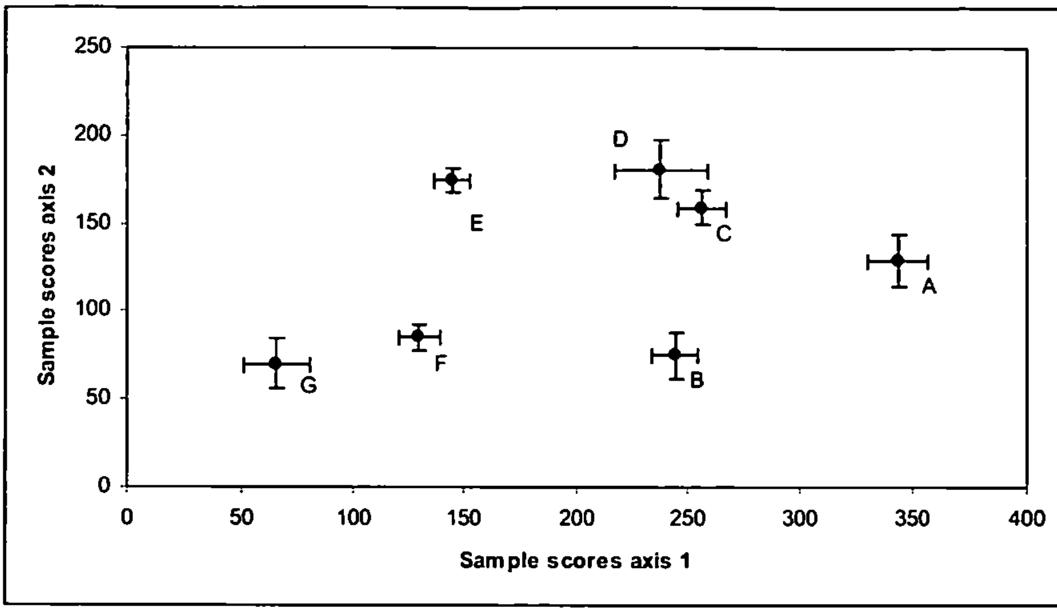


Figure 8.18 Average DCA sample scores and standard errors on axis 1 and 2 after removing sample 13, 37, 40 & 78, presented by TWINSPAN group

	axis 1	axis 2	axis3
Slope	-0.011	-0.073	**-0.159**
Soil depth	**-0.247**	0.008	**0.155**
Soil moisture	-0.056	0.041	**0.260***
pH	**-0.215**	**-0.293***	-0.103
Na	**0.149**	-0.006	0.112
Topographic index	-0.034	**0.163**	0.045
Total C	0.005	0.068	**0.198**
Total N	-0.041	0.061	**0.208**
C/N	**0.222**	0.083	**0.189**
P available	**-0.195**	-0.074	-0.094
K	-0.035	0.123	0.114
Ca	**-0.223**	**-0.159**	0.034
Mg	-0.015	0.002	0.086
grazing	**0.453***	-0.060	**-0.145**

*Table 8.17 Kendall's τ correlation coefficients of normalized environmental data with the first three axes of the detrended correspondence analysis after removing the outliers (13, 37, 40 & 78). Critical value at a two-tailed 0.05 significance level 0.137 (N = 93). Significant correlation printed in bold font. *Strongest correlation.*

8.4.3 Canonical correspondence analysis

Canonical correspondence analysis is an ordination technique that inter-relates species composition and environmental data (Chapter 7). The same data sets as for the DCA analysis were used. The procedure described below contains a number of steps to come to an optimum result, identifying the most important environmental variables and the relationships between the sample points and the ordination axes. Environmental variables that are not expected to be important or are correlated with others are taken out of the analysis to reduce the amount of noise in the data. Extreme sampling points are removed for the same reasons.

Step 1

The analysis started by using all samples, with all species and the total set of environmental parameters. The result is presented in Figure 8.19 with the TWINSPAN groups superimposed on the sampling points. Grazing pressure is the most important variable on the first axis (r = –0.653) and soil moisture is the most important variable on the second axis (r = 0.686). Together the first two axes explain 34.9 % of the variation in the data.

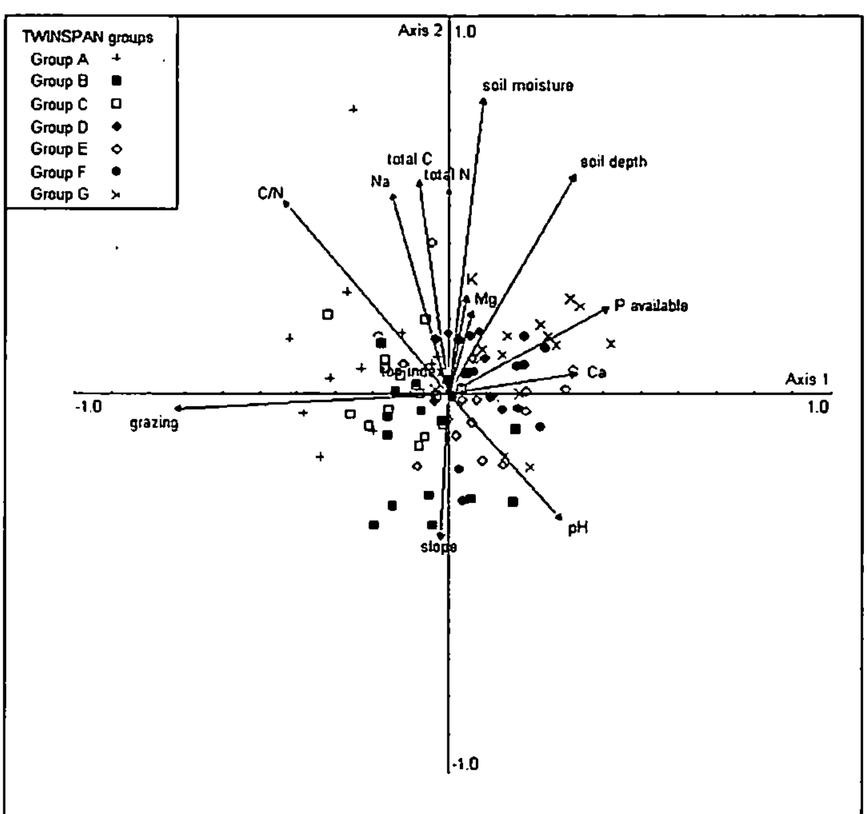


Figure 8.19 Sample ordination plot from CCA of the floristic data (all samples and variables included).

Step 2

For the second step, grazing pressure was taken out of the environmental data set, because of its crude scale. The remaining variables were all soil properties. Figure 8.20 shows the resulting ordination graph. On the first axis, available phosphorus is now the most important variable with a correlation coefficient of 0.417. Soil water content has again highest correlation with the second axis (r = 0.681). Together the axes explain 35.7 % of the variance in the data.

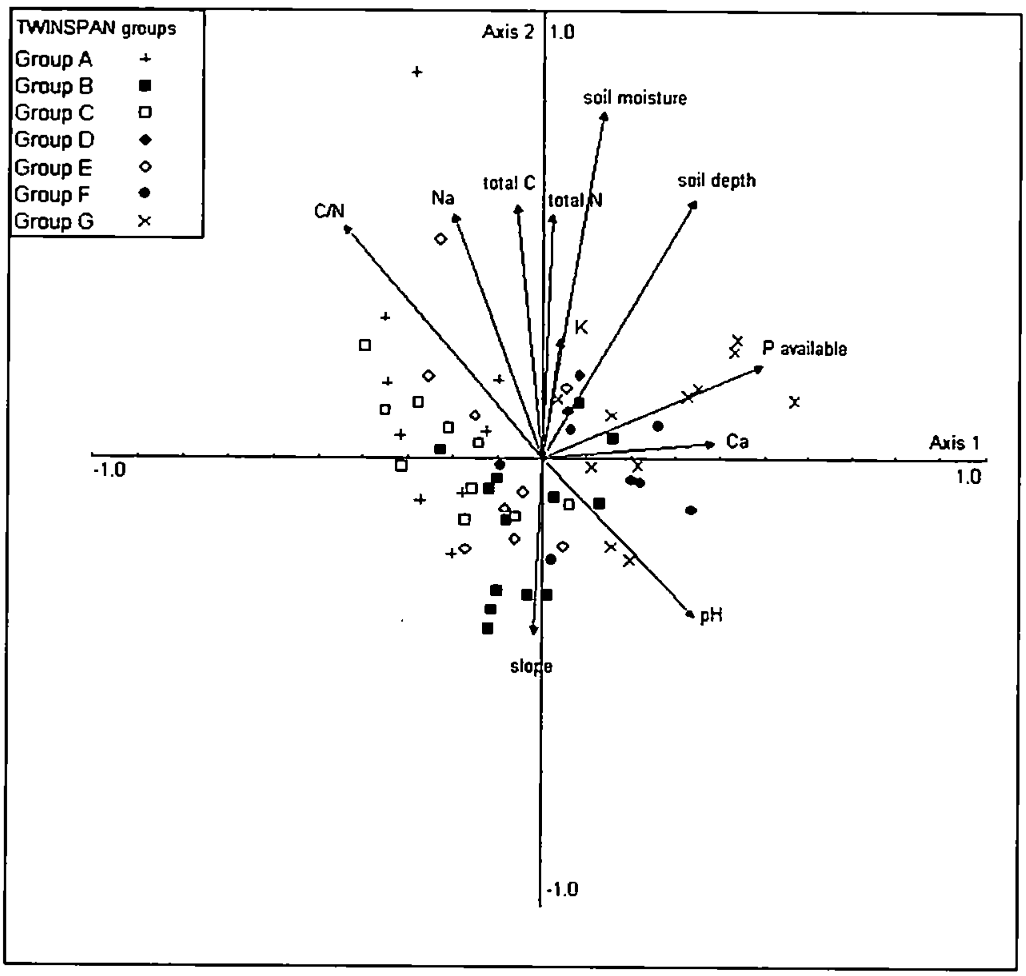


Figure 8.20 Sample ordination plot from CCA of the floristic data (all samples included and grazing is excluded from the environmental data set).

Step 3

High correlation existed between total organic carbon and nitrogen contents and the C/N-ratio which was indicated by high inflation factors, e.g. larger than 20 (respectively 11048.6, 8337.2 and 355.9), (Ter Braak and Smilauer, 1997). Where significant inter-correlations between variables occur, it is recommended that one or more variable(s) is/are removed. It was therefore decided to remove the total organic carbon and nitrogen contents from the environmental data set. The sodium content was also removed because high outlier values affected the results and sodium content was not expected to be a crucial factor in the analysis. The result is presented in Figure 8.21, which again shows available phosphorus content and soil moisture content as the two most important variables (r_1 = 0.430 and r_2 = –0.729). The two axes explain 43.3 % of the variance in the data.

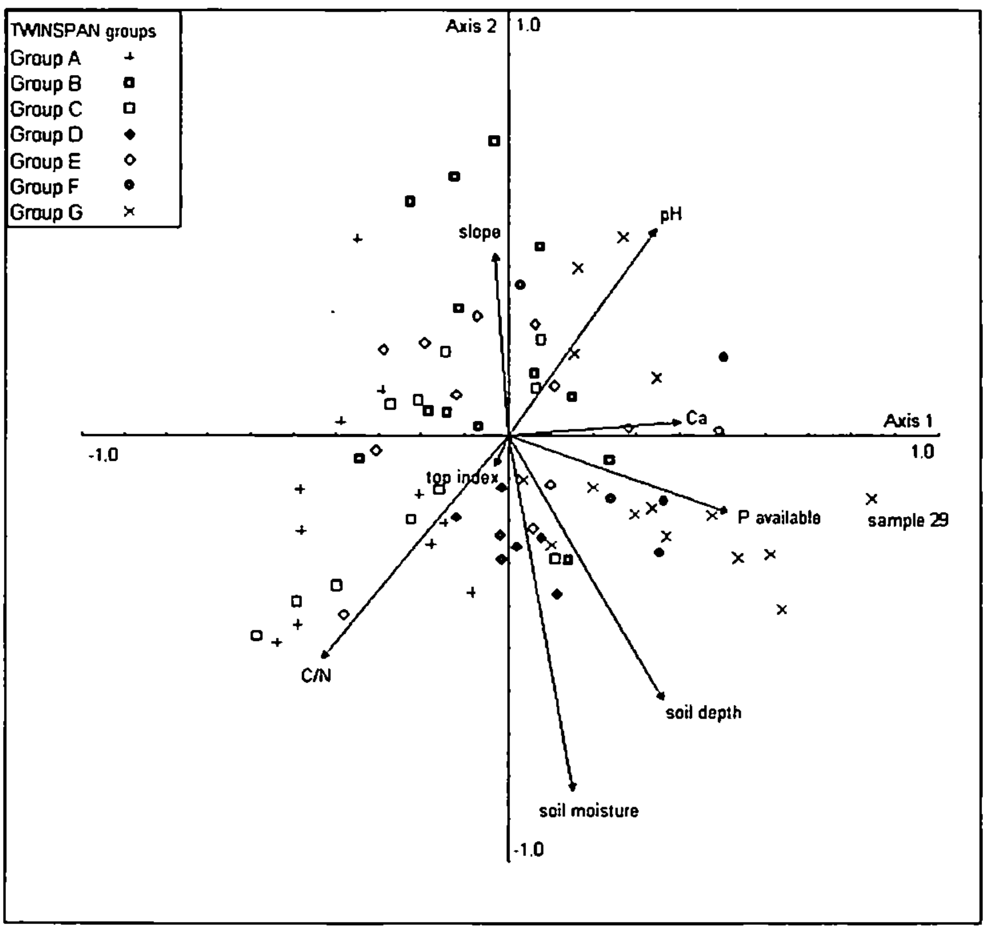


Figure 8.21 Sample ordination plot from CCA of the floristic data (grazing pressure, total C and N and the sodium content are excluded from the environmental data set).

Step 4

From Figure 8.21 sample 29 was identified as an outlier and therefore removed from the analysis. The result is presented in Figure 8.22. Available phosphorus content is again the most important factor on the first axis (r = 0.404) and soil moisture is the most important on the second axis (r = -0.729). Together the two axes explain 42.9 % of the variance.

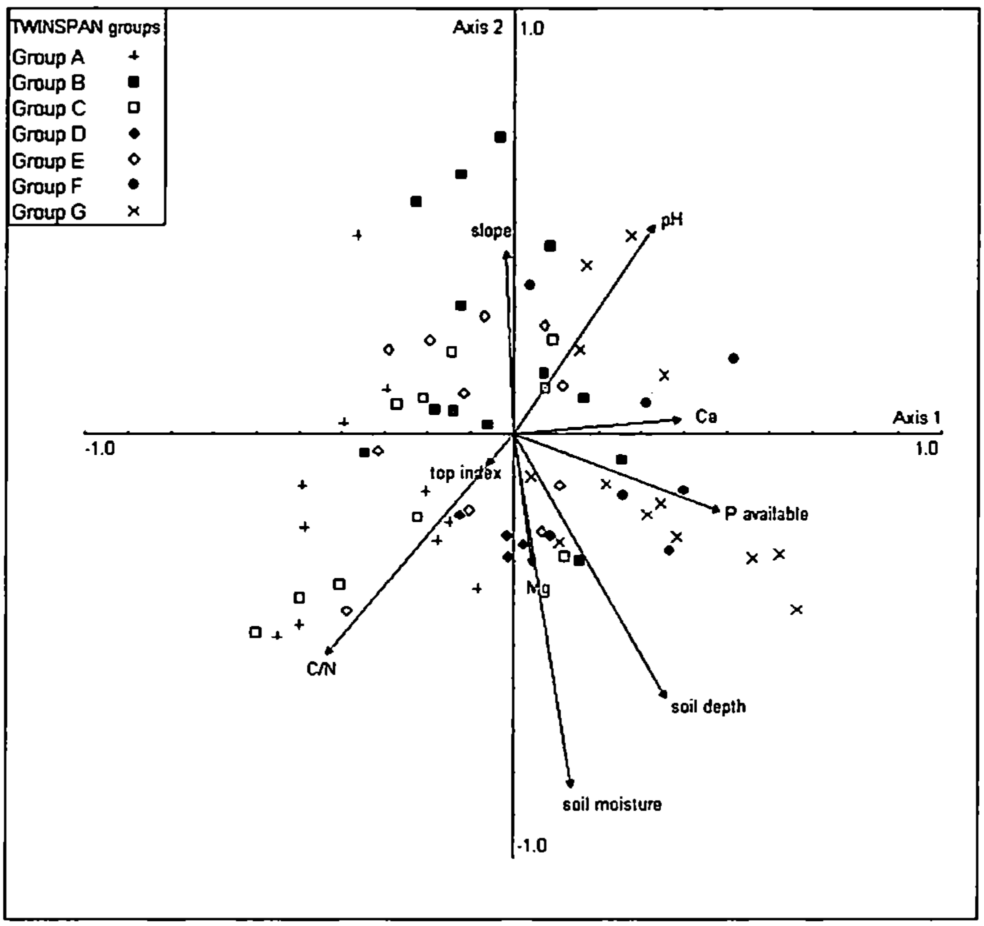


Figure 8.22 Sample ordination plot from CCA of the floristic data (sample 29, grazing pressure, total C and N and the Sodium content are excluded from the environmental data set)

Step 5

Only the most important variables were used for the final analysis and the parameters that have only small correlation coefficients were removed. Only available phosphorus, soil moisture, C/N, pH and soil depth are used in the ordination. Results are presented in Figure 8.23. Again available phosphorus and soil moisture have the highest correlation with respectively axis 1 and 2 (r_1 = 0.434 and r_2 = -0.729). The two axes explain 65.6 % of the variance in the data.

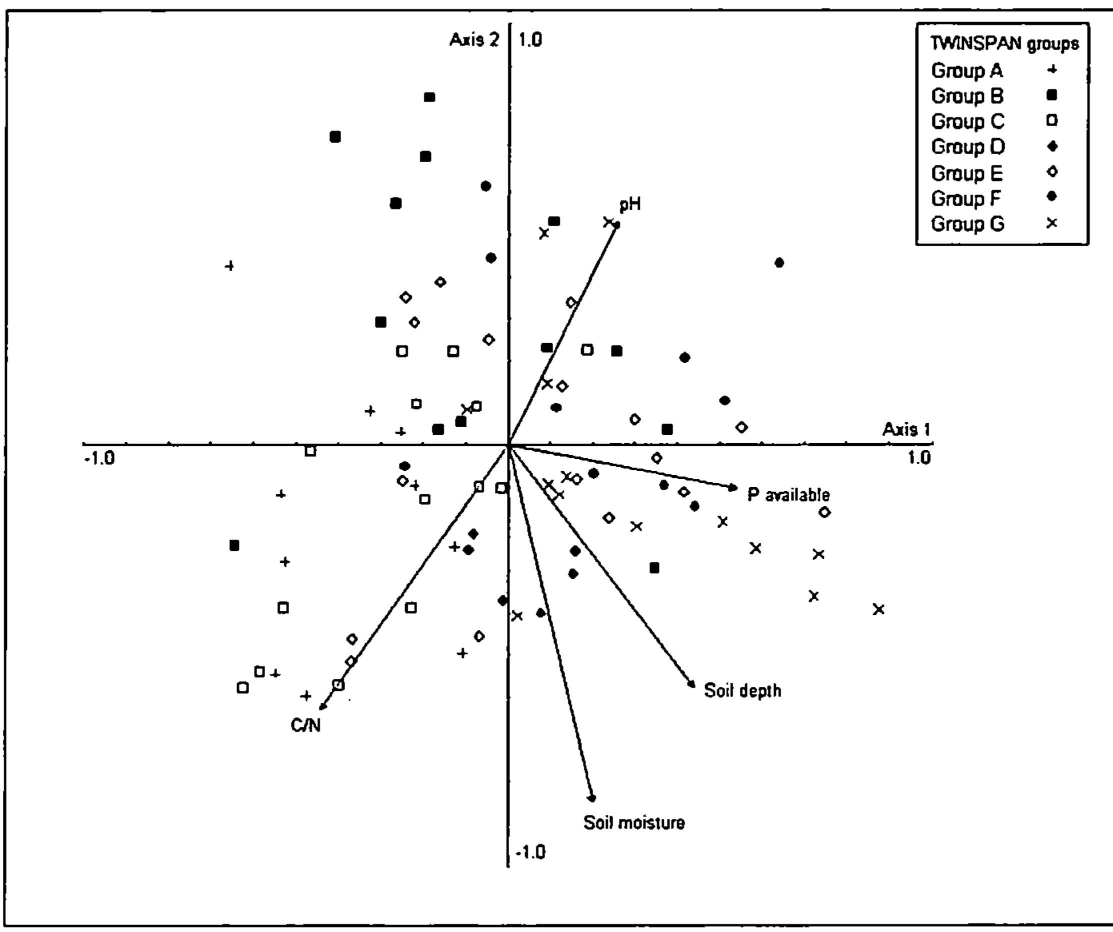


Figure 8.23 Sample ordination plot from CCA of the floristic data including only soil moisture available Phosphorus, C/N-ratio, pH and soil depth (sample 29 is excluded from the data set)

Step 6

The optimal set of data is presented in Figure 8.24. Grazing is reintroduced in the environmental data set because of its importance shown in step one. This, however, lowers the percentage of explained variance by the first two axes to 60.5 %. Grazing pressure has the highest correlation with axis one (r= 0.688) and soil moisture with axis 2 (r = -0.751). Available phosphorus is correlated with the third axis (r = 0.510). These three environmental variables are considered most important in determining the variation in the data (74.7 % is explained by these three). The relationships between the vegetation species and the ordination axes is shown in Figure 8.25.

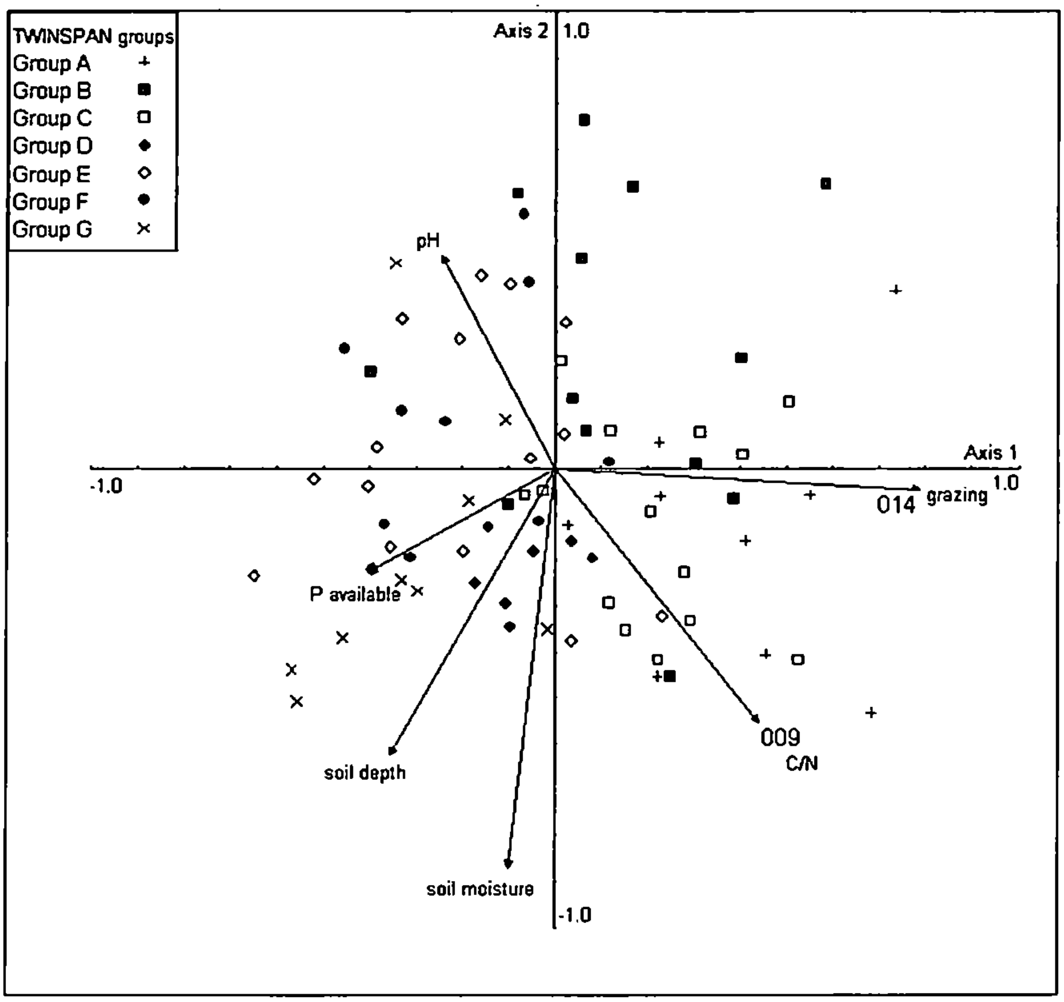


Figure 8.24 Sample ordination plot from CCA of the floristic data including only grazing pressure, soil moisture, available phosphorus content, C/N-ratio, pH and soil depth (sample 29 is excluded from the data set)

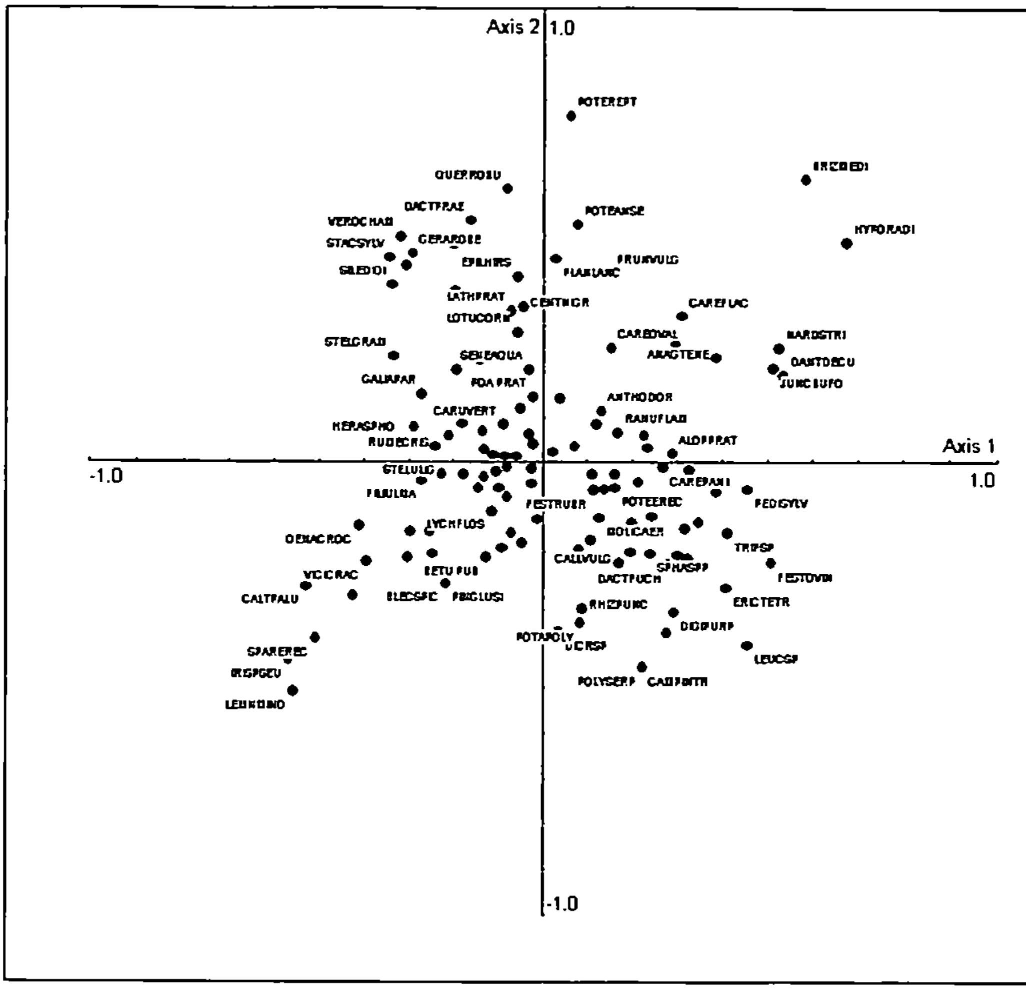


Figure 8.25 Sample ordination plot from CCA of the floristic data showing the relationship between species and the ordination axis, including only grazing pressure, soil moisture, available phosphorus content, C/N-ratio, pH and soil depth (sample 29 is excluded from the data set)

Figure 8.26 shows the TWINSPAN groups in relation to the ordination axis resulting from the final CCA analysis, described under step 6. Group G was clearly different from group A and C and group D was different from F. However, the other groups were strongly overlapped. Figure 8.27 shows the average sample scores for each group, which suggests that groups E and F resembled each other, but the other groups showed clear vegetation patterns and were associated with distinct environmental conditions.

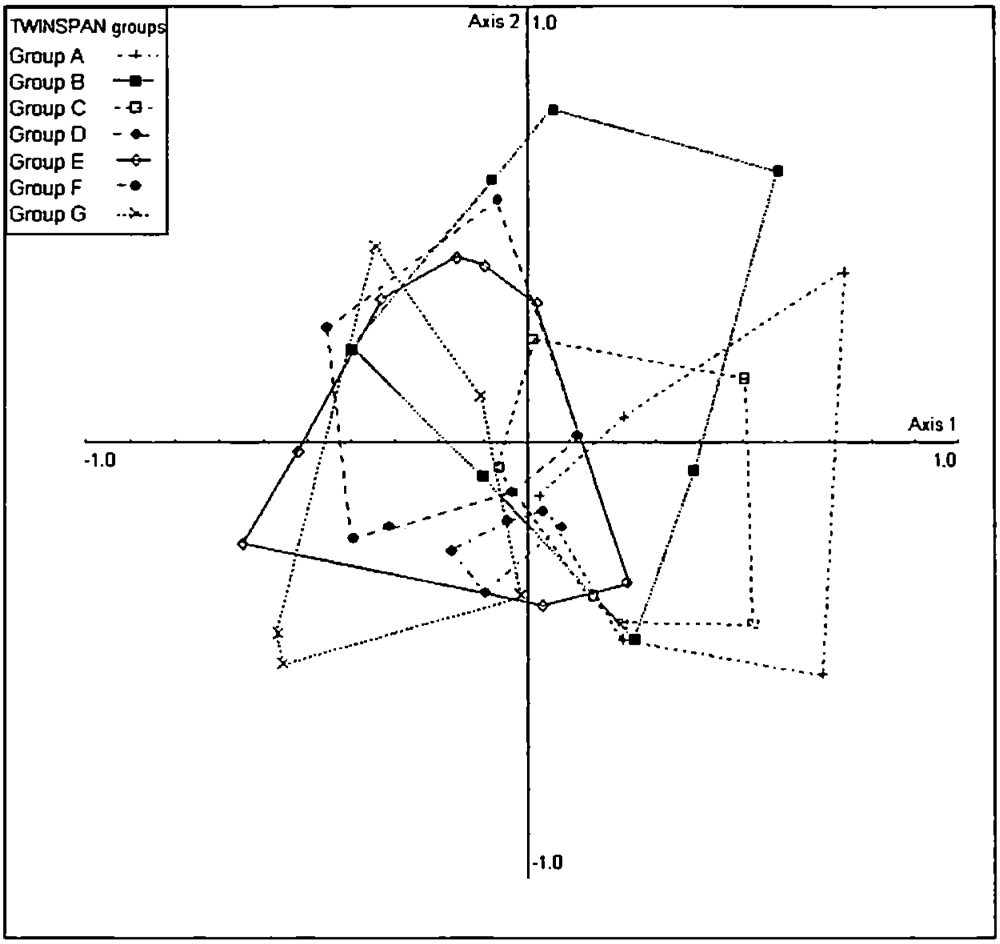


Figure 8.26 TWINSPAN groups in relation to the CCA ordination axes

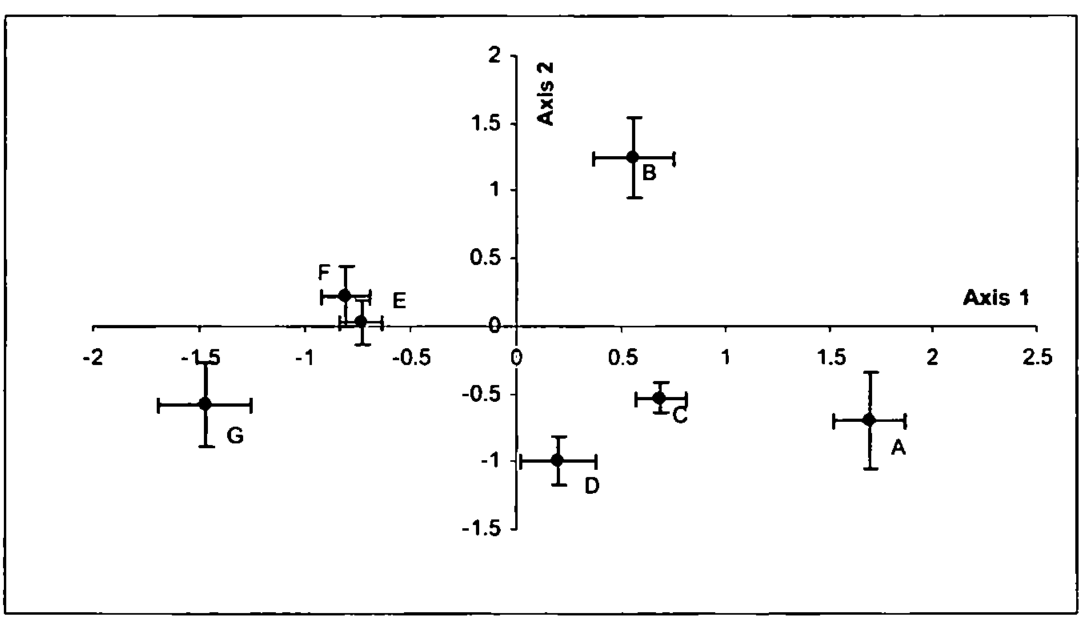


Figure 8.27 Average CCA sample scores and standard errors on axis 1 and 2, including only grazing pressure, soil moisture, available phosphorus content, C/N-ratio, pH and soil depth (sample 29 is excluded from the data set). Data are presented by TWINSPAN group.

Compared to the CCA results, DCA shows the TWINSPAN groups much more clearly. Instead of grazing pressure, soil water content and available phosphorus are the most important variables associated with axis 1, 2 and 3. DCA resulted in grazing pressure, pH and soil moisture showing the highest correlation with these axes.

8.5 Discussion

The 2000 survey was conducted because no conclusive results were obtained from the 1999 field survey and the DWT data, conducted a year earlier (Chapter 7). Vegetation data were classified into 7 groups by using two-way indicator species analysis (Hill, 1979a) in the computer package TWINSPAN. This technique was applied in this thesis because it has widely been used (e.g. Dinsdale *et al.,* 1997 and Kent *et al.,* 1999) and is commonly accepted as an important analysis tool. However, some authors have criticised the technique, because of its poor functioning when there is more than one important underlying gradient (Van Groenewoud, 1992; Belbin and McDonald, 1993) and its sometimes inappropriate selection of dichotomising points (Belbin and McDonald, 1993). The problems with TWINSPAN have been minimised in the PC-Ord analysis package, used for this thesis, by setting a very strict tolerance limit (0.0000001) and using 999 iterations for the calculation, following the suggestions of Oksanen and Minchin (1997).

Comparison of the vegetation groups with the NVC classification derived from TABLEFIT showed that M24c, M23a and b and M27c were mostly found in the sampled fields (Section 8.2). Although the selected 97 sampling locations only formed a very small proportion of the total area of Culm grassland in the region (over 750 sites in total), analysis of the DWT data (Section 7.2) should have ensured that the full range of vegetation was covered in the sampling scheme. However, one of the five Culm grassland communities, M16, was not represented in the data. This was probably because this plant community was less commonly found on the Culm grassland sites.

Physical and chemical characteristics of the sampling points were studied to identify those parameters most responsible for the floristic composition of the quadrats. The measurements were used to compare the different samples at the specific time that the samples were taken and no information was gathered on the fluctuation of the parameters through time. The time difference between taking the samples, with a maximum of 21 days between the first and the last sample, was inevitable with the large number of samples that were collected. Soil water content was the most likely parameter to show large change through time. However, the time effect was expected to be averaged out, because samples were taken at a random order. Figure 8.28 also shows no correlation between soil water content and the date of sampling. For the chemical parameters little variation was expected, because mainly bulk parameters were measured.

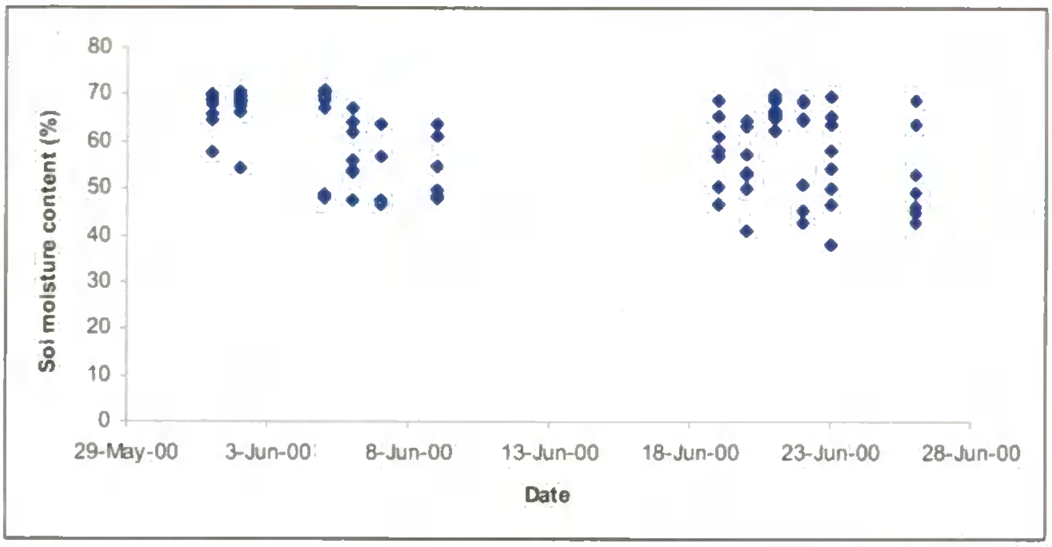


Figure 8.28 Correlation between soil moisture content (%) and the sampling date

DCA and CCA ordination techniques were used to identify the most important gradients in the data (Section 7.3.4). Similar problems as reported above for TWINSPAN existed in the past for DCA. Minchin (1987) reported errors in the performance of DCA and 'lack of robustness'. The version of DCA available in the PC-Ord computer package, used for this thesis, was corrected for these errors.

Both CCA and DCA indicated the grazing pressure to be the most influential factor, stressing the importance of management practices on the development of plant communities. Detrended correspondence analysis gave the clearest result, with pH and soil water content being shown as the most important factors after grazing. Group E, F and G were related to low grazing pressure and group A to the highest grazing pressure. This corresponded with the NVC description: part of group E, F and G can be classified as M27, which is reported to benefit from the protection from grazing (Rodwell *et al.*, 1991). Due to the subjective scale used for estimating the grazing pressure, grazing intensities could not be quantified in detail. Groups related to relatively alkaline conditions were F and G and more acidic conditions were found for A, C and D. Group B was associated with drier conditions and E and D with the wettest locations found. One of the important communities in group B is M24c, which is associated with most to fairly dry soil, and the M23 and M27 communities (group E and D) are related to moist soils (Rodwell *et al.*, 1991). From the canonical correspondence analysis phosphorus availability also appeared to be one of the important factors controlling plant community composition. The plant communities described in this chapter, however, were no clear and discrete entities, but they were distributed as a continuum along the environmental gradients. Along the environmental gradients, only gradual changes in floristic composition therefore occurred.

Together with the results presented in Part 2 of the thesis, the results of this study are used for the design of a decision support system (Chapter 9) to aid conservationists and planning authorities in the selection of suitable restoration locations. Although many factors are of great importance for the successful development of this semi-natural plant community, detailed knowledge of the soil conditions and vegetation patterns are crucial. Research by Goodwin *et al.* (1998) and Tallowin and Smith (*in press*) should therefore be taken into account in the selection process. For example, the relatively high phosphorus levels of agricultural fields could be a limitation for vegetation succession into a more natural stand, due to the long-term binding effect of phosphorus in the soil (Section 2.3.3). Additionally, the availability of nitrogen depends largely on the wetness of the soil (Section 2.3.3). Although levels of 0.7 to 1.6 % of total nitrogen were found in the samples, only a limited amount will be available for plant uptake due to the wet conditions on the sites.

PART IV

The Decision Support System

Chapter 9

A decision support system to identify potential restoration sites

9.1 Introduction

The final part of this thesis is concerned with the integration of the results presented in Parts 2 and 3 and the development of a management tool, designed to aid conservationists and regional planners in making decisions about where to focus Culm grassland restoration activities. In the last chapter, conclusions will be drawn from the various aspects of the research on the relationships between Culm grassland location and landscape topography and hydrology and of the work on the ecology of Culm grasslands. Implications for future work will also be discussed.

Part 2 of the thesis gave an overview of the relationships between landscape topography and Culm grassland location and examined the location of the wet grassland sites in relation to surface water hydrology and soil hydrology. In Part 2 various approaches to determine the best way to explain the position of Culm grassland in the landscape were tested. In Part 3 the DWT vegetation database was described and analysed and the sampling design was presented. The results of an extensive field study to describe species composition, general field characteristics and physical and chemical soil parameters were also presented and discussed. In other words, Part 2 (Chapter 4, 5 and 6) studied where Culm grassland is typically found and Part 3 investigated which parameters determined the variation within Culm plant communities.

In this chapter, the design of a Decision Support System (DSS) is presented to aid decision-makers in planning the expansion of the area covered by Culm grassland on a regional level. This tool will provide an overview of the existing sites and will show clearly where else in the area a potential for the development of Culm grassland exists. It is designed to help to select target areas and to predict plant community patterns, based on environmental and management characteristics. The information is presented in a Geographical Information System (GIS) and the information can thus be added easily to other GIS information used in regional land use planning. The chapter aims to fulfil the fourth objective listed in Chapter 1:

To integrate these findings (results of objective 1 to 3) in a Decision Support System, to aid in the identification of potential restoration sites.

To make efficient use of available resources and design a long-term plan for ecological conservation and restoration of important habitats in a region, decision-making strategies are needed. Strategic planning of habitat restoration ensures a more effective use of available funds. As examples, Kent and Smart (1981) introduced a method to assess semi-natural plant communities for regional and local conservation planning. Pastorok *et al.* (1997) described a decision framework to help to maximise the overall success of ecological restoration projects on a site-specific basis. The focus of their approach was mainly on a selected site and its relationship with the surrounding area, whereas in this thesis the process of site selection for restoration purposes was studied in more detail. The planning tool introduced in this study could only cover a small part of the total habitat restoration process and therefore addressed only some of the stages of the whole procedure. The results of the study need to be integrated with other sources of information available to environmental and nature conservation agencies. Furthermore, habitat restoration does not only depend on physical parameters, other factors evenly important. For example, the willingness of landowners to manage their land in an environmentally friendly way and the availability of suitable agri-environmental schemes to support this are crucial for the restoration to succeed.

Box (1996) argued that in most cases of habitat creation or restoration, an idealised plant community is created. However, creation of a more natural plant community by natural regeneration, colonisation and succession needed to be given greater consideration. Carefully planning and defining the desired output is therefore of crucial importance. Two approaches of Culm grassland restoration, which complement each other, can be adopted. The first is focused on improving poor quality 'existing' Culm grassland sites. The second is directed at creating 'new' sites on locations with suitable soil and environmental conditions, which is the approach of this study. The site selection procedure presented in this chapter is based on finding locations with conditions that are naturally favourable for Culm grassland-type wetlands, instead of having to create the conditions completely artificially. To achieve this aim, the process was divided into four components: Section 9.2 describes the site selection based on topography and hydrology. Section 9.3 describes the environmental parameters explaining the variation within the Culm grassland plant communities. Section 9.4 verifies the results and a discussion follows in Section 9.5.

9.2 Topography and hydrology

Soil physical properties and topography are key variables in determining wetland hydrology. Chapter 6 characterised the hydrology of Culm grassland sites. Various methods for description of the hydrological properties were applied and their explanatory value for the position of Culm grassland in the landscape was evaluated. The hydrological classification of the soil types (HOST) explained the location of existing sites most clearly. The sites were mainly found on soils with a HOST category of 9 or 24 (Chapter 6: Table 6.6). In Chapter 5, slope, curvature and upslope contributing area were shown to be important topographic parameters related to Culm grassland location. Chapter 6 indicated that the $\ln(a/\tan\beta)$ topographic index could be used to explain the location of most Culm grassland sites. Sites were found on locations with an index equal to or larger than 8. However, the exact value of 8 is valid only for the 50 m resolution grid. The result of the interpolation of elevation data to derive a digital elevation model (DEM) depends on the input data and also on the chosen resolution of the DEM. These small differences cause the calculation of slope and upslope contributing area to produce slightly different results for the various resolutions, which then affects the calculation of the topographic index (Quinn *et al.*, 1995). If a different grid resolution is needed, the calculations of the topographic index would have to be repeated.

These discriminating factors: HOST class, the topographic index value and the various other topographic parameters were used to set up the decision support system. The high percentage of Culm sites on soils with a HOST class of 9 or 24 was the reason to use the HOST classification as a first discriminating factor for the selection of suitable sites. The selection was refined by rating the sites according to the number of topographic criteria met:

- Gradient ≤ 4°
- Upslope contributing area > 1 ha
- Curvature = straight/concave
- Topographic index > 8

The topographic criteria were treated as equal and suitability levels ranged from 1 to 5, with 1 corresponding to the least suitable sites, which should not be confused with the unsuitable areas. The selection procedure is presented in Figure 9.1 and was based on the principle that the more criteria were met, the better the site would be for the creation or restoration of Culm grassland.

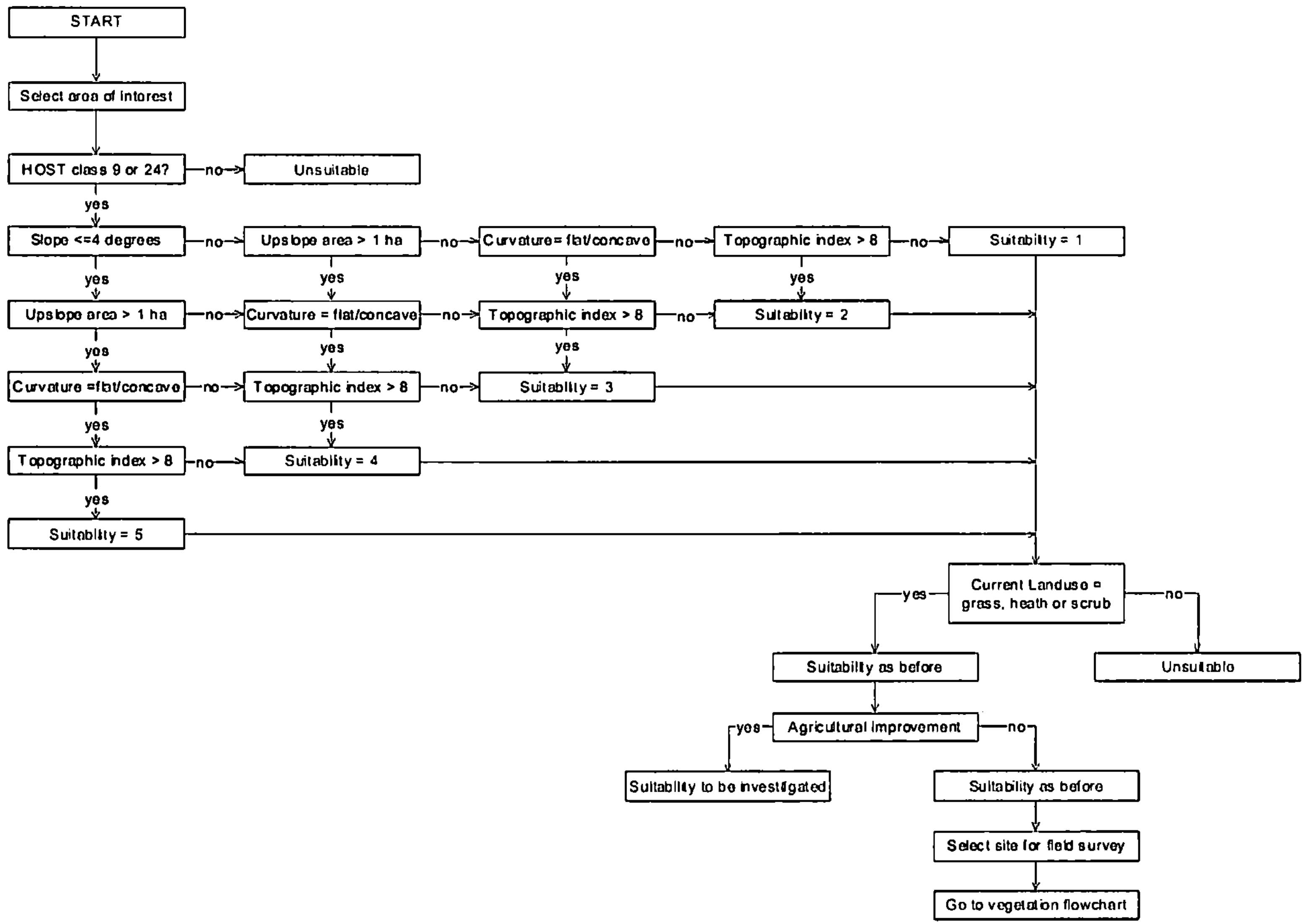


Figure 9.1 First section of the Decision Support System indicating potentially suitable Culm grassland restoration sites.

However, the 'best' sites could thus correspond to the wettest sites, supporting a relatively narrow range of plant communities. In terms of biodiversity, a selection of sites across different suitability classes, to stimulate the establishment of a wide range of plant communities, could be more desirable than focusing on sites only located on the areas with the 'highest' level of suitability for Culm grassland development (HMSO, 1994). It is important to realise that the suitability is not as clear-cut as presented in Figure 9.1, but that the suitability changes along a continuum.

The selection procedure of Figure 9.1 was applied to the Wolf, Thrushel, Carey and North Lew catchments and the results are presented in Figure 9.2. To indicate the relationship of these potentially suitable sites to the existing sites, the existing Culm grassland sites were also presented on the map. 89% of the existing sites were located on suitable locations. However, this information cannot be used for the estimation of the validity of the technique, because the same data have been used to derive the selection procedure. Validation of the presented technique is therefore tested on an independent area, elsewhere in the Culm Natural Area (CNA). The same selection criteria were applied to a 100 km^2 area around Holsworthy, which will be described in Section 9.4.

Due to limited resources and copyright issues, concerning the reproduction of soil maps, the decision-making rules concerning the HOST classification could not be applied to the 1:250,000 soil map and therefore it was not possible to estimate the error introduced by using this much smaller scale map for the identification of suitable restoration sites. However, due to the inevitable generalisation associated with the decrease of map scales, this probably resulted in the inclusion of unsuitable areas located in the midst of a suitable area and exclusion of suitable sites situated in the midst of unsuitable areas. Soil map units smaller than 0.5 km^2 were not represented on the 1:250,000 map (Findlay *et al.*, 1984), which is a much larger area than the average size of 5.1 ha of the existing Culm grassland sites (Section 5.2.1). For the 1:50,000 map, areas smaller than 2 ha were excluded and thus this scale is therefore more appropriate for the study of Culm grassland

In addition, the selected areas need to be compared to other regional plans and topographic maps to make sure selected sites do not conflict with other land uses. A discussion on this issue follows in Section 9.4.3. It is also important to take the locations of existing sites into account to be able to connect fragments by developing new Culm grassland areas in between the patches. Fragmentation of habitats causes geographical isolation and has therefore a negative effect on many plant and animal species.

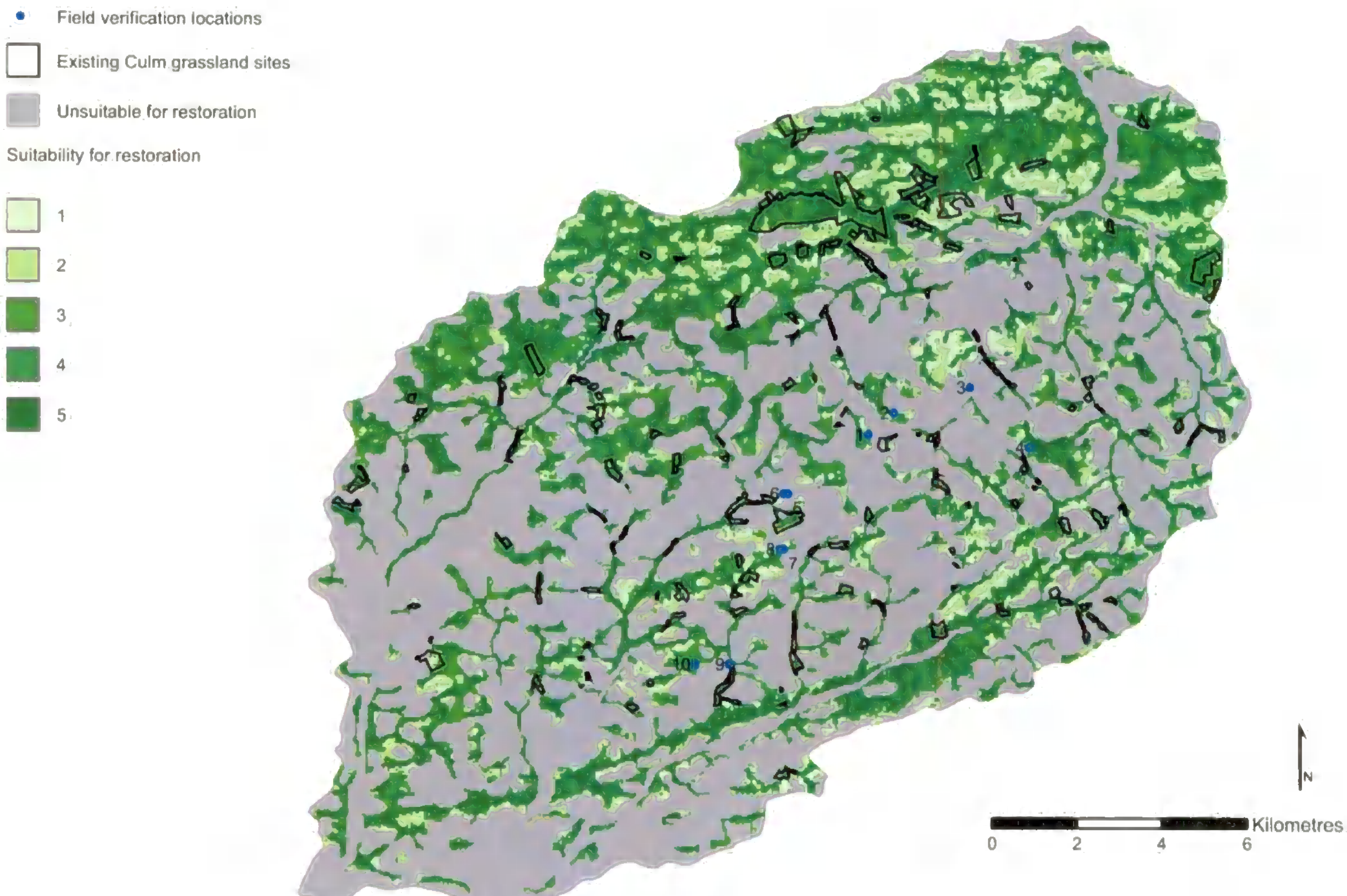


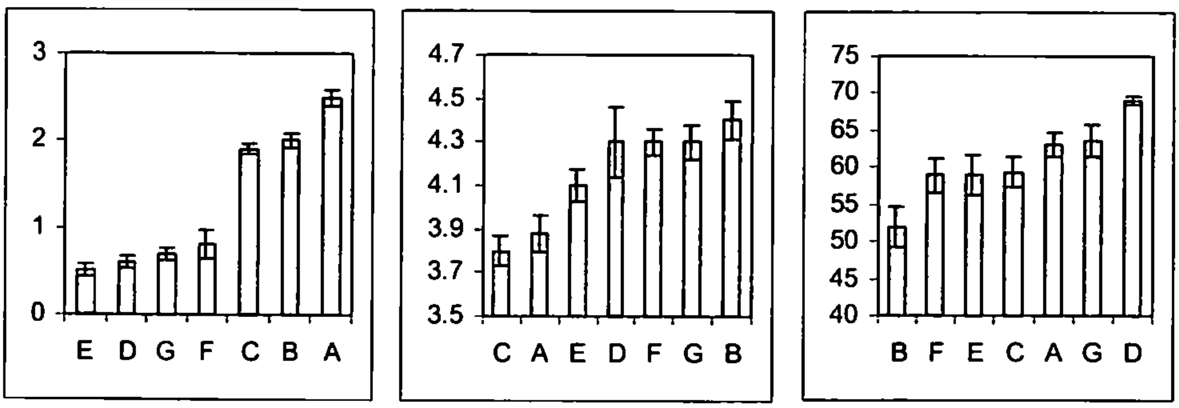
Figure 9.2 Suitabability for Culm grassland restoration, 1 = low and 5 = high.

Recolonisation after extinction of a species largely depends on the distance to the nearest fragment where the species still present (Farina, 2000). Section 9.5.4 will discuss some aspects of fragmentation in more detail. The next section will describe the second part of the DSS, in which plant communities were related to environmental and management parameters.

9.3 Environmental parameters and management controls

The composition of Culm grassland vegetation and its relationship to physical and chemical environmental parameters and grazing characteristics were described in Chapter 7. Data were analysed with the aid of detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA). The closest fit was obtained with DCA, which clearly showed the 7 TWINSPAN groups in relation to the ordination axes. Presentation of the environmental gradients in the same ordination space indicated the major parameters responsible for the variation in vegetation. This section will use the three parameters with the highest correlation to the environmental axes and the expected plant communities.

Figure 9.3 shows how the seven vegetation groups relate to the major environmental gradients. As described in Chapter 7, the parameter mostly associated with the first ordination axis was grazing (Figure 9.3a). Groups E, D, G and F were associated with very low grazing pressures, C and B with intermediate levels and A with the highest grazing pressure. The soil acidity was mostly associated with the second ordination axis. The trend of vegetation groups can be described by C and A occurring on the most acidic soils, E, D, F and G on the intermediate acidity levels and B on the least acidic soils (Figure 9.3b).



a *b* *c*

Figure 9.3 The average values and standard errors of the major environmental gradients (a) grazing pressure (b) pH (c) soil moisture in %, for the TWINSPAN groups (A-G.)

For soil water, associated with the third ordination axis, vegetation group B was found on the driest soils and D on the wettest, with the other groups in between (Figure 9.3c). However, the differences between the groups are small, as can be observed from Figure 9.4 a, b, and c, which shows the individual data points along the environmental axes.

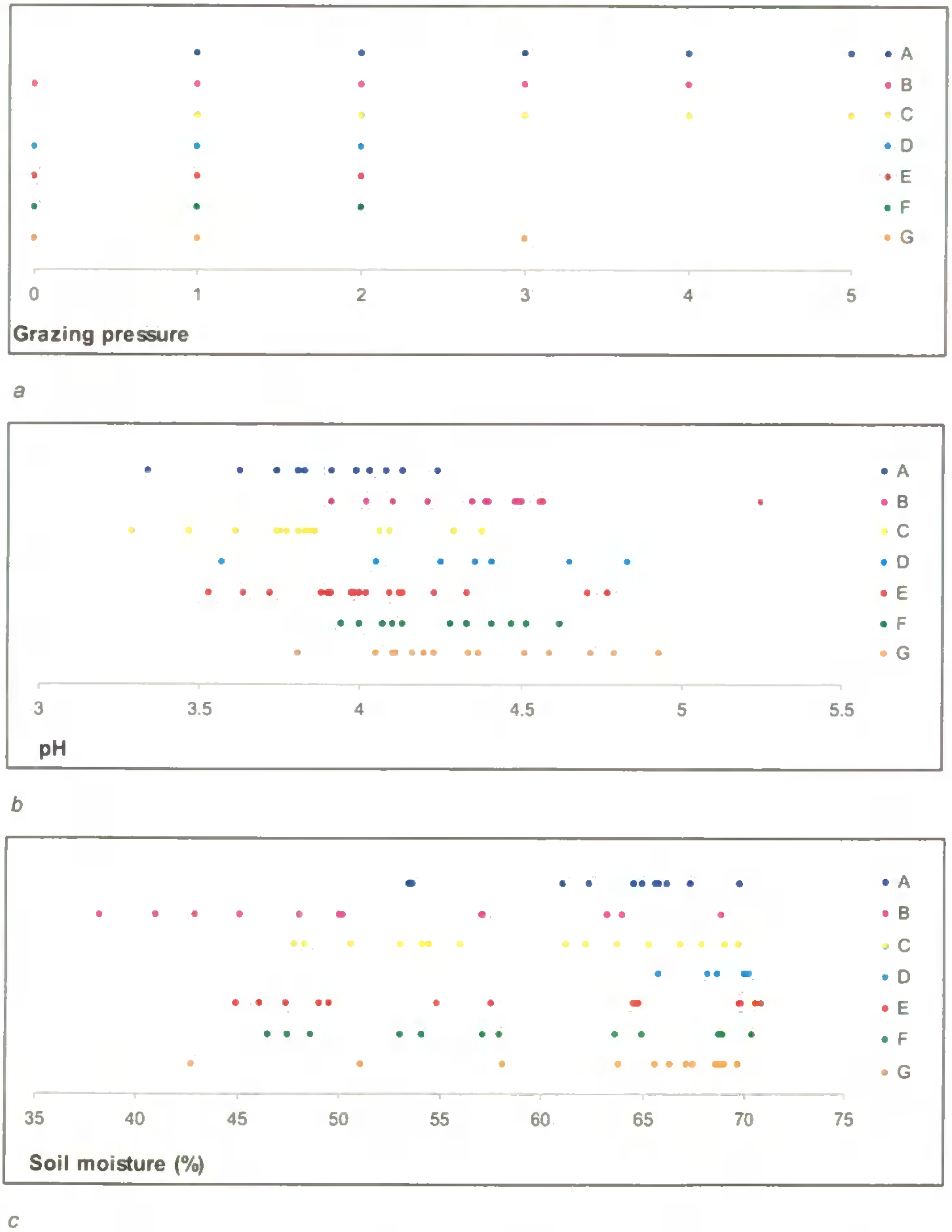


Figure 9.4 The measured values of all samples in TWINSPAN groups (A-G) for the three major environmental axes (a) grazing pressure (b) pH (c) soil moisture, derived from the DCA of the same data.

The correlation of the individual species with the ordination axes are shown in Figures 9.5, 9.6 and 9.7. The axes indicate the directions of maximum variation and the abundance of the the species is represented by the size of the dots. This gives an indication of how a species relates to the environmental gradient. Increasing grazing pressure showed an increase in *Potentilla erecta* and *Molinia caerulea* and a decrease in *Ranunculus repens* (Figure 9.5). The first two were constant species in plant community group A, which was associated with the highest grazing pressures. Both *P. erecta* and *M. caerulea* were listed by Grime *et al.* (1996) as species occurring in grassland and grazed but also ungrazed moorland. *Ranunculus repens* was one of the constant species in group F and G, which were associated with a low grazing pressure. Figure 10.5c also shows this species to be associated with lower pH values, which corresponded to the pH range of plant community groups F and G. Grime *et al.* (1996) listed *R. repens* as associated with wide-ranging habitats with grasslands and mires among the most important ones. However, according to Grime *et al.* (1996) *R. repens* was virtually absent from soils with pH values below 4.5, which contradicted the results of this research.

Further, *Carex panicea* and *Sphagnum spp.* were associated with higher grazing pressures (Figures 9.6a and c). The species were respectively constant and common members of group A, which was related to the highest grazing pressures. *Filipendula ulmaria* and *Poa trivialis* were related to lower grazing pressures (Figures 9.6d and f) and were constant or common species in group F and G. *F. ulmaria* was listed by Grime *et al.* (1996) as a species with a strategy intermediate between competitor (C) and a stress-tolerate competitor (S-R) and therefore does not thrive under highly disturbed circumstances. However, *P. trivilalis* has strategy intermediate between C-S-R strategist and competitive-ruderal (C-R) (Grime *et al.*, 1996) and should therefore be better adapted to the disturbance of grazing. *Molinia caerulea* and *Spagnum spp.* were also associated with wetter conditions (Figures 9.6b and e). These species were found as respectively constant and common of group A and D, but also occured regularly in one of the other vegetation groups. *Carex panicea, Ranunculus repens* and *Poa trivialis were* negatively correlated with the third ordination axis (Figures 9.6a, e and f). This corresponded to the descriptions of Grime *et al.* (1996) who described *M. caerulea* as generally occurring on wet acidic habitats and *C. panicea, R. repens* and *P. trivialis* more associated with moist conditions rather than wet. Figures 9.7a and b show *Angelica sylvestris* and *Valeriana officinalis* to be associated with wet conditions and relatively high pH values. For both species, pH values reported by Grime *et al.* (1996) were above 4.0.

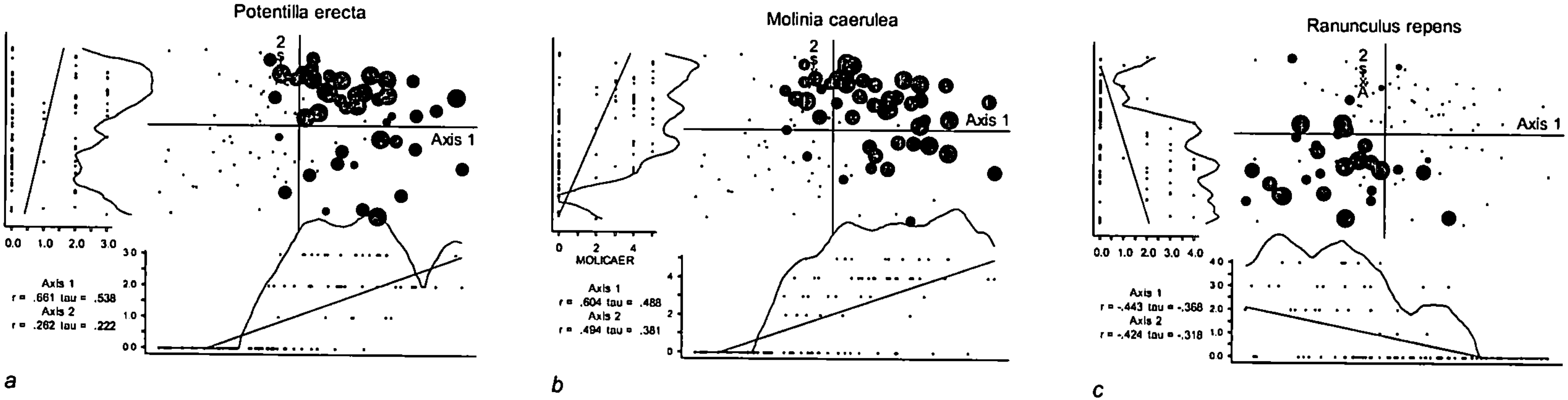


Figure 9.5 DCA correlation of selected species with axes 1 and 2

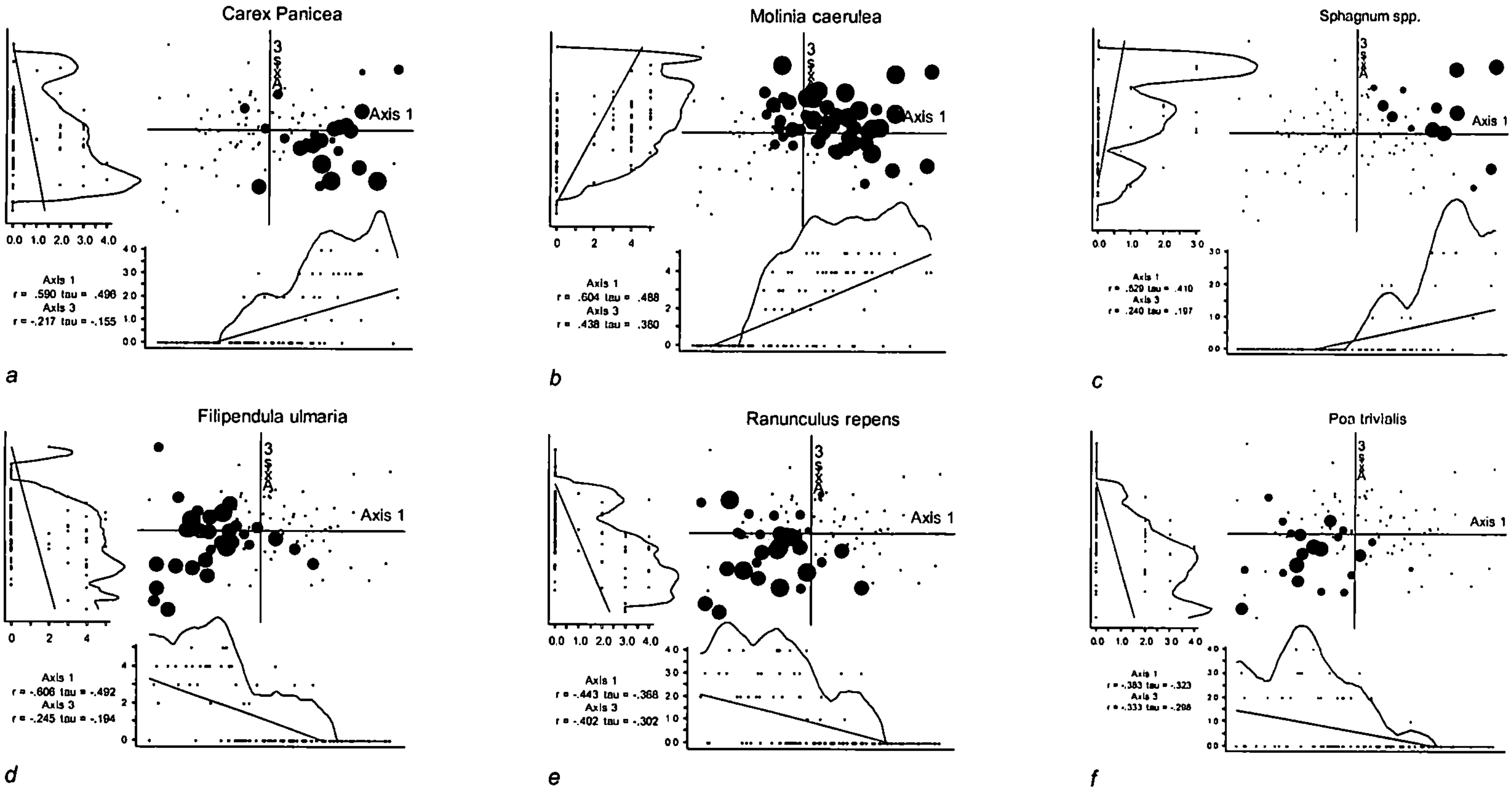
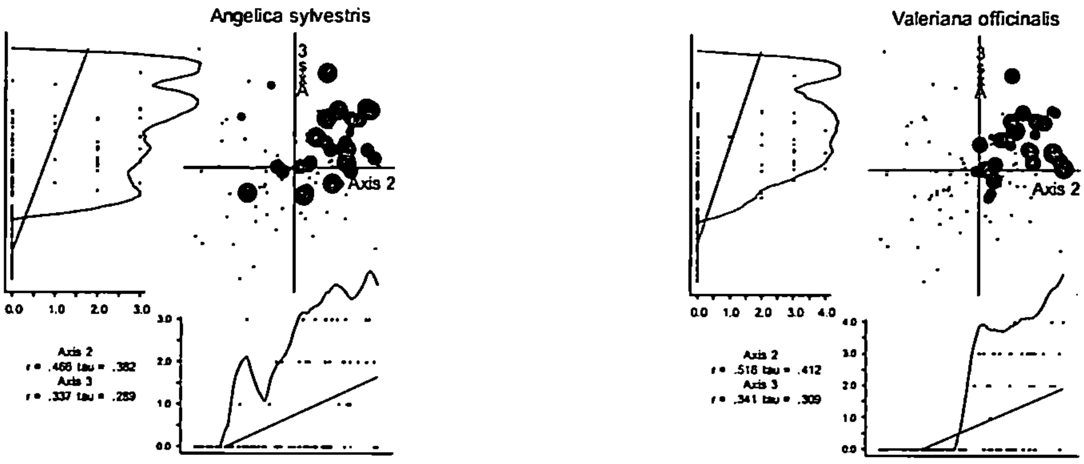


Figure 9.6 DCA correlation of selected species with axes 1 and 3



a *b*

Figure 9.7 DCA correlation of selected species with axes 2 and 3

The vegetation trends described above were used for the second part of the DSS to give an indication of the vegetation response that could be expected under various circumstances when applying the DSS (Figure 9.8). The procedure presented in Figure 9.8 assumed that all the other necessary steps (Figure 9.1) have been taken and that the selected location only needs to be examined for local soil/hydrological characteristics and site management. The presented gradients are those parameters that were revealed as most important in determining the variation within the Culm grassland vegetation and are an indication of what to expect from the vegetation development under various circumstances.

However, other studies have shown the importance of nutrients to the vegetation composition of wet grasslands (Goodwin *et al.*, 1998; Tallowin and Smith, *in press*) (Chapter 2). The reason that nutrients were not identified in this study as the major parameters determining the species composition could be that only sites were investigated that were already classified as Culm grassland, whereas in the other studies comparisons to improved fields were made as well. The difference in plant communities found in improved and semi-natural fields is probably mainly caused by the nutrient status. The more subtle differences in grazing management, pH and soil moisture determine the variation within the semi-natural vegetation, as was shown in this thesis.

However, the nutrient status of the sites should also be considered in the planning of Culm grassland restoration. Table 9.1 presents the overall average values determined for the soil samples (Chapter 8) to indicate the order of magnitude needed for Culm grassland in general. The possibilities for adjustment of the variables need to be evaluated and considered in the decision whether to restore Culm grassland on the site or not. The flowchart presented in Figure 9.8 should therefore only be treated as an indication of the procedure and the likely developments when changing the grazing management, soil acidity or soil water.

Nutrients	
Total nitrogen	0.9 %
Available phosphorus	5 mg kg^{-1}
Potassium	247 mg kg^{-1}
Sodium	187 mg kg^{-1}
Calcium	1395 mg kg^{-1}
Magnesium	469 mg kg^{-1}

Table 9.1 Overall average soil nutrient concentrations for Culm grassland.

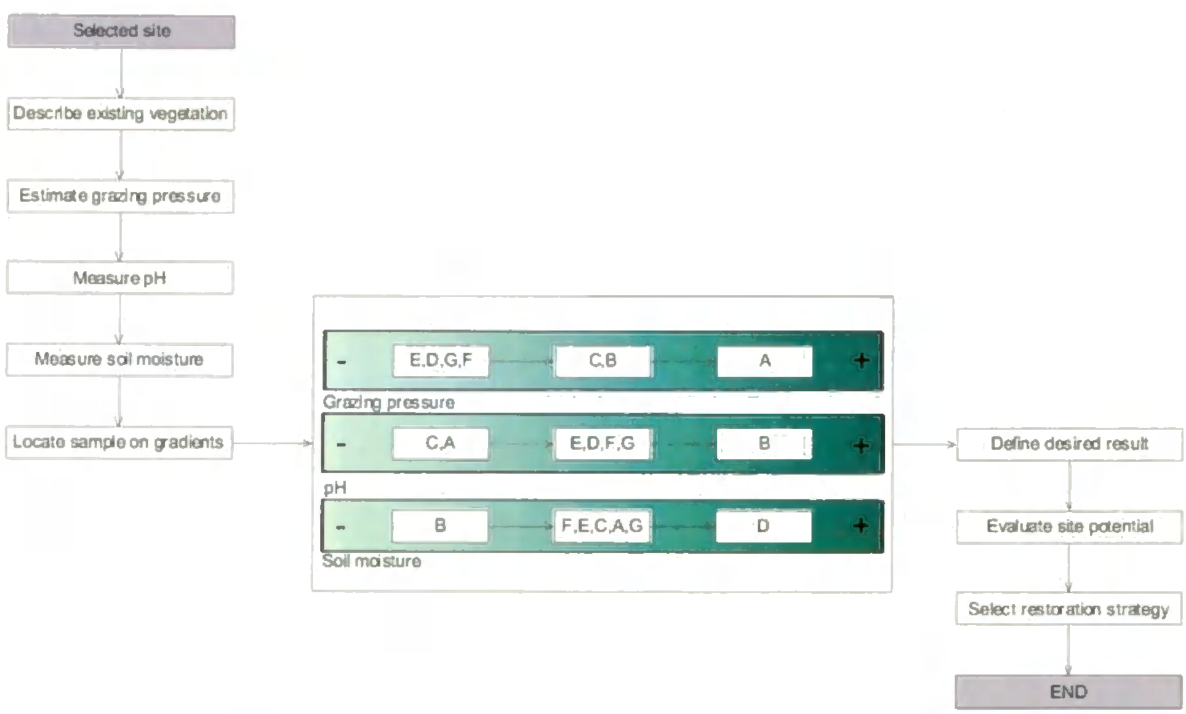


Figure 9.8 Second part of the Decision Support System indicating vegetation trends in relation to the environmental gradients

The low to high ranges for pH and soil moisture can be quantified from Figure 9.3 and 9.4. However, grazing pressure was measured on a subjective scale and quantification is therefore difficult. The values have not been included in Figure 9.8 because too little information is available to use them as absolute numbers. Grazing was found to be the most important factor, but due to the limited information available on the management and the subjectivity of the classification system used, this factor could not be quantified. Furthermore, no vegetation response experiments to investigate the precise effect of the changing the grazing pressure, soil water or pH on the species composition have been carried out in this study. Also the interactions between the environmental parameters and their combined effect on the composition of the vegetation have not been studied. Therefore presented trends are only an indication of the influence of individual effects.

In Figure 9.9 the vegetation groups are presented again, but now in two-dimensional plots with two of the environmental parameters on the axes. The outer points of each vegetation community are connected to indicate the space covered by each plant community group and to show how the groups relate to each other. For investigating a potentially suitable site, its environmental parameters can be located on the graphs and from this can be estimated which community might develop also based on the vegetation characteristics of the site. Below an example is given of how this information could be used.

Example:
Assume a site has been selected by following the first part of the DSS (Figure 9.1) for further investigation of suitability for Culm grassland restoration based on soil hydrology and topography. A field study shows that the grazing pressure at the site is intermediate, the volumetric soil moisture content in summer is approximately 60% and the soil pH is 4.5. The sample characteristics have to be located on the graphs in Figure 9.9. This example is indicated with an X. In Figure 9.9a shows that the conditions probably support vegetation similar to group B. Figure 9.9b indicates vegetation similar to group A, B, C and Figure 9.9 c shows that the sample is situated within B, C, E or F. Group B, which resembles the M24c and M23a NVC communities (Section 8.2) is the only plant community that is indicated by all three graphs and therefore the most likely to develop under 'Culm-friendly' management. The present vegetation on the site needs to be compared to the constant and common species of group B (Appendix D), to estimate the potential for the community to develop.

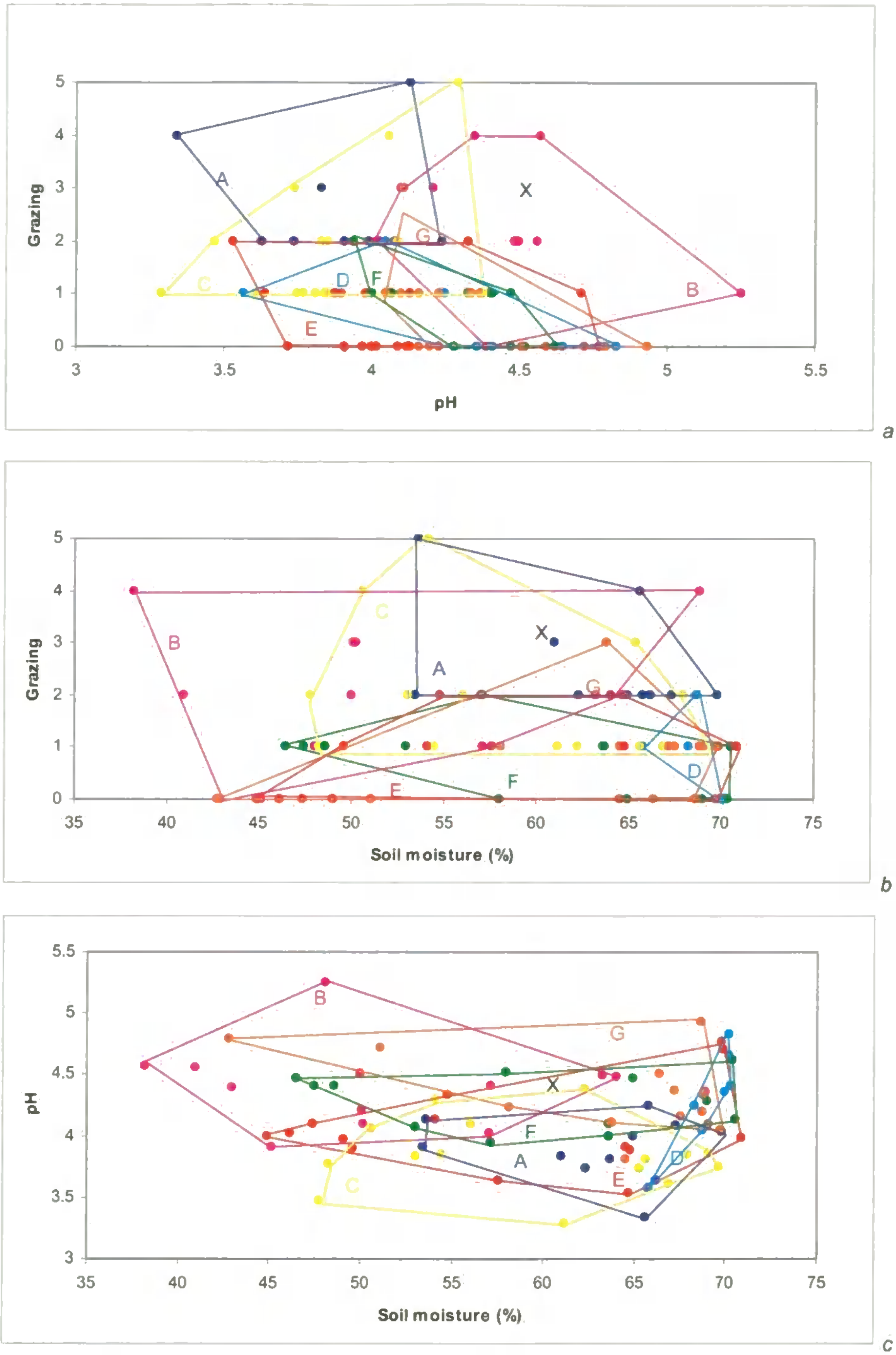


Figure 9.9 Relationships between the seven plant communities and the three most important environmental axes: Grazing pressure, pH and soil moisture. X: example described in the text.

The example described above shows how the information presented in this thesis could be used and how to estimate which vegetation could develop at a selected site. However, such information has to be handled with care and has to be seen only as an example, as the values will vary during the year and only a limited number of samples has been used for this study. Much more research had to be conducted into the response of the vegetation under different environmental conditions, before conclusive results can be presented.

In Chapter 8, the possible inclusion of the topographic index in the multiple regression ordination analysis to relate the vegetation to the GIS system was considered. It was expected that the topographic index would reflect the soil water patterns and therefore could possibly explain part of the observed vegetation gradients. However, results showed that the observed gradients were not correlated with the topographic index at the sampling location. Probably, due to the large scale difference between the field measurements and the scale of the GIS maps, the plant communities could not be correlated to soil and topographic characteristics derived from the 1: 50,000 maps.

9.4 Verification of the results

9.4.1 Introduction

The DSS presented in this chapter was evaluated by comparing the results with other sources of information. Section 9.4.2 shows the results of the application of the criteria to a different section of the Culm Natural Area (CNA): the 100 km^2 area around Holsworthy (National grid square: SS30). No information on the current land use was included in the system. A comparison with the Land Cover Map of Great Britain (1990) © NERC was therefore made in Section 9.4.3. Section 9.4.4 shows how the predicted areas related to the marsh land indicated on historical topographic maps. These maps indicated largely the situation before large scale agricultural improvements were carried out and therefore should have given good information of where wet grasslands and heaths were found. Field checks of the predicted sites are presented in Section 9.4.5.

9.4.2 The Holsworthy area

To test the validity of the decision rules presented in Section 9.3, the selection criteria were applied to a different section of the CNA. The area of 100km^2 around Holsworthy was chosen, because of the availability of a detailed soil map for the area.

Figure 9.10 HOST classification of the Holsworthy area (SS30). Based on the 1:25,000 SS30 soil map copyright Cranfield University (Soil Survey and Land Research Centre), 2001.

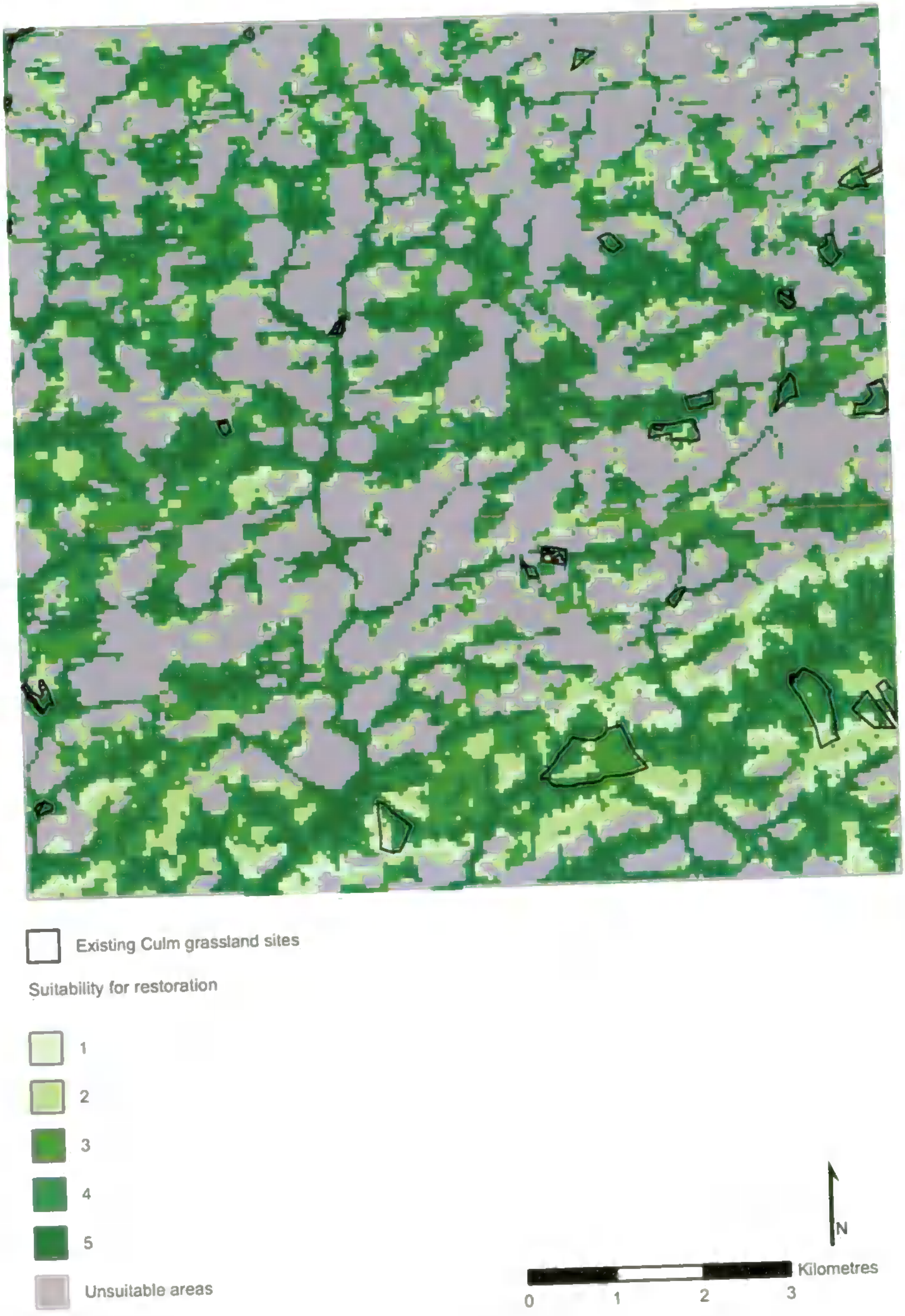


Figure 9.11 Suitability of sites in the Holsworthy area (SS30), 1 = low and 5 = high

The HOST classification was applied to the 1:25,000 soil map (Figure 9.10) (Harrod, 1978). The HOST categories found in the area were 9, 17, 21 and 24 (Chapter 6: Table 6.6), which corresponded to the classes of the Wolf, Thrushel, Carey and North Lew catchments.

The topographic parameters: gradient, upslope contributing area, curvature and the topographic index were calculated on a 1:50,000 scale with grid cells of 50 * 50 m^2, in a similar manner as was done for the Wolf, Thrushel, Carey and North Lew catchments. Application of the decision rules presented in Figure 9.1 resulted in selection of suitable restoration locations (Figure 9.11). The quality of the prediction was judged by calculating the area of the existing Culm grassland sites that are classified as suitable. For this independent testing area, it was found that 88 % of the area of existing Culm grassland sites was selected as potentially suitable sites. Compared to the initial 89% cover of the sites, which was used to the derive the selection criteria, this was a very close fit.

9.4.3 Land cover data

The DSS described in Section 9.3 was purely based on physical soil characteristics and landscape topography. However, many other factors need to be taken into account when deciding where Culm grassland sites can be restored. This section therefore compares the selected areas for restoration with The Land Cover Map of Great Britain (1990) © NERC to describe the land use in the area. The map had a resolution of 25 m and was based on the Landsat Thematic Mapper data using supervised maximum likelihood classifications (Fuller *et al.*, 1994).

Figure 9.12 presents the land cover for the regions classified as potentially suitable restoration sites. Land use varied from grazed grassland to coniferous woodland, as can be observed from the legend of Figure 9.12. For the selection of suitable Culm grassland restoration sites, the current land cover has to be taken into account for planning purposes. For example, it might not be desirable to remove woodland in order to create a wet grassland, if e.g. this woodland is already of a high quality or has the potential to develop into a diverse woodland community. Further, some land use types are inherently more revertible than others. Also the existing human structures such as villages, roads, railways and reservoirs might have been indicated as suitable, but obviously it is unlikely that these will be selected for wetland restoration purposes. A clear example of this is the suitability of Roadford reservoir, which is indicated as unclassified in Figure 9.12. This site would clearly be unsuitable for Culm grassland development.

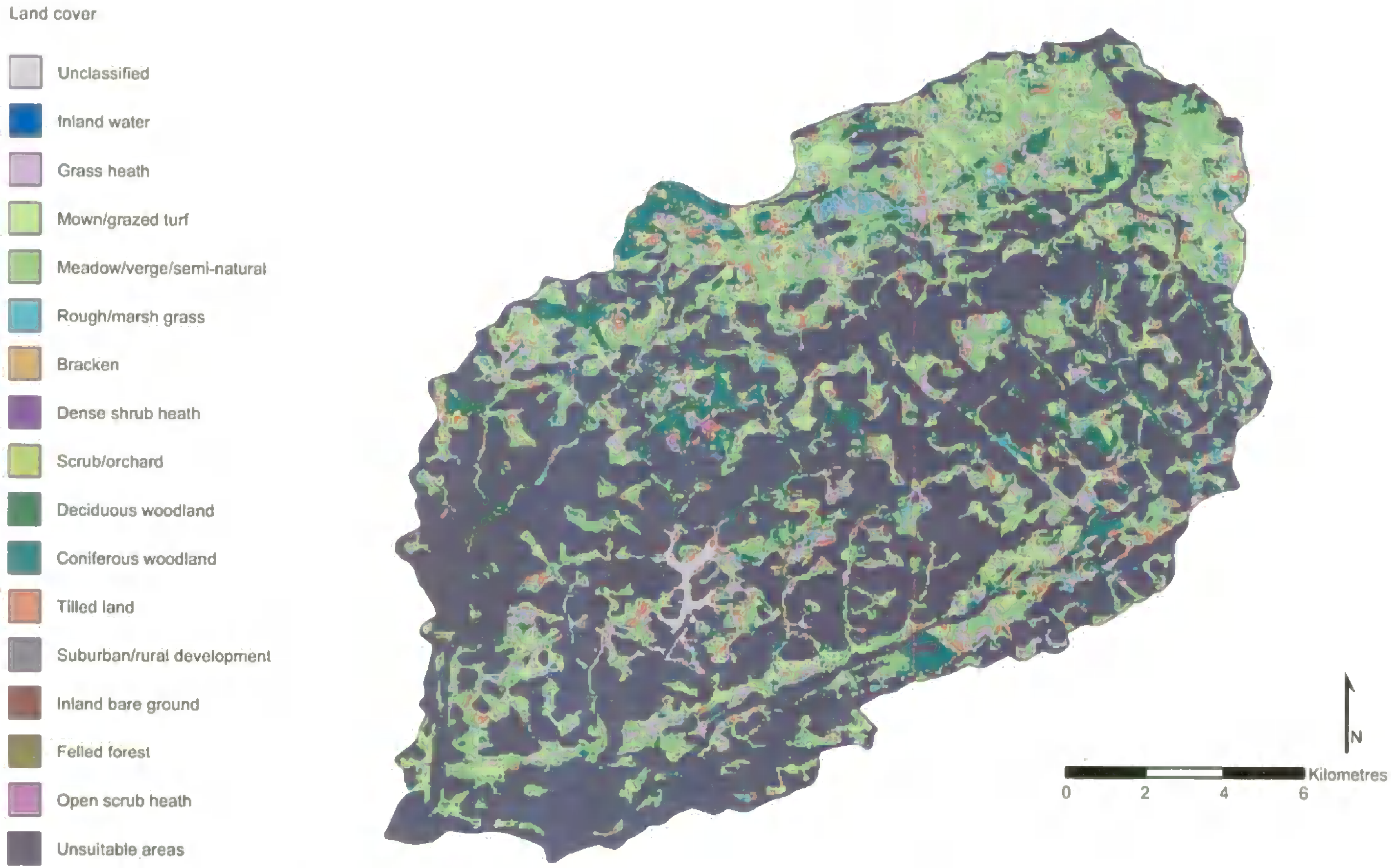


Figure 9.12 Current land cover in the suitable culm grassland restoration sites. The Land Cover Map of Great Britain (1990) COPYRIGHT Natural Environment Research Council, Acknowledgements CEH Monks Wood (formerly ITE Monks Wood)

However, based on the HOST classification and the topographic index the site had the right characteristics. Details of land use planning for the CNA were not studied in this thesis, because it was not included in the aim of the project and because of time constraints. However, land use information could form an important aspect of the DSS, if it would be used for 'real-world' planning purposes. Therefore, an indication of the area of the land use categories is given in Table 9.2. If a tool like this would be used by local and regional conservation agencies the land use information should be added to the system as an additional information layer in the GIS.

Land cover	Area (ha)
Unclassified	281.5
Inland water	0.5
Grass heath	1794.3
Mown/grazed turf	2035.8
Meadow/verge/ semi-natural	5907
Rough/marsh grass	521
Bracken	72.8
Dense shrub heath	12.3
Scrub/orchard	63.3
Deciduous woodland	1596
Coniferous woodland	739
Tilled land	820.3
Suburban/rural development	1
Inland bare ground	1
Felled forest	34.5
Open shrub heath	103.3

Table 9.2 Land cover information in the Wolf, Thrushel, Carey and North Lew catchments obtained from 'The Land Cover Map of Great Britain (1990)© NERC

9.4.4 Historical data

The validity of the methodology presented in this thesis was verified further by comparing the selected sites for Culm grassland restoration with the location of marshland and rough pasture at the beginning of the twentieth century. After the Second World War, agricultural improvement and drainage of land increased substantially to ensure enough land was suitable for food production (Cook, 1999). Historical maps from before this time period should, therefore, give a good impression of the situation before the main loss of Culm grassland occurred.

Figure 9.13 Suitable Culm grassland restoration areas in relation to the 6": 1 mile historical topographic map (OS, 1907). Suitability: 1 = low and 5 = high.

A section of the historical topographical map around Holsworthy of the year 1907 (O.S., 1907) was taken as an example to compare former marshland with the predicted suitable restoration sites. The result is presented in Figure 9.13. The information could only be compared visually, because the historical maps were not available as spatial GIS data and needed to be scanned from paper to form a background layer to the selected suitable restoration sites. From Figure 9.13, it appears that the suitable restoration areas largely overlap with marshes and rough pastures. However, some former wet grasslands were not selected as suitable sites, which indicated that the designed method did not necessarily select all wetland locations. These wetlands might have been of a different nature than Culm grassland or the selection method presented in this study might not have been precise enough to select all 'wet' areas. Also, some other, 'dry' areas were selected as potential restoration sites, but were not indicated as wet grasslands and marshes on the historical maps. This could have been due to the fact that also before 1907, drainage of the land had taken place, although not at such a large scale as later in the twentieth century (Cook and Williamson, 1999). Less accurate mapping techniques during the beginning of the last century should also be considered when judging the quality of the overlap.

Further, it is not known whether the rough pastures and marshes in general indicated on the historical maps were of the Culm grassland type. Therefore, these maps can only be used as an indication of the former extent of wetlands in the area and not as an absolute measurement of the area of Culm grassland. The use of historical maps is thus of limited value, but does provide some insight into the functioning of the system.

9.4.5 Field verification

Field verification of the selected sites was needed to further test the functioning of the presented DSS. However, due to the extensive restrictions because of the Foot and Mouth disease during the first half of the year 2001, none of the fields could be visited and access to the study area was limited to paved roads. Therefore, photographs could only be taken from a distance to give an impression of the potential restoration sites. Ten locations (Figure 9.2) were photographed and are presented in Plate 9.1.

Plate 9.1 Field verification of selected restoration sites. Numbers correspond to locations on Figure 9.2. Suitable sites: locations 1, 2, 4, 5 and 6. Unsuitable site: location 3.

7

8

9

10

Plate 9.1 (cont.) Field verification of selected restoration sites. Numbers correspond to locations on Figure 9.2. Suitable sites: locations 7, 8, 9 and 10.

The first two photo locations were positioned on the edge of the selected areas and the third just outside the selected zone (Figure 9.2). All three sites seemed fairly 'dry' judged from the vegetation: beech woodland (location 1) and well drained pasture (locations 2 and 3). Location 4 was situated on a spruce plantation, which is typical for much of the marginal agricultural land. Often, poorly drained fields were used for forestry to ensure some income out of otherwise unproductive land (Brandon, 1987; Harrod, 1987). Locations 5, 6, 7 and 9 were small stretches of land adjacent to small streams that did not appear to be used very intensively. Location 8 and 10 were both at the bottom ends of larger (semi-) improved fields. Generally, the selected restoration sites were located on damp to wet locations and therefore those positions would be worth further investigation in terms of possible Culm grassland creation.

9.5 Discussion and synthesis

9.5.1 Introduction

Successful restoration and creation of plant communities requires careful planning (Box, 1996; Gilbert and Anderson, 1998). The Decision Support System (DSS) presented in this chapter was designed to help in the selection of suitable Culm grassland restoration sites and to indicate the most important environmental gradients to which the vegetation responded. This tool is aimed at conservation agencies and authorities concerned with regional planning, because it could help to prioritise and provide target areas for restoration of valuable wet grassland ecosystems. Currently, only a small amount of the natural and semi-natural plant communities is protected in e.g. National Nature Reserves or Sites of Special Scientific Interest (SSSI) (Kent, 1987; 1989; English Nature, 2000). This method could help to plan the creation of other valuable wildlife sites and to link existing ones. However, the system presented covered only a small part of the planning process of nature conservation and regional nature management. Clearly, many more issues have to be taken into account before a restoration strategy is complete. The system presented in this thesis was designed to aid with the site selection process, one of the first steps in the restoration planning, and to estimate the possible vegetation developments based on environmental gradients and management practices.

9.5.2 The Decision Support System

The major advantages of the new approach were that the soil and topographic data used for the set up of the DSS were readily available and could be used within a GIS environment. Also it provided a clear picture on a regional scale, which enables the decision maker to look at a potential site in its wider perspective. However, the value of the DSS should not be overestimated. Since the tool was developed on a regional scale, its use on the local scale is limited. The information derived from the basic maps contained a certain amount of uncertainty due to the inevitable generalisation associated with regional scaled maps. Further, the DSS was developed based only on soil and topographical characteristics and no information on the current land use was included. The land cover information could, however, be added easily by including a separate data layer in the GIS and by excluding all areas that could not be used for Culm grassland restoration purposes. In the same way, topographic information could be added. Field verification of the suitability of the selected sites will be necessary to ensure that field conditions are right for restoration purposes. When using the system, it is important to bear in mind that the approach aimed to narrow down the potential restoration locations and not to give a final selection. The development of Culm grassland depends on the management plans for the whole region. The maintenance and improvement of the biodiversity is an important aspect of nature conservation regionally (Devon Biodiversity Partnership, 1998; Cornwall Biodiversity Initiative, 1997; 1998), nationally and internationally (EU, 2000). To achieve a rural area with a high biodiversity, it is important to maintain and enhance the (semi-) natural mosaic of different plant communities. Not only the diversity within the community is of great importance but also the variety of plant communities themselves.

Natural environmental gradients are related to climate, topography hydrology and soils. This study revealed grazing, pH and soil moisture as the most important characteristics, in determining species variability within existing Culm grassland sites. However, other studies (Hayati and Proctor, 1990; Van Oorschot 1994; Goodwin *et al.*, 1998) have shown the importance of factors such as phosphorus and nitrogen (Chapter 2) and these should not be ignored in the restoration process and are important factors when looking at the conversion of improved pastures to semi-natural habitats. Not all conditions can be easily adjusted and this is also not always desirable, as heterogeneous environmental conditions could support a higher biodiversity. Existing ecological factors have to be taken into account in the restoration process (Box, 1996) and the emphasis should be on changing conditions within their natural range or reverting conditions to their original state to encourage the desired vegetation community to develop and not on altering these to a 'new' desirable state. Management practices e.g. could be used to alter vegetation composition where needed. Soil acidity and moisture were identified as important parameters in determining the vegetation composition. However, in many cases these parameters reflect the natural situation and cannot or should not be changed. On the other hand, soil moisture conditions are likely to be greatly affected by drainage of agricultural land in other areas of the catchment. Maps indicating where field drainage has taken place in the past would have provided a very useful addition to the DSS. Unfortunately, maps for the area have not been retained (Sonia Thurley - Environment Agency, pers. comm.).

9.5.3 Methodology

The methods used to derive the topographical and hydrological characteristics of Culm grassland in general also have to be discussed in more detail. Characteristics of preferential locations were determined by comparison of the parameter distribution of Culm grassland sites with the total CNA. χ^2 tests were applied to establish if the differences in distributions were significantly different. However, because the tests were used on statistical populations with a very large number of cells, only small differences were needed for the outcome to be significant. Due to the nature of the data no other statistical testing method could be used, but visual examination of maps and charts confirmed that the sites were related to specific topographic conditions.

Another drawback of the method was that all the relationships between Culm grassland sites and the topographical and environmental parameters were based on the existing sites. These sites were probably still present, because they were the least interesting for agricultural improvement. Therefore, the grasslands could possibly also develop on other locations, which were not included in the research. In other words the use of the 'leftover' sites to determine the conditions needed for Culm grassland, might mean that other suitable locations could be missed. This problem was partially solved by comparing the results to historical maps of the beginning of the twentieth century, assuming that these give a good impression of the former extend of wet meadows and marshes. Although a reasonable overlap was achieved, photocopying and scanning of the historical maps meant that an location error was introduced. On the other hand, research into the economic consequences of fen restoration in eastern England conducted by Morris *et al.* (2000) indicated that wetland restoration is most likely to occur on less productive land. It is therefore unlikely that highly productive agricultural land will be taken out of production for nature conservation purposes and it could therefore be concluded that the presented method indicated the areas most likely to be used for wet grassland restoration. However, recent problems with BSE and the Foot and Mouth disease in the agricultural industry could cause large numbers of farmers to go out of business (The Observer, 2001, The Guardian, 2001), leaving also highly productive fields for other land use.

Further, the results presented in Chapter 8 showed that the *Erica tetralix – Sphagnum compactum* wet heath NVC community (M16) was largely missing from the data. The reason for this gap in the data is not clear, but possibly this plant community was under-represented in the original Devon Wildlife Trust survey, due to only little presence of the M16 community in the Culm Natural Area or because of missing out these sites due to their deviant heath-like characteristics. As a consequence, the environmental gradients described in Figure 9.8 might not have covered Culm grasslands of the M16 type and this must be kept in mind when applying the findings. Also no geological information was included in the system. However, geological formations could greatly affect the direction and speed of groundwater flow and also determine where springs can be found. Springs or flush lines in the area are often found on the Bude formation (Chapter 3), where water that percolates through the upslope soils suddenly reaches an impermeable layer and reaches the surface (Harrod, 1987). Some Culm grassland sites exist because they are fed by spring water and because the location of springs has not been taken into account in the selection procedure, these sites might not be included. Vegetation of NVC M25 is often associated with these areas (Rodwell *et al.*,1991). On the other hand, the good agreement of the sites with the topographic index and the soil hydrology suggested that at the regional and catchment scale topography and soils gave sufficient information on wetland occurrence.

The soil parameters measured in the field to describe the environmental gradients of the different Culm grassland communities provided a momentary picture of the situation, because samples were only taken at one time during the year. It did not really cause a problem, because comparison between the sites was the major purpose and variation during the sampling period was not expected to be very high. However, it is important to realise this when using information about the environmental gradients presented.

9.5.4 Scale and fragmentation

The scale of the maps used in this thesis was mainly suitable for regional planning purposes. For planning on the scale of local conservation areas or individual farms, more detailed information on the local conditions is needed (Cook and Norman, 1996). Therefore, although the selection of suitable sites could help to draw up a regional management plan, for more detailed work, field information needs to be gathered. Some other aspects of scale also have to be considered here. The amount of detail that can be presented on a map is limited. The minimum area on the 1:250,000 soil map is 0.5 km^2 (Findlay *et al.*, 1984), corresponding to approximately 3 by 3 mm on the map. A similar size unit on a 1:50,000 scale map, like the Wolf, Thrushel, Carey and North Lew soil map, will thus be approximately 2 ha (20,000 m^2) and 0,5 ha (5000m^2) on a 1:25,000 map, like the Holsworthy soil map. A minimum of four soil samples per cm^2 of the final map, corresponding to 25 ha on a 1:50,000 map is mentioned by Buringh *et al.* (1962, in Stein *et al.* 1994)). Therefore, local conditions could often provide a suitable Culm grassland environment but would not be selected using the decision rules. Many existing Culm sites were smaller than the minimum size of the soil units shown on the map. For example, local areas with peat soils were found in the field, but were not represented on the soil map because of their limited extend. However, every map is a generalisation of the real world and thus a certain amount of uncertainty is inevitable.

The question where to restore Culm grassland sites should also be put in perspective of the island biogeography theory of MacArthur and Wilson (1967) and metapopulation ecological theory, as described by Hanski (1999), because of the large degree of fragmentation of the remaining sites. The island biogeography theory is based on the equilibrium between species immigration and extinction on oceanic islands (Section

2.2.3). The immigration rate depends on the distance to other islands and the mainland and the extinction rate depends on the size of the island (Kent, 1989; Begon *et al.*, 1990). The same theory has been applied in nature conservation to study fragmented plant communities. It could be expected that the larger the size of a patch or fragment, the higher the number of species (Begon *et al.*, 1990; Lomolino, 2000; 2001). The theory of metapopulation ecology (Hanski, 1999) is based on similar principles, but applies them to individual species instead of plant communities and does not assume an unlimited source of species from the 'mainland' (Section 2.2.3)

Many researchers have studied these principles for different plant communities (e.g. Benayas *et al.*, 1999; Haig *et al.*, 2000). Bogaert, *et al.* (2001) discussed a method to use island biogeographical principles to quantify the disturbance on isolated habitats. However, due to complicated ecological mechanisms and response of species to climatic conditions and human impact, that confuse the theory, little evidence has been found that the island biogeography theory was valid. In this thesis, the correlation between size and species richness was studied, but only a weak correlation was found mainly because of the poor consistency of the data. No conclusions in terms of the validity of the species number – area relationship could be drawn from the analysis. However, Kent (1987; 1988) argues, that despite the lack of empirical evidence to support the theory, its basic principles remain important for nature conservation.

The restoration and creation of Culm grassland sites should be considered in relation to the location of the existing sites. To increase the species diversity of the sites, the size of a site is important and expanding existing sites could therefore be useful to maintain species diversity. The creation of wet grasslands zones to connect existing sites is important to ensure migration from species from one are into the other, therefore increasing the diversity of the sites. Also for insects, birds and animals that rely on these wet grasslands, it is important to be able to migrate from one area into the other. Due to the importance of size and connectivity with similar plant communities for the survival many ecological communities, it could thus be questioned if restoration efforts should concentrate on small isolated sites. The expansion and connection of existing sites would probably be a better use of resources. The problem of small areas with suitable soil conditions, which were not presented on the soil map, could therefore be irrelevant up to a certain scale. Maps on a 1:50,000 scale were suitable for the purpose, as they provided enough general information to be used for planning purposes, but also supplied sufficient detailed information.

9.5.5 Wetland functions

Many reasons could be proposed for conserving the natural and semi natural habitats of the world. Green (1996), for example, listed ethical, aesthetic, cultural and scientific values, material benefits and the maintenance of the ecological balance. Like many of the grasslands in the temperate zone, Culm grassland is not climax vegetation and without human management, it would fast develop into shrub- or woodland. Restoration of wet grasslands is primarily approached from the perspective of biodiversity and preservation of the appearance of the landscape. However, the wetlands could probably also function for water storage and nutrient and sediment traps, but little research has been conducted to investigate these possible functions of Culm grassland. Only Hogan (*unpublished*) has investigated the functioning of wetlands in general, including Culm grassland, in southwest England. For the environmental functions, the maintenance of wet grassland vegetation as such is not crucial and probably the wet woodlands that would develop after agricultural abandonment would function in similar ways.

This chapter has combined Part 2 and 3 of the study into a decision making tool. It provided an example of how the selection of suitable Culm grassland restoration sites could be performed on a regional scale. Also plant communities were presented along environmental and management gradients. However, many other factors influence the planning process and should be taken into account. The management tool should thus be considered as a building block in the complex procedure of regional nature management and not as the whole planning system or the only way forward. Furthermore, the study has not included the various possible restoration techniques and for each selected site such options should be carefully considered. An overview of the most common techniques has been presented and discussed in Section 2.3.5. The final chapter concludes and summarises the research and makes some recommendations for future work.

Chapter 10

Conclusions and recommendations

10.1 Introduction

The research has investigated various aspects of Culm grassland ecology and management. The project commenced with the description of Culm grassland in its wider context, including a literature review on research conducted on similar plant communities and a description of the most important physical and chemical parameters for wetland functioning. The work continued with a GIS investigation on the topographical and hydrological aspects of the Culm grassland environment and this was followed by a detailed field study on the vegetation and plant community composition and the determination of the most important environmental gradients determining the variation in the species composition. Results were integrated in a management tool, designed to provide a clear picture of potentially suitable Culm grassland restoration locations at a regional scale and to indicate some of the vegetation changes that could occur under various environmental and management conditions. This tool was then validated and tested. This last chapter of the thesis will draw conclusions of this study (Section 10.2) and will give some recommendations for future work (Section 10.3).

10.2 Conclusions

A number of conclusions are drawn from the research presented in this thesis. The first set of conclusions is related to the association between the location of Culm grassland and landscape topography and soil hydrology, described in Part 2 of the thesis. The second set of the conclusions is related to the work presented in Part 3, describing the Culm grassland plant communities and which soil and environmental characteristics are important to species composition. The third set of conclusions is drawn from the Decision Support System, described and tested in Chapter 9.

Landscape topography and soil hydrology:

1. Topographical parameters largely determined the position of the remaining Culm grassland sites. Generally, GIS investigations showed that the wet grasslands were related to level or gently sloping grounds, topographic 'hollows' represented by concave or straight slopes and areas with a large upslope contributing area. Comparisons with the $\ln(a/\tan\beta)$ showed that sites were mainly found on landscape

positions with a topographic index higher than 8, corresponding to the 'wetter' locations, if only landscape topography is taken into account.

2. The location of Culm grassland sites was associated with poorly drained soils. This was examined by applying the Hydrology Of Soil Types (HOST) classification to a 1:50,000 soil map in part of the area. Sites were mainly found on soils of HOST class 9 or 24. Soil hydrology was considered the most important discriminating factor in determining the suitability of a site for Culm grassland location.

3. The findings of the GIS study showed that readily available, regional scale soil and topographic maps could be used to explain 'natural' Culm grassland location, which indicates that these maps provide a useful source of information for determining the location of sites where Culm grassland could potentially be restored.

4. Quantification of the terms 'wet' and 'dry' on a catchment scale was done by modelling the number of days of soil saturation for a one year period (Oct. 1995 – Oct. 1996). However, the results showed an underestimation of the number of days of saturation in the Culm grassland sites, because only topographic parameters were taken into account and no soil conditions were considered. It was decided not to develop the modelling exercise any further, because it was expected that little improvements would be made and results would only be valid for the modelled season and would therefore not be generally applicable.

Culm grassland ecology:

5. Vegetation was sampled at 97 locations and seven plant communities were distinguished with the aid of TWINSPAN analysis. Group A mainly contained sedge, grass and herbaceous species, group B and C were dominated by grasses and rushes, group D was characterised by a combination of herbaceous species and grasses, group E was dominated by various herbaceous species and group F and G consisted mainly of rushes and herbs. Classification of the samples into NVC communities resulted in most samples belonging to M23a, M24c, M25c, M27c, which are part of the major Culm grassland communities. However, none of the samples resembled M16b, the fifth typical Culm community, closely. The communities are, however, distributed as a continuum in relation to the environmental gradients.

6. Both physical and chemical soil parameters were determined at every sampling location. In short, vegetation group B was associated with the driest soil and D with the

wettest soils, which also contained the highest organic matter content. Groups A and C occurred on the most acidic soils and group G was associated with the highest available phosphorus concentrations.

7. Although grazing pressure was estimated visually on a subjective scale, ordination analysis showed that this parameter determined most of the species variation. Other important environmental gradients were soil pH and soil moisture content. These gradients could be used in predicting the species composition under various environmental conditions. However, other soil characteristics, like nutrient levels, are also of major importance to the potential of wet grassland restoration.

8. Due to the experimental design, only species compositions within Culm grassland sites were studied and no comparisons were made with the plant communities of sites that could potentially be restored. This could be the most important reason why results do not indicate nutrient levels to be important.

Decision Support System:

9. The results discussed above were integrated into a decision-making tool to indicate suitable Culm grassland restoration sites, based on the 'natural' conditions present at the site. Environmental gradients were used to predict species composition. The goodness of fit was tested by applying the decision rules to an independent area and it was found that 88% of the Culm grassland sites were located on sites that were indicated as suitable.

10. Further verification of the DSS was carried out by comparing the potentially suitable restoration sites to land cover data, historical data and field photographs. Land cover data indicated that many of the selected areas were under types of land use that could not be easily restored to wet grasslands, which shows that current land use needs to be included in the decision making process. Comparisons with historical data and locations visited in the field showed a reasonably close fit.

11. The validity of the second part of the DSS still needs testing. Controlled experiments to determine species response to changes in grazing regime, soil pH and soil moisture have to be carried out to be certain of the changes that can be expected in the field when changes are made to restore the site.

10.3 Recommendations for future work

Analysis of the topographical and soil conditions, which determine the location and species composition of Culm grassland was undertaken in this study. The results were incorporated into a decision-making tool to integrate the findings into the nature restoration planning process. However, further experiments on vegetation responses and habitat restoration have to be carried out to be able to predict the outcome of the restoration activities accurately. The major drawback to the study presented in this thesis, was that research focused completely on the existing Culm grassland sites and on which factors were responsible for the species composition within those sites. Due to this approach potential sites might have been missed. Future work should also include sites that were selected as potentially suitable and compare the species on those sites to the species found in existing Culm sites. This could give a better indication of which techniques need to be applied if the site is to be restored. The outcome of the first part of the DSS could thus be used to select potential locations, and vegetation and soil sampling according to the methods presented in Part 3 could be applied to investigate differences between Culm and non-Culm sites. The reason that this approach was not adopted in this study was that the research on topographical and soil hydrological parameters influencing wet grassland location was carried out at the same time as the detailed field study was carried out and therefore no information on potentially suitable locations were available at that time. A follow-up study focusing on these aspects could perhaps provide better insights.

Since grazing pressure was indicated as the most important factor in determining the species composition of the Culm sites, the effects of grazing and field management need to be studied in further detail. In this thesis, only a subjective estimation of the grazing pressure was made, but no information was gathered on when the cattle was out in the field, for how long, what the field conditions were at that time, whether any mowing had taken place as well. An important aspect of grazing could be the trampling of the soil, enabling species present in the seed bank to germinate. Research into the impact of grazing could help to design a management system aimed at increasing the species richness of the site and supporting the conditions for rare species to become established.

For the re-establishment of species in a field the presence of the species in the seed bank or in a nearby field is important. To obtain crucial insights into the potential of an improved site to be restored, a study of the condition of the seed bank is necessary. Studies should focus on which of the original Culm grassland species still exists in the seed bank of an improved field and how long the seeds persist. In other words information on how long after the Culm grassland species have disappeared from the sites are the seeds still present in the seed bank. Other research could focus on the distance that seeds can be dispersed from the surrounding area to the field that is to be restored. This provides insight in whether a selected site has the potential of restoration based on the presence of species in the surrounding area.

In addition, research should not only focus on species richness and diversity, but should also investigate the functional aspects of these wetlands. Information is needed on what the impact of the wetlands is on e.g. flood prevention and river quality and whether the restoration of the sites can be strategically planned to ensure that restoration serves a multiple purpose. Not only would this be a more efficient use of resources, but it would probably also have wider support from different parts of the community.

Meeting the targets set in (inter)national and regional Biodiversity Action Plans requires careful planning of land use and the use of resources. Habitat restoration and creation measures are too costly to adopt a random trial and error strategy. Before restoration activities can be undertaken, the aims of the work need to be clearly defined and the possible outcomes need to be considered. Also, the restoration of a certain vegetation community or wildlife habitat is not an isolated process targeting one isolated site with conditions that can be manipulated indefinitely, but a practice in which the surrounding land use and natural processes need to be taken into account. Natural conditions need to be considered and the restoration activities should focus on creating a habitat that would naturally develop on the target location or one that could be maintained by the traditional management practices that were responsible for creating the target plant communities in the first place. Furthermore, the presence and location of similar plant communities or wildlife populations is of crucial importance to the success of the restoration measures and should therefore be taken into account in the planning process. Tools, like the one presented in this thesis, provide these insights and give information on the 'best' ways of connecting the existing sites according to the landscape topography and soil characteristics and which vegetation patterns to expect under various environmental conditions. The tool presented here is only an example of how to approach planning of wetland restoration activities. However, the methodology itself is not restricted to wet grasslands and could be applied to any (semi-) natural vegetation community, especially, when considering that often there are other habitats in the same region that need to be restored. Adopting the strategy presented in this thesis helps to plan the use of land at a regional scale.

Much of the land used for the nature conservation and restoration is owned by farmers. To ensure the success of these activities, close co-operation with the farming community is needed. Encouraging farmers to take part in agri-environmental schemes should be high priority, especially for them to adopt more environmentally friendly agricultural practices in turn for financial compensation. However, the current crisis in the farming industry caused by large scale outbreaks of animal diseases, like BSE and Foot and Mouth, could result in large areas of farmland being abandoned and neglect of these sites could pose a serious threat to semi-natural plant communities. Management of the land by farmers is crucial to the appearance of the landscape and support is needed for farmers to enable them to continue their profession. However, this should be done under the encouragement of environmentally friendly practice, to maintain and preferably extend the natural environment. Some of the land taken out of intensive production could potentially be used for restoration of Culm grassland if managed appropriately.

In the future, the various stakeholders including landowners, tenants and community groups must recognise the need to achieve environmentally responsible land management and conservation targets for Culm grassland. Particular attention must be paid firstly to maintenance and improvement of present areas identified as Culm grassland and secondly at establishing perhaps a more coherent, less fragmented set of existing and restored sites. Such is the fragmented nature of the present Culm grassland sites, that continuing pressure on this habitat could totally destroy the present appearance of the Culm landscape. The research discussed in this thesis has described a framework for indicating areas with the most potential to enhance the remaining vestiges of Culm grassland in a former biologically diverse landscape.

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Appendix A: Plant community groups - survey 2000

Species frequencies: I = 1-20%, II = 21-40%, III = 41-60%, IV = 61-80% and V = 81-100%

Species abundance between brackets: 1 = rare, 2 = occasional, 3 = frequent, 4 = abundant, 5 = dominant.

A

Carex panicea	V(2-4)	*Anagallis tenella*	I(2)
Molinia caerulea	V(2-5)	*Calluna vulgaris*	I(2)
Potentilla erecta	V(1-3)	*Carex echinata*	I(2)
Agrostis canina sens.str.	IV(2-4)	*Carex flacca*	I(1-4)
Dactylorhiza maculata	IV(1-2)	*Carex nigra*	I(2)
Anthoxanthum odoratum	III(2-4)	*Carex ovalis*	I(2)
Carex pulicaris	III(1-3)	*Carum verticillatum*	I(3)
Carex viridula ssp. oedocarpa	III(1-3)	*Cynosurus cristatus*	I(3)
Cirsium dissectum	III(2-4)	*Eriophorum angustifolium*	I(2)
Cirsium palustre	III(2-3)	*Festuca ovina agg.*	I(3-4)
Festuca rubra sens.str.	III(3-4)	*Galium palustre*	I(3)
Holcus lanatus	III(1-3)	*Hypochaeris radicata*	I(3)
Juncus acutiflorus	III(2-5)	*Juncus bufonius agg.*	I(2)
Lotus pedunculatus	III(1-3)	*Lathyrus linifolius*	I(1)
Sphagnum spp.	III(1-3)	*Lotus corniculatus*	I(1)
Succisa pratensis	III(2-3)	*Nardus stricta*	I(3-4)
Calliergon sp.	III(1-2)	*Plantago lanceolata*	I(2)
Pseudoscleropodium purum	III(1-3)	*Polygala serpyllifolia*	I(3)
Rhytidiadelphus squarrosus	III(1-3)	*Potamogeton polygonifolius*	I(4)
Thuidium tamariscinum	III(1-3)	*Prunella vulgaris*	I(2)
Danthonia decumbens	II(2)	*Rumex acetosa*	I(2)
Erica tetralix	II(1-3)	*Trifolium sp.*	I(3)
Juncus bulbosus	II(2-3)	*Aulacomnium palustre*	I(3)
Juncus conglomeratus	II(1-3)	*Campylopus introfexus*	I(2)
Juncus effusus	II(2-3)	*Eurhynchium praelongum*	I(1-2)
Luzula multiflora	II(1-2)	*Leucobryum sp.*	I(2)
Pedicularis sylvatica	II(1-2)	*Plagiomnium undulatum*	I(2)
Ranunculus flammula	II(2)	*Polytrichum commune*	I(3)
Salix repens	II(1-2)	*Rhizomnium punctatum*	I(1)
Scutellaria minor	II(2)		

B

Anthoxanthum odoratum	V(2-4)	*Carex nigra*	I(2)
Holcus lanatus	V(2-4)	*Carex ovalis*	I(1-3)
Juncus acutiflorus	V(2-4)	*Carex paniculata*	I(4)
Lotus pedunculatus	IV(2-4)	*Carex pulicaris*	I(2-3)
Calliergon sp.	IV(1-3)	*Carum verticillatum*	I(2)
Agrostis canina sens.str.	III(2-4)	*Cerastium fontanum*	I(1)
Carex flacca	III(1-3)	*Dactylis glomerata*	I(1-3)
Carex panicea	III(2-4)	*Dactylorhiza praetermissa*	I(1-2)
Cirsium palustre	III(1-2)	*Danthonia decumbens*	I(1-2)
Cynosurus cristatus	III(2-4)	*Epilobium palustre*	I(2)
Juncus conglomeratus	III(1-4)	*Filipendula ulmaria*	I(3-4)
Potentilla erecta	III(1-3)	*Galium aparine*	I(3)
Ranunculus flammula	III(1-3)	*Heracleum sphondylium*	I(2)
Achillea ptarmica	II(2-3)	*Hydrocotyle vulgaris*	I(2)
Carex viridula ssp. oedocarpa	II(1-3)	*Hypochaeris radicata*	I(2)
Centaurea nigra	II(3-4)	*Isolepis setacea*	I(1)
Cirsium dissectum	II(1-3)	*Juncus bulbosus*	I(2)
Festuca rubra sens.str.	II(2-4)	*Menyanthes trifoliata*	I(1-4)
Galium palustre	II(1-3)	*Myosotis secunda*	I(1)
Galium uliginosum	II(2-3)	*Nardus stricta*	I(1)
Juncus effusus	II(1-3)	*Potentilla anserina*	I(1-3)
Luzula multiflora	II(2)	*Potentilla reptans*	I(2)
Molinia caerulea	II(2-4)	*Prunella vulgaris*	I(1-3)
Plantago lanceolata	II(2-4)	*Quercus robur*	I(1)
Poa trivialis	II(1-3)	*Rumex acetosa*	I(2)
Ranunculus acris	II(1-2)	*Salix repens*	I(1)
Ranunculus repens	II(1-4)	*Senecio aquaticus*	I(2-3)
Eurhynchium praelongum	II(2-3)	*Serratula tinctoria*	I(1)
Pseudoscleropodium purum	II(2-3)	*Stachys officinalis*	I(2)
Rhytidiadelphus squarrosus	II(2-3)	*Stellaria graminea*	I(2)
Achillea millefolium	I(2)	*Stellaria uliginosa*	I(2)
Agrostis capillaris	I(2-4)	*Succisa pratensis*	I(1-2)
Agrostis stolonifera	I(2)	*Valeriana officinalis*	I(2-3)
Ajuga reptans	I(3)	*Veronica chamaedrys*	I(2)
Anagallis tenella	I(2-3)	*Brachythecium sp.*	I(1)
Angelica sylvestris	I(1-3)	*Fissidens taxifolius*	I(3)
Briza media	I(3)	*Thuidium tamariscinum*	I(2-3)
Carex echinata	I(2-3)	*Thuidium tamariscinum*	I(2-3)

C

Agrostis canina sens.str.	V(2-4)	*Carex pilulifera*	I(2)
Juncus acutiflorus	V(2-5)	*Carex viridula ssp. Oedocarpa*	I(2)
Molinia caerulea	V(2-5)	*Cirsium dissectum*	I(2)
Potentilla erecta	V(1-3)	*Dactylorhiza fuchsii*	I(2)
Anthoxanthum odoratum	IV(2-4)	*Dactylorhiza maculata*	I(1-2)
Holcus lanatus	IV(2-4)	*Deschampsia caespitosa*	I(4)
Lotus pedunculatus	IV(2-4)	*Digitalis purpurea*	I(1)
Cirsium palustre	III(1-2)	*Epilobium palustre*	I(1)
Galium palustre	III(1-3)	*Festuca ovina agg.*	I(4)
Luzula multiflora	III(1-3)	*Festuca rubra sens.str.*	I(1-2)
Rumex acetosa	III(2-3)	*Galeopsis tetrahit agg.*	I(2)
Succisa pratensis	III(1-4)	*Glyceria declinata*	I(2)
Viola palustris	III(1-3)	*Holcus mollis*	I(2-3)
Eurhynchium praelongum	III(1-3)	*Hydrocotyle vulgaris*	I(2)
Pseudoscleropodium purum	III(1-2)	*Hypericum tetrapterum*	I(3)
Rhytidiadelphus squarrosus	III(1-2)	*Juncus bulbosus*	I(2-4)
Angelica sylvestris	II(1-2)	*Juncus inflexus*	I(2)
Carex panicea	II(1-3)	*Lathyrus linifolius*	I(2)
Juncus conglomeratus	II(2-3)	*Lathyrus pratensis*	I(1-2)
Juncus effusus	II(1-4)	*Lotus corniculatus*	I(1-2)
Sphagnum spp.	II(1-3)	*Lychnis flos-cuculi*	I(3)
Calliergon sp.	II(1-3)	*Mentha aquatica*	I(2)
Thuidium tamariscinum	II(1-2)	*Myosotis secunda*	I(2)
Achillea ptarmica	I(1)	*Ranunculus acris*	I(2)
Agrostis stolonifera	I(2)	*Ranunculus flammula*	I(2)
Anagallis tenella	I(1)	*Rubus fruticosus agg.*	I(2)
Betula pubescens	I(1)	*Scutellaria minor*	I(2)
Callitriche stagnalis sens.str.	I(2)	*Serratula tinctoria*	I(1)
Calluna vulgaris	I(1)	*Valeriana officinalis*	I(1-2)
Cardamine pratensis	I(1)	*Aulacomnium palustre*	I(2)
Carex echinata	I(2-3)	*Brachythecium sp.*	I(1)
Carex hostiana	I(2)	*Calypogeia fissa*	I(2)
Carex nigra	I(1-2)	*Plagiomnium undulatum*	I(2)

D

Angelica sylvestris	V(1-3)	*Blechnum spicant*	I(1)
Molinia caerulea	V(5)	*Calluna vulgaris*	I(2)
Potentilla erecta	V(1-3)	*Carex echinata*	I(3)
Cirsium palustre	IV(1-2)	*Carex panicea*	I(1)
Juncus effusus	IV(2-3)	*Carex sylvatica*	I(2)
Valeriana officinalis	IV(2-3)	*Carex viridula ssp. oedocarpa*	I(2)
Agrostis canina sens.str.	III(2)	*Cirsium dissectum*	I(1)
Galium palustre	III(1-2)	*Eriophorum angustifolium*	I(1)
Juncus conglomeratus	III(2-3)	*Galeopsis tetrahit agg.*	I(1)
Lotus pedunculatus	III(1-3)	*Hypericum elodes*	I(1)
Sphagnum spp.	III(1-3)	*Juncus bulbosus*	I(2)
Eurhynchium praelongum	III(1)	*Lychnis flos-cuculi*	I(1)
Dryopteris carthusiana	II(1)	*Pinguicula lusitanica*	I(1)
Juncus acutiflorus	II(3-4)	*Potamogeton polygonifolius*	I(2)
Luzula multiflora	II(2-3)	*Ranunculus repens*	I(1)
Ranunculus flammula	II(1-2)	*Serratula tinctoria*	I(1)
Rumex acetosa	II(2)	*Succisa pratensis*	I(1)
Brachythecium sp.	II(1-2)	*Viola palustris*	I(1)
Calypogeia fissa	II(2-3)	*Calliergon sp.*	I(3)
Agrostis stolonifera	I(2)	*Pseudoscleropodium purum*	I(1)

E

Angelica sylvestris	V(1-3)	*Centaurea nigra*	I(2)
Lotus pedunculatus	V(1-4)	*Cirsium dissectum*	I(1)
Rumex acetosa	V(2-3)	*Dactylis glomerata*	I(4)
Cirsium palustre	IV(1-3)	*Dactylorhiza praetermissa*	I(1)
Juncus acutiflorus	IV(2-5)	*Dryopteris carthusiana*	I(2)
Valeriana officinalis	IV(2-4)	*Eupatorium cannabinum*	I(2)
Eurhynchium praelongum	IV(1-3)	*Galeopsis tetrahit agg.*	I(2)
Achillea ptarmica	III(1-3)	*Heracleum sphondylium*	I(2)
Filipendula ulmaria	III(3-5)	*Holcus mollis*	I(3-4)
Galium aparine	III(2-3)	*Juncus bulbosus*	I(2)
Galium palustre	III(2-3)	*Lotus corniculatus*	I(4)
Holcus lanatus	III(2-4)	*Luzula multiflora*	I(1-2)
Juncus conglomeratus	III(1-4)	*Myosotis secunda*	I(2)
Juncus effusus	III(2-4)	*Phalaris arundinacea*	I(2)
Molinia caerulea	III(2-5)	*Plantago lanceolata*	I(2)
Agrostis canina sens.str.	II(2-4)	*Poa pratensis sens.lat.*	I(2-3)
Deschampsia caespitosa	II(2-4)	*Poa trivialis*	I(2-3)
Epilobium palustre	II(1-2)	*Potentilla erecta*	I(2)
Festuca rubra sens.str.	II(2-4)	*Prunella vulgaris*	I(1)
Mentha aquatica	II(1-4)	*Ranunculus flammula*	I(2)
Ranunculus repens	II(1-4)	*Rumex crispus*	I(2)
Brachythecium sp.	II(1-3)	*Silene dioica*	I(2)
Calliergon sp.	II(2)	*Stellaria graminea*	I(1-2)
Calypogeia fissa	II(2-3)	*Stellaria uliginosa*	I(1-2)
Rhytidiadelphus squarrosus	II(1-2)	*Urtica dioica*	I(1)
Agrostis capillaris	I(1)	*Viola palustris*	I(1-2)
Agrostis stolonifera	I(1)	*Dicranum sp.*	I(2)
Ajuga reptans	I(1-2)	*Mnium hornum*	I(2)
Caltha palustris	I(2)	*Plagiomnium undulatum*	I(1)
Carex hirta	I(1)	*Pseudoscleropodium purum*	I(3)
Carex panicea	I(2)	*Rhizomnium punctatum*	I(2)

F

Juncus acutiflorus	V(2-5)	*Carex echinata*	I(4)
Lotus pedunculatus	V(2-4)	*Centaurea nigra*	I(2-3)
Agrostis canina sens.str.	IV(1-4)	*Cerastium fontanum*	I(2)
Cirsium palustre	IV(1-2)	*Epilobium hirsutum*	I(3)
Filipendula ulmaria	IV(2-5)	*Equisetum palustre*	I(2)
Galium palustre	IV(2-4)	*Eupatorium cannabinum*	I(1)
Holcus lanatus	IV(2-4)	*Galium aparine*	I(2)
Juncus effusus	IV(2-5)	*Hydrocotyle vulgaris*	I(1-2)
Poa trivialis	IV(2-4)	*Lathyrus pratensis*	I(2-3)
Ranunculus repens	IV(2-4)	*Luzula multiflora*	I(2)
Rumex acetosa	IV(2-3)	*Lycopus europaeus*	I(3)
Stellaria uliginosa	IV(1-2)	*Molinia caerulea*	I(2)
Eurhynchium praelongum	IV(1-3)	*Oenanthe crocata*	I(1)
Lychnis flos-cuculi	III(2-3)	*Plantago lanceolata*	I(2)
Brachythecium sp.	III(1-3)	*Potentilla anserina*	I(3)
Angelica sylvestris	II(2-3)	*Potentilla erecta*	I(1-2)
Anthoxanthum odoratum	II(2-3)	*Prunella vulgaris*	I(1-2)
Cardamine pratensis	II(1-3)	*Ranunculus acris*	I(3)
Epilobium palustre	II(2)	*Ranunculus flammula*	I(2)
Juncus conglomeratus	II(1-3)	*Rumex crispus*	I(2)
Mentha aquatica	II(2-3)	*Scutellaria minor*	I(1-2)
Myosotis secunda	II(1-3)	*Senecio aquaticus*	I(1-3)
Calliergon sp.	II(2-3)	*Urtica dioica*	I(1-2)
Rhytidiadelphus squarrosus	II(1-3)	*Valeriana officinalis*	I(3)
Achillea ptarmica	I(1)	*Vicia cracca*	I(1)
Agrostis capillaris	I(2)	*Viola palustris*	I(2)
Agrostis stolonifera	I(2)	*Mnium hornum*	I(1)
Ajuga reptans	I(1)	*Plagiomnium undulatum*	I(3)
Betula pubescens	I(2)	*Pseudoscleropodium purum*	I(2)

G

Juncus effusus	V(1-5)	*Equisetum palustre*	I(2-3)
Filipendula ulmaria	IV(2-4)	*Eupatorium cannabinum*	I(2)
Ranunculus repens	IV(2-4)	*Galium uliginosum*	I(3)
Eurhynchium praelongum	IV(1-2)	*Geranium robertianum*	I(2)
Cirsium palustre	III(1-2)	*Glyceria declinata*	I(3)
Galium palustre	III(1-4)	*Glyceria fluitans*	I(3-4)
Holcus lanatus	III(2-4)	*Holcus mollis*	I(3)
Lotus pedunculatus	III(2-4)	*Hydrocotyle vulgaris*	I(2)
Mentha aquatica	III(2-4)	*Hypericum tetrapterum*	I(1-2)
Myosotis secunda	III(2-3)	*Iris pseudacorus*	I(2)
Oenanthe crocata	III(2-5)	*Juncus acutiflorus*	I(2-3)
Poa trivialis	III(2-3)	*Juncus bufonius agg.*	I(2)
Stellaria uliginosa	III(1-3)	*Juncus bulbosus*	I(3)
Brachythecium sp.	III(1-2)	*Juncus conglomeratus*	I(4)
Agrostis canina sens.str.	II(2-3)	*Juncus inflexus*	I(2)
Ranunculus flammula	II(2-5)	*Lathyrus pratensis*	I(2)
Scutellaria minor	II(1-2)	*Lemna minor*	I(2)
Urtica dioica	II(1-3)	*Lycopus europaeus*	I(3)
Calliergon sp.	II(1-2)	*Phalaris arundinacea*	I(2-3)
Agrostis stolonifera	I(2-3)	*Potamogeton polygonifolius*	I(3)
Ajuga reptans	I(2)	*Prunella vulgaris*	I(2)
Alopecurus pratensis	I(1)	*Rhinanthus minor*	I(1)
Anthoxanthum odoratum	I(2)	*Rumex acetosa*	I(2)
Callitriche stagnalis sens.str.	I(2)	*Rumex crispus*	I(2)
Caltha palustris	I(2)	*Scrophularia nodosa*	I(1)
Cardamine pratensis	I(2-3)	*Senecio aquaticus*	I(2-3)
Carex laevigata	I(2)	*Silene dioica*	I(2)
Carex panicea	I(3)	*Sparganium erectum*	I(3)
Carex paniculata	I(2-5)	*Stachys sylvatica*	I(2)
Chrysosplenium oppositifolium	I(2)	*Valeriana officinalis*	I(2)
Dactylis glomerata	I(2)	*Calypogeia fissa*	I(1-2)
Deschampsia caespitosa	I(3)	*Plagiomnium undulatum*	I(2)
Epilobium palustre	I(1-2)	*Thuidium tamariscinum*	I(1)
Equisetum fluviatile	I(1)	*Thuidium tamariscinum*	I(1)

Appendix B: NVC results obtained with TABLEFIT

Terms are explained at the bottom of the table.

Quadrat	Group	CORINE	NVC	Goodness of fit	Compositional satisfaction	Mean species constancy	Dominance satisfaction	Dominance consistency
1	A	C37.312	M24c	43	64	76	36	48
		C31.11	M15a	43	65	68	34	54
		C31.11	M16b	38	82	54	23	44
		C31.11	M15	36	85	51	21	45
		C37.312	M24	35	54	65	32	45
2	D	C54.423	M6	60	100	52	56	86
		C54.423	M6a	58	100	59	45	85
		C37.312	M24c	53	58	69	58	73
		C31.11	M15a	47	55	56	52	80
		C37.312	M25	46	78	48	41	73
3	D	C37.312	M25c	60	82	87	41	76
		C37.312	M25	55	78	72	41	74
		C37.312	M24c	47	40	84	58	79
		C37.312	M25b	46	57	64	47	68
		C54.423	M6	41	70	49	35	67
4	D	C37.312	M25c	45	61	50	44	88
		C37.312	M24c	42	35	58	56	92
		C37.312	M24b	34	20	45	57	78
		C37.312	M25	32	49	34	39	77
		C37.312	M24	32	25	43	47	91
5	D	C37.312	M25	60	85	79	41	89
		C37.312	M25c	59	76	77	46	91
		C37.312	M24c	52	46	96	58	100
		C37.312	M25b	51	63	70	47	78
		C37.312	M24	48	47	100	49	100
6	E	C37.1	M27c	39	76	52	28	51
		C37.1	M27	39	100	55	16	38
		C37.217	M23	38	70	60	21	57
		C37.312	M24c	37	55	76	25	64
		C37.312	M25b	37	79	59	16	42
7	E	C37.217	M23	52	96	69	30	63
		C37.217	M23b	50	95	66	30	59
		C37.1	M27c	49	86	54	47	56
		C37.217	M23a	45	71	69	30	61
		C37.1	M27	39	100	56	16	42
8	E	C37.217	M23b	44	51	97	39	77
		C54.423	M6c	43	60	49	48	62
		C37.217	M23	41	49	90	37	76
		C37.1	M27c	37	53	71	29	63
		C44.A1	W4b	35	40	81	32	84
9	D	C37.312	M24c	53	55	83	53	84
		C37.312	M25b	51	72	60	44	73
		C37.312	M25	51	89	57	38	75
		C37.312	M25c	47	76	60	35	71
		C37.217	M23	42	91	78	4	42
10	C	C54.423	M6d	50	100	57	34	75
		C54.423	M6	49	100	56	33	69
		C37.312	M24c	48	66	85	33	77
		C37.312	M25b	48	97	73	17	58
		C37.312	M25	39	100	56	12	50

Quadrat	Group	CORINE	NVC	Goodness of fit	Compositional satisfaction	Mean species constancy	Dominance satisfaction	Dominance consistency
11	A	C37.312	M24c	60	64	97	58	81
		C37.312	M24	52	53	82	55	81
		C31.11	M16b	51	78	65	39	66
		C37.312	M24b	43	37	77	55	69
		C37.312	M25b	41	68	56	39	47
12	G	C37.217	M23	47	96	60	30	53
		C37.1	M27c	45	86	47	49	48
		C37.217	M23b	44	91	58	30	49
		C37.1	M28a	44	65	73	29	75
		C37.217	M23a	43	79	60	30	52
13	G	C53.143	S14c	31	61	55	22	40
		C53.4	S22b	27	85	33	29	26
		C37.1	M27	25	79	43	6	19
		C37.1	M27c	25	65	40	20	26
		C37.1	M28a	21	38	63	14	46
14	F	C37.1	M28	41	58	80	27	78
		C37.1	M27	36	79	48	27	45
		C37.1	M27a	35	60	60	25	53
		C37.1	M27c	34	66	45	33	44
		C37.1	M28a	32	41	75	27	84
15	G	C37.241	MG10c	38	68	61	24	48
		C37.1	M27c	35	62	40	41	47
		C37.217	M23b	32	56	48	30	53
		C37.241	MG10a	31	75	39	30	40
		C37.217	M23	30	54	45	28	52
16	F	C37.217	M23a	52	96	67	34	59
		C37.217	M23	46	91	60	31	56
		C37.217	M23b	43	91	54	29	52
		C54.423	M6	31	73	23	60	37
		C37.1	M28a	30	61	65	7	56
17	E	C37.1	M27a	48	69	77	37	61
		C37.1	M27	42	79	60	28	46
		C37.1	M27c	38	60	55	35	52
		C37.312	M25c	32	62	57	20	42
		C37.217	M23a	31	59	76	9	46
18	D	C37.312	M24c	73	76	84	77	71
		C37.312	M25c	60	100	65	54	54
		C37.312	M25	56	100	59	51	53
		C37.312	M25b	53	83	57	59	50
		C37.312	M24	51	60	67	56	62
19	F	C37.1	M27a	59	92	66	51	62
		C37.1	M27	44	79	47	49	49
		C37.1	M27c	40	60	38	58	48
		C37.1	M28a	38	57	73	26	73
		C37.217	M23a	36	71	59	17	51
20	F	C37.217	M23a	70	100	80	53	84
		C37.217	M23	52	100	80	19	62
		C37.217	M23b	46	100	69	17	47
		C37.1	M28a	43	79	77	12	72
		C37.312	M24c	40	74	64	20	58
21	E	C37.217	M23a	59	86	82	36	85
		C37.312	M24c	50	71	84	33	74
		C37.217	M23	47	79	77	21	70
		C37.217	M23b	44	81	70	19	58

Quadrat	Group	CORINE	NVC	Goodness of fit	Compositional satisfaction	Mean species constancy	Dominance satisfaction	Dominance consistency
		C37.312	M25c	36	83	56	12	50
22	E	C37.312	M25c	49	81	55	45	62
		C37.312	M24c	45	47	65	55	64
		C37.312	M24	40	46	64	47	63
		C37.312	M24b	36	32	61	57	53
		C37.312	M24a	34	40	52	45	56
23	C	C37.312	M24c	53	72	81	42	60
		C37.312	M25b	44	89	60	30	47
		C37.312	M25	43	100	55	26	44
		C37.312	M24	41	62	70	32	56
		C37.312	M25c	37	91	52	23	38
24	G	C53.217	S3	42	93	35	66	39
		C54.2l	S25b	41	56	43	61	48
		C37.217	M23	33	71	55	17	43
		C37.1	M27c	33	79	48	22	33
		C37.1	M27	28	89	45	6	22
25	B	C37.217	M23a	40	90	55	24	41
		C37.217	M23	33	96	48	13	28
		C38.23	MG3b	30	32	44	49	50
		C37.312	M24c	29	60	52	18	43
		C37.217	M23b	28	87	43	11	24
26	F	C37.217	M23a	53	86	63	42	66
		C37.217	M23	43	91	60	23	54
		C37.1	M28	40	79	69	13	55
		C37.217	M23b	40	91	55	23	47
		C37.241	MG10c	38	79	47	34	46
27	E	C37.217	M23a	41	71	59	31	49
		C37.312	M24c	34	55	65	28	42
		C37.312	M25	33	92	48	15	30
		C37.312	M25b	33	77	50	20	35
		C37.312	M25c	30	81	47	14	28
28	E	C37.213	MG9	48	69	54	47	66
		C37.217	M23b	45	72	62	35	54
		C37.213	MG9a	42	65	49	45	57
		C37.1	M27c	41	76	49	42	44
		C37.217	M23	39	65	55	35	50
29	G	C37.1	M28	41	51	94	30	93
		C37.1	M28a	36	40	91	32	97
		C37.1	M27	35	79	60	12	31
		C37.1	M28b	31	45	81	20	82
		C37.1	M27c	29	65	55	13	28
30	C	C37.312	M24c	67	82	90	60	67
		C37.312	M24	54	70	79	54	51
		C37.312	M25b	44	89	57	35	45
		C37.312	M25	44	100	55	30	47
		C54.423	M6d	44	88	36	60	48
31	A	C37.312	M24c	74	69	97	78	96
		C37.312	M24	60	62	87	61	85
		C37.312	M25	59	100	65	44	75
		C37.312	M25b	57	83	63	52	70
		C37.312	M24b	55	45	86	73	66
32	C	C37.312	M24c	60	80	72	52	70
		C37.217	M23a	58	92	58	52	75
		C37.217	M23	44	96	51	32	59

Quadrat	Group	CORINE	NVC	Goodness of fit	Compositional satisfaction	Mean species constancy	Dominance satisfaction	Dominance consistency
		C37.312	M24	42	68	61	33	53
		C37.217	M23b	41	95	48	30	51
33	F	C37.217	M23b	52	95	62	40	57
		C37.217	M23	52	96	61	39	58
		C37.217	M23a	40	67	52	38	52
		C37.1	M27c	35	76	39	42	41
		C37.241	MG10a	28	64	28	41	39
34	B	C37.312	M24c	54	97	72	35	53
		C37.312	M24	46	84	64	31	51
		C37.217	M23a	42	96	49	32	50
		C37.312	M25b	39	100	50	26	40
		C37.312	M24b	39	66	65	27	45
35	A	C37.312	M24c	33	62	64	17	43
		C35.11	U5c	32	64	51	24	41
		C37.217	M23a	28	64	48	15	37
		C54.25	M10a	26	53	41	27	41
		C54.423	M6b	26	68	45	11	37
36	C	C37.312	M24c	52	89	78	27	58
		C37.217	M23a	44	94	55	28	55
		C37.312	M24	42	76	67	22	53
		C37.217	M23	36	96	45	21	47
		C37.217	M23b	33	90	44	20	43
37	B	C38.22	MG1e	44	80	55	33	67
		C35.12	U4b	39	71	43	41	53
		C38.23	MG3b	35	37	46	52	60
		C18.2	MC9c	35	67	38	37	54
		C38.112	MG5b	33	52	48	31	69
38	E	C37.1	M27c	61	100	58	70	49
		C37.1	M27	44	100	56	32	39
		C38.22	MG1c	41	65	50	47	46
		C37.217	M23	41	82	58	28	39
		C37.217	M23b	40	82	60	29	34
39	B	C37.312	M24c	55	76	63	55	60
		C37.312	M24	46	74	62	37	55
		C37.312	M25b	45	97	47	40	52
		C37.312	M24b	43	60	68	41	50
		C37.217	M23a	42	71	53	35	61
40	B	C37.312	M26b	25	43	54	22	51
		C54.25	M10a	22	49	32	30	34
		C54.21	M13a	21	54	40	17	30
		C37.312	M24	21	52	46	11	32
		C16.34	SD17b	21	63	33	19	25
41	G	C37.1	M27c	62	72	69	60	82
		C37.1	M27	48	79	69	31	64
		C44.31	W7	37	40	65	39	87
		C37.1	M28	36	57	100	17	74
		C37.217	M23	35	43	57	37	70
42	E	C37.217	M23a	57	100	72	36	65
		C37.217	M23	54	100	70	33	64
		C37.217	M23b	51	100	67	30	59
		C37.312	M24c	50	74	64	43	58
		C37.312	M25c	35	83	48	24	43
43	C	C54.423	M6	70	75	71	72	84
		C37.312	M25b	69	82	95	61	73

Quadrat	Group	CORINE	NVC	Goodness of fit	Compositional satisfaction	Mean species constancy	Dominance satisfaction	Dominance consistency
		C54.423	M6d	65	98	83	44	79
		C37.312	M25	60	81	72	51	68
		C37.312	M24c	58	46	96	73	82
44	C	C37.312	M25b	64	98	79	48	62
		C37.312	M24c	61	70	97	55	73
		C54.423	M6	54	75	47	68	61
		C37.312	M25	52	100	65	35	54
		C37.217	M23a	52	81	80	29	64
45	C	C37.312	M25b	50	87	57	43	58
		C37.312	M24c	48	61	72	46	62
		C37.217	M23a	44	90	75	11	48
		C37.312	M25	43	92	52	32	53
		C37.312	M25c	40	88	53	29	43
46	E	C37.217	M23a	57	74	70	48	79
		C37.217	M23	39	79	62	15	60
		C37.217	M23b	37	79	63	12	47
		C37.312	M25c	33	83	57	4	43
		C37.312	M24c	32	53	67	20	65
47	C	C54.423	M6d	61	91	58	62	64
		C37.217	M23a	59	71	87	50	77
		C37.312	M25b	52	88	81	27	57
		C37.312	M25	50	100	73	23	55
		C37.312	M24c	50	61	100	42	75
48	E	C37.1	M27a	47	88	62	34	49
		C37.1	M27	40	100	48	29	40
		C37.1	M28a	31	52	63	20	62
		C37.1	M28	31	61	57	15	48
		C37.217	M23a	30	63	49	18	49
49	E	C37.1	M27a	44	78	64	31	46
		C37.1	M27	41	100	51	29	39
		C37.1	M27c	29	60	38	33	40
		C37.217	M23a	27	55	49	17	48
		C37.1	M28a	25	41	57	19	57
50	E	C37.312	M24c	29	53	54	20	51
		C37.312	M25c	28	81	41	17	33
		C37.217	M23b	28	72	49	8	39
		C37.217	M23	26	70	45	10	34
		C37.217	M23a	26	64	46	11	35
51	E	C37.1	M27c	56	100	59	48	61
		C37.217	M23a	52	78	76	33	70
		C37.1	M27	45	100	55	32	48
		C37.217	M23	44	79	63	24	64
		C37.217	M23b	33	66	52	19	50
52	F	C37.1	M27c	72	89	74	69	79
		C37.241	MG10a	62	100	70	51	65
		C37.217	M23	57	74	84	45	78
		C37.217	M23b	56	74	81	46	65
		C37.241	MG10c	54	74	84	39	71
53	B	C37.217	M23a	48	71	69	37	64
		C37.213	MG9	36	75	59	16	42
		C37.213	MG9a	32	70	55	15	33
		C35.12	U4b	30	50	53	35	37
		C18.2	MC9e	28	56	52	22	36
54	G	C37.1	M27c	67	93	67	72	58

Quadrat	Group	CORINE	NVC	Goodness of fit	Compositional satisfaction	Mean species constancy	Dominance satisfaction	Dominance consistency
		C37.1	M27	50	100	66	31	46
		C37.217	M23	49	77	71	32	63
		C53.143	S14c	49	81	80	24	58
		C37.1	M28	47	66	96	30	72
55	G	C37.241	MG10c	33	66	52	23	46
		C37.1	M27c	32	76	45	24	42
		C37.1	M27	31	79	50	14	36
		C37.1	M28	28	54	63	12	49
		C37.217	M23	27	61	47	14	48
56	G	C37.1	M27c	48	89	47	55	48
		C37.1	M28	44	73	75	24	59
		C37.217	M23	43	88	58	27	48
		C44.31	W7	42	65	52	42	54
		C37.1	M27	42	100	52	32	39
57	G	C37.1	M27c	34	58	26	60	45
		C44.31	W7	25	40	30	37	56
		C37.1	M27	24	68	28	30	38
		C37.1	M28b	23	52	49	12	41
		C37.1	M28	23	47	43	19	49
58	F	C37.217	M23a	58	94	71	41	69
		C37.217	M23	50	100	70	24	60
		C37.217	M23b	47	98	67	22	54
		C37.1	M28	37	70	63	17	58
		C37.1	M28a	35	58	66	21	69
59	F	C37.217	M23a	41	64	62	33	61
		C37.217	M23	41	79	62	21	54
		C37.1	M28	38	61	61	28	60
		C37.217	M23b	37	74	60	20	42
		C37.1	M28a	35	50	65	29	69
60	G	C37.1	M27c	67	100	60	72	62
		C37.217	M23	63	100	78	41	79
		C37.217	M23b	58	100	71	39	69
		C37.217	M23a	54	86	70	36	72
		C37.1	M28	44	76	70	21	62
61	B	C37.217	M23a	52	80	66	37	82
		C37.217	M23	42	79	61	22	68
		C37.312	M24c	38	64	67	20	66
		C37.217	M23b	35	81	52	16	53
		C37.1	M28a	18	44	49	5	54
62	C	C37.312	M24c	60	70	100	50	81
		C37.312	M25c	56	97	78	32	62
		C37.312	M25	56	100	71	34	64
		C37.312	M25b	53	83	69	39	62
		C37.217	M23a	45	75	79	21	66
63	C	C37.312	M24c	82	85	100	81	87
		C37.312	M25b	65	89	71	61	66
		C37.312	M25	62	100	66	52	69
		C37.312	M24	55	64	78	56	67
		C54.423	M6	54	75	36	75	70
64	F	C37.217	M23a	59	94	62	50	75
		C37.1	M28a	56	90	87	26	83
		C37.1	M28	49	87	79	19	66
		C37.217	M23	44	100	61	17	56
		C37.1	M27c	43	100	47	42	41

Quadrat	Group	CORINE	NVC	Goodness of fit	Compositional satisfaction	Mean species constancy	Dominance satisfaction	Dominance consistency
		C54.423	M6c	25	100	23	34	29
76	G	C37.217	M23b	50	79	60	44	61
		C37.217	M23	49	74	58	42	66
		C37.1	M27c	45	86	44	47	60
		C37.1	M27	34	100	46	16	42
		C54.423	M6c	33	86	27	51	41
77	G	C37.217	M23	66	100	72	52	80
		C37.217	M23b	60	92	66	52	68
		C37.217	M23a	57	86	78	36	79
		C37.241	MG10a	45	92	42	53	49
		C37.241	MG10c	40	74	54	34	48
78	A	C54.21	M13a	28	58	37	30	45
		C35.11	U5c	27	49	32	39	45
		C54.25	M10a	25	53	35	29	44
		C37.312	M25b	23	76	37	11	26
		C54.25	M10b	23	30	35	39	48
79	B	C37.312	M24c	56	67	85	50	68
		C37.217	M23a	51	81	74	31	65
		C37.312	M25b	50	87	66	35	53
		C54.21	M13a	43	70	65	32	52
		C37.312	M25	43	100	56	25	44
80	B	C37.312	M24c	44	79	69	25	43
		C37.217	M23a	41	76	53	35	47
		C37.217	M23	27	77	40	18	32
		C37.312	M24	25	60	53	6	30
		C37.312	M25b	21	68	35	12	26
81	B	C37.312	M24c	58	73	75	54	61
		C37.312	M25b	58	100	66	48	56
		C37.217	M23a	53	86	72	36	62
		C37.312	M24	49	68	72	41	62
		C37.312	M25	44	100	52	35	44
82	A	C37.312	M24c	69	67	85	76	75
		C54.423	M6d	53	88	41	64	67
		C54.423	M6	51	75	43	63	63
		C37.312	M25	43	81	44	45	56
		C37.312	M24	43	48	62	56	55
83	A	C37.312	M24c	65	76	84	60	72
		C37.312	M25b	58	97	60	53	61
		C37.312	M24	54	62	70	57	67
		C37.312	M24b	52	50	76	68	58
		C37.312	M25	46	92	48	42	54
84	B	C37.312	M24c	66	82	85	58	66
		C37.217	M23a	45	81	63	30	49
		C37.312	M24	44	64	70	38	52
		C37.312	M25b	41	81	51	35	46
		C54.21	M13a	38	68	53	32	48
85	F	C37.217	M23a	65	90	68	57	82
		C37.217	M23	58	100	67	42	72
		C37.217	M23b	49	90	58	38	61
		C37.1	M27c	45	100	47	43	46
		C37.312	M24c	36	60	61	25	58
86	C	C37.312	M24c	68	72	93	67	80
		C37.312	M25b	65	100	81	47	62
		C37.312	M25	52	100	64	35	56

Quadrat	Group	CORINE	NVC	Goodness of fit	Compositional satisfaction	Mean species constancy	Dominance satisfaction	Dominance consistency
		C37.312	M24	50	64	84	41	69
		C54.423	M6d	50	98	48	52	53
87	B	C37.312	M24c	46	80	66	32	45
		C37.217	M23a	32	75	43	27	39
		C37.312	M24	28	61	53	16	33
		C37.312	M25b	25	79	38	13	27
		C54.423	M6d	23	85	25	30	31
88	C	C37.312	M24c	71	76	100	68	85
		C37.312	M25b	69	100	91	50	66
		C37.312	M24	65	64	100	69	77
		C54.423	M6d	61	100	64	53	64
		C37.312	M25	58	100	75	38	63
89	E	C37.217	M23a	66	80	80	57	81
		C37.312	M24c	49	67	93	35	72
		C37.312	M25c	49	97	72	22	53
		C37.312	M25	41	100	61	15	45
		C37.217	M23	38	74	63	18	50
90	C	C37.312	M24c	68	85	100	55	72
		C37.312	M25b	59	100	82	37	53
		C37.217	M23a	55	80	76	38	69
		C37.312	M25	49	100	66	28	51
		C54.423	M6d	47	98	47	46	52
91	B	C54.12	M37	37	73	30	87	32
		C38.12	MG	8	33	43	69	33
		C54.21	M13a	33	50	61	33	43
		C37.217	M23a	32	55	64	23	43
		C54.532	M9b	24	32	58	33	42
92	D	C37.312	M24c	66	52	86	80	91
		C37.312	M25c	61	87	74	47	74
		C37.312	M25	59	89	63	51	78
		C37.312	M25b	57	68	61	60	72
		C37.312	M24	46	42	71	56	79
93	A	C37.312	M25b	73	100	81	67	61
		C37.312	M24c	73	76	97	77	68
		C37.312	M24	67	70	92	72	68
		C37.312	M25	58	100	64	52	53
		C37.312	M24b	58	52	90	82	60
94	A	C37.312	M24c	54	70	89	46	61
		C37.312	M24	53	64	84	49	62
		C54.21	M13a	52	77	73	37	64
		C37.312	M25b	51	93	66	37	51
		C37.312	M24b	45	47	83	55	53
95	A	C54.21	M13a	42	66	62	33	60
		C37.312	M24c	40	65	82	20	58
		C31.11	M16b	35	72	56	19	44
		C37.312	M25b	32	78	55	10	35
		C54.423	M6d	30	86	41	17	37
96	A	C37.312	M24c	75	94	89	60	83
		C37.312	M24	56	76	74	44	72
		C37.312	M24b	46	56	70	52	56
		C37.312	M25	46	100	52	35	57
		C37.312	M25b	43	88	47	41	51
97	A	C37.312	M24c	77	95	84	68	80
		C37.312	M24	62	87	78	47	72

Quadrat	Group	CORINE	NVC	Goodness of fit	Compositional satisfaction	Mean species constancy	Dominance satisfaction	Dominance consistency
		C37.312	M25b	57	100	60	50	60
		C37.312	M24b	55	66	79	54	62
		C37.217	M23a	46	81	51	41	66

Goodness of fit: overall indication of goodness of fit of a quadrat compared to an NVC community, calculated from the average of 4 goodness of fit values.

Compositional satisfaction: Goodness of fit of the sample composition

Mean constancy: Goodness of fit of the constancy class composition

Dominance satisfaction: Goodness of fit of the species that ought to have a high abundance

Weighted mean constancy: Goodness of fit of the weighting by its cover value

Appendix C: Environmental data of the 2000 field survey for the plant community groups

Vegetation group	Mean	Median	Standard Error
A	2.17	2.00	0.32
B	3.67	3.00	0.49
C	2.67	2.00	0.57
D	2.71	2.00	0.78
E	2.79	3.00	0.36
F	2.62	3.00	0.55
G	2.44	1.00	0.76
All	2.74	2.00	0.21

Table C.1 Gradient per vegetation group

Vegetation group	Mean	Median	Standard Error
A	49.8	53.0	4.9
B	51.2	41.0	4.9
C	57.7	60.0	3.8
D	67.9	69.0	3.5
E	60.2	65.0	3.5
F	63.9	75.0	4.9
G	64.6	75.0	4.6
All	59.0	65.0	1.8

Table C.2 Soil depth (cm) per vegetation group

Vegetation group	Mean	Median	Standard Error
A	61.8	64.7	2.0
B	52.4	50.1	2.4
C	59.3	61.2	2.0
D	69.1	70.0	0.6
E	58.9	61.1	2.7
F	58.9	58.0	2.4
G	63.6	67.2	2.3
All	59.8	63.6	1.0

Table C.3 Soil moisture (volume %) per vegetation group

Vegetation group	Mean	Median	Standard Error
A	3.9	4.0	0.1
B	4.4	4.4	0.1
C	3.8	3.8	0.1
D	4.3	4.4	0.2
E	4.1	4.0	0.1
F	2.9	4.3	0.1
G	4.3	4.2	0.1
All	4.1	4.1	0.03

Table C.4 Acidity (pH – $CaCl_2$) per vegetation group

Vegetation group	Mean C	Median C	Std. Err. C	Mean N	Median N	Std. Err. N
A	11.81	8.65	2.68	0.83	0.63	0.17
B	8.71	6.60	2.14	0.67	0.53	0.14
C	13.55	7.10	3.12	0.96	0.60	0.20
D	23.10	19.70	4.62	1.52	1.20	0.26
E	11.23	6.90	2.21	0.86	0.61	0.14
F	11.38	6.90	2.90	0.88	0.64	0.17
G	10.99	10.05	1.07	0.87	0.83	0.09
All	12.11	8.10	1.00	0.89	0.64	0.06

Table C.5 Total organic carbon and nitrogen content (%) per vegetation group

Vegetation group	Mean	Median	Standard Error
A	13.77	13.50	0.35
B	12.32	12.30	0.37
C	12.99	12.30	0.45
D	14.64	14.70	0.73
E	12.22	11.50	0.36
F	12.06	11.40	0.47
G	12.59	12.35	0.29
All	12.76	12.40	0.17

Table C.6 C/N ratio per vegetation group

Vegetation group	Mean	Median	Standard Error
A	3.13	3.69	0.51
B	3.91	2.93	1.40
C	2.30	1.99	0.35
D	5.72	3.75	2.54
E	4.00	3.00	1.00
F	5.51	3.62	0.83
G	12.05	6.00	3.49
All	5.13	3.21	0.74

Table C.7 Phosphorus availability ($mgkg^{-1}$ air dry soil) per vegetation group

Vegetation group	Mean	Median	Standard Error
A	214.4	154.1	65.6
B	149.2	125.2	23.7
C	215.8	133.9	47.0
D	313.7	181.4	88.1
E	307.6	171.6	79.8
F	261.0	154.4	69.4
G	282.0	139.2	93.5
All	247.3	151.6	27.0

Table C.8 Potassium ($mgkg^{-1}$ air dry soil) per vegetation group

Vegetation group	Mean	Median	Standard Error
A	477.0	105.0	370.0
B	106.7	102.0	6.9
C	105.4	103.7	5.2
D	148.9	168.6	20.2
E	270.0	91.0	167.0
F	104.2	94.7	6.93
G	108.3	106.7	5.09
All	187.4	101.7	56.0

Table C.9 Sodium ($mgkg^{-1}$ air dry soil) per vegetation group

Vegetation group	Mean	Median	Standard Error
A	692	617	85
B	1448	1184	187
C	1166	812	362
D	2109	2258	545
E	1216	935	182
F	1692	1077	433
G	1748	1763	149
All	1395	1117	108

Table C.10 Calcium ($mgkg^{-1}$ air dry soil) per vegetation group

Vegetation group	Mean	Median	Standard Error
A	191	180	34
B	739	192	496
C	201	180	28
D	1383	623	967
E	634	165	420
F	248	183	60
G	261	217	52
All	469	183	133

Table C.11 Magnesium ($mgkg^{-1}$ air dry soil) per vegetation group